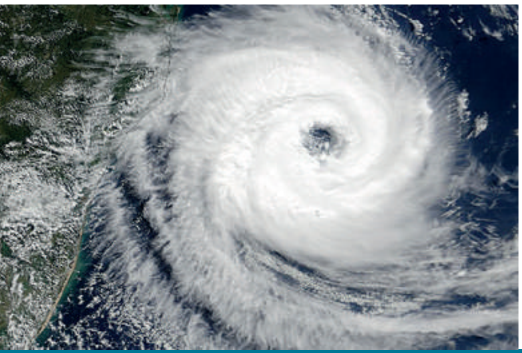
Explaining Ocean Warming:

Causes, scale, effects and consequences

Edited by D. Laffoley and J. M. Baxter

September 2016



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Foreword

Our triumphant march through the advancement of the sciences, medicine, technology and sociology has provided humans with an unprecedented level of human betterment and well-being. We live longer and at various levels of comfort and entertainment, and have spread this mode of living - albeit unequally -across the earth. And yet, after several thousand years we have arrived at a critical turning point in our development.

Scientific analyses of the global climate system have provided us with the ability to understand the challenges created by rising greenhouse gas levels in the atmosphere, but despite the remarkable level of understanding achieved to date, there is much more work to be done. In particular, while the oceans cover 71% of the Earth's surface, apart from the impact of rising sea levels on coastal areas caused by ocean warming and expansion and the melting of land-based glaciers, insufficient attention has been given to the range of problems associated with the warming of the oceans. The present report addresses that gap in our knowledge. It is the most comprehensive review available of the science and implications of ocean warming.

This report is well-timed, coming in the aftermath of the ground-breaking agreement achieved at COP21 in Paris on 12.12.15. The nations of the world decided to limit global warming to less than 2°C above the pre-industrial average temperature. It is hoped that the challenges to the benefits we receive from the ocean ecosystems as set out here will lead to a renewed interest amongst the political and social communities in the state of our oceans. To manage the risks will require both urgent actions and a quest for deeper scientific understanding. We will need this to protect the Earth's ecosystems through sustainable living.

Sir David King
UK Foreign Secretary's Special Representative on Climate Change

Preface

Ocean warming may well turn out to be the greatest hidden challenge of our generation. Whilst some may be aware of the challenges a warming ocean presents to coral reefs, few know about the other consequences this holds for the ocean. Ocean acidification emerged as a new story around 2004, with problems already being encountered due to changes in ocean chemistry, and yet add ocean warming and there is a far bigger story to tell. In this report, we assess the scale of the challenge and explore this issue from a range of different perspectives – oceanography, ecosystems and species. We also look at the impacts ocean warming might have on the every-day benefits we derive from the ocean – its 'goods and services'.

This is a very timely report. We know the ocean is warming. Until very recently, the debate on climate change has focused on specific themes such as land surface temperatures, melting ice caps in Greenland and Polar Regions, and shrinking glaciers in mountain ranges. It has only occasionally mentioned the ocean. When the ocean was included, the issues discussed generally related to dramatic changes to coral reefs, as we have seen in 2016 when water temperature rises turning beautifully-coloured reefs a ghostly white from bleaching.

The arguments of sceptics have focused on an apparent pause in warming and yet as this report is being produced we are faced with the 14th consecutive month of record-breaking global temperatures on land. In the ocean, 2015 was recently analysed to have been the warmest year within the 136-year records of extended reconstructed sea surface temperature and the fourth such record-breaking year since 2005. The scale of ocean warming is truly staggering with the numbers so large that it is difficult for most people to comprehend. A useful analysis undertaken by the Grantham Institute[1] in 2015 concluded that if the same amount of heat that has gone into the top 2000m of the ocean between 1955-2010 had gone into the lower 10km of the atmosphere, then the Earth would have seen a warming of 36°C. By factoring in the ocean, as this report shows, the perspective is fundamentally altered. What is perhaps more surprising, is that it is only in recent years that science on these cumulative ocean warming impacts has emerged and the story started to be revealed and heard.

The story that unfolds in the following pages should matter to everyone. Whether ocean warming impacts a particular group of organisms, alters the structures of ecosystems such as coral reefs, changes the very essence of environmental conditions, or indeed influences weather, it impacts on everyone to some degree as we are an ocean planet. It has profound implications not just for ecosystems but also for the significant number of coastal communities and valuable economies that depend on a healthy ocean. Up to now, the ocean has shielded us from the worst impacts of climate change. The costs is that its chemistry has been altered as it absorbed significant amounts of the extra carbon dioxide we put into the atmosphere, but it has also warmed at an alarming rate in recent decades.

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[1] Whitmarsh F, Zika J, Cazaja A. 2015. Ocean heat uptake and the global surface temperature record, Grantham Institute, Briefing paper No 14.

This report represents the most comprehensive review to date on ocean warming. To build up the report, leading scientists from around the world were invited to join with colleagues to contribute individual chapters. Each has been subject to peer review and tells in the scientist's own words the scale and nature of changes being driven by ocean warming, often in association with other stressors, such as ocean acidification and deoxygenation. It contains many recommendations from the scientists on capability gaps and research issues that need to be resolved if we are to tackle the impacts of ocean warming with greater confidence in the future. The focus of the report is on gathering facts and knowledge and communicating this to show what is now happening in and to the ocean. There is purposefully much less focus on political ramifications. We hope that this report will help stimulate further debate and action on such issues.

We hope that the timing of this report after COP21 in Paris in late 2015 will keep up awareness that, despite greater recognition now being given to the ocean in climate discussions, the scale, intensity and nature of changes continue to grow. This report builds on the IPCC's 2013 assessment, promotes their messages, and adds in new information published since then – over 25% of the peer reviewed papers quoted here have been published since 2014 - as well as highlighting lesser-known consequences of ocean warming on species, ecosystems and services for greater awareness and scrutiny in the future. Since the process was started to compile this report, IPCC has agreed to prepare a special report on climate change and oceans and the cryosphere. The papers in this report will, we hope, help that process and shape further thinking on the scale and consequences of climate change in our seas. Alongside this report, a second volume is in production, which will use the knowledge on ocean warming to revaluate the risks to society from the growing changes we see in the ocean.

Above all though, this report is the story of ocean warming and its consequences for all of us. It outlines cautionary tales about changes that are now underway in the ocean, often hidden and unseen, but nevertheless of great consequence. A warming ocean is one where changes to ecosystems, chemistry and processes are generating risks to the benefits we and many other species receive and depend on during our lives: changes that are not theory, but now a reality supported by hard facts. For this reason, the relationship we have with the ocean matters more than ever and we hope this report will be instrumental in inspiring greater and urgent action to care for it.

Carl Gustaf Lundin
Director
IUCN's Global Marine and Polar Programme

Dan Laffoley
Marine Vice Chair
IUCN's World Commission on Protected Areas

Executive Summary

The scale of ocean warming is truly staggering with the numbers so large that it is difficult for most people to comprehend.

Ocean warming may well turn out to be the greatest hidden challenge of our generation. Whilst some may be aware of the implications of a warming ocean for coral reefs, few know about the many other consequences for the ocean. In 1956 the influential meteorologist Carl-Gustav Rossby, now considered by some as the 'father' of ocean warming, speculated that over the course of a few centuries vast amounts of heat might be buried in the oceans or emerge, perhaps greatly affecting the planet's climate. He warned that "*Tampering can be dangerous. Nature can be vengeful. We should have a great deal of respect for the planet on which we live*". His theory has been borne out as the consequences of increasing human activities have indeed injected vast quantities of heat into the ocean, shielding humanity on land, in so doing, from the worst effects of climate change. This regulating function, however, happens at the cost of profound alterations to the ocean's physics and chemistry that lead especially to ocean warming and acidification, and consequently sea-level rise.

Key warming facts

- Sea surface temperature, ocean heat content, sea-level rise, melting of glaciers and ice sheets, CO_2 emissions and atmospheric concentrations are increasing at an accelerating rate with significant consequences for humanity and the marine species and ecosystems of the ocean.
- There is likely to be an increase in mean global ocean temperature of 1-4°C by 2100. The greatest ocean warming overall is occurring in the Southern Hemisphere and is contributing to the subsurface melting of Antarctic ice shelves. Since the 1990s the atmosphere in the polar regions has been warming at about twice the average rate of global warming.
- There is likely to be Arctic warming and ice loss, and possibly the essential removal, in some years, of the summer Arctic sea ice within the next few decades. In the Antarctic the extent of the sea ice has been growing at a rate of ~1.3% per decade, although there is strong inter-annual variability.
- Over the last 20 years there has been an intensification and distinct change in the El Niño events, with a shift of the mean location of sea surface temperature anomalies towards the central Pacific.
- Currently 2.5 Gt of frozen methane hydrate are stored in the sea floor at water depths of 200 – 2000 m. Increasing water temperature could release this source of carbon into the ocean and ultimately into the atmosphere.

Marked biological manifestations of the impacts from ocean warming and other stressors in the ocean have taken the form of changes in biogeographical, phenological, biodiversity, community size, and species abundance as well as ecological regime shifts. Such shifts often interfere, or are predicted to interfere, with the benefits we expect from the ocean. More precise interactions, such as the relative importance of direct physiological effects and indirect effects through other abiotic pathways, and species interactions remain largely unknown. The problem is that we know ocean warming is driving change in the ocean – this is well documented - but the consequences of these changes decades down the line are far from clear.

Whilst rising CO_2 levels and increasing warming can occasionally have positive effects, the overwhelming evidence and predictions shown in this report are for a cocktail of negative effects, which we are only just starting to understand, but about which we know enough to be very concerned. The warming signs are clear to see, not only the current prevalence of bleaching of coral reefs around the world, but the increasing confidence of predictions that all coral reefs will be so affected by 2050, unless we change our ways, and quickly. Ocean warming and climate change are ultimately contributing to global homogenization of biodiversity, as vulnerable species become extinct and "non-native" species from different biogeographic regions spread, overlap, and become established across the world's ocean.

All these changes and predictions for the future matter from moral, social, ecological and economic perspectives. The value of our relationship with the ocean sometimes seems difficult to cost, but is the ultimate relationship that enables life to exist on Earth. Where it is quantified it runs to trillions of dollars a year, directly and indirectly affecting many of the benefits we have so far taken for granted. The greatest losses will likely fall upon those people who rely upon the ocean for day-to-day subsistence – typically the poorest coastal nations. With issues of such importance at stake we need to vastly improve the science and knowledge available as we move forward into an increasingly compromised ocean world. This is a common conclusion by many scientists who have contributed to this report.

Key recommendations based on the evidence presented in the report are that there is a need for:

Recognition of impact severity. There is a need for a much greater recognition of the unequivocal scientific evidence of impacts on key marine and coastal organisms, ecosystems, and services even under the low emissions scenario (RCP2.6).

Concerted joined-up global policy action for ocean protection. There is a need to join up action across global conventions with respect to climate change and environmental protection.

Comprehensive protection and management. There is a need to ensure that we rapidly fill gaps in protective regimes, such as protecting the High Seas.

Updated risk assessments. A re-evaluation is needed on the risks that impacts from ocean warming and other stressors pose to humanity, to the viability of the very species and ecosystems involved, and to the provisioning of goods and services we derive from the environment.

Closing gaps in fundamental science and capability needs. There is a need to rapidly assess science, observing and modelling capacity and their needs in light of the widespread changes happening from ocean warming and other stressors.

Acting quickly to keep future options open. The concerns among the scientific community that as atmospheric CO_2 increases, the options for the ocean (i.e. mitigate, protect, repair, adapt) become fewer and less effective must now be recognized.

Achieving rapid and substantial cuts in greenhouse gases. Greenhouse gas mitigation at the global scale appears to be the overarching solution.

The evidence in this report shows a complex story of change in the ocean, change that is underway, is often already locked in for future decades, and is beginning to impact our lives. This is no longer a single story of challenges to coral reefs, but stories to changes across species and ecosystem scales, and across geographies and the world. It is pervasive change, driven by ocean warming and other stressors that is already operating across scales and in ways we only barely understand. It is critical that we sit up and recognize these issues and act, or we will be poorly prepared if at all for an uncertain changing future.

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> *"By absorbing a disproportionate amount of heat from global warming and by taking up the rapidly increasing emissions of carbon dioxide, the ocean has shielded the world from even more rapid changes in climate. However, the extent to which it can continue to do so in the near and distant future is far from clear."*
>
> *Chapter 1 author*

Ocean warming: setting the scene

1

Tampering can be dangerous. Nature can be vengeful.
We should have a great deal of respect for the planet on which we live
Rossby, 1956

Philip C. Reid

Professor of Oceanography
Senior Research Fellow, Sir Alister Hardy Foundation for Ocean Science
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Summary

- The crucial role that the ocean plays in climate regulation as the major heat, carbon and water reservoirs of the world is not generally recognized or appreciated by the public or policy makers.
- More than 93% of the enhanced heating since the 1970s due to the greenhouse effect and other human activities has been absorbed by the ocean, even affecting the deep ocean.
- Sea surface temperature, ocean heat content, sea-level rise, melting of glaciers and ice sheets, CO_2 emissions and atmospheric concentrations are increasing at an accelerating rate with grave consequences for humanity and the marine species and ecosystems of the ocean.
- The greatest ocean warming overall is occurring in the Southern Hemisphere and is contributing to the subsurface melting of Antarctic ice shelves.
- Crucially, as evident in the past two years, the heat and CO_2 accumulated in the ocean are not permanently locked away, but can be released back to the atmosphere when the ocean surface is anomalously warm, giving a positive rapid feed-back to global warming.
- By absorbing a disproportionate amount of heat from global warming and by taking up the rapidly increasing emissions of carbon dioxide, the ocean has shielded the world from even more rapid changes in climate. How long can it maintain this role?

1.1 Introduction

The evidence for a human influence on climate is clear and for a warming world “unequivocal” with many changes in Earth systems since the 1950s that are “unprecedented” (IPCC, 2013a; Reid *et al.*, 2016). This opening chapter provides an introduction to the major role of the ocean in global warming and the Earth’s energy budget as a background to the changes in sea temperature that are behind many of the observed impacts on biological communities that are presented in the rest of the report. I also draw attention to the knife edge that humanity is on if the ocean reduces the huge buffering it provides as a heat and carbon reservoir for the world.

After a brief description of the topography of the ocean, the key role that it plays in the global heat budget and the Earth’s Energy Imbalance (EEI) is outlined, followed by a summary of changes in global surface temperatures, sea surface temperature (SST), and Ocean Heat Content (OHC). The chapter concludes with comments on: impacts and the hugely important role that the ocean and recent changes in OHC are likely to have on future climate change. Table 1.1 provides a summary of the main consequences of ocean warming, other than biological, that are covered elsewhere in the report. The table also includes interactions with deoxygenation, ocean acidification and other stressors that are likely to have compounding consequences for ocean ecosystems and species (Levin and Le Bris, 2015; Sperling *et al.*, 2016). Box inserts on Argo and El Niño/Southern Oscillation (ENSO) are also provided to describe essential processes needed to measure ocean heat, as well as the dramatic changes intermittent events such as El Niño are bringing to the planet.

As Rossby - perhaps considered by some as the ‘father’ of ocean warming https://www.aip.org/history/climate/oceans.htm#M_13_ - noted back in a 1956 volume of Time magazine: “*Tampering can be dangerous. Nature can be vengeful. We should have a great deal of respect for the planet on which we live*”. This report notes the scale of changes now overtaking the ocean, something Rossby warned us about some 60 years ago.

Why is a warming ocean such a critical issue? It is because the water of the ocean covers ~71% of the surface of the globe (with an estimated, area of 360 600 000 km^2). The scale of this enormous volume of water (1,334,900,000 km^3) that covers the solid Earth is mind boggling when it is realised that it makes up ~97% of the world’s water (Costello *et al.*, 2015). As a consequence our world is a blue planet as seen from space.

The gigantic dimensions of the ocean and the key role it plays in our world are difficult to comprehend and all too easily ignored by us terrestrial dwellers. We also fail to appreciate the interconnectedness of the waters of the different ocean basins, coastal seas and estuaries that form “one body of water, one global ocean”. Because of its size and distance from human habitation the ocean in the past has seemed like an almost limitless natural resource, including as a source of food. This is far from the truth as humanity has had a very major impact on all aspects of the ocean’s functional systems and the organisms living in it, from the smallest microbe to penguins and whales.

Global warming as a result of human additions of greenhouse gases to the atmosphere is having a particularly large impact on the ocean. Current systems are changing, sea-level rise is increasing through the thermosteric (heat expansion) of water, ice sheets and glaciers are melting and biological processes at cellular to ecosystem scales are altering, all of which are strongly governed by temperature.

As the major water, heat and carbon reservoirs of the world, the ocean plays an especially crucial role in climate regulation (Reid *et al.*, 2009; Rhein *et al.*, 2013), facts that are not generally recognized or appreciated by the public or policy makers. Because of its high density and specific heat sea water takes up heat more than 4000 times as effectively as air, volume to volume, and can thus transport and store large quantities of heat. As a consequence, the ocean, due to its large surface area, volume and low albedo, has absorbed more than 93% of the heat generated by anthropogenic global warming since 1971 (Wijffels *et al.*, 2016), as well as buffering year-to-year variability in atmospheric, land and sea surface temperatures. Without this oceanic buffer global temperatures would have risen much more steeply than has occurred.

To achieve a global radiative balance, the ocean also has a key role in the redistribution of heat from the tropics to the poles, as part of the thermohaline circulation (Meridional Oceanic Circulation, MOC) known commonly as the ‘global conveyor belt’. Contrary to research up to 2010, e.g. Le Quéré *et al.* (2010) and a general belief that an increased stabilization of the

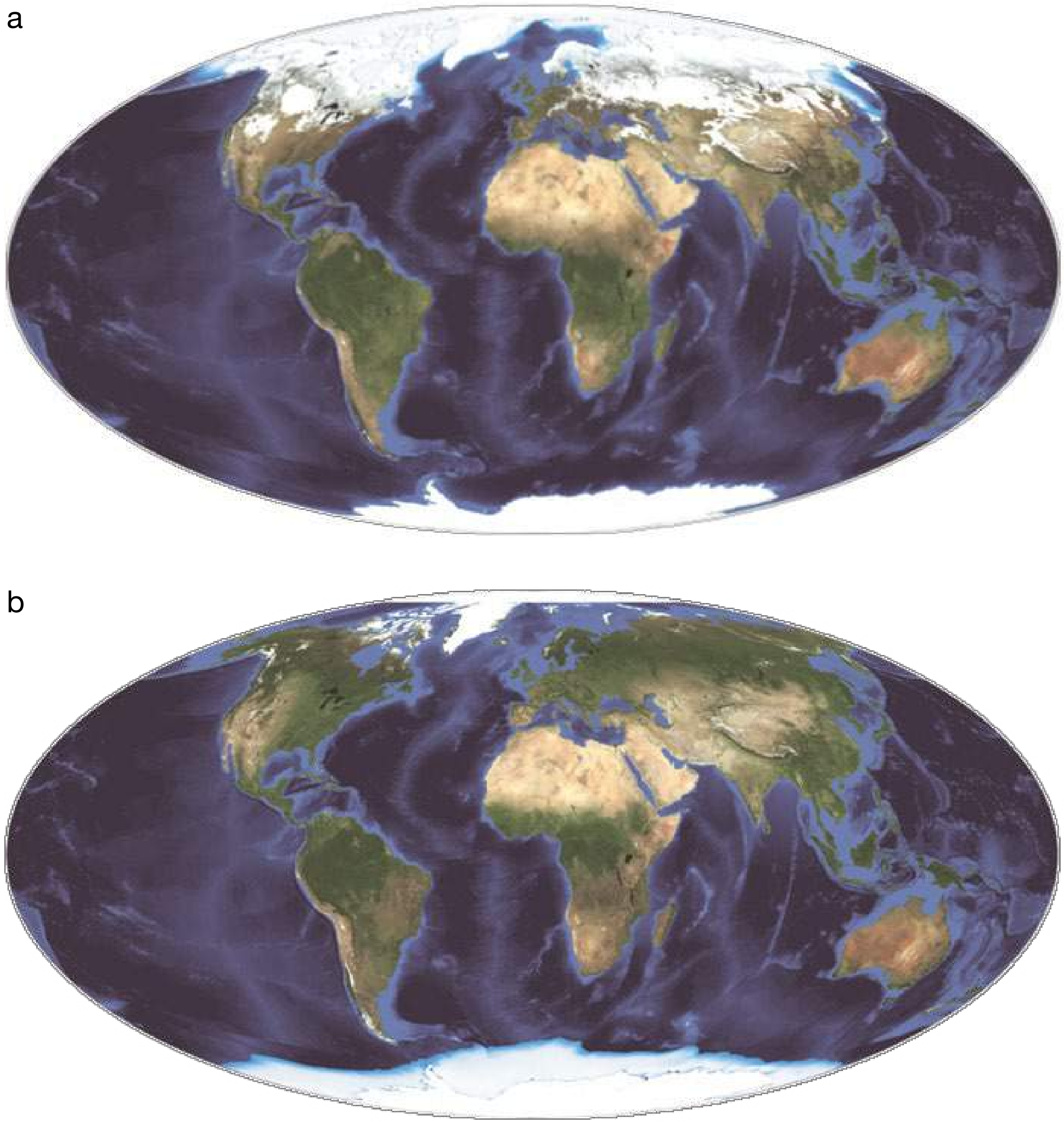


Figure 1.1 (a) shows the maximum extent of snow, ice and sea-ice in the Arctic winter and minimum in the Antarctic winter with land plant growth (greening) in the Northern Hemisphere winter and Southern Hemisphere summer. (b) The same for the Antarctic winter and Arctic summer, with the opposite seasonal patterns to 'a' for land plant growth. The two maps also give a coarse representation of ocean bathymetry: pale blue - shallow, dark blue – deep. Data based on MODIS surface reflectance; obtained from the GreenMarble initiative (http://services.imagico.de/greenmarble.php,see also: http://eoimages.gsfc.nasa.gov/images/imagerecords/74000/74518/readme.pdf). Maps produced by Jonathan Barichivich, Laboratoire des Sciences du Climat et de l'Environnement, Gif-sur-Yvette, France. (see Figure 2 for a more detailed representation of ocean topography).

ocean due to warming is likely to lead to a reduction in the uptake of CO_2, it appears that it has been taking up substantially more than previously thought (Ballantyne *et al.*, 2012; Reid *et al.*, 2016).

Seen from space, our world is not totally blue; it has both top (Arctic), and bottom (Antarctic) white caps from the snow, sea-ice and Antarctic and Greenland Ice sheets. The sea-ice and snow shows a strong seasonal cycle in its areal coverage, waxing and waning with the seasons (Figure 1.1).

Like the snow/ice extent terrestrial vegetation shows a pronounced inverse expansion/contraction with the seasons in each hemisphere. A similar expansion and contraction in plant growth occurs in the ocean, in this case measured from satellites as fluorescence (chlorophyll), (See: Figure 1.8 in Reid *et al.*, 2009).

Table 1.1 Effects, responses and interactions of ocean warming

Ocean warming effect	Current response
Changes in heat storage (Ocean Heat Content, OHC)	Increasing uptake of heat by the ocean as a response to the Earth's Energy Imbalance (EEI), buffering global warming Rising water temperatures at all depths Shallowing of the pycnocline Intensification of El Niño (ENSO) events
Changes in the strength/position of currents and heat transport.	Increased poleward heat transport in western boundary currents of the subtropical gyres Ditto in baroclinic shelf edge currents
Warming of adjacent land masses.	Warmer land surface temperatures Melting permafrost Retreating mountain glaciers and surface melting of the Greenland Ice sheet Terrestrial vegetation changing Increased extent and magnitude of forest fires
Rising sea levels due to direct thermosteric (heat expansion of water) plus other temperature related contributions from melting ice sheets and glaciers	Permanent land inundation, coastal erosion, flooding from storm surges, salt water intrusion into aquifers, loss of some coral atolls and islands.
A melting cryosphere (frozen world)	Basal melting and thinning of ice shelves in Antarctica destabilizing dammed up ice sheet glaciers Increasing overall Antarctic ice mass and sea ice Accelerated mass loss of the Greenland Ice Sheet including basal melting of marine terminating glaciers Accelerating reduction of sea ice in the Arctic and in the Bellingshausen/Amundsen Seas of Antarctica
Methane gas hydrate dissociation	Potential release of methane to the atmosphere from seafloor clathrates and permafrost
Intensification of the hydrological cycle	Enhanced atmospheric moisture transport towards the poles Rising humidity and increasing precipitation Increasing Eurasian river discharges Extreme droughts and floods Both negative and positive feedbacks to global warming Salinity increasing where evaporation dominates in the mid latitudes and decreasing in the rainfall dominated regions of the tropical and polar seas A strong feedback on polar SST from haline stratification
Negative feedback on the ocean carbon sink	Higher SST reduces pCO_2 uptake from the atmosphere Higher global SST and LST in part enhance the rate of increase in atmospheric CO_2
Deoxygenation	Reduced oxygen (O_2) solubility in warmer water. Reduced penetration of oxygen into deeper water due to enhanced stratification
Potential feedback from Ocean Acidification	Rising temperature reinforces Ocean Acidification. Possible feedback to global temperature from a reduced production of dimethylsulphide (DMS) by phytoplankton
Potential slowdown of the Biological Pump	Current status unclear

Ocean warming effect	Current response
The occurrence of more extremes in natural variability such as the El Niño/Southern Oscillation (ENSO) and in weather events	Changes in the occurrence, frequency and severity of cyclones/hurricanes Changes in the location and meandering of jet streams affecting downstream weather Landslides, collapses in fisheries Coral bleaching, enhanced disease prevalence, malnutrition and human migration Monsoons, forest fires and associated air pollution Positive feedback to temperature from burning peat
Changes in biological processes at cellular to ecosystem scales	Addressed in subsequent chapters

1.2 Background to ocean topography/terrain – a warming framework

An understanding of topography is essential to explain how the ocean distributes heat around the world and how warming is influenced by the different structure and depth of each of the ocean basins. Friction from topographic features on the bottom slows down currents, and topography/depth with the combined effects of the Coriolis Force influence mixing, upwelling and the path, meanders and eddy structures of ocean currents, that govern temperature in the upper and deep waters of the ocean.

The major western boundary currents of the subtropical gyres such as the Kuroshio and Gulf Stream that transport huge quantities of warm water from the tropics poleward, and the deep dense return flows that hug the edges of continents are all guided by bottom topography. Together these currents form part of the Meridional Oceanic Circulation. Baroclinic density driven currents also closely follow the topography of the shelf edge (Reid and Beaugrand, 2012). The Upper Circumpolar Deep Water (UCDW) of the Antarctic Circumpolar Current has little contact with the Antarctic Continent except where it rises to the level of the Western Antarctic Peninsula shelf to the east of the Ross Sea (Martinson, 2012) and in a warmer westward flowing shelf edge current adjacent to the Bellingshausen Sea (Zhang *et al.*, 2016). Penetration of ~3°C warmer water along deep troughs into the Bellingshausen Sea and onto the Western Antarctic Peninsula shelf has caused subsurface melting of West Antarctic ice shelves (Martinson and McKee, 2012; Zhang *et al.*, 2016) with consequent acceleration and thinning of some Antarctic glaciers, as the damming effect of the ice shelves is reduced (Sutterley *et al.*, 2014). Basal melting has also been reported for parts of East Antarctica (Rignot *et al.*, 2013) and a similar effect is seen beneath marine terminating glaciers in Greenland fjords (Rignot *et al.*, 2016).

The world on land that we know has been classified into major habitat types known as biomes that in turn have been divided into smaller ecoregions based on climate, temperature precipitation, relief, geology and soils with their characteristic vegetation and biota. Similar attempts to classify the different regions of the ocean have also been developed, e.g. the Biomes of Longhurst (2007) see also Reygondeau *et al*. (2013) and the Large Marine Ecosystems of e.g. Sherman (2015). However, neither of these systems take into full account the huge depth and topographic variability that is evident in the terrain of the ocean (Costello *et al.*, 2010) that is much greater than anything seen on land and dominated by the deep ocean (Figure 1.2). Only 11% of the area and 1% of the volume have depths shallower than 1000m and only ~7% of the area is covered by continental shelves with depths less than 200m.

While most of the deep ocean floor is relatively flat and featureless, there is substantial topographic variability marked by the mid ocean and other ridges that form along the edges of tectonic plates and are often associated with deep trenches. An estimated 60,000 isolated sea mounts and sub-marine volcanoes and close to 1 million sea hills and knolls also rise up from the ocean floor (Costello *et al.*, 2010). The large scale of the changes in topography seen in some parts of the ocean can be gauged against the Challenger Deep at ~11,000m depth in the Mariana Trench versus Mount Everest on land at 8850m above sea level. Because there is such a huge depth and in consequence pressure range in the ocean, each associated with its own specialized ecosystems (benthic for organisms living in and on the bottom and pelagic for those in the open water), oceanographers have classified

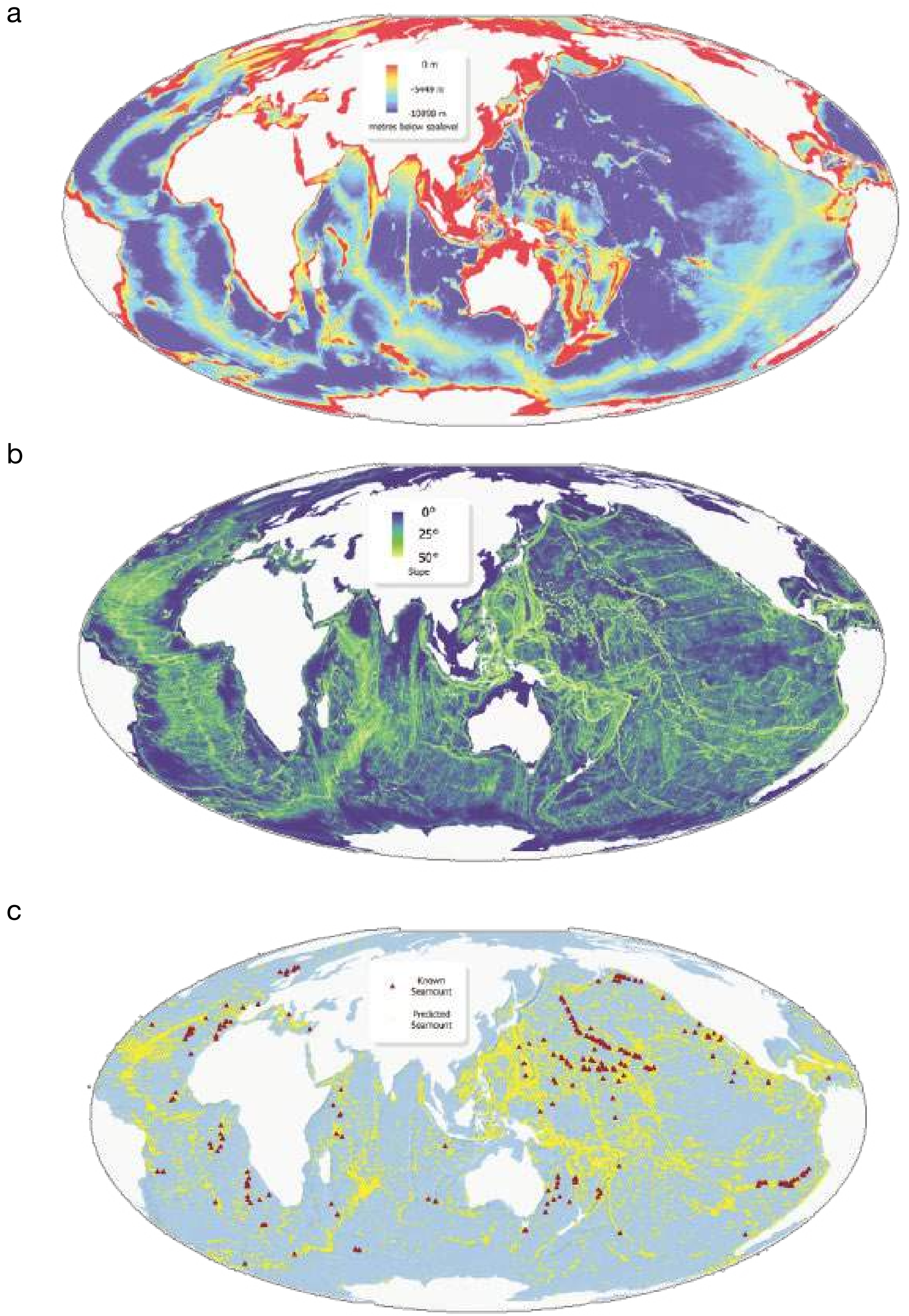


Figure 1.2 a) World bathymetry, b) slope of the bottom in degrees with a scale of low, dark blue to steep, yellow and c) occurrence of seamounts. Known seamount locations are indicated by red triangles and predicted seamounts in yellow. Note: the scale of the slope map exaggerates the areas of high slope because on a linear scale these areas would be almost invisible. The slope map highlights the location of the mid ocean ridges and deep sea trenches that form the boundaries of tectonic plates. The figures are higher definition versions to those presented in (Costello *et al.*, 2010) courtesy of Mark Costello, Leigh Marine Laboratory, University of Auckland, New Zealand.

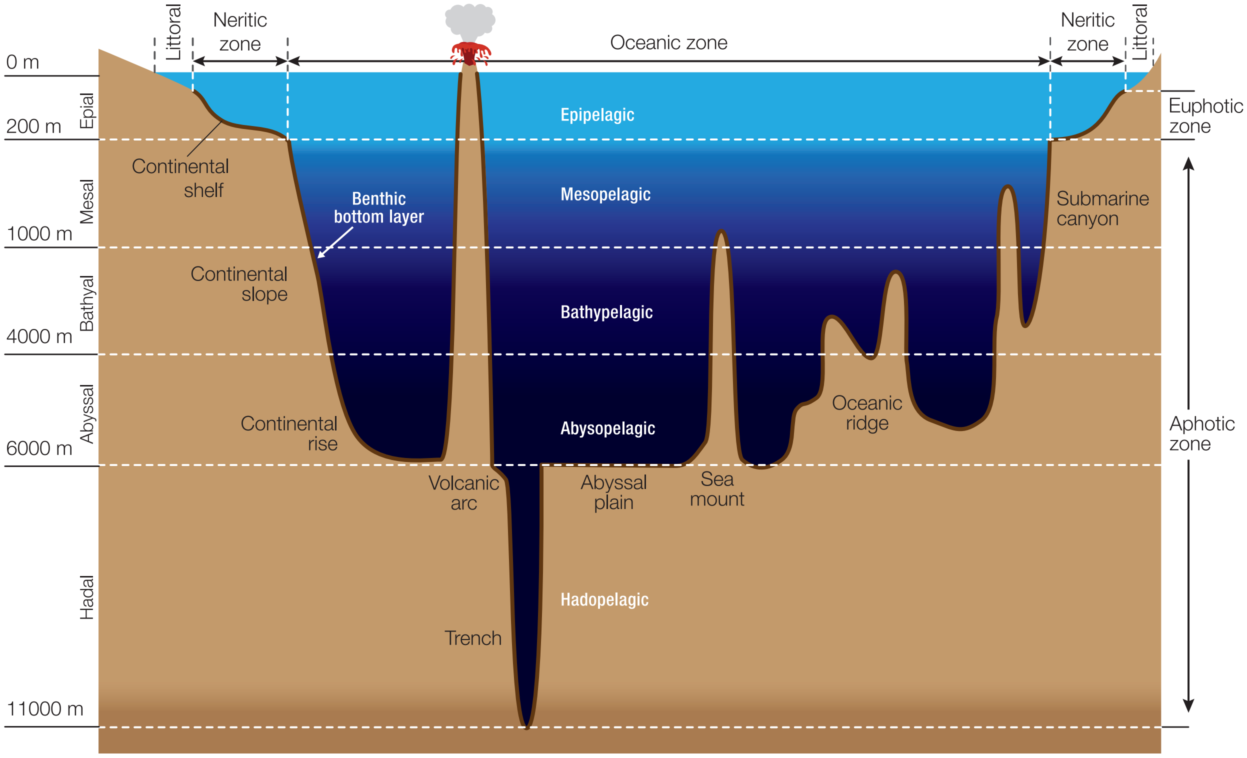


Figure 1.3 Depth zones of the ocean. The Continental Shelf extends out to 200m from the littoral intertidal zone, varying in width in different parts of the world (see Reid & Beaugrand, 2012) with on its outer edge the much steeper Continental Slope to 1000m. The Apial and Mesal depth zones are defined here for the first time as extending from 0 to 200m and 200m to 1000m respectively. The Bathyal zone extends from 1000 to 4000m, the Abyssal from 4000 to 6000m and the Hadal from 6000 to the deep bottom of ocean trenches. Pelagic zones have the same depth divisions and prefix as for the depth zones, but with the suffix - pelagic afterwards. Light for phytoplankton growth varies in the depth of penetration by latitude and water clarity averaging about 100m, with Aphotic waters below.

the ocean into different depth zones (Figure 1.3). The upper euphotic zone is where sufficient light penetrates to allow growth of plants. Specialized chemosynthetic ecosystems associated with deep sea vents and low oxygen zones also occur.

This large variability in depth and topography strongly influences the hydrography of the ocean, including current distribution, salinity, pH and oxygen concentration as well as light penetration and photosynthesis, and in consequence associated pelagic and benthic habitats. Terrain and topography need to be kept in mind when considering the changes in other physical and biological patterns related to ocean warming. Seamounts are especially important as they form productive centres of diversity and fisheries. The most variable topography and habitats with the richest diversity of corals and other species in the ocean are associated with the Indo-West Pacific islands, a region that includes the 'warm pool' with temperatures >28.5°C (see Wilkinson *et al*., 2016). This shallow oceanic region is also characterized by high rainfall and plays a critical role (through evaporation) in the hydrological cycle in Asia.

1.3 A major ocean contribution to the global heat budget

The Earth has absorbed more radiant energy from the sun than it is reflecting back into space at the top of the atmosphere (TOA) and as a result heat has accumulated in Earth systems since at least 1970 (Rhein *et al.*, 2013; Trenberth *et al.*, 2014; von Schuckmann *et al.*, 2016). More energy (heat) is retained at present than is returned to space to create what is termed an Earth Energy Imbalance (EEI). By scientific consensus the primary cause of the excess energy input, is rapidly increasing anthropogenic greenhouse gases (IPCC, 2013a). It is becoming increasingly apparent that the ocean has a major role as the main (93%) reservoir for the additional heat produced and accumulated by global warming, with ~3-4% for melting snow and ice and only ~1% for the atmosphere (Figure 1.4). The scale of the ocean buffer is enormous and only a small reduction in uptake or increased flux from the ocean to the atmosphere would have a huge impact on global air temperature, never mind the impact that the warming of the ocean is having on marine ecosystems.

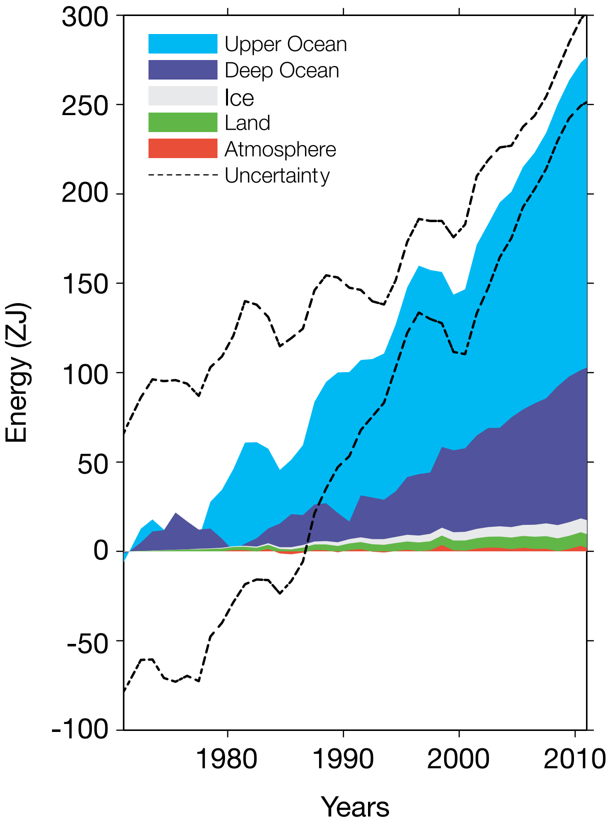


Figure 1.4 Energy accumulation in ZJ (1 ZJ = 10^{21} J) by different parts of the Earth's climate system relative to 1971 for the period 1971-2010 where measurements available. See original source for the start date of each variable. The ocean dominates the energy uptake with most of the warming absorbed by the upper ocean above 700m (light blue) and the rest in the deep ocean below (dark blue). A small percentage of the energy is involved in ice melt (light grey), continental land warming (green) and atmospheric warming (brown). Dashed lines 90% confidence intervals for all variables combined. Figure from (Rhein *et al.*, 2013).

Improved understanding of the risks associated with the ocean uptake and quantification of the energy gain by the Earth due to the EEI is needed to determine how the climate responds to radiative forcing. Approximately 30% of the incoming shortwave radiation at the TOA is reflected back into space by clouds and from the surface. The remaining heat is absorbed and distributed between different Earth systems, used to evaporate water and melt snow and ice, and eventually returned to space as infrared radiation. It is the balance between the absorbed visible solar radiation and the outgoing longwave radiation that determines the radiation budget of the world. Figure 1.5 shows the complexity of the various processes involved in the global energy flows that need to be measured to calculate the EEI. Note that the energy imbalance due to the EEI is a very small part (0.6 Wm^{-2}) of the total energy flows and input from the sun emphasising again the vulnerability of the Earth and ocean to global warming.

Improved measurements from satellites and especially sea surface altimetry from 1992, establishment of the tropical Pacific moorings in the same year and Argo measurements of temperature down to 2000m since 2000 (see Box 1.1) have made it possible to more accurately measure the many processes involved in the EEI. In 2009 Trenberth (2009) calculated a net absorption of heat (EEI) of 0.9 $W.m^{-2}$. More recent calculations based on both Top of the Atmosphere (TOA) calculations, OHC and models have refined the estimate of excess absorption of heat and its annual and decadal variability to an average of ~0.5 to 0.8 $W.m^{-2}$ (Hansen *et al.*, 2011; Trenberth *et al.*, 2014). IPCC gave a mean heat flux to the global ocean surface of 0.55 $W.m^{-2}$ between 1971 and 2010 (Rhein *et al.*, 2013).

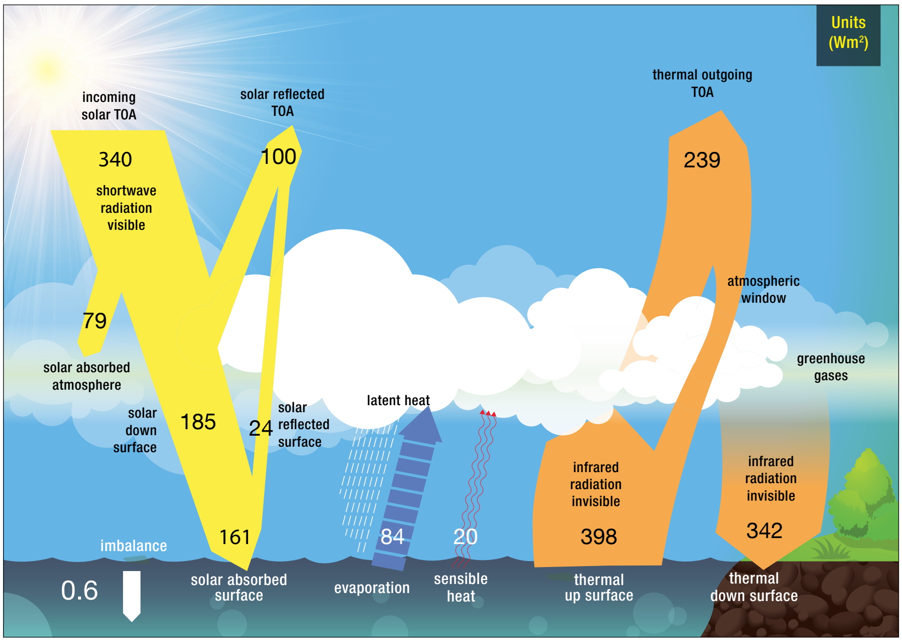


Figure 1.5 The left side of the figure shows the incoming shortwave visible solar radiation and its partial reflection back into space. The processes shown in the centre, with a slightly darker blue, are involved with the absorption of heat by the atmosphere. The right side of the diagram shows the reflection of infrared radiation back from the Earth's surface and the returning back radiation due to Greenhouse Gases. Absorbed solar radiation (ASR) is stored as various forms of heat, mainly in the ocean, but also on land and in the atmosphere, distributed and with varying delays emitted back to the atmosphere as part of natural variability. Simplified and modified diagram after Hartmann *et al.*, (2013).

The total flow of energy through the global climate system is estimated at ~122 PW Petawatts = (10^{15} W); equivalent to 239 W. m^{-2} (Trenberth *et al.*, 2014). It is calculated that the ocean has taken up 93% of the excess heat (EEI), with the melting of ice (latent heat) comprising ~4% and the heat absorbed by the atmosphere ~1% and land ~2% (Figure 1.6a).

A sufficiently accurate calculation of the EEI has only been possible in recent years and there are still issues of bias, measurement coverage and accuracy that need to be addressed to refine this crucial calculation needed to assess the future direction and intensity of global warming (von Schuckmann *et al.*, 2016).

The additional heat absorbed and warming of the Earth (Figure 1.6b) has led to:

1. rising global surface temperature (combined land and sea surface) that reached new records in 2014, 2015 and 2016;
2. droughts and floods;
3. a big increase in OHC;
4. melting of snow, permafrost, sea-ice, ice sheets and glaciers;
5. a more intensified hydrological cycle with both negative and positive feedbacks to global warming;

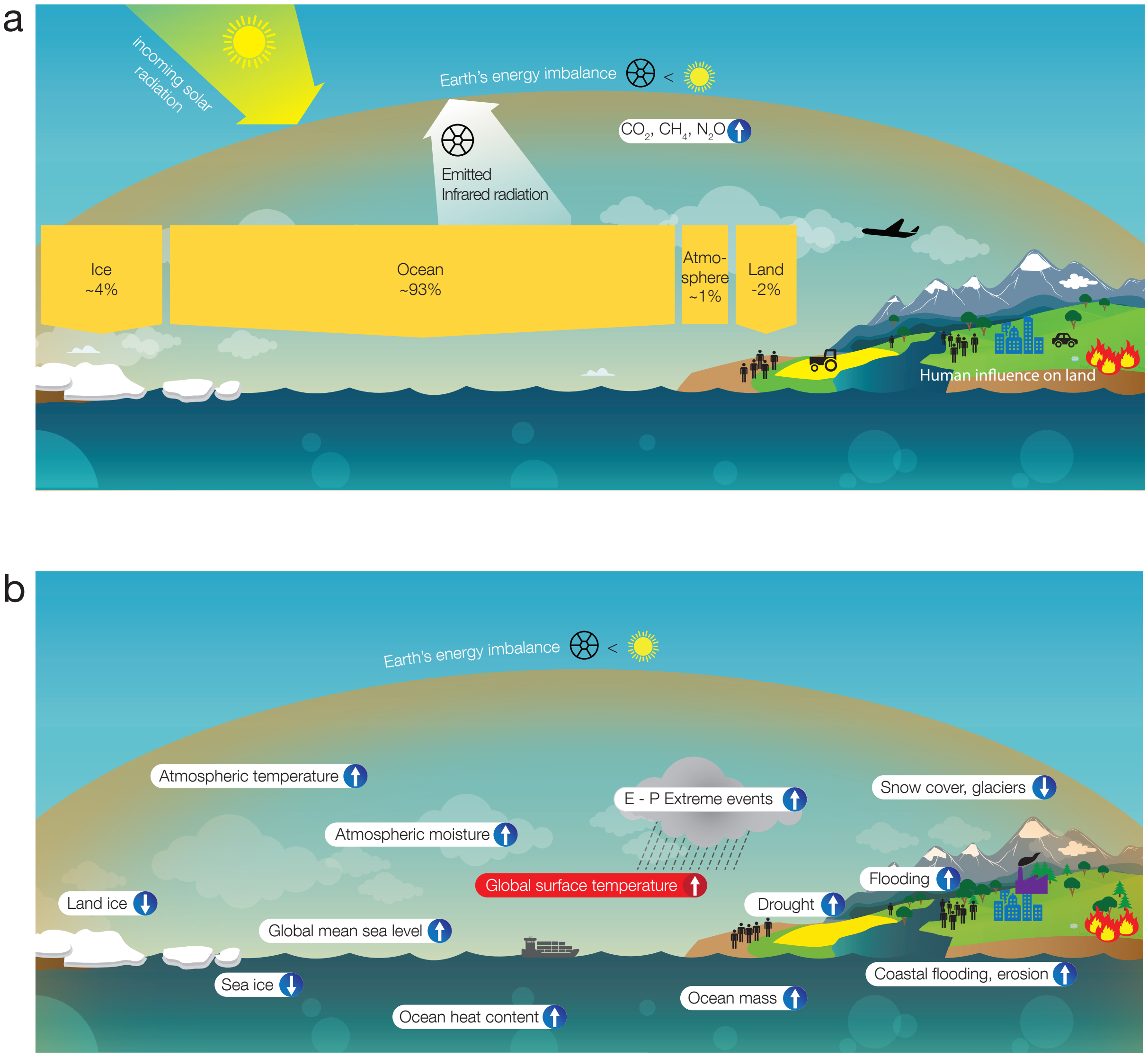


Figure 1.6 Schematic representations of: **a** the flow and storage of energy in the Earth's climate system. The global ocean is the major heat reservoir, with ~93% of EEI stored there. The rest goes into warming the land, atmosphere and melting ice and snow. And, **b** the consequences of EEI and the resulting global warming caused by human activities that is leading to rising surface temperature, ocean heat content, ocean mass, global mean sea level, atmospheric temperature and moisture, drought, flooding and erosion, increases in extreme events, and evaporation – precipitation (E–P), plus a reduction in ice sheets, glaciers, sea-ice and snow cover. Redrawn and modified after von Schuckmann *et al.* (2016).

6. Sea-level rise due to thermosteric expansion of water plus contributions from melting ice sheets, glaciers and snow and increased precipitation;
7. a likely contribution to more extremes in natural variability such as the El Niño/Southern Oscillation (ENSO);
8. the occurrence of more extreme weather events.

Box 1.1 Ocean Observations and the Argo Revolution.

Systematic observations of the atmosphere at meteorological stations on land and in the surface of the ocean from ships along their tracks have been made and coordinated by the World Meteorological Organization and its predecessor since 1853. It was recognized in the 1990s that similar observations of the ocean's interior were needed to help understand the changing state of the Earth's climate. Building on already developed technology, proposals were put forward in 1998/99 to establish an international cooperative programme (Argo) to measure in real-time high quality data on temperature, conductivity (for salinity) and pressure from an array of profiling floats. Starting in 2000, the Argo project achieved its initial aim of deploying 3000 floats in all ocean basins by November 2007 and by the end of 2015 ~1.5 million Argo profiles had been achieved (Riser *et al.*, 2016). Since then Argo has revolutionized our understanding of the changing status of upper ocean temperature, salinity and water circulation (Boutin *et al.*, 2013; Bowen *et al.*, 2014; Roemmich *et al.*, 2015; Durack *et al.*, 2016).

After deployment, mostly from ships, but sometimes from aircraft, Argo floats sink to 1000m and remain at that depth for ~9 days, when they sink to 2000m and then rise over a 6 hour period, measuring temperature, conductivity and pressure until they break the surface. On reaching the surface Argo transmits the accumulated data via a satellite to meteorological forecasting centres and two ocean data centres (in France and the USA) after which, it sinks to its 1000m 'parking' depth and repeats the cycle. The data are quality controlled and made available in real time and delayed mode formats for free without restrictions (see: http://www.coriolis.eu.org/Data-Products).

Argo is one of a number of physico-chemical and biological programmes that contribute to the Global Ocean Observing System (GOOS) http://www.ioc-goos.org/. GOOS is a permanent international collaborative system for observing, modelling and analysing global ocean variables that supports operational ocean services worldwide. Together these different observing systems and their operational products are greatly improving our understanding of the ocean and of ocean/atmosphere interactions such as the El Niño/Southern Oscillation (ENSO) that can have such a devastating impact on tropical countries.

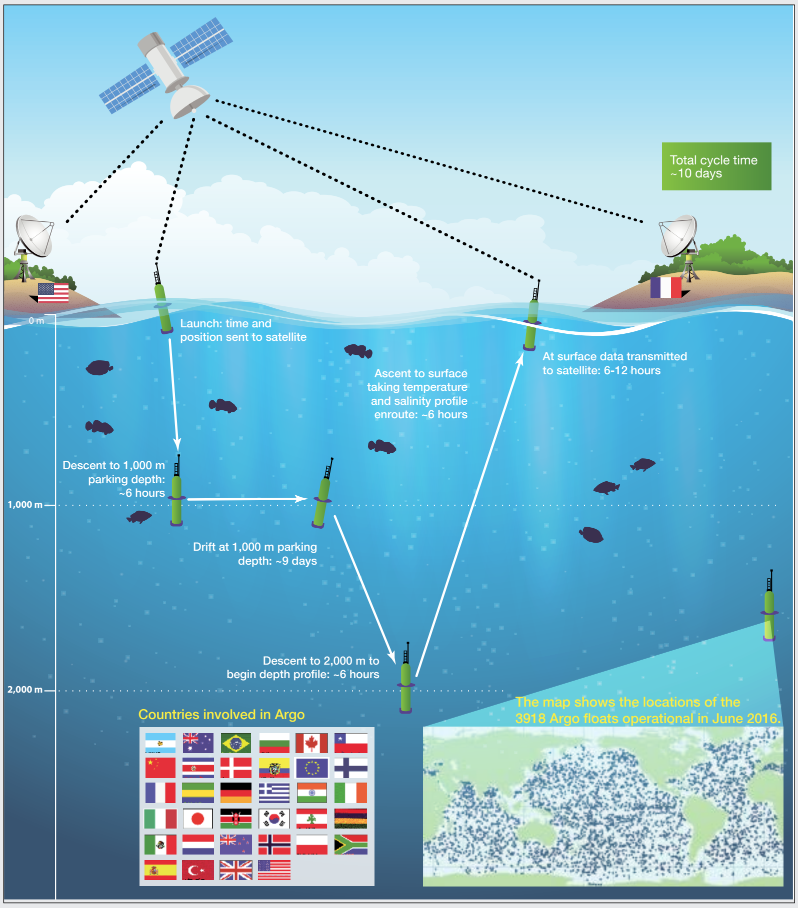


Figure 1 Argo cycle. Launch position/time to satellite and Global Data Assembly Centres (GDACs). Descent to 1000m parking depth, then 2000m. Salinity and temperature profiling ascent to surface. Data to satellite and GDACs and then free distribution to user community. Repeat 10 day cycle.

1.4 Global Surface Temperature

Since the 19th Century global surface temperature (combined land and sea surface temperature) peaked in the 1940s and then changed little, but has increased steadily since the 1970s (Hartmann *et al.*, 2013; Hansen *et al.*, 2016b) (Figure 1.7).

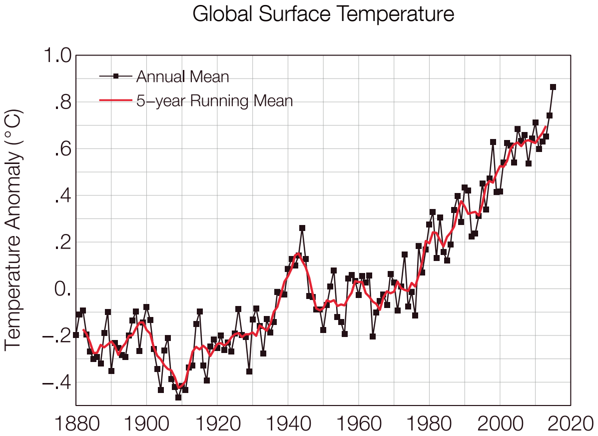


Figure 1.7 Global surface temperatures relative to 1951-1980 in the GISTEMP analysis, which uses data from GHCN meteorological stations, Antarctic research stations and NOAA sea surface temperatures. From Hansen *et al.*, (2016b).

The rate of change reduced from ~1998 and has been used by some sceptics as evidence for a slowing down in global warming. The rate has accelerated again in the last two years, when, for the first time in the instrumental time series, two years with record breaking global temperatures (2014, 2015) followed in sequence contradicting suggestions for a 'global warming hiatus' since ~1998 (Hansen *et al.*, 2015, 2016b). Reinforced by a strong El Niño (Box 1.2) this pattern of record temperatures has continued into 2016 with each of the first six months at least as the warmest on record and together as the warmest six month period since 1880 (Figure 1.8). Hansen and colleagues have calculated that the recent increases in temperature mean that global warming has now reached ~1°C since the 19th Century (Hansen *et al.*, 2016b); that is half way to what is considered as a 'dangerous interference with the climate system' (Hansen *et al.*, 2016a; Knutti *et al.*, 2016). A more ambitious target to pursue efforts to limit the increase to 1.5°C was agreed at the. 2015 UNFCCC Paris Agreement (Schellnhuber *et al.*, 2016).

1.5 Ocean warming: sea surface temperature

Average global SST (the temperature of the upper few metres of the ocean) has shown a warming trend of ~0.13°C per decade since the beginning of the 20th Century with a small sub-peak centred on 1940 (Figure 1.9). The temperatures of the last three decades have been warmer than at any time since instrumental records were first obtained on a routine basis around 1880. Thirteen of the warmest SST years on record since 1880 (with the exception of 1997 and 1998, have occurred since 2000. Against this background, from about 1998, the increase in global surface temperature and SST appeared to stall, flattening-out to form what has been called a 'hiatus' in temperature growth that did not fit the predictions of global climate models (Roberts *et al.*, 2015). Throughout this period, in contrast to SST, OHC increased (see next section). Once the two exceptionally warm years for 2014 and 2015 are taken

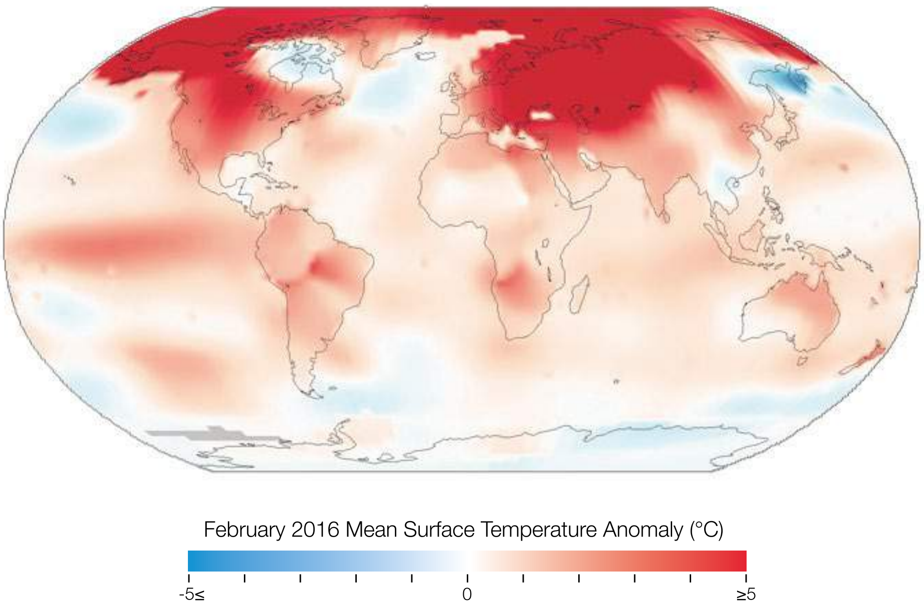


Figure 1.8 Record global surface temperatures for February 2016. Global map of mean surface temperature anomalies. The warmest temperature anomalies occurred in Asia, North America, and the Arctic and the coldest in the Northwest Pacific with cold anomalies also over Hudson Bay in Canada, the subpolar gyre in the North Atlantic, parts of the Southern Ocean and Antarctica. Note the higher temperatures in the central Pacific due to El Niño. From Voiland, (2016) based on GISS data.

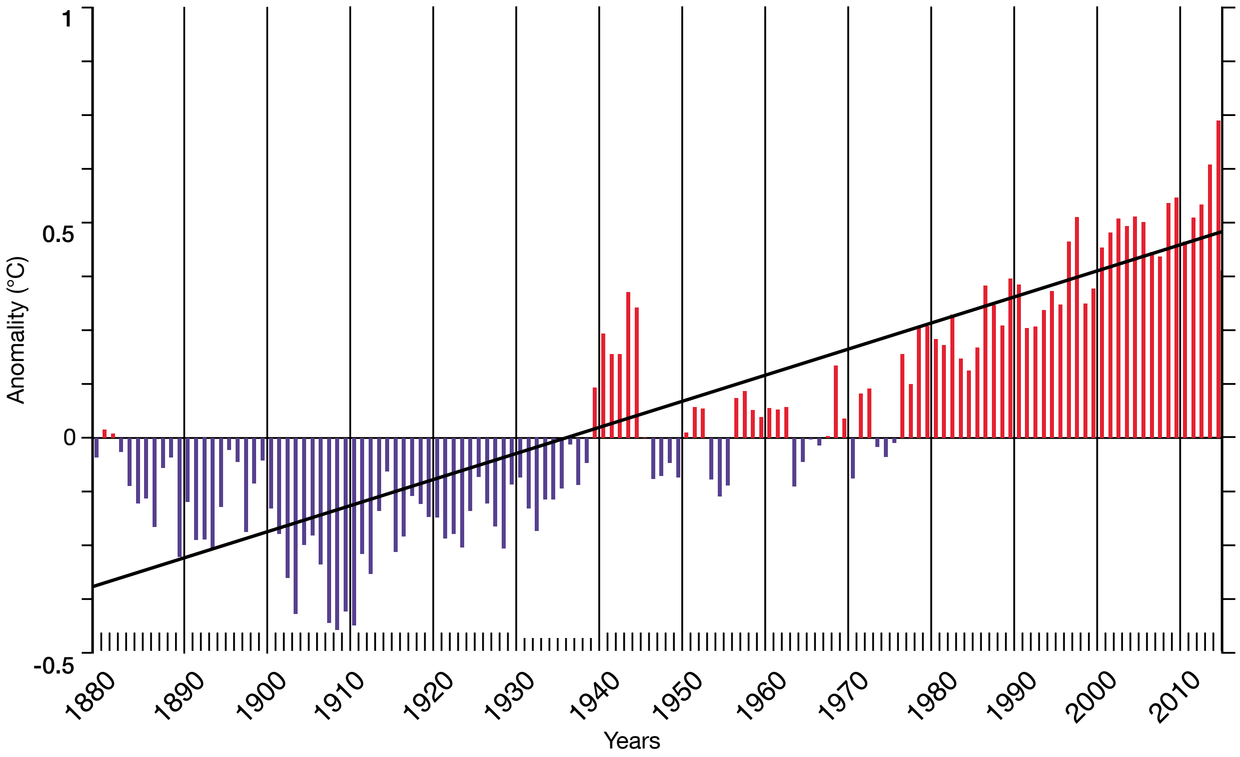
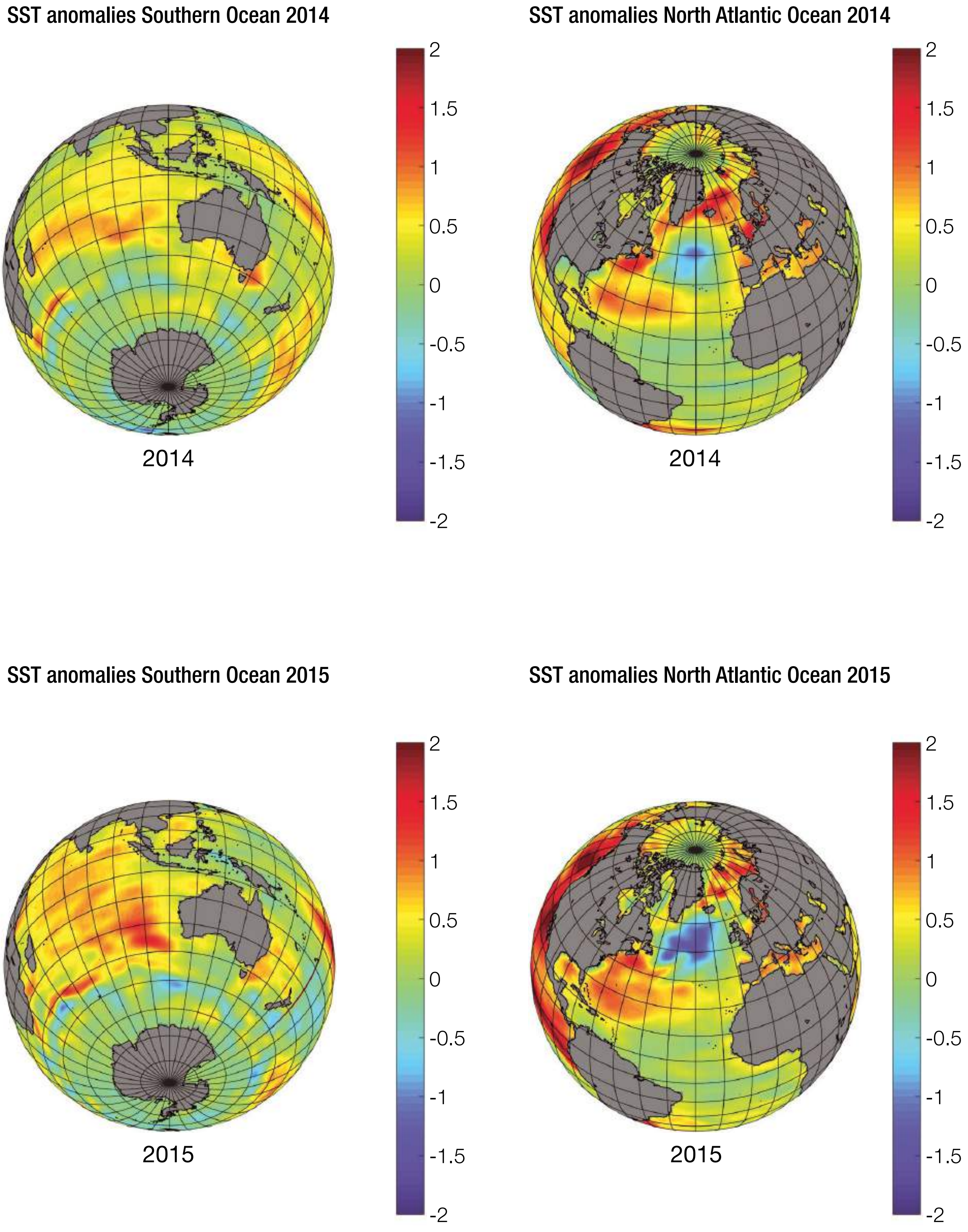


Figure 1.9 Annual global sea surface temperature anomalies from 1880 to 2015 with superimposed a linear trend (Base period 1951-1980), red positive, blue negative. From: http://www.ncdc.noaa.gov/cag/time-series/global/globe/ocean/ytd/12/1880-2016 .

into account, however, it is clear that the hiatus is a short term feature as both global surface temperature and SST and their rates of change have continued an upward and accelerating trend (Figures 1.7 and 1.9) (Smith *et al.*, 2015).

In contrast to global surface temperature the consecutive record SST years of 2014 and 2015 (Figure 1.10) were preceded by an earlier example in 2009 and 2010. Figure 1.10 presents global SST anomalies for the exceptionally warm years of 2014 and 2015. See Box 1.2 for a 'Pacific view' of the same data. The build-up of El Niño warmth in the eastern Pacific, including the 'warm blob' (Amaya *et al.*, 2016; Siedlecki *et al.*, 2016) is evident with strong warming in the Indian Ocean including the eastward propagation of the Aghulas Current recirculation and warmer anomalies encircling the cold North Atlantic. Subpolar Gyre 'cold blob' (Duchez *et al.*, 2016, Yeager *et al.*, 2016). The five most recent months of 2016 have, as for the global surface data, been the warmest months in the record with anomalies that reached at least 0.8° C. Due to this pronounced warming in the last decade especially, most of the ocean is much warmer than previously, with temperature anomalies greater than 1°C and anomalies that exceed 3 standard deviations in places. There are, however, pronounced regional differences in SST patterns with some areas with negative anomalies, including the Southern Ocean, the eastern North and South Pacific and since ~2009, and especially in the winter of 2013/2014, the exceptionally low temperatures in the North Atlantic Subpolar Gyre (Grist *et al.*, 2016) that have been referred to as the 'cold blob'. Warming has been particularly enhanced in the Arctic and adjacent seas due to what is known as polar amplification (Cohen *et al.*, 2014) and adjacent to the Western Antarctic Peninsula due to mixing from Upper Circumpolar Deep Water (UCDW) (Martinson, 2012). Cooler waters occur in the Southern Ocean and low SST around Antarctica as a whole has been linked to a general expansion of sea ice (Fan *et al.*, 2014). In European seas SST has increased more rapidly than the global average (Philippart *et al.*, 2011). Large inter-annual and decadal variability is superimposed on these global and regional patterns of change. In the Atlantic this variability is linked to climatic indices such as the NAO and the Atlantic Multi-decadal Oscillation (AMO), and in the Pacific with the PDO and ENSO. Modelling studies predict that the trend in SST is likely to continue in the 21st Century with mean global sea surface warming varying between 1°C and more than 3°C depending on the emission scenarios used, with the greatest warming in the tropics and subtropics (Collins *et al.*, 2013).



SST anomalies Southern Ocean 2014

SST anomalies North Atlantic Ocean 2014

SST anomalies Southern Ocean 2015

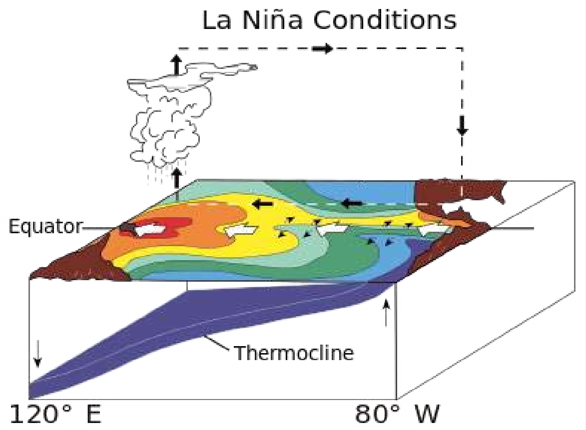
SST anomalies North Atlantic Ocean 2015

Figure 1.10 Maps of SST anomalies for 2014 and 2015 with a southern hemisphere polar and northern hemisphere semi-polar view, centred respectively on Malaysia and Greenland. Anomalies calculated on the mean of the period 1960-2013 for 2014 and 1960-2014 for 2015. Figure produced by Pierre Hélaouët, SAHFOS. based on GISS data http://data.giss.nasa.gov/gistemp/. See also SAHFOS Global Marine Ecological Status Report for 2014/15 (Edwards *et al.,* 2016).

Box 1.2 Major global oceanic variability linked to warming: El Niño Southern Oscillation (ENSO)

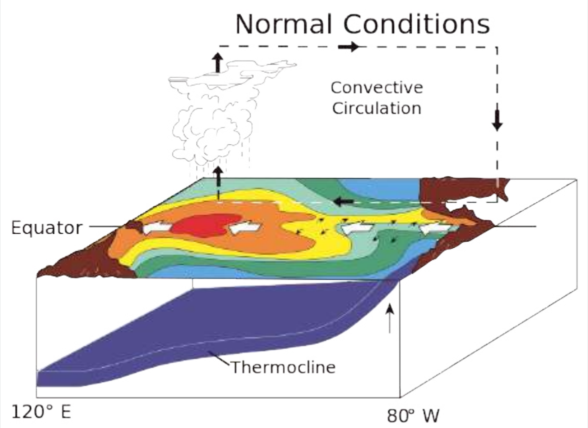
Approximately every 3 to 7 years the surface waters of the equatorial Pacific undergo an oscillation between exceptionally warm and cold surface temperatures named respectively as El Niño and La Niña with an intermediate neutral phase. These oceanic events combined with their atmospheric counterpart, the Southern Oscillation (SO), are termed the El Niño Southern Oscillation (ENSO).

El Niño and La Niña events, depending on their severity, may have enormous socio-economic and health effects in some regions of the world. South America is especially affected where El Niño may devastate the economies of Peru and adjacent countries due to a collapse in the largest fishery in the world and to high rainfall and its associated floods and landslides. In contrast, El Niño causes droughts in other parts of South America, effects that are also pronounced in Southern Africa, South-east Asia, Australia and Canada. Heat, drought and floods exacerbate disease prevalence, malnutrition and migration; El Niño and La Niña years are also associated with outbreaks of vector-borne diseases such as cholera, malaria and dengue fever (e.g.van Panhuis *et al.*, 2015). It is estimated that the current 2015/2016 El Niño had already severely impacting the livelihoods and health of 60 million people by April 2016, with 50 million people affected in Southern Africa alone by the end of May (United Nations Office for the Coordination of Humanitarian Affairs, 2016). In a marine context, because of reduced upwelling, the productivity of the whole of the Pacific is affected by El Niño. The consequences are felt at all levels of the food web and predicted to be dire for corals (Wilkinson *et al.*, 2016) from multiple stressors that include bleaching and increased storms. Such impacts are likely to be especially severe if El Niño frequency increases as projected by models (Cai *et al.*, 2014).

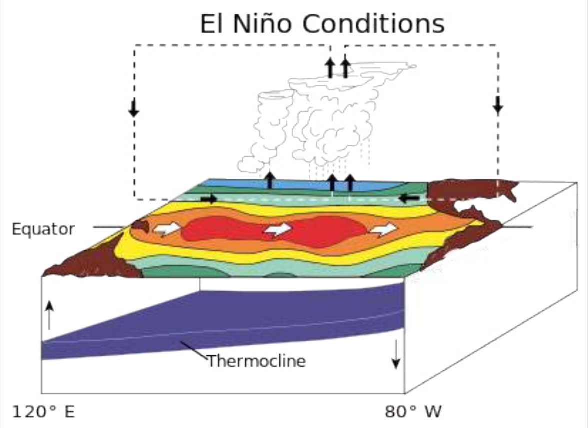


Accumulation of warm sea water in the east causes the sea level to slope downward from west to east with strong upwelling of cold water off South America. The thermocline slopes steeply in the opposite direction, extending down to ~200m in the west. Low pressure and associated intense cloud formation and precipitation create strong convective updraft as the upward limb to flow westwards and then down as part of the "Walker Circulation returning in strong easterlies above the ocean surface.”

There is a strong interaction between the atmosphere and ocean in the equatorial Pacific due to intense solar heating and a west to east sea surface temperature gradient. It is the contrast between the high pressure over the cold water in the east and the low pressure over the warm water in the west that drives the dominant easterly trade winds along the equator. Over time a see-saw in this west to east pressure difference



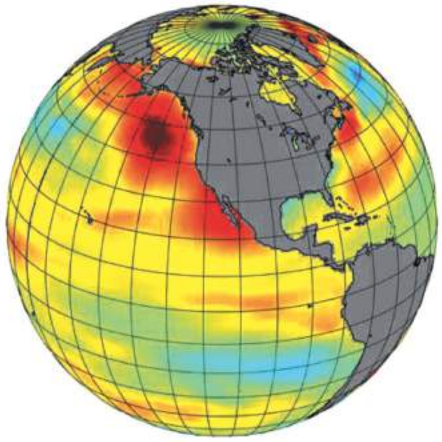
Warm temperatures extend half way across the Pacific. The slopes of both the surface and thermocline are less steep with shallower warm conditions in the west and upwelling of cold water off South America. The Walker Circulation follows a similar pattern to La Niña.



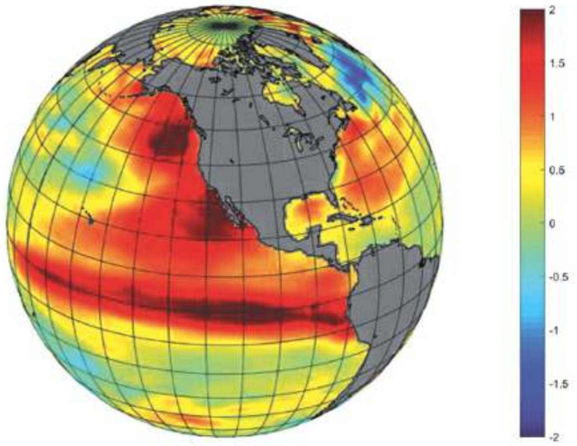
Warm conditions extend all the way across the Pacific with the sea surface sloping upwards from west to east and the thermocline flattening off, sinking in the east and restricting upwelling. The Focus of the Walker Circulation moves to over the central Pacific resulting in westward flowing surface winds flowing across half the Pacific reducing the intensity of the easterlies.

Redrawn from http: //www.pmel.noaa.gov/elnino/schematic-diagrams

Box 1.2 Cont.


Incipient 2014 El Niño and 'warm blob'

A map, based on the same data as in Figure 1.10, but centred on the eastern Pacific, to show the incipient 2014 El Niño and the 'warm blob'. Map courtesy of Pierre Hélaouët, SAHFOS.


2015 El Niño and 'warm blob'

Map showing the full 2015 El Niño plus again the 'warm blob'. Map courtesy of Pierre Hélaouët, SAHFOS.

occurs, known as the Southern Oscillation (SO) with negative extremes in pressure reflected in high SST in the east Pacific (El Niño) and the reverse (La Niña).

In neutral and La Niña states the trade winds maintain a pressure gradient and transport warm near surface waters (~0-100m) westwards leading to a damming up of warm water in the west Pacific 'warm pool'. The pressure gradient raises surface sea level about 80cm to 1m higher in the western Pacific, with upwelled cold water and a lower sea surface in the east Pacific. At the same time the trade winds enhance coastal upwelling off the west coast of the Americas and to either side of the equator and further cool the east Pacific. As a consequence the thermocline is shallow in the east and deeper, sloping steeply to the west. Over the warm pool in the west strong atmospheric convection, rising air and intense cloud formation and rainfall is promoted, with the air flowing to the east in the upper troposphere, later sinking as drier air over the east Pacific and flowing westward along the equator to amplify the trade winds. This rising warm air in the west and sinking air in the east forms what is known as the 'Walker Circulation'.

A typical El Niño event is preceeded by a reversal of the above pattern with a subsurface build up of anomalously warm water and its transfer from the west to the east Pacific (Ramesh and Murtugudde, 2013) that is also reflected in positive sea surface temperature anomalies in the east that can reach more than 4°C above normal, and a substantial increase in sea surface height. Upwelling of cold water off the west coast of the Americas reduces, further increasing the temperature. As a result the slope of the thermocline flattens off and becomes deeper in the east. The trade winds slow down, helping to add to the increase in temperature. They may reverse at times, and in the incipient stages of an El Niño bursts of strong westerlys reinforce the easterly movement of warm water (Levine and McPhaden, 2016). The transfer of the centre of surface warmth in the ocean to the east is tracked by the Walker Circulation with a movement of the region of intense vertical convection, cloud formation and heavy rainfall to over the islands of the central Pacific.

Strong El Niño events impact the downstream atmospheric circulation of the whole of the world because of the large release of ocean heat to the atmosphere that is distributed around the globe. Jet streams alter their courses, cyclone/hurricane patterns change, monsoons are affected and extremes of heat and precipitation characterize many parts of the world. Huge forest fires in Canada in 1998 (Hirsch, 1991) and the May 2016 onwards Fort MacMurry fire in Alberta have occurred in El Niño years as have the enormous forest fires and air pollution that have blighted Indonesia and Australia. La Niña events may have an equally large, if not greater, impact (Hoyos *et al.*, 2013), especially following large El Niños, e.g. the 2011 drought in the Horn of Africa and the huge floods in 1998 in Venezuela, China and Bangladesh.

1.6 The heart of ocean warming – our evolving knowledge of Ocean Heat Content (OHC)

The ocean's key role in climate variability as a consequence of its huge capacity to store heat, and the way that it has buffered climate change due to the EEI, has been emphasized above. Over the last few decades there has been a rapid and accelerating rise in heat storage in the ocean with downstream consequences for the atmosphere, hydrosphere and cryosphere (Wijffels *et al.*, 2016). All global systems are likely to have been affected and especially seasonal, decadal and regional variability in climate, ocean circulation, stratification, heat transport, biogeochemistry, and ocean ecosystems and fisheries. Climate models show good agreement with long-term trends in OHC and agree with ocean observations that show that major volcanic eruptions that inject aerosols into the stratosphere can lead to marked reductions in OHC (Balmaseda *et al.*, 2013; Ding *et al.*, 2014), but may be followed by a rapid recovery in surface temperature (Reid *et al.*, 2016). Recent observations demonstrate that the heat absorbed due to EEI can be redistributed to different depths and between different ocean basins over relatively short periods of time. Much of the spatial and temporal variability seen in patterns of heat gain is due to this redistribution by dynamic processes in the ocean rather than air-sea exchange at the surface. Different processes seem to have operated in each ocean basin.

In addition to his many other contributions to meteorology and oceanography, Rossby in his posthumous paper (Rossby, 1959) [first published in Swedish in 1956 (Rossby, 1956)] was the first to propose that because of its large specific heat capacity (water is able to absorb more than 4000 times as much heat as air) and huge volume, the world's ocean is the main factor in the Earth's heat balance. He recognized that the ocean takes up large amounts of heat from the atmosphere and is able to store it below the surface, out of contact with the atmosphere for periods of time ranging from seasons to many centuries (estimated as up to 1000 years). It was at about this time that the key role that CO_2 plays in global warming and its absorption by the ocean was also demonstrated (Plass, 1956; Revelle and Suess, 1957).

Hoffert *et al*. (1980) suggested that the temporary heat storage in the ocean acted like a thermal flywheel and he was the first to recognize polar amplification of warming. In early 1D modelling studies Hansen *et al.* (1981, 1983) recognized the crucial importance of improving understanding of ocean dynamics and especially heat storage and transport by the ocean, to better assess future climate over the next century. They also predicted many of the changes that we are now seeing from global warming, without at that time evidence for a clear greenhouse effect. The 'simple' climate models that were used in the 1980s and at the beginning of the 1990s represented the continents at times as a "wonderland" and the ocean as a static pool of sea water acting as an infinite source or sink of heat and humidity assuming that heat mixed down from the surface at a constant rate (Hansen *et al.*, 1993). More complex climate models that were under development were not able to correctly simulate ocean heat uptake and data for input was lacking. Necessary sub-surface temperature data were not available on a global scale until ~2000 as a result of an impressive data archaeology, compilation and rescue project that processed a huge amount of global ocean profile data (see: Levitus *et al*., 2000). Subsequently, Levitus *et al*. (2001) were able to confirm Rossby's suggestion that ocean heat dominates over other parts of the global heat budget. They estimated back then that ~84% of the increase in the heat content of the Earth was taken up by the ocean.

Oceanographers involved in the IPCC First Assessment Report (FAR) (IPCC, 1990) drew attention to storage and transport of heat by the ocean, but the importance and scale of the ocean's role was not generally appreciated by the wider scientific community. The assessment was limited because of the temporal and geographically restricted data that were available to measure ocean processes. Assimilating the few and spatially limited ocean observations into the General Atmosphere and Ocean Circulation models of the time often led to unrealistic rather than improved predictions. In 1990 ocean modelling was much less advanced than atmospheric modelling. This situation reflected the difficulties and costs of observing the ocean. Also, a much smaller cohort of oceanographers and institutions were involved in climate research, as is still the case now, compared to the meteorological community. To address these issues an Action Plan was proposed in the last chapter that included for the ocean the 1990 to1995 WOCE programme and new satellites to improve ocean monitoring (McBean *et al.*, 1990). The potential importance of heat storage in the ocean was recognized in FAR by reference to Rossby, but the data available to confirm any effects were limited to surveys in the North Atlantic and Pacific that showed at that time cooling in the upper layer down to 500m, but clear warming below this depth in the North Atlantic. This result, based on inadequate data coverage, did not raise any alarm bells.

Some of the positive initiatives in the FAR seem to have been lost in the 1995 IPCC SAR, where the Working Group (WG) 1 report (IPCC, 1996) emphasized modelling, and there was only one paragraph on sea temperature in the WG 2 report. Because of crude parameterization and a paucity of observations to validate models a number of issues were identified that continued to limit the progress of ocean process modelling relevant to climate. Models had improved, however, in the 5 years since FAR, evolving from mixed-layer ocean-atmosphere models to fully coupled atmosphere-ocean models. Even so there was limited coverage of ocean issues in the SAR with only two short paragraphs (4.3.5) that addressed ocean mixing below the surface layer. Only one page was devoted to improvements that were needed in ocean models (6.7.1.2). Against these shortcomings a whole chapter was devoted to sea-level change and another to marine biological responses to change and potential feedbacks to climate. It was not until the 2001 TAR (IPCC, 2001) that the first assessments at a global scale of ocean heat became available as a result of the efforts by Levitus and colleagues.

The 2007 IPCC Fourth Assessment Report (AR4) (IPCC, 2007a) broke new ground in respect to its coverage of physical ocean issues, with a full chapter devoted to the ocean and sea level. From a biological and time series context, however, (Richardson and Poloczanska, 2008) highlighted that marine systems were vastly underrepresented in the IPCC process. Marine ecosystems especially were described as being “under resourced, overlooked, under threat” and associated climate impacts poorly addressed by IPCC. In AR4 independent analyses of OHC based on close to 8 million profiles were updated to show an increasing trend in OHC in the top 700m. The results were considered then to be sufficiently accurate to close the Earth’s radiation budget, estimating at that time that the ocean accounts for more than 90% (Bindoff *et al.*, 2007) of the combined increase in heat of all Earth systems,

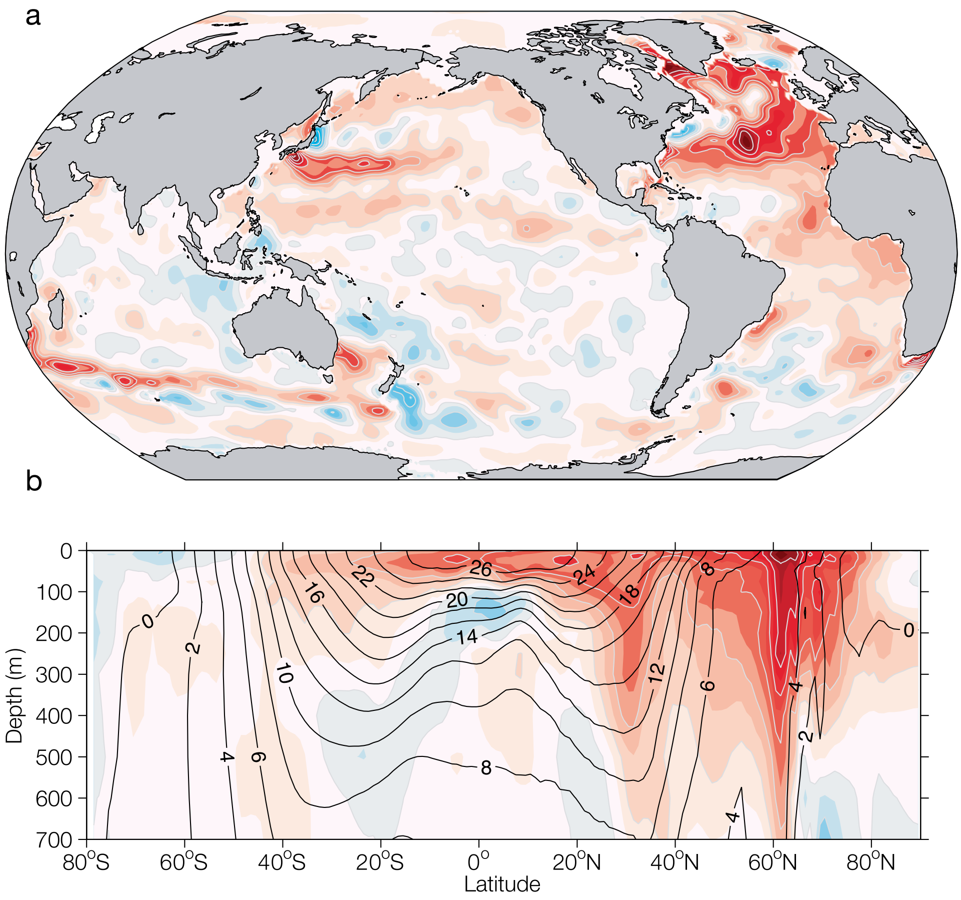


Figure 1.11 a. Depth-averaged 0 to 700 m OHC trend for 1971–2010, based on a grid of 2° longitude by 4° latitude, colours and grey contours in degrees Celsius per decade. From IPCC AR5 (Rhein *et al.*, 2013); b. Zonally averaged temperature trends (latitude versus depth). Colours and grey contours in degrees Celsius per decade for 1971–2010 with zonally averaged mean temperature over-plotted (black contours in degrees Celsius).’

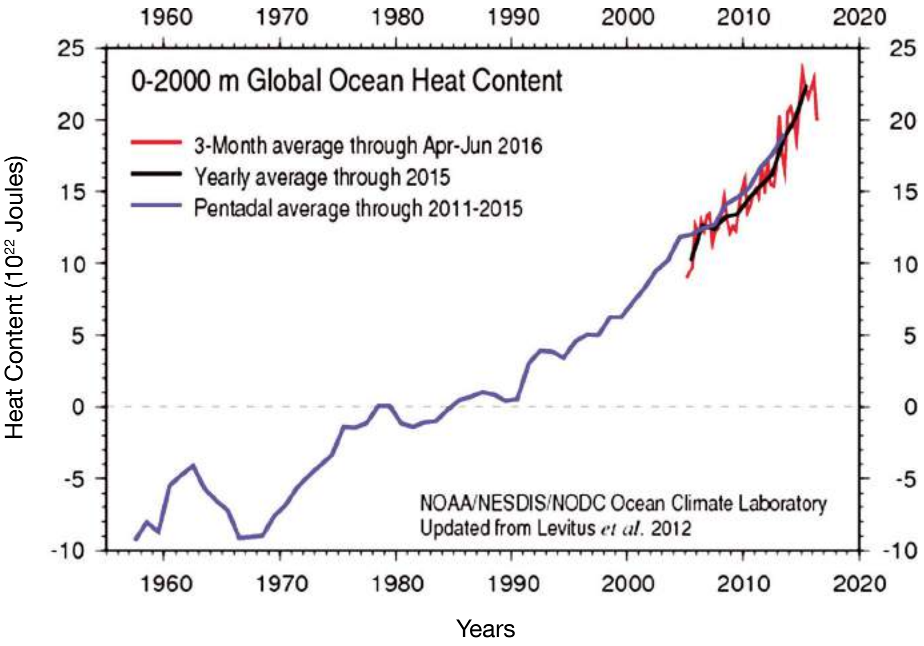


Figure 1.12 Plot of Global OHC 0-2000m as a pentadal trend from 1955-1959 to 2011-2015, with superimposed a yearly average from 2005-2015 and a three month average from January to March 2005 to April to June 2016; all averaged from 26 standard depths. From: https://www.nodc.noaa.gov/OC5/3M_HEAT_CONTENT/ Downloaded on 25 June 2016.

ocean, atmosphere, lithosphere and the heat generated by melting of components of the cryosphere. The ocean chapter included an acknowledgement for the first time that variability in OHC was critical for detecting effects from increasing greenhouse gases and for resolving the Earth's energy budget, but this comment was not referred to in the Technical Summary or the Summary for Policy Makers that both cited in error, in comparison with the main report, a more than 80% uptake of heat by the ocean and noted this only in relation to sea-level rise (IPCC, 2007b; Solomon *et al.*, 2007).

The key importance of OHC was eventually recognized in the IPCC AR5 report where the issue was brought right to the front of WGI Chapter 3 on Ocean Observations and included a box on 'Change in Global Energy Inventory' (Rhein *et al.*, 2013). The authors noted that the total absorption of heat for all depths of the ocean hugely dominates the energy imbalance of the global heat budget accounting for ~93% of the warming of Earth's systems since 1971 and as 90% in the Summary for Policy Makers (IPCC, 2013b). Given the magnitude of this storage there was no discussion of what would happen if the ocean reduced its rate of heat uptake or if only a small proportion of the heat gained was released. Estimates of OHC start to become reliable from about 1970 with further improvements following corrections for bias in XBT and other measurements (e.g. Domingues *et al.*, 2008; Levitus *et al.*, 2009). The largest fraction (~66%) of the OHC accumulated at a decadal scale since 1971 has been absorbed in the top 700m of the ocean's water column (Levitus *et al.*, 2012). The warming is ubiquitous (Figure 1.11), but especially, up to 2010 in the Northern Hemisphere and in the North Atlantic (Rhein *et al.*, 2013). It also coincides with a 4% increase in the temperature difference and thus density between the surface and 200m reflecting a shallowing of the pycnocline.

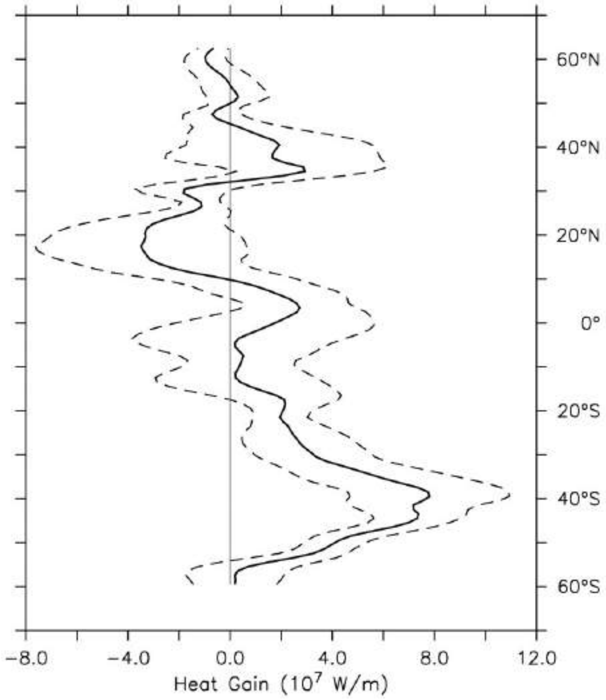


Figure 1.13 A plot of the heat gained by the ocean averaged for the depths 0 to 2000m over the 8 years 2006 to 2013 (107 W.m^{-2}), integrated against latitude and using one of the three interpolation methods applied by Roemmich *et al.* (2015).The results presented are based on a 1° latitude/longitude grid with 58 pressure (depth) levels and incorporated ~900,000 high quality Argo float profiles. The 95% confidence interval is shown as a dashed line. Redrawn as part of Figure 3b in Roemmich *et al.* (2015).

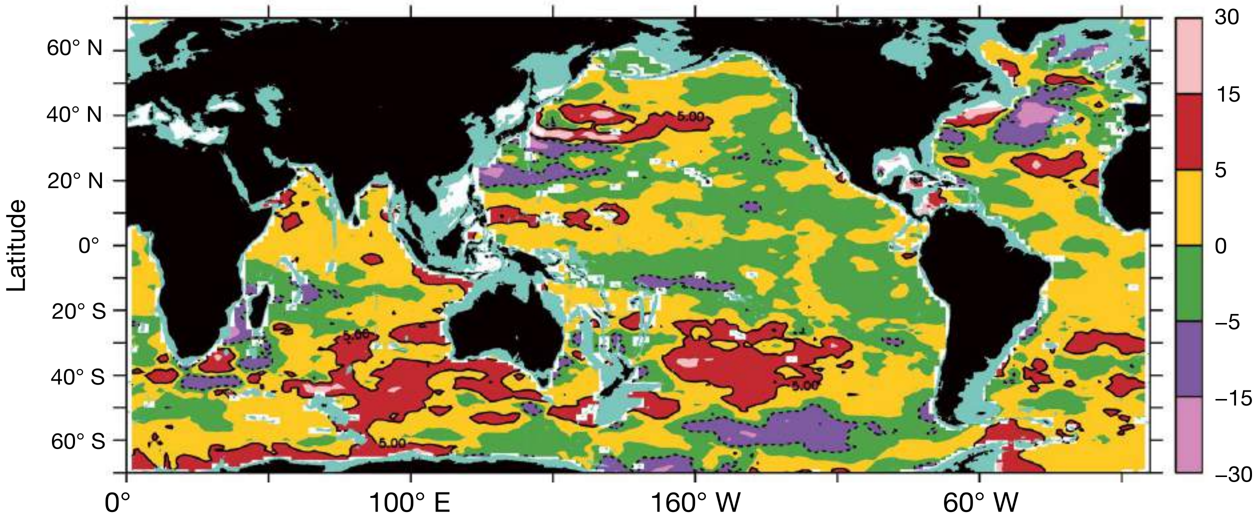


Figure 1.14 The spatial pattern of the trend in Ocean Heat Content (OHC) gain averaged for the depths 0 to 2000m over the years 2004 to 2010. Data as for Figure 13, but using a different interpolation method. A black contour line defines the areas where the heat gain was > than 5W.m^{-2}. A simplified version of Figure 3a in Roemmich *et al.* (2015). Figure courtesy of Dean Roemmich, Scripps Institution of Oceanography, USA.

It is estimated that approximately one third of the heat uptake in the surface to 2000m layer Figure 1.12 has been absorbed below 700m, and that this uptake was mostly above ~1500m (Levitus *et al.*, 2012). Roemmich *et al.* (2015) show that ocean heat gain over the 0–2,000 m layer continued at a rate of 0.4–0.6 W.m^{-2} during 2006–2013 which compares well with Levitus' estimate of 0.39 W.m^{-2} for the period 1955 to 2010.

In a review of the accumulation of heat by the ocean based on Argo results for the period 2006 to 2013 Roemmich *et al.* (2015) show that there has been a strong accumulation of heat in the mid latitudes of the Pacific and Indian Oceans at approximately 40° S (Figure 1.13) with weaker warming in the South Atlantic. Over this period most of the warming occurred in the Southern Hemisphere, a different pattern to the earlier study by Rhein *et al.* (2013). The maximum at 40°S coincides with the central cores of the subtropical gyres in the three ocean basins. The heat gained in these gyres is subducted down as a consequence of a strengthening circulation due to strong westerly winds. Secondary smaller peaks are seen at ~40N, again coinciding with part of the subtropical gyres, and centred just to the north of the equator in the tropics. The spatial pattern of heat gain in the 0 to 2000m water column (Figure 1.14 is in places the inverse of the map for the 0 to 700m depths from AR5.WG1 (Figure 1.11)

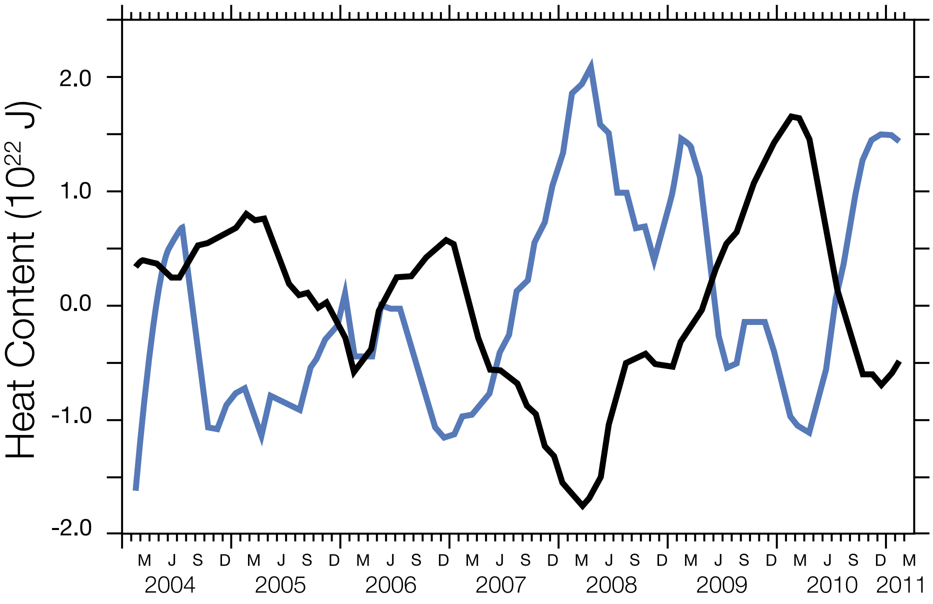


Figure 1.15 Monthly mean time series January 2004 to December 2010 of heat content for the depths 0-100m (black) and 100 to 500m (blue) averaged for the global ocean from 60°S to 60°N. Recalculated and drawn after. Roemmich and Gilson, (2011).

(Rhein *et al.*, 2013). Over the period studied the heat gain was divided equally between the 0 to 500m and 500 to 2,000m depth intervals. A key finding from Roemmich *et al.*'s work is that there is an inverse pattern between the OHC of the 0 to 100m and 100 to 500m layers and that global SST shows the same pattern as the top 100m. In an earlier study (Roemmich and Gilson, 2011) show that this alternation in the heat content of these upper layers of the ocean tracks inter-annual ENSO fluctuations, a result that fits with Hansen *et al.* (2016b) who note that global SST anomalies lag the Niño3.4 index by ~3 months. The finding by Roemmich's team has important ramifications for atmospheric warming as the heat accumulated over a number of years (La Niño/neutral ENSO) in the 100 to 500m layer is transferred to the upper layer in an El Niño year, "sloshing" from one side of the Pacific to the other and making it available for transfer and release to the atmosphere.

Systematic observations of temperature and other hydrographic measurements at depths below 2000m have only been taken by research cruises and at a few long-term time series stations (see http://www.oceansites.org/network/index.html). As a consequence, data are limited geographically and many of the measurements have only become available in the last three decades. Because of the lack of data and poor geographical coverage calculating heat absorbance for these deeper waters on a global scale is difficult and less precise (Domingues *et al.*, 2008). There is clear evidence, however, that the deep and abyssal ocean basins are absorbing substantial amounts of heat and contributing to thermosteric sea-level rise (Purkey and Johnson, 2010; Llovel *et al.*, 2014). Modelling studies based on different emission scenarios indicate that temperature increases of 0.5 to 1.5°C will extend down to depths of 1km by the end of the 21st Century. Gleckler *et al.* (2016) using CMIP5 models estimate that ~half of the OHC that has accumulated since the beginning of industrialization has occurred in recent decades and that more than one third has accumulated below 700m and is increasing.

1.7 Implications of the heat build-up in the ocean and the role of ENSO

It is well known that the ~10°C annual mean temperature difference between London and St Anthony, Newfoundland, at approximately the same latitude, is because heat from the warm Gulf Stream and its extension, the North Atlantic Current, is released from the ocean and taken up by the westerly weather systems to bathe Europe in warmth. Western boundary currents like the Gulf Stream have a key role in transporting warm tropical and sub-tropical water towards the poles and strongly influence the weather of downstream land masses. The ocean loses heat to the atmosphere when the surface is warm and vice versa when it is cold. This means that as the ocean warms up due to global warming it is likely that there will be a positive feedback from an increased release of heat to the atmosphere. Near surface water will also become more stratified (layered), isolating it from the colder waters below so that they heat even more, and further enhance heat release to the atmosphere. A possible example of a heat build-up of this nature may have occurred in 2013/2014 when what has been called the 'warm blob' in the North Pacific formed with temperatures that were > 3 standard deviations above the mean (Amaya *et al.*, 2016). This event had pronounced downstream weather consequences as well as major effects on the marine ecosystem (Siedlecki *et al.*, 2016). Similar effects on ecosystems were seen in the extreme warming that occurred off Western Australia in 2011 (Wernberg *et al.*, 2013, 2016). Modelling studies show that sea-ice loss in the Arctic Ocean and resulting release of ocean heat is transferred by the atmosphere up to 1500 km to the south, leading to an accumulation of ground heat with implications for permafrost degradation (Lawrence *et al.*, 2008).

The exceptional nature of the two record years for global SST and global temperatures in 2014 and 2015 in sequence and high likelihood that 2016 will also be a record year implies that the rise in global SST may be accelerating. The observations by Roemmich, Nieves and colleagues (Nieves *et al.,* 2015); and Roemmich and Gilson, 2011; Roemmich *et al.,* (2015) of a subsurface (at 100 to 500m depth) build-up of heat over several years in the Pacific and Indian Oceans especially, has profound implications for the future warming of the Earth. In a strong El Niño year this subsurface heat is suddenly transferred into the surface layer for release to the atmosphere (Roemmich and Gilson, 2011). Making available to the surface layer (0 to 100m) a number of years of subsurface warming has great relevance to global warming as the Pacific surface warming pattern is also evident at a global scale. This is especially so as modelling projections indicate that as the ocean warms in the 21st Century, El Niño events will double in frequency and become more intense (Cai *et al.*, 2014), providing again a strong positive feedback to climate.

1.8 Interactions and feedbacks from and to temperature

"Carbon dioxide is the control knob that regulates global temperature" with the Southern Ocean, and to a smaller extent the North Atlantic, playing a dominant role as major sinks for CO_2 (Hansen *et al.*, 2016a). The solubility of CO_2 in sea water is regulated by temperature with colder water taking up more and warmer less (Reid *et al.*, 2009). Approximately 50% of the extra anthropogenic CO_2 produced each year is retained in the atmosphere and about 25% is taken up each year by the ocean and land sinks. Global emissions of CO_2 have continued to grow at a high rate (Friedlingstein *et al.*, 2014). While atmospheric levels of CO_2 are growing at an accelerating rate, there is now strong evidence that the ocean and especially the Southern Ocean (Munro *et al.*, 2015), is taking up increasing quantities of atmospheric CO_2. This recognition is in contrast to a general belief held until recently (Wanninkhof *et al.*, 2013) that there had been a slowdown in uptake. Lower temperatures due to enhanced meltwater from ice sheets and associated increases in sea-ice cover around Antarctica and a slowdown in the Southern Ocean and Atlantic Meridional Circulations are postulated as the driving force behind the controlling 'knob' of Hansen *et al*. (2016a). The story is more complicated as atmospheric concentrations of CO_2 are also affected by temperature. Annual variability in the rate of increase in CO_2 was shown by Wang *et al.* (2014) to be closely positively correlated with tropical land temperature and by Reid *et al.* (2016) the same, but highly significantly correlated with global surface temperature (sea and land). The correlation implies that the temperature is in part controlling the rate of increase in atmospheric CO_2. This relationship is likely linked to El Niño as in these years more CO_2 is released to the atmosphere from both sea and land sinks during periods of heightened global warmth and extensive positive SST anomalies. Betts *et al.* (2016) estimate that the current El Niño has contributed an additional 1ppm to the growth rate of CO_2 in 2016.

Levels of CO_2 measured at Mauna Loa exceeded 400ppm for the first time in April 2014 and annually in 2015, and are continuing to increase in the atmosphere at a rapid rate. It is expected that an annual global mean level of 400 ppm, an important psychological marker and warning of the rate of change, will be passed for the first time in 2016 http://www.esrl.noaa.gov/gmd/ccgg/trends/global.html#global_data (Betts *et al.*, 2016). In the 2007 IPCC AR4 report it was estimated that CO_2 would need to be kept below 450ppm to avoid dangerous climate change (Schneider *et al.*, 2007), see also Oppenheimer *et al.* (2014). At current rates of increase 450 ppm could be with us within 20 years. Hanson calculated that CO_2 would need to be reduced to 350ppm to achieve an equilibrium EEI. The rapid current rate of increase is of grave concern and emphasizes the very urgent need to reduce carbon emissions.

In parallel with rising SST, an increasing uptake of CO_2 by the ocean has contributed to ocean acidification although interactions with climate change are unclear (Reid *et al.*, 2009). Temperature has two contrasting effects on the dissolution of carbonate minerals. In the first, higher temperatures increase their saturation state (Ω) and may thus mitigate the reverse effect of ocean acidification on saturation state that leads to increased dissolution of minerals like calcite and aragonite. The second effect, based on the general dissolution of minerals at higher temperature, overrides the first and is especially effective on biogenic forms of high-magnesium calcite (Ries *et al*., In press). This important recent experimental discovery means that ocean warming will reinforce ocean acidification, with organisms that have shells/skeletons that are made of the more soluble forms of calcium carbonate being especially vulnerable. A recent study has suggested that ocean acidification might amplify global warming by reduced production by phytoplankton of dimethylsulphide (DMS), the largest natural source of sulphur to the atmosphere (Six *et al.*, 2013).

The Biological Pump provides the main mechanism by which CO_2, taken up from the atmosphere and utilized in primary production, is transferred as particulate and dissolved organic matter to the deep ocean carbon reservoir (Reid *et al.*, 2009; Honjo *et al.*, 2014). The remaining direct uptake by sea water of CO_2 by the gas-exchange pump and the solubility pump is estimated to account at present for ~10% of the transfer of carbon as dissolved inorganic carbon to the deep ocean (Honjo *et al.*, 2014). Temperature mediated variation in the biological uptake of CO_2 by the ocean from the atmosphere has been proposed as a major factor contributing to the alternation between glacial and interglacial cycles in the Pleistocene (Matsumoto, 2007). Cool glacial temperatures strengthened the flux to the deep ocean and lowered rates of degradation reducing atmospheric concentrations of CO_2. There is concern that present warming will have the opposite effect leading to increased outgassing to the atmosphere as a positive feedback. In the Biological Pump, particulate planktonic debris and DOM produced in the euphotic zone sink to deeper depths at rates and amounts that are highly dependent on the composition of the original plankton and its associated inorganic ballast (diatom frustules, radiolarian exoskeletons) (i.e. Moigne *et al.*, 2014). Enroute pro- and eukaryotic organisms break down the sinking material. On reaching bathypelagic depths prokaryotic organisms predominantly, continue the breakdown and remineralization of the sinking material back to CO_2, which completes the cycle by outgassing to the atmosphere in upwelling regions. Modelling has shown that atmospheric concentrations of CO_2 are highly sensitive to the depth of this remineralization (Kwon *et al.*, 2009). The Biological Pump has a fundamental role in climate variability, and yet because of the complexity of the processes involved and their spatial, large depth and temporal variability, is still poorly quantified and understood. This complexity is illustrated by Kemp and Villareal (2013) who show that the traditional view that increased stratification reduces carbon export by a change from diatoms to small phytoplankton does not always apply.

Methane (CH_4) and nitrous oxide (N_2O) are greenhouse gases that are 21 and 310 times more potent than CO_2 with important sources that are affected by ocean warming (Reid *et al.*, 2009). A potential enhanced release of a) methane from clathrates (an ice form of methane) buried in sediments on the ocean floor and from melting permafrost, and b) of nitrous oxide from expanding anoxic zones may add to the rate of global warming as the ocean heats up (Kirschke *et al.*, 2013; Voss *et al.*, 2013; Skarke *et al.*, 2014).

Deoxygenation of the ocean (Keeling *et al.*, 2010) is another consequence of ocean warming that is of high relevance to ocean productivity and marine species (Wright *et al.*, 2012). A warming ocean reduces the solubility of oxygen in sea water, increases stability (stratification) and decreases ventilation of sea water in higher latitudes. These factors, with changes in the mixing/ renewal time and the size, location and transport of water masses can reduce the transfer of oxygen below the mixed layer. Oxygen is crucial for all aerobic marine life and is removed from sea water by the growth and respiration of the pelagic, and in large part the microbial community, as it breaks down the rain of organic particles from productive upper waters as part of the Biological Pump. Vertically migrating biota may intensify deoxygenation by the transfer of nutrients and carbon to deeper water. Extensive areas of low oxygen intermediate water between ~200 and 700m in the tropics are known as 'oxygen minimum zones' (OMZ). In these regions the depth of vertical migration by marine plankton closely tracks the upper margin of low oxygen waters with potential implications for the biological pump, future food webs and fisheries (Bianchi *et al.*, 2013). When oxygen levels drop to suboxic levels of <5 µmol/L and below, the potent greenhouse gas nitrous oxide may be formed as a positive feedback to climate change and breakdown of organic debris is dominated by bacteria and protozoa. A critical, toxic level for most higher marine life, including fish, termed hypoxic, is reached when levels fall below 60 $\mu molL^{-1}$. Only a few enclosed basins, e.g. the Black and Baltic Seas, the deep Cariaco Trench and some estuaries and fjords develop anoxic conditions where oxygen levels drop to zero (Richards and Vaccaro, 1956; Carstensen *et al.*, 2014; Rabalais *et al.*, 2014; Capet *et al.*, 2016; Montes *et al.*, 2016). There is now clear observational evidence that there has been a substantial global decline in oceanic dissolved oxygen with regions of low oxygen waters shoaling (coming closer to the surface) and expanding in their areal coverage in the last few decades (Stramma *et al.*, 2010; Helm *et al.*, 2011; Capet *et al.*, 2016; Montes *et al.*, 2016).

Eighty percent of the water exchanges on the Earth take place in the ocean, influencing the global water cycle and salinity and strongly interacting with SST (Durack *et al.*, 2016). Rising temperatures have led to an almost global increase in trophospheric humidity, a response that fits well the Clausius-Clapeyron relationship that the humidity of air increases by 0.7% per 1°C of temperature (Hartmann *et al.*, 2013). Continental evaporation has also increased in line with expectations from rising temperatures, but multidecadal variability appears to be governed by ENSO (Miralles *et al.*, 2014). Based on salinity the increased humidity has led to an intensified hydrological cycle (Durack *et al.*, 2012), but there is only limited global evidence from rainfall or river flows that this has occurred. However, Gloor *et al*. (2013) show that the catchment of the Amazon, the world's largest river, has experienced a substantial wetting trend since approximately 1990, and Zhang and Wu (2012) demonstrate that increased poleward transport of atmospheric moisture explains an accelerating increase in Arctic river discharges. Reducing salinity in polar regions and a consequent increased stability (layering) of the water from more meltwater due to global warming has a strong feedback on polar SST.

1.9 Tropical warming, polar amplification, the cryosphere and weather

The tropical belt of the Earth has expanded as a result of global warming with a resulting poleward movement of wind systems. At the same time the polar regions have been warming, in the case of the Arctic, at rates well above the global average (polar amplification) (Cohen *et al.*, 2014) and both the Greenland and Antarctic ice sheets are melting (Church *et al.*, 2013; Khan *et al.*, 2014), but see also (Zwally *et al.*, 2015). In Antarctica (Turner *et al.*, 2015) the pattern of change has been different (Marshall *et al.*, 2014) with warming largely restricted to Western Antarctica and reflected more widely in subglacial melting of ice shelves by warm sea water (Rignot *et al.*, 2013). The contrasting response of sea ice between the two poles, with a major decline in the Arctic and an expansion in the Antarctic is especially marked (Parkinson and Di Girolamo, 2016). Other possible consequences of a contraction in the contrast between the poles and the tropics are a poleward movement of storm tracks and changes in the monsoons. It is expected that the intensity of tropical cyclones will increase with global warming, but links with climate change are still far from clear (Walsh *et al.*, 2016). The contrast between the tropics and poles may also be contributing to a greater meandering in the jet stream and blocking weather systems that produce more extremes of weather such as drought, flooding, cold spells, and heat waves (Overland *et al.*, 2015).

1.10 Sea-level rise

Sea-level rise has been well articulated and addressed thoroughly in all IPCC reports compared to the less well known consequences of warming to species and ecosystems that are the focus of this report. Global warming contributed more than 80% of the rise in sea level between 1993 and 2010 due to thermosteric expansion of sea water from the increased heat content of the ocean (~39%) and 43% from the melting of ice with warm sea water again playing a major role (glaciers (~27%), Greenland ice sheet and its glaciers (~15%), Antarctic Ice Sheet and its glaciers (~1%) (Table 13.1 in Church *et al*., 2013). A recent update reports strong evidence for an acceleration in global sea-level rise (Clark *et al.*, 2015). Scenarios for "likely" future sea-level rise range from a minimum of 2.8cm for a low scenario (RCP2.6) to 0.52m to 0.98m for the high emission scenario (RCP8.5), neither of which take into account a potential collapse of the base of some Antarctic ice shelves.

1.11 Conclusions

In this introduction I have attempted to provide an overview of current knowledge on ocean warming as a background to the changes in sea temperature that are behind many of the observed impacts on biological communities that are presented in the rest of the report. Ocean warming is a complex issue that we are still striving to fully understand. Given the magnitude of the heat stored in the ocean, its interactions and feedbacks with the carbon and water budgets and key role in the Earth's energy budget future research to understand the processes involved should have a very high priority. There is a need to improve measurements of ocean heat content and ocean dynamics to better determine the mechanisms involved in its redistribution and release to the atmosphere, as well as its implications for marine ecosystems.

A lack of long-term observations of the ocean and a much slower development of ocean climate models compared to measurements and models of the atmosphere are the main reasons why the key role of the ocean in the global energy budget has not been fully recognized until recent decades. This is against a background that the heat reservoir role of the ocean and its implications for climate change were identified by Rossby 60 years ago. Two decades later astounding predictions, based on simple models, by Hansen *et al*. (1981) of expected global warming and its consequences, including the melting of Arctic sea ice, have been fully realized. So we have had ample warning of the changes that are to come and are ignoring these warnings at our peril.

Funding of ocean science has been a low priority in the past and governments have a long record of cutting long term observations. There is a real danger that the number of Argo floats in the ocean, that have been largely instrumental in providing us with the data that have led to our current knowledge of ocean warming, are in danger of being reduced due to policy bias and/ or budgetary cuts by governments. From a biological perspective the Continuous Plankton Recorder survey is also threatened by funding shortfalls, and the long-term measurements of CO_2 at Mauna Loa have also experienced funding difficulties. Instead a high priority should be placed on maintaining and strengthening existing ocean monitoring programmes, expanding measurements into polar seas the deep ocean and marginal seas that are presently poorly covered, in tandem with the development and application of new observation and analysis systems for *in situ* and satellite measurements (see: Durack *et al.*, 2016; von Schuckmann *et al.*, 2016). An improved global ocean observing system, interfaced with modelling, is needed that resolves ocean dynamics, biological and biogeochemical processes at a range of spatial and temporal scales. Internationally funded and coordinated it needs to be maintained for at least 100 years so that decadal variability can be evaluated.

A new recognition of the importance of the ocean by the International Panel on Climate Change is evident in their recent announcement that a special report on the ocean will be produced before the next IPCC Assessment. The speed and consequences of recent global and ocean warming should give an increased impetus to attempts to reduce CO_2 emissions. It is clear, however, that the urgent need to take action on climate change is still not properly recognized. This is evident in the slow uptake of signatories to the 2015 Paris Agreement of the United Nations Framework Convention on Climate Change (UNFCC). As of the 29th June 2016 only 19 states of the 178 that signed the agreement and that account for less than 2% of global greenhouse gas emissions had ratified the agreement! A total of 55 countries or a group of countries that produce 55% of greenhouse gas emissions are needed to bring the agreement into force. The Paris Agreement aims to pursue efforts to limit the global rise in temperature to 1.5°C and keep below 2°C. According to (Hansen *et al.*, 2016a) we achieved 1°C above pre-industrial levels in 2015. On current trends we are likely to reach 1.5°C in 20 years time. This slow response by governments and a lack of recognition of the urgent need to take action is against evidence for recent record years for global surface temperature, ocean temperatures, sea-level rise, ice melt and atmospheric levels of CO_2.

Concluding this examination of the facts about ocean warming I draw attention to the following points:

- We have known about global warming for about 60 years, but the heat and carbon management role of the ocean have only been properly recognized in the international debate on climate in the last decade or so, and afforded their proper significance by the scientific community within the last few years.
- There is strong scientific evidence to show that ocean warming is caused by excessive emissions of carbon dioxide into the atmosphere from human activities. More than 93% of the enhanced heating since the 1970s due to the greenhouse effect and other human activities has been absorbed by the ocean.
- Data show a sustained and accelerating upward trend in ocean warming. A warming trend for sea surface temperature has been observed since the beginning of the 20th Century with 13 of the warmest years since records began in 1880 occurring since 2000.
- Ocean warming is not just a sea surface phenomenon. Analysis of ocean heat content estimates that approximately two thirds of the excess heat has been taken up by the upper ocean in the surface to 700m depth layer with one third absorbed into the deep ocean below 700m depth.
- The distribution of recent ocean heat uptake since 2006 is not uniform with data showing a strong accumulation of heat in the mid-latitude regions of the Pacific and Indian Oceans, with weaker warming in the South Atlantic. The greatest warming overall is occurring in the Southern Hemisphere.
- Crucially relevant to the last two years, the current year and the future, is that heat accumulated in the ocean is not permanently locked away. Warming in the 100 to 500m layer can be transferred back to the upper layer. This transfer happens periodically making it available at the surface of the ocean for release back to the atmosphere – a positive feed-back loop.
- By absorbing a disproportionate amount of heat from global warming and by taking up the rapidly increasing emissions of carbon dioxide, the ocean has shielded the world from even more rapid changes in climate. However, the extent to which it can continue to do so in the near and distant future is far from clear.
- Carbon dioxide – the root cause of ocean warming – is also causing ocean acidification. Temperature, ocean acidification and deoxygenation, which together are driving responses in species and ecosystems, are impacting the benefits derived from the ocean in the form of 'goods and services' as described elsewhere in this report.
- The scale, nature and problems associated with ocean warming are progressive and on current data getting worse. The rates of increase in both temperature and CO_2 are of grave concern and emphasize the urgent need to stem further

warming by dramatically reducing CO_2 emissions from our activities.
- The clear evidence for a massive discharge of ocean heat and CO_2 to the atmosphere in the 2015/2016 El Niño and resulting high global temperature has profound implications for the rate of warming in the future if, as projected, El Niño years become more frequent.

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“Rapid and substantial reduction of CO_2 emissions is required in order to prevent the massive and effectively irreversible impacts on ocean ecosystems and their services.”

“It is thus of critical importance that changes in the ocean are taken into account in climate talks, and a relevant architecture for this must now be developed. “

Chapter 2 authors

The cascading effects of climate -related changes in the ocean

2

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Summary

- The ocean moderates anthropogenic climate change by absorbing significant parts of the heat and CO_2 that accumulate in the atmosphere. The ocean also receives all water from melting ice.
- This regulating function happens at the cost of profound alterations of the ocean's physics and chemistry, especially leading to ocean warming and acidification, and consequently sea-level rise.
- These changes significantly affect the ocean's ecology (organisms and habitats) and, consequently, ecosystem services and coastal human societies (e.g. fisheries, aquaculture, tourism, food security).
- As atmospheric CO_2 increases, the solutions (i.e. mitigate, protect, repair, adapt) become fewer and less effective, thus decreasing the long-term ability of humankind to cope with both on-set and gradual changes in the ocean.
- Such an assessment provides further compelling arguments for rapid and ambitious CO_2 emission reductions at the international level, notably through the revision cycle of countries' 2030 pledges (i.e. Intended Nationally Determined Contributions, INDCs) approved by the Paris Agreement in 2015.

2.1 Introduction

Together, the atmosphere and the ocean allow life on the Blue Planet. These life-support systems are, however, altered by human activities, as exemplified by contemporary climate change that generates worldwide disturbance in extreme events patterns, gradual environmental changes, widespread impacts on life and natural resources, and multiple threats to human societies. An impressive body of knowledge on "emerging" issues such as ocean warming and acidification has recently accumulated. Regarding ocean acidification, the number of scientific papers increased by 35% per year between 2000 and 2013 compared to an increase of 4.8% per year for all scientific fields (Riebesell and Gattuso, 2014; Yang *et al.,* 2015). Another significant indicator is the development of three chapters specifically dedicated to the ocean in the contribution of the IPCC Working Group 2 to the Fifth Assessment Report (AR5). These chapters together represent a more than 400-page synthesis of the existing literature, at the global (Pörtner *et al.,* 2014; Wong *et al.,* 2014) and regional (Hoegh-Guldberg *et al.,* 2014) levels. Scientists also undertook massive efforts to disseminate their understandings outside of the scientific community, and now the issue of ocean climate-related changes is the subject of numerous policy concerns (e.g. Goal 14 of the Sustainable Development Goals[1], Our Ocean Conferences in 2014 in the USA and in 2015 in Chile, and Ocean days and side events at the 21st Conference of the Parties to UNFCCC[2] in 2015). Progress to develop the scientific understanding of what is happening in the ocean as well as to better include the ocean-related issues in policy agenda at various scales, must, however, be reinforced for at least three reasons. First, and although COP 21 allowed some major progress, the source of the problem, i.e. the high concentration of greenhouse gases (GHG) in the atmosphere, has not yet been eradicated. Mitigation efforts at the global scale must thus be pursued, not to say drastically accelerated. Here the scientific community, including the ocean community, has a major role to play to "keep the pressure on" through advances in knowledge, from processes at work to impacts and thresholds (Briggs *et al.,* 2015; Stocker, 2015; Magnan *et al.,* 2016). Second, Science still faces key research challenges to develop multiple-driver studies at the community to ecosystem levels, and to find answers to societal problems. Riebesell and Gattuso (2015) emphasize four of these challenges regarding ocean acidification: to concentrate on reference organisms and keystone species, including ecosystem engineers; to identify commonalities and develop unifying concepts; to focus on species, processes and ecosystems considered most vulnerable or most resilient to ocean change; and to cover the range of processes from sub-cellular to ecosystem dynamics and biogeochemical cycling. A fifth one of course deals with better understanding the interactions with human societies, from impacts to short- to long-term responses. A third reason is that the societal side of the problem has been understudied up to now. Yet, as climate change will amplify, changes in the ocean as well as impacts on society will also increase. Whatever the global mitigation efforts will be in the coming decades, some impacts are already unavoidable due to latency in the climate and ocean systems. This means that dealing with climate and ocean changes is not only about "avoiding the unmanageable" (i.e. prevent dangerous physical and biological changes through massive GHG emission mitigation), but also about "managing the unavoidable" (i.e. adaptation) (Bierbaum *et al.,* 2007).

This chapter does not pretend to provide answers to the challenges raised above. It rather seeks to lay some foundations for future transdisciplinary research on ocean changes and their consequences on human societies. It is mainly inspired from a scientific paper (Gattuso *et al.,* 2015) and on a Policy Brief (Magnan *et al.*, 2015a) that provide a synthesis of the recent and future changes to the ocean and its ecosystems, as well as to the goods and services provided to humans. This chapter follows the "chain of impacts" principle to emphasize cascading effects, going from changes in the ocean's physics and chemistry to marine and coastal species, and then to human societies through the ocean's ecosystem services. It considers the global scale and focuses on key organisms and ecosystem services for which robust scientific studies have been recently published (Howes *et al.,* 2015; Weatherdon *et al.,* 2015). The chapter notably explores two contrasting GHG emission scenarios developed by the IPCC for the end of the 21st Century: the high emissions trajectory (Representative Concentration Pathway 8.5, RCP8.5) and a stringent emissions scenario (RCP2.6). The latter scenario is consistent with the Paris Agreement[3] of keeping mean global temperature increase below 2°C in the 21st Century. We then discuss possible solutions and end with four key messages to be considered in international climate negotiations under the UNFCCC.

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[1] http://www.un.org/sustainabledevelopment/oceans/

[2] United Nations Framework Convention on Climate Change

[3] UNFCCC. The Paris Agreement (FCCC/CP/2015/L.9/Rev.1). Available at: http://unfccc.int/resource/docs/2015/cop21/eng/l09r01.pdf.

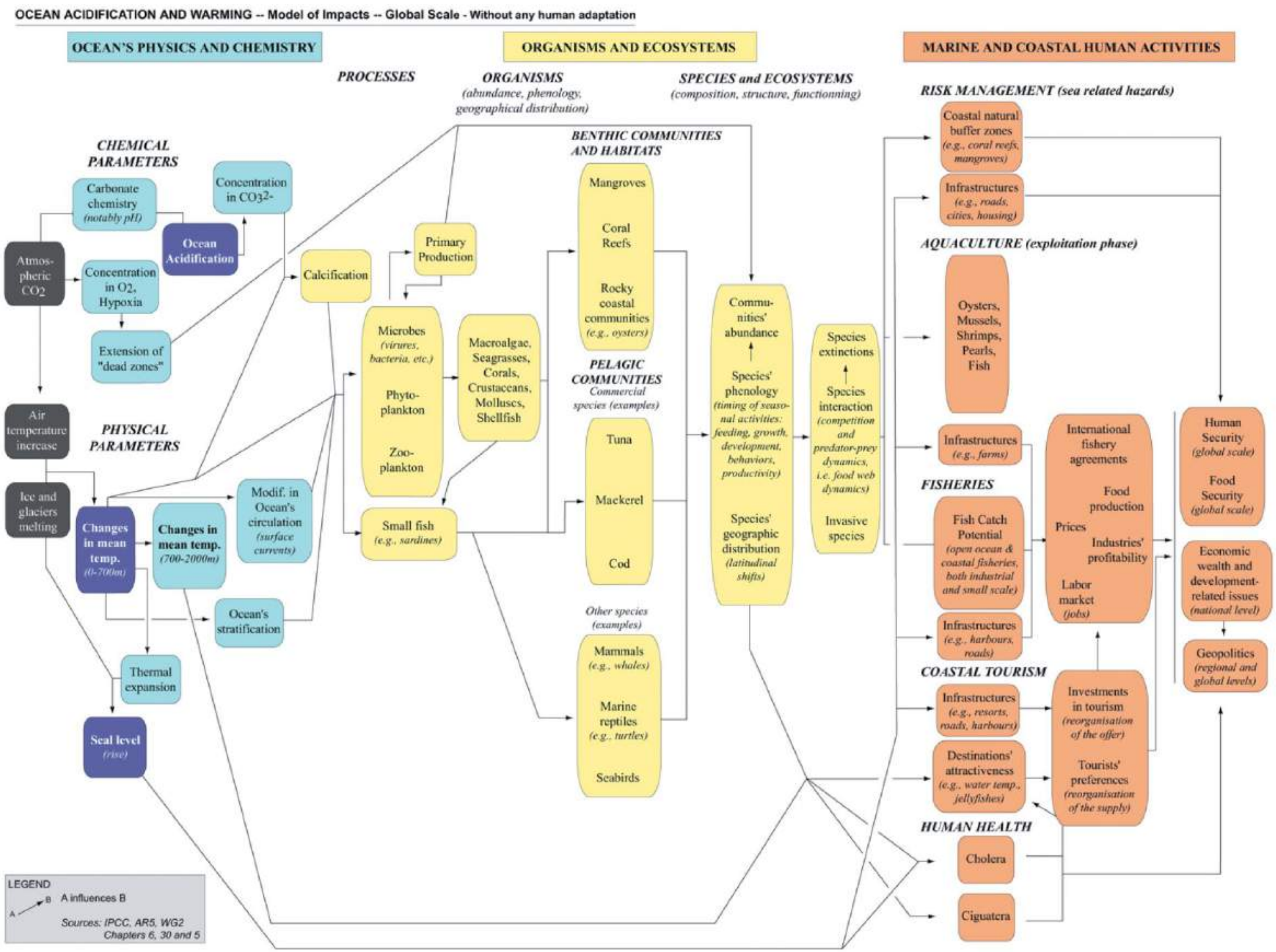

Figure 2.1 The chain of impacts of ocean acidification, ocean warming and sea-level rise.
Sources: the authors, derived from Pörtner *et al.* (2014), Hoegh-Guldberg *et al.* (2014).

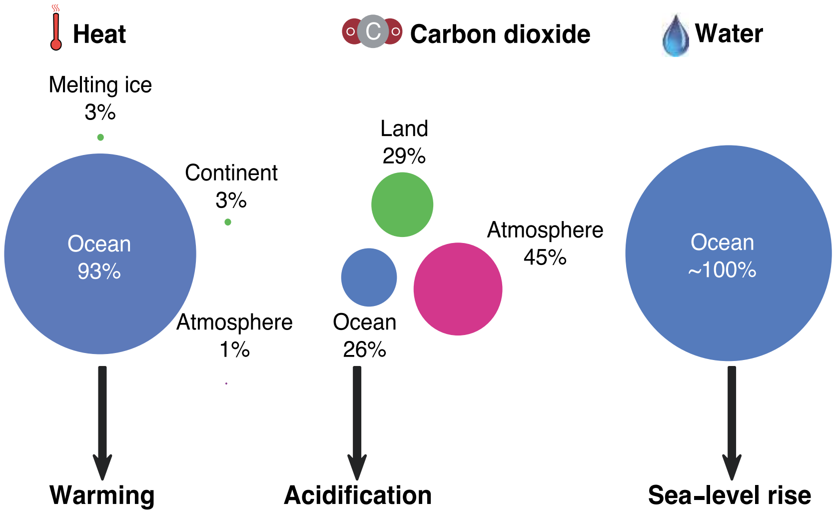

Figure 2.2 Distribution of heat, carbon dioxide and ice-melt water in the main Earth reservoirs and consequences for the ocean.

2.2 Cascading effects

2.2.1 General overview of the "chain of impacts"

Together, ocean warming, ocean acidification, and sea-level rise drive a "chain of impacts" that links changes in the ocean to humans (Figure 2.1). Changes in the basic parameters of the ocean have started to induce major consequences on organisms and ecosystems in terms of abundance, phenology, geographical distribution, invasive species, prey-predator relations, and species extinction (for a synthesis, see Hoegh-Guldberg *et al.,* 2014; Pörtner *et al.,* 2014; Howes *et al.,* 2015). Due to a domino effect, key human sectors are now at threat, especially fisheries, aquaculture, coastal risks management, health and coastal tourism (for a synthesis, see Weatherdon *et al.,* 2015). Severe implications at both the national and the international levels are to be expected from such cascading effects (Magnan *et al.,* 2015b). Changes in fish catch potential in a given area, for example, will challenge international fishery agreements between the countries concerned (e.g. in the western and eastern part of the Pacific, in North Atlantic, in polar seas), which in turn will have consequences on the industry (profitability, jobs, etc.), markets and prices in several countries, and their international competitiveness. Yet, the more that changes in the ocean challenge current international agreements, the more they will question food and human security, geopolitics and development at the global scale. As with climate change at large, changes in the ocean are definitely a global concern, extending beyond restricted national boundaries. This is all the more true, as the scientific community tells us that the impacts on key marine and coastal organisms, ecosystems and ecosystem services are already detectable from high to low latitudes, transcending the traditional North/South divide.

2.2.2 The ocean as a "climate integrator"

The first building block in the chain of impacts (see left hand side of Figure 2.1) refers to the direct interface between the atmosphere and the ocean. "Climate" is indeed not a result only of atmosphere dynamics, but actually of fine and multi-temporal atmosphere-ocean interactions. As a result, climate change not only affects the atmosphere, but also the ocean (including enclosed seas) that must thus be considered as a "climate integrator" (Figure 2.2). The ocean has, (i) absorbed 93% of the earth's additional heat since the 1970s, moderating global warming; (ii) captured 26% of human-derived CO_2 emissions since 1750, limiting the increase in atmospheric temperature; and (iii) collected virtually all water from melting ice. Without the ocean, present climate change would thus be far more intense and challenging for human life.

2.2.3 Ocean physics and chemistry

This regulating function, however, happens at a cost, as the rise in GHG concentration[4] over the industrial age has driven a series of major environmental changes in the ocean, especially warming, acidification and sea-level rise. There is strong evidence that the ocean has warmed between 1971 and 2010, and it is very likely that warming was occurring earlier (Rhein *et al.*, 2013). Warming has occurred at all depths but is most pronounced at the surface. Over the last four decades, it is estimated that the temperature of the upper 75m has increased by around 0.11°C per decade. The uptake of carbon dioxide (CO_2) in sea water causes a decrease in pH (i.e. increase in acidity), as well as in the availability of carbonate ions (CO_3^{2-}) that are one of the building blocks required by

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[4] From 278 to 400 ppm.

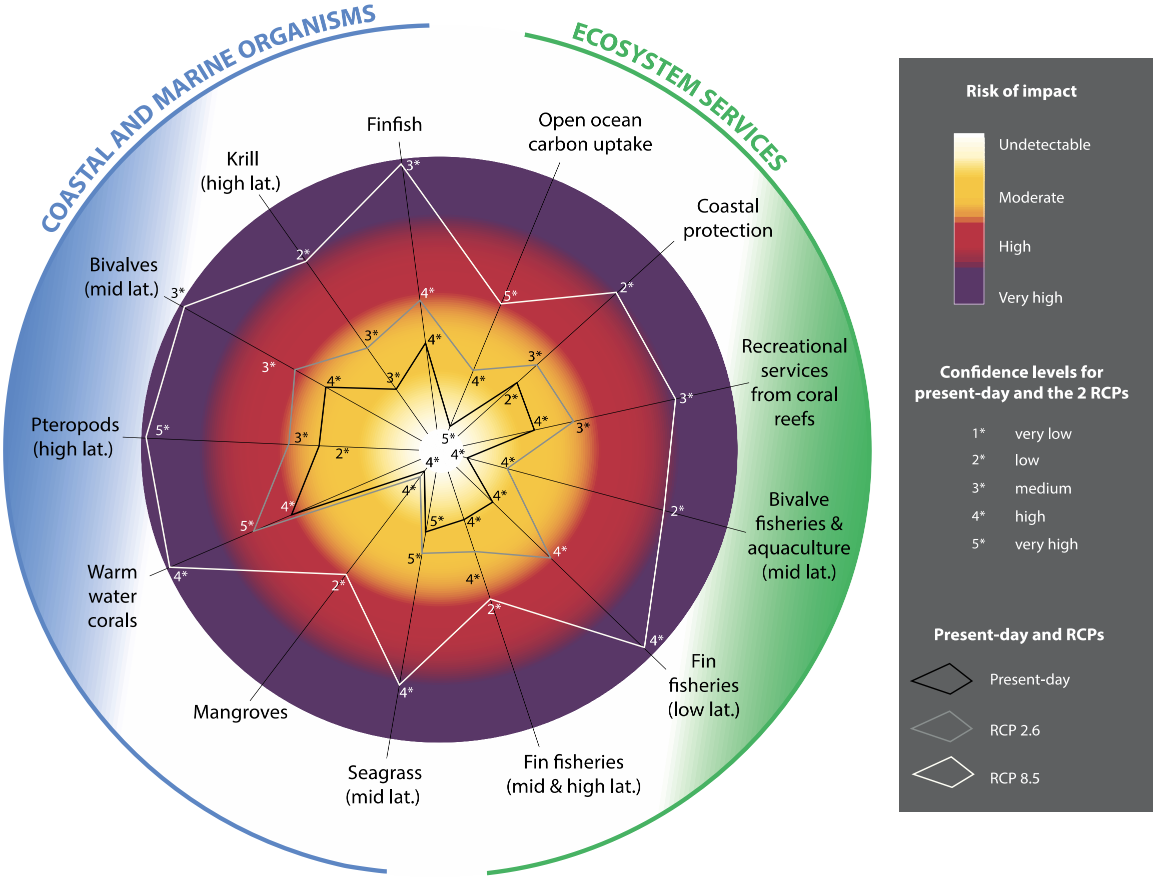

Figure 2.3 Contrasting risk of impacts to ocean and society from different anthropogenic CO_2 emissions. Source: the authors, adapted from Gattuso *et al.* (2015).

many marine plants and animals to make their skeletons, shells and other calcareous structures. This process is known as "ocean acidification". There is high confidence that surface ocean pH has declined by 0.1 pH units since the beginning of the industrial age, representing an increase of ocean acidity by around 30% in 250 years (Gattuso *et al.,* 2014). This ocean warming (i.e. thermal expansion) and melting of continental ice sheets has caused sea-level rise. It has been measured that global mean sea level has risen by approximately 1.7mm/year over the 1901-2010 period, with an acceleration between 1993 and 2010 (+3.2mm/year) (Church *et al*., 2013).

Future conditions for the ocean depend on the amount of carbon that will be emitted in the coming decades. The more stringent scenario (RCP2.6) allows less than one-sixth of 21st Century emissions expected under the business-as-usual scenario (RCP8.5). One must, however, be aware that the ocean's capacity to absorb CO_2 will decrease with increasing emissions: the fraction of anthropogenic emissions absorbed by the ocean in the 21st Century is projected to decline from 56% for RCP2.6 to 22% for RCP8.5. This suggests that ocean physics and chemistry in 2100 will be significantly different under these two emissions scenarios. Obviously, the ocean will be much warmer under RCP8.5 than under RCP2.6, the global mean change in sea surface temperature differing by nearly a factor of 3 when compared to preindustrial levels (+3.2°C *vs.* +1.2°C). In parallel, global surface acidity changes will decrease by 0.07 and 0.33 pH units under RCP2.6 and RCP8.5, respectively (relative to preindustrial values). Eventually, it is projected that mean global sea-level rise will be multiplied by a factor of 1.4 under RCP8.5 compared to RCP2.6, relative to the preindustrial period (respectively +0.86m *vs.* +0.60m)[5].

2.2.4 Organisms and ecosystems

Acknowledging that impacts on key marine and coastal organisms, ecosystems and ecosystem services are already detectable, Science warns that several of these environments and services will likely face high risk of impacts before 2100 (Figure 2.3), even with the moderate CO_2 emissions scenario (RCP2.6).

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[5] This multiplying factor reaches 1.6 when the reference period considered is the 1990-1999 decade (+0.67m under RCP8.5 and +0.41m under RCP2.6).

While warm-water corals are at the frontline of ocean changes, mid-latitude seagrass, high-latitude pteropods and krill, mid-latitude bivalves, and finfishes are also already affected. In a stringent emissions pathway (RCP2.6), ocean changes carry high risks of impact for warm-water corals as well as for mid-latitude bivalves, the risk of other impacts remaining moderate – although worrying. In the higher emissions scenario (RCP8.5), the situation will be greatly aggravated: several key marine organisms (e.g. corals, pteropods, finfish, and krill) would face very high risk of impact, such as mass mortalities or species displacement (Beaugrand *et al.,* 2015; Gattuso *et al.,* 2015; Nagelkerken and Connell, 2015). These results, which are derived from experiments, field observations and modelling, are consistent with evidence from high-CO_2 periods in the geological record, giving credence to those worrying future projections.

2.2.5 Ecosystem services

Impacts to the ocean's ecosystem services follow a similar trajectory of "moderate" to "high to very high" risks of impact with RCP2.6 and RCP8.5, respectively (see Figure 2.3). Fisheries and aquaculture (e.g. fin fisheries at low latitudes), which are key for the survival for millions of people (i.e. a source of dietary protein and income), are expected to be severely affected under business-as-usual RCP8.5, putting global food security at high risk of disruption. This threat therefore must be considered together with the fact that climate change will also severely affect agriculture on land. Likewise, the risk of impact on ecosystem services such as coastal protection (e.g. by oyster beds, coral reefs, and mangroves) would become high or very high by 2100, thus exacerbating the risks of marine flooding in low-lying areas.

Of course, these impacts of ocean warming and acidification will be cumulative or synergistic with other human-induced stresses such as over-exploitation of living resources, habitat destruction and pollution. This opens the perspective of significant disruption to job markets, international fishing agreements, geopolitics, etc., as mentioned above. In addition, given the extent of the expected changes, it must be acknowledged that no country is immune to these impacts, making this a worldwide problem and highlighting the importance of successful climate negotiations if the international community is to avoid moving towards an unsustainable future.

2.3 Solutions at risk

2.3.1 A threatened diversity of solutions

Various options are available to address ocean impacts, with some evidence of success (Billé *et al.,* 2013). They can be grouped into four categories (Figure 2.4): mitigating CO_2 emissions; protecting marine and coastal

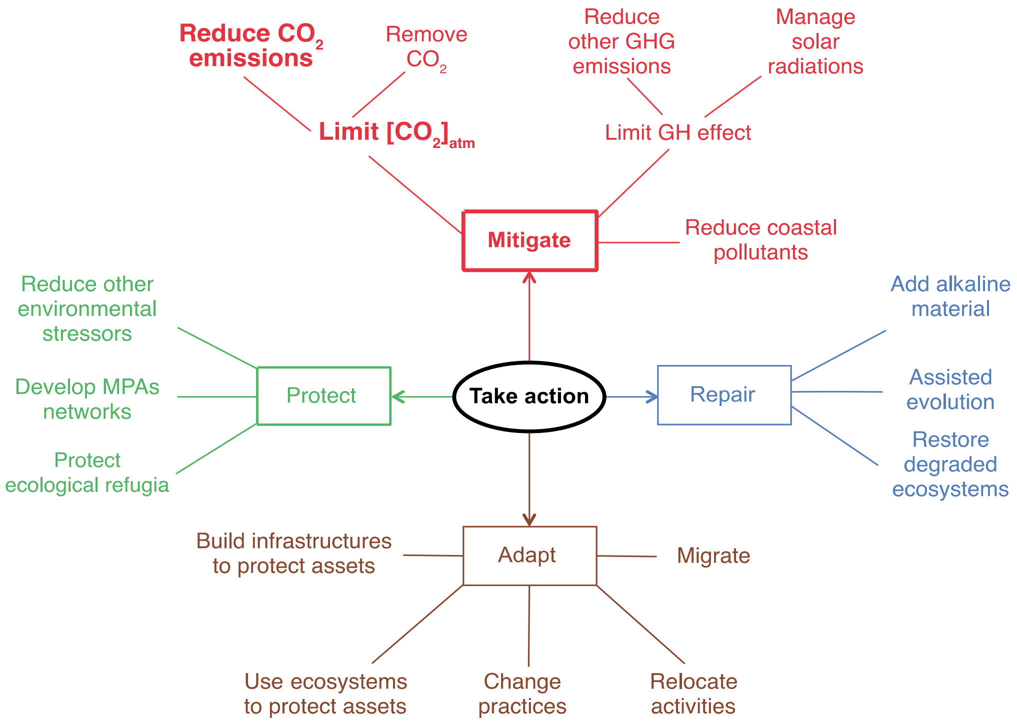

Figure 2.4 Solutions to face climate and CO_2 – related changes in the ocean. Source: adapted from Billé *et al.* (2013) and Gattuso *et al.* (2015).

ecosystems (e.g. protected areas, or regulation of natural resources exploitation); repairing ecosystems that have already experienced damage (e.g. assisted evolution of corals and/or coral farming); and adapting (e.g. economic activities diversification, or coastal setback zones). Despite the encouraging sign of emerging responses, the number of options and their efficiency narrow as the ocean warms and acidifies (Gattuso *et al.,* 2015). A key rationale behind this is that the more ecosystems are impacted, the less they will be resilient to gradual and on-set changes, thus exacerbating negative impacts and the adverse consequences for humans. That is to say, moving above the +2°C path will significantly limit the manoeuvring space of coastal societies to implement effective action. This matter actually concerns humankind at large given that it is not only coastal societies that depend on these vital ocean services.

2.3.2 CO_2 emission reduction as the overarching solution

The previous sections lead to a clear conclusion: rapid and substantial reduction of CO_2 emissions is required in order to prevent the massive and effectively irreversible impacts on ocean ecosystems and their services. In line with this and according to Gattuso *et al.* (2015), it appears that RCP2.6 is not a "green utopia" where everything would be fine, but actually a "minimum ambition" to be consistent with United Nations Framework Convention on Climate Change (UNFCCC) fundamental objective of preventing *dangerous anthropogenic interference with the climate system ... within a time-frame sufficient to allow ecosystems to adapt naturally to climate change, to ensure that food production is not threatened, and to enable economic development to proceed in a sustainable manner* (United Nations, 1992). From a purely scientific point of view, RCP2.6 will already bring major changes in the functioning and resources of the ocean.

Although international climate negotiations under the UNFCCC have only minimally considered the impacts of GHG emissions on the ocean and, in turn, its role as a key area of solutions to tackle climate change and enhance adaptation (Stocker, 2015), COP21 brought some progress as the text of the Paris Agreement recognizes 'the importance of ensuring the integrity of all ecosystems, including oceans'. In parallel, some emerging works propose, for example, to enlarge the scope of the negotiations to a wider panel of "planetary vital signs" than only air temperature increase by the end of the century (Briggs *et al*., 2015). Some of these vital signs should reflect changes in the ocean, referring to its warming and/or its acidification, for example. Given the contrasted futures summarized in the present contribution, the ocean obviously provides further compelling arguments for rapid and rigorous GHG emission (notably CO_2) reduction. Accordingly, any post-2015 global climate regime that will not significantly contribute to minimize the impacts on the ocean will remain incomplete and inadequate.

2.4 Conclusions

This contribution emphasizes four main cascading conclusions. First, the ocean strongly influences the climate system and provides fundamental services to humans. As a result, it must be recognized as a key component of the action, from local to international levels, against climate change. Second, unequivocal scientific evidence shows that impacts on key marine and coastal organisms, ecosystems, and services are already detectable and that high to very high risks of impact are to be expected by 2100, even under the low emissions scenario (RCP2.6). These impacts will occur across all latitudes, making this a global concern beyond the North/South divide. Third, there are concerns among the scientific community that as atmospheric CO_2 increases, the options for the ocean (i.e. mitigate, protect, repair, adapt) become fewer and less effective. Fourth, GHG mitigation at the global scale appears to be an overarching solution that will determine the future of the others (protect, repair, adapt). As a result, rapid and substantial reductions of GHG emissions are required, meaning that the ocean community will have to "keep the pressure" on the international climate negotiation process to ensure, first, that the mitigation efforts adopted in Paris in 2015 are effectively implemented and, second, that the global ambition is progressively increased. It is thus of critical importance that changes in the ocean are taken into account in climate talks, and a relevant architecture for this must now be developed.

Acknowledgements

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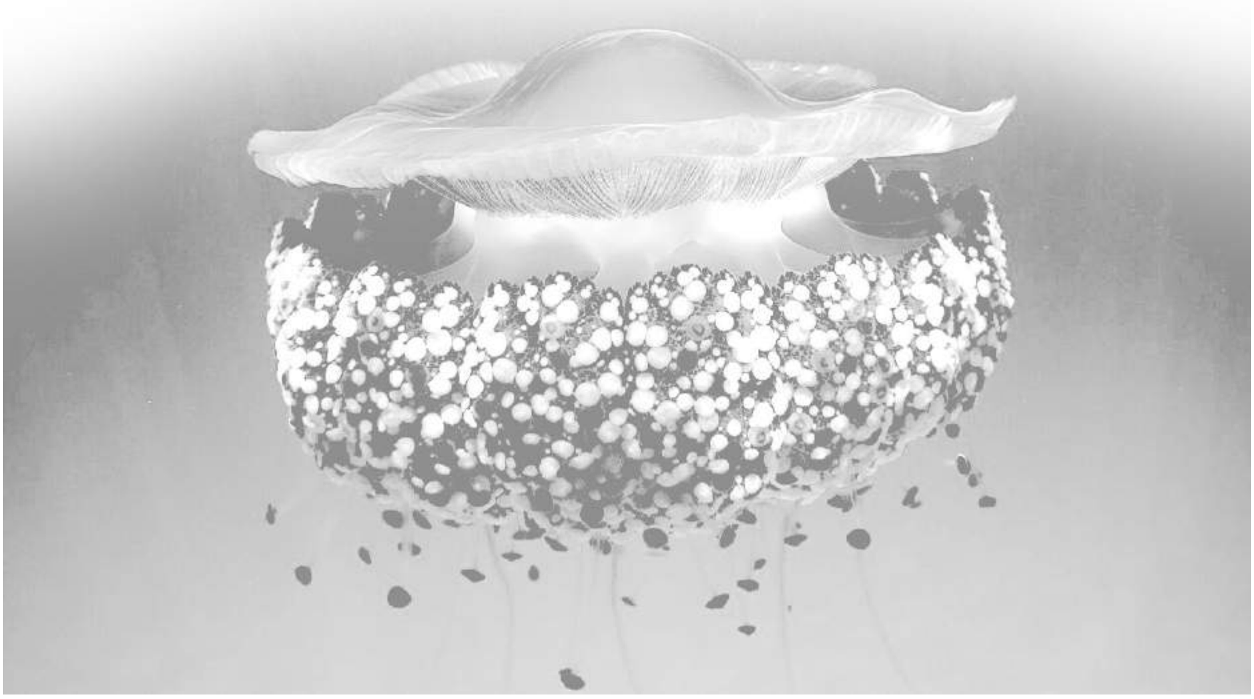
The significance of warming seas for species and ecosystems

3

The first two opening chapters have set the scene for ocean warming and how its effects are cascading down through ecosystems and species. In this chapter we explore in more depth these matters by taking a close look at the impacts and consequences for selected species and ecosystems in the ocean.

The story of the effects of ocean warming on some species and habitats, such as coral reefs, is far better known than for many others, and yet the consequences for these lesser known groups may be equally or even more concerning. For some species and ecosystems, the sections represent some of the first in-depth examination of ocean warming consequences, and together all the sections tell a compelling story of changes affecting the ocean.

The consequences for goods and services – the benefits we derive from the ocean – is explored in the Chapter 4.



> *"The impacts of the increase in seawater temperature on micro-organisms, which represent the vast majority of the biomass (organic carbon) in the ocean, will significantly alter the biogeochemical cycles and the functioning of the food webs at the global scale."*
>
> *Section 3.1 authors*

3.1 Impacts and effects of ocean warming on micro-organisms

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Summary

- Ocean warming is expected to have a range of effects on the biodiversity and functioning of marine microbial assemblages.
- The impacts of the increase in seawater temperature on micro-organisms, which represent the vast majority of the biomass (organic carbon) in the ocean, will significantly alter the biogeochemical cycles and the functioning of the food webs at the global scale.
- Ocean warming is predicted to lead to a global reduction in oceanic primary productivity and to favour the consumption and cycling of the organic matter in the surface layers of the ocean through heterotrophic processes, overall reducing the carbon export to the deep sea.
- Complex biotic and abiotic interconnections and feedbacks have to be considered, which might counteract or balance the trends observed or predicted by current models.
- Viruses and the balance between different virus-mediated processes have the potential to enhance or reduce the carbon sequestration efficiency of the ocean. Further research is needed to unveil the dynamic feedbacks between ocean warming and the huge diversity of virus-microbe interactions, as well as on their consequences on the overall marine ecosystem functioning.
- Oceanic zones experiencing oxygen depletion are increasing worldwide due to ocean warming, likely driving significant changes in the diversity and functioning of the microbial assemblages.
- Ice melting and altered patterns of circulation and precipitation induced by climate warming can cause shifts in viral replication strategies, and it will increase the transfer of freshwater microbes into marine ecosystems, possibly giving rise to novel virus-host interactions influencing ecosystem functioning.
- Overall, there is a clear need to shed light on the yet undiscovered diversity and functional role of marine microbes, to improve our understanding and ability to predict the impact of ocean warming on the biodiversity and functioning of marine ecosystems.

Ocean warming effects	Consequences
Increased oceanic primary productivity due to microorganisms	Reduced export of organic carbon to the ocean interior
Increased prokaryotic heterotrophic metabolism	Stimulation of respiration processes and decrease in the carbon-storage capacity of the ocean
Accelerated prokaryotic turnover rates	Decrease in the efficiency of the carbon-storage capacity of the ocean
Increased consumption of organic matter by microbes	Increased role of microbes in the oceanic food webs
Increased relative contribution of microbes to total biomass	Increased importance of microbes in the biogeochemical cycles and overall ecosystem functioning
Acceleration of enzymatic activities degrading organic matter	Acceleration of microbial-mediated organic matter degradation
Increased rates of viral infections	Increased role of viruses in the oceanic food webs
Increased virus-induced microbial mortality	Increased removal of organic matter available for higher trophic levels and increased role of the microbial food web
Increased role of the microbial taxa thriving under oxygen depletion due to the increased ocean stratification and consequent expansion of oceanic oxygen minimum zones	Changes in biodiversity and functioning of the oceanic microbial food webs; eukaryotes more sensitive than prokaryotes and viruses to oxygen deficiency
Changes in viral replication strategies	Alteration of the virus-microbe interaction with consequences on the microbial biodiversity and ecosystem functioning
Increased input of freshwater microbes to the ocean due to ice melting and altered patterns of circulation and precipitations	Changes in biodiversity, in virus-host interactions and overall marine food web functioning
Varying responses and sensitivity of different groups of prokaryotes	Changes in the relative importance of bacteria and archaea in different regions; consequences on the biogeochemical cycles

3.1.1 Global relevance of marine microbes

Marine microbes inhabit all oceanic habitats, from the deep sea floor to the surface microlayer of the oceanic water masses. They are known to live in environmental conditions, which are hostile to other organisms, spanning extreme ranges of temperature, salinity, oxygen and redox potential (Ducklow, 2000). This vast array of biological and ecological capabilities makes marine microbes the most abundant group of organisms in the ocean (Aristegui *et al.,* 2009). Carrying out a striking diversity of metabolic processes, marine microbes can influence practically the entire set of geochemical processes, in turn driving the functioning of the ocean (Falkowski *et al.,* 2008).

Two-thirds of the Earth surface are covered by the ocean, and half of the global primary production (i.e. the generation of new living biomass from inorganic compounds) takes place in the sea, where carbon processing is mostly driven by microbial heterotrophs and autotrophs (Field *et al.,* 1998). Limiting the dissertation to single-cell organisms, the microbial food web can be simplified into functional groups: two of these include autotrophic microbes (either prokaryotes or unicellular eukaryotes) and heterotrophic prokaryotes. Organisms capable of autotrophic production, usually defined as "primary producers", can assimilate inorganic carbon (mainly CO_2) and convert it into organic carbon (i.e. living biomass). This process in marine microbes can occur by photosynthesis or by chemosynthesis. Photosynthetic organisms can use CO_2 as a carbon source and light to fuel primary production, while chemoautotrophic organisms can incorporate inorganic carbon using energetic reduced chemical compounds in the absence of light. The organic carbon produced by autotrophs is in turn consumed by the "secondary producers" (i.e. heterotrophic organisms), that regenerate CO_2 and nutrients through respiration processes. The heterotrophic consumption and recycling of organic matter through the so-called microbial loop (Azam, 1998; Azam and Malfatti, 2007) accounts for about one-half of the global biogeochemical cycling of carbon, nitrogen, phosphorus, sulphur and iron, thus playing crucial roles at the global scale and supporting food webs, in turn keeping the ocean healthy and productive (Falkowski *et al.,* 2008). Global ocean respiration estimates point to numbers at least as high as oceanic primary production (del Giorgo and Duarte, 2002; Karl *et al.,* 2003; Riser and Johnson, 2008). The majority (greater than 95%; del Giorgo and Duarte, 2002) of respiration in the ocean is carried out by heterotrophic prokaryotes, with half of it (approx. 37 Gt of C per year) taking place in the euphotic layer (del Giorgio and Williams, 2005). Mixotrophic microbes, possessing the potential for both autotrophic and heterotrophic metabolism, fall between these two major functional groups, including either bacteria, archaea or protists (Béjà, *et al.,* 2000; Unrein *et al.,* 2007; Zubkov and Tarran, 2008; Moore, 2013; Qin *et al.,* 2014).

The marine ecosystems, and especially the open ocean and the deep sea, contain the majority of microbes present on Earth (Whitman *et al.,* 1998). Microbes are generally concentrated in surface sediments, with abundances up to 4 orders of magnitude higher, per unit of volume, than in the waters of the photic zone (Danovaro *et al.,* 2008). Recent evidence has indicated that in the ocean the pelagic and benthic realms host similar numbers of bacteria and archaea, totalling more than 10^{29} prokaryotic cells (Karner *et al.,* 2001), as well as a huge number of viruses (Danovaro *et al.,* 2015; Figure 3.1.1). Recent studies have highlighted that different microbial components inhabiting deepsea benthic ecosystems show varying sensitivities to changes in temperature conditions and food supply, concluding that climate change will primarily affect archaea, with important consequences on global biogeochemical cycles, particularly at high latitudes (Danovaro *et al.,* 2016).

A wide variety of widespread marine bacteria have been isolated and studied in detail, including the dominant oceanic photoautotrophs of the cyanobacterial genera *Synechococcus* and *Prochlorococcus*, the dominant heterotrophic bacteria of the SAR11 (Rappè *et al.,* 2002) and Roseobacter clades (Buchan *et al.,* 2005). Conversely, for most of the diversity of marine archaea, their metabolic potential remains unknown (Cavicchioli, 2010). Archaea are ubiquitous members of marine microbial assemblages (DeLong, 1992, 2007; Fuhrman, 1992) and their relative importance increases in deep waters (with abundances equivalent to those of bacteria at depths >1,000 m) (Karner *et al.,* 2001) and in marine sub-surface sediments (i.e. >1-m depth below the sediment surface) (Lipp *et al.,* 2008; Xie *et al.,* 2013). Evidence is also accumulating for widespread heterotrophic or mixotrophic lifestyles among archaeal members (Ouverney *et al.,* 2000; Ingalls *et al.,* 2006; Qin *et al.,* 2014; Santoro *et al.,* 2015), but the physiology and energy metabolism of other groups of marine archaea remains poorly understood.

Viruses are by far the most abundant biological entities known in the biosphere, with current estimates of the global viral abundance in the order of 10^{30}-10^{31} viruses, outnumbering prokaryotes by at least one order of magnitude (Suttle, 2005, 2007). Studies conducted in the last two decades have revealed that marine viruses play critical roles in shaping pelagic and benthic microbial assemblages and ecosystem dynamics (Proctor and Fuhrman, 1990; Brussaard, 2004; Suttle, 2005; Danovaro *et al.,* 2008). Viruses are known to infect all life forms in the ocean, from the largest mammals to the smallest marine microbes, and being not able to self-replicate, they use the host cell's machinery to propagate. Viral infections can cause the death of the host cells thus representing an important source of mortality of marine microbes (Suttle, 2007). Despite the fact that viruses can cause spectacular epidemics within a wide range of organisms, most marine viruses infect prokaryotes and protists, the most abundant organisms in the ocean (Fuhrman, 1999; Weinbauer, 2004), with profound impacts on their diversity and functional potential, both in terms of genetic and metabolic properties (Rower and Thurber, 2009). By controlling the host cells, viruses can influence the structure of microbial assemblages, their genetic diversity and overall functioning (Figure 3.1.2). Since autotrophic and heterotrophic prokaryotes and protists play pivotal roles in biogeochemical cycles and global ocean functioning, viral infections, by controlling the abundance and activity of these microbes, can have important ecological consequences. For instance, by killing the hosts after the completion of their replication cycle, viruses can transform living biomass into dissolved and particulate organic matter, which can then be used again by other microbes stimulating their growth (Thingstad and Lignell, 1997; Noble and Fuhrman, 1999; Middelboe *et al.,* 2003a, b; Miki *et al.,*

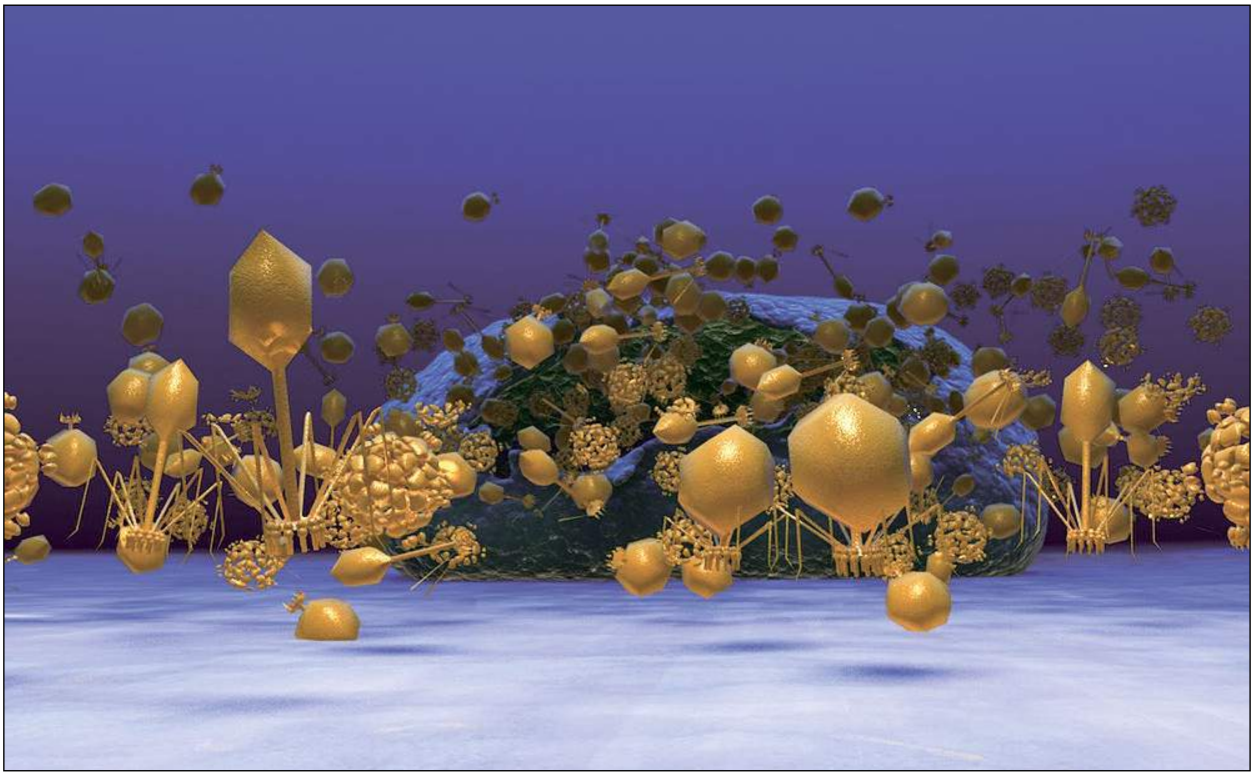

Figure 3.1.1 An image illustrative the multitude of viruses in marine environments. (Graphic Michael Tangherlini).

2008). This process, called "viral shunt" (Wilhelm and Suttle, 1999), fuels prokaryotic heterotrophic production by releasing dissolved organic compounds and/or support autotrophic production by enhancing nutrient regeneration pathways (Fuhrman, 1999; Suttle, 2005) (Figure 3.1.3), but it can also decrease the efficiency of the carbon transfer to higher trophic levels (Fuhrman, 1992; Bratbak *et al.,* 1994). The impact of viruses on prokaryotes in different pelagic ecosystems can be quantitatively comparable or even higher (especially in deep waters) than grazing by protists (Fuhrman and Noble, 1995; Guixa-Boixereu *et al.,* 2002; Wells and Deming, 2006b; Bonilla-Findji *et al.,* 2009).

Figure 3.1.2 An illustration of the impact of viruses on microbial cells: The viral infections, through cell lysis represent an important source of mortality for bacteria and archaea. (Graphic Michael Tangherlini).

The impact of viruses on bacteria and archaea is particularly high in deep-sea benthic ecosystems (Danovaro *et al.,* 2008a), where a major portion of the newly produced prokaryotic biomass is transformed into organic detritus through virus-induced cell lysis. After host cell lysis, the released viruses might infect other hosts, persist in the environment or decay. The factors controlling virus decomposition may contribute in shaping the diversity and functioning of viral communities, with possible consequences on the flow of energy and nutrients in marine systems (Wommack and Colwell, 2000; Suttle, 2007; Corinaldesi *et al.,* 2010; Jover *et al.,* 2014; Dell'Anno *et al.,* 2015).

While several viruses infecting the dominant oceanic bacterial autotrophs and heterotrophs have been

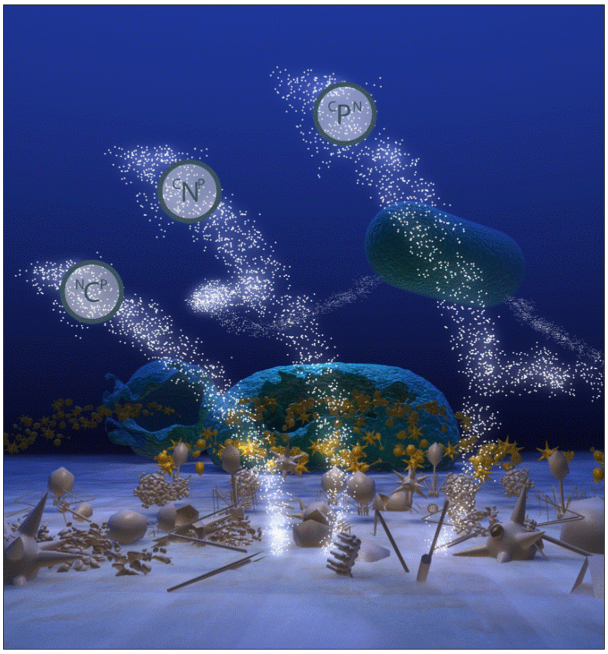

Figure 3.1.3 The death of microbial cells releases and important source of elements (C, N and P) that play a pivotal role in global biogeochemical cycles. (Graphic Michael Tangherlini).

identified and studied in detail (Zhao *et al.,* 2013), viruses infecting the dominant archaea inhabiting the oceans, despite being widespread and important (Angly *et al.,* 2006; Krupovic *et al.,* 2011; Brum *et al.,* 2015a; Chow *et al.,* 2015), have escaped proper identification and cultivation so far. Despite the increasing recognition of the crucial importance of archaea in biogeochemical and ecological processes (Wuchter *et al.,* 2006; Valentine, 2007; Orcutt *et al.,* 2011; Lloyd *et al.,* 2013; Molari *et al.,* 2013; Li *et al.,* 2015), the extent to which viral infection influences archaea in the ocean is unknown (Cavicchioli, 2010). This gap in knowledge limits understanding of the overall microbial dynamics occurring in the oceans, and hence the ability to forecast the actual impacts of ocean warming on the microbial marine assemblages, whose diversity and functioning still remains largely unexplored.

3.1.2 Ocean warming and its expected impacts on marine microbial world

Over the past decades, global average temperatures have risen by 0.65-1.06 °C (IPCC, 2014). The ocean has the capacity to store >1000 times the heat compared with the atmosphere (Levitus *et al.,* 2005) and it has been estimated that more than 90 % of the excess heat has been stored in the ocean in the last 50 years (Roemmich *et al.,* 2012). Ocean climate models predict that global warming will enhance the stratification of the oceanic water masses (Sarmiento *et al.,* 1998; Toggweiler and Russell, 2008), reducing their oxygen concentration with consequent expansion of so-called oceanic "dead zones" (Diaz and Rosenberg, 2008). Moreover, the increase in global temperatures is causing altered patterns of precipitation and run-off, ice and snow melting and consequent seawater freshening in different areas, including coastal zones (Hakkinen, 2002). Also the deep-water masses are warming, now storing 16–89% more heat (Levitus *et al.,* 2000), including in the deep Mediterranean Sea, now 0.12 °C warmer than few decades ago (Bethoux *et al.,* 1990). These modifications in the ocean are impacting deepsea animals (Danovaro *et al.,* 2004; Ruhl and Smith, 2004; Ruhl, 2008), and will likely influence also the microbes. However, although the impact of climate change is expected to have a range of effects on marine ecosystems, most of current knowledge does not take into account the microbial world. This could be due to the widespread assumption that sensitivity to climate increases with trophic level (Voigt *et al.,* 2003; Raffaelli, 2004), with microbial primary producers (phytoplankton) and decomposers (heterotrophic prokaryotes) considered less sensitive to environmental change than their consumers or predators. This is in contrast with recent evidence indicating that microbes have higher sensitivity to changes in thermal energy than organisms at the higher trophic levels (McClain *et al.,* 2012). Moreover, minor effects at the base of the food web can be amplified exponentially across trophic chains, highlighting the importance of better understanding the effects of climate warming on microbes.

In the last decades, research in marine biology and ecology has demonstrated that microbes (including protists, bacteria, archaea and viruses) dominate both in terms of abundance and biomass in the ocean (Whitman *et al.,* 1998; Ducklow, 2000; Fuhrman *et al.,* 2008; Danovaro *et al.,* 2015; Worden *et al.,* 2015). Scientific interest is indeed increasing on the interconnection between the present climate changes and the consequences on the biodiversity and functioning of marine microbial assemblages. The ongoing sea-surface warming is modifying marine ecosystems and has the potential to alter the cycling of carbon and nutrients in the ocean (Belkin, 2009; Kirchman *et al.,* 2009; Gattuso, 2015). Some effects depend on direct temperature changes of the seawater masses to which the micro-organisms are exposed, while others may occur indirectly due to changes in the interconnections and interactions among the different microbial species. In turn, the effects of climate warming on microbes, including possible positive and/or negative feedback type microbial responses, can have cascading effects on biogeochemical cycles, food webs, and the overall metabolic balance of the ocean. Given that the vast majority of the biomass (organic carbon) in the oceans consists of micro-organisms, it is expected that protists, bacteria, archaea and the viruses responsible for their mortality will play important roles in the overall response of the marine ecosystems to climate change (Danovaro *et al.,* 2011). Despite the extensive research on the potential effects of increasing CO_2 concentration and global warming on ecosystems (Hughes, 2000; Hays *et al.,* 2005; Doney *et al.,* 2009), our knowledge on the impacts of climate change on marine micro-organisms and especially of the role of viruses in such changes is still largely unknown.

Single-cell marine organisms, including autotrophic protists, bacteria and archaea (i.e. primary producers) and heterotrophic microbes (i.e. secondary producers), can be affected in their species composition, phenology, productivity, size structure, nutritional value, abundance and biogeographical distribution, in response to the predicted changes in stratification and vertical mixing of water masses due to ocean warming (Sarmento *et al.,* 2010; Danovaro *et al.,* 2011; Lewandowska *et al.,* 2014; Mojica *et al.,* 2015). Potential impacts are expected on net biomass production rates and turnover, on the assemblage composition and functions of heterotrophic and autotrophic micro-organisms, as well as on the viral communities able to infect them. Indeed, the effects of ocean warming on viruses, despite being difficult to predict, may include indirect responses based on the effects of rising temperature on the physiology and ecology of their hosts, leading for example to shifts in viral life strategies (e.g. induction of lytic infections in prokaryotes), or direct effects of rising temperatures on viral infectivity and decay rates (Danovaro *et al.,* 2011).

The biological and environmental factors influencing the biology and ecology of marine microbes are still largely unknown, especially for benthic ecosystems (Karner *et al.,* 2001; Biddle *et al.,* 2006; Lipp *et al.,* 2008; Lloyd *et al.,* 2013; Molari *et al.,* 2013). Previous studies reported that sea-surface temperature is one of the major drivers of the benthic prokaryotic abundance and biomass of the global oceans (Wei *et al.,* 2010). The importance of temperature in shaping the microbial assemblages has been highlighted recently also by the global survey of the diversity and functioning of surface ocean's microbes in the framework of the Tara project (Brum *et al.,* 2015a; Lima-Mendez *et al.,* 2015; Sunagawa *et al.,* 2015). Overall, consistent evidence is emerging, suggesting that long-term changes in surface temperatures leading to stratification will likely have great impacts on oceanic microbes.

Besides the environmental and ecological effects, climate change and especially climate warming have been shown in the last decades, to enhance morbidity and mortality in many regions of the world (Patz *et al.,* 2005). The impact of ocean warming on marine microbial communities, primarily in coastal areas, can have direct links with the health of the marine and terrestrial biota, including humans (Colwell, 1996; Harvell *et al.,* 2002). Increasing cOncern has emerged due to the evidence of positive correlations between the increase in sea-surface water temperatures and the increased abundance of pathogenic microbes, including infectious vibrios (Baker-Austin *et al.,* 2012; Vezzulli *et al.,* 2012, 2013) and other potentially harmful protists, bacteria, and viruses (Danovaro *et al.,* 2009; Lejeusne *et al.,* 2010). Clearly, future research efforts are needed to investigate these issues in more detail and to forecast and prevent detrimental effects of climate warming on the good environmental status of the ocean.

3.1.3 Potential impact of ocean warming on microbial food webs

Global warming and the increase in seawater temperature can affect all of the microbial food web functional compartments. Possible effects might include changes in metabolic rates (physiological response) or in species composition, with the final outcome depending on the trade-off of synergistic and antagonistic processes taking place within the food web. Slight changes in the biomass stock or activity of any of the compartments of the marine microbial food web should have major impacts on the global carbon cycle and could accelerate or compensate the processes associated with global change.

Multiple lines of evidence suggest that changes in phytoplankton biomass and productivity are related to ocean warming (Behrenfeld *et al.,* 2006; Polovina *et al.,* 2008; Boyce *et al.,* 2010). Current evidence suggests that in a warmer ocean primary producers will tend to be smaller (e.g. Falkowski and Oliver, 2007; Moràn *et al.,* 2010). Moreover, current evidence has highlighted that global phytoplankton biomass and productivity are generally declining (Behrenfeld *et al.,* 2006; Boyce *et al.,* 2010; Henson *et al.,* 2010; Hofmann *et al.,* 2011; Sommer *et al.,* 2012). This trend is predicted to persist in the future, despite possible opposite increasing trends in specific regions (Gregg *et al.,* 2003; Chavez *et al.,* 2011). Two major processes influence these trends. The physically induced upper-ocean warming, enhancing vertical stratification, can indirectly affect microbes by reducing the nutrient flux towards the upper ocean (Behrenfeld *et al.,* 2006; Doney, 2006; Boyce *et al.,* 2010; Hofmann *et al.,* 2011; Polovina *et al.*, 2011). Secondly, global warming can have direct effects on microbial metabolic rates, with evidence of a growing imbalance in favour of heterotrophic over autotrophic processes as temperatures increase (Müren *et al.,* 2005; López-Urrutia *et al.,* 2006; Sommer and Lengfellner, 2008; Sommer and Lewandowska, 2011).

The influences of the various physical and biological processes on marine microbial autotrophs have been generally explored in isolation, focusing on photoautotrops only (Behrenfeld *et al.,* 2006; Martinez *et al.,* 2009; Boyce *et al.,* 2010; Henson *et al.,* 2010; Hofmann *et al.,* 2011). To date, the possible interactions and the cumulative effects of these processes on marine microbial assemblages is still largely unknown (Sommer and Lewandowska, 2011; Holding *et al.,* 2013; Olonscheck *et al.,* 2013), as well as the potential effects of ocean warming on marine chemoautotrophic microbes (Middelburg, 2011). Recent studies attempting to assess the relative effects of physically and biologically mediated effects of warming on marine plankton communities have highlighted that warming can reduce phytoplankton biomass under nutrient-rich conditions, but not under nutrient-poor conditions (O'Connor *et al.,* 2009; Lewandowska *et al.,* 2014). These results highlight that the impact of ocean warming on the autotrophic components can depend upon a multitude of complex biological interconnections within the microbial food webs. These can include variable responses of the higher-order secondary consumers (grazers), changes in the efficiency by heterotrophic prokaRyotes to recycle nutrients (Taucher and Oschlies, 2011), and

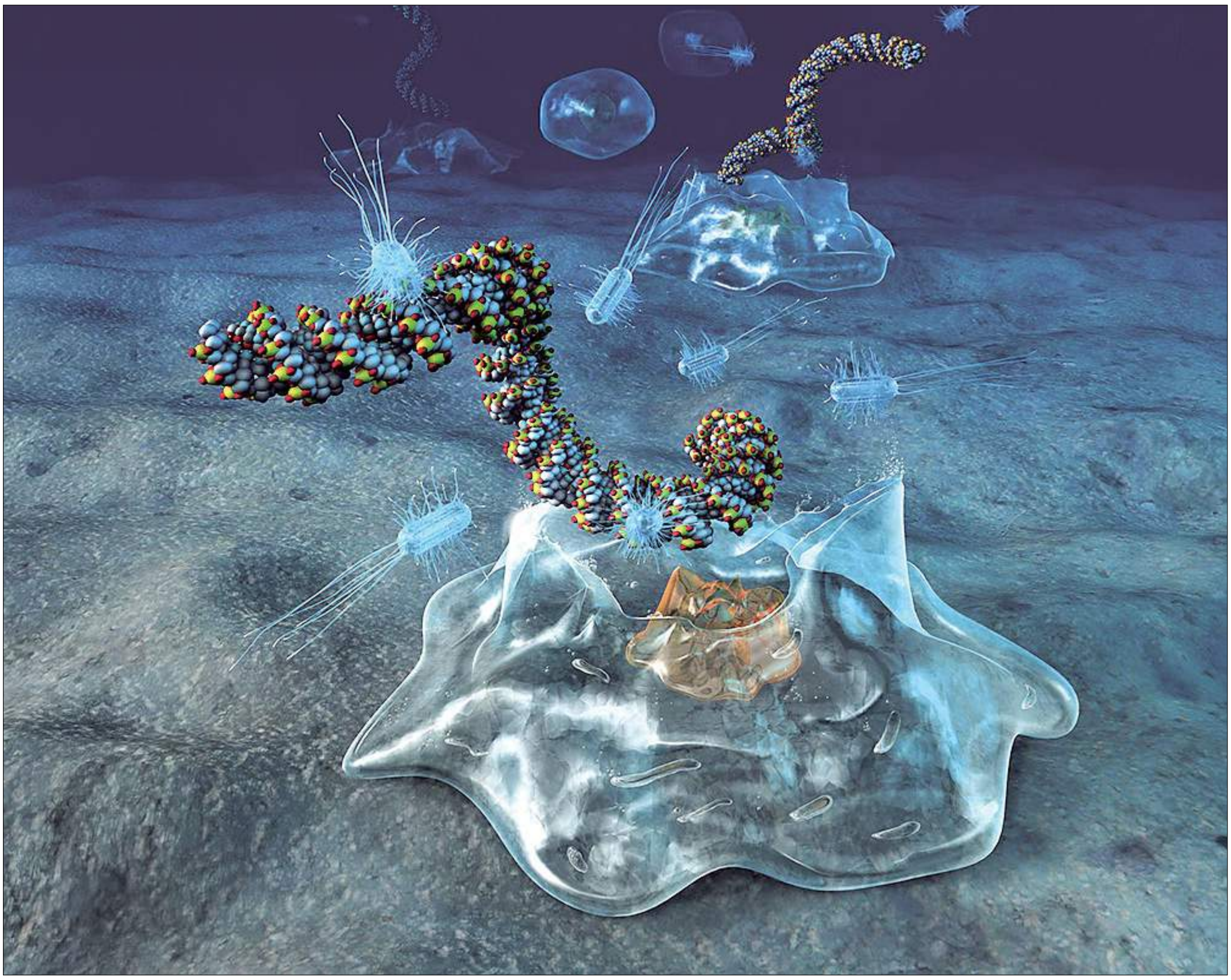

Figure 3.1.4 The lysis of microbial cells releases not only cellular components but also the DNA that is contained into the cells. This DNA, once out of the cells, is named extracellular DNA. (Graphic Michael Tangherlini).

other factors which are generally overlooked by global models and laboratory experimental approaches (e.g. local decreases in the input of land-derived nutrients as a consequence of altered patterns in precipitation and runoff). Overall, the lack of a consensual and unequivocal theoretical and experimental framework on how phytoplankton will respond to climate change (e.g. Falkowski and Oliver 2007, 2008; Peters, 2008) reduces our ability to make predictions of the effects of warming on oceanic microbes and on the associated ecosystem processes.

The negative impact of ocean warming on net primary production might reduce the organic matter available for prokaryotic heterotrophic consumption. However, temperature is also known to stimulate phytoplankton exudation (Watanabe, 1980; Zlotnik and Dubinsky, 1989; Morán *et al.,* 2006) and consequently a temperature increase would increase the availability of organic compounds sustaining heterotrophic bacteria and archaea (Sarmento *et al.,* 2010).

Heterotrophic bacteria and archaea play major roles in the marine microbial food web, and their metabolic activity and interactions with other compartments within the trophic web are influenced by changes in temperature (Sarmento *et al.,* 2010). Current evidence indicates that ocean warming can significantly increase respiration rates of heterotrophic prokaryotes (Rivkin and Legendre, 2001; López-Urrutia and Morán, 2007; Wohlers *et al.,* 2009; Sarmento *et al.,* 2010). Consequently, a warmer ocean would significantly increase the importance of heterotrophic prokaryotes in the control of oceanic carbon and nutrient fluxes, reinforcing the already dominant role of microbes in the global biogeochemical cycles. The metabolic processes underlying heterotrophy appear to respond more strongly to temperature than does primary production, so that increased temperature results in a shift to heterotrophy in the overall ecosystem metabolism, coupled with enhanced accumulation of dissolved organic matter (DOM) (Wohlers *et al.,* 2009), which includes a fraction of dissolved DNA (extracellular DNA; Figure 3.1.4) (Corinaldesi *et al.,* 2007b, 2014). The use of extracellular DNA is a useful additional or even important component of the diet of marine microbes (Figure 3.1.5). The DOM pool ranges from small molecules directly available for cellular uptake to large macromolecules or colloids that may require extracellular digestion prior to assimilation. The diversity of marine organic carbon compounds necessitates an elaborate network of heterotrophic strategies to decompose it (Cuna *et al.,* 2010). Most ocean models assume that DOM compounds are oxidized by a homogeneous class of prokaryotic heterotrophs through extracellular enzymatic activities and complex networks of metabolic processes that modify, transport, and/or re-mineralize organic molecules. The quantitative role of heterotrophic or mixotrophic unicellular eukaryotes in these processes is still almost completely unknown (Worden *et al.,* 2015). Ocean warming might cause a shift in the spectrum of extracellular enzymatic activities acting both in surface and in deeper ocean layers (Cuna *et al.,* 2010). The increasing length of the polar ice melt season are expected to result in an ice-free Arctic during summer within the next 100 years (Johannessen *et al.,* 1999; Laxon *et al.,* 2003). In this regard, polar ice melting was found to affect the spectra of bacterial extracellular enzymes and to increase the relative importance of polysaccharide hydrolysis and turnover (Sala *et al.,* 2010). However, robust evidence is currently lacking on the response of extracellular enzymatic activities to increased seawater temperature.

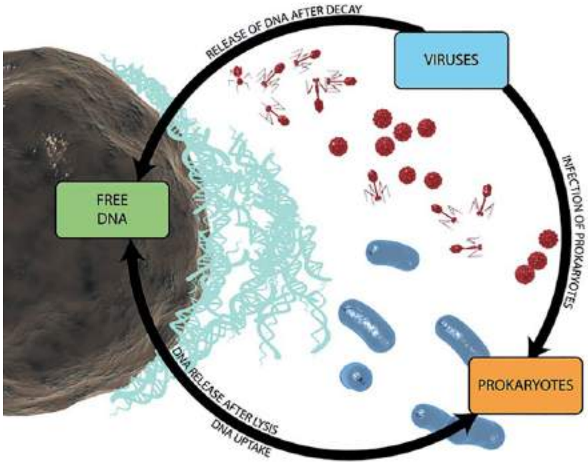

Figure 3.1.5 The DNA released due to viral infection (extracellular DNA) is re-utilized but other microbes, sustaining their metabolism. (Graphic Michael Tangherlini).

An additional and particularly relevant consequence of global warming is the expected decrease in the oxygen concentration of oceanic water masses (Diaz and Rosenberg, 2008). Oxygen concentrations in the ocean are governed by the balance between photosynthesis, aerobic heterotrophic respiration, and physiochemical processes. A decrease of 3-12 mmol kg^{-1} in oxygen concentration is forecast by 2100 due to climate change (Oschlies *et al.,* 2008; Keeling *et al.,* 2010), with 18–50% of this decline due to ocean warming reducing oxygen solubility. Also the increased stratification, hampering the oxygen supply to the surface ocean from the deeper water masses, contributes to the ongoing ocean deoxygenation (Sarmiento *et al.,* 1998; Keeling *et al.,* 2010). Decreases of 0.1–0.4 mmol kg^{-1} year^{-1} in dissolved oxygen have already been seen (Stramma *et al.,* 2008), with possible local greater rates of loss due to concomitant anthropogenic eutrophication (Diaz and Rosenberg, 2008; Middelburg and Levin, 2009; Cai *et al.,* 2011). Oxygen concentrations in the water column typically show an oxygen minimum zone (OMZ) at approximately 200–1200 m, due to the higher ventilation of shallower waters and the reduced oxygen consumption in the deeper waters (Paulmier *et al.,* 2008; Helm *et al.,* 2011). In some OMZs, oxygen can reach very low concentrations (hypoxia) or be completely depleted (anoxia) (Ulloa *et al.,* 2012). These OMZs are expanding in the oceans because of global warming (Emerson *et al.,* 2004; Whitney *et al.,* 2007; Bograd *et al.,* 2008; Stramma *et al.,* 2008), with major consequences for the distribution of organisms, including macro-organisms, whose sensitivity to oxygen levels is highly nonlinear (Vaquer-Sunyer and Duarte, 2008). Oxygen depletion can lead to changes in behaviour, distribution, functioning, and even mortality of organisms. As oxygen concentrations decline, the habitat available for aerobic organisms in pelagic and benthic ecosystems becomes less favourable or decreases in extent, with possible changes in the biodiversity and functioning of these regions (Rabalais *et al.,* 2010). Although OMZs are inhospitable to aerobically respiring organisms, these areas support highly active and diverse microbial communities (Wright *et al.,* 2012). The sensitivity is variable among different organisms, but eukaryotes can be expected to be more sensitive than several groups of prokaryotes (Ulloa *et al.,* 2012; Oikonomou *et al.,* 2014). The wider extent of OMSs in a warming and oxygen-starved ocean, would thus make microbes, and especially bacteria and archaea quantitatively even more important than in present conditions. As viruses also have been shown to maintain high abundance and infectivity potential under oxygen depleted conditions (Weinbauer *et al.,* 2003; Danovaro *et al.,* 2005; Corinaldesi *et al.,* 2007a, b, 2014), the loss of bacteria and archaea through viral lysis might increase relative to that caused by eukaryotic grazers. Expanding OMZs, leading also to an increase in anoxic benthic ecosystems (Ulloa *et al.,* 2013), might potentially increase the global relevance of the already high rates of virus-host interactions known to occur in marine sediments (Danovaro *et al.,* 2008).

3.1.4 Potential impact of ocean warming on microbes-viruses interactions

The complex networks of microbial interactions, including virus-host dynamics, are shaped by abiotic and biotic factors. Historically, abiotic factors have been considered to have a stronger effect, but in the last decades, the knowledge of the importance of the biotic factors has increased (Lima-Mendez *et al.,* 2015; Worden *et al.,* 2015).

Despite the well recognized roles of viruses infecting microbes in marine ecosystems, further efforts are needed to quantify and include their relevance in large-scale global oceanic models (Suttle, 2005, 2007; Danovaro *et al.,* 2011). Viruses can influence the functioning of pelagic and benthic microbial food webs and ecosystems, profoundly impacting biogeochemical cycles and shaping the diversity of microbial assemblages both in short and evolutionary time scales. As viral replication and life cycle are closely linked with host metabolism, increases in temperature will likely influence the interactions between viruses and the cells they infect.

The evidence gathered so far on the importance of temperature as driver of the global viral abundance and production is scant and contrasting, suggesting that in different oceanic regions viruses will respond differently to changes in surface temperatures caused by climate change (Danovaro *et al.,* 2011). While recent perturbation experiments have reported that short-term changes in temperature do not directly influence viral abundance (Feng *et al.,* 2009), other studies have reported either positive, negative or inconsistent correlations depending on the system investigated (Rowe *et al.,* 2008), with strongest positive relationships observed for temperate open ocean areas (Danovaro *et al.,* 2011). Overall, grouping together the available global data shows a decreasing pattern of viral abundance with increasing temperature (Danovaro *et al.,* 2011) but this relationship is weak, indicating that factors influencing virioplankton distribution are more complex than those predicted by temperature alone. Notably, for sediments the data set is still too limited to draw firm conclusions on the relationship between viral abundance and temperature. Considering viral infections and viral replication, the results from current experimental investigations on the relationship between temperature and viral production rates are contrasting. While high-latitude cold-water systems show higher viral production rates at higher temperatures, the opposite has been documented for pelagic systems at tropical and mid-latitudes, where higher temperatures seem to reduce viral production rates (Danovaro *et al.,* 2011).

There are some viruses that display diverse replication strategies, but the lytic and lysogenic viral infections are currently considered to be more frequent in marine systems (Ripp and Miller, 1997; Wommack and Colwell, 2000; Weinbauer, 2004). The lytic strategy implies host infection and subsequent cell lysis, while the lysogenic cycle involves the integration of the viral DNA into the host genome, with no immediate cell lysis. Depending on several factors still not well understood, some viruses can switch between lysogenic or lytic strategies (Williamson and Paul, 2006; Long *et al.,* 2008). The relative importance of lysogenic viral infections is known to vary widely among different marine environments from undetectable to more than 100% (Weinbauer and Suttle, 1996, 1999; Weinbauer, 2004). Even if a few reports suggest possible induction of temperate viruses by increases in temperature (Cochran and Paul 1998; Wilson *et al.,* 2001), other studies have reported greater influence of nutrient availability and host metabolic state (Jiang and Paul, 1996; Weinbauer and Suttle, 1999; McDaniel *et al.,* 2002; Williamson and Paul, 2006). Current evidence suggests that there may be changes in viral life strategies due to the decrease in primary productivity as a result of global warming. Indeed, an increase in the relative importance of lysogens over lytic viruses has been reported in periods of low microbial productivity, across different trophic conditions and in different oceanic areas (Angly *et al.,* 2006; Payet and Suttle, 2009). Ocean warming, leading to increased stratification and nutrient limitation, in turn reducing primary productivity levels (Sarmiento *et al.,* 2004), might make lytic infections less frequent. This would reduce the amount of microbial biomass removed through viral lysis, thus increasing its availability for predators and grazers at the higher levels in the trophic web. This suggested pattern may occur first in the polar oceans, which host some of the most rapidly warming regions on the planet (Doney *et al.,* 2012; Ducklow *et al.,* 2012a; Brum *et al.,* 2016).

The complex cascading effects of virus-host interactions triggered by warming-induced changes in environmental conditions extend beyond the possible shifts in viral lifestyles. As discussed above, the increase in global temperatures, can accelerate prokaryotic heterotrophic production and growth rates (Rivkin and Legendre, 2001). On one hand, the higher host metabolism can fuel higher rates of viral production. On the other hand, the more active cells could also speed up the activity of extracellular enzymes (including those degrading DNA, RNA and proteins) potentially enhancing the decomposition of viral structural and functional constituents, in turn increasing the so-called “viral decay” rates (Noble and Fuhrman, 1997; Wommack and Colwell, 2000; Dell’Anno *et al.,* 2015). The balance between these processes induced by ocean warming can strongly influence the resulting net response of the virus-host interactions to the increase in temperature.

Global warming is enhancing glacial melting, extreme weather events and altered patterns of precipitation, leading to seawater freshening. This is expected to affect in particular the poles and coastal ecosystems (Peterson *et al.,* 2002). Currently available data are still rather limited to allow global conclusions. However, it can be considered that viral abundance in low-salinity aquatic systems can reach values higher than in most of the marine ecosystems (Danovaro *et al.,* 2011). For both marine and freshwater viruses, the host range remains largely unknown. Despite freshwater viruses appearing to be taxonomically distinct from most marine viruses, some viruses appear to be shared across systems (Sano *et al.,* 2004; Angly *et al.,* 2006; Wilhelm *et al.,* 2006; Wilhelm and Matteson 2008; Bonilla-Findji *et al.,* 2009). Recently, pioneering works have started to study the contribution of freshwater microbes to marine systems, the increased opportunity for crossing over of marine and freshwater taxa, and the possible range of novel virus-host interactions, which might evolve in a future scenario of climate change. Sano *et al.* (2004) have suggested that freshwater viruses can survive and replicate in the marine environment. Also Breitbart and Rohwer (2005), examining the DNA sequences within viral genomes, identified identical phage sequences in freshwater, terrestrial and marine systems, highlighting the possibility that a subset of viruses can have wide host ranges, and that these viruses will likely continue to infect microbial hosts regardless of the system into which they are introduced. Viruses are known to be involved in the transfer of DNA across different micro-organisms through horizontal gene transfer (McDaniel *et al.,* 2010). As new genetic information contained in the DNA of freshwater viruses will increasingly be available to the marine microbial assemblages, one possible outcome of ocean warming might be the enhancement of the virus-mediated lateral transfer of genes (and associated functions) across different freshwater and marine microbes. However, different outcomes have to be considered, as changes in seawater salinity have been also reported to inhibit the ability of viruses to infect their hosts. This process, possibly due to inefficient adsorption of viruses to the cells in conditions of reduced salinity (Sobsey *et al.,* 1975; Harvey and Ryan, 2004), might counteract the development of novel virus-host interactions induced by seawater freshening processes.

The ocean has great potential to buffer the ongoing threats caused by climate change, serving as major sink for the anthropogenic CO_2 emissions. One of the major processes enabling carbon sequestration from the atmosphere to the ocean interior is the “biological carbon pump”, consisting of microbial primary producers (i.e. autotrophs) incorporating CO_2 into biomass (Falkowski *et al.,* 2004; Falkowski and Raven, 2007). Microbial secondary producers (i.e. heterotrophs) drive this pump in the opposite direction, consuming organic carbon and releasing CO_2 back into the atmosphere. Ultimately, the organic carbon produced at the ocean surface is exported down to the deep sea (Duce *et al.,* 2008). However, only a very small amount of this organic carbon is estimated to reach the ocean sea floor (Middelburg and Meysman, 2007), as most of it is consumed and recycled by microbes within the top 500m of the water column. Warming of ocean surface water and the predicted decrease in primary production might cause a decline in the strength of the biological pump (Riebesell *et al.,* 2009), with consequent decrease in the export of carbon to the deep sea and positive feedbacks on the ongoing climate changes. With as much as one quarter of the primary production in the ocean ultimately flowing through the viral shunt (Suttle, 2007), the viral infections influencing autotrophic and heterotrophic microbes and the overall microbial food webs can strongly influence the efficiency of the biological carbon pump and the extent of the carbon sequestration into the deep ocean. As such, the changes in the virus-host interactions triggered by the increase in seawater temperatures have to be considered as a further factor influencing the carbon storage capacity of the ocean.

The increase in the viral production with increasing temperature, as observed at high-latitude cold-water systems, would stimulate the heterotrophic metabolism and recycling of the organic matter at the ocean surface, decreasing the carbon sequestration efficiency of the biological pump (Danovaro *et al.,* 2011). This is expected to exacerbate the food limitation characterizing the largest biome of the biosphere, the deepsea ecosystems (Smith *et al.,* 2008), which primarily depend on the efficiency of organic carbon export from the photic zone. However, some authors have highlighted that virus-host interactions can contribute to the carbon export in several other ways, with opposite effects on the efficiency of the biological carbon pump. For instance, Lawrence and Suttle (2004) reported that viral infection can increase the export of carbon and other organic molecules to the deep ocean by promoting the sinking of virus-infected cells, possibly due to density increase or loss of motility of the infected cells. Moreover, virus-induced lysis can enhance the release and sinking of dense, refractory and carbon-rich colloidal aggregates (Mari *et al.,* 2005), favouring in this way carbon export to the ocean interior. Another virus-mediated process potentially increasing the efficiency of the biological carbon pump is the selective retention of nutrients available to support higher primary production rates at the surface, while increasing the relative portion of refractory carbon exported to the ocean interior. Indeed, viruses, through host cell lysis, have been suggested to selectively retain minerals (such as iron) and nutrients in the photic zone by releasing highly labile cellular contents, including amino acids and nucleic acids, while promoting the sinking of more refractory and carbon-rich structures (such as cell-wall material) (Suttle, 2007; Danovaro *et al.,* 2011). Moreover, the virus particles, being predominantly composed of proteins and nucleic acids, are generally enriched in nitrogen and phosphorus compared with the typical contents of a microbial cell (Jover *et al.,* 2014). As such, ocean warming, through the enhanced production of new viruses and increased cycling of organic matter through the viral shunt, might increase in this way the efficiency of the biological carbon pump.

Overall, a potential increase of viral lysis and of the amount of organic carbon entering the viral shunt due to increased seawater temperatures might either increase or decrease the efficiency of the biological carbon pump, depending on the net balance between different processes and on the specific virus-host interactions evolving in a warmer ocean.

3.1.5 Conclusions and recommendations

A better understanding of the microbial responses to present climate change and scenarios of global warming would enhance our ability to predict and adapt to the consequences of such changes. It is currently unclear whether the complex networks of interactions among microbes will ultimately stabilize or destabilize the functioning of the marine ecosystems and the dynamics driving the marine and global biogeochemical cycles. Several microbe-microbe and virus-microbe interactions have the potential to actively respond to and interact with the current ocean warming, but gaps in knowledge are still limiting the possibility to fully understand or predict the net impacts on the marine ecosystems.

General knowledge based on consistent experimental evidence and theoretical models point to a global reduction in oceanic primary productivity caused by global warming, with relative increase in heterotrophic secondary production processes leading to enhanced consumption and cycling of the organic matter in the surface ocean. The overall effects would be a reduction in the carbon storage efficiency of the ocean, but complex biotic and abiotic interconnections and feedbacks have to be considered, which might counteract or balance the observed trends.

Viruses have the potential to either positively or negatively affect the carbon sequestration efficiency of the oceans, depending on the balance between different virus-mediated processes promoting or decreasing the export of organic carbon from the ocean surface to the deep sea.

Ocean warming is also causing the expansion of zones experiencing oxygen deficiency, with important consequences for biogeochemical cycling and an increased role for the microbial world, and especially bacteria, archaea and viruses, at the expense of eukaryotes which are generally more sensitive to reduced oxygen levels. This will likely make the already dominant role of microbes in the functioning of the marine ecosystems even more pronounced in a scenario of a warming ocean.

Ice melting and altered patterns of circulation and precipitation induced by climate warming might lead to changes in the dominant virus life strategies and a rise in novel virus-host interactions due to the increased inputs of freshwater microbes into marine ecosystems.

Overall, there is a clear need to shed light on the yet undiscovered diversity and functional roles of marine microbes, to improve our understanding and possibility to predict the impact of ocean warming on the biodiversity and functioning of marine ecosystems.

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3.2 Impacts and effects of ocean warming on plankton

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Summary

- Extensive changes in plankton ecosystems around the world over the last 50 years including production, biodiversity and species distributions have had effects on fisheries production and other marine life. This has been mainly driven by climate variability and ocean warming.
- There has been a poleward shifts in the distribution of many plankton and fish species around the planet. For example, during the last 50 years there has been a northerly movement of some warmer water plankton by 10° latitude in the north-east Atlantic and a similar retreat of colder water plankton northwards (a mean poleward movement of between 200–250 km per decade).
- The seasonal timing of some plankton production has also altered in response to recent climate changes. Many planktonic organisms are now appearing earlier in their seasonal cycles compared to the past. This has consequences for plankton predator species, including fish, whose life cycles are timed in order to make use of seasonal production of particular prey species.
- When global warming rises above the key threshold of 2°C (by 2050) it has been estimated that between 50% and 70% of the global ocean may experience a large change in marine biodiversity indicating a major effect of climate warming on marine biodiversity. Additionally, melting of Arctic waters may increase the likelihood of trans-Arctic migrations of species between the Pacific and Atlantic oceans.
- Future warming is likely to continue to alter the geographical distribution of primary and secondary pelagic production, affecting ecosystem services such as oxygen production, carbon sequestration and biogeochemical cycling. These changes may place additional stress on already-depleted fish stocks as well as have consequences for mammal and seabird populations.

Ocean warming effects	**Consequences**
Biogeographical shifts of plankton Poleward movement of species Geographical (spatial) adjustment to optimum ecological niche/thermal preference	Community structural changes In some cases plankton can become invasive species or cause new Harmful Algal Blooms Competitive exclusion of native species
Phenological shifts of plankton Changes in seasonal appearance of plankton Seasonal (temporal) adjustment to optimum ecological niche/thermal preference	Decreased temporal synchrony of community and trophic levels leading to potential mismatch between plankton, fish and other marine wildlife
Whole marine ecosystem shifts (regime shifts) Response to shifting thermal boundaries and decoupling of community structure Differing sensitivity of species responses to increasing temperature	Abrupt ecosystem shift (difficult to predict and manage). Change in exploitable fish and shellfish species and carrying capacity
Reduced body-size of plankton (in ectotherms) Response to resource/nutrient limitation Fitness gains from earlier reproduction and adopting smaller size Earlier maturation	Potential devaluation of fisheries (possible reduction of biomass and move towards smaller species) Increase in carbon residence times in surface waters (possible reduced carbon drawdown)
Increase in plankton biodiversity in cooler climates Increase in environmental/water-column stability Increase in mutation rates Move towards smaller size structure of community	Positive feedback on climate warming with a possible shift from diatoms to small flagellates Increasing biodiversity not necessary of benefit to large monospecific populations of exploitable fish species

3.2.1 Introduction

Plankton include the free floating photosynthesizing life of the oceans (algal phytoplankton, bacteria and other photosynthesizing protists), at the base of the marine food-web which provide food for the animal plankton (zooplankton) which in turn provide food for many other marine organisms ranging from the microscopic to baleen whales. The carrying capacity of pelagic ecosystems in terms of the size of fish resources and recruitment to individual stocks as well as the abundance of marine wildlife (e.g. seabirds and marine mammals) is highly dependent on variations in the abundance, seasonal timing and composition of this plankton. Global change caused by human-activities has had large consequences for the Earth's biosphere through such effects as habitat destruction, climate warming, pollution, introduction of non-native species, loss of biodiversity, unsustainable exploitation of resources and alterations to nutrient cycles. These changes have accelerated over the last 50 years as human populations have sharply grown, coupled with unsustainable economic practices. In marine environments the main drivers of change include climate warming, pollution, deoxygenation and unsustainable levels of fishing. Furthermore, and unique to the marine environment, anthropogenic CO_2 is also associated with ocean acidification. Ocean acidification has the potential to affect the process of calcification and therefore certain planktonic organisms dependent on calcium carbonate for shells and skeletons (e.g. coccolithophores, foraminifera, pelagic molluscs, echinoderms) may be particularly vulnerable to increasing CO_2 emissions. It is also worth noting that while pelagic systems are undergoing large changes caused by climate change they have also been identified as a means of mitigating climate change through possible human manipulation of these systems through geoengineering processes. It has been shown at small-scales that the addition of iron to certain oceanic environments (ocean fertilization) can increase productivity and net export of carbon to the deep ocean. However, this approach is still controversial with largely unknown long-term ramifications for marine ecosystems at the large-scale. For example, it could lead to negative effects such as the stimulation of Harmful Algal

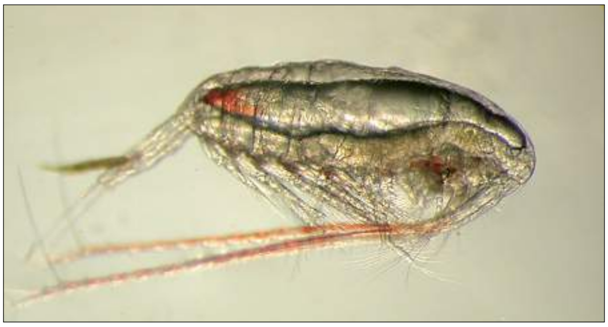

Figure 3.2.1 *Calanus finmarchicus.* © Fisheries and Oceans Canada.

Box 3.2.1 Invasive species and the geographic movement of organisms

Climate warming will open up new thermally defined habitats for previously denied non-indigenous species (e.g. newly observed warm-water species in the North Sea seen over the last few decades) and invasive species allowing them to establish viable populations in areas that were once environmentally unsuitable. Therefore, species can arrive naturally as a part of shifting thermal boundaries, however, human-caused introductions (e.g. ballast water exchange, aquaculture) have become a significant cause for concern over recent decades. The introduction of non-native species into a new environment can have significant economic and ecological consequences (Vitousek *et al.*, 1997) as well as introducing potentially Harmful Algal Bloom forming species (Hinder *et al.*, 2011). While it should be noted that not all introductions lead to invasions or the establishment of viable populations some species can establish themselves (approximately 10% of introductions are successful). Over the last 100 years there have been an estimated 16 exotic phytoplankton taxa introduced into the North Sea (Nehring, 1998). For example, (Edwards *et al.*, 2001b) showed how the Pacific diatom *Coscinodiscus wailesii*, after being introduced into the North Sea in 1977, managed to spread and establish itself relatively quickly throughout the region where it remains as an important component of the North Sea phytoplankton community.

Apart from these thermal boundaries limits moving progressively poleward, and in some cases expanding, the rapid climate change observed in the Arctic may have even larger consequences for the establishment of invasive species and the biodiversity of the North Atlantic due to the decreasing areal coverage of Arctic ice. Since the late 1990s large numbers of a Pacific diatom *Neodenticula seminae* (Figure 1) have been found in samples taken in the Labrador Sea in the North Atlantic associated with the decreasing ice coverage. *N. seminae* is an abundant member of the phytoplankton in the subpolar North Pacific and has a well defined palaeo history based on deep sea cores. According to the palaeo evidence this was the first record of this species in the North Atlantic for at least 800,000 years. The reappearance of *N. seminae* in the North Atlantic, and its subsequent spread southwards and eastwards to other areas in the North Atlantic, after such a long gap, could be an indicator of the scale and speed of changes that are taking place in the Arctic and North Atlantic oceans as a consequence of climate warming (Reid *et al.*, 2007). This diatom species could be the first evidence of a trans-Arctic migration in modern times and be a harbinger of a potential inundation of new organisms into the North Atlantic. The consequences of such a change to the function, climatic feedbacks and biodiversity of Arctic systems are at present unknown.

Figure 1 *Neodenticula seminae* samples from the Gulf of St Lawrence, Northwest Atlantic, light microscopy. © Phycological Society.

Blooms (HABs) or hypoxia but further investigations are needed (Güssow *et al.*, 2010). While there are a myriad of pressures and intertwined multiple drivers on the marine environment and on pelagic ecosystems some of which are synergistic (e.g. the interaction of temperature, ocean acidification and hypoxia) in this section, the focus is solely on the effects of ocean warming on planktonic communities.

Box 3.2.2 Marine biodiversity, past, present and future

In general, still relatively little is known about marine biodiversity. Although over 200,000 marine species have been described, scientists believe this represents only 10% of marine biodiversity; in other words, the number of species in the sea may approach 2 million. It is therefore difficult to predict the outcome of climate change on global marine ecosystems. Until now, attempts to understand the implications of climate change on marine biodiversity have either extrapolated results from just a few key species, or have applied ecological niche models to many species. However, both approaches are limited by our poor knowledge of species distribution. In a recent study a new approach based upon the theory that the way biodiversity is distributed in the ocean is as a result of the interaction between the multidimensional domain of environmental tolerance of species and fluctuations in the environmental regime was used to address this limit in our knowledge (Beaugrand *et al.*, 2015). The study generated tens of thousands of theoretical species, each having a unique response to local changes in climate (sea surface temperature) which were allowed to colonize the sea providing the local environment was suitable. The study reconstructed oceanic biodiversity for the past, the present and also for a range of projections of biodiversity for the end of the 21st Century. The results showed that provided future global warming remains below 2°C, which is the amount of warming the international community considers to be below the threshold that would place natural systems at risk of grave damage, only 15% of the global ocean surface would experience a change in biodiversity of greater magnitude than occurred over the last 20,000 years since the Last Glacial Maximum. As a result the study provided evidence that if humanity kept global warming below 2°C, the effects on marine biodiversity predicted by the model may be within 'acceptable levels of change'. However, more alarming, the other three levels of global warming that were examined each indicated that they would place the marine biosphere at risk of increasingly, significant changes. When warming reaches the dangerous threshold of 2°C the model predicts that between 37% and 46% of the surface ocean would experience a change in marine biodiversity that is greater in magnitude than occurred between either the Mid-Pliocene or the Last Glacial Maximum, and the present day, respectively. When global warming rises above the dangerous threshold of 2°C, it was estimated that between 50 and 70% of the global ocean may experience a change in marine biodiversity indicating a major effect of climate warming on marine biodiversity (Figure 1).

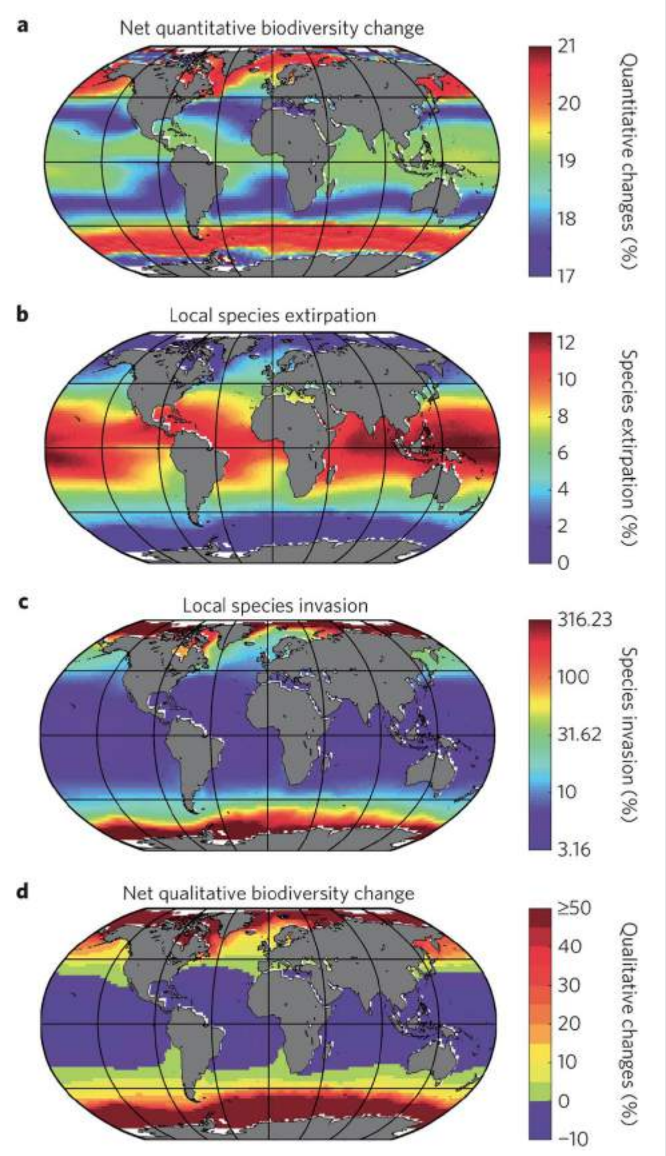

Figure 1 Expected sensitivity of biodiversity to a 2°C increase in temperature. a–c, Net quantitative changes in biodiversity (a), local species extirpation (b) and invasion (c). d, Net qualitative biodiversity changes resulting from the difference between species invasion and extirpation. All changes are expressed as a percentage. Based on Beaugrand *et al.* (2015).

3.2.2 Definition of ecosystem

The marine pelagic realm, the habitat for planktonic organisms, is the largest ecological habitat on the planet; occupying 71% of the planetary surface fuelling the vast majority of marine biological production that drives the marine food-webs. In terms of ecosystem services the pelagic realm plays a huge role. For example, occupying such as large part of the Earth's biosphere, the pelagic realm plays a fundamental role in modulating the global environment via its regulatory effects on the Earth's climate and its role in planetary oxygen production, carbon drawdown and other biogeochemical cycling. Changes caused by increased warming on marine pelagic communities are likely to have important consequences on ecological structure and function, thereby leading to changes to marine biological production and significant feedbacks on the Earth's climate system. Biologically speaking, changes in temperature have direct consequences on many physiological processes (e.g. oxygen metabolism, adult mortality, reproduction, respiration, reproductive development) and control virtually all life-processes from the molecular to the cellular to whole regional ecosystem level and biogeographical provinces. Ecologically speaking, temperature also modulates, both directly and indirectly, species interactions (e.g. competition, prey-predator interactions and food-web structures). Ultimately, changes in temperature can lead to impacts on the biodiversity, size structure and functioning of the whole pelagic ecosystem.

Global warming of pelagic surface waters also increases the density gradient between the surface layer and the underlying nutrient-rich waters. The availability of one of the principal nutrients (nitrate) that limits phytoplankton growth has been found to be negatively related to temperatures globally (Kamykowski and Zentara, 1986, 2005). While, temperature has direct consequences on many biological and ecological traits it also therefore modifies the actual marine habitat by influencing oceanic circulation and by enhancing the stability of the water-column and hence nutrient availability. The amount of nutrients available in surface waters directly dictates phytoplankton growth and is the key determinant of plankton size, community and foodweb structure. A global analysis of satellite derived chlorophyll data has shown a strong inverse relationship between Sea Surface Temperatures (SST) and chlorophyll concentration (Behrenfeld *et al.*, 2006). Furthermore, other abiotic variables like oxygen concentration (important to organism size and metabolism (Pörtner and Knust, 2007)), nitrate metabolism (Berges *et al.*, 2002) and the viscosity of sea water (important for the maintenance of buoyancy for plankton and their morphological traits) are also directly linked to temperature. Climate warming is expected to contribute to an overall decline in global ocean oxygen levels (deoxygenation) via reduced oxygen solubility from warming and reduced ventilation from stratification and circulation changes (Keeling *et al.*, 2010). This coupled with increased nutrients from human activities is thought to have led to an increase in hypoxic events termed Oxygen Minimum Zones (OMZs) around the world (Rabalais *et al.*, 2010).

3.2.3 Global and regional significance

About 70% of the world population lives within 60 km of the coast. Humanity uses on average 8% of the aquatic primary production, this fraction reaching 25% for upwelling and 35% for non-tropical continental-shelf ecosystems. It is also estimated that approximately 80 million tonnes of fish and invertebrates are caught every year and marine ecosystems are valued as a source of new marine bioresources, medicines, biofuels, and an important carbon regulator. At the global scale, phytoplankton comprise approximately half of total global primary production and play a crucial role in climate change through biogeochemical cycling and the export of the greenhouse gas to the deep ocean by carbon sequestration (mainly as detrital material) in what is known as the 'biological pump'. Phytoplankton have thus already helped mitigate some of the climate effects of elevated CO_2 observed over the last 200 years, with the ocean taking up to about 40% of anthropogenic CO_2 (Zeebe *et al.*, 2008). The biological pump is strongly regulated by the resident zooplankton community as they process a large part of the primary production through grazing and produce fast sinking faecal pellets that contribute significantly to export flux. Additionally, zooplankton also contribute to carbon sequestration via diel vertical migrations (Hansen and Visser, 2016) and through what is known as the 'lipid pump'. For example, a recent study has shown that one species, the copepod *Calanus finmarchicus* (Figure 3.2.1) overwintering in the North Atlantic (diapause), sequesters an amount of carbon equivalent to the sinking flux of detrital material. The inclusion of this newly described lipid pump almost doubles the previous estimates of deep-ocean carbon sequestration by biological processes in the North Atlantic (Jónasdóttir *et al.*, 2015). In terms of feedback mechanisms on Earth's climate it is speculated that these biological pumps will be less efficient in a warmer world due to changes mainly in the phytoplankton composition. These changes favour small flagellates (Bopp *et al.*, 2005) and less overall nutrient mixing due to increased stratification. It is also predicted that warmer temperatures would shift the metabolic balance between production and respiration in the world's ocean towards an increase in respiration thus reducing the capacity of the ocean to capture CO_2 (Lopez-Urrutia *et al.*, 2006). At the regional scale, plankton fuel production and energy flow through almost all known marine ecosystems. Apart from playing a fundamental role in the Earth's climate system and in marine food-webs, plankton are also highly sensitive contemporary and palaeo indicators of environmental change and provide rapid information on the 'ecological health' of the ocean. A plankton species, defined by its abiotic envelope, in effect has the capacity to simultaneously represent an integrated ecological, chemical, and physical variable.

3.2.4 Trends and impacts

Observations from around the world show that many pelagic ecosystems, are responding to changes both physically and biologically in regional climate caused predominately by the warming of air and sea surface temperatures and to a lesser extent by the modification of precipitation regimes and wind patterns. The biological manifestations of rising SST have variously taken the form of biogeographical, phenological, biodiversity, physiological, maximum body-size, and species abundance changes, as well as whole ecological regime shifts. Any observational change in the marine environment associated with climate change, however, should be considered against the background of natural variation on a variety of spatial and temporal scales. Recently, long-term decadal observational studies have focused on known natural modes of climatic oscillations at similar temporal scales such as the El Niño-Southern Oscillation (ENSO) in the Pacific, and the North Atlantic Oscillation (NAO) in the North Atlantic in relation to pelagic ecosystem changes (see reviews by Drinkwater *et al.* (2003) and Overland *et al.* (2008)) . Many of the biological responses observed have been associated with rising temperatures. However, approximating the effects of climate change embedded in natural modes of variability, particularly multidecadal oscillations like the Atlantic Multidecadal Oscillation (AMO) (Edwards *et al.*, 2013) is difficult. At the species level, some of the first consequences of climate warming are often seen in a species phenology and in species geographical distribution responses. Phenology, or repeated seasonal life-cycle events, such as annual migrations or spawning are highly sensitive indicators of climate warming. This is because many terrestrial and marine organisms, apart from photoperiod, are dependent on temperature as a trigger for seasonal behaviour. In the terrestrial realm phenology events such as bird migrations, egg-laying, butterfly emergence and flowering of certain plants are all getting earlier in response to milder spring weather (Parmesan and Yohe, 2003). In terms of the pelagic phenological response to climate warming, many plankton taxa have also been found to be moving forward in seasonal cycles (Edwards and Richardson, 2004). In some cases a shift in seasonal cycles of over six weeks was detected, again a far larger shift than observed for terrestrial based observations. Summarizing a terrestrial study of phenology using over 172 species of plants, birds, insects and amphibians, Parmesan and Yohe (2003) calculated a mean phenological change of 2.3 days per decade. It is thought that temperate pelagic environments are particularly vulnerable to phenological changes caused by climatic warming because the recruitment success of higher trophic levels is highly dependent on synchronization with pulsed planktonic production (Edwards and Richardson, 2004). Furthermore in the marine environment, and just as important, was the response to regional climate warming that varied between different functional groups and trophic levels, leading to mismatch in timing between trophic levels (Figure 3.2.2). For example, while the spring bloom has remained relatively stable in seasonal timing over five decades, mainly due to light limitation and photoperiod rather than temperature dictating seasonality (Edwards and Richardson, 2004; Sommer and Lengfellner, 2008), many zooplankton organisms as well as fish larvae have moved significantly earlier in their seasonal cycles. Similarly, other pelagic phenological changes in response to climate warming have been observed in other areas of the North Atlantic and from other oceans around the world (Mackas *et al.*, 2012a).

Some of the strongest evidence of large-scale biogeographical changes observed in the ocean comes from the ocean-basin scale Continuous Plankton Recorder survey. A study encompassing the whole of the NE Atlantic Ocean, over a 50 year period, (Beaugrand *et al.*, 2002; Beaugrand, 2009) highlighted the northerly movements of the biodiversity of a key zooplankton group (calanoid copepods). During the last 50 years there has been a northerly movement of warmer water plankton by 10° latitude in the

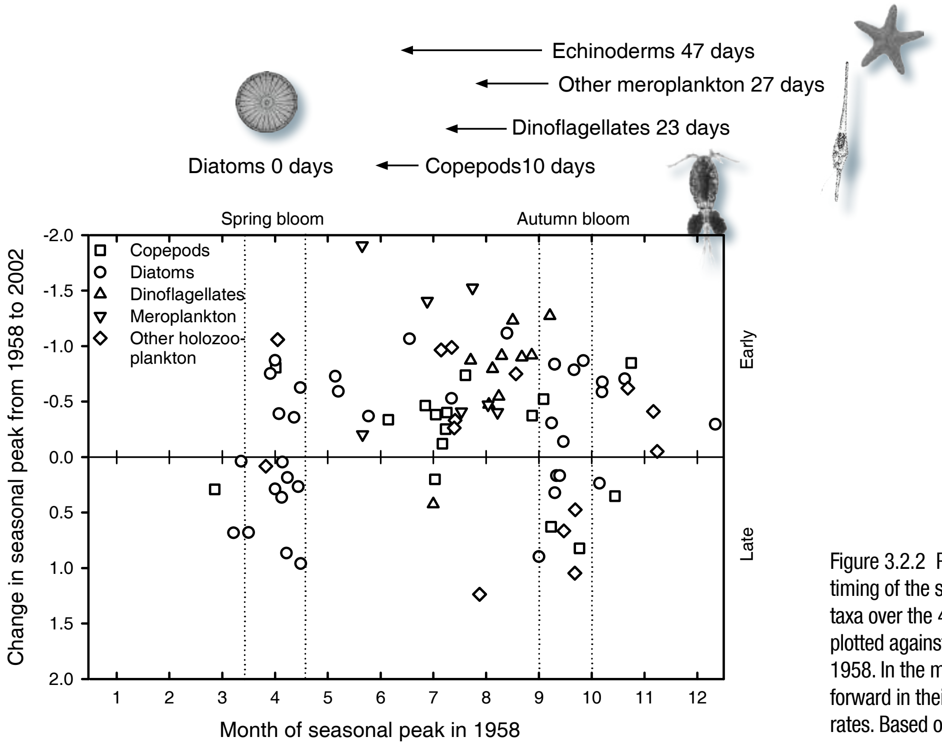

Figure 3.2.2 Phenological shifts: the change in the timing of the seasonal peaks (in months) for the 66 taxa over the 45-year period from 1958 to 2002 plotted against the timing of their seasonal peak in 1958. In the majority of cases most taxa are moving forward in their seasonal cycles but at different rates. Based on Edwards and Richardson (2004).

north-east Atlantic and a similar retreat of colder water plankton northwards (a mean poleward movement of between 200–250 km per decade) (Figure 3.2.3). This geographical movement is much more pronounced than any documented terrestrial study, mainly due to advective processes and in particular the shelf-edge current running north along the northern European continental shelf. The rapid movement of plankton northward is only seen along the continental shelf, where deeper water is warming much more rapidly. Further along the shelf, plankton are upwelled from this deeper water to make an appearance in the surface plankton community. Hence the plankton have moved 10° latitude northwards via mainly deep water advective processes not seen in the movement of surface isotherms. In other areas in the North-east Atlantic the plankton shifts were more moderate and varied between 90 to 200 km per decade, but still faster than any other documented terrestrial study which has a meta-analytic average of 6 km per decade (Parmesan and Yohe, 2003). Similar to the North Atlantic, in the North-east Pacific there has been a general increase in the frequency of southern species moving northward (Mcgowan *et al.*, 1998). Climate variability and regional climate warming have also been associated with variations in the geographic range of marine diseases and pathogens (Vezzulli *et al.*, 2012). In comparison to terrestrial systems, epidemics of marine pathogens can spread at an extremely rapid rate.

Contemporary observations of satellite *in-situ* blended ocean chlorophyll records indicate that global ocean net primary production has declined over the last decade (Behrenfeld *et al.*, 2006). Although this time-series is very limited in terms of length it does show a strong negative relationship between primary production and SST and is evidence of the closely coupled relationship between ocean productivity and climate variability at a global scale. In the North Atlantic and over multidecadal periods, both changes in phytoplankton and zooplankton species and communities have been associated with Northern Hemisphere Temperature (NHT) trends and variations in the NAO index. These have included changes in species distributions and abundance, the occurrence of sub-tropical species in temperate waters, changes in overall phytoplankton biomass and seasonal length, change in mean size-structure of community, and changes in the ecosystem functioning and productivity of the North Atlantic (Edwards *et al.*, 2001a, 2002; Beaugrand *et al.*, 2002; Beaugrand and Reid, 2003; Edwards and Richardson, 2004). The increase in overall phytoplankton biomass in the North Sea has been associated with an increase in smaller flagellates which favour warmer and stratified conditions (Edwards *et al.*, 2002). Over the whole NE Atlantic there has been an increase in phytoplankton biomass with increasing temperatures in cooler regions but a decrease in phytoplankton biomass in warmer regions (Richardson and Schoeman, 2004). This is

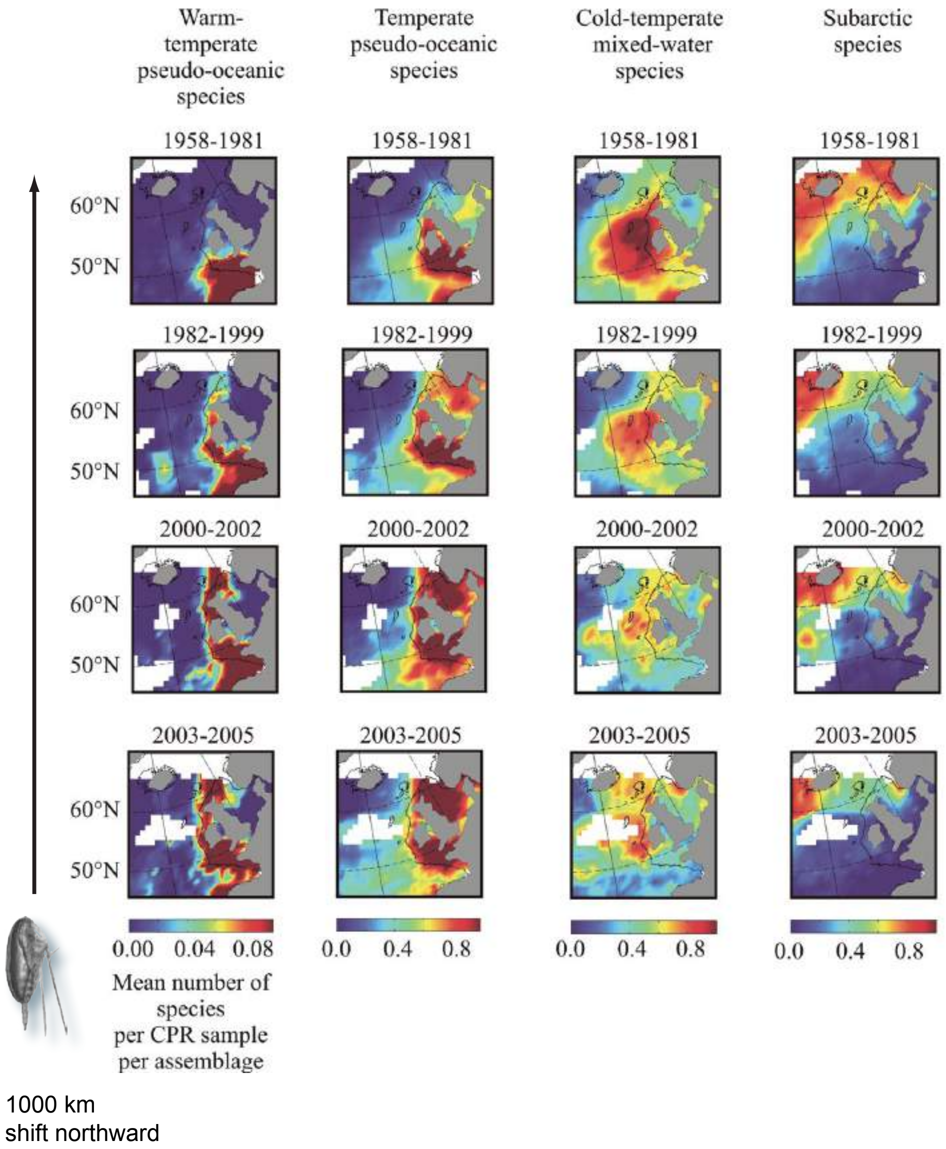

Figure 3.2.3 Biogeographical shifts: biogeographical changes in plankton assemblages spanning five decades. Warm-water plankton (e.g. warm-temperate species) are moving north and cold-water plankton (e.g subarctic species) are moving out of the North Sea. Particular rapid movement is seen along the European Continental Shelf up to 1000 km over 50 years. Based on Beaugrand *et al.* (2003).

possibly a trade-off between increased phytoplankton metabolic rates caused by warming temperatures in cooler regions but conversely a decrease in nutrient supply in warmer regions. Regional climate warming in the North Sea has also been associated with an increase in certain Harmful Algal Blooms (HABs) in some areas of the North Sea (Edwards *et al.*, 2006; Hinder *et al.*, 2012). In the North Sea the population of the previously dominant and ecologically important zooplankton species, (the cold water species *Calanus finmarchicus*) has declined in biomass by 70% since the 1960s (Figure 3.2.4). Species with warmer-water affinities are moving northward to replace this species but these species are not as numerically abundant or nutritionally beneficial to higher trophic levels. This has had inevitably important ramifications for the overall carrying capacity of the North Sea ecosystem.

The ecological changes that have occurred in the North Sea since the late 1980s (predominately driven by change in temperature regime and more warmer winters) have also been documented for the Baltic Sea for zooplankton and fish stocks (Alheit *et al.*, 2005).The related changes that have taken place in these Northern European waters are sufficiently abrupt and persistent to be termed as 'regime shifts' (Beaugrand, 2004). Similarly in the Mediterranean, zooplankton communities have also been linked to regional warming and the NAO index (Molinero *et al.*, 2005; Conversi *et al.*, 2010). All these observed changes appear to be closely correlated to climate-driven sea temperature fluctuations. Indirectly the progressive freshening of the Labrador Sea region, attributed to climate warming and the increase in freshwater input to the ocean from melting ice, has resulted in the increasing abundance, blooms and shifts in seasonal cycles of

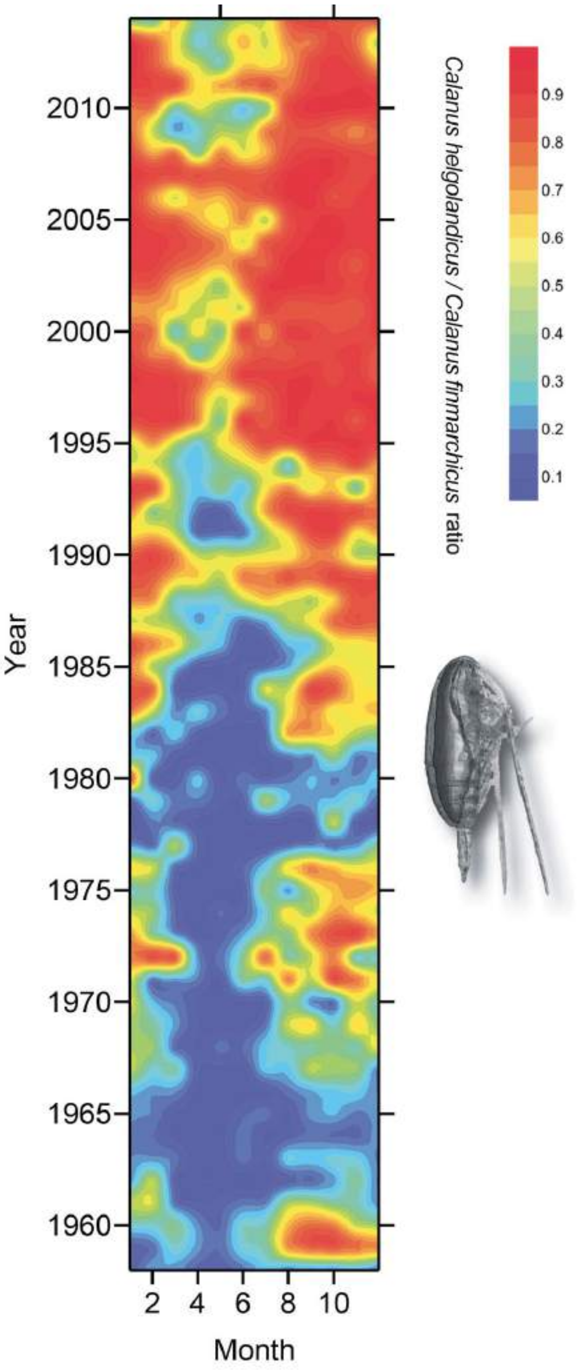

Figure 3.2.4 A simple abundance ratio between the warm-water copepod species (*Calanus helgolandicus)* and the cold-water species (*Calanus finmarchicus*) per month from 1958-2014 in the North Sea. Red values indicate a dominance of the warm-water species and blue values the dominance of the cold-water species. (0= total *C. finmarchicus* dominance, 1=total *C. helgolandicus* dominance).

dinoflagellates due to the increased stability of the water-column (Johns *et al.*, 2003). Similarly, increases in coccolithophore blooms in the Barents Sea (Figure 3.2.5) and HABs in the North Sea are associated with negative salinity anomalies and warmer temperatures leading to increased stratification (Smyth *et al.*, 2004).

In the Benguela upwelling system in the South Atlantic, long-term trends in the abundance and community structure of coastal zooplankton have been related to large-scale climatic influences (Mackas *et al.*, 2012b). Similarly, changes in mesozooplankton abundance have also been related to large-scale climate influences in the Californian upwelling system (Ohman *et al.*, 2009). The progressive warming in the Southern Ocean has been associated with a decline in krill (Figure 3.2.6; Atkinson *et al.*, 2004) and an associated decline in the population sizes of many seabirds and seals monitored on several breeding sites. In the Southern Ocean the long-term decline in krill stock has been linked to changes in winter ice extent which in turn has been related to warming temperatures (Atkinson *et al.*, 2004). Changes in the abundance of krill have profound implications for the Southern Ocean food web. Recent investigations of planktonic foraminifera, from sediment cores encompassing the last 1400 years, have revealed anomalous changes in the community structure over the last few decades. The study suggests that ocean warming has already exceeded the range of natural variability (Field *et al.*, 2006). A recent major ecosystem shift in the northern Bering Sea has been attributed to regional climate warming and trends in the Arctic Oscillation (Grebmeier *et al.*, 2006). Decadal changes in zooplankton related to climatic variability in the west sub arctic North Pacific (Chiba *et al.*, 2008) and in the Japan/East Sea (Chiba *et al.*, 2006) have also been observed.

At the North Atlantic scale over the last 50 years, overall plankton biodiversity has been shown to have increased. In particular, increases in diversity are seen when a previously low diversity system like Arctic and cold-boreal provinces undergo prolonged warming events. The latitudinal increase in biodiversity both for phytoplankton and zooplankton have been related to the warming North Atlantic over the last 50 years (Beaugrand *et al.*, 2010). Moreover, the increases in copepod diversity have been paralleled by a decrease in the mean size of zooplanktonic copepods. For example, warming in the temperate to polar North Atlantic has led to a reduction in the average body lengths of 100 copepod species from 3-4 mm to 2-3 mm (Beaugrand *et al.*, 2010). Similarly, phytoplankton (dinoflagellates) show a relationship between temperature and diversity which could be linked to the phytoplankton community having a higher diversity but an overall smaller size-fraction and a more complex foodweb structure (i.e .microbial-based versus diatom based production) in warmer more stratified environments. Reduced body size as an ecological response to climate warming has

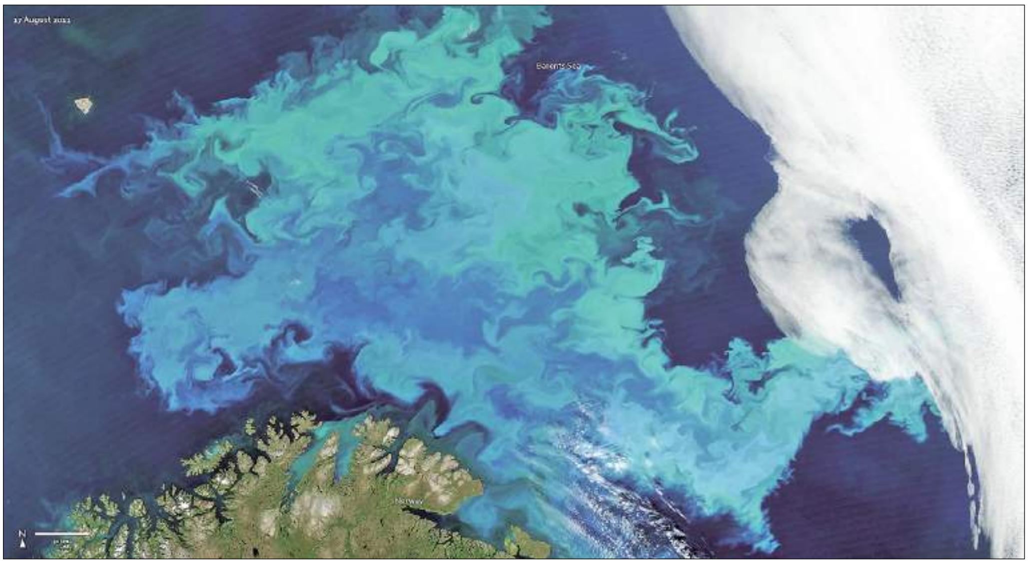

Figure 3.2.5 Coccolithophore bloom in the Barents Sea. © NASA/Goddard Space Flight Center.

many diverse explanations including nutrient availability (Sheridan and Bickford, 2011). Increased warming and a move towards a dominance of smaller organisms may influence the networks in which carbon flows (i.e. increase in surface carbon residence times) and may have negative consequences for the biological carbon pump and North Atlantic fisheries. Climate warming will therefore increase planktonic diversity throughout the cooler regions of the world's oceans as temperature isotherms shift poleward. In a recent study using a new model for how biodiversity is arranged in the ocean, future projections estimate that there could be a decrease in biodiversity in warm-water regions of the ocean but as much as a 300% increase in polar regions of the world (Beaugrand *et al.*, 2015).

Figure 3.2.6 A northern krill *Meganyctiphanes norvegica.* © Øystein Paulsen.

3.2.5 Conclusions

At the species level, some of the first manifestations of climate warming are often seen in a species phenology (i.e. timing of annual occurring life-cycle events) and in species geographical distribution responses. This is mainly because temperature continually impacts the life cycle of the species and naturally the population will respond over time, providing it is not biotically restrained or spatially restricted, attaining its optimum position within its bioclimatic envelope. This can occur within a temporal niche as in seasonal succession (observed as a phenological response) or in its overall biogeographical distribution (observed as a geographical movement in a population). These biological changes as well as those changes observed in biodiversity and planktonic abundance and productivity are perhaps the key indicators signifying the large scale changes occurring in the world's ocean as a consequence of climate warming. The studies highlighted in this section collectively indicate that there is substantial observational evidence that many pelagic ecosystems, are responding both physically and biologically to changes in regional climate caused predominantly by the warming of sea surface temperatures (SST), ocean current changes and changes to nutrient regimes. These biological manifestations of climatic variability have rapidly taken the form of biogeographical, phenological, biodiversity, community size changes, species abundance changes and whole ecological regime shifts. Overall, ocean primary production is expected to continue to change, however, the global patterns of these changes are difficult to project. Existing projections suggest an increase in productivity in high latitude systems like the Arctic and Southern Ocean and a decrease in productivity in the tropics and mid-latitudes. Due to their sensitivity to change some of the most convincing evidence for the biological response to climate change in the ocean comes from phytoplankton and zooplankton communities. Most of this observational evidence derives from long-term surveys and historical datasets that can reveal change in the context of multi-decadal natural variability and shifting baselines. However, such datasets particularly for open ocean systems are rare and regionally based (Edwards *et al.*, 2010). To improve our information on ocean changes these historical datasets will need to be maintained and where possible expanded into new areas of the world's ocean where there are little or no sustained observations.

Apart from playing a fundamental role in the Earth's climate system and in marine food-webs, plankton are also highly sensitive contemporary and palaeo-indicators of environmental change and provide rapid information on the 'ecological health' of the ocean. With the realization that ocean ecosystems are vulnerable to human threats such as overfishing, climate change, eutrophication, habitat destruction, pollution and species introductions there is an increasing imperative to observe ocean biology in a more integrated fashion in order to provide the long-term baselines needed for management actions and research. Many new international research initiatives such as Global Earth Observation System of Systems (GEOSS) and Group on Earth Observations Biodiversity Observation Network (GEOBON) are being set up to address these issues and monitor these changes using 'Essential Ocean and Biodiversity Variables' (EOVs and EBVs). Future biological monitoring of these open-ocean ecosystems, through an integrated and sustained observational approach, will be essential in understanding the continuing impacts of climate and environmental change on oceanic systems. This in turn may allow us through international collaboration to mitigate and adaptively manage some of their more detrimental impacts (Edwards *et al.*, 2010).

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3.3 Impacts and effects of ocean warming on seaweeds

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Summary

- Seaweeds (marine macroalgae) encompass a diverse group of marine plants comprising >13,000 species. They provide habitat, food and many other important ecological functions, and the value of ecosystem services (e.g. fishing, tourism, biodiversity) from seaweed habitats is conservatively estimated to be US$30,000 ha^{-1} year^{-1}. Seaweeds have complex life cycles with several stages that are sensitive to direct physiological effects of warming on metabolism and reproduction, and indirect effects associated with warming-mediated changes in abiotic conditions (e.g. light) and species interactions such as herbivory.
- Ocean warming has caused significant changes in seaweed distribution, especially at Arctic and temperate latitudes. Cool-water species have been contracting and warm-water species extending their range edges poleward. Recent range-changes have been from 26 km to 1250 km. In addition, many seaweed populations have changed their depth distribution and relative abundance.
- Ocean warming has caused significant changes in seaweed communities, and the evidence is substantial and globally comprehensive. Gradual warming, marine heatwaves and over-grazing range-shifting herbivores have forced and augmented regime-shifts in at least seven regions across four continents. Here, highly complex productive seaweed forests have been replaced by structurally simple coralline crusts, filamentous turfs or small fleshy seaweeds.
- Key challenges include establishing appropriate baselines to assess further change against, as well as identifying the mechanisms that underpin warming-induced changes in seaweed ecosystems.
- The ecological and socio-economical flow-on effects of changing seaweed ecosystems require better understanding. In particular, the knowledge of the range of services provided by seaweed dominated ecosystems, and the value of these services to regional economies, is rudimentary.
- Solutions for mitigating impacts of warming are required. Options include managing additional local stressors, boosting resilience through assisted breeding and selection of resistant genotypes, restoration through translocation or substitution with functionally similar species. Knowledge of the relative merits and feasibility of these solutions are largely unknown.

Ocean warming effects	Consequences
Increasing mean ocean temperature	Shifting habitat suitability Increasing physiological stress leading to reduced resilience Failure to reproduce in marginal populations leading to population attrition and eventually local extinction and range contraction Population expansion and poleward range extension of warm-water species
Increasing frequency of marine heatwaves	Rapid population collapse and poleward range contraction of cool-water seaweed populations
Increasing poleward flow of western boundary currents	Increasing poleward propagule pressure leading to range expansion of warm-water seaweeds and other species including sub-tropical and tropical herbivores Increasing grazing pressure leading to seaweed population collapse and/or reinforcing ecosystem transitions. Increase risk of marine heatwaves at mid-latitudes
Increasing glacial melt and retreating sea ice in Arctic and Antarctic	Release of new space for seaweed colonization Changes to spatial and depth distribution Increased light penetration and production in some area Low salinity and turbidity limiting survival and light in other areas

3.3.1 Introduction

Marine macroalgae, commonly known as seaweeds, are a large, heterogeneous group of plants (*sensu* Bolton, 2016; Figure 3.3.1) that are found in most coastal areas of all climate zones (Lüning, 1990). Seaweeds have three basic environmental requirements: sea water, sufficient light to drive photosynthesis, and for most species a firm attachment point at some stage in their life cycle. Beyond that, species-specific distribution and growth are primarily controlled by temperature, irradiance and photoperiod, nutrients, waves, currents, salinity and herbivores (Van den Hoek, 1982a; Kirst, 1989; Lüning, 1990; Hurd, 2000; Wernberg *et al.*, 2013a; Vergés *et al.*, 2014a).

Globally there are currently 13,761 species of seaweeds that have been identified (Guiry and Guiry, (2016), accessed on 18th of February, 2016). They can be divided into three main groups, distinguished by their thallus pigmentation: red algae (phylum Rhodophyta; 7,113 species), green algae (phylum Chlorophyta; 2,760 species) and brown algae (phylum Ochrophyta; 3,888 species). These groups have evolved along separate pathways, and differ considerably in many features in addition to photosynthetic pigments. They are, however, all important marine primary producers serving a multitude of ecological functions and providing valuable ecosystem services (Lüning, 1990; Smale *et al.*, 2013; Bennett *et al.*, 2016).

Seaweeds are more complex organisms than generally realized (Figure 3.3.1). They range in size from a few millimetres to tens of metres, and in thallus structure from single filaments and coenocytes to highly elaborate growth forms with specialized tissues (Lüning, 1990; Hay, 1994). Many seaweeds have complex life cycles involving both micro- and macroscopic phases and alternation between haploid and diploid stages that can be either isomorphic or heteromorphic (Coelho *et al.*, 2000; Garcia-Jimenez and Robaina, 2015). Because of their complex life cycles, there are many stages where temperature and other abiotic factors can affect seaweeds, and the sensitivity can change throughout a species life cycle.

3.3.2 Global and regional significance of seaweed ecosystems

Seaweeds play an important role in marine ecosystems as ecologically important primary producers, ecosystem engineers and habitat formers. They are the dominant organisms on many intertidal and shallow subtidal rocky reefs along approximately 25% of the world's coastlines (Figure 3.3.2), where their species-specific distributions often shape local marine communities (Wernberg *et al.*, 2003; Buschbaum *et al.*, 2006; Ingólfsson, 2008; Tuya *et al.*, 2009; Egan *et al.*, 2014). Seaweed dominated habitats are particularly prevalent and important at temperate to polar latitudes (Figure 3.3.2). For example, kelp forests – dense stands of large brown seaweeds – are among the most productive ecosystems on Earth (Mann, 1973) and they are arguably some of the most ecologically and socio-economically important habitats in temperate waters (Steneck *et al.*, 2002; Smale *et al.*, 2013; Bennett *et al.*, 2016).

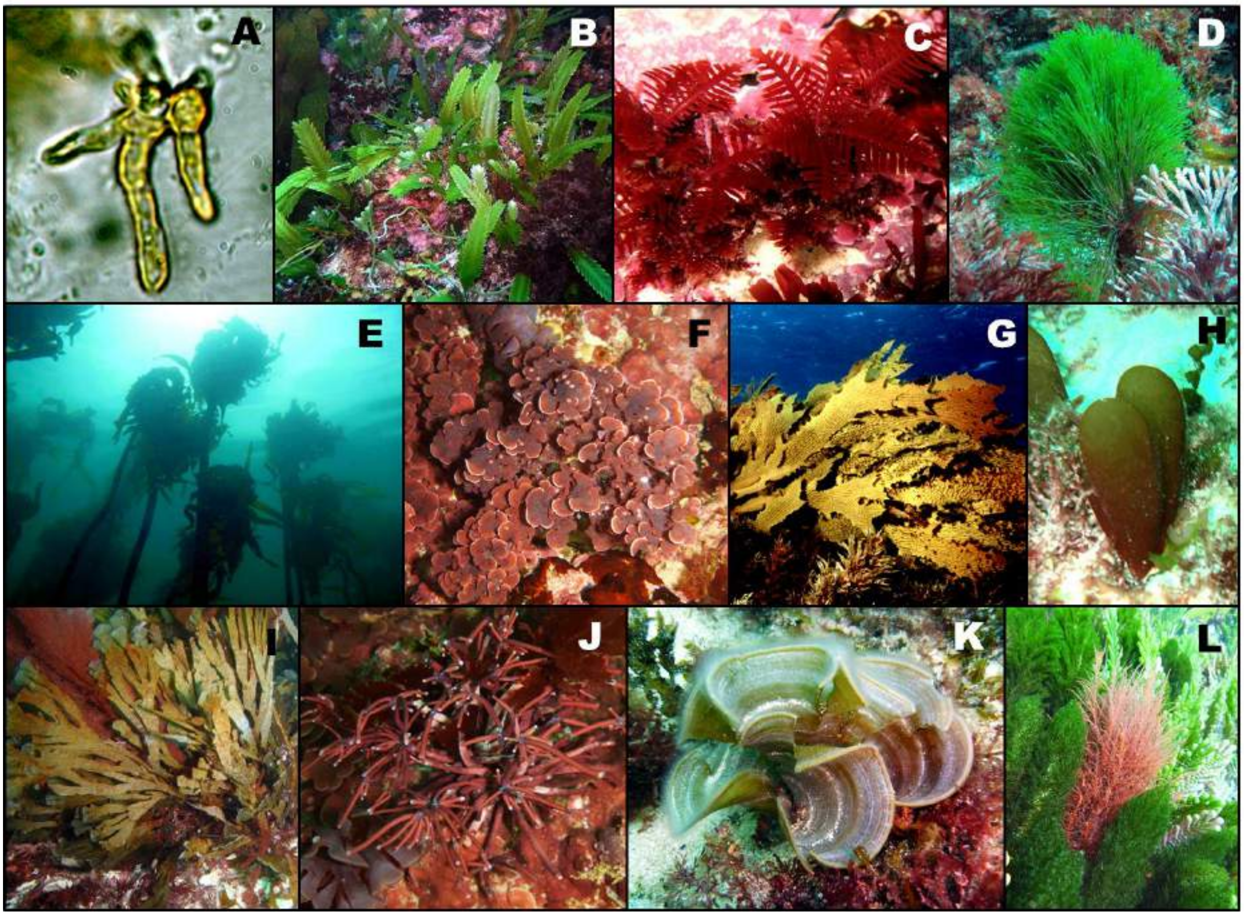

Figure 3.3.1 Seaweeds are a diverse group of marine plants. They are classified into red (C, F, H, J, L), brown (A, E, G, I, K) and green (B, D, L) algae based on their main pigments. Seaweeds display a broad range of morphologies including clusters of strings (D, J, L), fleshy blades (B, C, I, K), gelatinous bulbs (H) and highly differentiated structures with holdfasts, stipes and canopies (E, G), and some have calcified tissues (F, J, K). They can have complex life histories alternating between micro macroscopic phases (A *vs.* G) and range in size from a few centimetres to more than 10 metres (E). Male gametophyte of *Ecklonia radiata* (A, ~0.1 mm), *Caulerpa scalpelliformis* (B, ~10 cm), *Orthocladia rectangularis* (C, ~5 cm), Penicillus nodulosus (D, ~5 cm), *Ecklonia maxima*(E, ~10 m), *Metamastophora flabellata* (F, ~10 cm), *Ecklonia radiata* (G, adult sporophyte, ~1 m), *Gloiosacchion brownii* (H, ~10 cm), *Zonaria turneriana* (I, ~15 cm), *Metagoniolithon radiatum* (J, ~5 cm), *Padina* sp. (K, ~10 cm), *Caulerpa obscura* (green) and *Hypnea ramentacea* (red) (L, ~10 cm). The species shown here are all from Western Australia except *E. maxima* (E), which is from South Africa. © Photo A. Mohring M.; Photos B, C, D, E, F, G, H, I, J, K, L. Wernberg T.

Kelps and many other seaweeds produce large amounts of biomass (Mann, 1973), affect their physical environment (Dayton, 1985; Hurd, 2000; Wernberg *et al.*, 2005) and increase the habitable surface area considerably (Boaden, 1996). Many marine species depend on these seaweed habitats for feeding, mating and nursing areas or protection from predators. Consequently, seaweeds provide the structural and trophic framework supporting diverse associated communities and complex food webs (Steneck *et al.*, 2002; Wernberg *et al.*, 2004, 2013b; Graham, 2004; Ling, 2008; Harley *et al.*, 2012; Smale *et al.*, 2013; Steneck and Johnson, 2013; Bertocci *et al.*, 2015; Graiff *et al.*, 2015; Paar *et al.*, 2015; Bennett *et al.*, 2016). The ecological importance of seaweeds extends well beyond their main habitat. As much as 80% of the primary production from kelp forests is exported to adjacent communities with lower primary production (e.g. deep sea, sandy beaches), where it subsidises and enhances secondary production (Krumhansl and Scheibling, 2012).

In addition to their ecological importance, seaweeds underpin valuable ecosystem services. Specifically, many commercial and recreational fisheries depend directly on seaweeds, including abalone, lobsters, and several species of fish (Bolognaand Steneck, 1993; O'Connor and Anderson, 2010; Fraser *et al.*, 2011; Rosenfeld *et al.*, 2014; Bennett *et al.*, 2016). Several seaweeds are edible and are harvested or grown for food or additives used in medicines and cosmetics, as well as industrial chemicals (Kain (Jones) and Dawes, 1987; Lüning, 1990; Smit, 2004; FAO, 2014). Others can be used for biofuel production, provide coastal

Box 3.3.1 Maerl

Maerl beds are accumulations of unattached live and dead coralline algae – heavily calcified red seaweeds – which form over thousands of years (Box Figure 3.3.1). They occur from the tropics to the poles and from the low intertidal down to 100m depth in the clear water of the Mediterranean (Blake and Maggs, 2003; Hall-Spencer *et al.,* 2010; Peña *et al.,* 2014). They provide a wide range of ecological niches and support high biodiversity (Barbera *et al.,* 2003; Grall and Hall-Spencer, 2003).

Figure 1 Maerl bed. ©SNH.

Maerl beds have high conservation status in European legislation due to their longetivity, high biodiversity and benefits for commercial species as nursery areas (Hall-Spencer *et al.,* 2010). In addition to being highly productive communities, maerl beds are considered an important source of calcareous sediment and they contribute to the pH balance of sea water (Canals and Ballesteros, 1997; Hall-Spencer *et al.,* 2010).

Maerl beds face many threats worldwide, including habitat destruction (from dredging, fishing gear, fish farms), the spread of invasive species, sewage pollution, and the combined pressures of ocean acidification and ocean warming (Grall and Hall-Spencer, 2003; Hall-Spencer *et al.,* 2010; Peña *et al.,* 2014). Due to very slow growth rates (<1cm per year, on average around 1mm/year), recovery from disturbances take a very long time or is impossible (Barbera *et al.,* 2003; Blake and Maggs, 2003; Hall-Spencer *et al.,* 2010; Brodie *et al.,* 2014).

Ocean warming is expected to have severe effects on maerl beds as their fragmented ranges and poor dispersal capacity makes them vulnerable to local extinction (Hall-Spencer *et al.,* 2010). Maerl species are expected to be affected directly, but information about thermal limits is missing. So far only indirect effects of warming via water quality and increases of invasive species have been associated with negative impacts of warming. Also, there is the possibility of regime shifts as fleshy seaweeds may be favoured over maerl under warming conditions, leading to major changes in maerl bed functioning and productivity (Hall-Spencer *et al.,* 2010; Noisette *et al.,* 2013).

protection or contribute to carbon capture and storage (Løvåsand Tørum, 2001; Duarte *et al.*, 2013a, Hill *et al.*, 2015).

The monetary value that these seaweed ecosystems contribute to society is difficult to estimate, mainly because of a lack of studies valuing ecosystem services specifically provided by seaweeds (in contrast to, for example, corals) (Bennett *et al.*, 2016). However, in Australia Bennett *et al.* (2016) estimated the direct contribution to gross domestic product (GDP; activities such as fishing and reef-related tourism) from the seaweed-dominated Great Southern Reef to be at least A$1,400 $ha^{-1}year^{-1}$, and account for more than 15% of regional economies. However, this estimate does not include substantial indirect values such as coastal protection, nutrient cycling, carbon storage and biodiversity. Estimates for more broadly defined marine macrophyte communities which do consider these indirect values place seagrass and seaweed beds as the third most productive systems globally, providing ecosystem services valued at ~US$30,000 $ha^{-1}year^{-1}$ (Costanza *et al.*, 2014). Even this is most likely a considerable under-estimation; coral reefs were recently found to be worth more than 40 times previous estimates, mainly because of new studies valuating additional ecosystem services (Costanza *et al.*, 2014). Properly valueing seaweed dominated ecosystems will likely reach similar conclusions (Bennett *et al.*, 2016).

3.3.3 Trends and impacts

Temperature plays a pivotal role in the biogeography of seaweeds. Distribution limits of individual species typically follow major marine isotherms (Van den Hoek, 1982b; Lüning, 1990), giving rise to strong relationships between seaweed communities and the temperature signatures of major ocean gradients (Broitman *et al.*, 2001; Schilsand Wilson, 2006; Tuya *et al.*, 2012; Wernberg *et al.*, 2013a). For seaweeds, these patterns are a product of two types of temperature thresholds: lethal boundaries, determined by the capacity to survive during the unfavourable season, and growth and reproduction boundaries, determined by the ability to grow and reproduce during the favourable season (Van den Hoek, 1982b; Lüning, 1990). In addition to these direct physiological effects determining the potential ecological niche, there is increasing evidence of indirect effects mediated by changing, sometimes novel, species interactions and abiotic conditions. Specifically, the consumption of temperate seaweed by range-shifting tropical herbivores also contribute to set, maintain, or change distribution limits of seaweeds, thus shaping the realized niche (Haraguchi *et al.*, 2009; Vergés *et al.*, 2014a, b; Bennett *et al.*, 2015a; Franco *et al.*, 2015; Takao *et al.*, 2015). Similarly, coastal darkening and ice free zones, indirect abiotic effects caused by retreating

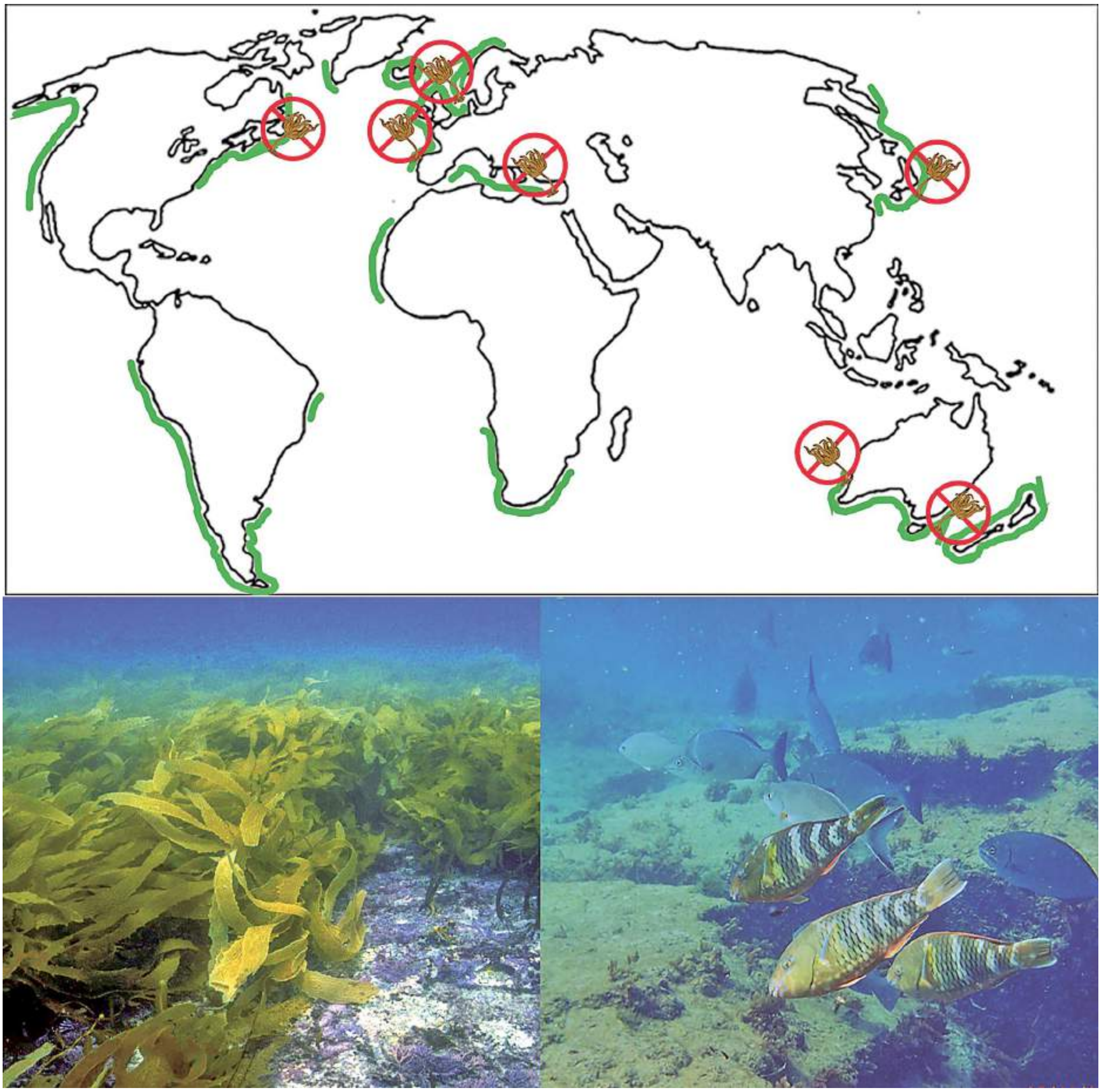

Figure 3.3.2 Seaweeds dominate intertidal and shallow subtidal rocky reefs along ~25% of the world's coastline. The map show the global distribution of seaweed forests (green, adapted from Steneck and Johnson, 2013). However, ocean warming has led to regime-shifts in several regions (red symbols), where complex, highly productive seaweed forests have been lost and replaced by structurally simple coralline crusts, filamentous turf or small foliose seaweeds. The photos show rocky reef habitats in Western Australia before (2005) and after (2013) a marine heatwave caused a 100 km range contraction of kelp (*Ecklonia radiata*). At the same time, subtropical and tropical herbivorous fishes such as parrotfish (*Scarus* sp.) increased substantially in abundance and they now suppress the recovery of kelp forests (Wernberg *et al.*, 2016a). © T. Wernberg.

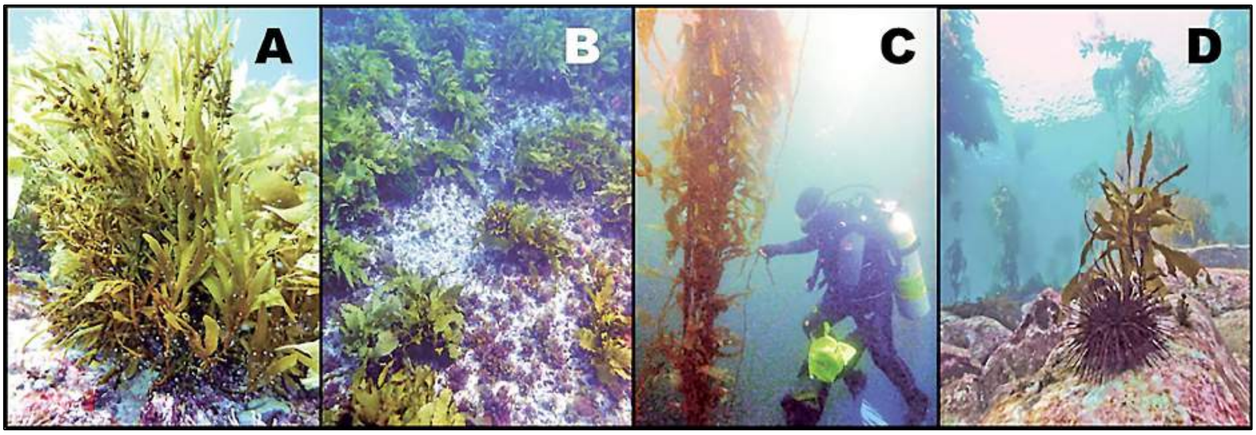

Figure 3.3.3 Seaweeds under threat from warming. In Western Australia, the ~0.5-1 m tall fucoid *Scytothalia dorycarpa* (A) succumbed to direct physiological stress associated with an extreme marine heatwave, causing a 100 kilometre range-contraction and leaving behind big gaps in the surrounding canopy cover leaving patches of *Ecklonia radiata* (B) (Smale and Wernberg, 2013) (In Tasmania, giant kelp (*Macrocystis pyrifera*) (C) has been in dramatic decline due to decreasing nutrient levels and increasing temperatures, and together with common kelp (*Ecklonia radiata*) has been severely impacted by range-extending sea urchins (*Centrostephanus rodgersii*) (D) (Johnson *et al.*, 2011). © Photos A, B, C. Wernberg T.; Photo D. Ling S.

ice-borders, are shaping local seaweed communities on Arctic and Antarctic rocky shores. The net effects can, however, be in opposing directions as ice free zones provide new habitat for seaweed colonization, increasing biomass and diversity, whereas glacial melt reduces salinity and increases turbidity, altering production rates and causing an upward shift of seaweed distributions (Bartsch *et al.*, 2012, 2016; Deregibus *et al.*, 2016). In other words, changes in temperature directly alters the distribution and abundance of seaweeds, associated species and abiotic conditions which in turn has unprecedented indirect consequences for interactions, food web structure and habitat configuration in seaweed dominated ecosystems (Wernberg *et al.*, 2011a; Harley *et al.*, 2012; Vergés *et al.*, 2014a; Straub *et al.*, 2016).

Kelps are cool-water organisms and kelp forests and other temperate to polar seaweed ecosystems are particularly under threat from direct and indirect effects of ocean warming (Figures 3.3.2 and 3.3.3) (Johnson *et al.*, 2011; Wernberg *et al.*, 2011a; Vergés *et al.*, 2014a). Globally many rocky reefs previously dominated by kelp forests have experienced regime-shifts due to warming in the past 2-3 decades, where kelps have been replaced by turfs or crustose coralline algae (Connell and Russell, 2010; Andersen *et al.*, 2011; Ling *et al.*, 2015). This has been observed in western Australia (Wernberg *et al.*, 2016a), Tasmania (Ling *et al.,* 2015), eastern Canada (Filbee-Dexter *et al.*, 2016), southern Norway (Andersen *et al.*, 2011; Moyand Christie, 2012) and northern Spain (Díez *et al.*, 2012; Voerman *et al.*, 2013).

In Nova Scotia, warming over several decades has exceeded the temperature threshold of the main canopy-forming seaweeds (*Saccharina latissima*, *Laminaria digitata*) causing an 85-99% decline in kelp forests and a shift to turf-dominated rocky reefs and invasive seaweeds (Filbee-Dexter *et al.*, 2016). Sediments are now stabilizing the new turf state, making it virtually irreversible (Filbee-Dexter *et al.*, 2016). A similar regime-shift has occurred in southern Norway, where sugar kelp (*Saccharina latissima*) (Figure 3.3.4) has been lost and replaced by filamentous seaweeds following decades of warming and eutrophication (Moyand Christie, 2012). In Norway most sugar kelp forests along the more sheltered areas disappeared in, 2002 after several warm summers, and a reduction in sugar kelp distribution has also been observed in Sweden, Denmark and Germany, with increased sea temperatures, nutrients and epiphytism, and particle levels suggested as the main reasons (Andersen *et al.*, 2011; Bekkby and Moy, 2011; Moy and Christie, 2012)

Figure 3.3.4 Sugar kelp (*Saccharina latissima*) and other filamentous brown algae. © SNH.

In contrast to changes seen over decades of gradual warming, in Western Australia kelp forests collapsed when extreme temperatures exceeded the physiological limit during a marine heatwave (Smale and Wernberg, 2013; Wernberg *et al.*, 2013b). Over a few months kelp (*Ecklonia radiata*) and strapweed (*Scytothalia dorycarpa*), an endemic fucoid, disappeared from extensive areas, causing a 100 km range contraction of both species and substantial re-configuration of the benthic ecosystem (Figures 3.3.2 and 3.3.3 A,B). These seaweeds have also been replaced by turfs, recovery being suppressed by herbivorous fishes (Bennett *et al.*, 2015a; Wernberg *et al.*, 2016a).

3.3.3.1 Physiological impacts

Seaweeds have a temperature range within which they can survive, and an optimum temperature where processes like growth and photosynthesis are reaching their maximum. These direct physiological effects of temperature are associated with the mechanics of cellular processes (protein stability, enzyme activity, membrane permeability, etc.) (Davison, 1991; Kordas *et al.*, 2011).

Temperature dependency of physiological performance has been documented for many seaweeds, including crayweed (*Phyllosphora comosa*), a temperate fucoid endemic to south-eastern Australia. Flukes *et al.* (2015) demonstrated how photosynthesis, growth and survival were negatively affected at current summer maximum temperatures. This implies that unless rapid adaptation occurs, continued warming of south-eastern Australia, which has been warming four times faster than the global average, will have strong negative impacts on the distribution and abundance of *P. comosa* (Flukes *et al.*, 2015). Similarly, reproduction (sporogenesis) in *Laminaria digitata*, (Figure 3.3.5) a summer reproductive kelp, was negatively affected during warm summers at Helgoland (Germany) indicating that reproduction is the limiting life cycle stage and that future summer warming could further restrict the distribution of this species (Bartsch *et al.*, 2013).

In most cases, however, warming is likely to be sublethal with physiological effects manifesting through altered requirements for, or availability of, resources such as light and nutrients or reduced capacity to respond to other perturbations. Photosynthesis and respiration rates in seaweeds are temperature dependent (Davison, 1991; Wiencke *et al.*, 2006; Staehrand Wernberg, 2009; Wernberg *et al.*, 2016b) and warming increases the light requirements to maintain a positive metabolic balance. This implies a reduction in depth of the compensation point and an increased sensitivity to reduced water quality (Staehr and Wernberg, 2009). Subtle differences in physiological performance breadth (temperature range over which net photosynthesis is greater than 80% of maximum, Eggert *et al.*, 2003; Wernberg *et al.*, 2016b) were found to correspond with differences in distribution as well as responses to a marine heatwave for three seaweeds along a temperature gradient in Western Australia (Wernberg *et al.*, 2016b). *Scytothalia dorycarpa* had a narrower performance breadth over cooler temperatures than *Sargassum fallax*; the species were distributed towards cooler and warmer latitudes, respectively and over three consecutive warm summers *S. fallax* populations expanded where *S. dorycarpa* populations perished or diminished (Smale and Wernberg, 2013; Wernberg *et al.*, 2016a).

Figure 3.3.5 *Laminaria digitata* exposed at extreme low water spring. © John M Baxter.

Warming-induced changes in nutrient and light availability have also been associated with changes in seaweed populations. For example, a dramatic 95% decline in Australian giant kelp (*Macrocystis pyrifera*) forests has been attributed to increasingly frequent incursions of warm nutrient poor water from the East Australia Current (Johnson *et al.*, 2011, Figure 3.3.3D), and in the Arctic warming has led to changes in abundance and depth distribution of several seaweeds, although the responses reflect a complex interaction between the opposing forces of reduced ice cover (more light) and glacial melt reducing salinity and increasing turbitidy (less light) (Krause-Jensen *et al.*, 2012; Bartsch *et al.*, 2016).

Most seaweeds can adjust their metabolic machinery to accommodate variation of temperature regimes

(Davison, 1991; Eggert, 2012). However, these changes can have consequences for the ability to respond to changes in other environmental factors. Sporophytes of the kelp *Ecklonia radiata* exhibit substantial differences in physiology under different climatic conditions with warm-adjusted kelp showing 50% lower photosynthetic rates and 90% lower respiration rates at optimal temperature in comparison to cool-adjusted kelps (Staehrand Wernberg, 2009). The kelp optimizes its metabolic balance under elevated temperatures through a reduction in the temperature sensitivity of photosynthesis and respiration (Wernberg *et al.*, 2010). However, these changes are linked to supressed capacity to respond physiologically to changes in light levels and disturbance regimes – and therefore lower kelp forest resilience - presumably because the cellular processes involved in temperature control also are critical to regulating responses to other conditions such as light levels (Wernberg *et al.*, 2010).

For some species warming might have a direct positive physiological effect but with negative indirect consequences. Endo *et al.* (2013) found that *Sargassum patens* had a higher growth rate under elevated temperatures, which led to lower phlorotannin (defensive compound) concentration in the upper parts of the thallus, making the apical meristems more palatable to herbivorous fishes feeding during warm summer temperatures. A similar effect was seen for the kelp *Agarum clathratum* in Nova Scotia (Simonson *et al.*, 2015). Overall, however, effects of temperature on the secondary chemistry of seaweeds are still poorly understood.

3.3.3.2 Impact on reproduction and early life-cycle stages

Life cycle events are often tightly cued to seasonal changes in environmental conditions and many seaweeds exhibit distinct temporal patterns in reproduction and recruitment, often with species- and life-stage specific temperature thresholds (Steinhoff *et al.*, 2011; Bartsch *et al.*, 2013; Mohring, 2013; Andrews *et al.*, 2014; Bennett *et al.*, 2015b).

Temperature-mediated mismatches in the timing of life cycle events could have substantial impacts on seaweeds. For example, the annual brown seaweed *Desmarestia viridis* accumulates sulphuric acid during growth from recruit to adult. Summer temperatures trigger a synchronized die-off by mass releases of sulphuric acid at the time of reproductive maturity (Gagnon *et al.*, 2013). However, *D. viridis* has a low temperature tolerance, and further warming could initiate die-off before reproductive maturity (Gagnon *et al.*, 2013).

Early life stages are usually more sensitive to warming than the later stages, and the thresholds for impact can be abrupt. For example, in Arctic Norway 98% of kelp zoospores (*Saccorhiza dermatodea*) germinated between 2-12°C, but above 12°C (the projected local temperature at the end of century) germination declined by 80% at 17°C (Steinhoff *et al.*, 2011). Similarly, in Tasmania early development of *Ecklonia radiata* gametophytes and sporophytes peaked between 15-22°C, but decreased above 22°C where no sporophytes developed (Mabin *et al.*, 2013). Temperature responses for early life stages sometimes reflect a trade-off between growth and survival. For germlings of *Fucus serratus* in Scotland (Figure 3.3.6), increasing temperature had a positive effect on growth while simultaneously also causing lower survival (Nielsen *et al.*, 2014). A similar response has also been reported for kelp (*E. radiata*) gametophytes in Australia, where gametophytes grown under warm conditions were larger but had lower survival than those grown under cool conditions (Mohring *et al.*, 2014).

Figure 3.3.6 *Fucus serratus.* © John M Baxter.

3.3.3.3 Impacts of herbivores

A widely documented consequence of ocean warming is the poleward range shift in the distribution of many marine taxa, including herbivorous fishes and sea urchins (Ling *et al.*, 2009a; Bates *et al.*, 2013; Feary *et al.*, 2014; Vergés *et al.*, 2014a; Figures 3.3.2 and 3.3.3D). The effects have been most pronounced where ocean current run poleward, pushing warm water and subtropical and tropical species towards temperate latitudes (e.g. western boundary currents, Vergés *et* *al.*, 2014a). Herbivorous fishes have traditionally been considered to play a minor role in structuring temperate benthic communities (Choat, 1982). However, evidence is emerging that range-expanding subtropical and tropical fishes are having strong impacts on ecologically important temperate seaweeds - overgrazing by tropical herbivores has been documented on temperate reefs in the Mediterranean Sea (Vergés *et al.*, 2014b), around Japan (Haraguchi *et al.*, 2009), and in Australia (Vergés *et al.*, 2014a; Bennett *et al.*, 2015a).

In the Mediterranean Sea, canopy seaweeds (*Sargassum vulagere* and *Cystoseira compressa*) have become 65% less abundant where two species of tropical rabbitfishes have become dominant (Vergés *et al.*, 2014b). In Japan, kelps (*Ecklonia cava*) declined due to the combined effects of ocean warming and fish and urchin herbivory (Haraguchi *et al.*, 2009) whereas in Western Australia subtropical and tropical herbivorous fishes have kept seaweeds from recovering after they were decimated by an extreme marine heatwave (Bennett *et al.*, 2015a; Wernberg *et al.*, 2016a; Figure 3.3.2). A common feature in these cases has been that herbivores have not simply increased in abundance but also in functional diversity; temperate fish were found to feed only on adult seaweeds, whereas new subtropical and tropical fishes such as rabbitfishes feed both on adult seaweed and on seaweed recruits (Vergés *et al.*, 2014b; Bennett *et al.*, 2015a).

Overgrazing can also occur by warm temperate species, as documented in Portugal where intense fish and urchin herbivory at a warm location restricted kelps to crevices with zero survival in open habitat. This contrasted with a cool location where herbivory was virtually absent (Franco *et al.*, 2015). In south-eastern Australia, the warm-temperate sea urchin *Centrostephanus rodgersii* expanded its range into Tasmania as a consequence of ocean warming. Here, populations expanded due to overfishing of urchin predators (large lobsters), triggering overgrazing resulting in widespread decimation of foliose seaweeds and establishment of extensive urchin barrens (Ling *et al.*, 2009b, 2015; Johnson *et al.*, 2011), which are characterized by low structural complexity and primary productivity, and low food web complexity) (Filbee-Dexter and Scheibling, 2014). Shifts from kelp forests to urchin barrens have also been observed in Canada, Norway, New Zealand and many other places (Filbee-Dexter and Scheibling, 2014 and references therein). In some systems barrens have existed for more than 40 years (Newfoundland, Canada), while other systems are undergoing repeated regime shifts between urchin barrens and kelp beds, either as a consequences of variation in top predators (sea otters, Aleutian Islands and California) or changing oceanographic conditions (California, Maine and northern Chile) (Filbee-Dexter and Scheibling, 2014 and references therein).

3.3.3.4 Interactions between warming and other stressors

Warming is arguably the most pervasive environmental stressor associated with global climate change. However, warming rarely operates independently of other regional and local conditions. Instead multiple stressors interact cumulatively and exposure to one stressor can affect the tolerance to another stressor (Campbell *et al.*, 2011; Wernberg *et al.*, 2011a; Nema *et al.*, 2012; O'Brien *et al.*, 2015; Simonson *et al.*, 2015, Xiao *et al.*, 2015).

Warming can reverse grazer-macroalgal interactions, and wave action and temperature have been found to have interactive effects on macroalgal assemblage structure (Mrowicki and O'Connor, 2015). Similarly, warming can affect the direction of interactions between seaweeds with competitive (negative) interactions under cool conditions and facilitative (positive) interactions under warm conditions (Wernberg *et al.*, 2010; Bennett and Wernberg, 2014; Bennett *et al.*, 2015c).

Studies in Nova Scotia have shown that warmer temperatures increase outbreaks of kelp encrusting bryozoans (*Membranipora membranacea*) (Saunders and Metaxas, 2008; Scheibling and Gagnon, 2009) as well as altering feeding and metabolic rate of herbivores (O'Connor, 2009). The cumulative effects of direct temperature damage to kelps, increased encrustation by bryozoans, which increases kelp fragmentation and reduces kelp reproduction, and higher herbivory rates resulted in weakened seaweeds that were more vulnerable to disturbances during storms (Chapman *et al.*, 2002; Simonson *et al.*, 2015).

Warming can also interact with other anthropogenic changes in the environment. High pCO_2 (ocean acidification) and elevated temperature can interact synergistically in their effects on early life stages of the giant kelp *Macrocystis pyrifera* with detrimental effects on germination and mortality of zoospores (Gaitán-Espitia *et al.*, 2014). Similarly, the cumulative effects of warming and UVB radiation have been found to severely inhibit growth and photosynthesis of three habitat-forming seaweeds (*Ecklonia radiata*, *Scytothalia dorycarpa*, *Sargassum* spp.) from Western Australia (Xiao *et al.*, 2015). Interestingly, responses showed that species-specific sensitivity and acclimation potential might alter the balance and competitiveness between these dominant canopy-formers in the future (Xiao *et al.*, 2015).

It is noteworthy, however, that warming is not always a stressor and that the combined effects of multiple stressors are not always negative. For example, in the Arctic, zoospores of the kelp *Alaria esculenta* were found to be less vulnerable to UV radiation in warm (7°C) compared to cold (2°C) conditions (Olischläger and Wiencke, 2013). Whether or not the cumulative effects of multiple stressors are agonistic or antagonistic likely depends on species, life stages, season or where in the tolerance range the stressors are. Importantly, a recent review of marine climate change experiments showed both an over-representation of single-factor studies and an under-representation of marine macrophytes including seaweeds (Wernberg *et al.*, 2012). Moreover, only very rarely do studies adopt a complete life cycle approach (Russell *et al.,* 2012) where the vulnerability of all life stages are assessed (see Bartsch *et al.*, 2013 for a rare example). This highlights strong knowledge gaps in the understanding of cumulative effects of multiple stressors on seaweeds, and what life stages will be limiting seaweed distribution and performance in the future.

3.3.3.5 Impacts of pathogens

It is expected that seaweed disease outbreaks will increase in occurrence and severity because ocean warming and other anthropogenic stressors make seaweeds more susceptible to opportunistic pathogens while also increasing their virulence (Gachon *et al.*, 2010; Campbell *et al.*, 2012; Egan *et al.*, 2014).

Warming has been linked to shifts in surface bacterial assemblages leading to bleaching and reduced levels of chemical defences in the red seaweed *Delisea pulchra*. (Campbell *et al.*, 2011). Similarly, microbial communities have been linked to bleaching in kelp (*Ecklonia radiata*) where bleached individuals suffered lower photosynthetic efficiency reducing overall kelp performance (Marzinelli *et al.*, 2015). In general, however, little is known about the role and prevalence of pathogens in natural seaweed populations (but see also Bengtsson *et al.*, (2012) and Campbell *et al.*, (2015).

3.3.3.6 Range shifts

To date, only one seaweed species has been declared globally extinct (Brodie *et al.*, 2009). However, the multitude of effects of warming on seaweed physiology and ecological interactions ultimately lead to changes in distribution as a consequence of local extinctions (Bates *et al.*, 2014). Several warming-related shifts in seaweeds distribution ranges have been documented globally (Sorte *et al.*, 2010; Wernberg *et al.*, 2011b, 2016a; Harley *et al.*, 2012; Poloczanska *et al.*, 2013; Straub *et al.*, 2016; Table 3.3.1). These range shifts have included both contractions at the equatorward range-edge, and expansions at the poleward range-edge (Straub *et al.*, 2016). It is noteworthy that range contractions and expansions are fundamentally different processes, and require substantially different evidence to document. Range contractions require the elimination of all individuals of a species whereas range expansions only require the successful establishment of one or a few individuals in a new habitat (Bates *et al.*, 2014). Contractions are often preceded by periods of declining abundance and failed recruitment while adult individuals persist in the unfavourable area (Hampe and Petit, 2005; Bates *et al.*, 2014), in other cases contractions can be abrupt, when temperatures greatly exceed thermal tolerances (Smale and Wernberg, 2013; Wernberg *et al.*, 2016a).

In northern Spain, range contractions have been reported for several canopy-forming seaweeds including *Fucus serratus* and *Himanthalia elongata* (Figure 3.3.7) which have shifted westwards in the Bay of Biscay in response to warming since the late, 19th Century (Duarte *et al.*, 2013b). *H. elongata* shifted 330 km over 120 years, whereas *F. serratus* shifted, 197 km over 114 years and also declined dramatically in abundance in its remaining range. For both species the rate of contraction

Figure 3.3.7 *Fucus serratus* and *Himanthalia elongata* luxuriant growth on shore in Orkney. © John M Baxter.

Table 3.3.1 Summary statistics for recently observed climate-driven range-shifting seaweeds. The taxa listed are those for which sufficient data exists to estimate range-shift distance and speed (from Straub *et al.,* 2016)

	Extension (22 taxa)	**Contraction (n=9 taxa)**
Median shift (range)	192 km (26 – 593)	116 km (35-1250)
Median time (range)	50 years (2 – 75)	31 years (1- 66)
Taxa (n=41)	*Ahnfeltia plicata* *Bifurcaria bifurcata* *Chondrus crispus* *Codium adhaerens* *Desmarestia aculeata* *Desmarestia ligulata* *Dumontia contorta* *Ecklonia maxima* *Fucus serratus* *Fucus vesiculosus* *Halidrys siliquosa* *Halopithys incurva* *Himanthalia elongata* *Hypnea musciformis* *Laminaria ochroleuca* *Padina pavonica* *Palmaria palmata* *Pelvetia canaliculata* *Sargassum flavifolium* *Sargassum illicifolium* *Turbinaria ornata* *Valonia utricularis*	*Assemblage (collection of species)* *Durvillea potatorum* *Ecklonia radiata* *Fucus serratus* *Fucus vesiculosus* *Himanthalia elongata* *Sargassum micracanthum* *Sargassum yamamotoi* *Scytothalia dorycarpa*

appears to have accelerated in recent years (Duarte *et al.*, 2013b). The ecological implications of these two range contractions are largely unknown (Duarte *et al.*, 2013b), although both species (and several other large, retreating canopy-forming seaweeds) are important habitat-formers for smaller epiphytes and mobile animals (Hawkins and Hartnoll, 1985; Wernberg *et al.*, 2004; Ingólfsson, 2008; Thomsen *et al.*, 2010).

The warm-water kelp *Laminaria ochroleuca* was first recorded in England in 1948, and subsequently expanded its range eastwards to the Isle of Wright at a rate of 5.4 km per year, as well as expanded northwards to Lundy Island at a rate of 2.5 km per year (Straub *et al.*, 2016). Recent re-surveys of the inhabited area suggest that *L. ochroleuca* also expanded from the initially colonized sheltered coastline to moderately wave-exposed open coasts, accompanied by a significant increase in abundance, most likely in response to recent warming (Smale *et al.*, 2014). In the area where *L. ochroleuca* most recently colonized, it competes with the native dominant *L. hyperborea*. As both species appear morphologically and functionally similar, it was initially assumed they would have similar ecosystem function with little impact on the colonized ecosystem (Terazono *et al.*, 2012). However, even small morphological differences may incur large cascading ecosystem effects. For example, Smale *et al.* (2014) showed that epiphyte load on the smoother stipe of *L. ochroleuca* was dramatically lower than on the rough stipes of *L. hyperborea* (Figure 3.3.8). Thus, a reduction of the epiphytic habitat can be expected if *L. ochroleuca* replaces *L. hyperborea*, potentially with dramatic effects on associated fauna (Christie *et al.*, 2009),

Figure 3.3.8 Heavy epiphytic growth on the stipes and fronds of *Laminaria hyperborea*. © SNH.

trophic interactions (Smale *et al.*, 2014) and biodiversity (Thomsen *et al.*, 2010).

These range shifts are potentially irreversible with great impacts on ecosystems (Madin *et al.*, 2012; Wernberg *et al.*, 2016a). Additionally, species where there is no suitable habitat at their cold range limits will be particularly vulnerable to warming as they can only contract, but not expand their range as no new colonization is possible (Burrows *et al.*, 2011, 2014). This also poses the risk of range contractions leading to extinctions where endemic species run out of habitat. This is a particularly important issue in the southern hemisphere where there are no sub-Antarctic landmasses (Wernberg *et al.*, 2011b). An often overlooked consequence of range-contractions is the risk of losing genetic diversity. Several European seaweeds have a disproportionally large fraction of their genetic diversity concentrated at their warm range-edge (a consequence of glacial refugia) (Provan and Maggs, 2012).These unique genetic linages are threatened by local extinctions of the species. For example, while the persistence of the canopy-forming seaweed *Bifurcaria bifurcata* is not threatened, local extinction in Morocco, which is expected by the end of the century, would cause a reduction in global genetic diversity of this species (Neiva *et al.*, 2015). Another example is the seaweed *Fucus vesiculosus*, where local extinctions at its southern range edge in the eastern Atlantic have been documented over the past 30 years, causing the loss of several genetic lineages (Assis *et al.*, 2014). Similarly, for the red seaweed *Chondrus crispus*, where a unique genetic diversity in rear-edge populations in Iberia are in danger of local extinction due to ongoing warming, thus affecting their overall genetic diversity (Provan and Maggs, 2012). All studies concluded that loss of unique lineages, reducing the genetic pool of the seaweeds, compromises their adaptive potential to respond to future warming and interactive stressors (Provan and Maggs, 2012; Assis and Perrin, 2014; Neiva *et al.*, 2015).

A critical problem is that information on species' range boundaries is scarce and largely qualitative due to lack of baseline information and regular surveys (Wernberg *et al.*, 2011a; Bates *et al.*, 2015; Marcelino and Verbruggen, 2015; Straub *et al.*, 2016).

3.3.4 Conclusions and recommendations

There is overwhelming evidence that seaweeds are impacted by ocean warming globally, affecting species as well as associated communities, altering whole ecosystems with likely substantial impacts on valuable ecosystem services.

Effects include direct physiological limitations of metabolism and reproduction as well as indirect effects mediated through changes in ecological interactions such as herbivory and competition. The relative importance of direct physiological effects and indirect effects through other abiotic pathways and species interactions is still poorly understood. It is also clear that warming often compounds effects of other natural and anthropogenic stressors magnifying their effects. Still, only relatively few studies have tested the effects on seaweeds of warming in combination with other factors and rarely has the vulnerability of all life stages been tested. It is recommended that more studies attempt to isolate the mechanisms that drive changes in seaweed populations, especially to distinguish direct from indirect effects of warming and the role of multiple stressors. It is also recommended that more studies adopt a complete life-cycle approach to identify which life stages will be limiting the distribution and performance of seaweed populations in the future.

There is substantial evidence from several continents that warming affects the biogeography of seaweeds, but changes in distribution are often hard to establish due to lack of consistent high resolution baseline information. Some regions, such as South America, are greatly under-represented. This is likely a consequence of data deficiency. It is recommended that more effort is directed to establishing and monitoring species abundances and boundaries to enable early detection of changes.

The long-term ecological and economic consequences of warming are still to be realized for most seaweed dominated systems. The impacts are, however, likely to be substantial considering the array of ecological functions and ecosystem services provided by seaweeds. There are however substantial knowledge-gaps around the variety of ecological services seaweed systems provide and, in particular, the values these services contribute to local and regional economies. It is recommended that more studies establish the nature and value of ecological functions seaweeds provide to better understand the flow-on effects on humans of warming-mediated changes in seaweed communities.

To date there has been limited focus on solutions and mitigation options. It is recommended that more studies focus on solutions by investigating opportunities for maintaining ecological functions through species replacements (i.e. establish ecological redundancy among different seaweeds) or boosting resilience of cool-adapted populations through assisted *a priori* breeding with warm-adapted populations. Similarly, the viability of reducing impacts of warming by managing additional local stressors such as eutrophication, pollution and overfishing requires more attention. Finally, it is recommended that rehabilitation programmes be developed and their viability tested.

3.3.5 References

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“Mangroves are invading marsh-dominated ecosystems around the world, representing one of the most dramatic plant range shifts occurring today.”

“Changes in plant production caused directly by temperature or indirectly by species shifts will fundamentally alter carbon cycling and storage.”

Section 3.4 authors

3.4 Impacts and effects of ocean warming on tidal marsh and tidal freshwater forest ecosystems

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Summary

- Tidal wetland responses to warming involve complex feedbacks between plants, microbes and physical processes, the balance of which will ultimately determine if these ecosystems can keep pace with accelerated sea-level rise.
- Plant primary production is likely to increase with warming based on evidence from latitudinal gradients of tidal marsh biomass and experimental manipulations.
- Rates of decomposition are likely to increase based on first principles and lab incubations, but microbial responses to temperature are poorly characterized and confidence in this forecast is low.
- Models suggest that the net effect of warming on marsh carbon sequestration and the capacity to keep pace with relative sea-level rise will be small and related primarily to the indirect effect of temperature on rates of sea-level rise.
- Temperature-driven displacement of tidal marsh plants by mangrove trees will increase carbon sequestration at the boundaries of these ecosystems.
- Temperature will increase methane emissions through a combination of direct effects on the micro-organisms that produce methane and indirect effects on micro-organisms that consume methane or compete with methane producing microbes.

Ocean warming effect	Consequences
Warming air and soil temperatures, longer growing seasons, and higher minimum temperatures	Low latitude salt marsh distributions decline due to conversion to mangrove forest, while high latitude marshes expand onto mud flat Because marsh species respond individually, future community composition is uncertain Increased plant production likely, which will generally improve ecosystem services Decomposition rate change is highly uncertain, but will affect marsh vulnerability to sea-level rise Carbon sequestration may increase This is highly uncertain, but affects marsh vulnerability to sea-level rise Methane emissions have a high likelihood of increasing, which affects climate-motivated restoration activities
Accelerated sea level rise and increasing salinity	Decreased tidal wetland area due to conversion to open water. Highly uncertain due to limited information on marsh ability to grow vertically and migrate inland Tidal freshwater forest area declines due to salinity intrusion and geomorphic constraints
Warming-driven decline in tidal wetland area, higher inundation frequency, and plant community composition change	Wildlife will be affected by changes in marsh area, habitat type and inundation frequency

3.4.1 Introduction and background

The boundary of land and sea typically appears as a sharp line on maps, but is in fact a dynamic boundary that rises and falls daily with the tides, annually with sea level, and at decadal or millennial timescales with relative sea level. Coastal wetlands occur in this dynamic, intertidal zone where they provide a wide variety of ecosystem services including habitat for aquatic and terrestrial wildlife, nutrient removal, protection of human infrastructure from storm surge, and carbon sequestration. These services arise from complex ecological interactions between tidal wetland plants, microbes, animals, hydrology and geomorphology that collectively describe the ecology of tidal wetland ecosystems. All biogeochemical processes respond to temperature, but biological responses to warming are expected to be particularly consequential for the future of tidal wetland ecosystem services.

Carbon cycling is a phenomenon that reflects important ecological characteristics of a tidal wetland such as plant community composition, nutrient availability, primary production, decomposition rates, and herbivory. Carbon cycling also reflects hydrological and geomorphic features that ultimately regulate the biology and factor into the stability of marshes against accelerated sea-level rise, such as flooding frequency and the mineral sediment supply. This section focuses on carbon cycling because it weaves together key aspects of the ecology and management of both tidal marshes and tidal freshwater forests.

Tidal marshes are global hotspots of carbon storage and one of three ecosystems that combine to account for about half of the total marine soil carbon stocks (Duarte *et al*., 2005). Globally, intertidal marshes, mangroves and seagrass meadows bury carbon at rates roughly equivalent to terrestrial forests (McLeod *et al.,* 2011). The global area of tidal wetlands is much smaller than that of forests, but ecological, hydrological and geological factors combine to help tidal wetland build large carbon stocks in a smaller area (Alongi *et al.,* 2014). This feature makes tidal wetlands particularly attractive for climate mitigation activities (Howard *et al.*, in press). As sea-level rise accelerates, coastal wetlands have the potential to sequester soil carbon at an increasingly rapid pace provided that plants survive flooding and continue to build soil elevation.

Despite the extraordinary leverage these ecosystems exert over the global carbon cycle, the dynamics of coastal wetland carbon pools are not presently represented in earth system models. Compared to upland soils, the sequestration potential of tidal wetland soils is extremely high because rising sea level gradually increases the potential soil volume, and the rate at which carbon is transferred to deeper, more anoxic soil horizons. Thus, tidal wetlands are not subject to the limits on carbon storage typical of upland soils. Coastal wetlands have only recently been recognized as important carbon sinks, and therefore the response of carbon cycling to climate change in tidal wetlands is largely unexplored. The future sink strength and carbon stock stability of these systems is uncertain because global change drivers such as temperature and elevated CO_2 perturb the complex biotic and abiotic feedbacks that drive high rates of soil carbon sequestration, and biogeochemical processes such as decomposition, methane (CH_4) emissions and hydrologic export. Thus, an important reason to study the effects of warming on coastal wetlands is to understand the stability of soil carbon pools, and to determine whether these important ecosystems will continue to gain elevation via carbon sequestration as rates of sea-level rise accelerate.

3.4.1.1 Global and regional significance

Coastal blue carbon ecosystems occupy the intertidal margins of shorelines worldwide, extending from the freshwater tidal rivers downstream to shallow coastal waters that support emergent or submerged vascular plants. The presence of vascular plants distinguishes these coastal ecosystems from ocean blue carbon systems, which are dominated by phytoplankton and tend to support relatively low rates of primary production and carbon burial. This distinction has biogeochemical significance because the combination of high rates of plant production, low rates of decomposition, and sea-level rise explains the high rates of carbon sequestration and large area-based carbon stocks found in tidal wetlands and seagrass beds (Kirwan and Megonigal, 2013). These processes occur largely independently of salinity which is the reason salinity regimes are not a formal part of the definition of coastal blue carbon ecosystems.

Tidal marshes are the subset of coastal wetland blue carbon ecosystems dominated by either herbaceous plant species or mixtures of herbaceous plants and shrubs, and are found across the full range of salinity regimes from tidal freshwater to tidal hypersaline (Figure 3.4.1). In tidal freshwater areas and at relatively high soil elevations, tree species can replace herbaceous species creating tidal freshwater forest. Mangrove forests are found in tropical and subtropical climates where they occupy all intertidal areas regardless of salinity (see Section 3.6). The distinction between woody and herbaceous vegetation is important from both a wildlife habitat perspective and a carbon perspective because woody biomass can be a long-term (i.e. decadal- or century-scale) carbon sink. It is common

Figure 3.4.1 The global distribution of salt marshes and relative abundance. Saltmarshes are far less abundant in the tropics (areas in grey) where mangroves dominate. An interactive version can be found at http://maps.tnc.org/globalmaps.html. Hoekstra *et al.,* 2010.

to discriminate between shrubs and trees because the difference in stature has consequences for ecological processes generally, and for the size of aboveground carbon sinks specifically. There are many ways to separate the two classes but a common approach is based on height and/or diameter. For example, the US Forest Service defines trees as > 4.6 m in height and >7.6 cm in diameter, and smaller woody plants as shrubs (US Forest Service).

Tidal marshes and tidal wetland forests occur worldwide, but they are most extensive in temperate climates (Figure 3.4.1). Saltmarshes are far less abundant in tropic and subtropical regions where mangrove forests occur. The major global distributions of mangrove forest and tidal marshes intersect at subtropical latitudes (Ghiri *et al.,* 2011), which represents the limit of temperature tolerance for mangrove tree species. Mangrove forests are presently expanding into tidal marshes at the historical mangrove-marsh ecotone where their distributions overlap (Saintilan *et al.,* 2014), a phenomenon linked to warming and which has important implications for carbon sequestration (Doughty *et al.,* 2015).

3.4.1.2 Trends and impacts

Global air temperatures are projected to rise 0.3-4.8°C by 2100, a range of outcomes that varies with assumptions about future greenhouse gas emissions (IPCC, 2014). Warmer air temperatures will cause water bodies and soils to also warm. Over time this means that soil temperatures will rise to many tens of metres depth (Huang *et al.,* 2000), a possibility that has particularly important implications for tidal marshes with highly organic soils that can be several metres deep.

The direct effects of warming are accompanied by the direct effects of rising CO_2 levels on plants and a variety of indirect effects such as rising sea level. Carbon dioxide concentrations are projected to continue rising and may exceed 700 ppm by the year 2100 (IPCC, 2014). There is evidence that elevated CO_2 acting alone can help stabilize tidal marshes by increasing elevation gain, primarily through root production (Langley *et al.,* 2010). Warming may either reinforce or negate the effects of elevated CO_2 on elevation, but there is little known about how the two global change factors interact in tidal marshes or tidal freshwater forests.

Rising temperatures are driving accelerated rates of sea-level rise. In addition, many sea coasts are experiencing land subsidence due to natural and anthropogenic phenomena that exacerbate sea-level rise by causing land to sink. The combination of these effects (i.e. relative sea-level rise) tends to increase the frequency of tidal inundation, which in turn changes plant community composition and wildlife habitat value (Krauss *et al.,* 2009; Swanson *et al.*, 2014). When increasing rates of relative sea-level rise cross a poorly-understood critical threshold, tidal marshes and forests are threatened with conversion to open water (Cadol *et al.,* 2013).

The two largest components of sea-level rise are additions of water from land-grounded ice sheets and the thermal expansion of ocean waters. Local sea level trends deviate from the global mean change because of factors including rising or sinking of land, dynamic responses of ocean currents, gravitation effects of glaciers, terrestrial water storage change and to a lesser effect changes in atmospheric pressure (Carson *et al.,* 2016). The capacity of a marsh to respond to sea-level rise depends upon the availability of mineral and organic material to build soil and the availability of space for wetlands to migrate landwards with sea-level rise (Morris *et al.,* 2002; Orr *et al*., 2003; Kirwan *et al.,* 2010; Spencer *et al.,* 2016).

3.4.2 Consequences

Warming is expected to influence the aboveground and belowground feedback loops that regulate soil carbon sequestration, elevation gain, methane emissions and hydrologic export of carbon and nitrogen (Figure 3.4.2). Temperature effects on plant production will influence processes that regulate carbon inputs, outputs, and burial, with implications for soil carbon sequestration and marsh stability against sea-level rise. Changes in production will lead to different outcomes for ecosystem function depending on the relative responses of shoots versus roots. Changes in decomposition affect soil organic matter pools directly through mass loss, or indirectly through mass gain if increased soil organic matter decomposition increases nitrogen availability and therefore plant growth. Finally, changes in plant and microbial metabolism will have consequences for CH_4 emissions to the atmosphere, and dissolved or particulate forms of carbon and nitrogen to adjacent aquatic ecosystems.

3.4.2.1 Primary production

The effects of temperature on plant production has been explored through latitudinal gradients and experimental manipulations (Figure 3.4.3). All of the experimental manipulations to date have been through passive warming using chambers (Figure 3.4.3, left panel), which

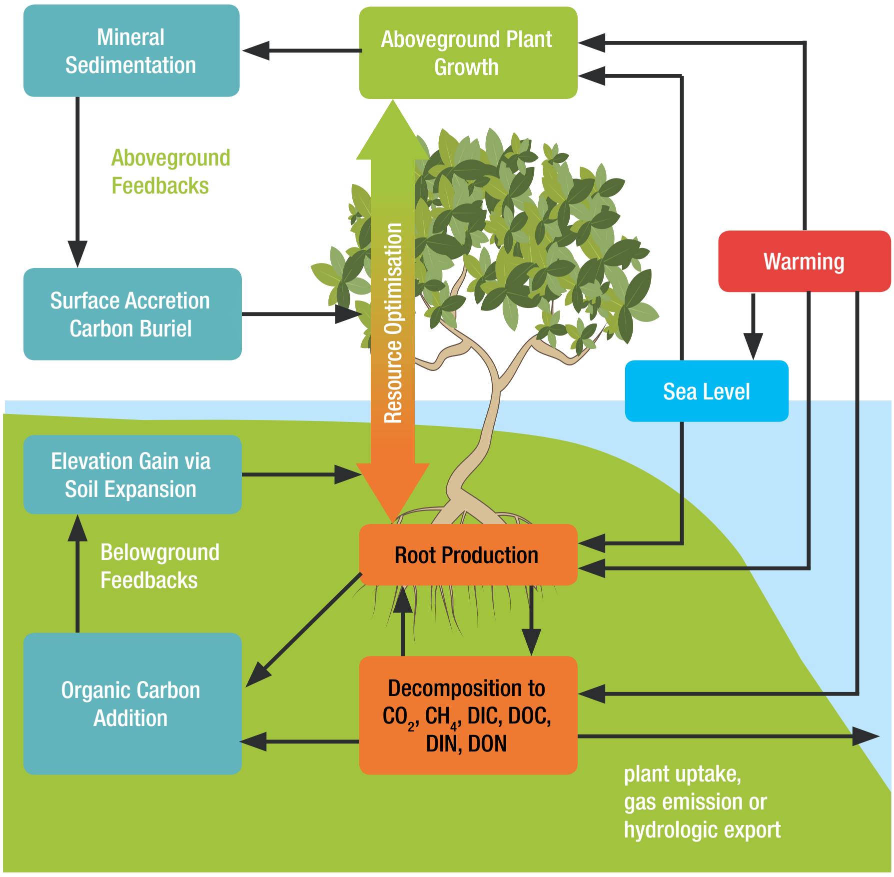

Figure 3.4.2 Conceptual model of temperature effects on key ecosystem processes that regulate carbon input, output, and burial, and export of CH_4 and dissolved forms of carbon and nitrogen. Modified from Kirwan and Megonigal (2013).

typically causes a 2-4°C increase in air temperature, but negligible changes in soil temperature. In general, warming tends to increase production rates (Gray and Mogg, 2001; Loebl *et al.,* 2006; Charles and Dukes, 2009; Gedan and Bertness, 2009), but the effects tend to be location or species specific. A latitudinal gradient of *Spartina alterniflora*-dominated saltmarshes showed an increase of 27 g m^{-2} yr^{-1} per 1°C increase in temperature (Kirwan *et al.,* 2009). Similarly, experimental air warming in a *S. alterniflora* marsh in NE United States suggests an increase in biomass on the order of about 50 g m^{-2} per degree of warming (Gedan *et al.,* 2010). Experimentally warming a *Spartina patens*-dominated NE United States saltmarsh also increased biomass (Gedan and Bertness, 2009), while warming a different NE United States saltmarsh increased biomass in some

Figure 3.4.3 Two approaches to experimentally warming tidal marsh ecosystems. Left: Chambers erected on a Florida USA saltmarsh raise air temperature by 2-3°C. The chamber has negligible effects on soil temperature. Right: A brackish marsh in Maryland USA is actively heated (1.7-5.1°C) aboveground by infrared lamps and belowground by cables to a depth of 1.5 metres. © Adam Langley (left) and Roy Rich (right).

Box 3.4.1 Species Interactions

Warming is expected to influence ecological interactions, but there are few experimental manipulations that test this hypothesis. Bertness and Ewanchuk (2012) studied the role of climate in regulating species interactions by transplanting nine locally common saltmarsh plant species into unvegetated mudflats on the north side (cool) and south side (warm) of Cape Cod, US. Soil surface temperature in the two regions differ by 2-3°C. Species were planted with and without neighbours. The presence of plant neighbours tended to improve growth rates on the south (warm) side of Cape Cod, but reduce growth rates on the north (cool) side of Cape Cod. This difference in plant interactions seemed to be mediated by the effects of temperature on soil salinity, both of which are greater in the southern sites. The study suggests that interspecific interactions can switch from competitive to facultative in a warming environment, which may help plant communities adapt to climate change. But this conclusion only applies in the aggregate. Another lesson of the study is that predicting the response of such interactions for a given plant species or plant functional group will be exceedingly difficult, limiting forecasts of warming on plant community composition.

species (e.g. *S. alterniflora*), but not others (e.g. *S. patens* and *Distichlis spicata*) (Charles and Dukes, 2009). By contrast, warming increased *D. spicata* biomass by ~250±70 g m^{-2} yr^{-1} (mean±SD, averaged over 2 years) in a SE United States brackish marsh, representing a doubling of saltmarsh plant biomass (Coldren *et al.,* 2016). These three *in-situ* warming experiments span a large latitudinal range. The observation that warmer air temperatures resulted in more plant growth in one or more plant species at each site indicates that saltmarsh plants may respond positively to warming across their full latitudinal range, and thus may exhibit increased carbon storage in a future, warmer climate.

Collectively these studies show that warming effects on plant biomass will vary among species, making it important to consider how warming will influence plant community composition. There is little research to judge the consequences of warming for organismal-level processes such as physiological adaptation to temperature; population-level processes such as reproduction, dispersal, and genetic selection; community-level processes such as interspecific competition and introduction of invasive species; or the ecosystem-level consequences of functional group shifts such as from herbaceous species to woody shrubs. Further research on these topics is needed to develop robust forecast models of tidal marsh and forest responses to warming.

3.4.2.2 Decomposition

Because most of the carbon stored in saltmarshes lies belowground, root biomass and organic matter decomposition responses to warming are both critical to understand yet more difficult to assess than aboveground responses. Though warming-induced increases in plant production are expected to increase carbon inputs to soils, warming may also stimulate microbial decomposition of organic matter.

Latitudinal gradient studies suggest that warming will increase decomposition rates at the same time it increases production (Kirwan *et al.,* 2009, 2014). The net effect of higher carbon input and output in the short term (decades) will be for warming to enhance carbon storage (Kirwan and Mudd, 2012). However, the long term effects of warming are more complex than latitudinal patterns suggest, and will be strongly mediated by sea-level rise and gradual increases in total soil-profile decomposition rates as carbon accumulates in the soil profile. Model simulations of a typical *Spartina alterniflora* marsh suggest that carbon storage is enhanced for several decades, followed by weakening and potentially declining carbon storage rates. This pattern is supported by two experimental manipulations of air temperature in New England marshes (Charles and Dukes, 2009; Gedan *et al.,* 2011), but these studies suggest that long-term ecosystem responses to warming will also be controlled by ecological interactions in the form of changes in plant functional groups (Charles and Dukes, 2009; Gedan *et al.,* 2011).

Changes in plant community composition are as important for decomposition rates as for productivity. Plants exert a strong control over soil organic matter decomposition rates in tidal wetlands (Mueller *et al*., 2015), but effects vary dramatically across plant species. For example, Bernal *et al.* (in revision) demonstrated that an invasive genotype of *Phragmites australis* can accelerate soil organic matter decomposition compared to rates in native North American plant communities. The result of shifting plant communities in response to warming and ensuing sea-level rise represents a large

Box 3.4.2 Plant Community Control of Soil Carbon Decomposition

Warming has the potential to destabilize soil organic matter pools by directly increasing rates of soil microbial decomposition or indirectly through changes in plant community composition. The plant-mediated indirect effects have received little attention. Bernal *et al*. (in revision) collected soil from a depth of 50-100 cm to test the effects of three plant species on the decomposition of a relatively old and stable pool of soil organic matter. A stable isotope technique allowed the influence of plants on decomposition to be separated into effects at the soil surface (0-40 cm depth) versus deep soil (40-80 cm depth). The presence of plants dramatically increased soil organic matter decomposition rate, most likely due to a combination of labile carbon and O_2 additions from plants (Mueller *et al.,* 2015). Plants also deepened the part of the soil profile where organic matter was lost, with 72% occurring at the soil surface in the absence of plants, but <44% in the presence of plants. These effects varied strongly across species. *Schoenoplectus americanus* enhanced soil organic matter decomposition at the soil surface, *Phragmites australis* enhanced decomposition at depth, and *Spartina patens* had no discernable effect on decomposition. Because *P. australis* is invasive in this study marsh and across the US, it seems that changes in plant community composition are fundamentally changing carbon dynamics and may lead to the loss of soil carbon. Warming may have similar effects through altered plant community composition.

A largely unexplored question is whether changes in salinity and associated increases in sulphate concentration will influence rates of soil organic matter decomposition (Sutton-Grier *et al.,* 2011). The limited evidence available is equivocal. In many cases sulphate addition has caused an increase in decomposition rates (Weston *et al.,* 2006). However, in a comparison of 10 wetland soils, D'Angelo and Reddy (1999) did not find a difference in decomposition rates under sulphate-reducing or methanogenic conditions. This may be explained by the fact that the terminal step in microbial respiration where sulphate acts does not necessarily control all of the earlier steps in organic matter degradation (Sutton-Grier *et al.,* 2011). There has been limited work on the impacts of different terminal electron acceptors on organic carbon mineralization in soils that differ in organic matter quality.

uncertainty for predicting future ecosystem carbon dynamics in tidal marshes and forests.

Initial attempts to measure the sensitivity of organic matter decomposition to warming in marshes range from no responses (Charles and Dukes, 2009) to responses that are larger than those reported in most terrestrial temperature response studies (Kirwan and Blum, 2011). Some models of the process have used a relatively high sensitivity (Q_{10}= 3.44), but more recent analyses suggest a much lower sensitivity to warming (Q_{10}=1.3-1.5, Kirwan *et al.,* 2014). Because the sensitivity of refractory carbon to warming has never been evaluated in coastal wetlands, the initial model assumed that both labile and refractory pools respond identically to warming, even though strong differences in temperature effects on labile versus recalcitrant have been observed (Frey *et al.,* 2013). Therefore, the precise response of soil carbon decomposition to warming represents a key knowledge gap, and new model experiments informed by field experiments are critical for accurate forecasts of coastal carbon cycling. It is important that warming experiments heat both aboveground and belowground portions of the ecosystem.

3.4.2.3 Microbial metabolism

Temperature accelerates enzymatic reactions that breakdown organic substrates. Indeed, this is the mechanism by which Arrhenius-based models traditionally forecast changes in soil carbon pools – generally declines – due to warming (Wieder *et al.,* 2013). More recent decomposition models incorporate mechanistic details of microbial population dynamics such as extracellular enzymes, carbon use efficiency (CUE), and turnover, with a wider range of outcomes from declines to gains in soil carbon (Hagerty *et al.,* 2014; Li *et al.,* 2014). These new models show that predicting changes in soil carbon pools in response to temperature requires detailed knowledge of microbial biomass, physiology and ecology, and that the understanding of these processes is not presently sufficient to predict whether warming will increase or decrease soil carbon pools.

Changes in microbial metabolism induced by temperature affect the efficiency with which organic matter is converted into microbial biomass, a property known as carbon use efficiency (CUE). Theoretically, warming should reduce CUE by changing the balance between energy production and biosynthesis; at higher temperature, the demand for cell maintenance energy increases, leaving less substrate for biosynthesis of new cell materials (Allison *et al.,* 2010; Manzoni *et al.,* 2012; Sinsabaugh *et al.,* 2013). However, experimental results are variable with some showing the expected decrease (DeVêvre and Horwáth, 2000; Steinweg *et al.,* 2008) and some find no effect of temperature on CUE (Dijkstra *et al.,* 2011; Hagerty *et al.,* 2014). By comparison, the turnover rate of microbial products does respond strongly to temperature (Hagerty *et al.,* 2014), indicating that it may be important to understand temperature effects on microbial growth as well as death. Microbial mortality is caused by predation and grazing by specialized bacteria and fungi, protozoa, nematodes, and other organisms making up the food web. Much less studied in soils is microbial turnover caused by viruses (Kimura *et al.,* 2008), which may be important as controls on microbial turnover in low and mid-latitude marine ecosystems (Fuhrman, 1999; Mojica *et al.,* 2016). The temperature sensitivity of CUE and its underlying biochemistry in terrestrial ecosystems have mostly been determined under aerobic conditions in mineral soils. Because tidal marshes and forests contain large stores of soil C, it is essential to consider fundamental microbial processes such as CUE and turnover.

3.4.2.4 Methane emissions

Methane (CH_4) emissions are an important feature of the tidal wetland carbon budget because CH_4 is a powerful greenhouse gas and relatively small rates of release can offset large rates of CO_2 sequestration (Poffenbarger *et al.,* 2011). Each gram of CH_4 released from a marsh into the atmosphere offsets 32-45 grams of sequestered CO_2 in terms of the climate impact of these gases (Neubauer and Megonigal, 2015). The balance between rates of CO_2 sequestration and CH_4 emissions is important to understand when the goal is to quantify the effects of an activity such as restoration, creation or management on greenhouse gases. Warming also has the potential to change the balance of CO_2 and CH_4 fluxes.

Subjecting anaerobic soils to a range of temperatures typically shows that warming will increase microbial production of CH_4 (Fung *et al.,* 1991; Meng *et al.,* 2012). Similarly, measuring CH_4 emissions in the field as temperature changes across seasons suggests that warming will increase CH_4 emissions from tidal wetlands (Dunfield *et al.,* 1993; Megonigal and Schlesinger, 2002; Yvon-Durocher *et al.,* 2014). However, the value of such studies is limited either by the absence of real field conditions (soil incubations) or by the assumption that seasonal variation is entirely due to temperature (field studies). Because of complex interactions between many processes, *in situ* temperature manipulation experiments are needed to determine whether warming will increase or decrease CH_4 emissions.

The effect of temperature on CH_4 emissions is more complex than the effect on CH_4 production alone for several reasons. One is that emissions of CH_4 are the net outcome of two separate microbial processes -- production and oxidation – that can have different temperature responses. Because the amount of CH_4 consumed in oxidation can exceed the amount emitted (Megonigal and Schlesinger, 2002), both must be considered in predictions of future CH_4 emissions. The few Q_{10} values reported for CH_4 oxidation are near 2.0, a value similar to other aerobic biochemical processes. The Q_{10} values reported for net CH_4 emissions in field and laboratory studies are often much higher (Dunfield *et al.,* 1993). Megonigal (1996) proposed that even a modest difference in the apparent activation energy (equivalent to Q_{10}) of CH_4 production (60 kJ mol^{-1}) versus oxidation (50 kJ mol^{-1}) causes CH_4 oxidation to consume an increasingly smaller fraction of CH_4 production as soils warm (Figure 3.4.4). The implication is that warming may increase CH_4 emissions from tidal marshes by decreasing percent of CH_4 oxidation.

In principle, warming can influence CH_4 emissions indirectly by affecting other coupled aerobic-anaerobic processes that regulate CH_4 emissions. Methanogens

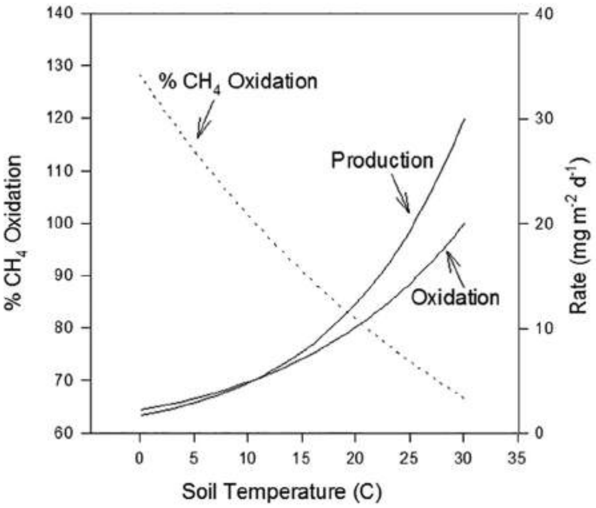

Figure 3.4.4 A model illustrating the potential for CH_4 oxidation to decline as a fraction of methane production with increasing temperature (Megonigal, 1996).

compete with a variety of other micro-organisms for the organic compounds that support respiration (Megonigal *et al.*, 2004). These organisms generally outcompete the methanogens and suppress CH_4 production wherever there is an abundance of nitrate (denitrifying bacteria), oxidized iron (iron-reducing bacteria) or sulphate (sulphate-reducing bacteria) (Neubauer *et al.,* 2005). Bullock *et al.* (2013) demonstrated that rising temperature increases iron reduction rates more than iron oxidation rates, with the result that the abundance of iron oxides declines with warming. Thus, warming may cause increased rates of CH_4 production by releasing methanogens from competition with iron-reducing bacteria.

Climate warming will also change CH_4 emissions through other indirect mechanisms that regulate the supply of metabolism-regulating compounds. Methane production is sensitive to the supply and quality of organic carbon (Megonigal and Schlesinger, 1997; Vann and Megonigal, 2003; Mozdzer and Megonigal, 2012), which can change through temperature-driven changes in plant growth or plant species replacement (Gough and Grace, 1998; Baldwin *et al.,* 2001; Langley and Megonigal, 2010; Mueller *et al.,* 2016). Sea-level rise will increase the supply of sulphate - a critical substrate for the respiration of sulphate-reducing bacteria – which typically outcompete methanogens for organic compounds, thereby suppressing CH_4 production (Neubauer *et al.,* 2005; Weston *et al.,* 2006).

3.4.2.5 Model forecasts

Numerical models are one approach to forecasting temperature effects on tidal marsh elevation and carbon sequestration. There are several robust tidal marsh elevation models (Fagherazzi *et al.,* 2012), but only a few attempt to mechanistically model soil organic matter (SOM) accumulation. The Callaway model (Callaway *et al.,* 1996; Callaway and Takekawa, 2013) and the modification named WARMER (Swanson *et al.,* 2014) simulate burial by varying SOM decay rates as a function of age and soil depth, but there are no feedbacks of temperature or flood duration on decomposition rate. The Marsh Equilibrium Model (MEM) of Morris *et al.* (2002) and similar models add a constant fraction of annual primary production to the SOM pool, which means that SOM storage (the inverse of decomposition) effectively varies only indirectly as a function of flooding on plant production. The Kirwan and Mudd (2012) marsh elevation-carbon model is the only model in this group to date in which SOM decomposition rates respond to temperature.

Kirwan and Mudd (2012) simulated the response of a tidal marsh to a step change in air and soil temperature (Figure 3.4.5). The model was parameterized for a tidal marsh dominated by *Spartina alterniflora* in a setting with low suspended sediment concentrations and a constant rate of sea-level rise. The model found that warming increased soil carbon accumulation rates in the years immediately following a sudden increase in temperature. Warming increased plant productivity, which led to enhanced mineral deposition rates, soil elevation gain, and soil organic matter accumulation. However, several factors caused the initial increase in accumulation to decline over time. Enhanced soil carbon sequestration led to a larger absolute soil carbon pool over time, and thus a steady increase in the absolute amount of carbon lost to decomposition. At the same time, gains in marsh surface elevation became too high for optimum plant growth. The net result of these changes was that warming had little impact on net carbon gain after a century in the model runs with both plant and decomposition effects (Figure 3.4.5, black line; Kirwan and Mudd, 2012). Warming increased organic matter accumulation more when the decomposition response was taken out of the model, highlighting the need for research on decomposition responses to temperature, which are poorly understood (Kirwan and Megonigal, 2013).

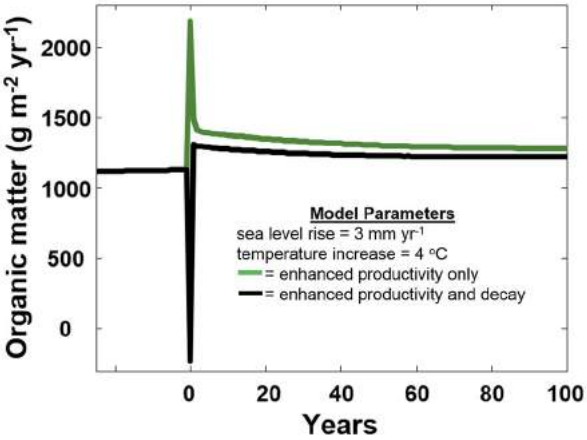

Figure 3.4.5 Modelled response of organic matter sequestration to an instantaneous 4°C increase at year 0 and a constant rate of sea-level rise. The black line is the effect of warming on both plant growth and microbial decomposition; the green line is with warming of plant growth only (i.e. no warming of decomposition). The sharp change in accumulation at year 0 is a model artifact arising from an immediate increase in decomposition, but a one year lag before the enhanced plant growth reaches the soil profile in the model. Adapted from Kirwan and Mudd (2012).

Box 3.4.3 Carbon Consequences of Mangrove Displacement of Tidal Marsh

Perhaps the clearest evidence of warming impacts on tidal marshes are studies that show ongoing mangrove displacement of tidal marsh. Kelleway *et al.* (2016) quantified the lateral encroachment of mangroves into two south-eastern Australian saltmarshes over a period of 70 years. Mangrove encroachment increased aboveground biomass as expected due to the accumulation of woody biomass, but most of the increase in stocks was due to higher rates of soil carbon sequestration which added as much as 230 Mg C km^{-2} yr^{-1}. This is one example of a mechanism by which warming may increase carbon storage it tidal wetland, thereby counteracting global warming.

The Kirwan and Mudd (2012) model forecasts that the positive impact of temperature on *S. alterniflora* production increases with the rate of sea-level rise. This behaviour arises for three reasons. First, plant productivity increases with inundation frequency, so proportional increases in growth caused by warming are larger in absolute terms when the rate of sea-level rise is faster. Second, faster rates of sea-level rise tend to offset gains in surface elevation that would otherwise decrease inundation frequency and eventually limit primary production. Third, sea-level rise enhances elevation gain (i.e. increase in soil volume) through sediment deposition, so that the carbon concentration in the soil profile and its impact on decomposition is reduced (Mudd *et al.,* 2009; Kirwan and Mudd, 2012). However, these model results are based on simple parameterizations that apply to a specific wetland type, and they remain untested in natural environments.

3.4.2.6 Mangrove invasion of tidal marsh

Mangroves are invading marsh-dominated ecosystems around the world (Figure 3.4.6), representing one of the most dramatic plant range shifts occurring today (Perry and Mendelsshon, 2009; Doyle *et al.,* 2010; Record *et al.,* 2013; Saintalin *et al.,* 2014) and indicating that carbon storage changes are already occurring (Kelleway *et al.*, 2016) or imminent (Doughty *et al.,* 2015). The expansion of mangroves into higher latitudes on a global scale is driven predominantly by declining frequency of severe freeze events (Osland *et al.,* 2013; Cavanaugh *et al.,* 2014). For example, in North America, the black mangrove, *Avicennia germinans*, intermingles with salt marsh species and can expand its distribution during freeze-free intervals (Stevens *et al.,* 2006) or when saltmarsh vegetation is stressed or killed (McKee *et al.,* 2004). Though air temperatures drive global patterns of mangrove expansion, finer-scale changes in mangrove extent respond to many other environmental factors such as erosion, land subsidence and accretion (Giri and Long, 2014). Thus, some mangrove expansion may be due to re-emergence from previous populations that had disappeared due to disturbance. Regardless, the declining frequency of freeze-related disturbances has generated an overall trend of poleward mangrove range expansion (Saintilan *et al.,* 2014; Section 3.6). Woody mangroves encroaching into herbaceous marshes will likely significantly increase wetland carbon storage at these ecotones between temperate marshes and tropical mangroves.

Figure 3.4.6 Young mangrove seedlings establish in a tidal marsh previously dominated by grasses. © Adam Langley.

Mangrove area in south-eastern Florida (US) has doubled over the past three decades at the northern edge of the historical mangrove range, with a corresponding loss of salt marsh (Cavanaugh *et al.,* 2014). Mangroves are also expanding into vast areas of marshland on the Louisiana and Texas US coasts (Comeaux *et al.,* 2012; Osland *et al.,* 2013), rendering a large portion of the US coastline subject to dramatic change in the next few decades. At a site in north-eastern Florida, Doughty *et al.* (2015) showed that mangrove area increased by 69% in only 7 years (Figure 3.4.7). This increase in mangroves also created a 25% increase in carbon storage over the landscape in less than a decade (Doughty *et al.,* 2015). Though extreme climatic events (reduction of freezes) are driving wetland plant

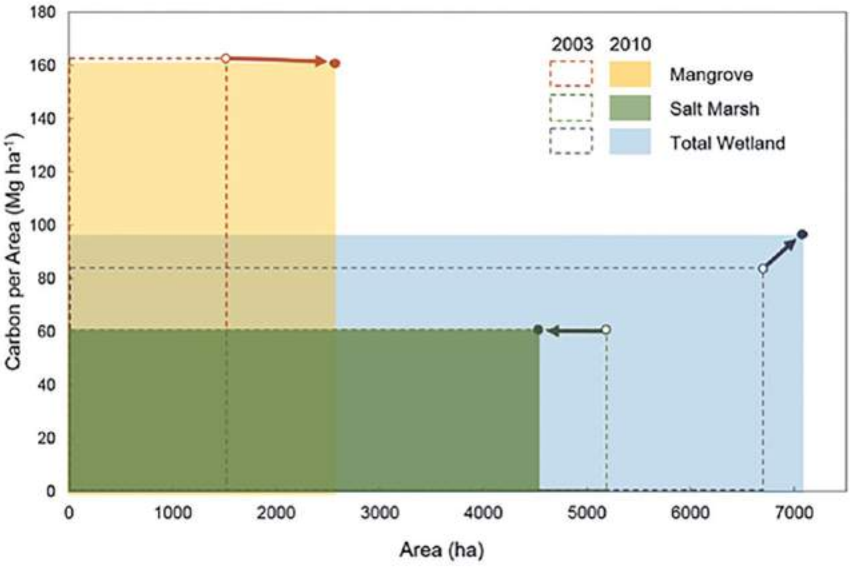

Figure 3.4.7 Carbon storage increases in Florida, US mangrove-marsh ecosystems due to mangrove encroachment. Taken from Doughty *et al.* (2015).

community composition changes, chronic warming will likely continue to alter the carbon sequestration potential of these rapidly shifting ecotones. Root dynamics in transitional wetlands are of particular interest because mangrove roots can potentially oxygenate the soil more than marsh roots, increasing microbial decomposition of organic matter and increasing carbon release (Tran and Chapman, unpublished data). Understanding these dynamics is an important challenge especially where organic matter is a driver of surface elevation maintenance to SLR. As coastal ecosystems provide some of the highest carbon sequestration rates on earth, understanding their shifting carbon storage capacity, particularly with rising seas, holds particular importance (Chmura *et al.,* 2003; Donato *et al.,* 2011).

3.4.2.7 Sea-level rise

Temperature is a major driver of accelerated sea-level rise. The impact of sea-level rise on tidal wetlands is to shift spatial boundaries, the vertical and horizontal ranges in the coastal zone that wetlands occupy. The response of an individual wetland to sea-level rise is nested within the larger landscape response as estuaries, open coasts, barrier systems and other large landforms adjust to the changing balance between increased wave energy (including tides) and the redistribution of sediment (Pethick and Crooks, 2000). If tidal wetlands are unable to adjust to this progressive and accelerating shift, they will drown out and transition to subtidal habitat such as mud flat or seagrass meadows.

The persistence of tidal wetlands in the face of accelerated sea-level rise is favoured by a high mineral sediment supply and low slopes. Settings with low sediment supply and limited space for marshes to migrate to will see a progressive conversion of vegetated wetland area to mudflat and open water (Spencer *et al.,* 2016). Numerical models suggest that tidal range also regulates the transition from a stable to unstable marsh by setting the elevation range over which plants can grow (Kirwan and Megonigal, 2013). Relative sea-level rise is most rapid in large river deltas and other areas of rapid subsidence (Kirwan and Megonigal, 2013). Thus, the most sensitive marshes to sea-level rise are those with rapid relative sea-level rise, and small tidal ranges and sediment inputs. Though there is a great deal known about the processes by which tidal marshes gain elevation, large gaps remain in our understanding about how these interact with hydrogeomorphic phenomena and land use patterns at large spatial scales. As a result, current forecasts of marsh loss due to sea-level rise may be overestimated (Kirwan *et al.*, 2016). Tidal freshwater marshes and forests as a rule occur at the head of tidal rivers where the nearby uplands have relatively slopes. As a result of this geomorphic setting, these systems may be particularly vulnerable to loss of area with accelerated sea-level rise.

3.4.2.8 Organismal, population and community responses

Warming is expected to cause changes in the distribution and abundance of tidal marsh plants and animals (Figure 3.4.8). Many tidal marsh plant species presently exist across large gradients of latitude, suggesting there is potential for individual species or genotypes to adapt to warming. It is reasonable to expect heat-tolerant plant species to expand into higher latitudes and cold-adapted plant species to contract in area (Adam, 2002; Mustin *et al.,* 2007). The physiological potential

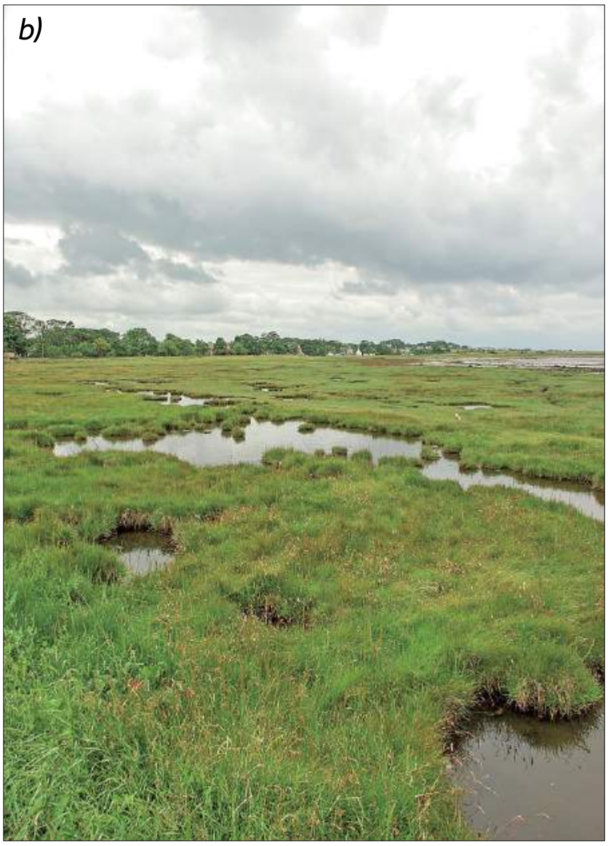

Figure 3.4.8 a) Geese fly over a tidal marsh. © Matt Kirwan.
b) Fringing salt marsh in Firth of Forth, Scotland. © John M Baxter.

of heat-tolerant plant species to migrate may fail to be realized if there are physical or ecological barriers to dispersal. Physical barriers include habitat fragmentation or circulation patterns that direct the movement of plant propagule. Ecological barriers include competition with existing species (see Box 3.4.1). It is difficult to predict changes in the distributions of species because they will be highly dependent on the traits of individual species and on ecological interactions among species in often novel plant community associations.

Warming will influence wildlife indirectly through changes in the tidal marsh plant communities that provide habitat. For example, it has been suggested that shorebird use of coastal wetlands will shift as warming and associated changes in precipitation cause a shift from marsh to saltpan habitat (Mustin *et al.,* 2007). Even without a dramatic shift in plant community composition, increased inundation depth and frequency driven by accelerated sea-level rise can alter wildlife habitat. Accelerated sea-level rise will increase the length of time that marshes are inundated, a change with important implications in tidal marshes where even slight differences in elevation impact the ability of species to inhabit, feed and breed (Swanson *et al.,* 2014). For example, Swanson *et al.* (2014) used a marsh elevation model to forecast that accelerated sea-level rise in San Francisco Bay (US) will degrade habitat for the California clapper rail (*Rallus longirostris obsoletus*) (Figure 3.4.9) and salt marsh harvest mouse (*Reithrodontomys raviventris*) (Figure 3.4.10) by decreasing vegetation cover. Because

Figure 3.4.9 California clapper rail. © Melanie/Flickr.

Figure 3.4.10 Saltmarsh harvest mouse. © Aric Crabb / Oakland Tribune.

the model simulation was limited to vertical elevation change in the existing boundaries of these marshes, it is possible that some of the projected habitat loss will be offset by shoreward migration of marshes.

3.4.3 Conclusions and recommendations

Warming is one of many global changes that affect the structure and function of tidal wetland ecosystems, and forecasting the effects of warming is hampered by limitations in observational data, experimental evidence, and models. Key among these is information on how both plant growth and interspecies competition are influenced by temperature. Temperature-driven shifts in species composition will dramatically alter tidal marsh ecology, biogeochemical cycling, and ecosystem services. Such shifts will arise from species-specific responses of which very little is known. Changes in plant production caused directly by temperature or indirectly by species shifts will fundamentally alter carbon cycling and storage. Forecasting these effects will require information on changes in belowground production and depth distributions, which are not commonly measured.

The processes that regulate decomposition rates are poorly understood. Perhaps the most important consequence of this gap is the challenge of forecasting the effects of warming on marsh stability against sea-level rise. Because soil carbon is a large fraction of tidal wetland soil volume (Morris *et al.,* 2016), an increase in decomposition rate caused directly by warming or indirectly by increased plant production (Wolf *et al.,* 2007; Mueller *et al.,* 2015), has the potential to destabilize existing soil organic matter pools. The feedbacks between plant activity, microbial activity, and carbon storage are complex and will remain a research challenge for decades.

Ultimately, forecasts of tidal marsh responses to warming will require improved models informed by manipulative experiments and process-level observations. Presently there are few tidal marsh warming experiments, and none of these manipulate soil temperature deeper than a few centimetres. Manipulative experiments should focus on observations that inform models (and vice versa) and seek to elucidate feedbacks between plant responses, microbial responses, nutrient cycling and elevation change.

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3.5 Impacts and effects of ocean warming on seagrass

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Summary

- Seagrass communities currently provide valuable ecosystem services to human populations (e.g. fisheries habitat, sediment stabilization, carbon storage).
- Shallow coastal regions where seagrasses dominate experience climate warming superimposed upon high natural seasonal and daily variability in temperature. Thus, many seagrass genera are currently experiencing stress from a greater frequency and intensity of temperature maxima which will continue as temperatures increase over the next few decades (4°C by 2100).
- Global seagrass decline has increased from 1% yr^{-1} before 1940 to 7% yr^{-1} presently. Factors accounting for seagrass loss rates of over the last few decades, particularly nutrient enrichment and associated declines in water quality, will continue to be compounded by climate change stressors.
- While some seagrass populations are more resistant to extinction as a result of genetic diversity, a broad geographic distribution, or the ability to recolonize, there are limits to population sustainability under a high frequency and intensity of high-temperature events.
- Persistent, structurally complex seagrass species do not recover quickly from major mortality incidents as clonal propagation is slow and recruitment from sexual reproduction is limited. Thus, a global phase shift to more ephemeral, opportunistic seagrass species, macroalgae or bare sediment is likely, consequently minimizing future seagrass ecosystem services.
- An active management approach to re-establish long-lived persistent species will be required to sustain seagrass ecosystems under climate change.
- Socio-economic approaches could be implemented (e.g. marine spatial planning) to preserve seagrass ecosystem functions and ecological services to local human populations.

Ocean warming effects	Consequences
Increasing the frequency and intensity of high temperature extremes above normal seasonal and daily maxima	Increased mortality of temperate and polar seagrass species
Raising the temperatures above thermal tolerance of tropical seagrass species currently living at their thermal limits	Increased mortality of tropical seagrass species
Lower oxygen solubility, enhancing seawater hypoxia (low oxygen conditions) and raising the concentration of sulphides in the sediment	Deterioration of below-ground tissues as seagrass depend on water column oxygen diffusion to their roots growing under low oxygen conditions in the sediment Also, root exposure to sulphides, a known phytotoxin
Greater evaporation and salinization which also lowers oxygen solubility in seawater (see above)	Stress to seagrass from hypersaline conditions raising metabolic costs compounded with elevated temperature and hypoxia stress
Higher temperatures support greater microbial respiration stimulating nutrient recycling, oxygen consumption and sulphide production	Exacerbation of eutrophication (nutrient over-enrichment), sulphide toxicity and disease leading to greater mortality of seagrass
Thermal stress lowers the viability of persistent long-lived seagrass populations with slow growth rates	Replacement of persistent long-lived seagrass species with colonizing, opportunistic seagrass species, macroalgae or bare sediment which provide fewer or no ecosystem services to human populations (e.g., fisheries habitat)

3.5.1 Introduction

Open-oceans are tracking atmospheric warming evidenced by a slow average temperature increase of 0.106°C decade^{-1} (1998-2014; Smith *et al*., 2015), although a more rapid rate is found in high latitude oceans of 0.4°C decade^{-1}. In contrast, shallow coastal waters experience atmospheric warming superimposed upon high natural seasonal and daily variability in water temperature. Thus, organisms from shallow coastal regions with restricted circulation and long water residence times, such as estuaries and coastal lagoons, are acutely vulnerable to climate-driven warming that elevates seasonal and daily temperature maxima and promotes extreme thermal events. This vulnerability is likely to be most pronounced in tropical regions where many organisms are currently living at their thermal limits (Koch *et al*., 2014) and at the distributional limits of temperate (Carr *et al.*, 2012) and polar species. Rising thermal maxima in coastal waters is causing seagrass range contractions in polar and temperate regions as the frequency of warming events increase under climate change (Jarvis *et al*., 2013), particularly in regions where warming is accentuated, such as in the Mediterranean Sea. Warming in the Mediterranean (0.4°C decade^{-1}) is four times the average rate in the open ocean and the frequency of extreme warming events in the Mediterranean Sea and other coastal regions globally is increasing (Marbà and Duarte, 2010; Thomson *et al*., 2015).

Seagrasses are dominant in estuaries and coastal lagoons characterized by high rates of sedimentation and protection from high energy environments by outer reefs or shallow banks. Climate warming during periods of seasonal or daily high temperature extremes in these coastal regions are likely to result in biogeographic shifts in seagrass species. These shifts will be controlled by individual species' thermal tolerance, competitive interactions and current and future ecosystem-level stressors. In this section, ocean warming effects on globally and regionally significant seagrass genera are reviewed with a focus on life history strategies, competitive species interactions and cumulative impacts. Recent trends in seagrass abundance are presented and potential management approaches suggested to enhance seagrass resilience to climate change.

3.5.2 Definition of species/ecosystem

The total area of seagrass distribution globally is estimated to be between 300,000 and 600,000 km^2 (Duarte *et al*., 2005). Seagrasses are taxonomically limited to a relatively few species (60 to 70, Short *et al*., 2011) with similar lineages, and represent the only marine submerged benthic flowering plants or angiosperms. They have the ability to reproduce sexually as well as asexually through clonal propagation and fragmentation. Although several species are now threatened by extinction due to human coastal

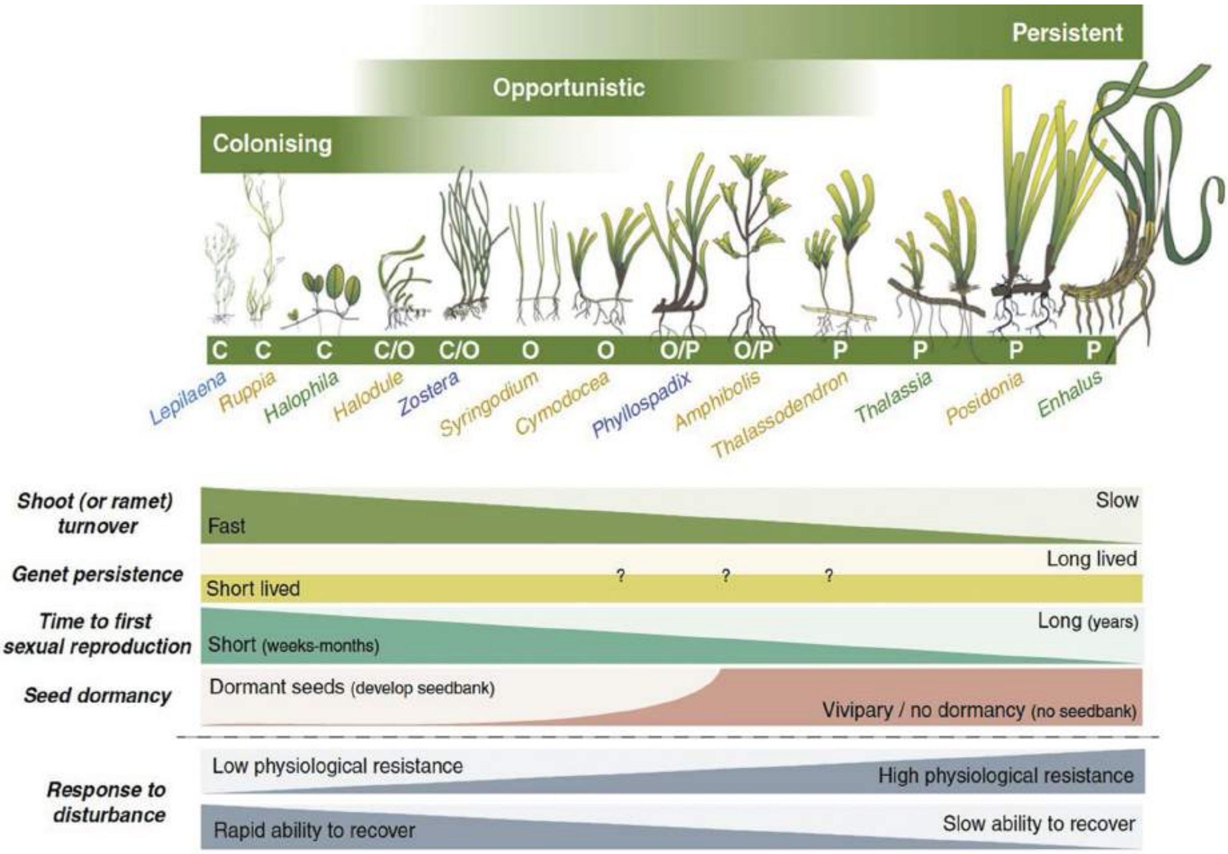

Figure 3.5.1 Major global genera of seagrasses illustrating their diverse architecture, life history strategies and ability to respond to disturbance. Similar colour of the genus represent four evolutionary lineages. Reprinted with permission (Elsevier) from Kilminster *et al*., 2015.

development (Orth *et al*., 2006; Short *et al*., 2011), seagrasses have survived the past 60 to 100 million years (Les *et al*., 1997, 2003; Janssen and Bremer, 2004) and are now dominated by 13 major genera (Figure 3.5.1) with the greatest species diversity in the tropics. These major genera are distinguished by their variety of form and size (Figure 3.5.2) with similar tissue differentiation that gives rise to a common three dimensional structure, including above ground (leaves and short shoots) and below ground (rhizomes and roots) components (Figure 3.5.1).

Extensive clonal development in seagrasses produce meadows of shoots that can comprise contiguous

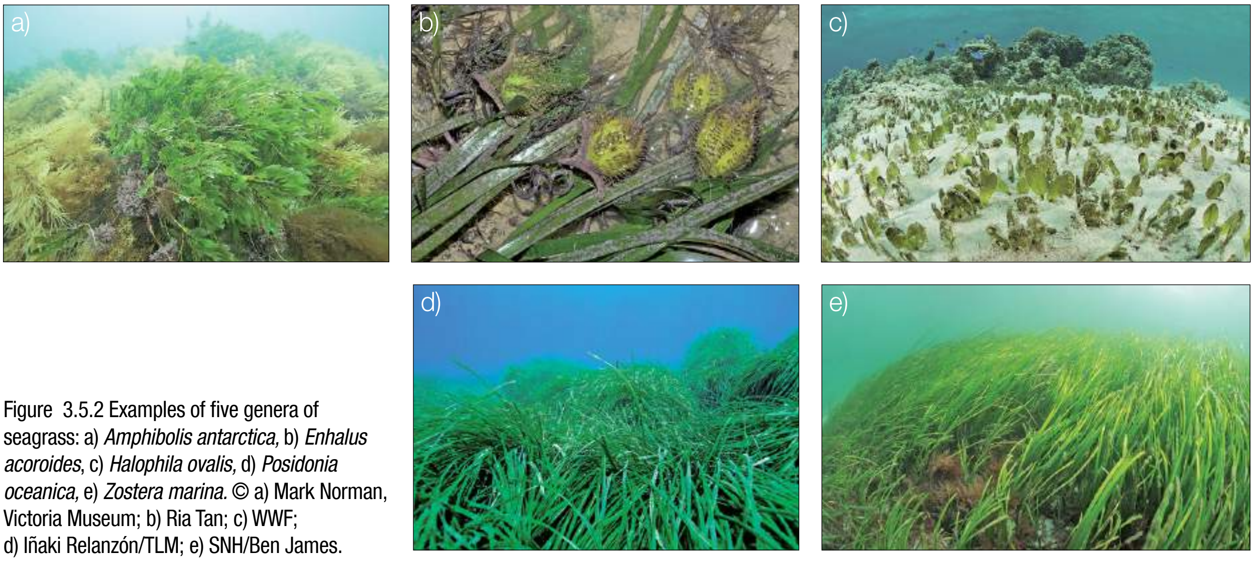

Figure 3.5.2 Examples of five genera of seagrass: a) *Amphibolis antarctica,* b) *Enhalus acoroides*, c) *Halophila ovalis,* d) *Posidonia oceanica,* e) *Zostera marina.* © a) Mark Norman, Victoria Museum; b) Ria Tan; c) WWF; d) Iñaki Relanzón/TLM; e) SNH/Ben James.

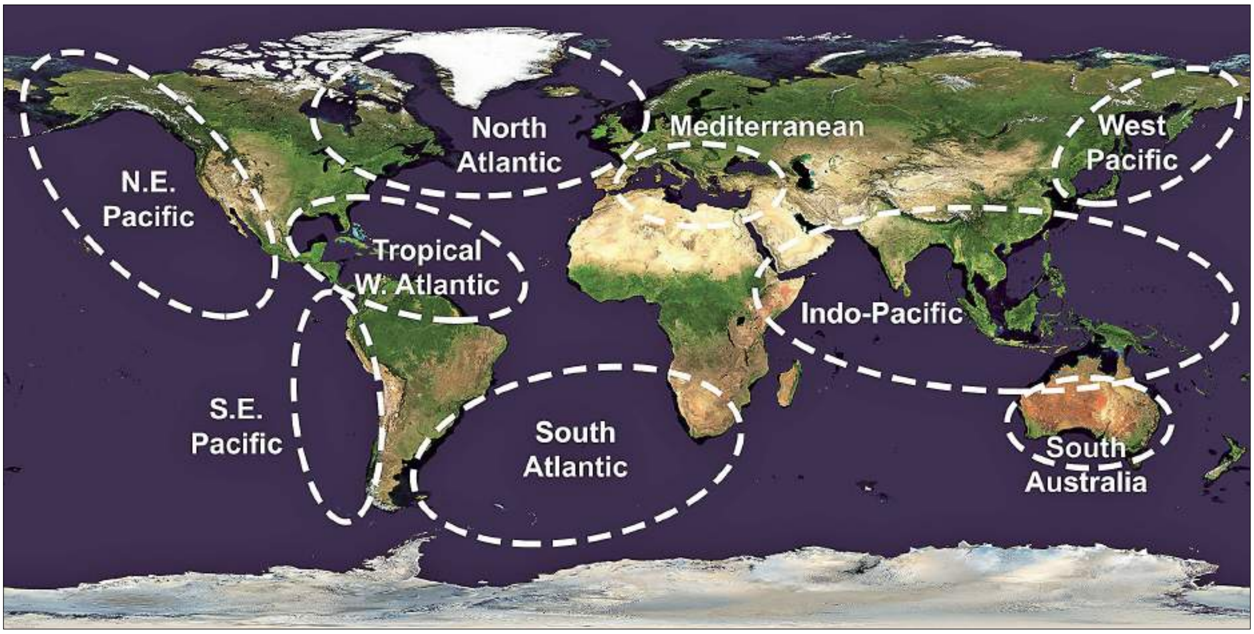

Figure 3.5.3 Seagrass bioregions depicting their global distribution in tropical, temperate and lower polar regions (after Fourqurean *et al.,* 2012).

seagrass beds reaching extents of 10,000s km^2 (Marbà and Duarte, 2010) and create important benthic habitat for a diversity of marine organisms. Below-ground biomass, which in some seagrass genera represents 50% or more of their total biomass (Duarte and Chiscano, 1999), also provides habitat and resources (photosynthetically fixed organic carbon) for organisms living in the sediment. Their below-ground roots and rhizomes restrict the majority of genera to areas where sediments are accreting or where soft sediment enable root and rhizome penetration. Long-lived, persistent seagrass genera provide habitat structure in coastal and estuarine ecosystems both above and belowground. Their preservation is critical in protecting a large diversity and abundance of marine species in coastal habitats.

3.5.3 Global Regional Significance

Seagrasses are cosmopolitan in nature spanning tropical (>24°C), temperate (4-24°C) and polar (<4°C) coastal regions with a wide range of average temperatures (Green and Short, 2003; Orth *et al*., 2006) and are divided into nine global bioregions (Figure 3.5.3). Seagrass global and regional significance is highlighted by their global distribution and quantified through a contribution of ecological services (Costanza *et al*., 1997, 2014). Ecological services are attributes of an ecosystem that provide benefits to human populations and resilience of resident organisms and other ecosystems within the landscape. Seagrasses are well recognized as having three primary ecological services. The first is the role as a habitat for shellfish and finfish, particularly early life stages (Figure 3.5.4a). This attribute has established seagrass communities

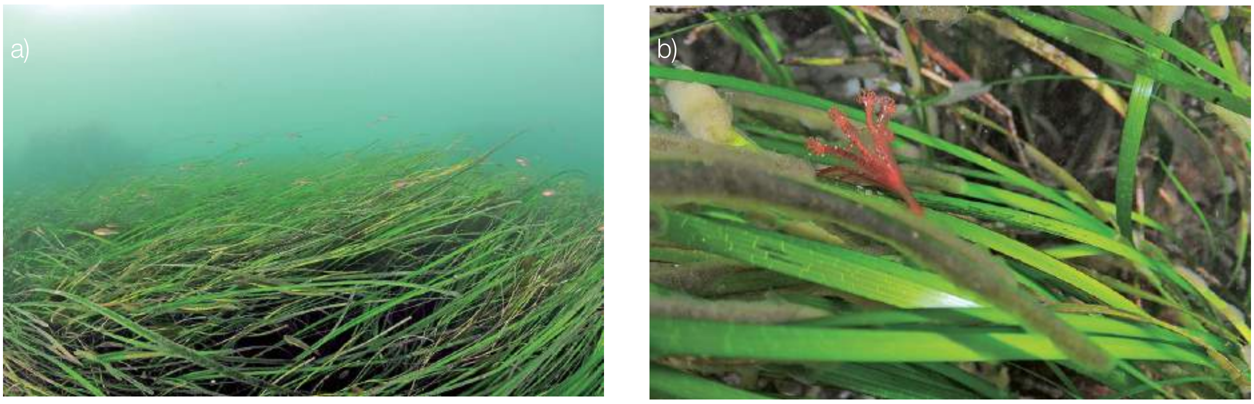

Figure 3.5.4 a) *Zostera marina* bed providing shelter for a shoal of small fish; b) small stalked jellyfish using a blade of *Zostera marina* as a point of attachment © SNH/Ben James.

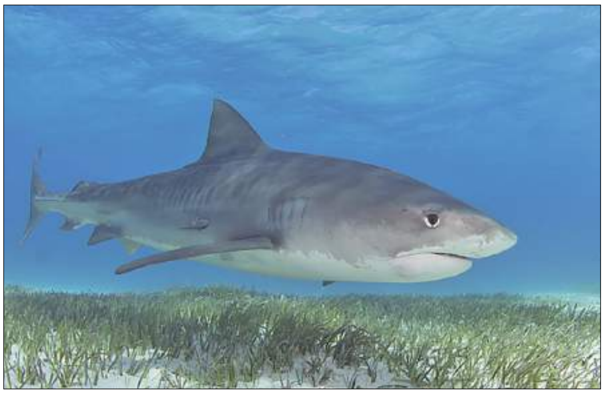

Figure 3.5.5 Shark swimming over seagrass bed. © Florida International University.

as a nursery ground for many ecologically and economically important species (e.g. shrimp, crabs, fish; Beck *et al*., 2001; Heck *et al*., 2003; Barbier *et al*., 2011). Seagrass structure significantly increases the biodiversity of the benthos in coastal environments, supporting both resident and transient marine species (Figure 3.5.4b). Secondly, seagrasses have primary production rates that equate to those of upland forests and coral reefs (Duarte and Chiscano, 1999), providing organic carbon that drives food webs and ultimately fisheries production for human consumption. Primary productivity includes the seagrasses themselves, but also other primary producers or epiphytes that grow on their leaves and shoots, shown to directly support fisheries production, as well as export of organic matter to interconnected ecosystems (e.g. beaches). Many important threatened and endangered large marine animals (megafauna) also graze on seagrasses (e.g. sea turtles, manatees, dugongs) and use this habitat for feeding and reproduction (e.g. sharks, dolphin) (Figure 3.5.5). The third attribute is the ability of seagrasses to entrain and stabilize sediments. Sediment in the water column settles amongst seagrass shoots improving overlying water quality for the seagrass community and adjacent ecosystems which require high irradiance, for example coral reefs in tropical regions. Belowground biomass holds sediment and nutrients that would otherwise be resuspended into the water column. In this way, seagrasses contribute to the maintenance of high water quality and foster internal nutrient recycling. Furthermore, rhizome and root material accumulate, creating a highly organic sediment which sequesters carbon from the environment (Duarte *et al*., 2005) and stores it below-ground (Figure 3.5.6). Seagrass "blue carbon" sequestration has recently been estimated globally to represent 4.2 to 8.4 Pg (1 Pg = 10^{15} g or 1 billion tonnes) of carbon storage (Fourqurean *et al*., 2012). Seagrass capacity to sequester carbon has been estimated at approximately 27.4 Tg C yr^{-1} (1 Tg = 10^{12} g or 1 million tonnes), a significant contribution to the marine carbon sink given the small total area (0.2%) of seagrass habitat in the world's ocean (Duarte *et al*., 2005). The large persistent seagrass genera (Figure 3.5.1) account for the majority of organic carbon storage. For example, the *Posidonia* genus in the Mediterranean has a large living biomass contributing approximately 7 metric tons of carbon ha^{-1} (Fourqurean *et al*., 2012). Thus, the loss of the persistent, long-lived seagrass would compromise the "blue carbon" sequestration potential of seagrass ecosystems and decrease marine carbon storage.

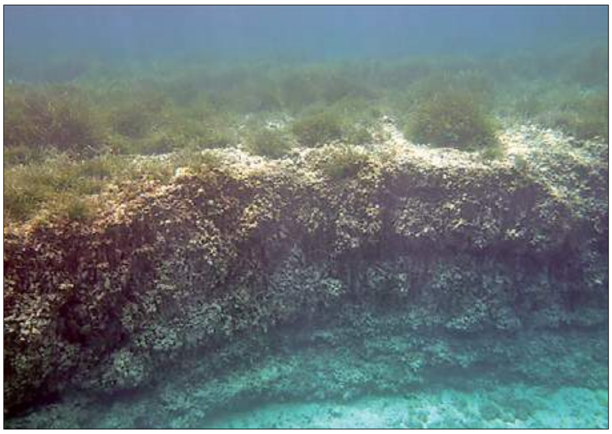

Figure 3.5.6 Seagrass "blue carbon" illustrated at an escarpment of a Mediterranean seagrass (*Posodonia oceanica*) with extensive organic carbon accumulation (Portlligat Girona, Spain). © Group of Aquatic Macrophyte Ecology, GAME-CSIC.

3.5.4 Trends and impacts

Although seagrasses are considered to be ecologically and economically important, as well as contribute to marine carbon storage, they are declining globally at an accelerating rate, from around 1% yr^{-1} before 1940 to 7% yr^{-1} today (Duarte, 2002; Orth *et al*., 2006; Waycott *et al*., 2009). These trends reflect local and regional impacts of large human populations inhabiting coastlines where seagrasses dominate (Duarte, 2002). There are a number of specific factors that have contributed to seagrass loss rates over the last few decades, including physical damage from fishing activities (e.g. trawling, dynamite fishing, propeller scars) (Figure 3.5.7), changes in land use and armouring coastlines, reclamation, siltation from coastal development, and salinization from decreased freshwater flows and tailings from desalinization plants (Short and Wyllie-Echeverria, 1996; Orth *et al*., 2006; Waycott *et al*., 2009). At the global scale, extensive nutrient enrichment and overall reduction in water quality of coastal zones has reduced light penetration to seagrasses worldwide (Lotze

Figure 3.5.7 Propeller scar though a seagrass bed in Redfish Bay, Texas. © Texas Parks and Wildlife Dept.

et al., 2006; Short *et al*., 2011). The global coastal eutrophication problem was documented more than 20 years ago (Short and Wyllie-Echeverria, 1996) and has been steadily increasing. Because of their large below-ground biomass, seagrasses require a high amount of sunlight or irradiance to reach the benthos (~10-25% of surface irradiance; Dennison *et al*., 1993). The rapid extinction of light through sea water by plankton and other particulates prevents seagrasses from maintaining a net positive growth and successful reproduction. Furthermore, the additional biomass of water column plankton and microbial activity from excess nutrient availability under eutrophication can lead to low oxygen conditions in seagrass communities.

The present concern is that the impacts which have driven rapid loss rates of seagrasses over the last few decades are being compounded by climate change stressors, and therefore will accelerate rates of seagrass decline (Short and Neckles, 1998; Duarte *et al*., 2008; Waycott *et al*., 2009; Hoegh-Guldberg and Bruno, 2010; Marbà and Duarte, 2010; Jordà *et al*., 2012). Under a scenario of a warmer climate, elevated seawater temperatures could subject many coastal estuaries and lagoons to a series of additional stressors with cascading effects (Figure 3.5.8). Increasing seawater temperature elevates seagrass community respiration rates, and therefore the consumption rate of oxygen, raising the respiration to production ratio (R:P). Elevating temperature also increases microbial activity and sulfate reduction rates, a major biogeochemical pathway that breaks down organic matter in marine ecosystems. Sulphate reduction results in an accumulation of inorganic and gaseous sulphides that are known phytotoxins known to cause seagrass decline (Koch *et al*., 2007; García *et al*., 2013). This microbial up-regulation also increases the activity of microbes associated with disease and promotes nutrient recycling. Increased air temperature can also result in greater evaporation and salinization, lowering the capacity of sea water to hold oxygen. Greater heating of surface waters further promotes stratification, a physical process that inhibits reoxygenation of the water from the atmosphere, and has been shown to cause seagrass and fish mortality under hypoxic (low oxygen) conditions (Koch *et al*., 2007). As seagrasses and sediments retain the largest pool of nutrients in shallow soft-bottom habitats, high seagrass mortality rates release nutrients and foster eutrophication conditions. This has been observed to lead to large-scale secondary seagrass mortality events as a consequence of phytoplankton blooms and sediment suspension (Rudnick *et al*., 2005; Burkholder *et al*., 2007). Therefore, elevating temperature can promote hypoxia in coastal environments and lead to a cascade of other indirect impacts (Figure 3.5.8).

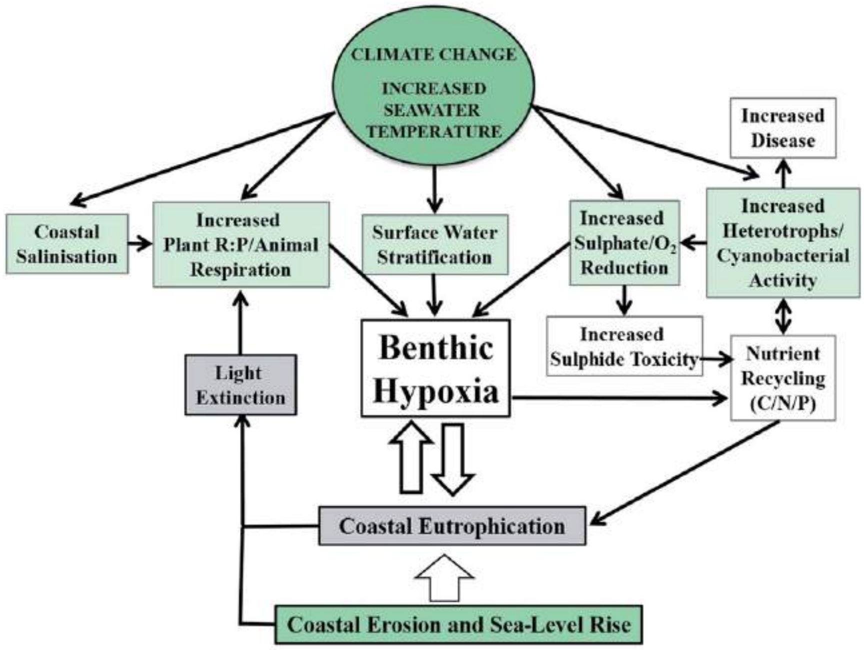

Figure 3.5.8 Ocean warming leads to primary (light green boxes) and secondary (white boxes) impacts on shallow seagrass ecosystems that exacerbate coastal eutrophication and light extinction in a negative feedback process. Sea level rise and subsequent coastal erosion would also promote eutrophication and lower light availability to seagrass ecosystems.

Sea-level rise and an increase in the partial pressure of CO_2

(lower pH) are also predicted to accelerate with ocean warming and climate change (IPCC, 2013). There are concerns that sea-level rise leading to coastal erosion will exacerbate eutrophication and increase light extinction (Figure 3.5.8). Even without deteriorated water quality, the exponential decline in irradiance with water depth dictates a lower light environment for seagrasses as sea levels rise. In lagoons where seagrasses are associated with reefs, and other barriers, sea-level rise effects on wave heights and physical scouring in lagoons may reduce maintenance of seagrass beds. Based on modelling scenarios for lagoonal seagrasses of the Great Barrier Reef in Australia, 20% of present seagrass distribution (assuming continued reef accretion) is predicted to be lost by 2100 with a predicted 1 metre rise in sea level (Saunders *et al*., 2014). If warming limits coral reef accretion, Saunders *et al*. (2014) predicted a total loss of seagrass habitat for the Barrier Reef. As a result, they make the case for more detailed modelling of interdependent ecosystem responses to climate change. While the majority of climate drivers, such as rising ocean temperature and sea levels, predict a major decline in seagrasses, higher CO_2 has been shown to potentially raise photosynthetic rates and allow seagrasses to store more carbohydrates and raise their thermal tolerance if light is not limiting (reviewed in Koch *et al*., 2014; Zimmerman *et al.*, 2015). However, the response of seagrass to elevated CO_2 may be species specific and potentially unlikely to overcome other constraints on seagrass growth (Cox *et al.,* 2016). Finally, cumulative stress in coastal environments where higher CO_2 has already been realized under coastal eutrophication (as a result of higher ecosystem respiration rates) continue to drive seagrass global decline (Short *et al*., 2011).

3.5.5 Consequences

The consequence of greater thermal loads on seagrass ecosystems will be expressed at the ecosystem scale as described above (Figure 3.5.8) and influence local populations based on individual genera thermal tolerance and life history strategies. As illustrated in Figure 3.5.1, there exists a spectrum of seagrass forms across the 13 genera, each with various life history strategies. The persistent seagrass genera are characterized by a large amount of above and below-ground biomass. These genera are typically tolerant of modest stress and show physiological resilience due to the availability of large energy reserves (carbohydrates) in belowground rhizomes. For example, carbohydrate reserves are thought to account for the ability of the Mediterranean seagrass, *Posidonia* (Figure 3.5.2d), to asexually grow as a single clone for a millennium when conditions are relatively stable (Marbà and Duarte, 1998; Arnaud-Haond *et al*., 2012). However, because of their very slow growth rates, on the order 1-10 cm y^{-1}, persistent seagrass typically does not recover quickly from major mortality events (Marbà and Duarte, 1998; Kendrick *et al*., 2005) and may have problems recovering from mortality unless they have the capacity for successful sexual reproduction.

A new recruitment model on seagrass movement by McMahon *et al*. (2014) shows a high capacity for sexual reproduction in seagrasses, including persistent genera (*Posidonia*, *Thalassia*). Sexual reproduction has the ability to transport seeds, fruit and new shoots great distances (10s to 100s of kilometres). In contrast to decades or millennia for asexual reproduction replacing seagrass beds in slow growing persistent genera, the time frame for sexual production is on the order of weeks. Therefore, natural recruitment within larger metapopulations of persistent genera may become dependent on recruitment from sexual reproduction under rapid climate change and disturbance occurring over decades, rather than 1000s of years (2012; Jarvis *et al*., 2012; Kendrick *et al*.). Genetic evidence indicates that persistent seagrass species may have the capacity to establish in preferential habitats through dispersal, suggesting the possibility of climate adaptation through sexual reproduction and recruitment (Oetjen *et al*., 2010). However, seagrass genetic diversity is lowest in populations at their range boundaries (Olsen *et al*., 2004; Arnaud-Haond *et al*., 2007; van Dijk *et al*., 2009; Arriesgado *et al*., 2016) and reproduction at range boundaries has been shown to be limited to clonal growth (Arriesgado *et al*., 2016). Thus, there may be constraints on adaptive potential driven by genetic diversity of populations between bioregions.

Even within seagrass populations, sexual recruitment can be low following severe warming events after mortality. For example, sexual recruitment accounted for negligible shoot recruitment (2%) in the Mediterranean seagrass (*Posidonia*) following major warming events and was ineffective at arresting rapid population declines (5% y^{-1}; Marbà and Duarte, 2010). Warming-induced abortion of seeds during heat waves can also limit recovery of seagrass populations via sexual reproduction (Balestri and Cinelli, 2003; Jarvis *et al*., 2013). Furthermore, on average many persistent genera have low sexual propagule and seed production rates and lack a seedbank from which to recruit (Figure 3.5.1). Constraints to recruitment, regardless of ocean current transport of seeds, fruits and propagules, may partially explain the presence of seagrasses in only 4% of the possible suitable habitat estimated by Waycott *et al*. (2009). While the importance of seed production is acknowledged (Inglis, 2000; Orth *et al*., 2006), there is a need for a better understanding of seagrass sexual reproduction and its potential to ameliorate losses of seagrasses globally (Inglis and Waycott, 2001; Kendrick *et al*., 2012; Kilminster *et al*., 2015). Currently, minimal information exists on the survival rates of new recruits and the likely bottleneck of seedling survival (Díaz-Almela *et al*., 2009; Olsen *et al*., 2012; Strazisar *et al*., 2015), one of the most sensitive life-history stages in the development of plants, as well as the ability of reproductive adults to successfully reproduce. Furthermore, seagrass seedbanks have recently been observed to be short-lived in some genera, even those classified as colonizing (e.g. *Ruppia*, Strazisar *et al*., 2016) or opportunistic (e.g. *Zostera*, Jarvis *et al*., 2014), thus sexual reproduction alone may not be a successful life history strategy to overcome a high frequency of disturbance, including high temperature events (Díaz-Almela *et al*., 2007) likely to increase with climate change.

Large-scale die-off of seagrass in response to temperature extremes, compounded by interactive stressors (Figure 3.5.8), have been documented for several long-lived or persistent genera across the planet, e.g. *Thalassia*, *Amphibolis*, *Zostera*, *Posidonia* (Robblee *et al*., 1991; Zieman *et al*., 1999; Seddon *et al*., 2000; Moore *et al*., 2013; Thomson *et al*., 2015). As global warming compromises persistent genera, or the climatic conditions are no longer tolerable for temperate species, there will be shifts in species with the competitive advantage of species that are opportunistic and colonizing (Figure 3.5.1). There is some evidence that these species are becoming more dominant and replacing longer-lived persistent species that require decades or longer to become reestablished (Thomson *et al*., 2015). The frequency of disturbance is critical as a result of the long lag time for re-establishment of some persistent species. If the frequency of high temperature events is greater than the time for recovery, it is unlikely that the larger, slow growing genera will persist. This tolerance window, across both combined stressors and time is likely to define species shift within the seagrass community (Figure 3.5.9). This shift may be from one seagrass species to another, or to macroalgae, which have shorter life spans and high reproductive rates, or result in bare sediment and a complete collapse of ecological services and value of the seagrass ecosystem. Genetic diversity may also become a factor, as many seagrass species are not genetically diverse within populations as a result of their clonal reproductive nature or restricted dispersal capacity. Genetic diversity is constrained further by range contractions and restoration efforts that do not consider genetics (Williams, 2001). The ability of higher thermally tolerant seagrasses to recruit and become established in polar and temperate regions is only now being assessed (McMahon *et al*., 2014).

Even though there is a current lack of understanding on how individual seagrass genera and species will respond to ocean warming, current population trends provide insight into vulnerabilities and potential opportunities. Out of 72 seagrass species from 13 genera examined by Short *et al*. (2011), 39% of species with known population trends (56 species) were declining, while only 9% were increasing (Table 3.5.1). The species most at risk defined by the IUCN Red List (http://www.iucnredlist.org/) criteria endangered or vulnerable were those with small ranges or endemics unlikely to expand their range and adapt to climate change under current extinction probabilities. Other genera, such as *Phyllospadix*, possess endangered and vulnerable species due to extensive coastal

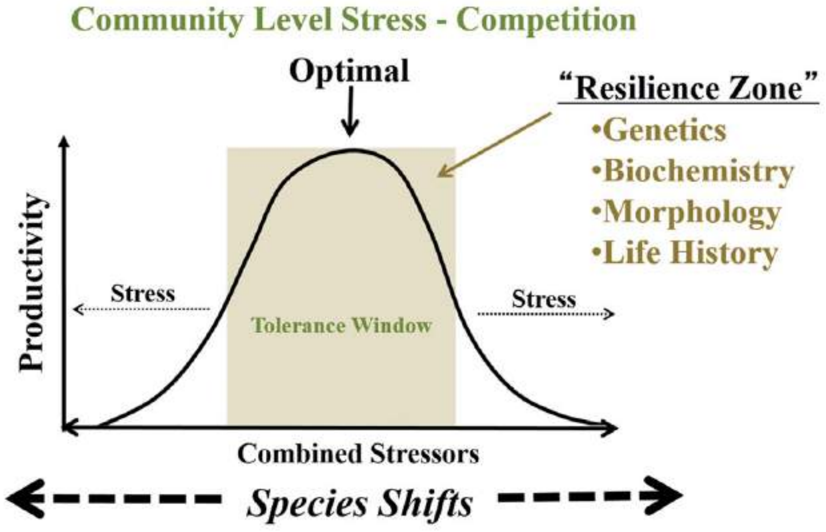

Figure 3.5.9 At the organismal scale, seagrass species will shift based on their resilience defined by genetics, biochemistry, morphology and life history as well as community competition.

development in the North Pacific bioregion, thus current anthropogenic stress limits range expansion. Shallow species were also found by Short *et al*. (2011) to be more threatened that those with deeper distributions. Shallow species will be subject to greater temperature extremes with ocean warming compounding ongoing declines unless they have a broad distributions. Broad distributions of persistent seagrass genera with species showing declining populations are listed as species of least concern (Table 3.5.1). These genera may have species with local population declines, but their broad range provides an opportunity for them to expand in response to climate change. The genera with species that had increasing populations were primarily characterized as having colonizing, opportunistic life history strategies. Species in these genera also have the opportunity to sustain populations under increased disturbance from climate change.

Table 3.5.1 Proportion of species within 13 seagrass genera that have populations increasing (I), decreasing (D), stable (S) or unkown (U), their IUCN Red List Category (EN = endangered, VU = vulnerable, NT = near threatened, LC = least concerned, DD = data deficient), life history strategy designation (Figure 1) and bioregion: 1 = Temperate North Atlantic, 2 = Tropical Atlantic, 3 = Mediterranean, 4 = Temperate North Pacific, 5 = Tropical Indo-Pacific, 6 = Temperate Southern Oceans. The numbers in parentheses are the number of species from each genus assigned to the attribute. Adapted from Short *et al.*, 2011.

Genus	Spp (#)	Red List	Trend	Life History	Bioregion
Amphibolis	2	LC (2)	Stable (2)	O/P	6 (2)
Cymodocea	4	LC (4)	Stable (3)	O	5 (3)
			Unknown (1)		1,3 (1)
Enhalus	1	LC (1)	Decreasing (1)	P	5 (1)
Halodule	7	LC (3)	Decreasing (2)	C/O	5 (2)
		DD (4)	Increasing (1)		2 (4)
			Stable (1)		1,2,3,4,5 (1)
			Unknown (3)		
Halophila	17	V (3)	Decreasing (5)	C	2 (3); 4 (2)
		NT (2)	Stable (4)		5 (8); 6 (1)
		LC (10)	Increasing (3)		2,3,5 (1)
		DD (2)	Unknown (5)		4,5,6 (1)
					2,3,4,5,6 (1)
Lepilaena	2	DD (2)	Unknown (2)	C	6 (2)
Phyllospadix	5	EN (1)	Decreasing (2)	O/P	4 (5)
		VU (1)	Stable (3)		
		LC (3)			
Posidonia	8	VU (1)	Decreasing (3)	P	6 (7)
		NT (1)	Stable (4)		3 (1)
		LC (6)	Unknown (1)		
Ruppia	6	LC (5)	Stable (5)	C	6 (4); 3 (1)
		DD (1)	Unknown (1)		1,2,3,4,5,6 (1)
Thalassia	2	LC (2)	Stable (2)	P	2 (1); 5 (1)
Thalassodendron	2	LC (2)	Unknown (2)	P	6 (1); 5,6 (1)
Syringodium	2	LC (2)	Stable (2)	O	2,3 (1); 5,6 (1)
Zostera	14	EN (2)	Decreasing (9)	C/O	6 (4); 4 (5)
		VU (2)	Stable (3)		5,6 (2); 4,5 (1)
		NT (2)	Increasing (1)		1,3,4 (1)
		LC (8)	Unknown (1)		1,3 (1)

3.5.6 Conclusion and recommendations

Climate warming and other global change effects will exacerbate current seagrass stress in many coastal lagoons and estuaries where they provide critical habitat and numerous ecological services for wildlife and human populations. Thus, one of the most significant restoration goals at a local scale should be to lessen current stressors (Saunders *et al*., 2013), particularly coastal eutrophication, sedimentation and coastal reclamation and armouring (Short *et al*., 2011) and provide a framework for increased resilience (Unsworth *et al*., 2015). Reducing stress would widen the tolerance window for persistent species that take many years to recover. Reducing physical disturbance such as boating, fishing and mining activities to "healthy" seagrass ecosystems that persist currently under high water quality conditions is also important to maintain global seagrass ecosystem services. Maintaining seagrass communities retains their ability to provide habitat and mitigate further loss of "blue carbon" to the atmosphere. Socio-economic approaches could be implemented at the local scale through marine spatial planning with the goal to preserve ecosystem function and ecological services to local human populations. Marine protected areas are also being established to prevent physical disturbance in highly valuable seagrass habitats (Orth *et al*., 2006), but require water quality management programmes at the watershed and regional scales to be successful (Kenworthy *et al*., 2006). Internationally, carbon credits from seagrass sequestration of carbon could also be employed as a strategy to maintain seagrass ecosystems on a global scale.

A new paradigm in ecological restoration is the need for active management and restoration (Koch *et al*., 2015). Higher frequency and intensity of disturbances associated with climate change, for example thresholds of thermal limits being exceeded for both temperate and tropical species, are expected to result in declines in persistent seagrass species. The reality of these losses has shifted the management community of natural coastal ecosystems from principally "protection" to also actively promoting the re-establishment of important habitat-forming species (Marion and Orth, 2010; van Katwijk *et al*., 2016). This approach has been ongoing in the Chesapeake Bay for many years with respect to seagrass restoration, and coral nurseries have been established in many tropical regions. While active reintroduction of persistent species fosters the chance for recovery of degraded ecosystems, the conditions for establishment, survival and reproduction have to be present and the frequency of disturbances have to be low for even modest success. There is also a need for the recognition of genetic diversity through the establishment and interconnectedness of metapopulations. Genetically diverse populations are needed to assist in "rescuing" species from extinction by increasing the connectivity amongst populations (Chust *et al*., 2013). If original long-lived persistent species, e.g. polar and temperate species, cannot be re-established, consideration should be given to assisted migration of more thermally tolerant species, as natural recruitment processes may be slower than the rate at which climate warming will shift coastal zone thermal regimes.

Finally, with regard to temperature, local and global warming needs to be minimized in an effort to stabilize and slow the rate of ocean warming. On a local scale, increased circulation and tidal exchange, that can also maintain a low energy environment required by seagrass communities, as well as restoration of freshwater flows in estuaries, could assist in thermal regulation of coastal waters during summer months. At the global scale, a commitment to limiting greenhouse gases and fossil fuel combustion by shifting to renewable energy and development of alternative energy is ultimately required to maintain seagrass ecosystems. Although nearly 24% of all seagrass species can presently be assigned to a Red List conservation status (Short *et al*., 2011), it is likely that our current trajectory of ocean warming will lead to more species being assigned to endangered or threatened. Major species shifts toward those adapted to higher temperature are predicted, but also bare sediment conditions will persist and seagrass communities will be dominated by opportunistic and colonizing seagrass and macroalgal species that don't provide a full suite of seagrass ecosystem services and are more ephemeral. Public awareness of seagrass' ecological importance, ecosystem services and present state globally will be critical to solve the current and future crisis of seagrasses approaching threatened and extinction status (Orth *et al*., 2006; Short *et al*., 2011).

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> *"Given the severity of the threat from sea-level rise in particular, it is essential that ways are developed to increase the resistance and resilience of mangroves, and increase adaptive capacity."*
>
> *Section 3.6 authors*

3.6 Impacts and effects of ocean warming on mangrove species and ecosystems

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Summary

- Mangrove ecosystems have critical values to people.
- Over 30% of mangrove areas have been lost in the last 100 years.
- There are now three endangered and two critically endangered mangrove species.
- Temperature rise causes precipitation changes and sea-level rise, that both have impacts on mangroves.
- Precipitation changes affect mangrove productivity and species diversity.
- Most mangroves are not keeping up with sea-level rise which is causing mangrove dieback.
- Mangrove crabs are essential bioengineers in mangroves, and are themselves impacted by raising temperatures.
- Ocean warming will affect connectivity among mangrove faunal communities.

Ocean warming effects	Consequences
Mangrove habitat conversion	Increasing species under threat of extinction Fragmented habitats
Temperature rise	Moderate impacts on trees High impacts on fauna with low thermal plasticity Changes in some species ranges Reduction in connectivity between mangrove fauna populations
Increased atmospheric CO_2	Enhances productivity and growth of some mangrove trees Lack of research on impacts on mangrove fauna
Precipitation changes	Reduction in mangrove diversity, photosynthesis and growth with reduced rainfall and humidity Impacts on mangrove crabs
Storms and high energy waves	Significant impacts on mangroves Reduced protection with narrower mangroves
Sea-level rise	Major impacts on mangroves Seaward edge mortality and retreat Low tidal range area most vulnerable Landward mangroves at risk if migration blocked

3.6.1 Introduction

This section describes the spectacular coastal mangrove ecosystem, their unique characteristics and the direct benefits they afford to people. It also outlines the human destruction of mangroves that has happened in the last few decades, and the growing impacts from climate change associated with ocean warming, with focus on literature published in the last two years. The mangrove adaptation among angiosperms (flowering plants) started during the late Paleocene in the SE Asia /SW Pacific region, and mangroves have been further developing over the last 60 million years along with an associated unique fauna. During that time mangroves have survived climate and sea-level changes, however, the rate of current changes combined with heavy coastal modification and habitat fragmentation as a result of human development, are resulting in some mangrove species becoming more vulnerableto the effects of ocean warming.

3.6.1.1 Definition of species/ecosystem

Mangroves are a taxonomically diverse, yet small in number, group of tropical tree species, which through parallel evolution, have developed physiological and morphological adaptations that enable them to growth in intertidal habitats (Polidoro *et al.,* 2014). While mangroves are by definition a biogenic community primarily of trees and associated fauna, the word also refers to the wetland habitat in which they occur.

Mangrove ecosystems occur on low energy, low gradient tropical coastlines, between mean and high tide levels (Figure 3.6.1). There are approximately 70 species of true mangroves, represented by 17 families (Polidoro *et al*., 2014), with the majority found in SE Asia. Compared to other forest types, mangrove forests generally lack an understorey and usually exhibit distinct zones of species controlled by elevation and tidal inundation. In this saltwater wetland, the specially adapted trees have aerial roots (Figure 3.6.1) and salt regulation strategies.

The ecosystem is characterized by a highly specialized and peculiar resident fauna, mainly comprising crabs, gastropods and mudskippers, and non-permanent

Figure 3.6.1 Seaward edge of mangroves in the Pala Lagoon, America Samoa. The seaward edge is at mean tide level. Foreground species is *Bruguiera gymnorrhiza,* with *Rhizophora mangle* further away. © J. Ellison.

fauna, such as fish with a life cycle connection to adjacent habitats (Figure 3.6.2). Mangroves are an open-air evolutionary laboratory where most of the resident marine fauna show evolutionary trends from the sea to a terrestrial or limnic (fresh water) life style. Such transitions are based on key adaptations in physiology, respiration, foraging behaviour and reproduction, often only found in mangrove-associated species. The ecosystem also includes a diverse non-vascular flora of algae, ferns and mistletoes, growing on the trees.

Figure 3.6.2 Mangrove crabs *Uca occidentalis* and gastropods *Terebralia palustris* at a mangrove creek in Kenya. © S. Cannicci.

3.6.1.2 Global significance

The largest areas of the World's mangrove forests are established in deltas and estuaries (Giri *et al*., 2015), or coastal areas that are dominated by tidal or riverine processes as opposed to wave energy. Mangroves protect coastal communities from wave erosion, tropical cyclones, storm surges, and even moderate tsunami waves (Figure 3.6.3) (Cochard *et al*., 2008; Nurse *et al*., 2014). Mangrove forests and their substrates filter terrestrial runoff water, and so protect offshore seagrass beds and coral reefs from suspended sediment discharged by rivers (Vo *et al*., 2012). Mangroves provide a wide range of products for coastal people, such as fish, crabs, timber and fuel wood, and bioactive compounds for tanning and medicinal purposes (Ewel *et al*., 1998; Spalding *et al*., 2010).

Ample evidence exists for the direct contribution of established mangroves to accretion in the vertical plane through peat formation (Lee *et al*., 2014), which

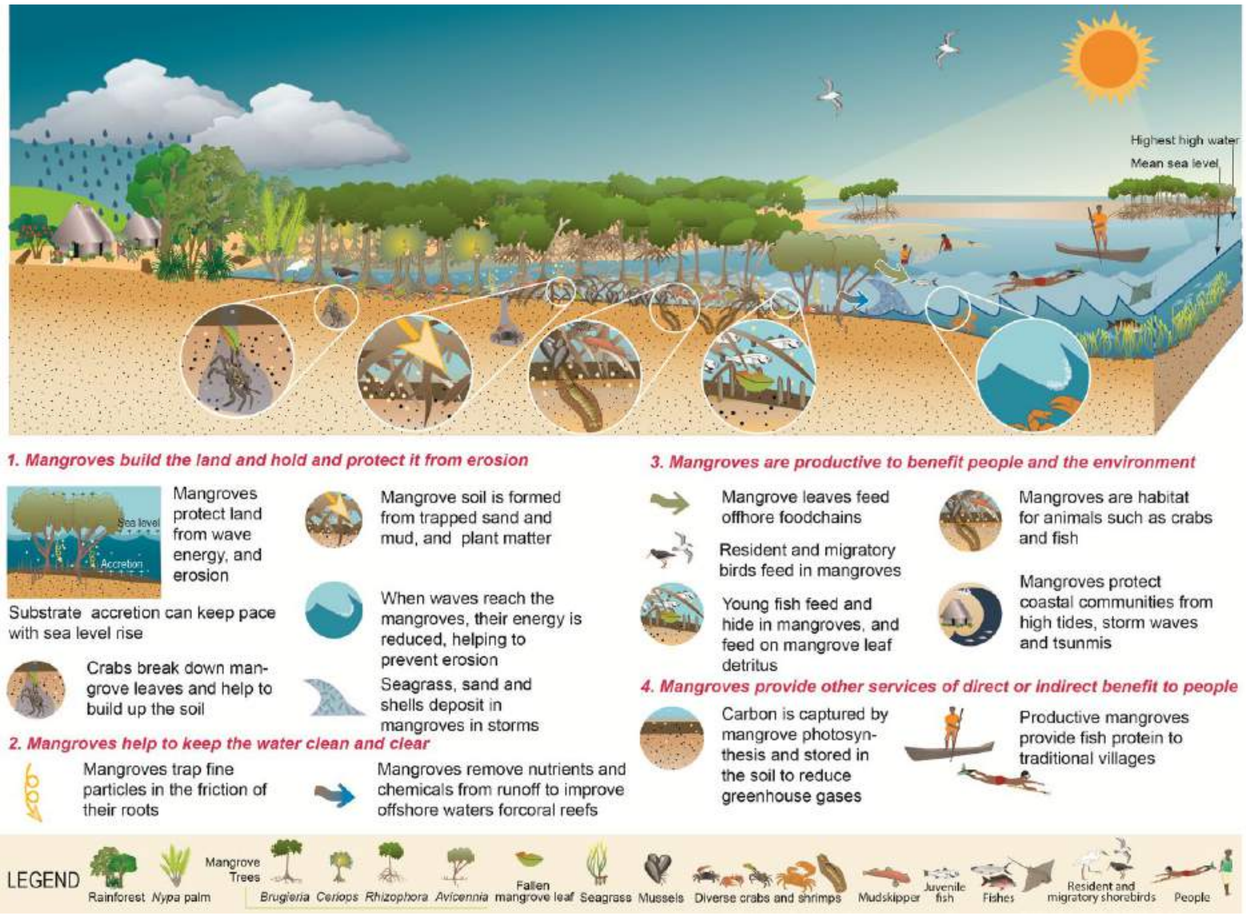

Figure 3.6.3 The mangrove habitat and values of the ecosystem to people (Illustrator: Jan Tilden).

contributes to the mitigation of sea-level rise as well as carbon sequestration. Mangrove-sediment carbon stores are approximately five times larger than those found in temperate, boreal and tropical terrestrial forests (Bouillon, 2011; Donato *et al.*, 2011).

3.6.2 Trends and impacts

Despite these values, mangrove global area is less than half of what it was just over a century ago, with many mangrove areas lost in the last few decades as a result of direct human impacts (Spalding *et al*., 2010; Giri *et al*., 2011). The most substantial changes to the world's mangrove cover result from direct conversion of mangrove areas to urban and industrial spaces, toand for aquaculture and to agqriculture (Spalding *et al*., 2010). Mangrove area worldwide has fallen from over 200,000 km^2 early last century to 188,000 km^2 in 1980, to 137,760 km^2 in 2000 (Giri *et al*., 2011) with rising rates of loss after 1980. Asia has suffered the highest losses, largely due to human impacts (Long *et al*., 2014; Polidoro *et al*., 2014), and high rates of loss have also been recorded in Africa (Kirui *et al*., 2013). Reductions in mangrove areas in Asia have resulted in three mangrove species being classified as endangered and two critically endangered, and globally, six others species are considered vulnerable (Polidoro *et al*., 2014).

Mangroves are furthermore sensitive to climate change associated with the enhanced greenhouse effect and ocean warming. These ecosystems sensitivities are reviewed below.

3.6.2.1 Temperature rise

Warmer temperatures raise the metabolism of coastal marine species and can be fatal to those already living at the upper end of their temperature range (Wong *et al*., 2014). The IPCC (2013) observed a warming of both the ocean surface and land temperatures over the last century, of about 1°C. With future temperatures expected to be up to 4.8°C warmer by 2081–2100 relative to 1986–2005 (IPCC, 2013), negative impacts from temperature rise alone are not expected despite mangrove trees showing a depression in photosynthesis rates at temperatures of over 30°C (Alongi, 2015). Impacts on mangroves of a sea surface temperature increase of over 3°C are projected to be moderate and may approachto high (Gattuso *et al.*, 2015), but with low confidence levels, as interaction with the combined pressures from other impacts are difficult to assess.

Mangrove response to temperature rise is otherwise likely to show changing species composition and phenological patterns (e.g. timing of flowering and fruiting), expanding mangrove ranges to higher latitudes where range is limited by temperature, and is not limited by other factors such as a supply of propagules and suitable physiographic conditions (Gilman *et al*., 2008). There are recent reports of mangrove expansion to higher latitudes with increased winter temperatures (Osland *et al*., 2015), reviewed by Saintilan *et al*. (2014) and confirmed by Armitage *et al*. (2015). Around Tampa Bay, Florida (27-28°N), analysis of four large marshes since the 1870's showed 72% conversion of marsh to mangrove wetlands (Raabe *et al*., 2012). Such range expansions, however, include very few species, and it has been commented that poleward expansion is not possible for all species (Parida *et al*., 2014). Some authors further comment that poleward mangrove expansion is not solely due to climate warming, but rather is a result of a combination of human activities such as estuary infilling and increases in nutrient inputs, and other factors such as wave variation (Lundquist *et al*., 2014; Walcker *et al*., 2015). By contrast, in southern China introduced *Spartina alternifolia* has expanded greatly in the last two decades and replaced mangroves (Zhang *et al.*, 2012;, Wang *et al*., 2015), such as seen atAt Yunxiao, near Xiamen, where introduced *Spartina* has recently invaded the seaward edge of native mangroves (Figure 3.6.4).

Present knowledge about the impact of global warming on mangrove associated fauna is very scarce (Alongi, 2015), and much is inferred from the growing literature on intertidal invertebrates and tropical ectotherms. Tropical intertidal species are subjected to very high temperature variations throughout their daily activity and are known to have wide thermal niches, i.e. the range of temperatures in which the species can survive, grow and reproduce.

Figure 3.6.4 Introduced *Spartina* recently invading mangroves from the seaward edge at Yunxiao, near Xiamen, China. © J. Ellison.

However, recent studies showed that they live close to the upper limits of these niches (Somero, 2002; Helmuth *et al*., 2010), making them extremely vulnerable to further temperature increase. Moreover, recent meta-analytical approaches predict that climate change will affect the biodiversity and the distribution of low latitudes populations and communities, which live in a thermally homogeneous environment and thus show little thermal plasticity (Deutsch *et al*., 2008; Dillon *et al*., 2010; Sunday *et al*., 2011). Within this theoretical frame, it should be expected that mangrove-associated invertebrates would either migrate polewards together with the floral component, following their thermal niche, or go extinct, since they cannot cope with the rise in temperature. The few studies available at present show that crab populations living near the upper latitudinal limits of the mangrove range are coping with temperature rise better than the equatorial ones. In the United States, in the last century, the American mangrove tree crab, *Aratus pisonii* not only kept pace with the northward expansion of mangroves, but it even expanded its range limit at a faster rate than the trees, and it is now colonizing temperate saltmarshes (Riley *et al*., 2014). On the other hand, an equatorial population of the East African mangrove crab *Perisesarma guttatum*, belonging to the same family as *A. pisonii*, proved to be strongly affected by temperature increase. In a study conducted on tropical and subtropical populations of *P. guttatum* and fiddler crab *Uca urvillei*, Fusi *et al*. (2015) found that the latter species showed a very wide thermal niche, while the former demonstrated little thermal plasticity. In particular, Kenyan populations of *P. guttatum* were shown to live at the higher limit of their thermal window and compensated for acute heat stress by means of energy-costly physiological and behavioural mechanisms, which, in the long run, may not be sustainable. Crabs of the Sesarmidae have fundamental roles in the carbon and nutrient cycles within mangrove ecosystems (Lee, 1998; Cannicci *et al*., 2008) and their vulnerability to climate change is projected to result in major changes in ecosystem functioning, especially in the Indo-Pacific region.

Another strong impact of global warming on mangrove associated populations is from the effect that temperature has on their larval development and dispersion potential (O'Connor *et al*., 2007). Since mangroves are mainly associated with estuaries, deltas and creeks, they often are patchily distributed on tropical coasts. This uneven distribution can limit the connectivity between mangrove invertebrate populations, reducing their intrinsic genetic variability and, ultimately, affecting their overall phenotypic and thermal, plasticity. To cope with these limitations, mangrove crabs and molluscs have evolved highly specialized reproductive behaviour, which allow them to spawn during the fastest ebbing tides of their reproductive seasons, to maximize larval dispersal and population connectivity (Skov *et al*., 2005). However, in a warmer ocean, the larval duration of benthic species will be shorter, due to the increase in metabolic rate and faster growth rate, and the dispersal potential of these life-stages could be significantly lower, resulting in further reduced connectivity between mangrove populations (O'Connor *et al*., 2007; Hoegh-Guldberg and Bruno, 2010).

3.6.2.2 Increased atmospheric CO_2

Atmospheric CO_2 concentrations have increased at about 2 ppm per year over the last decade, and further increased concentrations are very likely (IPCC, 2013). Increased CO_2 enhances the growth of mangrove trees (Wong *et al*., 2014), being a reactant in photosynthesis. Experimental work on mangrove *Rhizophora mangle* seedlings grown in doubled levels of CO_2 demonstrated significantly increased biomass, total stem length, branching activity and total leaf area compared with seedlings grown in ambient levels of CO_2 of 350 μmol mol^{-1} (Farnsworth *et al*., 1996) (N.B. current atmospheric levels of CO_2 have now reached 400 μmol mol^{-1}). The benefits of increased CO_2 may, however, only occur where mangroves are not limited by high salinity or humidity (Ball *et al*., 1997). Using a biogeochemical process model Luo *et al*. (2010) found that increasing atmospheric CO_2 concentration differentially affects net primary productivity of different mangrove species, with the greatest stimulating effects seen where mangroves suffer greater soil salinity stress.

Mangrove responses to increasing atmospheric CO_2 will be complex (Alongi, 2015), benefiting some species, while others show little change or a decline. Species patterns within estuaries may change based on the ability of each species to respond to spatial and temporal differences in salinity, nutrient availability, and other drivers in relation to increasing CO_2 levels (Alongi, 2015).

The digging and burrow-maintenance activities of the mangrove crabs of the families Sesarmidae and Ucididae have a major impact on soil biochemistry and carbon fluxes (Lee, 1998; Cannicci *et al*., 2008; Kristensen, 2008). Recently, it has been observed that the behaviour of these crabs result in an enhanced emission of CO_2 by mangrove forests (Pülmanns *et al.et al*., 2014). Both in Brazil, a *Ucides* spp. dominated area, and in New Caledonia, a sesarmid dominated one, burrow maintenance by crabs resulted in an increased reduction potential of the soil surrounding the burrows (Leopold *et al*., 2013; Pülmanns *et al*., 2014). This activity alters the microbial carbon oxidation from mainly anaerobic to partially aerobic, which results in higher CO_2 efflux rates. The implications of this consequence of crab burrowing behaviour both for mangrove ecosystems and global CO_2 emissions are yet to be analysed in detail. There is little research to date on the direct effects of increase in atmospheric increase in CO_2 and ocean acidification on mangrove crabs.

3.6.2.3 Precipitation changes

Climate change projections of precipitation changes show that these will not be uniform (IPCC, 2013). Mangroves feature taller, more productive and more diverse forests on coasts with higher rainfall, and have narrower extent, and lower diversity, height and biomass on more arid coastlines (Duke *et al*., 1998). On drier coasts, increasing salt tolerance occurs at the expense of growth (Duke *et al*., 1998), resulting in lower height of the canopy. For example, at the saline, arid Lake MacLeod, Western Australia, tree heights of *Avicennia marina* are <4.0 m, compared with wetter sites at the same latitude on the east coast of Australia where mangrove canopies are commonly >10 m (Ellison and Simmonds, 2003).

Increases in salinity in mangroves may result from reduced rainfall, more seasonal rainfall and reduced humidity. Reduced rainfall is expected to cause reduction in mangrove diversity, photosynthesis, and growth rates along with substrate subsidence (Smith and Duke, 1987; Rogers *et al*., 2005, 2006; Whelan *et al*., 2005). Reduced humidity is expected to cause reduced productivity and species diversity (Clough and Sim, 1989; Cheeseman *et al*., 1991; Cheeseman, 1994; Ball *et al*., 1997). Decreasing freshwater discharge from the River Indus has caused the quantity of water flow reaching the delta to reduce significantly, causing raised salinity of water within the landward mangroves to 50 ppt, resulting in large areas of mangrove loss in the last few decades (Giri *et al*., 2015). Storms bringing salt water further inland contribute to the impacts of salinity on mangroves (Kitula *et al*., 2015). With fresh water becoming more scarce, mangrove forests of arid coastlines such as NW Australia, Pakistan, Mexico and the Arabian Peninsula are likely to decline with future climate change (Alongi, 2015).

Salinity also has a strong influence on the development and growth of mangrove crabs and molluscs inhabiting mangroves. It is remarkable that very few mangrove crab species produce salinity tolerant larvae, even if they colonize habitats that are *per se* subject to variations in salinity, such as estuarine mangroves experiencing huge seasonal variation in freshwater input (Diele and Simith, 2006). Indeed, the vast majority of mangrove crab larvae show very low tolerance to both hypo- and hyper-saline conditions, and berried females have evolved specific behaviours to optimize the larval journey to the open ocean, ranging from spawning during the fastest ebb tides (Skov *et al*., 2005) to migrating off-shore to spawn (Hill, 1994). However, salinity proved to be an important parameter for juvenile and adult crabs as well, with growth of the juvenile stages of various species of the commercially important mangrove crab genus *Scylla*, intensively and extensively reared along all SE Asia, shown to be strongly influenced by salinity, with a general trend of reduced growth in hyper-saline conditions (Gong *et al*., 2015). Salinity also played a role in determining zonation and space partitioning among similar species. In Kenya, for instance, two congeneric species of burrowing crabs that feed on leaf litter, showed differential tolerances to hyper-salinity (Gillikin *et al*., 2004). In particular, *Neosarmatium africanum* (Figure 3.6.5A), the species occupying the landward belt of

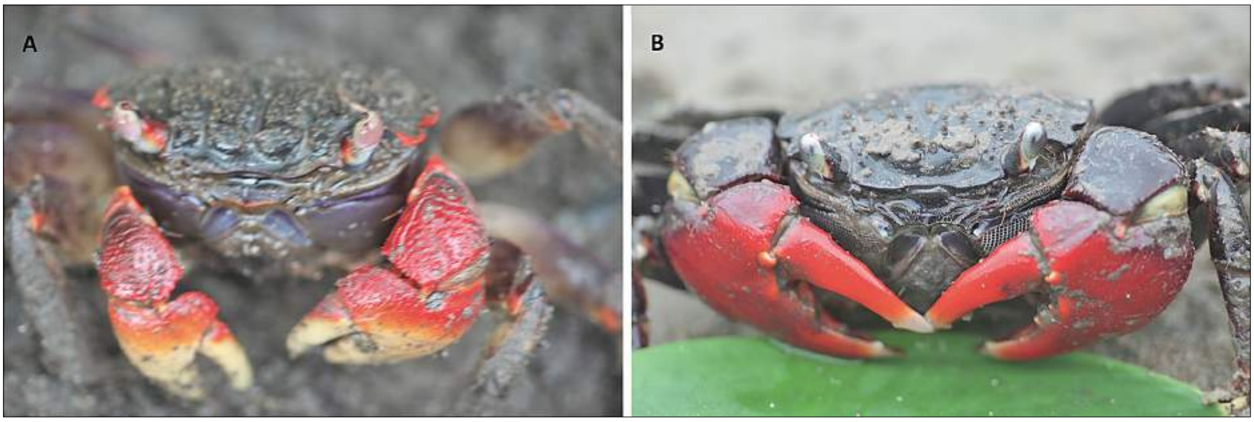

Figure 3.6.5 Mangrove burrowing crabs of Kenya. A. *Neosarmatium africanum* B. *Neosarmatium smithi.* © S. Cannicci.

the forest showed a higher tolerance to hyper-saline conditions, more common in its microhabitat, than *N. smithi* (Figure 3.6.5B) which is dominant in the seaward belt, where the pore water salinity is similar to the sea water.

3.6.2.4 Storms and high energy wave impacts

Climate change projections warn of an intensification of tropical and extra-tropical cyclones, combined with larger extreme waves and storm surges (IPCC, 2013). While storms provide sediment to mangroves to benefit accretion (Figure 3.6.3), wave action has increasing impact on trees. Increased inundation occurs with sea-level rise. Severe storms and hurricanes potentially may have significant impacts on mangroves, especially when combined with sea-level rise and squeeze from human land-uses or topography on the landward side (Godoy and Lacerda, 2015). Mangroves are among the 10 major terrestrial and marine ecosystems considered most vulnerable to tipping points due to their narrow environmental tolerances, their geographically restricted distribution, their proximity to dense human populations in coastal zones, their patchy and fragmented location in the country and their reliance on a few key framework species (Laurence *et al*., 2011). A comprehensive review of existing studies by Gedan *et al.* (2010) found strong support that coastal wetlands provide context-dependent protection of shorelines from storm surge flooding. With loss of mangrove wetlands due to human impacts (Spalding *et al*., 2010), such protection will be diminished.

At present, only one study has tried to quantify the effect of typhoon disturbance on diversity and abundance of crab communities in mangroves. Working in a Biosphere Reserve in Vietnam, Diele *et al*. (2013) showed that there was no significant difference in diversity and abundance of crab species between patches of old monoculture of *Rhizophora apiculata* and typhoon gaps where trees were downed. Interestingly, the biodiversity seemed to

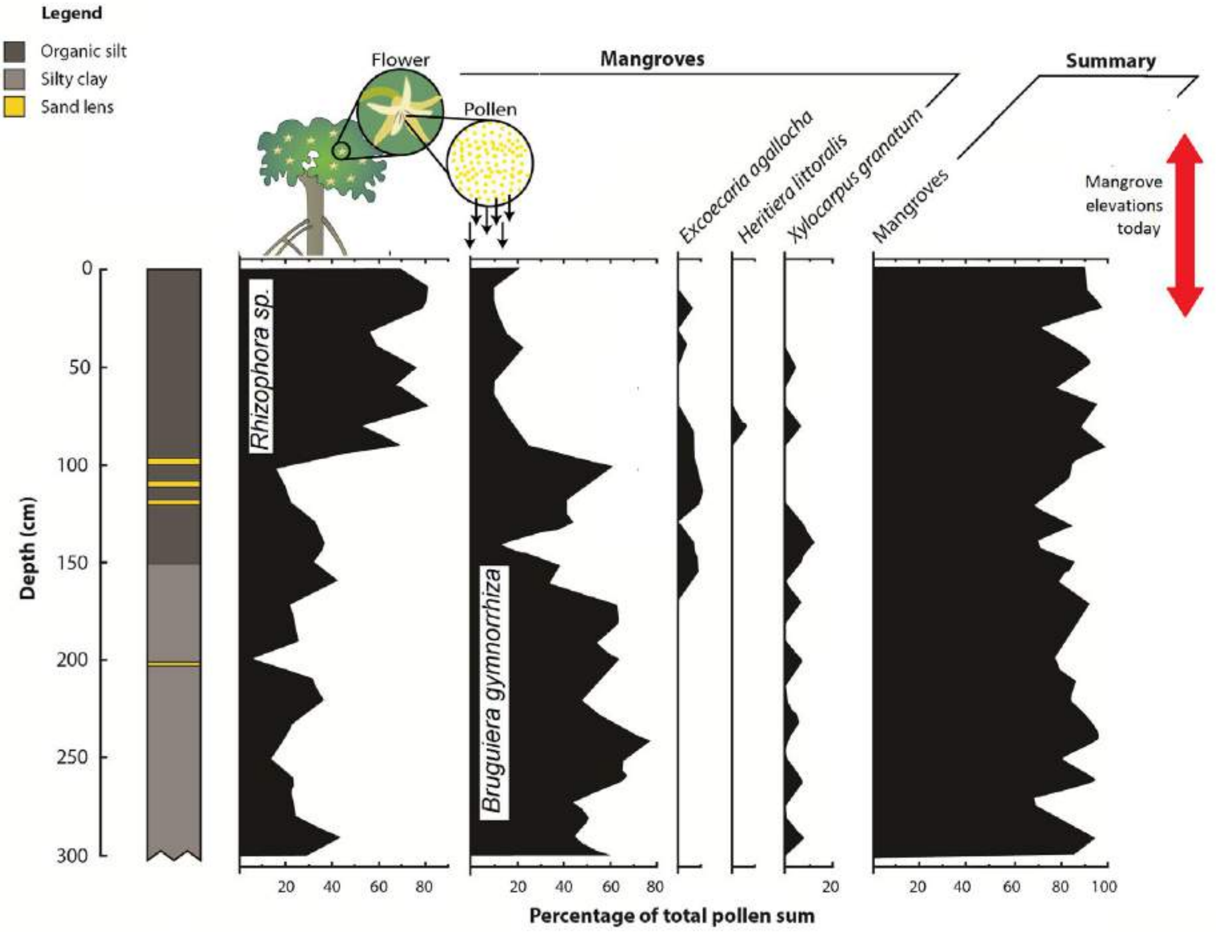

Figure 3.6.6 Mangrove palaeohistory at Tikina Wai, Fiji, during long-term RSLR of over 2 mm per year. Mangroves today grow at elevations shown by the red arrow, yet mangrove pollen dominates sediment deposits down to 3 m or more owing to accretion. Over time, from the base up, a landward community of *Brugueira* is replaced by a seaward community of *Rhizophora*, showing slow landward retreat (adapted from Ellison and Strickland, 2015).

increase, with new species colonizing the gaps, but total biomass decreased, with smaller crabs colonizing the gaps.

3.6.2.5 Sea-level rise impacts

Sea-level rise in the last few decades has largely resulted from ocean warming and thermal expansion (Church *et al*., 2013). The IPCC (2013) observed that sea-level rise since the mid-19th Century has been larger than the mean rate during the previous two millennia (high confidence). Over the period 1901 to 2010, global mean sea level rose by 0.19 [0.17 to 0.21] m. A global rise in mean sea level is projected for 2081–2100 relative to 1986–2005 of 0.2–0.98 m, depending on different emissions scenarios. The highest scenario would give a rate at the end of the 21st Century of 8–16 mmyr^{-1} (Church *et al*., 2013). There is strong consensus in the literature that sea-level rise is the major impact of climate change on mangroves (Gilman *et al*., 2008; Ellison, 2014, 2015; Parida *et al*., 2014; Alongi, 2015). Impacts will be exacerbated in locations of higher relative sea-level rise (RSLR) owing to local factors of coastal subsidence (Ellison and Strickland, 2015).

Mangrove accretion rates as determined from surface elevation tables and a sediment surface marker horizon are widely used and recommended for monitoring intertidal surface-elevation trajectories in coastal wetlands (Lovelock *et al*., 2015). Analysis of mangrove surface elevation data shows that about 50% of sites are not keeping up with RSLR, particularly low islands and subsiding locations (Alongi, 2015), with fringe mangroves more vulnerable than basin settings (Sasmito *et al*., 2016). Lovelock *et al*. (2015) also found that for the majority of locations, the current rate of sea-level rise exceeded the soil surface elevation gain, and mangroves with low tidal range and low sediment supply could be submerged as early as 2070, such as the Gulf of Thailand, the south-east coast of Sumatra, the north coasts of Java and Papua New Guinea and the Solomon Islands.

In conditions where RSLR exceeds net sediment accretion rates, mangrove zones retreat landward, as demonstrated from the tectonically subsiding coastlines of SW Papua (Ellison, 2005) and Tikina Wai, Fiji (Ellison and Strickland, 2015) (Figure 3.6.6). Mangrove species at the landward margin are particularly vulnerable to sea-level rise if recruitment inland is blocked owing to coastal development or topography (Di Nitto *et al*., 2008). Such species that occur at the landward edge, or upstream in tidal estuaries include *Brownlowia tersa, Bruguiera sexangula, Nypa fruticans, Phoenix paludosa, Lumnitzera racemosa, Lumnitzera littorea, Sonneratia caseolaris, Sonneratia lanceolata* and *Xylocarpus granatum* (Polidoro et al., 2014).

There is empirical evidence of an increase in mangrove extent at landward margins reviewed by Crase *et al*. (2015), and loss of mangroves from the seaward edge, which is a key sign of sea-level rise impacts (Gilman *et al*., 2008). Examples of records of mangrove seaward edge retreat attributed to sea-level rise are compiled in Table 3.6.1, and located in Figure 3.6.7.

Mangrove species occur within specific ranges between mean and high tide levels (Figure 3.6.3), and as such are vulnerable to habitat changes resulting from sea-level rise. Prolonged submergence and increased salinity reduces photosynthesis and seedling survival rates (Mangora *et al*., 2014), drowning of aerial roots of some adult species may cause death (Yáñez-Espinosa and Flores, 2011), along with changes in species dominance as zones move

Table 3.6.1 Mangrove seaward edge loss attributed to rising sea level

Location	Change reported	Source
Southern Sundarbans	Erosion and mangrove loss of seaward margins, with tidal currents a factor along with RSLR	Raha *et al*. (2014), Giri *et al*. (2015)
Southern Sundarbans	Mangrove retreat of up to 2.8 km 1968- 2014 with RSLR of 5 mm yr^{-1}	Ghosh *et al*. (2015)
Tutuila, American Samoa	Seaward edge retreat over four decades of 25-72m yr^{-1}, with RSLR of 2 mm yr^{-1}	Gilman *et al*. (2007)
Hungry Bay, Bermuda	Seaward edge retreat with RSLR of 2.6 mm yr^{-1}	Ellison (1993)
Douala, Cameroon	Over 60% of the mangrove seaward edge retreated at up to 3m yr^{-1} 1975-2007, with 89% loss of an offshore mangrove island	Ellison and Zouh (2012)

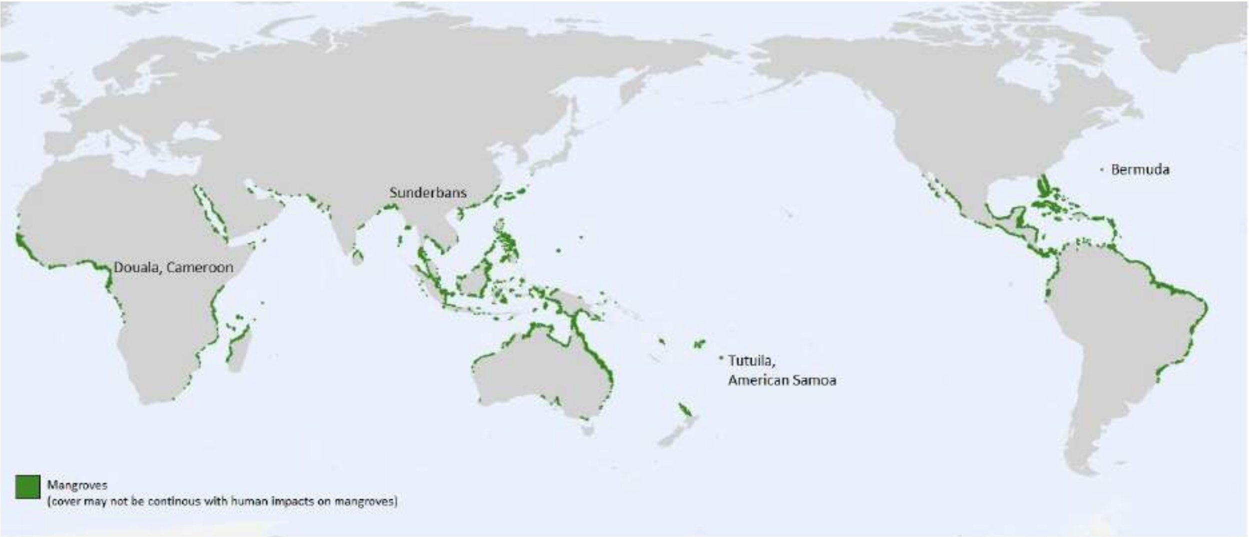

Figure 3.6.7 Locations with seaward edge dieback of mangroves owing to relative sea-level rise.

inland (Crase *et al*., 2015). Greater exposure is expected in areas with smaller tidal ranges compared to those with larger tidal ranges (Ellison, 2015). In Brazil, on northern macrotidal coasts, mangroves are mostly expanding landwards, whereas along southern microtidal coasts, mangroves are disappearing faster as a result of sea-level rise and saline intrusion (Godoy and Lacerda, 2015). Coastal squeeze of the narrower microtidal mangroves is also a major concern.

3.6.3 Conclusion and recommendations

The direct effects of the projected temperature increase driving ocean warming are likely to be mostly beneficial to mangroves, increasing mangrove productivity and biodiversity particularly at higher latitudes. The benefits of increase in atmospheric CO_2 are subject to the limiting factors of salinity, humidity and nutrients (Ball *et al*., 1997). Rainfall and humidity changes are of more significance to mangroves, particularly reduced rainfall decreasing productivity and biodiversity and causing relative subsidence exacerbating impacts from sea-level rise.

Projected sea-level rise is the main impact of ocean warming on mangroves, as such intertidal ecosystems are particularly vulnerable to changes in the frequency of tidal inundation. Accretion rates are already shown to be lagging behind RSLR at many places (Alongi, 2015; Lovelock *et al*., 2015), and landward relocation will be dependent on habitat availability, with many coastal lowlands having human modifications and barriers to such migration. Given the severity of the threat from sea-level rise in particular, it is essential that ways are developed to increase the resistance and resilience of mangroves, and increase adaptive capacity. As stated by the IPCC assessment of key vulnerabilities (Oppenheimer *et al*., 2014), loss of mangrove ecosystems would endanger the livelihoods of unique human communities (Figure 3.6.8) and cause economic damage.

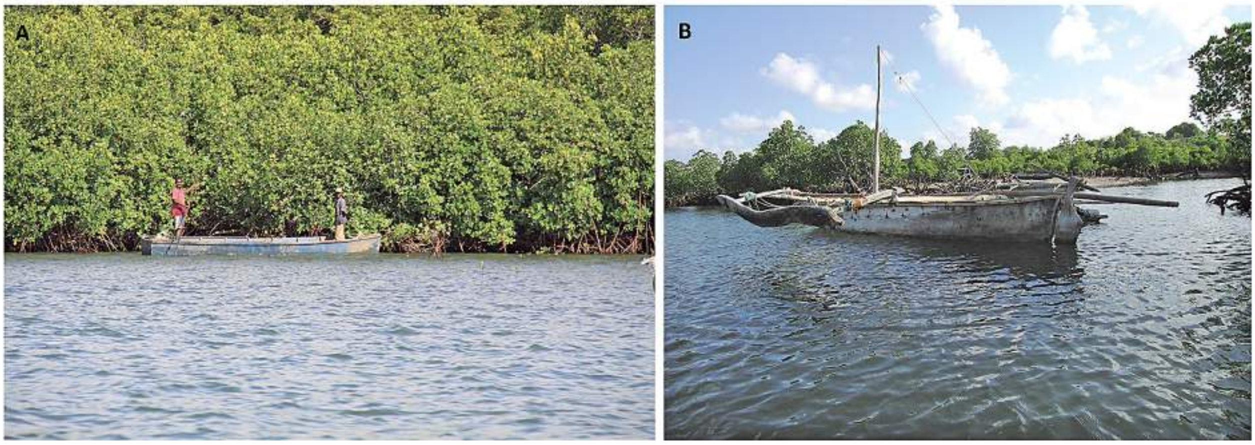

Figure 3.6.8 Traditional fishing in mangroves. A Tikina Wai in Fiji, where villages manage mangroves through monitoring and resource management committees. © R Anders. B. Traditional Ngalawa fishing in mangroves, Tanzania. © S. Cannicci.

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3.7 Impacts and effects of ocean warming on intertidal rocky habitats

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Summary

- Intertidal rocky habitats comprise over 50% of the shorelines of the world, supporting a diversity of marine life and providing extensive ecosystem services worth in the region of US$ 5-10 trillion per year.
- They are valuable indicators of the impacts of climate change on the wider marine environment and ecosystems.
- Changes in species distributions, abundance and phenology have already been observed around the world in response to recent rapid climate change.
- Species-level responses will have considerable ramifications for the structure of communities and trophic interactions, leading to eventual changes in ecosystem functioning (e.g. less primary producing canopy-forming algae in the North-east Atlantic).
- Whilst progress is made on the mitigation[1] required to achieve goals of a lower-carbon world, much can be done to enhance resilience to climate change. Managing the multitude of other interactive impacts on the marine environment, over which society has greater potential control (e.g. overfishing, invasive non-native species, coastal development, and pollution), will enable adaptation[1] in the short and medium term of the next 5-50 years.

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[1] See IPCC Assessment Reports (2005 onwards) for usage.

Ocean warming effect	Consequences
Species range extensions and retractions	Changes in composition and structure of intertidal communities Reduced primary production and supply of detritus to inshore food webs Some reduction in provisioning and regulating services
Changes in vertical shore distributions	Changes in composition and structure of intertidal communities Reduced extent of suitable habitat for intertidal organisms Some reduction in provisioning and regulating services
Shifts in phenology	Promotion of multi-brooding warm-water species Increased reproductive failure of single-brooding cold-water species Changes in composition and structure of intertidal communities Trophic mismatches may have ramifications for commercial fisheries
Species invasions	Promotion of nuisance and fouling species Reduced diversity of native species Changes in composition and structure of intertidal communities Potential positive and negative effects on commercial fisheries and regulatory and cultural services
Proliferation of sea defences (adaptation to rising and stormier seas)	Loss and disturbance of natural sedimentary habitats and species Changes in connectivity as a result of ocean sprawl Assisted spread (via stepping stones) of non-native species Assisted range shifts (via stepping stones) of native species Potential positive and negative effects on primary production and cultural services
Range extension, species invasion and proliferation of sea defences combined	Promotion of biotic homogenization with negative implications for all ecosystem service provision

3.7.1 Introduction

The intertidal zone is the most accessible part of the ocean. Shoreline habitats have been heavily-exploited since the time of hunter-gatherers and increasingly used for recreation by modern societies. It is also the best-studied part of the ocean with formal scientific investigation going back to the time of Aristotle (Hawkins *et al.,* 2016). We focus here on rocky shores for three main reasons. Firstly, they have been subject to extensive broad-scale and long-term studies in many parts of the world – particularly in the North-east Atlantic and North-east Pacific. They have also been the focus of considerable field experimentation because of their ease and tractability for manipulative study (Connell, 1972; Paine, 1994; Hawkins *et al.,* 2016). Thus, the link between pattern and process in these systems is well-established, enabling better interpretation of the direct and indirect effects of climate change. Secondly, rocky intertidal organisms must contend regularly with both marine and atmospheric (at low tide) conditions on a daily basis, and so are subject to challenges posed by both aquatic and aerial environmental regimes, which are amplified by climate change. Thirdly, fluctuations in intertidal species have been found to mirror changes in other species further offshore (Southward, 1980; Helmuth *et al.,* 2006b; Mieszkowska *et al.,* 2014a). Rocky shores have, therefore, long been used as easily-observed indicators of the influence of climate fluctuations on the wider marine environment (e.g. Southward and Crisp, 1954; Southward, 1963, 1980, 1991; Southward *et al.,* 1995). They have proved valuable sentinel systems in early detection of recent rapid climate change (Barry *et al.,* 1995; Sagarin *et al.,* 1999; Mieszkowska *et al.,* 2006, 2014b; Hawkins *et al.,* 2009), as well as for forecasting and predicting future trends (Helmuth *et al.,* 2006b; Poloczanska *et al.,* 2008;Hawkins *et al.,* 2009; Wethey *et al.,* 2011).

Intertidal rocky habitats are directly and indirectly affected by the global environmental changes associated with current climate warming and ocean acidification. In addition they are subject to frequent invasions by non-native species, which has contributed to the global homogenization of biota (e.g. Trowbridge, 1995; Streftaris *et al.,* 2005; Allen *et al.,* 2006; García Molinos *et al.,* 2016). Global-scale influences are often, however, less obvious than acute regional- and local-scale impacts from both land and sea (see Thompson *et al.* (2002) for review). Regional-scale impacts can include the consequences of overfishing on mobile fish and shellfish using the intertidal as feeding or nursery grounds, and eutrophication of enclosed seas. Local-scale impacts can include eutrophication at the scale of enclosed bays or inlets, point-source pollution, coastal development, over-harvesting for food, curios and bait, trampling due to recreational activity, and sedimentary input. Some of these local impacts can scale up to have regional-scale effects (Huston, 1999; Airoldi *et al.,* 2005a). For example, urban coastlines are frequently modified by engineered developments such as port, road and rail infrastructure, industry and housing, as well as sea defences built to reduce erosion or flood risk. This has led to additive effects in terms of hardening and linearization of long stretches of coastlines, and replacement of natural sedimentary habitats by artificial rocky shores, which often support impoverished biodiversity compared with natural shores (discussed further below).

In this section, we discuss rocky intertidal habitats and the observed and predicted effects of climate change on the species and communities that inhabit them. We first summarize the biodiversity and ecosystem services supported by rocky shores, along with the major factors determining the distribution of species at global, regional and local scales (drawing largely on Raffaelli and Hawkins (1996) and Thompson *et al.* (2002)). The responses of rocky shore species to past climate fluctuations and recent rapid change are then presented, with consideration of the consequences for communities and ecosystem functioning. We focus largely on the North-east Atlantic biogeographic region because of the wealth of broad-scale and long-term studies that provide a baseline, although other global examples are presented. To inform adaptive management to climate change, we then explore the mechanisms and drivers of change, and consider potential interactions with other impacts acting at regional and local scales. Some positive suggestions for adaptation are proposed, including ecologically-sensitive design of sea defences that are built in response to rising and stormier seas.

3.7.2 Intertidal rocky shores and their global and regional significance

3.7.2.1 Definition and extent

At the interface between land and sea, intertidal rocky habitats connect the marine environment with terrestrial habitats beyond the influence of sea spray. The seaward transition towards the subtidal zone is part of a continuum from rocky shore to submerged reef, but the lower intertidal boundary may be considered the lowest level exposed to the air during lowest tides. Shore platforms and reefs often give way, both horizontally and vertically, to depositing boulder and cobble fields, gravel or sand.

Intertidal rocky habitats occur extensively along both open and sheltered coasts globally, comprising well over 50% of the shorelines of the world (Emery and Kuhn, 1982; Davis and Fitzgerald, 2004). The extent of intertidal hard substrata is increasing due to the proliferation of engineered coastal structures such as breakwaters, groynes and sea walls, built to protect people, property and infrastructure from rising and stormier seas (Thompson *et al.,* 2002; Firth *et al.,* 2013a, 2016a). These artificial rocky habitats are not, however, the same as natural rocky shores. Although they are often colonized by common rocky shore organisms, they are frequently found to support less diverse communities (Moschella *et al.,* 2005; Pinn *et al.,* 2005; Firth *et al.,* 2013b, 2016b; Aguilera *et al.,* 2014), with opportunistic and invasive species taking advantage of the novel habitat (Bulleri and Airoldi, 2005;

Glasby *et al.,* 2007; Vaselli *et al.,* 2008; Bracewell *et al.,* 2012; Firth *et al.,* 2015). Nevertheless, in light of the predicted reduction in spatial extent, through loss of natural intertidal rocky habitats as sea levels rise ("coastal squeeze", e.g. Jackson and McIlvenny (2011)), these artificial structures may provide surrogate habitats for rocky shore organisms (see Para. 3.7.5).

3.7.2.2 Biodiversity and ecosystem services

Rocky shores are home to a wide variety of marine flora and fauna that have upwardly colonized the intertidal zone from fully marine conditions. Thus, they host far fewer organisms of terrestrial evolutionary origin. Seaweeds and sessile animals (e.g. barnacles, sea anemones, bivalves and sponges) find secure attachment on the hard substratum. Mobile animals (e.g. snails, crustaceans and fish) forage for food over the reef at high tide, some taking refuge in abundant pits, pools and crevices when the tide is out (Silva *et al.,* 2008, 2010, 2014; Taylor and Schiel, 2010). Some rocky shore species are considered of particular conservation concern on account of their rarity, for example the highly endangered limpet *Patella ferruginea* and *Scutellastra mexicana* (García-Gómez *et al.,* 2011, 2015). Others are of conservation value due to their importance in ecosystem functioning, for example the reef-building worm *Sabellaria alveolata* (Dubois *et al.,* 2002; Frost *et al.,* 2004).

Intertidal rocky habitats support a number of important ecosystem services for human well-being (The Economics of Ecosystems and Biodiversity: TEEB, 2010). Based on an interpolation of figures presented in a recent valuation of global ecosystem services (Costanza *et al.,* 2014), the estimated value of services supported by intertidal rocky habitats globally may be somewhere in the realm of US$ 5-10 trillion per year. In terms of *production services*, marine photosynthesis accounts for 50% of total global primary production, of which a considerable proportion is attributable to marine macrophytes in the coastal zone where seaweeds and seagrass detritus drive food webs (Beardall and Raven, 2004; Chung *et al.,* 2011). Highly productive macroalgae are common on rocky shores; the overall productivity of rocky habitats tends to be an order of magnitude higher than sedimentary ones (Bourget and Ricciardi, 1999). Habitat amelioration by seaweed canopies (Thompson *et al.,* 1996; Moore *et al.,* 2007; Teagle *et al.,* 2016; Walls *et al.*, 2016) and trophic exchange (Menge *et al.,* 1997) can lead to successional development of diverse benthic and pelagic marine communities. Detached macroalgae can even subsidise low productivity of terrestrial ecosystems by export through strandlines (Ince *et al.,* 2007). In terms of *provisioning services*, rocky shores are inhabited by a number of edible species that can be exploited as a food or bait resource, for example seaweeds, mussels, winkles, oysters and limpets (Keough *et al.,* 1993; Kyle *et al.,* 1997; Airoldi *et al.,* 2005b; Martins *et al.,* 2010). They can further provide nursery habitat for juvenile commercial fish and shellfish (Rangeley and Kramer, 1995; Silva *et al.,* 2010). Common and abundant macroalgal species may also be harvested for biofuel production (Maceiras *et al.,* 2011) and for biochemical derivatives used for additives to food, cosmetics and pharmaceuticals (Pereira *et al.,* 2013). Both harvested seaweeds and those collected from strandlines are also used as fertilizer or soil conditioners. In terms of *regulatory services*, intertidal communities can take an important role in regulating environmental conditions. For example, macroalgae (Figure 3.7.1) are important for carbon sequestration and macro-nutrient (nitrogen and phosphorus) removal (Chung *et al.,* 2011), while bivalves and macrophytes are important for water purification (Kohata *et al.,* 2003). Biofiltration is particularly important for regulating water chemistry and controlling potentially-harmful phytoplankton blooms (Hily, 1991; Allen *et al.,* 1992; Newell, 2004; Fouillaron *et al.,* 2007). Water filtration by diverse rocky-reef assemblages can therefore be linked to societal benefits for coastal communities (Lamberti and Zanuttigh, 2005). Biogenic reef-forming species and kelp beds also provide regulatory services in terms of natural coastal protection, by attenuating wave energy and stabilizing sediments (Mork, 1996; Naylor and Viles, 2000; Borsje *et al.,* 2011). Finally, in terms of *cultural services*, where rocky shores are close to, and easily-accessed by, coastal communities and tourists, they can support a number of direct and indirect uses. They are highly valued for recreational uses such as rock-pooling, angling, snorkelling and

Figure 3.7.1 *Laminaria digitata.* © John M Baxter.

environmental education (Firth *et al.,* 2013a). As coastal habitats become increasingly threatened by a number of interacting pressures (Thompson *et al.,* 2002; Knights *et al.,* 2013), and canopy algae are suffering widespread declines in many parts of the world (Airoldi and Beck, 2007; Connell *et al.,* 2008; Mangialajo *et al.,* 2008; Mineur *et al.,* 2015), conservation of rocky shores becomes increasingly important to ensure maintenance of these essential ecosystem services.

3.7.2.3 Factors influencing biodiversity in intertidal rocky habitats

The distribution of species on rocky shores around the world is largely driven by broad-scale climatic regimes, associated with latitude and modified by ocean currents and upwelling regimes (Hutchins, 1947; Helmuth *et al.,* 2006b; Fenberg *et al.,* 2015). There are warm- and cold-water adapted species, leading to different species pools able to live in different biogeographic areas. The species pool is ultimately determined by phylogeographic processes associated with the evolutionary origin of species and their subsequent spread in response to tectonic and climatic processes over long geological timescales, including opening and closing of ocean basins (Rivadeneira *et al.,* 2015). Natural biogeographical processes have been altered, however, by human-mediated transport of species around the world. In the ocean this has occurred via transport of organisms fouling ships and in ballast water, and also via accidental and deliberate introductions associated with aquaculture and the ornamental aquarium trade. Marine canals can also enable species to take short-cuts between biogeographic regions. For example, the Suez Canal has acted as a conduit of numerous species from the Indo-Pacific biogeographic realm of the Red Sea to the Mediterranean (so-called Lessepsian migration: Por (1978)). This has had a profound effect on the eastern and wider Mediterranean. Expansions and contractions of glaciation have also had a strong influence on species pools. For example, during the trans-Arctic interchange which occurred approximately 3.8 million years ago, groups of organisms migrated into the North-east Atlantic from the North Pacific (Cunningham and Collins, 1994). Recent changes in ice cover in the Arctic, opening up the North-west Passage, have again led to species entering or re-entering the Atlantic from the Pacific (e.g. Reid *et al.,* 2007). This is likely to accelerate if warming continues (Wisz *et al.,* 2015).

Within broad biogeographic constraints, the biological communities that develop on rocky shores are ultimately determined by the ability of different species to first recruit, and then to tolerate local environmental stress gradients acting at different spatial and temporal scales, and by biological interactions with neighbouring organisms (see reviews by Hutchins, 1947; Lewis, 1964; Little and Kitching, 1996; Raffaelli and Hawkins, 1996). Regional-scale variation in salinity, pollution, and nutrient and sediment loads influence species distributions, particularly around estuaries and near to human settlements. At local scales, rocky shores are characterized by steep and largely-predictable environmental gradients, both vertically (low to high shore) and horizontally (sheltered bays to exposed headlands). Intertidal organisms experience desiccation stress and temperature fluctuations during emersion. These stressors increase unidirectionally along the vertical gradient, from low to high shore, as emersion time increases (Foster, 1971; Raffaelli and Hawkins, 1996). Since some organisms are more tolerant to desiccation and temperature fluctuations than others (e.g. Connell, 1961a; Schonbeck and Norton, 1978; Dring and Brown, 1982), species distributions are limited along this vertical gradient. Along horizontal wave exposure gradients, physical disturbance regimes (e.g. from wave energy and scouring by suspended sediments) change, but the influence of wave action on organisms is not unidirectional. Some species thrive in wave-swept conditions, for example suspension feeders such as mussels (Moschella *et al.,* 2005; Vaselli *et al.,* 2008). Others favour shelter, for example intertidal canopy-forming macroalgae in the North-east Atlantic (Lewis, 1964; Jonsson *et al.,* 2006). Some kelp canopy species, however, prosper in wave-exposed conditions (e.g. *Postelsia palmaeformis* in the North-west Pacific: Blanchette (1996), and *Laminaria* species in Europe: Hawkins and Harkin (1985), Smale *et al.* (2015)). Biological interactions such as grazing can also set distribution limits along wave exposure gradients (Hawkins, 1981; Harley, 2003; Jenkins *et al.,* 2005; Taylor and Schiel, 2010). For example, establishment of large brown algae on European shores is prevented by grazing, but persistence is determined by wave action (Jonsson *et al.,* 2006). Microhabitats such as rock pools, crevices and gullies modify and provide refuge from physical stressors, creating a mosaic of environmental conditions and enabling rocky shores to support diverse communities of marine life. These microhabitats further shape spatial patterning on shores as they provide shelters from and in which grazers (Noël *et al.,* 2009; Skov *et al.,* 2011) and predators (Fairweather, 1988a; Johnson *et al.,* 1998b) forage, sometimes creating "haloes" of bare rock (Fairweather, 1988b). Where larger consumers are present, they are also important for providing refuge from predation and grazing pressure (Menge and Lubchenco, 1981), influencing the potential for species to co-exist.

Environmental conditions experienced by rocky shore communities vary, relatively predictably, on short (tidally and daily) and medium (seasonally) time scales. For example, tidal cycles, and diurnal and seasonal weather patterns lead to variation in stresses experienced during low tide windows and disturbance from wave energy and scouring. Occasional natural catastrophic events occur, however, such as extreme cold winters (Crisp, 1964; Todd and Lewis, 1984) or hot springs and summers (Hawkins and Hartnoll, 1985; Harley, 2008; Smale and Wernberg, 2013), extreme storms (Perkol-Finkel and Airoldi, 2010; Benedetti-Cecchi *et al.,* 2015) and toxic algal blooms (Southgate *et al.,* 1984), which are less predictable in their occurrence and effects. Superimposed on local

Box 3.7.1 Shifting ranges

In recent years, range extensions have been recorded for a number of rocky intertidal species in the North-east Atlantic. Around the UK, a number of southern warm-adapted species have shown northwards and eastwards extensions along the Welsh and Scottish coastlines, and eastwards extensions into the cooler Eastern English Channel basin (Figure 1). In some cases, artificial structures (e.g. piers, breakwaters) have probably aided range extensions by acting as stepping stones between previously-isolated rocky intertidal habitats.

Likewise, in California, the northern limits of a number of rocky intertidal species have expanded up the coast in recent years (Figure 2). For *Mexacanthina l. lugubris*, the expansion is thought to be due to a combination of factors, including the spatial availability of habitat and food, high abundances near their historical range limit, and increasing sea surface temperatures. Other species, however, such as the limpet *Lottia gigantea*, have experienced a range contraction, presumably due to sporadic recruitment success and naturally low abundances towards its northern limit.

Responses to climate change are species-specific and dependent on coastal context, with the same species responding differently in different locations.

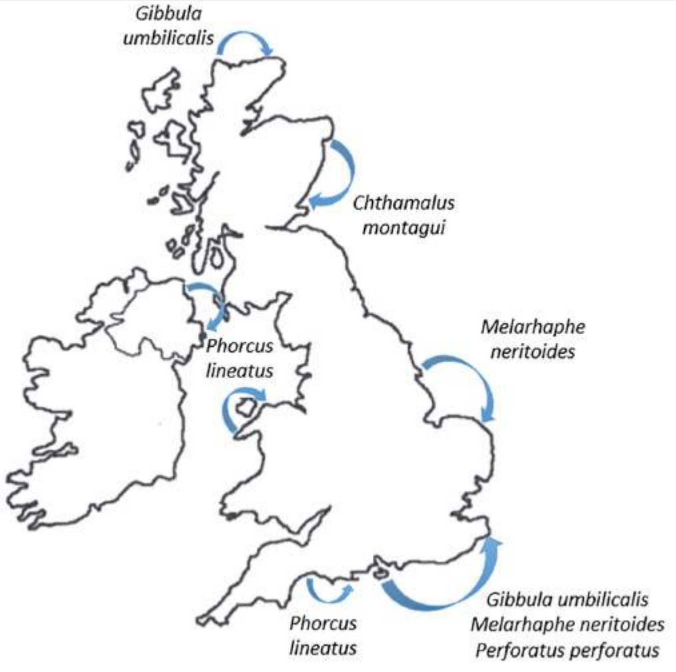

Figure 1 Some examples of range extensions in rocky intertidal species around the UK. Arrows indicate the limit to which each of the species ranges have reached and the direction of extension (Herbert *et al.*, 2003, 2009; Mieszkowska *et al.*, 2005, 2006, 2007; Hawkins *et al.*, 2009).

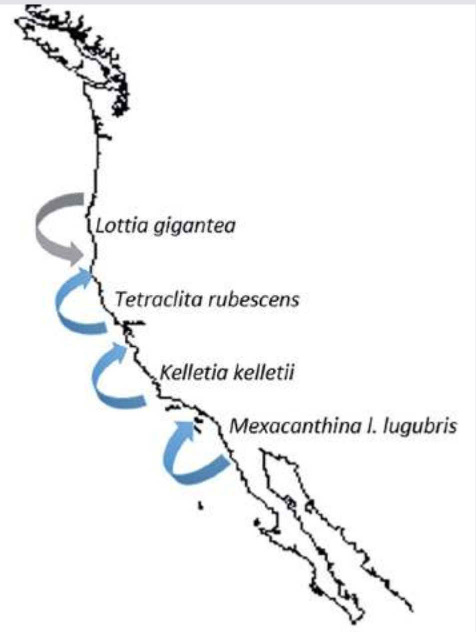

Figure 2 Some examples of range extensions and contractions in rocky intertidal species along the Californian coast. Arrows indicate the limit to which each of the species ranges have reached and the direction of shift (Zacherl *et al.*, 2003; Dawson *et al.,* 2010; Fenberg and Rivadeneira, 2011; Fenberg *et al.*, 2014).

gradients are broad-scale (with geographic setting) and longer-term climate fluctuations, and more recent rapid anthropogenic climate change. The signal of climate fluctuations and change is of low amplitude and long wavelength compared to the noise of weather and tidal cycles. The 'openness' of intertidal populations, because larvae and propagules are often recruited from outside sources, can often lead to unpredictable variability and patchiness of species distributions both spatially and temporally (Underwood and Fairweather, 1989; Burrows *et al.,* 2010). Disentangling the effects of climate change from species responses to shorter-term fluctuations and natural variability is a challenging, yet key, task for predicting impacts and their subsequent mitigation (Southward *et al.,* 1995; Hawkins *et al.,* 2008, 2009; Mieszkowska *et al.,* 2014b).

3.7.3 Climate change: trends and impacts

IPCC Assessment Reports (2007, 2014) have briefly reported some of the responses to climate change observed in rocky intertidal habitats. Here we summarize the main trends and impacts on species, assemblages and communities recorded in the literature, and outline the key drivers and mechanisms of change.

3.7.3.1 Geographical distribution and abundance of species

One of the global "fingerprints" of climate change, recorded consistently across natural systems, is the steady shift of the geographical ranges of species towards the poles as the climate warms (Walther *et al.,* 2002; Parmesan and Yohe, 2003; Root *et al.,* 2003; Burrows *et al.,* 2011; Sunday *et al.,* 2012; Bates *et al.,* 2014). Range extensions occur over time as a result of increasing abundance in populations towards the leading (often poleward) range limits, leading to expansions into previously uncolonized habitat. For example, the predatory gastropod *Mexacanthina lugubris lugubris* recently expanded its northern range limit into southern California, which was likely facilitated by high abundances and a wealth of habitat availability and food resources at its historical northern range limit (in northern Baja California Mexico; Box 3.7.1 Figure 2, Fenberg *et al.* (2014)). Conversely, retractions at the trailing (often equatorward) edge are a result of declining abundance, leading to local extinctions of populations due to lack of recruitment. However, range contractions associated with lack of recruitment and low abundances toward poleward limits have also been observed (Box 3.7.1 Figure 2, Fenberg and Rivadeneira (2011)). Changes in abundances are often driven by altered survivorship and reproductive success under fluctuating ambient conditions, punctuated by advances and retreats caused by extreme events (Hutchins, 1947; Crisp, 1964; Southward, 1980; Southward *et al.,* 1995; Wethey *et al.,* 2011; Poloczanska *et al.,* 2013; Smale and Wernberg, 2013; Spinuzzi *et al.,* 2013; Bates *et al.,* 2014; Firth *et al.,* 2016a).

In the North-east Atlantic biogeographic region, long-term and broad-scale study of intertidal rocky habitats has revealed clear patterns of ecological change in response to climate fluctuations. In particular, building on early time series studies (Southward and Crisp, 1954, 1956; Southward, 1963, 1967, 1991), there is growing evidence of changes in the abundances and distributions of species in the English Channel (Southward, 1991; Southward *et al.*,1995; Hawkins *et al.,* 2008, 2009; Mieszkowska *et al.,* 2014a). Barnacles are valuable "model systems" in rocky intertidal ecology. They are easily quantified and compete for clearly definable resource space (Connell, 1961a). In recent decades, fluctuations have been recorded in the relative abundances of warm- and cold-water barnacle species on North-east Atlantic rocky shores, with warm-water species (*Chthamalus stellatus* and *C. montagui*) flourishing in the warmer 1950s (Southward and Crisp, 1954) and the colder-water species (*Semibalanus balanoides*) doing well in the cooler 1930s, 1960s and 1970s (Moore and Kitching, 1939; Southward, 1967, 1991; Hawkins *et al.,* 2003). Consistent warming since the late 1980s, which has exceeded previous levels (Box 3.7.2 Figure 1, Hawkins *et al.* (2008, 2009), Firth *et al.* (2015)), has led to a subsequent decline in *S. balanoides* and an increase in the warm-water *Chthamalus* species, which are now more abundant than in the 1950s (Box 3.7.3 Figure 1, Mieszkowska *et al.* (2014a)). Poloczanska *et al.* (2008) used a 40-year time series to develop models involving interactions between the two species to investigate the processes explaining past fluctuations and predicting future shifts. They showed that, although *S. balanoides* is the faster-growing dominant competitor (Connell, 1961a), warm years negatively affected its recruitment, thereby releasing *Chthamalus* species from competition. Using future climate predictions under alternative emissions scenarios (low, medium-low, medium-high and high future scenarios as defined by the UK Climate Impacts Programme: Hulme *et al.* (2002)), they predicted that *S. balanoides* would eventually go extinct in south-west Britain, and that barnacle populations in the British Isles would eventually resemble those in Portugal and Spain

Box 3.7.2 Sea surface temperature (SST) – long-term trends, short-term fluctuations & species responses

Long-term records of sea surface temperature (SST) such as those off Plymouth, UK (Figure 1) show considerable fluctuations over the last 140 years, with warmer periods (1890s, 1950s) alternating with colder spells (1900-20, 1962-87) before the recent period of accelerated warming. The record is punctuated by extremely cold winters such as 1962-63 associated with North Atlantic oscillation negative index years. More recently there were cold winters in 2008-09 and 2010-11. These broad-scale oceanographic patterns of temperature are modulated by local micro-environmental variation – especially in the intertidal when exposed to air at low tide. Figure 2 illustrates this in intertidal mussels which are much warmer than their predator the starfish, *Pisaster ochraceous*. *In situ* temperatures can be logged by deploying sensors within limpet shells ("robolimpets"). Figure 3 shows that differences due to microhabitat and shore level can be as important as geographic setting.

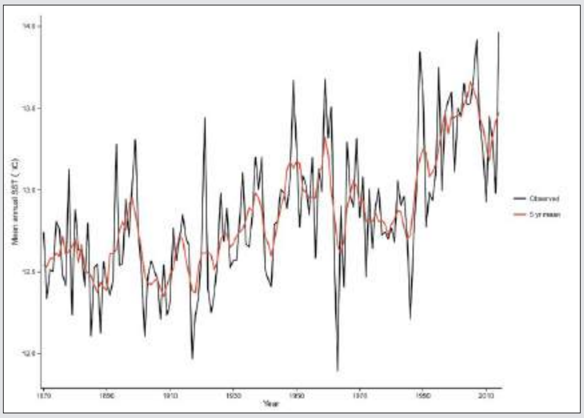

Figure 1 Mean annual sea surface temperature (SST) 1870-2014 off Plymouth, UK (Met Office Hadley Centre). Black line indicates annual mean temperature; red line indicates 5-year running average.

Figure 2 Thermal imagery of the seastar *Pisaster ochraceous* feeding on a bed of *Mytilus californianus* mussels illustrates how intertidal animals can experience different body temperatures when exposed to identical ambient temperature (Helmuth, 2002).

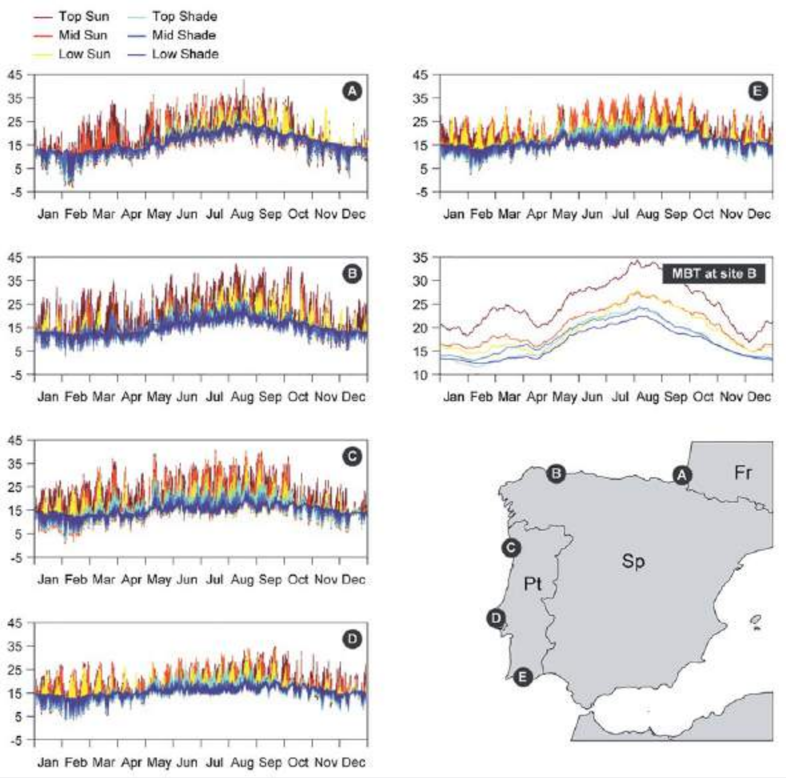

Figure 3 Body temperature profiles obtained by "robolimpets" deployed in different microhabitats (depicted by different line colours): (A-E) profiles recorded at 5 sites along the Atlantic coast of the Iberian Peninsula; (MBT at site B) 30-day rolling average of daily maxima at La Caridad (adapted from Seabra *et al.*, 2011).

Box 3.7.3 Long-term monitoring & historical data reveal community and phenological responses in rocky intertidal indicator species

Barnacles are good indicators of climate change responses. Long-term monitoring at Cellar Beach, UK, shows that the warm-water Chthamalid barnacles predominated in the warm 1950s; in the cooler 1960s, 1970s and early 1980s the more northerly-distributed *Semibalanus balanoides* was generally more abundant. From the 1990s onwards, the warm-water *Chthamalus* increased in abundance whilst *Semibalanus* became much rarer (Figure 1). Changes in barnacles mirror changes offshore in plankton and fish in the Western English Channel. Fluctuations in warm-water pilchards and cold-water herring have been reconstructed back to the middle ages using historical methods. Over the last 60 years such fluctuations broadly match those in barnacles (Figure 2). In addition to shifts in distribution and changes in abundance, phenological shifts have occurred. A southern species of limpet, *Patella depressa*, is now reproductively active for most of the summer in the UK, whereas it used to only reproduce once at most. Conversely the northern species, *Patella vulgata*, has shown failure years recently as its reproductive season has been pushed later (Figure 3).

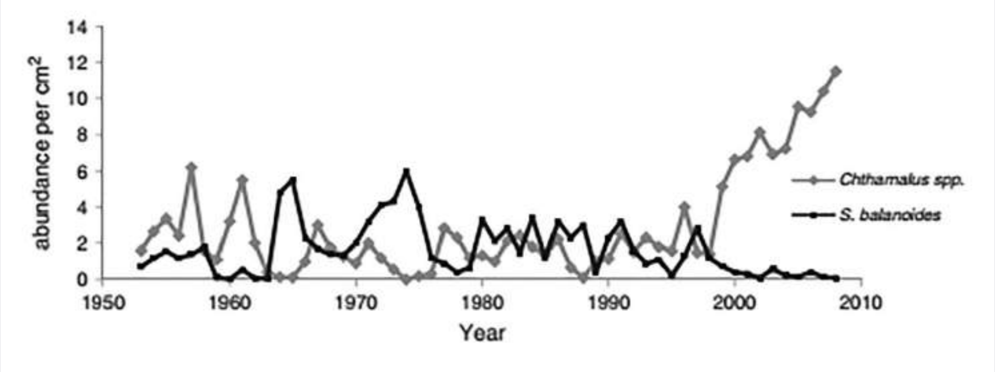

Figure 1 Abundance per cm^2 of the warm-adapted *Chthamalus* spp. and cool-adapted *Semibalanus balanoides* in the mid-shore region at Cellar Beach, Southwest UK, 1950s-2000s (Mieszkowska *et al.*, 2014a).

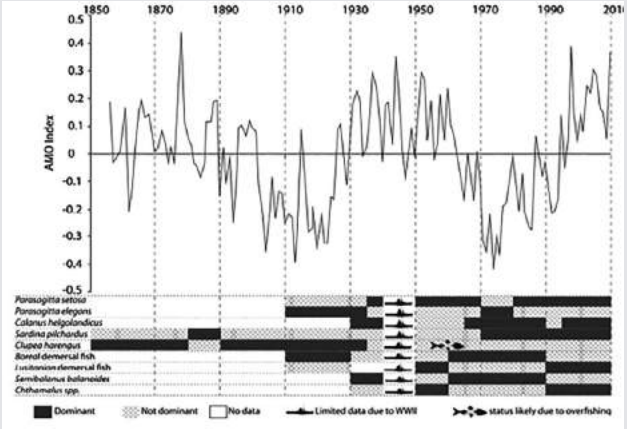

Figure 2 Annual Atlantic Multidecadal Oscillation (AMO) with phases of key taxa of warm- and cold-water biogeographic origins in the western English Channel (Mieszkowska *et al.,* 2014a).

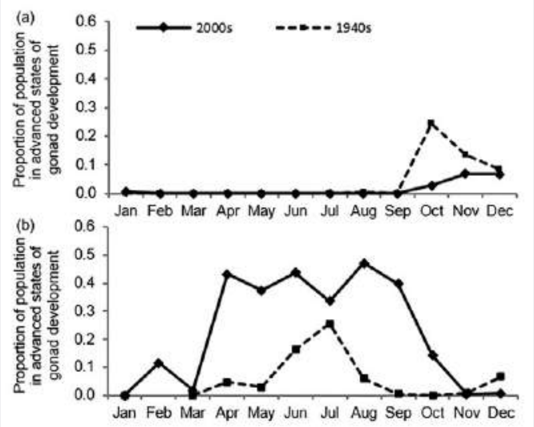

Figure 3 Mean monthly proportion of limpets in the SW of England in advanced states of gonad development in the 1940s (1946-1949) and the 2000s (2003-2007): (a) northern cool-adapted species *Patella vulgata* and (b) southern warm-adapted species *P. depressa* (adapted from Moore *et al.,* 2011).

(Box 3.7.4 Figure 1, see also Hawkins *et al.* (2008, 2009)). Wethey *et al.* (2011) have already shown that *S. balanoides* has fluctuated between abundant and absent at its current southern limit in Galicia over the last 50 years, which they suggest is a precursor of local extinction and hence range contraction.

Importantly, the fluctuations in barnacle species described here have long been known to mirror wider changes in the Western English Channel ecosystem (Box 3.7.3 Figure 2, Southward, 1980; Southward *et al.,* 1995; Hawkins *et al.,* 2003; Mieszkowska *et al.,* 2014a). Thus they provide easily-sampled indicators of change offshore in the English Channel in plankton (Genner *et al.,* 2009), fish (Genner *et al.,* 2004, 2009) and squid (Sims *et al.,* 2001). Similar fluctuations in warm- and cold-water species have also been reflected in other intertidal taxa of the North-east Atlantic, including algae (Lima *et al.,* 2007; Yesson *et al.,* 2015), other barnacle species (Herbert *et al.,* 2007), trochids (Mieszkowska *et al.,* 2007) and limpets (Southward *et al.,* 1995; Kendall *et al.,* 2004; Hawkins *et al.,* 2008). It must be stressed, however, that whilst southern warm-water species have generally increased in abundance beyond baselines established in the warm 1950s and cooler 1960s, the responses are often species-specific, reflecting life history characteristics, and dependent on coastline context. Some species have exhibited range extensions in the English Channel, including *Perforatus perforatus* (Herbert *et al.,* 2003), *Patella ulyssiponensis* (Hawkins *et al.,* 2009), *Gibbula umbilicalis* (Mieszkowska *et al.,* 2006; Herbert and Hawkins, *pers. obs*.), *Melarhaphe neritoides* (Hawkins *et al.,* 2009) and *Phorcus lineatus* (Mieszkowska *et al.,* 2005, 2007) (Box 3.7.1 Figure 1). Meanwhile other species have not, including both *Chthamalus* spp. (Herbert *et al.,* 2007, 2009). The lack of range expansion in these species is thought to be due to a combination of hydrographic barriers, habitat limitation and dispersal capability of different species (Herbert *et al.,* 2009; Keith *et al.,* 2011). In contrast to the English Channel, Chthamalid barnacles have, for example, shown range shifts in the Irish Sea and the North Sea along more continuous coastlines (Hawkins *et al.,* 2009). *Patella depressa* has made very small advances along the English Channel coast, primarily on artificial structures such as sea defences (Hawkins *et al.,* 2008). It is highly likely that several range extensions along the English Channel coast have been assisted by artificial structures acting as stepping stones (Moschella *et al.,* 2005; Firth *et al.,* 2013a), for example range extensions recorded in *Gibbula umbilicalis*, *Perforatus perforatus*, *Melarhaphe neritoides*, and *Patella ulyssiponensis*. This has also been seen in the recovery of the reef-building worm *Sabellaria alveolata* (Figure 3.7.2) in the northern Irish Sea and its spread southwards toward North Wales; on the Wirral it colonized sea defences as a novel habitat interfacing with sand (Firth *et al.,* 2015). Hence, the continued proliferation of artificial structures, both as a mitigational (e.g. marine renewable energy infrastructure) and adaptational (e.g. sea defences) response to climate change, is likely to have an additive effect, aiding shifts in species distributions with climate warming (Firth *et al.,* 2016a). It has been suggested that artificial structures may even provide opportunities for assisted migration of species at risk from climate change (Hoegh-Guldberg *et al.,* 2008). The negative implications of urban sprawl becoming an additional driver of biological homogenization by facilitating the spread of non-native species at local, regional and global scales (Airoldi *et al.,* 2015), however, may outweigh potential positive effects (Kühn and Klotz, 2006; McKinney, 2006; Bishop *et al.,* 2016; Firth *et al.,* 2016a).

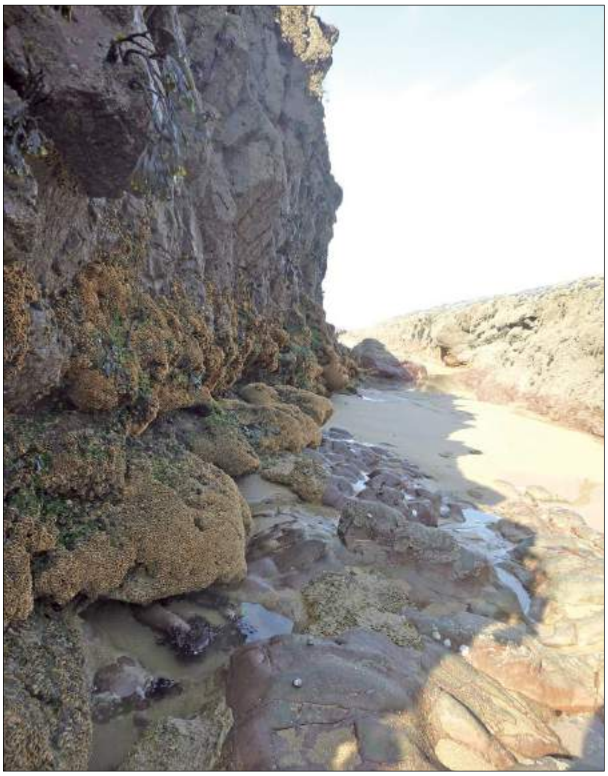

Figure 3.7.2 The honeycomb worm (***Sabellaria alveolata***) is a species of conservation interest in the UK. The worms build networks of sandy tubes to live in, which provide habitat for other intertidal animals and algae. On boulder shores, the worms perform an important function by cementing mobile boulders into stable reef habitats, which allows more mature intertidal communities to develop. © Ally Evans.

3.7.3.2 Vertical shore distribution: climate-driven changes in zonation

In addition to predicted effects on geographical species distributions, climate change is likely to promote changes in vertical shore distribution patterns in intertidal rocky habitats. Evidence of this to date is, however, limited (but see Harley and Paine, 2009; Harley, 2011). Upper distributional limits of species on rocky shores, especially those at upper- and mid-shore levels, are often set directly by physical factors, such as temperature and desiccation (Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985; Harley, 2003). Biological interactions, such as competition, grazing and predation, become more important controlling factors lower down the shore, generally setting lower distributional limits (Connell, 1972; Lubchenco, 1980; Hawkins and Hartnoll, 1985; Harley, 2003), and also setting upper limits of some mid- and low-shore species (Hawkins and Hartnoll, 1985; Jenkins *et al.,* 1999, 2005; Boaventura *et al.,* 2002a).

Organisms inhabiting intertidal shores must withstand prolonged emersion, which may become increasingly stressful with rising air and sea surface temperatures. Although the effects of temperature on the survival and physiological performance of invertebrates and algae are relatively well-understood (Somero, 2002, 2005; also discussed further below in *para. 3.7.3.4*), it is evident that different organisms experience different body temperatures when exposed to identical climates (Box 3.7.2 Figure 2, Helmuth (2002)). Non-lethal effects of heat stress (e.g. tissue damage, alteration of metabolic rates, activation of heat-shock responses) which carry considerable energetic costs, can lead to changes in activity and reproductive output, and hence influence population dynamics and community structure on rocky shores. Hot weather has also been observed to cause mortality at the upper limits of many intertidal species, particularly seaweeds (Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985), but also invertebrates (Harley, 2008; Firth and Williams, 2009). The upper intertidal limits of the canopy-forming alga *Fucus serratus* (Figure 3.7.3), for example, have been “pruned back” at its southern range edge along the Iberian Peninsula (Pearson *et al.,* 2009). This appears to be a result of reduced resilience to desiccation from extreme temperatures compared to populations in cooler regions further north. Since canopy algae provide important refuge habitat for other intertidal organisms, this is likely to have implications for overall community composition and structure. Warmer summers, with more frequent warm events and rising sea levels, may therefore be expected to truncate shore zones, reducing the extent of suitable habitat for intertidal species. It is important to note, however, that the temperatures experienced by organisms on rocky shores can be ameliorated by wave splash, which may reach different distances up the shore depending on the exposure of the coastline as well as localized weather and larger-scale climatic conditions (Harley and Helmuth, 2003; Helmuth *et al.,* 2006a). With predicted increasing storminess, greater wave splash may enable species to persist higher on the shore in certain locations. To complicate things further, biological interactions, such as competition between overlapping species and predator-prey interactions, are likely to be modulated by climate change (Sanford, 1999, 2002; Poloczanska *et al.,* 2008; Kordas *et al.,* 2011). As an example, Harley (2011) found that climate warming substantially reduced predator-free space in intertidal rocky habitats in the North-east Pacific region over a 52-year period of warming. Upper shore limits of mussels (*Mytilus californianus* and *M. trossulus*) and barnacles (*Semibalanus balanoides* and *Balanus glandula*) shifted down the shore, whereas the foraging limit of the predatory sea star *Pisaster ochraceus* was unaffected by thermal stress. This led to a thermally-forced reduction in predator-free space. Consequently, the vertical extent of mussel beds was reduced by approximately half in some locations, and several local extinction events were recorded. Thus, a complexity of interacting factors may lead to unexpected changes in vertical species distribution patterns into the future. It is likely that species will be pushed further down the shore and may need to rely on subtidal refuges.

Figure 3.7.3 ***Fucus serratus.*** © John M Baxter.

3.7.3.3 Phenological shifts

Changes to the synchronous timing of ecological events in response to interannual changes in temperature are now well known in the marine environment (Poloczanska *et al.,* 2013). Recurring life cycle events responding to changing environmental cues include the timing of reproduction and migrations (e.g. Sims *et al.,* 2001; Edwards and Richardson, 2004; Moore *et al.,* 2011; Pankhurst and Munday, 2011). In addition to direct spatial and temporal distributional effects, this may lead to mismatches in the timing of ecological interactions between species and their prey. There may therefore be considerable ramifications for populations of higher trophic-level species, including commercial fishery species, which often depend on synchronized planktonic production (Edwards and Richardson, 2004; Beaugrand and Kirby, 2010; Sumaila *et al.,* 2011).

In rocky intertidal habitats, phenological shifts have been observed in the congeneric limpets *Patella depressa* and *P. vulgata* in the North-east Atlantic region (Box 3.7.3 Figure 3, Moore *et al.* (2011)). *Patella depressa* is a warm-water Lusitanian species that occurs between Spain and North Wales, while *P. vulgata* is a more cold-water species extending from the Algarve as far north as northern Norway. The two species inhabit the same shore zone and habitat type, and co-occur and compete where their ranges overlap (Boaventura *et al.,* 2002b; Firth *et al.,* 2009). Peak spawning time in the southern species, *P. depressa*, has shifted from mid-July in the 1940s to mid-April by the warmer early 2000s, with links to sea surface temperature (Moore *et al.,* 2011). The advance in peak reproductive development of this species is double the average observed for terrestrial and freshwater systems (Root *et al.,* 2003), indicating that marine species may be responding faster to climate warming (see also Poloczanska *et al.,* 2013). In addition to this temporal shift in reproductive development, the duration of the reproductive season of *P. depressa* has also lengthened over time and a much higher proportion of the population is reaching advanced stages of gonad development than previously. Concurrently, *P. vulgata* populations have experienced more frequent failure years due to delayed periods of development and spawning (Moore *et al.,* 2011). This is thought to be the first observation of a cool-adapted species showing a delayed reproductive season as a response to warming. This delay may lead to trophic mismatches if larvae are spawned into the plankton when there is little planktonic food available, particularly given observed advances in the phenology of a number of other autumn-blooming plankton species (Edwards and Richardson, 2004). Increased larval mortality may lead to recruitment failures and local extinctions at southern range edges (Connell, 1961b; Svensson *et al.,* 2005).

3.7.3.4 Mechanisms of change

Most organisms inhabiting intertidal rocky habitats, such as algae and invertebrates, are ectothermic and their metabolic processes are driven by temperature. In algae, both respiration and photosynthesis are temperature-dependent. Thus, warmer temperatures generally lead to faster growth and productivity (Oh and Koh, 1996), although greater respiration can reduce any benefits of faster photosynthesis (Fortes and Lfining, 1980; Terrados and Ros, 1992). In invertebrates, warmer seawater temperatures tend to promote greater activity, such as increased filtering rates in suspension-feeders (Schulte, 1975; Riisgård *et al.,* 1993) and increased foraging in mobile grazers (Thompson *et al.,* 2004), detritivores and predators (Sanford, 1999). This in turn can lead to faster growth and greater reproductive output. For many intertidal organisms, the majority of physiological processes function better when the tide is in, although there are some exceptions (e.g. some algae photosynthesize when the tide is out provided desiccation is not extreme; Dring and Brown (1982)). Thus, during the *tide-in* phase, warmer temperatures resulting from climate change may drive metabolism and be beneficial for many organisms in temperate regions, in terms of activity, growth and reproductive output. This is only beneficial, however, up until respective optima are reached, beyond which sub-lethal effects, heat comas and mortality will occur. Some species are also active when the tide is out, often at night (e.g. limpets, *Patella* spp.: Santini *et al.* (2004)) and provided conditions are humid (e.g. dogwhelks, *Nucella lapillus* (Figure 3.7.4): Burrows and Hughes (1989)). Low tide windows can present highly stressful conditions, such as extreme high (especially at lower latitudes and during the day) or extreme low (especially at higher latitudes and during the night) atmospheric temperatures. Such extremes cause stress, slowing metabolism, activity, food intake and hence growth, and in some cases leading to damage or death (e.g. Somero, 2002; Firth and Williams, 2009; Firth *et al.,* 2015). The increased likelihood of more extreme hot weather in the future, therefore, may be expected to cause more costly stress levels during the *tide-out* phase – in essence putting a brake on metabolism, growth and occasionally causing mortality events.

Figure 3.7.4 ***Nucella lapillus*** © John M Baxter.

In certain circumstances, temperature may be a contributor, but not the direct mechanism of organism damage or death. For example, in 2013, massive die-offs were documented in populations of the sea star *Pisaster ochraceus* at many rocky intertidal sites along North-east Pacific coastlines (Stokstad, 2014; Jurgens

Box 3.7.4 Modelling the future

Long-term data and in-parallel experimentation can be used for statistically-based population modelling and for validating and calibrating mechanistic models. These approaches can be used to both understand past changes and forecast future status of populations. Long-term barnacle data (similar to that in Box 3.7.3) has been used to create models incorporating competition between the competitively superior cold-water northern species *Semibalanus balanoides* and the warm-water Chthamalids. During warm springs, the warm-water species were released from competition with the cold-water species. Using future climate scenarios, predictions for the future status of these populations indicate that Chthamalids will replace *S. balanoides* as the dominant barnacles on intertidal rocky shores (Figure 1).

Statistical modelling has also been used to predict how warmer and windier conditions will influence the abundance of the dominant canopy-forming seaweed *Ascophyllym nodosum* ("eggwrack") (Figure 2). Increased wave exposure and warmer temperatures were predicted to lead to fewer shores being dominated by this seaweed.

Shores in northern Europe (UK, Ireland), therefore, will increasingly resemble those further south in Europe (Spain, Portugal), with more southern species of barnacles and less seaweed cover.

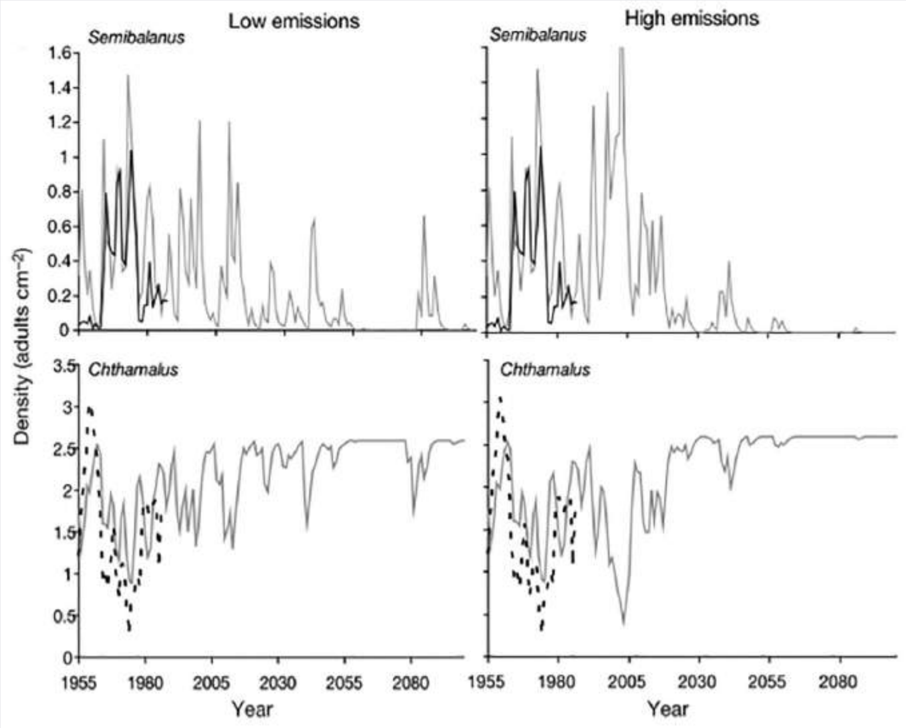

Figure 1 Competition-based model simulating future populations of the northern barnacle species *Semibalanus balanoides* and the southern species *Chthamalus* spp. under high and low emissions scenarios (Hawkins *et al.*, 2009, adapted from Poloczanska *et al.*, 2008).

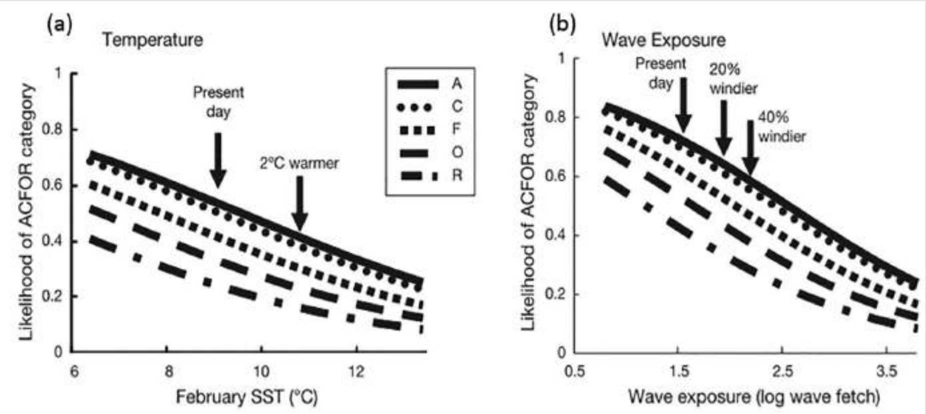

Figure 2 Outputs of multinomial logistic regression modelling of present-day distributions of *Ascophyllum nodosum* versus winter sea surface temperature (SST; February) and wave fetch. The predicted shifts along the ACFOR category (Abundant, Common, Frequent, Occasional and Rare) with (a) increased SST of 2ºC and (b) wind speeds of 120 and 140 % are highlighted, showing subsequent decreases in this key species (Hawkins *et al.,* 2009).

et al., 2015). In as little as three days, individual sea stars developed lesions, lost structural integrity and limbs, changed in behaviour, and ultimately died. Hewson *et al.* (2014) suggested that this "sea star wasting syndrome" was likely to be caused by a virus called Sea Star Associated Densovirus (SSaDV). Although the ultimate trigger for the viral outbreak has not yet been established, many sites, especially where earlier and more recent outbreaks were recorded in southern California and Washington, had been associated with warming events (e.g. the 1997 El Niño event: Stokstad (2014)). However, sites in Oregon had cooler water temperatures during recent observations of wasting, making predictions of whether temperature is a driver of the die-offs more difficult to confirm (Menge *et al.,* 2016). Regardless of the ultimate cause of these mortality events, *Pisaster ochraceus* has long been known to significantly affect the structure and functioning of intertidal communities as an important predator of mussels and other invertebrates. Indeed, it was one of the species for which the term "keystone species" was first coined (Paine, 1969). Furthermore, sea star wasting syndrome is not restricted to *P. ochraceus*; outbreaks in several sub-tidal sea star species have also been observed (pacificrockyintertidal.org). If the spread of SSaDV is indeed facilitated (at least in part) by warmer temperatures, then climate warming can be expected to lead to further outbreaks in the future. The potential mass depletion of these voracious predators would have cascading effects on local ecological communities. It is not yet clear whether new cohorts recently recruited along the Oregon coast (Menge *et al.,* 2016) will be affected or whether they will be able to restore depleted populations and local ecological balance.

At the other end of the spectrum of temperature-induced responses, warmer climatic conditions have enhanced performance and facilitated range extensions in many warm-water species at their poleward limits (see Para. 3.7.3.1). Range shifts and population expansions tend to be driven by increased reproductive output and recruitment (Wethey *et al.,* 2011; Bates *et al.,* 2014). Warm-temperate, sub-tropical and tropical species are often capable of multiple broods (e.g. Lewis, 1986; Ribeiro *et al.,* 2009). In animals that are direct-developers, population expansions stem directly from brood size and frequency leading to more juveniles being born and surviving initial developmental stages. In animals with a planktonic phase, increased brood number and size, larval development, survival and metamorphosis can all be enhanced under warmer conditions. Earlier timing of recruitment can mean juveniles can grow and thus be less susceptible to winter mortality, which may already be reduced due to milder winters (Helmuth *et al.,* 2006b). Moreover, greater numbers of planktonic larvae at range edges can increase the probability of crossing hydrographic boundaries such as headlands (Gaylord and Gaines, 2000; Keith *et al.,* 2011), thereby enabling range shifts to occur (Herbert *et al.,* 2003; Keith *et al.,* 2011). The rocky intertidal species that have exhibited the greatest extension in range in the North-east Atlantic region are those with quite short-lived larvae, such as the trochid *Gibbula umbilicalis* in the English Channel (Box 3.7.1 Figure 1; Mieszkowska *et al.* (2006), Hawkins *et al.* (2009)). These shifts seem to have occurred via a series of small steps, with populations consolidating once hydrographic barriers had been breached. In contrast, some animals with longer larval duration, such as barnacles, seem to have been less able to make and consolidate range extensions (Herbert *et al.,* 2007, 2009). This may be because breeding populations require high adult population densities, because to reproduce, adults need to be within penis range of each other (Kent *et al.,* 2003). Such circumstances will only arise when cues for gregarious settlement have been successful. This so-called "Allee effect" (Kent *et al.,* 2003) may be important at range edges for both externally and internally fertilizing species.

3.7.3.5 Predicted community and ecosystem consequences

Distributional and phenological responses of individual species to climate change have considerable ramifications for the structure of communities and trophic interactions, leading to eventual changes in ecosystem functioning (Hawkins *et al.,* 2009). There is limited evidence for such changes in intertidal rocky habitats, but inferences can be made on the basis of localized observations and theory. For example, temperature-induced mortality events in important keystone species (such as *Pisaster ochraceus* in the North-east Pacific region; see para. 3.7.3.4) would be likely to have cascading effects on local and regional community structure. Similarly, contraction of vertical shore distributions of canopy-forming algae (such as *Fucus serratus* along the Iberian Peninsula; see para. 3.7.3.2) would effectively reduce the extent of suitable habitat for a number of intertidal species, again with implications for overall community structure and ecosystem functioning.

Figure 3.7.5 Very sheltered boulder shore with dense *Fucus* spp. and *Ascophyllum nodosum* cover. © John M Baxter.

Fucoid canopies are dense stands of *Fucus* and/or *Ascophyllum* seaweeds (Figure 3.7.5). They are important ecosystem engineers in temperate intertidal rocky habitats, providing food and habitat for a number of other species (Thompson *et al.,* 1996). Their abundance and density can, therefore, considerably influence the overall structure and functioning of rocky shore communities. In northern Europe, fucoid canopies are common and abundant features of most sheltered, and some more exposed, rocky shores (Ballantine, 1961; Hawkins and Harkin, 1985). At mid-latitudes, such as in Northern France, the British Isles and Ireland, and in moderately-exposed locations, patchy shores are typical (Lewis, 1964; Hartnoll and Hawkins, 1985). Further south in warmer parts of Europe, however, rocky shores tend to be devoid of large canopy-forming algae (Ballantine, 1961; Boaventura *et al.,* 2002c). Fucoid abundance is largely determined by the success rate of propagules "escaping" from grazers such as limpets, which is more likely among dense cover of *Semibalanus balanoides* barnacles as they restrict gastropod movement and provide refuges for juvenile plants (Hawkins, 1981; Hartnoll and Hawkins, 1985; Johnson *et al.,* 1997, 1998a; Burrows and Hawkins, 1998). Fucoid canopy cover is predicted to decline in response to climate change (Box 3.7.4 Figure 2) due to a combination of greater physiological stress (Pearson *et al.,* 2009; Martínez *et al.,* 2012; Ferreira *et al.,* 2014; Zardi *et al.,* 2015) and increased grazing pressure (Jenkins *et al.,* 2001, 2005; Ferreira *et al.,* 2015). At mid-latitudes in particular, escape rates are predicted to decline due to a combination of reduced recruitment in drier summers (Ferreira *et al.,* 2015), greater grazing pressure as southern species of limpets and trochids increase in abundance and ranges extend further north (Southward *et al.,* 1995; Mieszkowska *et al.,* 2006), and reduced barnacle density as populations of *Semibalanus balanoides* are replaced by slower-growing *Chthamalus* species (Hawkins *et al.,* 2008, 2009; Poloczanska *et al.,* 2008). Predicted stormier weather is also likely to contribute to declines in algal canopies because of increased dislodgement and the likelihood of higher limpet abundances with elevated wave exposure (Jonsson *et al.,* 2006). There is evidence that the canopy-algae *Ascophyllum nodosum* is already being denuded by limpet grazing towards its southern range limit (Lorenzen, 2007), as well as in sheltered locations such as Strangford Lough further north, where local increases in wave action have interacted with limpet grazing to reduce cover (Davies *et al.,* 2007). No conclusive pattern is yet clear (Yesson *et al.,* 2015), but going forward, intertidal rocky ecosystems in northern Europe are likely to become increasingly like those further south. Fucoid canopies may even become restricted to refuges such as estuaries, as has been observed in southern Europe (Lorenzen, 2007; Neiva *et al.,* 2012). This, in turn, would have implications for the diverse array of species that shelter in and under canopies (Thompson *et al.,* 1996; Moore *et al.,* 2007). There would also be reduced primary production and supply of detritus to the food chain in inshore waters.

Production and nutrient cycling are probably the most important ecosystem services supported by functioning intertidal rocky habitat communities (Costanza *et al.,* 1997; see para. 3.7.2.2). Loss of macroalgal canopies is not the only reason that productivity of rocky shore systems is predicted to decline with climate change. In the North-east Atlantic it is well known that northern species of invertebrates grow faster and outcompete slower-growing, but more physiologically-hardy, southern species. For example, *Semibalanus balanoides* outcompetes *Chthamalus stellatus* (Connell, 1961a; Poloczanska *et al.,* 2008). Thus, as southern species advance northwards, secondary production is likely to be reduced. In areas where upwelling occurs, however, upwelling processes are likely to intensify in response to climate change, thus additional nutrients brought up from deeper waters may supplement productivity in intertidal and nearshore communities (discussed further in Para. 3.7.4). In any case, on the basis of available evidence, we can be confident that community structure and ecosystem functioning of rocky intertidal habitats will change into the future. It remains to be seen whether they will continue to support current levels of important ecosystem services we rely upon as species and communities modify and adapt to the changes they face.

3.7.4 Drivers of change

As highlighted throughout this section, temperature is a key driver of observed and predicted ecological responses to climate change in intertidal rocky habitats, in part because temperature drives metabolic processes in ectothermic intertidal organisms. During the *tide-in* phase, warmer water temperatures may boost metabolism with some physiological benefits for certain species, for example by promoting increased foraging activity, growth and reproductive output. In contrast, increased *tide-out* temperatures are likely to cause stress in some species, with sublethal and/ or lethal consequences. Milder winters may, on the other hand, reduce the incidence of winter mortality. Superimposed upon long-term warming, however, are shorter-term weather fluctuations, often influenced by hemispheric-scale processes such as the El Niño Southern Oscillation (ENSO) events and the North Atlantic Oscillation (NAO). Certainly, the last few years in the North-east Atlantic have shown extreme NAO index "negative" winters, such as 2010/11 – the coldest since 1962/63, which was a 300-year cold event (Wethey *et al.,* 2011). There have also been NAO "positive" winters, such as 2013/14, which was extremely stormy (Matthews *et al.,* 2014). Here we emphasize two important points. Firstly, climate change is not just about temperature; the intertidal zone will be very strongly influenced by changes in storminess and the return-time of extreme events influencing wave action gradients and disturbance regimes (Perkol-Finkel and Airoldi, 2010; Walsh *et al.,* 2014; Benedetti-Cecchi *et al.,* 2015), as well as sea-level rise on a centennial scale (Jackson and McIlvenny, 2011; Church *et al.,* 2013) (Box 3.7.5 Figures 1 and 2). Secondly, whilst temperature (including aerial temperature) is undoubtedly extremely important, it is necessary to consider, not only average temperatures (warming), but also the frequency and extent of extreme events (Wethey *et al.,* 2011; Smale and Wernberg, 2013).

For rocky shore species and communities under threat from climate change, there are several sources of refuge that can ameliorate stressful conditions at a variety of spatial scales. These can, in some sense, be considered indirect drivers of change, as they additively or interactively modulate direct ecological responses. At the small scale (<1 m), shores with variable topography and aspect can provide shading and moisture in a mosaic of different microhabitats. These features modify species abundances and distributions in relation to the sharp vertical (temperature, desiccation) and horizontal (wave action) environmental gradients. Such small-scale processes can often over-ride the very gentle geographical gradients of climate change with latitude (Box 3.7.2 Figure 3; Seabra *et al.*, (2011); Lima *et al.,* (2016)). On top of this are mesoscale (100-1000 km) processes, driven by upwelling systems and coastal topography, which can further modulate the effects of climate change. For example, estuarine regions can provide refuge for cold-water species at lower latitudes. This has been well-demonstrated along the Iberian Peninsula for a variety of intertidal species, including fucoids (Lorenzen, 2007; Neiva *et al.,* 2012), *Carcinus maenas* (Silva *et al.,* 2006) and *Patella vulgata* (Fischer-Piette, 1955), although the underlying processes are not clear. Enclosed seas (e.g. Irish Sea, North Sea), meanwhile, can lead to counter-intuitive species distributions. For example, warm-water species such as *Sabellaria alveolata* have expanded southwards in the Irish Sea (Frost *et al.,* 2004), and several warm-adapted intertidal species have spread southwards into the Southern North Sea (Mieszkowska *et al.,* 2005; Philippart *et al.,* 2011). This is because enclosed seas, whilst often warmer in the summer, are also colder in the winter. This emphasizes the importance of coastline context for identifying and predicting ecological responses to climate change in different places.

Upwelling is a phenomenon caused by winds blowing along the coast, pushing surface waters offshore, while bringing nutrients and cold water from the deeper ocean to the surface. Upwelling systems strongly influence rocky intertidal communities along the eastern boundaries of the world's oceans. These systems, known as Eastern Boundary Upwelling Systems (EBUS) include the California, Humboldt, Benguela and Canary upwelling zones. In these regions, nutrient-rich water is brought to the surface and fuels production within intertidal and nearshore communities. Where upwelling is particularly intense, for example around headlands, reductions in sea-surface temperature can also be important in structuring species distribution and abundance patterns at regional scales (Blanchette *et al.,* 2008; Fenberg *et al.,* 2015; Reddin *et al.,* 2015). Under future climate change projections, it is predicted that land temperatures will increase faster than coastal waters, creating a scenario favouring stronger upwelling-producing winds (Bakun *et al.,* 2010; Di Lorenzo, 2015; Wang *et al.,* 2015). Increased cold-water upwelling may, therefore, provide refuge from climate warming in some locations. Effects, however, are unlikely to be consistent across latitudes. Models predict that upwelling intensification will be

Box 3.7.5 Beyond warming – ecologically-sensitive adaptation to rising and stormier seas

Engineered coastal structures (such as breakwaters, seawalls and groynes) are proliferating around coastlines globally as a societal response to rising (Figure 1) and stormier (Figure 2) seas. Their construction can cause loss of and disturbance to sensitive natural habitats and species. They tend to provide poor-quality habitat themselves, supporting low biodiversity and non-natural communities of marine life. They are often colonized by weedy and opportunistic species. Therefore, where structures act as stepping stones between previously-isolated rocky habitats (Figure 3), they can facilitate the spread of non-native species and contribute to biotic homogenisation over large geographical areas.

In light of this, it is becoming increasingly necessary to incorporate ecologically-sensitive design into

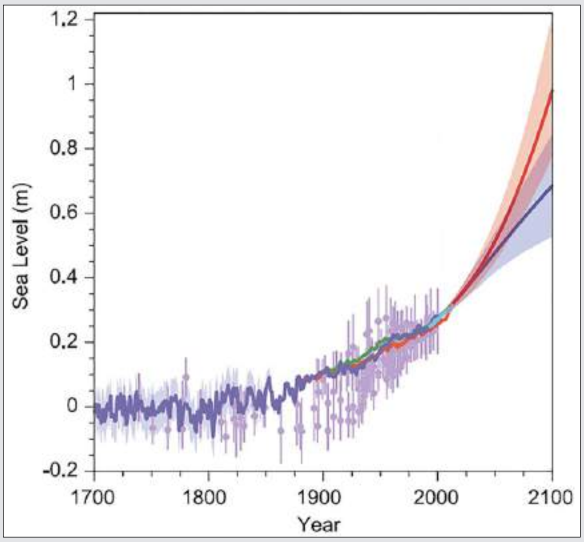

Figure 1 Past and future sea-level rise. For the past, proxy data are shown in light purple and tide gauge data in blue. For the future the IPCC projections for very high emissions (red) and very low emissions (blue) are shown (Church *et al.*, 2013; IPCC AR5 Figure 13.27).

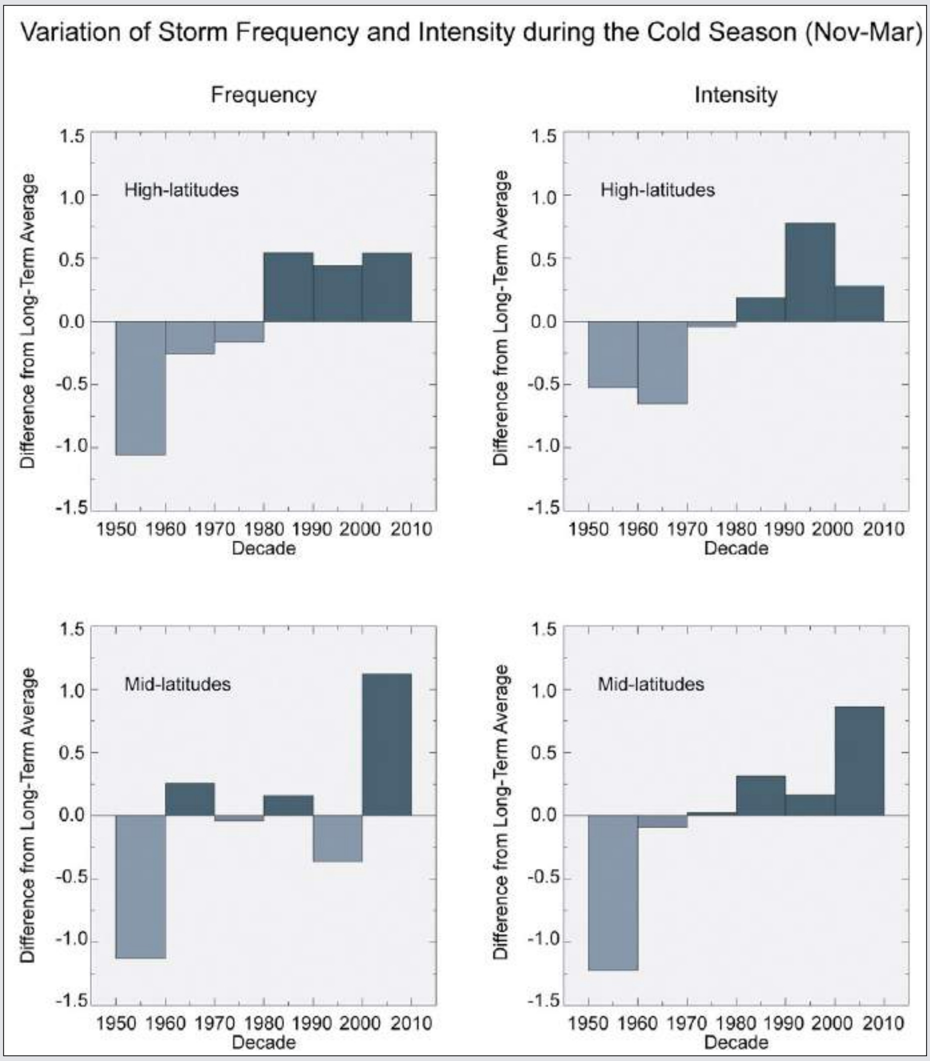

Figure 2 Variation of storm frequency and intensity during the cold season (November – March) for high latitudes (60-90° N) and mid latitudes (30-60° N) of the Northern Hemisphere over the period 1949-2010. The bar for each decade represents the difference from the long-term average. Storm frequencies have increased in middle and high latitudes, and storm intensities have increased in middle latitudes (updated from CCSP, 2008).

Box 3.7.5 Cont.

coastal developments, not only to minimize their environmental impacts, but also to maximize potential ecological and socio-economic benefits. By *eco-engineering* additional microhabitats (e.g. artificial rock pools; Figure 4) into coastal structures, it is possible to enhance their biodiversity and support similar ecosystem functions to natural rocky shores. A number of different eco-engineering designs have been tried-and-tested in different parts of the world. It is essential that this potential good practice is communicated to end-users to ensure every opportunity is taken to deliver environmentally-desirable outcomes of coastal and marine developments.

Figure 3 Elmer coastal defence scheme: structures can act as stepping stones and facilitate dispersal of species. © Arun District Council.

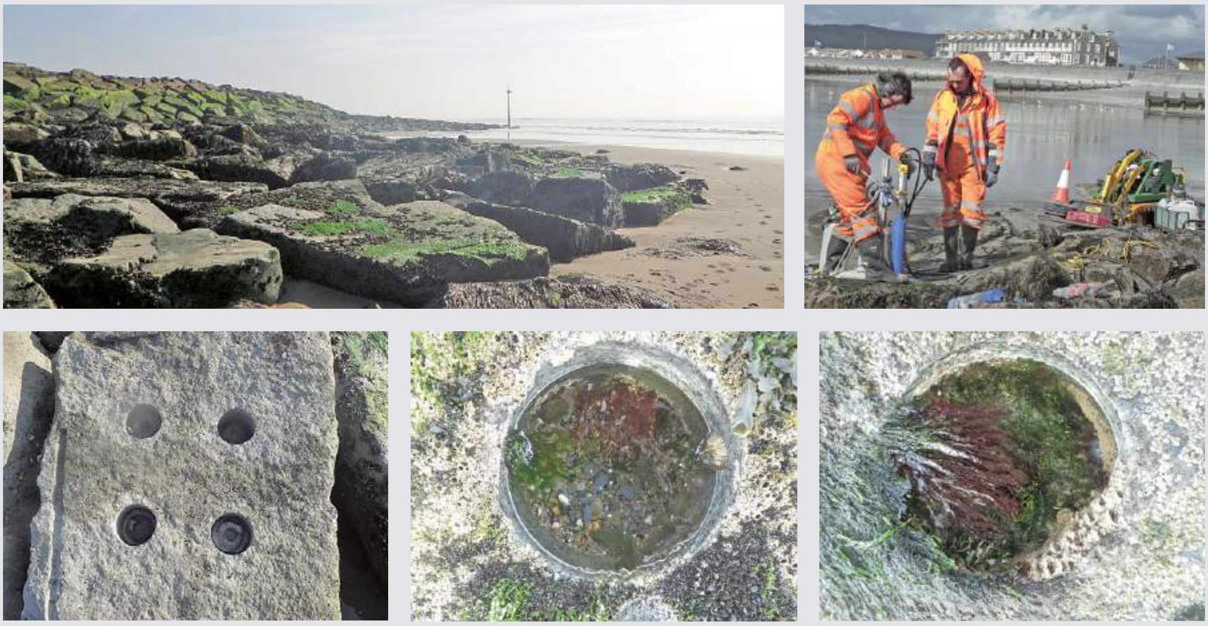

Figure 4 Artificial rock pools installed in an intertidal breakwater in Wales, UK, provided important habitat for marine life and performed a similar function to natural rock pools on nearby rocky shores (Evans *et al.,* 2016). © Ally Evans.

particularly marked at higher latitudes, where coastal upwelling is generally less intense. This, in turn, may cause homogenization of upwelling-influenced habitats across latitudes (but notably not in the California EBUS), and have cascading effects on the abundance and distribution of intertidal and nearshore flora and fauna (Wang *et al.,* 2015). There is evidence that upwelling has already intensified in most of the EBUS (Sydeman *et al.,* 2014; Varela *et al.,* 2015). While this may potentially be beneficial in terms of marine food production as the EBUS already produce >20% of global fisheries, there are a number of other biological consequences of a net increase in upwelling. For example, deeper waters have lower pH and oxygen levels than at the surface. Thus, an increase in upwelling may exacerbate emerging threats to coastal ecosystems, such as acidification and anoxic events (Chan *et al.,* 2008; Bakun *et al.,* 2015). Reduced pH can affect metabolism and energy budgets in marine organisms, particularly in organisms that produce calcium carbonate for shells or skeletons (Kroeker *et al.,* 2010; Harvey *et al.,* 2013, 2016). For example, calcification rates in *Mytilus californianus* mussels in Washington State, USA, have decreased significantly, probably due to declining pH (Pfister *et al.,* 2016). Mussel beds are the dominant space occupier of many temperate rocky shore coastlines around the planet. They provide habitat for other species (particularly for juveniles; Lohse (1993)), are an important food source for intertidal predators (e.g. whelks and sea stars), and have been harvested by humans for food for millennia (Rick and Erlandson, 2008). If this trend of shell thinning continues, the ability for *M. californianus* (and other mussel species) to play an important role in shaping the structure, functioning, and diversity of temperate rocky coastlines in the future may be in doubt.

Although these various drivers of change are relatively well-understood in isolation, it is difficult to predict how each will interact to shape intertidal rocky habitats in different parts of a rapidly-changing world (but see Crain *et al.,* 2008; Harvey *et al.,* 2013; Lemasson *et al.,* 2016). Species are likely to be affected variably at different locations within and at the edge of their geographic ranges, at different positions along vertical and horizontal shore gradients, and differently during the *tide-in* and *tide-out* phases. The balance of processes will also vary with regional modulation by upwelling or enclosure of seas/bays, and by other local environmental gradients and microhabitat variation. Furthermore, the region of evolutionary origin of species may predetermine their responses to interacting climate-driven processes (Rivadeneira *et al.,* 2015). Long-term contextual monitoring of natural systems (Hawkins *et al.,* 2013; Mieszkowska *et al.,* 2014b), coupled with experimental investigation of multi-stressor effects on species and communities (e.g. Przeslawski *et al.,* 2005; Firth and Williams, 2009; Atalah and Crowe, 2010; O'Gorman *et al.,* 2012), will be essential for disentangling the drivers and mechanisms of past, present and predicted future trends.

3.7.5 Concluding remarks – the need for adaptive management

There is now irrefutable evidence that climate-driven changes are occurring in intertidal rocky habitats, with important implications for the species and communities that inhabit them and the ecosystem services they support. Many of the examples described in this section are from the North-east Atlantic region, partly because of the extent of long-term and broad scale data available from this part of the world, but also because there is evidence that it has experienced faster warming than other regions (Burrows *et al.,* 2011). Climate-driven changes similar to those recorded in the North-east Atlantic have been observed elsewhere, along the Pacific coasts of North and South America (Barry *et al.,* 1995; Rivadeneira and Fernández, 2005; Harley *et al.,* 2006), Australia (Lathlean *et al.,* 2015), and New Zealand (Schiel *et al.,* 2016). Such shifts are occurring worldwide. In general, more species are advancing poleward than are retreating (Parmesan and Yohe, 2003), with some evidence from the northern hemisphere that cold-water species can persist in the face of climate change, if they outcompete southern species (e.g. Poloczanska *et al.,* 2008). Nevertheless, the composition, structure and functioning of communities on intertidal rocky shores is certain to change (Box 3.7.6).

Climate-driven changes interact with other global phenomena, such as ocean acidification, and also with regional- and local-scale impacts. In intertidal rocky habitats, these can include eutrophication, sedimentation, over-exploitation of seaweeds and shellfish, trampling from recreational use, and coastal development (Thompson *et al.,* 2002). This combination of impacts is already having considerable negative impacts on rocky shore communities, particularly by causing declines of canopy-forming algae, and instead favouring proliferation of fast-growing ephemeral algae and invasive species (Airoldi, 2003; Connell *et al.,* 2008; Perkol-Finkel and Airoldi, 2010; Airoldi and Bulleri, 2011). Algal canopies confer resilience to climate change for other organisms

Box 3.7.6 Rocky intertidal winners & losers in the North-east Atlantic

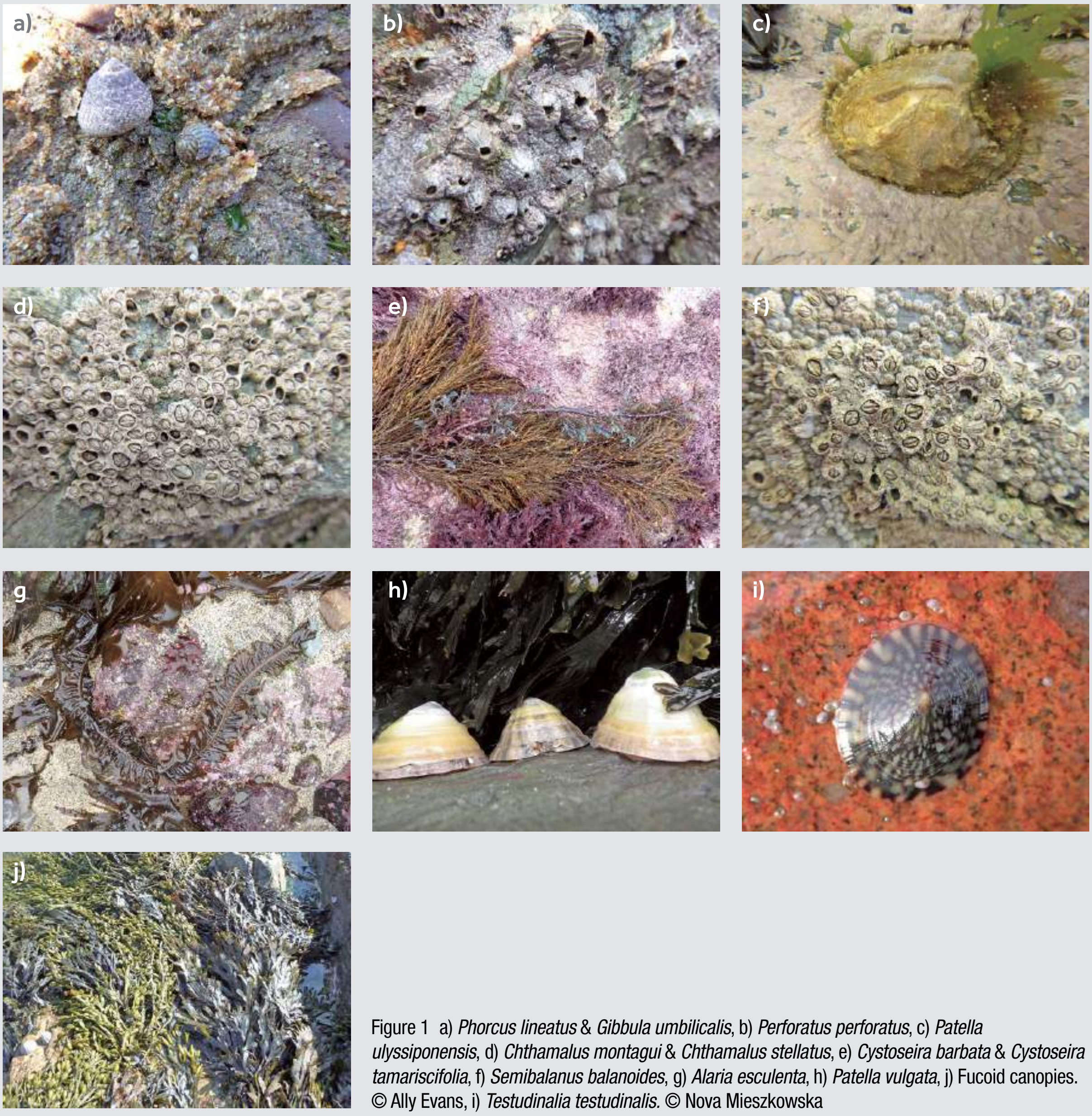

Figure 1 a) *Phorcus lineatus* & *Gibbula umbilicalis*, b) *Perforatus perforatus*, c) *Patella ulyssiponensis*, d) *Chthamalus montagui* & *Chthamalus stellatus*, e) *Cystoseira barbata* & *Cystoseira tamariscifolia*, f) *Semibalanus balanoides*, g) *Alaria esculenta*, h) *Patella vulgata*, j) Fucoid canopies. © Ally Evans, i) *Testudinalia testudinalis.* © Nova Mieszkowska

by providing refuge habitat and ameliorating local ambient conditions (Thompson *et al.,* 1996; Moore *et al.,* 2007; Teagle *et al.,* 2016; Walls *et al.,* 2016). Their loss, therefore, increases stress on more delicate understorey algae and invertebrates with community- and ecosystem-level implications. As a temperate phenomenon, these habitat engineers are likely to be under particular pressure from continued warming, with added physiological stress and increased grazing pressure (see para. 3.7.3.5). Thus direct (physiological stress) and indirect (more grazing or predation) effects of climate change may potentially be exacerbated in intertidal rocky habitats by a plethora of interactions with other impacts.

Through the complex localized and regional-scale responses described in this section, climate change is ultimately contributing to global homogenization of biodiversity, as vulnerable species become extinct and "non-native" species from different biogeographic regions spread, overlap, and become established across the world's ocean. Invasive species have been particularly successful during the spell of recent warming (Dukes and Mooney, 1999; Stachowicz *et al.,* 2002; Sorte *et al.,* 2010), and the likelihood of further successful invasions will increase with projected climate change (Walther *et al.,* 2009; Bellard *et al.,* 2013; Rius *et al.,* 2014), in particular with increased frequency and intensity of disturbance events (Perkol-Finkel and Airoldi, 2010; Airoldi and Bulleri, 2011; Benedetti-Cecchi *et al.,* 2015). This is not a surprise, since invasive species tend to be fast-growing opportunistic species, able to withstand variable conditions (e.g. *Undaria pinnatifida*: Dean and Hurd (2007), *Austrominius modestus*: Harms (1999), *Carcinus maenas*: Naylor (1962), *Mytilus* spp.: Pollard and Hodgson (2016), which have all been involved in invasions worldwide). There is growing evidence that the proliferation of artificial hard structures in the marine environment has had an additive effect with climate warming, and facilitated range shifts in non-native species (Ruiz *et al.,* 2009; Bracewell *et al.,* 2012; Mineur *et al.,* 2012; Spinuzzi *et al.,* 2013; Airoldi *et al.,* 2015). Artificial structures essentially act as stepping stones to aid the spread of species responding to climate-driven change. There is strong evidence for this already in the Eastern English Channel (Mieszkowska *et al.,* 2005; Moschella *et al.,* 2005; Hawkins *et al.,* 2008, 2009; Firth *et al.,* 2013a) and Irish Sea (Firth *et al.,* 2015). Much of this "ocean sprawl" has come about as a mitigational response to climate change (e.g. wind, wave and tidal energy generation infrastructure), and also as a societal adaptation to rising and stormier seas (e.g. coastal defences). There is growing interest in the concept of *ecological engineering* to design artificial structures with ecological implications in mind (Chapman and Underwood, 2011; Firth *et al.,* 2013a, 2014; Dafforn *et al.,* 2015; Dyson and Yocom, 2015). By incorporating physical engineered features, their habitat quality may be enhanced, thus enabling them to support more diverse and more natural communities of marine life. For example, artificial rock pools can be retro-fitted by drilling holes in breakwater units (Box 3.7.5 Figure 4; Evans *et al.* (2016)) or appending "flower pots" to seawalls (Browne and Chapman, 2011, 2014), and large habitat units can be cast in concrete to incorporate different microhabitats whilst also contributing to the body of structures (Firth *et al.,* 2014; Perkol-Finkel and Sella, 2014, 2016; Sella and Perkol-Finkel, 2015). Such interventions can be targeted for specific management outcomes, and can confer resilience to climate change by providing refuge for intertidal organisms during the *tide-out* phase. Ecologically-sensitive design of artificial structures may become increasingly important as natural intertidal rocky habitats are "squeezed" by sea-level rise (Jackson and McIlvenny, 2011); artificial habitats may eventually become important surrogate habitats for rocky shore organisms (e.g. Perkol-Finkel *et al.,* 2012).

The mitigation essential to achieve goals of a lower-carbon world will take time. The inertia of the climate system is such that even should emissions be reduced, there will be a phase-lag of at least 50 years over which warming will flatten out. In the meantime, much can be done to enhance resilience to climate change, by managing those impacts and interactions over which society has greater potential control in the short to medium term of the next 5–50 years (Knights *et al.,* 2013). In general, climate change exacerbates other impacts, and reducing these other impacts confers resilience to climate change. For example, the likelihood of non-native species invasions appears greater in a warmer, more disturbed world; over-exploited populations are susceptible to climate change, and climate change can increase vulnerability to over-exploitation; and harmful algal blooms are more likely in warmer and more stratified eutrophic seas. In mitigating (e.g. developing marine renewable energy generation) and adapting to (e.g. building sea defences) climate change, care must be taken to ensure ecological consequences are taken into consideration at both local and regional scales.

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3.8 Impacts and effects of ocean warming on coral reefs

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Summary

- Despite covering less than 0.1% of the sea floor area, coral reefs provide nearly US$9.8 trillion globally of social, economic and cultural services each year and provide habitat for over 25% of marine fish species.
- The rate of warming in coral reef areas has increased from ~0.04°C/decade over the past century to 0.2°C/decade over recent decades (1985-2012). Across this period, reefs were exposed to prolonged, high temperatures that caused bleaching once every six years. However, within the last three decades, as the planet has warmed the frequency of bleaching stress has increased three-fold.
- The latest climate models predict that ocean warming will cause annual coral bleaching for almost all reefs by 2050. They also predict that disease is as likely to be a future cause of coral mortality as coral bleaching. Unabated temperature increases will produce serious consequences for coral reef ecosystems and dependent communities.
- The proportion of reefs in which ocean chemistry will allow coral reefs to grow has decreased from 98% (ca. 1780) to 38% (ca. 2006) due to ocean acidification and continues to drop.
- Tropical cyclones can reduce thermal stress but can physically damage reefs. Ocean warming may increase the severity of cyclones. Warming-related coral bleaching has likely reduced the ability of reefs to recover from cyclone damage.
- Sea-level rise is predicted to accelerate. Historically reefs have not been able to keep up with rapid sea-level rise, and this is even less likely in the future if ocean warming and acidification slow reef growth.
- Loss of coral reefs would diminish the services these ecosystems provide, such as coastal protection from storm waves, habitat for reef fauna, and tourism. Predictions of ecosystem service losses from ocean warming and acidification globally reach US$1 trillion/year by 2100.
- Reducing atmospheric CO_2 is critical for coral reefs to continue. While reduced emissions will slow ocean warming and acidification, current CO_2 levels already exceed the 320-350 ppm needed for healthy coral reefs. While this is pursued, enhancing reef resilience through targeted management actions will help reefs to resist and recover from disturbance. Local actions to mitigate climate change impacts may be necessary to preserve reef resources.

Ocean warming effect	Consequences
Ocean warming	Recent warming has been linked to reduced calcification rate and an increased likelihood of thermal stress events
Thermal stress can result in coral bleaching and disease	Bleaching and disease can lead to reduced reproduction, coral death, poorer habitat for fish and other fauna, decreased biodiversity and (ultimately) local extinction
Ocean acidification	Reduced growth of coral skeleton slows recovery after acute events; increased erosion of reefs and reduced strength of reef structures makes them more susceptible to physical damage
Tropical cyclones (changing storm tracks and intensities)	Physical destruction of reefs results in the loss of habitat and coastal protection – although mixing of cool waters can temporarily offset thermal stress
Sea-level rise	Reefs that are unable to keep pace with rate of sea-level rise may cease to exist Higher sea levels can increase sedimentation and turbidity on reefs
Additive and synergistic effects of multiple global stressors	Many of these impacts, especially ocean warming and acidification act together, either adding or multiplying the separate effects These have already resulted in significant flattening of coral reef ecosystems

3.8.1 Introduction and significance

Coral reefs are ecologically and economically important marine ecosystems, found across the world's tropical and sub-tropical oceans. In addition to their inherent beauty, reefs provide a variety of social, economic and cultural services to coastal communities and visitors with an estimated value of US$9.8 trillion per year (Costanza *et al.,* 2014). Despite covering less than 0.1% of the ocean floor, reefs are the most biodiverse marine ecosystem – comparable to rainforests (Reaka-Kudla, 1997). These 'Rainforests of the Sea' provide habitat and feeding grounds for over one-quarter of marine fish species and myriad other marine animals (Spalding *et al.,* 2001). The complex three-dimensional structure formed by corals not only supports complex ecosystems, but also dissipates wave energy to protect coastlines from erosion and damage. Coastal protection and recreation activities (including tourism) supply the greatest economic benefits from coral reefs (Costanza *et al.,* 2014). Coral reef organisms have also been the source of numerous important drugs and medical treatments (Leal *et al.,* 2013). While the focus of this section is on shallow reef-building corals, there are also myriad ecosystem services provided by deep-water and high-latitude "cold water" corals.

The services provided by coral reefs can be severely disrupted by a wide range of chronic and acute environmental disturbances (Anthony *et al.,* 2015). Most important are the impacts of global stressors resulting from human-caused increases in atmospheric CO_2. These include thermal stress (linked to coral bleaching and disease); ocean acidification (reducing the growth of corals and the strength of reefs); tropical storms (which can physically damage reefs); and sea-level rise (with which coral reefs may not be able to keep up, and which could increase sediments, nutrients, and toxic pollutants on reefs).

Coral reefs are a key indicator ecosystem for the impacts of climate change on the marine environment – thermal stress events related to ocean warming have and are predicted to result in dramatic impacts on coral reefs. Corals thrive in conditions close to their upper temperature limits, maximizing growth and reproduction. However, rising above corals' temperature thresholds can result in coral bleaching – reducing coral growth and reproduction; increasing susceptibility to diseases; and even coral death. Such events reduce the cover and diversity of corals, and flatten the three-dimensional structure coral reefs provide (Baker *et al.,* 2008). This eliminates habitat for resident animals while also reducing coastal protection. Tropical cyclones also can flatten structures, causing the same downstream effects on coral ecosystems and the human populations they support. This can be hastened as reef structures are weakened by ocean acidification – caused by absorption of rising atmospheric carbon dioxide into sea water.

This section briefly outlines key functions of coral reefs and how environmental stressors can disrupt them. After considering observed historical impacts, we examine environmental stress linked to impacts on reefs over longer time-scales: how stress has varied in the past and predictions of future trajectories. While we focus on ocean warming, we also discuss acidification, storms and sea-level change. We also summarize potential loss of ecosystem services as a result of these stressors. We consider recent efforts to improve the resilience of coal reefs to climate change through resilience-based management. We conclude with recommendations for global and local actions to improve the likelihood that future generations will continue to benefit from coral reefs.

3.8.2 Definition of ecosystem: what are coral reefs?

Animal, vegetable or mineral? Corals are all three. Corals are animals that exist in mutually beneficial partnership (symbiosis) with microscopic plants that live inside the corals' tissue (Stanley, 2006). These symbiotic zooxanthellae generate energy through photosynthesis, just as terrestrial plants do. Through this partnership, corals gain up to 90% of their energy requirements from the zooxanthellae, enabling them to construct calcium carbonate skeletons that underpin the three-dimensional structure of reefs (Stanley, 2006). The resulting reef systems can be thousands of kilometres in length and provide homes to a wide array of plants and animals. The term 'coral reef ecosystem' encompasses corals and the various organisms that live in or on the reef structure (3.8.2a), and many that live in surrounding waters but rely on food the reef provides.

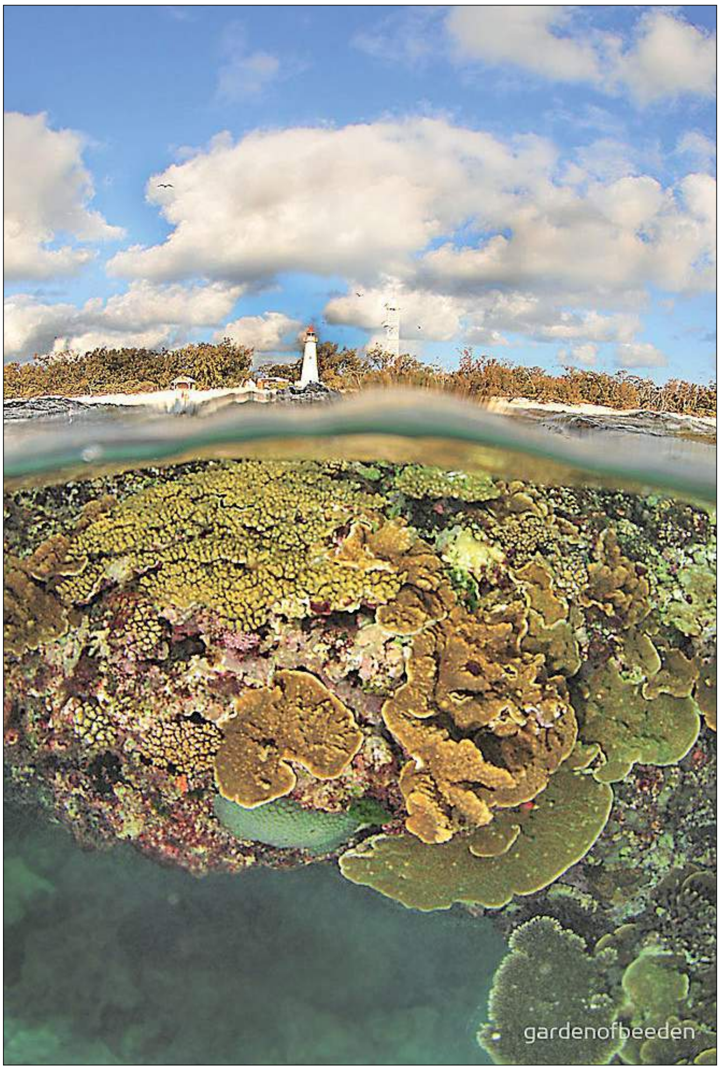

Figure 3.8.1 Vibrant and diverse corals at Lighthouse Reef exemplify the reefs around Lady Elliot Island in the southern Great Barrier Reef. © R. Beeden, GBRMPA.

Under certain environmental conditions, the symbiotic partnership is no longer beneficial, and can become toxic for the corals (Glynn, 1993). Stress can result from changes in salinity, temperature, light levels and water quality. Of these, impacts from temperature stress affects corals on a broad spatial scale – referred to as "mass bleaching". Sustained high water temperature of even 1 to 2°C above a coral's tolerance level has resulted in bleaching (Glynn and D'Croz, 1990), a process in which the coral expels their zooxanthellae, leaving the white skeleton visible through the transparent coral tissue (Figure 3.8.2b). Bleached corals are susceptible to injury and starvation. If stressful temperature conditions abate within days to weeks, corals can regain zooxanthellae and survive. However, if stress persists for several weeks or longer, corals can starve to death (Figure 3.8.2c; Glynn, 1993). Other stressors such as high nutrient levels or ocean acidification can make corals more susceptible to temperature stress (Anthony *et al.,* 2008; Wooldridge *et al.,* in press).

Bleaching, even at low levels, can have follow-on impacts. The corals' weakened condition following thermal stress causes slowed growth (Leder *et al.,* 1991) and greater susceptibility to coral disease outbreaks (Miller *et al.,* 2009; Mydlarz *et al.,* 2009; Burge *et al.,* 2014). Other impacts on corals from bleaching

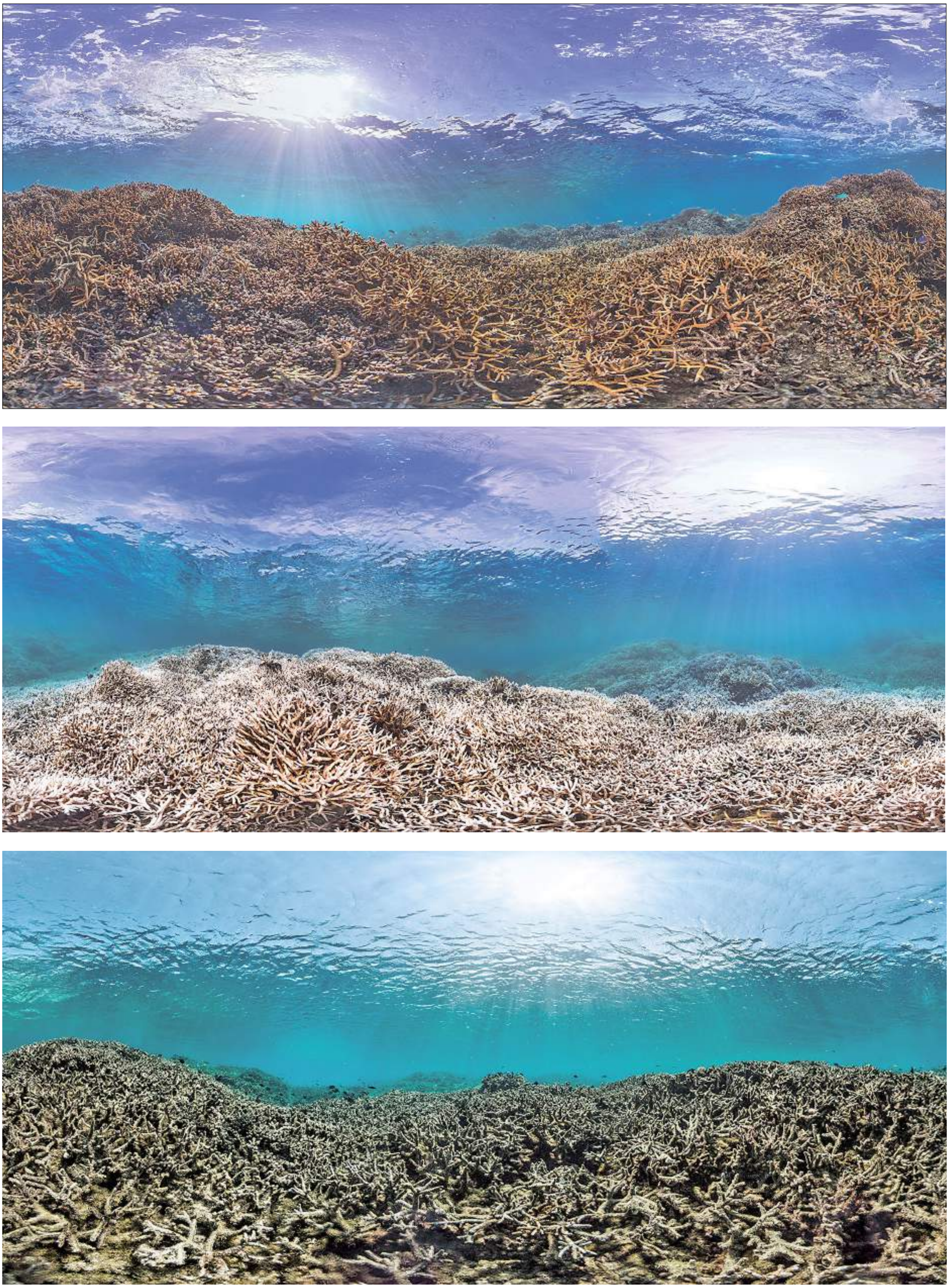

Figure 3.8.2 Airport Reef in American Samoa photographed by XL Catlin Seaview Survey. (a) December 2014 – still a healthy coral reef; (b) by February 2015, prolonged high temperatures bleached the corals; (c) by August 2015 corals died after sustained thermal stress. © Images courtesy of R. Vevers, XL Catlin Seaview Survey.

and/or disease include reductions in reproduction, three-dimensional structural complexity, coral cover, and biodiversity, and potentially local extinction of coral species (reviewed in Baker *et al.,* 2008; Brainard *et al.,* 2011, Brainard *et al.,* 2013). Broader ecosystem impacts include poorer habitat for fish and invertebrate species,and provision of fewer ecosystem goods and services for dependent human communities (Munday *et al.,* 2008; Doshi *et al.,* 2012). While corals appear to have been able to adapt to past rates of ocean warming (Logan *et al.,* 2013), there is no evidence that they can keep up with the accelerating rise in ocean temperature (Donner *et al.,* 2005; Hoegh-Guldberg *et al.,* 2007).

3.8.3 Impacts of rising ocean temperatures on reefs

Observations of coral bleaching prior to 1983 were limited, with less than 30 records available (Oliver *et al.,* 2009). Since that time, the number of people observing bleaching has increased. The number especially increased during and since the first well-documented global bleaching event in 1998 and the subsequent availability of satellite remote sensing tools that predict when and where bleaching occurs (e.g. Liu *et al.,* 2014; Heron *et al.,* 2016). While the increased number of observers may in and of itself cause a reporting bias (Oliver *et al.,* 2009), it is clear that there have been recent episodes of severe, widespread, and even global-scale bleaching. While ReefBase (Oliver *et al.,* 2009) used to maintain a central repository of well-documented survey reports – including reports of "no bleaching" – there is a great need to reinvigorate such an effort to assist in identifying regional/global bleaching patterns, as well as to support the development of satellite monitoring tools.

Five years with notably numerous bleaching reports to ReefBase were 1982-3, 1987, 1998, 2002 and 2005 (Oliver *et al.,* 2009). While bleaching in 1982-83 was widespread and perhaps global (Coffroth *et al.,* 1989), the 1998 event was the first to be confirmed as widespread in each of the Indian, Pacific and Atlantic basins, defining it as a global coral bleaching event. An estimated 16% of global coral reefs died in 1998 (Wilkinson, 2002). The second confirmed global bleaching event occurred during 2010 (Tan and Heron, 2011; Moore *et al.,* 2012; van Woesik *et al.,* 2012; Furby *et al.,* 2013; Alemu and Clement, 2014). The third confirmed global bleaching event began in mid-2014 in the Pacific and has continued to the time of this writing in mid-2016 (Eakin *et al.,* 2016). To-date, bleaching and mortality have been reported in many reef areas – the worst impacts being seen in the islands of the central equatorial Pacific Ocean (Kiritimati with >80% mortality and Jarvis Island with >95% mortality). Many bleaching events have been regional in scale: the eastern tropical Pacific was most affected during the 1982-83 event (Glynn, 1984); the Caribbean in 1987 (Williams and Bunkley-Williams,1988); the Great Barrier Reef (GBR) in 2002 (Berkelmans *et al.,* 2004); and the Caribbean again in 2005 (Wilkinson and Souter, 2008; Eakin *et al.,* 2010). These regional events were local manifestations of globally increasing ocean temperature in combination with regional climatic variability. The rapid recurrence of regional- and global-scale bleaching reflects the serious impact the current trajectory of ocean warming is having on both short- and long-term persistence of healthy coral reefs.

Since the first report of Black Band Disease in the Caribbean in 1973 (Antonius, 1973), various types of infectious coral diseases have been identified, affecting various coral species around the world (Burge *et al.,* 2014). Through this period, the understanding of the various diseases and their environmental drivers has rapidly progressed. The longest compiled datasets of repeated coral disease observations are from the Great Barrier Reef (from 1998, Willis *et al.,* 2004; Heron *et al.,* 2010), the Hawaiian archipelago (from 2004, Caldwell *et al.,* 2016) and parts of the Caribbean (from 2003, Miller *et al.,* 2009; Weil *et al.,* 2009). An increasing number of coral diseases were reported in the Caribbean in the 1980s and beyond (Goreau *et al.,* 1998; Aronson and Precht, 2001), with a strong connection being made between some diseases and thermal stress during the 2005 bleaching event (Rogers and Muller, 2012; Muller and van Woesik, 2014). Abundance of disease on the GBR increased by as much as 20-fold during and following the high temperatures that caused coral bleaching in 2002 (Willis *et al.,* 2004). Outer shelf reefs showed the greatest amount of disease, while disease prevalence was found to be greater during summer than in winter (Willis *et al.,* 2004). White syndrome disease prevalence on the GBR has been linked to the amount of coral cover and temperature stress during the preceding summer (summarized in Heron *et al.,* 2012). Prevalence of coral disease in the Hawaiian archipelago appears to have increased through the past decade, with episodic events indicating links to environmental drivers (Caldwell *et al.,* 2016).

The strength of links between thermal stress and bleaching and disease provides an opportunity to investigate impacts of rising temperatures on coral reefs using environmental data products. This approach is benefitted by the spatially vast and temporally complete nature of ocean temperature data products, especially those from satellites. Monitoring products for the risk of bleaching and disease events are considered essential support tools for the prediction and management of these disturbance events (Spillman *et al.,* 2011; Beeden *et al.,* 2012). Furthermore, projected ocean warming provides insight into how reefs may be impacted in coming decades.

3.8.4 Historical temperature trends on reefs

The year 2015 was recently analysed to have been the warmest year within the 136-year Extended Reconstructed Sea Surface Temperature (ERSST) climate data record from 1880 – and the fourth such record-breaking year since 2005 (NOAA National Centers for Environmental Information, 2016). While the record in 2015 was due in part to one of the strongest El Niño events on record, this event was superimposed upon a long-term warming trend. Global land-ocean temperature has increased at 0.07°C/decade since 1880 and at more than twice that rate since 1970 (0.17°C/decade; NOAA National Centers for Environmental Information, 2016). For context, the global temperature rate of increase over the past 420,000 years was 0.001°C/decade (ice core analysis, Petit *et al.,* 1999) – over 100 times slower than in recent decades. A large part of this recent warming has resulted from the great capacity of water to absorb heat – the ocean has absorbed 90% of the excess heat from anthropogenic climate change (IPCC, 2013). In fact, around half of the global ocean heat content increase since 1865 has occurred in the last two decades (Gleckler *et al.,* 2016).

Coral reefs have been especially hard hit by warming through the past century. Using the ERSST ocean temperature dataset, Heron *et al.* (2008) examined coral reef-containing locations to determine regional time-series for the 128-year period 1880-2007 (Figure 3.8.3). When averaged across each of nine coral reef regions, ocean temperatures increased in the range 0.02–0.06°C/decade (Table 3.8.1) – similar to the global rate of warming. The Fifth Assessment Report of the Intergovernmental Panel on Climate Change reported SST trends in coral reef provinces during a recent 60-year period (1950-2009; Hoegh-Guldberg *et al.,* 2014) and Heron *et al.,* (in review) reported trends during the satellite record (1985-2012). All reef regions except the north Atlantic accelerated in their warming during recent decades, exceeding the rate of global temperature increase (Figure 3.8.3, Table 3.8.1).

Since the 1980s, satellite remote sensing instruments have measured ocean surface temperature providing datasets at a higher spatial resolution than the century-long records (~4 km, compared with up to ~200 km). This has enabled examination of temperature trends near the scale of individual reefs. A recent study examined linear trends at global reef locations over the period 1985-2012 (Heron *et al.,* in review), the first such analysis approaching the standard climate time-scale of 30 years, using a NOAA Climate Data Record for SST[1]. Annual temperature trends on reefs were 0.20°C/decade when averaged globally but ranged from -0.48 to +0.66°C/decade across reef locations (Table 3.8.1). However, very few reefs saw a cooling trend; 97% of reef locations warmed through the analysed period. An example of the spatial variation in annual trends is

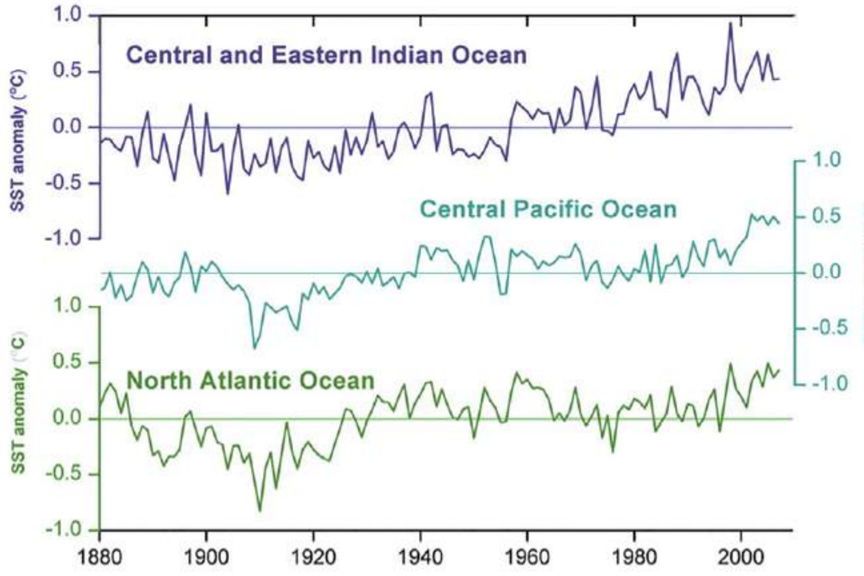

Figure 3.8.3 Sea-surface temperature (SST) time-series for reef-containing locations within three regions showing trend of increasing temperatures through the period 1880-2007. After Heron *et al.* (2009).

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[1] The Warm Pool is an ocean region in the western Pacific where SST is >28 °C year-round.

Table 3.8.1 Trends in annual temperature averaged across coral reef regions. Horizontal lines and curly brackets indicate approximate correspondence where the studies defined reef regions differently

Coral reef region	Temperature trend (°C/decade)		
	1880-2007	1950-2009	1985-2012
Middle East and Western Indian Ocean	*0.050*	*0.100*	*0.32*
Central and Eastern Indian Ocean	*0.059*	*0.097*	*0.21*
Southeast Asia	*0.044*	*0.131*	*0.20*
Great Barrier Reef and Warm Pool [2]	*0.052*	*0.073*	*0.08*
Western Pacific Ocean	*0.040*		
Central Pacific Ocean	*0.035*		*0.24*
Eastern Pacific Ocean	*0.024*	*0.094*	
Caribbean Sea	*0.037*	*0.024*	*0.17*
North Atlantic Ocean	*0.036*		
	After Heron *et al.* (2008)	After Hoegh-Guldberg *et al.* (2014)	After Heron *et al.* (in review)

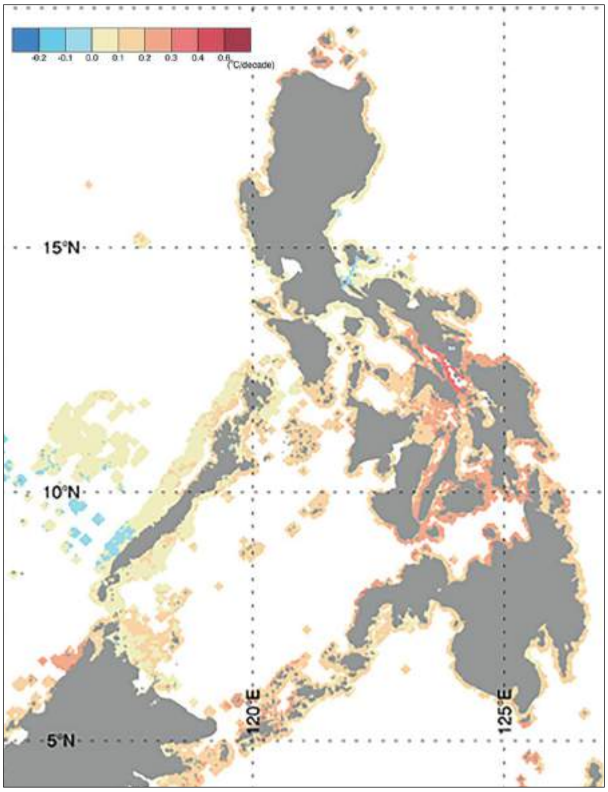

Figure 3.8.4 Linear trends in annual satellite-derived sea surface temperature around the Philippines for the period 1985-2012.

provided for the reef locations of the central Philippines (Figure 3.8.4). Globally, the highest annual warming trends were predominantly observed in the Middle East and the Pacific Ocean, while the Australian region had the highest number of reefs at which temperatures cooled during the studied period (Table 3.8.1; Heron *et al.,* in review). Reef-scale trends were also calculated for temperature from the three-month warm season, to consider potential effects during the period where coral bleaching is most likely. Averaged across global reef locations, warm-season temperatures increased at 0.16°C/decade (Heron *et al.,* in review) with 89% of reefs warming during the 28-year period. This has increased the exposure of coral reefs to thermal stress events that are linked to bleaching and disease.

3.8.5 Historical thermal stress impacts on reefs

As corals exist close to their thermal maximum, they are at risk of stress with relatively small increases in temperature. Temperatures exceeding the 'normal' summertime maximum experienced locally by as little as 1°C can cause coral bleaching. Global thermal stress monitoring products employ this temperature threshold to predict where and when bleaching may occur (Liu *et al.,* 2014; Heron *et al.,* 2016). These satellite-based temperature products use the Degree Heating Week (DHW) metric, which combines the magnitude and duration of unusually warm temperature to define the thermal stress (Liu *et al.,* 2003). Bleaching- and mortality-level stress occurs at DHW values at or above 4 and 8°C-weeks, respectively (Liu *et al.,* 2003; Eakin *et al.,* 2010). For broader-scale and less frequent datasets (typically monthly resolution), equivalent thresholds for accumulated thermal stress are Degree Heating Month (DHM) values of 1 and 2°C-months, respectively (Donner *et al.,* 2005).

Past-century records show not only an increase in temperatures, but also an increase in thermal stress.

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[2] pathfinder.nodc.noaa.gov

Box 3.8.1 The long and the short of thermal stress on corals

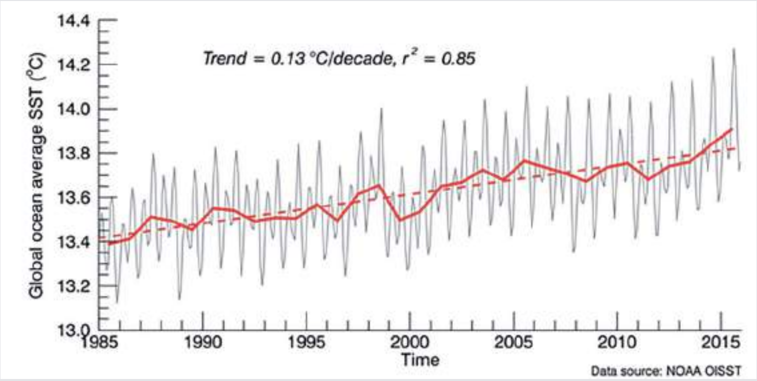


Figure 1 Global ocean sea surface temperature trend

Environmental impacts on reefs can generally be described as either "acute" – stress occurring as a short pulse; or "chronic" – long-term stressors (Anthony *et al*., 2015). Acute events include weeks-to-months of unusually warm water, heavy rainfall, or tropical storms. Chronic stressors include poor water quality, long-term warming and sea-level rise. Direct human impacts also fit into these categories; e.g. fishing: the use of bombs to kill fish (acute), compared with on-going unsustainable overfishing (chronic). Global ocean warming is a chronic stressor (Figure 1 dashed red line) that increases the background temperature level upon which acute short-term temperature variability (solid red line) is superimposed, making it more likely that natural variability (solid grey line) will exceed temperature thresholds that cause ecosystem impacts. While those short-term fluctuations can be considered 'natural', the underlying chronic warming causes these fluctuations to more often exceed limits within which organisms can remain healthy.

From June 2014 to June 2016, thermal stress impacted over 98% of coral reef locations globally (orange Warning level or higher on Figure 2), with 66% being exposed to the prolonged high temperatures that cause coral bleaching (red Alert 1 to 2). Many reefs experienced bleaching twice, and bleaching and mortality of corals were observed in all three tropical ocean basins. At the time of this writing, the event still continued.

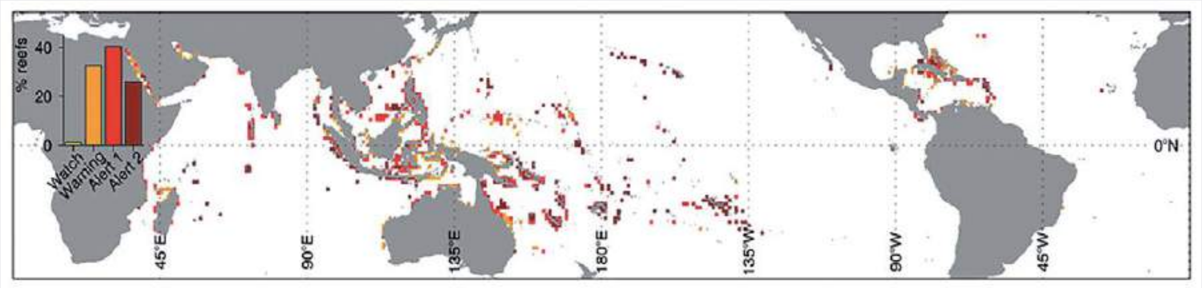


Figure 2 Coral reef thermal stress levels.Data source: NOAA OISST, mapped at 1° resolution

DHM values for the GBR and Warm Pool region (Figure 3.8.5) exemplify this for the nine reef regions studied by Heron *et al.* (2009). The IPCC Fifth Assessment Report (Hoegh-Guldberg *et al.,* 2014) indicated that the number of years that bleaching-level thermal stress (DHM ≥ 1 °C-month) occurred during 1981-2010 was double that in 1951-1980. This dramatic increase in the occurrence of bleaching stress is consistent with the observed acceleration in temperature increase and the observations of bleaching post-1982.

Reef-scale satellite monitoring of thermal stress revealed that reef locations were, on average, exposed to bleaching-level stress once every ~6 years in the 28-year record (1985-2012), while mortality-level stress occurred once every 21 years (Heron *et al.,* in review). There was substantial spatial variation in the frequency of both bleaching and mortality stress events within and between reef regions (e.g. Figure 3.8.6). The study noted a three-fold increase in the number of global reef locations exposed to bleaching stress from the first seven years (1985-91, 8%) to the latest seven years (2006-2012, 26%), further emphasizing the increased frequency of thermal impacts. Increases in temperature and thermal stress events will, if they continue unabated, produce serious consequences for coral reef ecosystems and their dependent human communities.

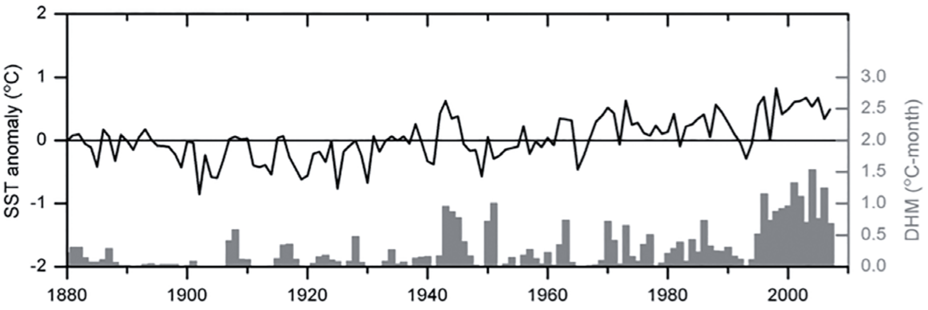


Figure 3.8.5 Sea-surface temperature (SST) and accumulated thermal stress (Degree Heating Months, DHM) time-series for reef-containing locations in the Great Barrier Reef and Warm Pool region showing increases through the period 1880-2007 (after Heron *et al.,* 2009).

3.8.6 Temperature and thermal stress projections

Model projections used in the IPCC Fifth Assessment Report predict that sea surface temperature will continue to increase through the 21st Century, in proportion with cumulative emissions of heat-trapping gases (Gattuso *et al.,* 2015). These emissions scenarios, called Representative Concentration Pathways (RCP), include one mitigation scenario (RCP2.6), two stabilization scenarios (RCP4.5 and RCP6.0) and one high-emission scenario (RCP8.5) (van Vuuren *et al.,* 2011). Surface temperature increase by 2100 is predicted to range from 0.6 to 2.0°C, relative to 1986-2005, depending upon the emissions pathway employed (IPCC, 2013). However, the near-term projections (to 2035) show limited deviation across the four emissions pathways, indicating a period of 'committed warming' due to past emissions (Donner, 2009). The divergence of trajectories in the latter half of this century primarily results from potential emissions in the next two decades. Temperatures under the highest emissions pathway (RCP8.5) may be more than 2°C higher than those under the lowest impact pathway (RCP2.6) by 2100 (Gattuso *et al.,* 2015). This is why it is so important to reduce emissions immediately to avoid the long-term declines in marine resources. Unfortunately, human-caused emissions are still following the high-emission scenario (RCP8.5).

Climate model projections of temperature have, for nearly 20 years, predicted devastating impacts for

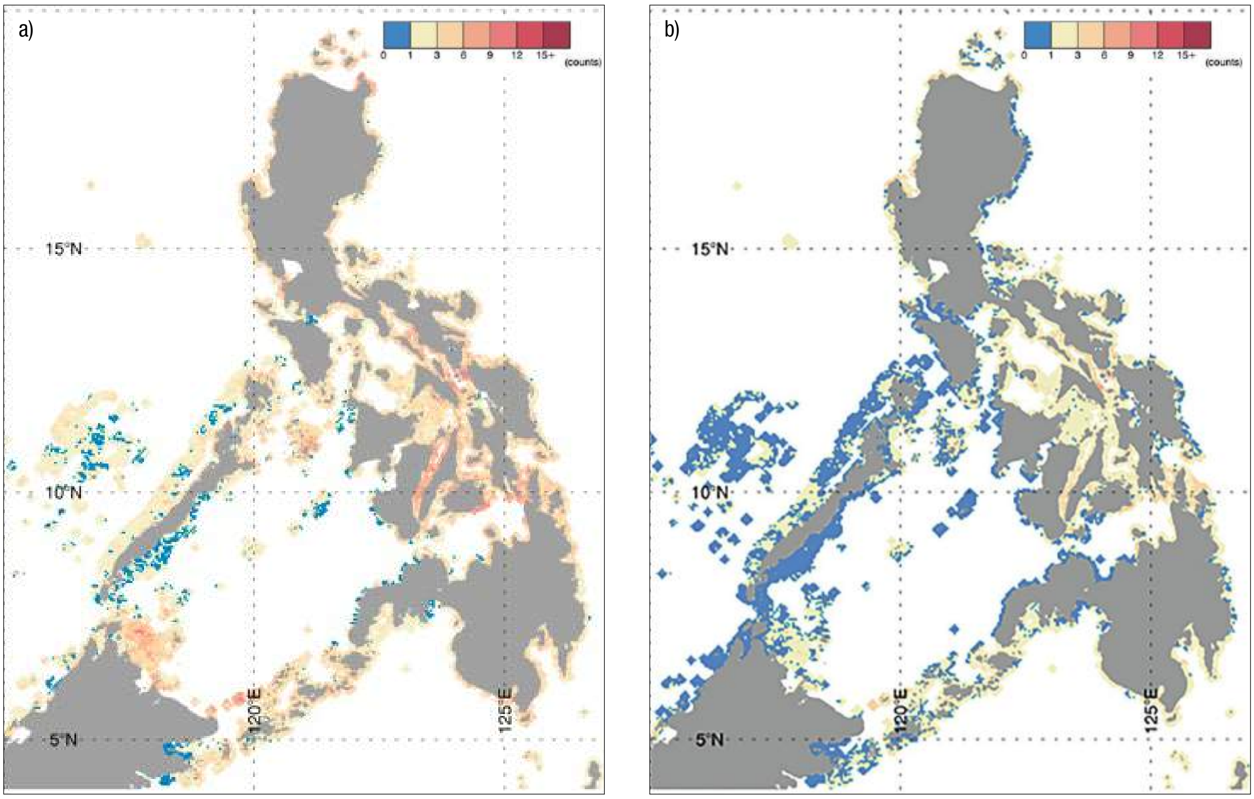


Figure 3.8.6 Number of thermal stress events around the Philippines during the period 1985-2012. (a) Bleaching-level stress (Degree Heating Weeks, DHW, ≥ 4 °C-weeks); (b) Mortality-level stress (DHW ≥ 8 °C-weeks).

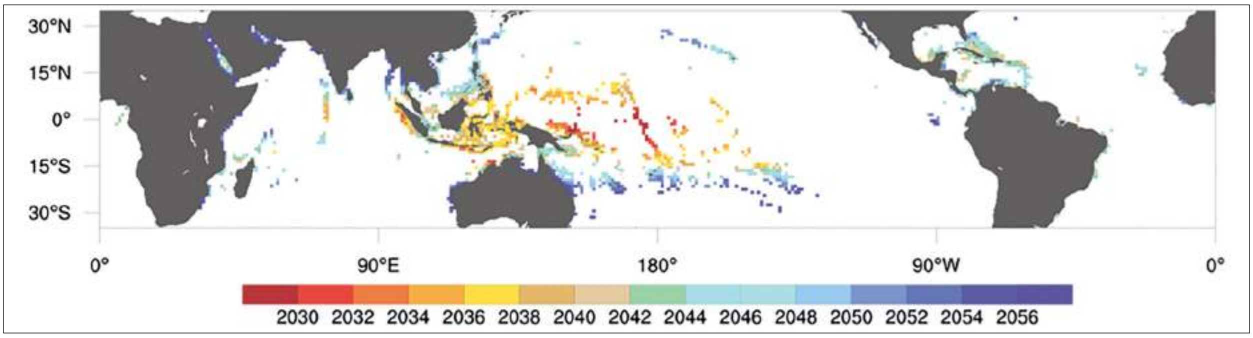


Figure 3.8.7 Global projections of the year annual severe bleaching conditions start for all reef locations under Representative Concentration Pathway (RCP) 8.5. After van Hooidonk *et al.* (2014).

coral reefs within the 21st Century. Seminal work by Hoegh-Guldberg (1999) suggested that bleaching-level stress would be reached annually within decades. Analysis used in the IPCC Fifth Assessment Report predicted the loss of corals from most global locations by 2050 under the current warming trajectory (Hoegh-Guldberg *et al.,* 2014). Global projections of when bleaching-level thermal stress will occur annually showed that the spatial patterns were nearly the same at all concentration pathways; the difference was only in the timing between the 2030s and 2050s (van Hooidonk *et al.,* 2013, 2014). Locations for which the onset of annual severe bleaching (Figure 3.8.7) occurs later, include the South Pacific, western Indian Ocean and parts of South-east Asia, while earlier start years occur across the central equatorial Pacific Ocean and in parts of the Caribbean. Managers in early-onset locations should immediately work to reduce other (non-thermal) stressors to promote recovery following disturbance events. In later-onset locations, managers should enhance protection of reefs (e.g. limited access, no-take zones) to increase the likelihood that they will persist through other disturbances (van Hooidonk *et al.,* 2013, 2014).

Corals have exhibited some ability to adapt to rising temperatures, helping reefs persist through past disturbance and temperature rise. Adaptive processes may include short-term increases in bleaching temperature thresholds (e.g. through symbiont shuffling following bleaching-level exposure) and/or long-term threshold changes (e.g. genetic selection through long-term temperature change or repeated exposure to bleaching-level exposure) (Logan *et al.,* 2013). Calculations of thermal stress (DHM) using different historical periods to define baseline temperatures suggested that some corals might have already responded (i.e. adapted) to 20th Century warming (Logan *et al.,* 2013). Projections of coral responses that included temporary increases to the temperature threshold resulted in a delayed onset of frequent bleaching by around 10 years under the high-emission scenario (Logan *et al.,* 2013). If corals can rapidly adapt within as little as 40 years, the frequency of severe bleaching could be reduced by as much 80% under the high-emission scenario (RCP8.5) (Logan *et al.,* 2013). While such rapid and continuing adaptation may be unlikely, further research on these adaptive processes is essential to help us understand whether corals can respond in time to projected warming. Clearly, the ability of corals to adapt to increasingly stressful temperatures will influence predictions of future bleaching.

Because climate projections are run at coarse spatial scales (i.e. large grid cells), some researchers have endeavoured to re-present this information at higher resolution, known as 'downscaling', particularly in coastal locations. Frieler *et al.* (2013) downscaled climate model projections to ~50 km resolution and determined that even under the most optimistic emissions scenario (RCP2.6) combined with the most favourable assumptions of coral adaptation, one-third of global reefs would experience severe thermal stress at least once every five years within this century. At this frequency, it is believed that corals have insufficient time to recover between disturbances (Baker *et al.,* 2008). Frieler *et al.* (2013) suggest that globally-averaged warming needs to be limited to below 1.5°C to preserve >10% of coral reefs worldwide.

Finer-scale, downscaled information, such as within tens of kilometres, provides the opportunity for targeted management activities at a regional scale (McLeod *et al.,* 2010), such as enhanced protection and reduced local stress at key locations. Downscaling of climate projections to support spatial conservation planning has been undertaken in a limited number of specific coral-reef regions. Projections for reefs across the Caribbean

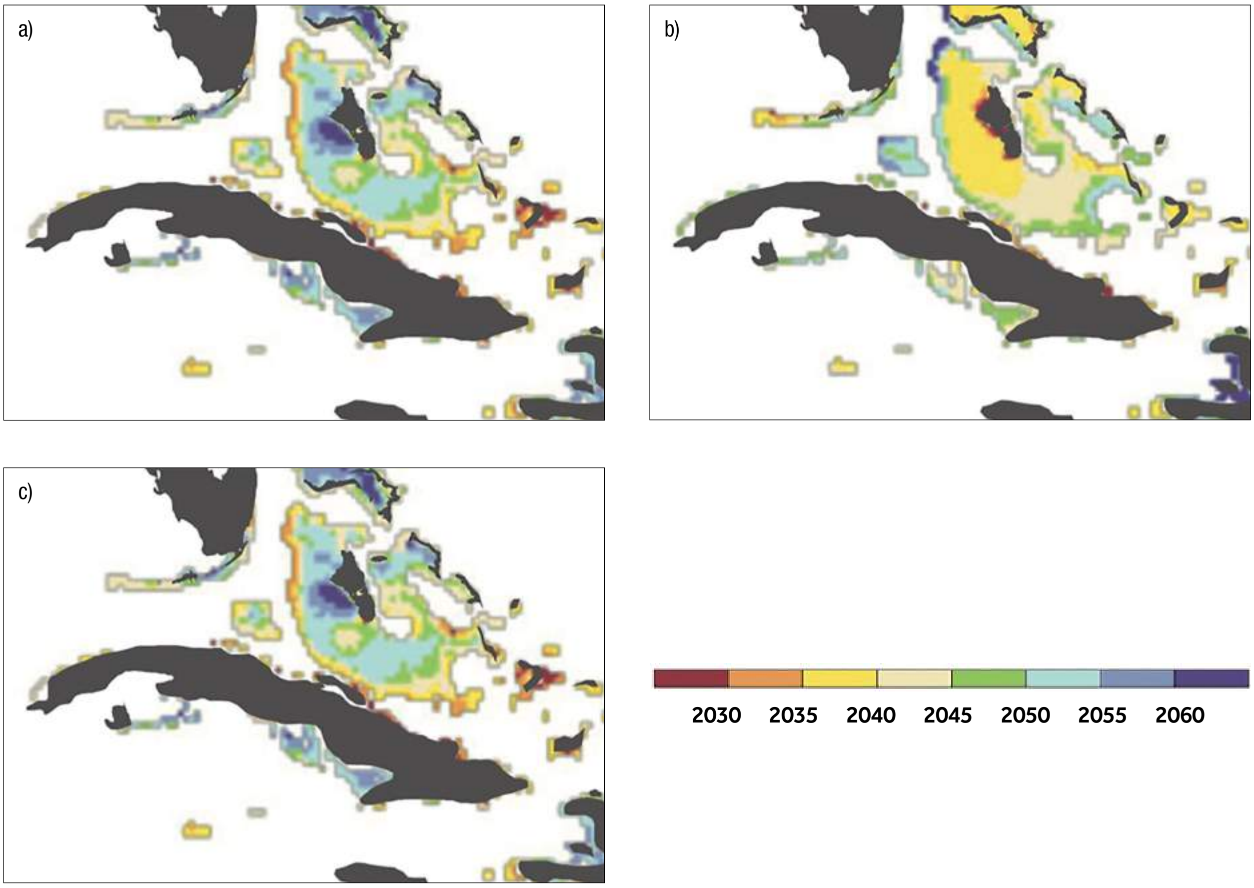


Figure 3.8.8 Onset year of annual severe thermal stress from native-resolution (coarse) climate projections (a), and downscaled using dynamical (b) and statistical (c) techniques. Downscaled projections provide information at a scale more relevant to reef management. Mean onsets ± SD are 2040 ± 10.3 years, 2041 ± 10.3 years and 2043 ± 10.5 years, respectively. Spatial domain is [85.5-72.5°W, 17.5-26.5°N]. After van Hooidonk *et al.* (2015).

(van Hooidonk *et al.,* 2015) were downscaled using two methods: (1) dynamical, where coarse projection model outputs are used to force a higher-resolution regional model resulting in local-scale variations in sea temperature; and (2) statistical, where historical patterns in high-resolution temperature are used to interpret the broad projections at the local scale. Each technique has costs and benefits: statistical downscaling is less computationally intensive (i.e. faster and cheaper) than dynamical downscaling; however, the dynamical approach has greater potential to incorporate unprecedented spatial patterns in SST (whereas statistical downscaling cannot).

Van Hooidonk *et al.* (2015) compared output from these downscaling techniques with the projections from the coarse-resolution global models. While the native resolution and both downscaled projections resulted in similar onset years for annual severe bleaching stress when averaged across the Caribbean (~2040) and similar standard deviation about the mean year (~10 years), the downscaled projections showed much finer spatial variations in the onset year (Figure 3.8.8). This spatial variability offers the potential for focused management response. The results of statistical and dynamical downscaling were comparable, except in one location (Andros Island, Bahamas) where regional currents were predicted to change. This suggests that statistical downscaling can provide useful information but should be interpreted with the recognition that it may miss changes in local dynamics. It is important to note that these are only differences among models and both may differ from realized changes.

Magris *et al.* (2015) used both historical observations and downscaled projections of chronic temperature trends and acute stress to characterize thermal regimes for Brazilian reefs. The acute stress metric was calculated as the duration of reduced ecosystem function of the reef (e.g. impaired recovery, growth and reproduction) due to thermal stress events. The combined historical and projected measures were used to guide potential management actions such as reduction of anthropogenic stressors and zoning for multiple-use or protection.

Projected increases in temperature can also inform outbreak predictions of some coral diseases. Maynard *et al.* (2015b) considered future increased susceptibility of the coral host to disease as well as changes to disease pathogen abundance and virulence, linking these to three distinct temperature signals. Reefs in the South Pacific, around Florida and in parts of the Arabian Sea were predicted to be among the latest to experience all three temperature signals related to disease outbreak (Figure 3.8.9). At RCP8.5, at least two of the three disease conditions were projected to occur before the onset of annual severe bleaching at 96% of reefs (cf. van Hooidonk *et al.,* 2014; Figure 5), indicating that impacts on coral communities from disease in coming decades may be even more important than bleaching. The risk of disease is also dependent upon local threats, such as increased sedimentation and nutrients from coastal development and terrestrial pollution; marine pollution and damage; and physical damage from fishing activities (particularly destructive fishing). Effective management intervention may alleviate these local threats and thereby mitigate disease risk to reefs as temperature rises.

3.8.7 Historical ocean acidification on reefs

While CO_2 emissions have induced (and are projected to continue) ocean warming, uptake of atmospheric CO_2 by the ocean has also altered ocean chemistry. Around 26% of human-related CO_2 emissions during the industrial era (since ca. 1780) have been absorbed in the ocean (Feely *et al.,* 2012). This has resulted the ocean becoming less alkaline (i.e. acidifying), with decreased oceanic pH (by 0.1 pH units) and carbonate ion concentration. This changed chemical balance is usually reported using the aragonite saturation state (Ω_{arag}) – a measure of the

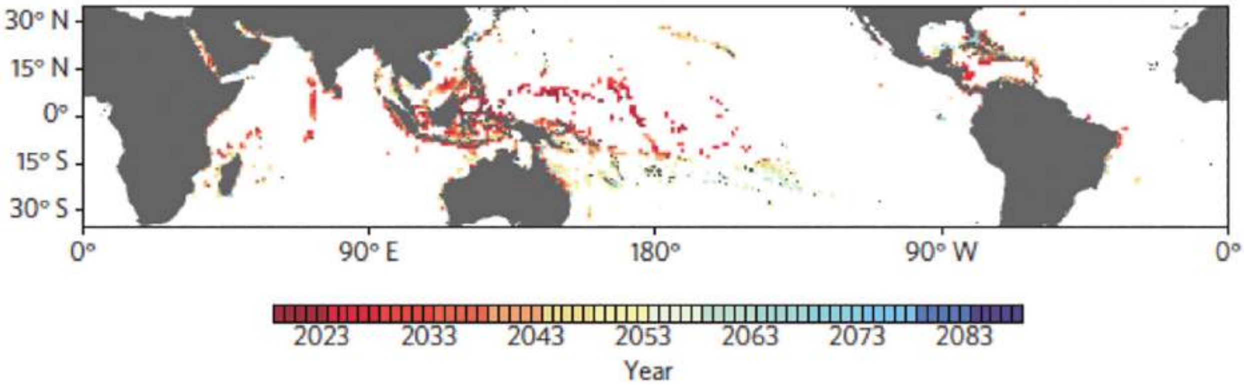


Figure 3.8.9 The year in which three temperature factors related to disease outbreak (host susceptibility, pathogen abundance, pathogen virulence) were all projected to occur. After Maynard *et al.* (2015b).

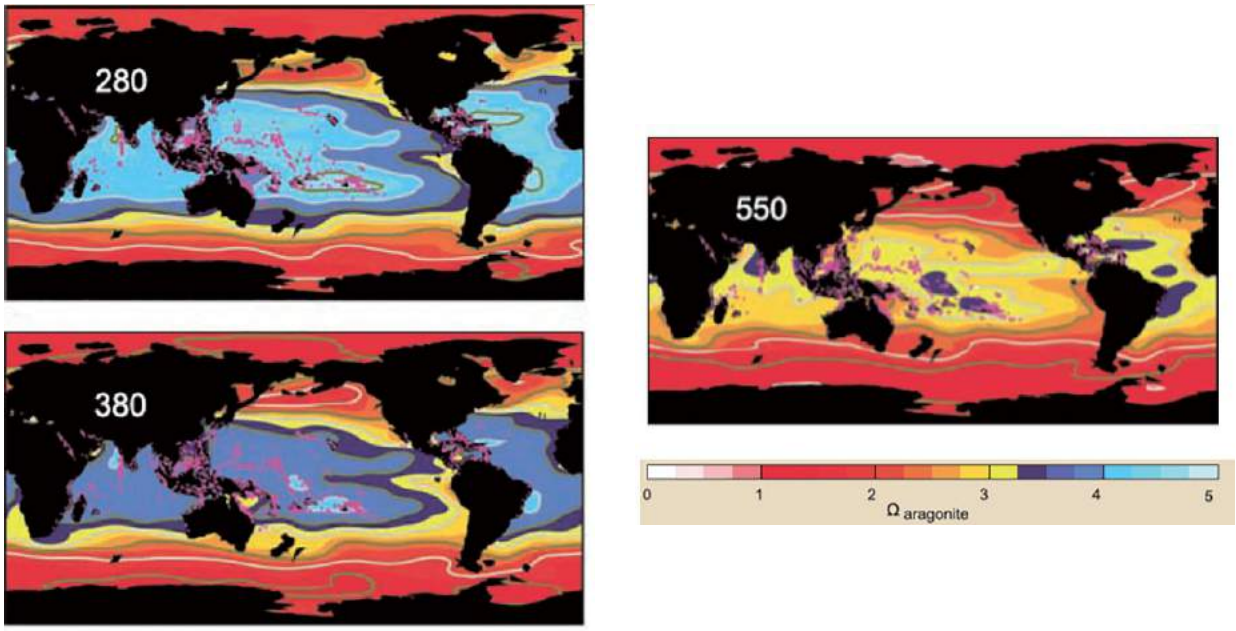


Figure 3.8.10 Modelled surface aragonite saturation state for the global ocean for various atmospheric concentrations of CO_2 (ppm): (a) 280 ppm (ca. 1780), (b) 380 ppm (ca. 2006), (c) 550 ppm (ca. 2050). After Hoegh-Guldberg *et al.* (2007).

amount of aragonite (the type of calcium carbonate forming coral skeletons and nearly all mollusc shells) that is dissolved in seawater. Ω_{arag} is generally highest in tropical waters and decreases poleward (Figure 3.8.10) and is important for reef-building corals as it describes the capacity of corals to form their limestone skeleton. In general, a saturation state must exceed a value of one for precipitation to occur; however, due to physical, chemical, and biological erosions on reefs, the Ω_{arag} threshold at which reef growth exceeds reef erosion is around 3.3 (Hoegh-Guldberg *et al.,* 2007). Ocean surface waters are considered optimal for maintaining coral accretion where $\Omega_{arag} > 4.0$, with less desirable categories of adequate (3.5-4.0), low (3.0-3.5) and extremely marginal (<3.0) becoming more and more apparent in reef waters (Guinotte *et al.,* 2003).

Modelling of global historical aragonite saturation state indicates long-term decline since the pre-industrial era (Cao and Caldeira, 2008). When atmospheric CO_2 was 280 ppm (ca. 1780; Figure 3.8.10a), waters surrounding over 98% of global coral reefs had $_{arag}$ above 3.5. This was cut by almost two-thirds (to 38%) by the time CO_2 concentration reached 380 ppm (ca. 2006; Figure 3.8.10b). During this period the average Ω_{arag} surrounding reefs decreased from 4.1 to 3.4, at an overall rate of -0.03 per decade but much faster in recent decades (Cao and Caldeira, 2008). In the Caribbean, Ω_{arag} decreased from 4.05 to 3.90 from 1996 to 2006, a decline rate of -0.13 or -3.4% per decade (Gledhill *et al.,* 2008). This rate was consistent with recent trends across the Pacific (Feely *et al.,* 2012) and at Lord Howe Island, the most poleward coral reef in the world (Anderson *et al.,* 2015). However, the decline is event faster at some reefs. Ω_{arag} at Davies Reef in the central Great Barrier Reef declined at -0.20 or -4.7% per decade between 1981 and 2012 (Anderson *et al.,* in review).

Fortunately, coral reefs have some local protections. Coral metabolic processes can influence the carbonate concentration in the immediate vicinity of corals, with daily Ω_{arag} variations as great as 1.0 due to changes in local CO_2 concentration during photosynthesis (Albright *et al.,* 2013). Furthermore, algal and/or seagrass beds can locally-enhance Ω_{arag} values, potentially buffering the effects of broad-scale ocean acidification (Anthony *et al.,* 2011; Manzello *et al.,* 2012; Unsworth *et al.,* 2012). Recent work that restored pre-industrial Ω_{arag} levels on a reef showed that modern calcification rates are clearly lower than they were before industrialization (Albright *et al.,* 2016).

3.8.8 Projected ocean acidification on reefs

Oceanic waters are predicted to continue a trajectory towards lower pH and Ω_{arag}. Atmospheric CO_2 concentration is projected to reach 550 ppm around 2050 under RCP8.5 (van Vuuren *et al.,* 2011), a level at which all existing coral reefs would be exposed to regional waters with $\Omega_{arag} < 3.5$ (Hoegh-Guldberg *et al.,* 2007; Figure 3.8.10c). Though projected to experience the greatest absolute decrease in Ω_{arag}, tropical oceans will continue to have relatively higher values than more poleward locations, suggesting they are the most conducive to maintaining carbonate accretion. However, tropical reefs are projected to be the most affected by bleaching-level thermal stress. These opposing factors suggest that there are no long-term refugia from both warming and acidification, which is demonstrated by considering the Ω_{arag} value projected for reef locations at the time when reefs are exposed to annual severe bleaching (RCP8.5; van Hooidonk *et al.,* 2014). High-latitude reefs predicted to have delayed thermal stress (Figure 3.8.7) have the lowest Ω_{arag} values (Figure 3.8.11), slowing any recovery from bleaching events.

Even if aggressive action is taken to reduce CO_2 emissions to stay within the RCP2.6 projections, atmospheric CO_2 concentration will peak at 440 ppm around 2050 (van Vuuren *et al.,* 2011), exposing all reefs to waters with $\Omega_{arag} <$ 3.75 and many below 3.25 (Hoegh-Guldberg *et al.,* 2007).

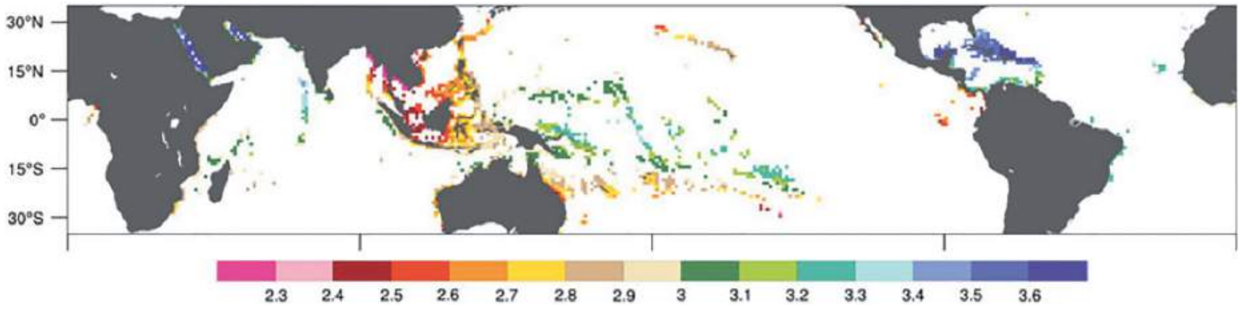


Figure 3.8.11 The aragonite saturation state (Ω_{arag}) at the time that reefs start to experience annual severe thermal stress based on model projections under RCP8.5 (shown in Figure 3.8.7). After van Hooidonk *et al.* (2014).

Areas adjacent to algal or seagrass beds that modify the local chemistry may represent one of the few options for the survival of coral reefs (Anthony *et al.,* 2011).

3.8.9 Other environmental factors influencing coral reefs

Tropical cyclones (TCs, also known as hurricanes and typhoons) of low intensity have the potential to mitigate thermal stress that would otherwise lead to bleaching (Manzello *et al.,* 2007); however, more severe TCs can result in physical destruction of reef structure from which recovery can take decades (e.g. Beeden *et al.,* 2015). Physical damage to corals can lead to increased coral disease (Lamb and Willis, 2011). Calculating historical trends in TC incidence at varying intensity levels has been confounded by advances in monitoring capability through the observational record (the intensity of cyclones occurring as recently as the 1970s and 80s may have been underestimated). Using consistent measurement techniques, there has been no trend in the number of TCs, nor has there been any significant trend in the number of severe TCs (sustained winds greater than 112 knots), since 1970 (Klotzbach and Landsea, 2015). While uncertain, the frequency of TCs is projected to show little change or slightly decrease in the coming decades but the incidence of severe TCs may increase in some areas (Knutson *et al.,* 2010). It is important to note that coral reefs have survived and thrived in the past in areas with frequent and severe TCs. It is likely that other impacts such as coral bleaching have reduced the ability of reefs to recover after these storms, making their future impact much more critical to reef survival (Edwards *et al.,* 2011).

Global sea level rose by 0.19 m from 1901 to 2010 at rate that increased to reach 3.2 mm per year during period 1993-2010 (Rhein *et al.,* 2013). Recent sea-level rise has most likely been the fastest in at least 2800 years (Kopp *et al.,* 2016). This has occurred primarily as a result of thermal expansion of ocean waters and movement of terrestrial water (e.g. glacial ice) into the ocean. Sea level is projected to further rise by about 0.74 m by 2100 under RCP8.5 (Rhein *et al.,* 2013), although there are concerns that the potential for ice melt is actually much greater than current estimates. While individual coral colonies have been observed to grow at the historical and projected rates of sea-level rise, entire reefs may not be able to keep up with this rate, particularly if growth rates are diminished due to increased temperature and ocean acidification. During past rapid sea-level rise, many reefs have been unable to keep up and have instead re-located coastward in dramatic 'back-steps' (Blanchon *et al.,* 2009). Changes in sea level may also influence the localized influx of terrestrial sediment and turbidity, which can adversely affect physiological processes such as photosynthesis and recruitment (Field *et al.,* 2011).

A further consideration for the future of coral reefs is the potential availability of suitable habitat. Freeman *et al.* (2013) analysed environmental parameters including temperature, aragonite saturation state (Ω_{arag}), salinity, current speeds, photosynthetically active radiation (PAR) and surface phosphate concentration to characterize conditions conducive to coral habitation. Applying climate projections to these characterizations suggested that the global area of habitat suitable for corals would decrease 82% by 2100 under RCP8.5. Indian Ocean reef sites were identified as being most representative of projected future conditions – these reefs may be best situated to provide suitable habitat for reefs into the future.

3.8.10 Impacts to ecosystem services

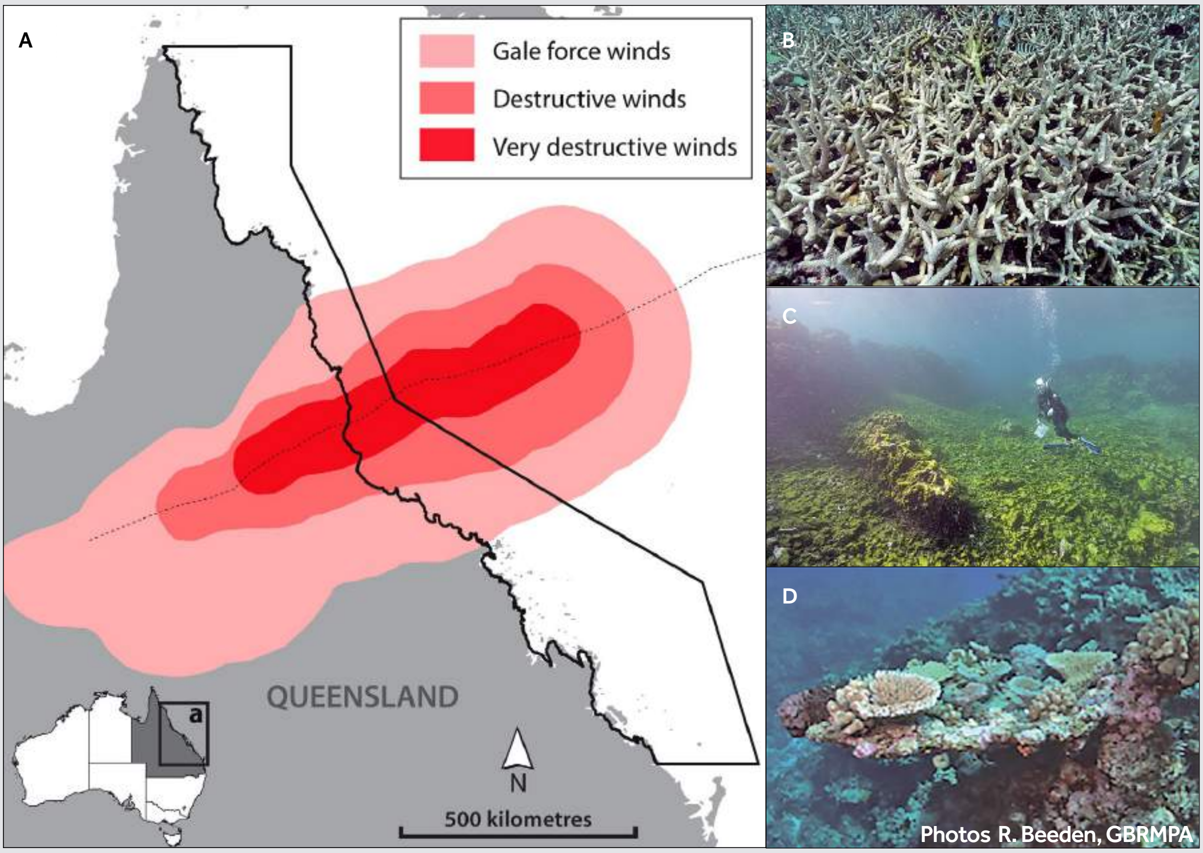
Cumulative impacts on coral reef ecosystems potentially have dramatic consequences for the myriad services they provide (Gattuso *et al.,* 2015) and the numerous people who rely upon those services. Coral reefs afford protection to coastlines by reducing wave energy during storm surge (associated with tropical storms) and other high water events (Spalding *et al.,* 2014). Predicted increases in sea levels will likely lead to more frequent and severe coastal inundation and erosion. Ocean acidification will likely reduce the strength of reef structure, increasing the loss of reefs during disturbance events (bleaching, tropical cyclones) and thereby decreasing coastline protection. This would also remove critical habitat for tropical fish and other reef fauna. While certainly impacting industrial fisheries (projected to decline, even under the lowest emissions pathway RCP2.6; Gattuso *et al.,* 2015), the effect of fish habitat loss on subsistence fishers would likely be even more dramatic. Coral reefs have also been an important source of substances used to develop new pharmaceuticals (including from coral, symbiotic coral microbiota, sponges and macroalgae; Leal *et al.,* 2013).

In addition, loss of corals (in quantity and/or quality) is expected to negatively affect the tourism industry (Gattuso *et al.,* 2015). A recent study following a coral bleaching event in South-east Asia suggested an economic loss of services to dive tourists on the order of US$49-74 million for the six-month period during and following bleaching (Doshi *et al.,* 2012). This estimate did not include loss of other economic benefits to the broader community (e.g. dive industry, accommodation, restaurants, other activities). Tourism costs associated with the loss of corals from warming and acidification have been estimated as high as US$12 billion per year, with annual costs from the loss of reef ecosystem services up to US$1 trillion by 2100 (Gattuso *et al.,* 2015).

There is evidence that the geographic range over which some marine species exist has already shifted – generally to higher latitudes and/or deeper waters, consistent with increased ocean temperature (Precht and Aronson, 2004; Yamano *et al.,* 2011; Hoegh-Guldberg *et al.,* 2014). However, as noted, corals are unlikely to experience range shifts due to the opposing latitudinal effects of warming and ocean acidification (van Hooidonk *et al.,* 2014) and reduced availability of suitable habitats at higher latitudes (Kleypas *et al.,* 1999), leading to shrinking geographic range and ultimately their demise. Technologies for the persistence and/or replenishment of corals after disturbance events include assisted coral evolution (van Oppen *et al.,* 2015) and coral farming (Rinkevich, 2005; Gattuso *et al.,* 2015). Rapid development of these may be necessary for the long-term existence of corals and the services they provide.

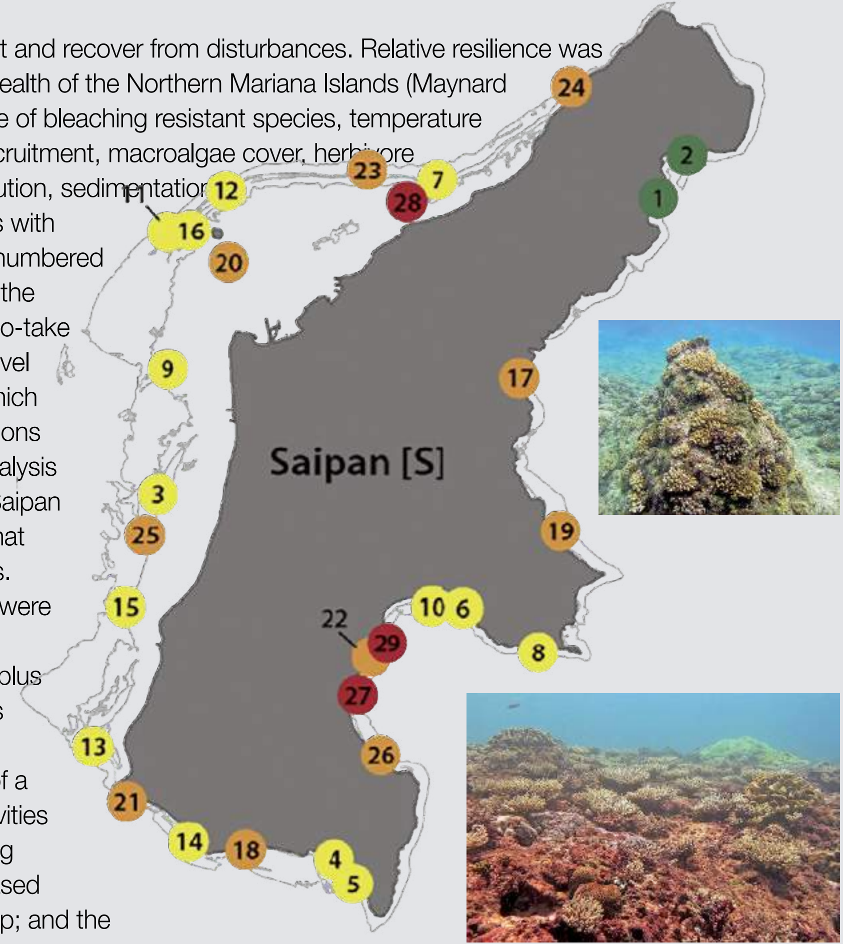
Box 3.8.2 Tropical cyclone damage

In 2011, Tropical Cyclone (TC) Yasi tracked across the Great Barrier Reef (GBR) before crossing the Queensland coast as the highest intensity cyclone landfall in 93 years. TC Yasi was both intense and large; gale force winds extended across a swath of ~600 km (panel A). An estimated 15% of GBR reef area was impacted (panel B), with 4% sustaining severe damage to corals and damage to reef structure (panel C). Many reefs were reduced to fields of rubble and overgrown by algae. In the worst hit areas, reefs were completely scoured and ~100-year-old corals were dislodged. Some recovery from the TC impacts was observed by 2013 with new coral recruits (panel D) and reduced algal cover. However, the rate of coral cover increase was around one-third to one-half of the previously documented rates on the GBR, potentially due to the extensive structural damage (Beeden *et al.,* 2015).



Photos R. Beeden, GBRMPA

Box 3.8.3 Reef resilience – local-scale assessment and management



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Resilience is the capacity to resist and recover from disturbances. Relative resilience was assessed for Saipan, Commonwealth of the Northern Mariana Islands (Maynard *et al.*, 2015a) based on: presence of bleaching resistant species, temperature variability, coral diversity, coral recruitment, macroalgae cover, herbivore diversity, herbivore biomass, pollution, sedimentation and fishing access. The two sites with the highest assessed resilience (numbered 1 and 2, at right) were located in the Bird Island Marine Sanctuary, a no-take marine protected area – a high level of management protection for which no further local management actions could therefore be employed. Analysis of the two least resilient sites in Saipan identified management actions that could reduce vulnerability of reefs. At Achugao (#28), these actions were the management, regulation and enforcement of fishery activities; plus bleaching monitoring and actions to support post-bleaching recovery. At Tuturam (#29), any of a broad range of conservation activities could enhance resilience including reducing terrestrial run-off; increased tourism outreach and stewardship; and the actions listed for Achuago. Including managers and reef stakeholders throughout the resilience assessment maximized support for the process and for the implementation of identified management actions.

3.8.11 Resilience and resilience-based management

As the frequency and intensity of climate change impacts increase, there is increasing need to enhance reef resilience – the capacity to resist impacts of and to recover following disturbance events. Resilience can also be described as the ability to maintain key ecosystem functions through disturbance. In addition to climate-related pressures, there are various local factors that can affect the ability of reefs to cope with stress events. These include pollution, nutrient loading, sedimentation and overfishing. Some of these pressures on reefs occur as discrete events (acute: anchor damage, terrestrial run-off) while others operate over longer timeframes (chronic: poor water quality, overfishing). Many environmental disturbances are acute events (e.g. thermal stress, storm damage). The cumulative effects of chronic stressors can exacerbate the impacts of acute events (Anthony *et al.,* 2015); e.g. corals are more susceptible to thermal bleaching in locations with higher nutrient loading (Wooldridge, 2009; Wooldridge *et al.,* in press). Enhancing reef resilience may be the difference between corals' survival and death for some levels of future stress.

Management actions to directly mitigate local stressors, or to reduce local activities that exacerbate climate-related stress events, can decrease reef vulnerability and therefore support continued provision of ecosystem services – this is the ethos of resilience-based management (Bestelmeyer and Briske, 2012). Importantly, resilience concepts incorporate both the ecological system and ecosystem services to communities that depend upon it (Chapin *et al.,* 2010). Different reefs can have different levels of vulnerability, and can be impacted by different local stressors. As such, undertaking assessments of the resilience of reefs and identifying potential stressors are the first steps to enable management responses. Guidance to assess reef resilience on the basis of various physical, biological and habitat factors has been refined in recent years (McClanahan *et al.,* 2012). Different reef-dependent communities and industries will have different capacities to incorporate management actions. Spatial variation in both assessed resilience and available management options enables the selection and prioritization of management actions to improve conditions on reefs (Maynard *et al.,* 2015a). The capacity to introduce resilience-based management activities can depend upon: existing management strategy; local/regional availability of resources; adaptability of existing governance structures (traditional and/or political); impacts upon and adaptability of ecosystem-dependent industries; and community support. Success at such management has typically been highest at sites where conservation is ingrained in local customs (Cinner *et al.,* 2016). However, local management practices alone are insufficient if we do not address the underlying global driver – rising CO_2 caused by human activity (Bruno and Valdivia, 2016).

3.8.12 Conclusions and recommendations

Ocean warming on coral reefs has accelerated during the past century and this is predicted to continue, resulting in more frequent and severe coral bleaching and disease. Unless the cause of this warming (CO_2 emissions) is urgently reduced, bleaching is likely to strike almost all of the world's coral reefs every year by 2050. This will result in severe coral mortality, as is now occurring around the world, and destroy most of the world's coral reef ecosystems.

Coincident with this, ocean acidification has reduced the rate of coral growth and weakened reef structure, increasing the likelihood of physical damage from tropical cyclones. Ocean warming and acidification also slow the growth of reefs, making them unable to keep up with rising sea levels. Because the worst bleaching is occurring in the tropics and the most rapid acidification at high latitudes, there will be no refuge from the impacts of rising atmospheric CO_2. These global stressors often act synergistically (e.g. acidification weakens reef structure increasing susceptibility to storm damage; thermal stress slows coral growth and kills corals), increasing the impact on reefs.

Loss of coral reefs would affect the services provided by the ecosystem, including coastal protection, fish habitat and tourism. Estimated costs from the loss of coral reef services reach US$1 trillion each year by 2100. The greatest losses will likely fall upon those people who rely upon reef services for day-to-day subsistence – typically the poorest coastal nations.

Reducing CO_2 levels in the atmosphere globally is the first essential step for the continued existence of coral reefs. It is critical that CO_2 pollution be rapidly and strenuously addressed. Any other option would, at best, only delay the inevitable loss of coral reef ecosystems and their services. Enhancing the resilience of corals through the reduction of local stressors will support the resistance to and recovery from acute disturbance events. Improved land-use practices (especially coastal development) to reduce terrestrial pollution and the establishment and enforcement of no-take marine protected areas are two key actions that are feasible for most global reef areas. To ensure the success of short- and long-term management strategies that respond to the impacts of warming and acidification on coral reefs, coral-dependent communities and industries will likely need to adapt some existing practices. This may require increased levels of support and investment. However, if we don't address atmospheric CO_2, no level of local conservation will be enough to save the world's coral reefs.

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“Increases in the atmospheric and upper ocean water temperatures are not quickly transferred to the deep sea. However, the increase in deep ocean water temperature is projected to continue for centuries after the atmospheric temperatures have levelled off or even decreased.”

“The deep sea plays an essential role in storing (>35,000 Gt) and absorbing (~25%) the vast amounts of carbon from the atmosphere, however, this will impact the regulating capacity that the deep sea currently undertakes and will no longer be able to reduce the impacts of climate change globally.”

Section 3.9 authors

3.9 Impacts and effects of ocean warming on deepsea communities

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Summary

- The deep sea covers a vast proportion of the planet (50% below 3000 m) and supports both a wide range of habitats and biological communities. Its very nature, i.e. deep and remote, has resulted in difficulties in studying this region as well as being extremely expensive to do so. The number of in-depth studies undertaken is restricted to a small number of locations.
- Increases in the atmospheric and upper ocean water temperatures are not quickly transferred to the deep sea. However, the increase in deep ocean water temperature is projected to continue for centuries after the atmospheric temperatures have levelled off or even decreased.
- The deep sea plays an essential role in absorbing (~25%) and storing (>35,000 Gt) vast amounts of carbon from the atmosphere, however, this will impact the regulating capacity that the deep sea currently undertakes and will no longer be able to reduce the impacts of climate change globally.
- Currently 2.5 Gt of frozen methane hydrate are stored in the sea floor at water depths of 200 – 2000 m. Increasing water temperature could release this source of carbon into the ocean and ultimately into the atmosphere.
- Impacts of climate change on deep sea faunal communities are not fully known. It is hypothesized that long term changes in surface productivity, as a result of a warming ocean, will lead to fundamental changes in the deep sea community as they are reliant on this flux of material reaching the sea floor.
- Currently there are few data to base predictions of current and future impacts of ocean acidification. However, it can be expected that calcifying fauna such as deepsea corals and bivalves are, and will be, under threat.
- The lack of long-term time-series studies i.e. a baseline, therefore makes it difficult to envisage the impact of future climate-driven changes against natural biological variability over time.

Ocean warming effects	Consequences
Upper ocean warming is slowly increasing water temperature in the deep sea	The slow transfer of heat into deeper waters, will result in the deep sea benthic communities continuing to be impacted beyond the time when atmospheric temperatures have stabilized or are declining
Phytoplankton community composition i.e. diatom to dinoflagellate ratio	Change in food composition, quality and quantity for deepsea benthic communities This will also have an impact on the food web
Warming creating opportunities for species to move into new areas	Non-native species are reducing benthic species diversity Some faunal groups are now found to be absent as a result of the invasive species
Numbers of calcifying organisms e.g. cold water corals	Reduced benthic species and functional diversity and changes in community composition Will also reduce nursery grounds for already vulnerable long-lived deepsea fish species
Oxygen availability: increasing the numbers and areas of Oxygen Minimum Zones	Reduction in species diversity and impacting on community composition allowing only for species with specialized features to inhabit these low oxygen regions

3.9.1 Introduction

The deep sea encompasses both the pelagic and benthic realms, and is the largest ecosystem on Earth. It is commonly defined as waters and sea floor found at depths greater than 200 m. The benthic environment accounts for ~90% of the oceanic sea floor, whilst the pelagic realm is >1 billion km^3 and accounts for >98% of the volume of the planet that is inhabited permanently by a diverse fauna (Thurber *et al.,* 2014). However, it is this vastness and remoteness which has resulted in it often being overlooked, so much so that new habitats are still being discovered; in the last 30 years alone seven new deepsea habitats have been identified out of a current total of 27 (Ramirez-Llodra *et al.,* 2010). To date it is estimated that ~5% of the deep sea has been explored and of that < 0.1% of that has been studied in great detail (Ramirez-Llodra *et al.*, 2010); however, based on the research undertaken, the deep sea is known to be home to a huge range of different taxa as well as numerous species, many of which are yet to be discovered, let alone described.

It was long thought that deepsea benthic ecosystems existed in a steady-state environment with few regions experiencing dramatic changes in temperature, salinity, oxygen or high current speeds, and were therefore shielded from the effects of the variable conditions in the upper ocean. This large ecosystem was also thought to act as a buffer to global climate change by absorbing large quantities of both heat and carbon dioxide from the atmosphere. In support of this suggestion it has been estimated that the deep sea stores >35,000 Gt of carbon, and in addition it has also managed to absorb about 25% of the carbon that has been released through human activities (Canadell *et al.*, 2007; Sabine and Feely, 2007).

It is only recently that we have begun to understand that deepsea communities are in fact being affected by the changing climate (Glover *et al.*, 2010; Hughes and Narayanaswamy, 2013). To be able to determine this, long term data sets are required from the deep sea, both biological, looking at species richness and diversity as well as composition, and hydrographic. However, very few such data sets exist covering the time scales required (several decades long) to be able to determine climate related impacts. Biological data sets are quite rare and a lot of current research often focuses on a few species or at higher assemblage levels meaning predictions about how whole ecosystems respond to climate change are unreliable (Birchenough *et al.*, 2015). The two most well-known deep water long-term time series are both situated at abyssal depths, one in the North East Pacific – Station M, and the other in the North East Atlantic - the Porcupine Abyssal Plain site (Figure 3.9.1) (Glover *et al.,* 2010 and references therein). At both locations major changes in faunal

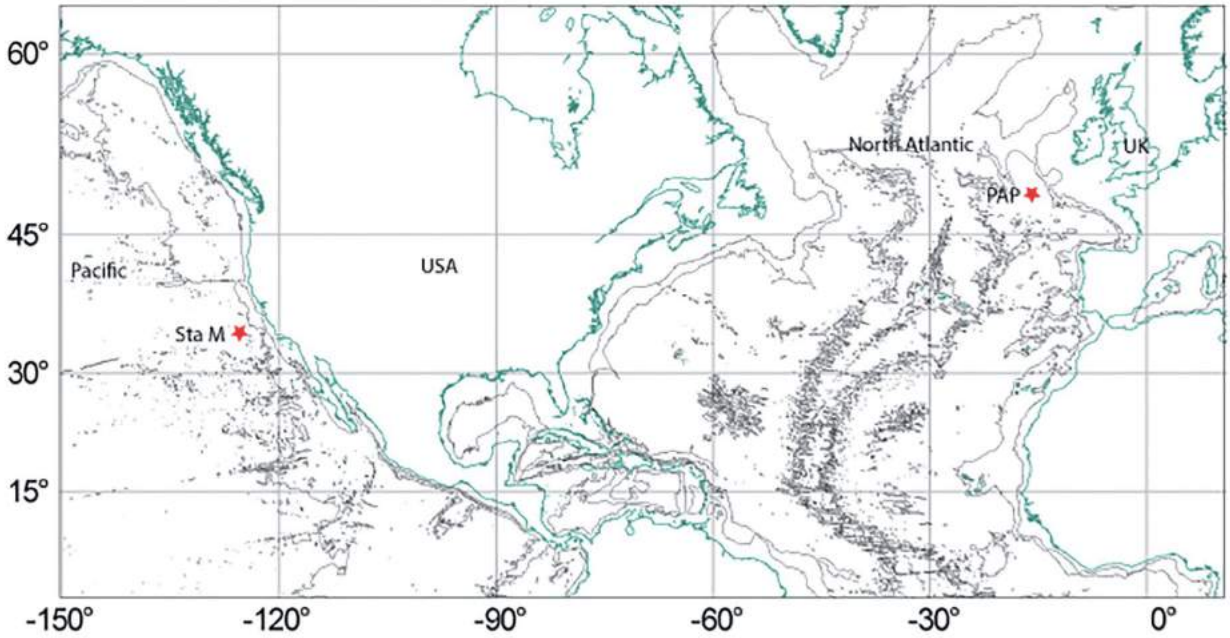

Figure 3.9.1 Chart showing the locations of two abyssal stations (Sta M: Station M in the Pacific; PAP: Porcupine Abyssal Plain station in the North Atlantic) which have been sampled regularly for over 20 years with the aim of detecting changes in food supply to the seafloor as a result of changes occurring in the atmosphere and upper ocean.

abundance across the size spectra were found to be related to changes in the quantity of food supply coming from above. Some deep water hydrographic data sets do exist, for example, Purkey and Johnson (2010) found that abyssal plains in the Southern Ocean, showed a statistically significant increase in temperature whilst further north, Bryden *et al.* (2005) found that there had been a 50% reduction in North Atlantic Deep Water flowing southwards.

3.9.2 Definition of the ecosystem

The deep sea is highly heterogeneous in nature with many broad scale habitats (hundreds of kilometres wide), as well as many smaller ones (metres wide), ranging from plunging canyons and trenches, biogenic habitats (e.g. cold water coral reefs), vast undersea mountainous ridges and individual seamounts that are in stark contrast to the soft sediment continental margins and abyssal plains that account for most of the deepsea benthic environment. Some of the more unusual habitats include those of a chemosynthetic nature including hydrothermal vents and seeps. Many of the habitats listed above are known to have high levels of diversity and are often centres of high biomass. It is this variety of unique habitats which make the deep sea quite different to other marine ecosystems (Ramirez-Llodra *et al.,* 2010).

The mid-ocean ridges provide a hard substrate for sessile (stationary) animals to anchor to. Seamounts, usually isolated peaks that rise up from the surrounding sea floor (Narayanaswamy *et al.,* 2013) are also generally rocky in nature. Both the seamounts and the mid-ocean ridges create a habitat elevated from the sea floor, which is in stark contrast to the soft sediment found in the surrounding area. The numerous fauna found on the seamounts and ridges are often vulnerable and include long lived epifauna such as corals and sponges. These in turn create a habitat for other fauna which often make them hotspots for biodiversity as well nursery grounds for deep water fish species and therefore in turn rich fishing grounds (Clark *et al.,* 2010).

Hydrothermal vents are often found on the mid-ocean ridges which are regions where the spreading of the tectonic plates allows the magma to rise close to the surface of the sea floor, or in some cases break through the sea floor. The fluid expelled by the hydrothermal vents can reach temperatures in excess of 400°C. However, the pressure exerted at the depths some of these vents are found, almost reaching 5000m in some instances, is so high that the fluid does not boil. This is in stark contrast to most deepsea habitats (excluding for example the Mediterranean) where the temperature is generally no higher than about 4°C. The vents are ecosystems fuelled by chemical reactions rather than energy from the sun; bacteria grow in this mineral rich water, utilizing the chemical energy and making organic material to be consumed by a vast array of unusual and endemic fauna. These fauna include large tube worms and giant clams, both of which have developed a special symbiotic relationship with the bacteria.

Biogenic habitats are three dimensional structures found on the sea floor that are created by the organisms themselves and can extend for tens of kilometres. The most common biogenic habitat is that made by the cold-water scleractinian corals, *Lophelia pertusa* and *Madrepora oculata* (Figure 3.9.2). These structures can be colonized by a vast range of both benthic and demersal organisms (Serpetti *et al.,* 2013) as well as forming nursery grounds for a variety of deep water fish species (Miller *et al.,* 2012). Other organisms creating biogenic habitats include sponges, tube worms as well as worm like fauna that create extensive burrow systems in the sediment such as sipunculids and echiurans (Hughes *et al.,* 2005; Shields and Kedra, 2009). These provide microhabitats for microbes and meiofauna.

The continental margins are geologically hugely variable, and themselves support a vast diverse array of habitats. The margins can be deemed passive, when an ocean rift splits a continent in two, and active, when the crust sinks through into the mantle creating deep ocean trenches (Ramirez-Llodra *et al.*, 2010). The soft sediments hide a surprisingly high level of diversity often in relation to depth, food availability as well as local environmental conditions (Rex and Etter, 2010; Narayanaswamy *et al.,* 2013). The abyssal plains are large flat expanses of sediment ranging in depth from ~4,000 to 6,000 m water depth (Smith *et al.,* 2008), that can be thousands of metres thick, with the uppermost layers containing the organic matter sinking from the surface. Even at abyssal depths, biodiversity is found to be enhanced in areas with higher organic matter input (e.g. Smith *et al.,* 2008).

Figure 3.9.2 Cold water coral reef. © Changing Oceans Research Group.

Trenches are usually V-shaped and are situated >6,000m below sea level but with occasional shelves jutting out that accumulate organic matter falling from above. They have been known to harbour higher levels of organic matter than the surrounding abyssal plains, enriching the area and enhancing microbial activity. Diversity in general is thought to be lower than the surrounding abyssal plains (Ingels *et al.,* 2016).

Although these habitats are quite unique, they are all influenced by events occurring at the surface such as transport of heat and carbon dioxide absorption, through ocean circulation and mixing.

3.9.3 Global and regional significance

3.9.3.1 Why is the deep sea important?

To most of the human population, the deep sea is seen as unimportant, it is out of sight and therefore out of mind. A cartoon drawn for the New Yorker magazine in the early 1980s highlights this issue perfectly, where a group of ladies are observed having a cup of tea and one has turned to the rest and says, “I don’t know why I don’t care about the bottom of the ocean, but I don’t” (New Yorker, 1983). However, it is vitally important, that we do realize how important the deep sea is. The services that the deep sea provide are numerous and much greater than is generally acknowledged. These services include amongst others, provision of food through fishing as well as hydrocarbon resources through extraction. In the near future (<2 years) metal and mineral resources will also be mined to supplement the increased demand to fuel the modern green economies (Hein *et al.,* 2013). In addition, the deep sea may well be a source of as yet undiscovered medical resources which may provide treatment for a number of human diseases (Maxwell *et al.,* 2005), as well as being known to significantly reduce the impact of human released CO_2 on the climate.

3.9.3.2 Biogeochemical cycling

The biological pump, i.e. the settling of organic matter to the deep sea, is a major flux of the global carbon cycle and varies both temporally and spatially. Deepsea benthic fauna are crucial to the cycling of this carbon and form a major part of the Earth’s biodiversity.

There are two main routes for carbon to be kept out of the atmosphere and sequestered into the deep sea. Firstly, there is the activity of the biological pump, whereby a variety of organisms, including microbes, degrades the organic material as it sinks through the water column. This may result in the carbon being used by organisms in the water column or on the sea floor through respiration thus producing carbon dioxide. If respired the carbon dioxide will be retained in the deeper waters, until thermohaline circulation drives the water to the surface allowing for the eventual release of the carbon dioxide back into the atmosphere. This entire process takes about 1,000 years. The second alternative route is for the carbon to be buried in the sediments themselves resulting in it being prevented from coming into contact with the atmosphere over a time frame of thousands to millions of years (i.e. geological timescales).

However, it is not just carbon that the deep sea acts as a reservoir for; methane, another gas known to influence climate change, is found extensively throughout the deep sea (e.g. Wallmann *et al.,* 2012). The methane often forms hydrates which essentially trap the majority of the methane at the sea floor, and what is released is generally consumed by deepsea fauna. The process of anaerobic oxidation of methane leads to the formation of authigenic carbonates, which results in more carbon being trapped for an indeterminate period of time (Aloisi *et al.,* 2002). However, it should be noted that throughout the history of the Earth, there have been periods where major disturbances have led to the release of methane which have resulted in massive extinction events. In some instances, more than 70% of the marine invertebrate species are known to have been lost (Kemp *et al.,* 2005), the proportion of those from the deep sea is not known.

3.9.3.3 Biodiversity

Diversity in the deepsea has been described as comparable or even possibly rivalling that of the tropical rainforest (Grassle, 1989), due to the relatively stable nature of the deepsea environment (Piacenza *et al.*, 2015). It was only in the 1960s that high levels of species diversity in the deep sea became apparent. Changes in sampling techniques that were more pertinent to the deep sea (Hessler and Sanders, 1967) as opposed to shallow water habitats revolutionized our understanding with Snelgrove and Smith (2002) finding as many as 100 species per 0.25m^2 of sea bed sampled. Numerous studies since the 1960s have tried to establish patterns of faunal standing stock and diversity in the deep sea. Standing stock, is somewhat easier, with abundance declining with increasing depth, related to the flux of material reaching the sea floor, whilst with biomass, where surface productivity is high, flux of particulate organic carbon to the sea floor is also increased and this is then reflected in the higher levels of biomass observed. Diversity, however, is very different, with trends varying depending on the size and type of fauna being studied as well as the ocean basin of interest. For example, macrofauna (fauna generally retained on a 0.25 mm mesh sieve) diversity in the North Atlantic exhibits a unimodal distribution, with the peak occurring at intermediate to bathyal depths (e.g. Maciolek *et al.,* 1987a, b). However, the depth at which the diversity peak occurs in this depth range varies, with Cosson-Sarradin *et al.* (1998) finding high levels at 2,000 m in the tropical NE Atlantic, whilst Paterson and Lambshead (1995) and Gage *et al.* (2000) found peaks at 1,400 to 1,800m water depth, whilst yet others found diversity maxima occurring at depths of 450 to 550m in the Faroe-Shetland Channel region (Narayanaswamy *et al.,* 2005, 2010).

In their review of the diversity of life on the sea floor, McClain and Schlacher (2015) concluded that it would be better to ask more specific questions in a bid to better understand the way ecosystems function on the sea floor. The distribution of species and diversity in this vast diverse ecosystem is by no means uniform; variations in conditions between geographical locations and different topographies and complex interactions between species and their environment dictate distributions of life in the deepsea. The structure and composition of the sediments on the sea floor play a large role in what species can exist there. Many deepsea studies have found that the more heterogeneous the sediment, i.e. more variable the grain size, the more species were found to coexist in that one area (e.g. Etter and Grassle, 1992; Levin *et al.*, 2001; Narayanaswamy *et al.*, 2005).

3.9.3.4 Ecosystem goods and services

The deepsea habitats in general are much less understood and by comparison receive less attention than their shallow water terrestrial neighbouring counterparts. It is fully acknowledged that the deep sea is a challenging environment to study, and this has resulted in it being overlooked in terms of the important ecosystem functions and services that it provides. The dependence on these provisioning services is ever increasing; the number of regions where there is increasing dependence and growing exploitation on these provisioning services is increasing rapidly (Morato *et al.,* 2006; Benn *et al.,* 2010). Deep water fishing for example has increased dramatically over the past 40 years (Morato *et al.,* 2013) with almost 30 deep water species being commercially targeted (Norse *et al.,* 2012). However, the long-life cycle of many of these fish species, in some instances they are known to live for more than 100 years (Caillet *et al.,* 2001), has meant that harvesting these stocks is unsustainable. The use of certain gear types has not only resulted in the indiscriminate capture of non-target species but in some regions has been observed to damage the very structure of the sea floor (Puig *et al.,* 2012) which in turn impacts the faunal standing stock, diversity and composition as well as carbon turnover (Pusceddu *et al.,* 2014). As Thurber *et al.* (2014) highlighted in their paper, many functions occurring in the deep sea result in the regulating and provisioning services found there being strongly connected.

3.9.4 Trends and impacts

3.9.4.1 How will climate change effects be transmitted to the deepsea benthos?

As highlighted previously, the deep sea appears to have a great capacity to absorb heat and remove carbon in different forms and ways from the atmosphere. However, by doing so, this process itself has an impact on the deep sea which results in it becoming warmer and less basic, as well as reducing the amount of oxygen available (Figure 3.9.3). In turn these combined environmental changes will potentially have a detrimental effect on the fauna living in the ocean. In particular, these changes undoubtedly impact the phytoplankton communities in the surface waters, e.g. changing the community composition, and because of their position at the bottom of the food chain this will influence the standing stock, species composition and functional diversity of the benthos. Little is known regarding how benthic faunal biodiversity responds to long-term productivity changes and how this connects with the overlying species and structure of the deep sea ecosystem. Organisms in the deep ocean exist in a more stable environment than that of their shallow water counterparts, and as such may be less resistant to changes in their environment. Small changes in water temperature, salinity and currents could have a much greater effect on the ecosystems of the deep sea (Hughes and Narayanaswamy, 2013). However, lack of decadal scale time-series studies mean that the full impact of these combined changes in environmental conditions on the deep sea fauna is still not known.

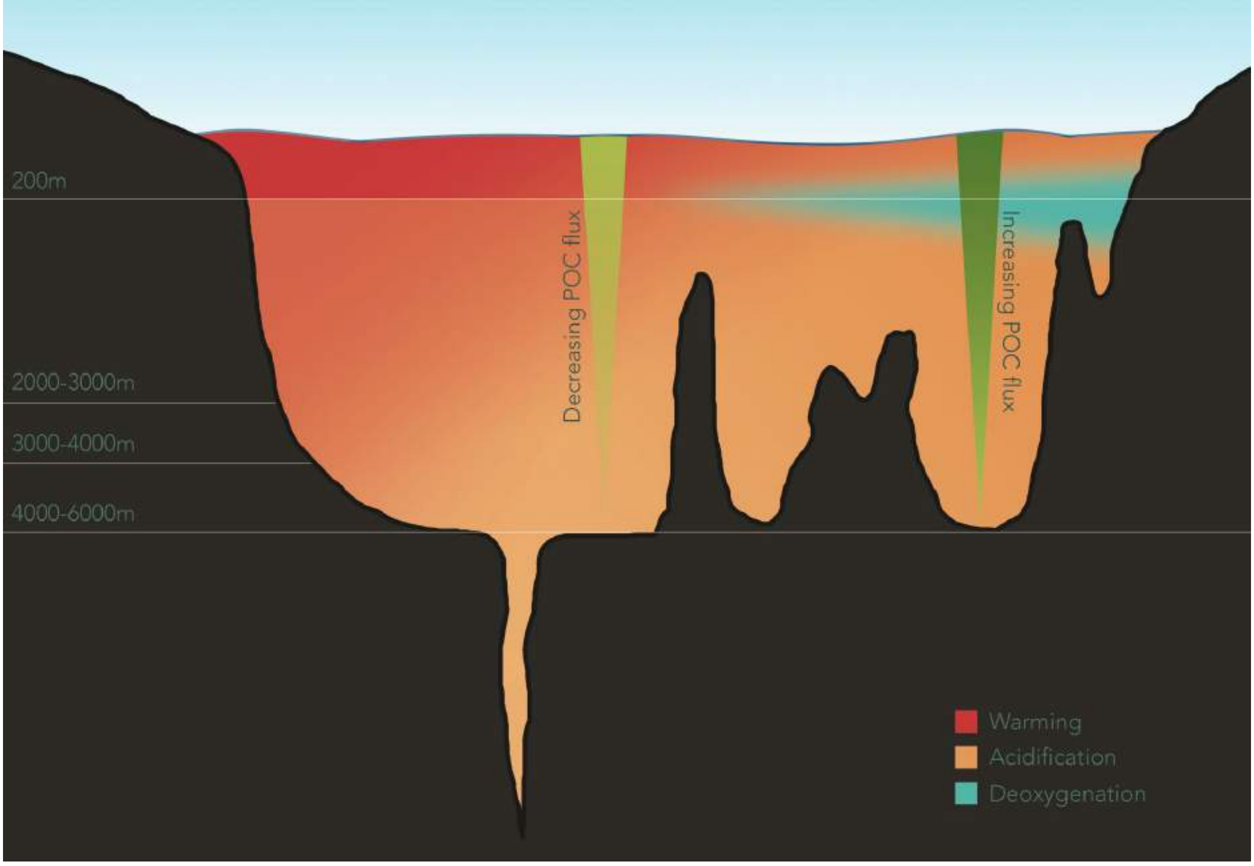

Figure 3.9.3 A cross section schematic of the deep sea illustrating how increased warming of the oceans, acidification and de-oxygenation may overlap. These, climate induced stressors will impact most strongly on the margins and at bathyal regions, although the impact will be felt at full ocean depth (Modified from Levin and Le Bris, 2015).

3.9.4.2 Temperature

It has long been established that the increasing atmospheric temperature is directly related to increases seen in the temperature of the global ocean. Around 80% of the heat in the earth's atmosphere is absorbed by the ocean (Levitus *et al.,* 2005) and during the past 100 years, surface temperatures have increased by 0.7°C (Trenberth *et al.,* 2007). These temperature rises are not rapidly transmitted to the deepsea which has risen by an estimated 0.2-0.3°C over the same time period (Mora *et al.,* 2013). As a result of this, the rise in deepsea temperatures is predicted to continue for centuries after atmospheric temperatures level off or fall (Hansen *et al.,* 2005; Purkey and Johnson, 2010).

As highlighted, the deep sea is generally thermally stable; an increase in water temperature of 1°C or even less may impact the species and faunal groups found in different ways. The increase in temperature may allow species to invade from other regions and have a devastating effect on the benthic community. An example of this is in the deep waters of the Antarctic continental shelf (~600m), whereby an increase in water temperature has allowed the lithodid crabs, more commonly known as king crabs, to colonize this region as these new temperatures are above the lower thermal limits for this group. This has resulted in a notable decrease in diversity of the epifaunal communities and in some instances whole groups of organisms have disappeared, e.g. echinoderms (Smith *et al*., 2012).

There is also a threat that warming temperatures in depths between 200 to 2,000m could liberate 2.5 Gt of methane hydrate frozen in the low temperature and high pressure sea floor. If this reaches the atmosphere it will only serve to accelerate global warming (Mienert, 2012). Microbial activity at methane seep sites in the deep sea act to oxidize the methane that is released from the reservoirs in the sea bed, but warming sea temperatures could cause the release of methane to occur too rapidly for it to be oxidized (Marlow *et al.*, 2014).

Deep water coral species inhabiting the Mediterranean are already close to their upper thermal tolerance threshold, as the deep waters in this region are already between 13 to 14°C. Small rises in water temperature of the deep Mediterranean will have a devastating impact not only on the deepwater coral species here, but the fauna found living in association with them (Ramirez-Llodra *et al.*, 2010).

3.9.4.3 Changes in oxygen availability in relation to changing temperature

The solubility of oxygen decreases with the increasing temperature of the ocean, resulting in a warmer ocean being able to contain less oxygen overall (Levin and Le Bris, 2015). Deoxygenation of the first 500m layer of the ocean is mostly caused by reduced oxygen solubility in the surface waters (Shaffer *et al.*, 2009). A warmer ocean will also lead to increased stratification. As surface waters warm they become less dense and the difference in density between surface and bottom waters becomes greater thus reducing the vertical mixing. Decreased oxygen levels and declining levels of mixing will cause a decline in oxygen levels in the deep sea (Figure 3.9.3). By the year 2100 the oxygen load of the ocean is predicted to drop by as much as 7% (Keeling *et al.*, 2009) and the volume of ocean considered hypoxic is set to increase by 50% (Oschlies *et al.*, 2008).

Oxygen Minimum Zones (OMZ) play an important role in the world's oceans and act as barriers for benthic as well as pelagic organisms. Differences in the environmental conditions within the OMZs mean they are considered to be of unique ecological importance, containing differences in community composition relative to the surrounding well oxygenated waters (Moffitt *et al.*, 2015). As the number and area that OMZs cover increase, organisms that are tolerant of these conditions will increase in number as they will be able to gain an advantage over species that are not able to tolerate the decrease in oxygen levels. Although numbers of individuals in the OMZs may increase, the species diversity and community composition found in these locations will decrease and change dramatically.

De-nitrification in the ocean occurs within the OMZs and thus both the physical presence and extent of these regions are linked to the nitrogen cycle of the ocean (Moffitt *et al.*, 2015). Expansion of both the number and size of these reducing oxygenated zones (OMZ) could have a drastic effect on the ecosystems of the deepsea benthos by reducing the species and functional diversity, as well as the composition of the fauna. Moffitt *et al.* (2015) highlighted that during the geologically recent de-glaciation, OMZs were recorded as covering a depth band of over 2,000 m in the Subarctic Pacific and over 3,000 m in the Humboldt Current and Equatorial Pacific. The upper limit of the OMZs extended up to within a few hundred metres of the surface of the ocean. This highlights the capacity for OMZs to become both much more extensive as well as intensive in today's ocean if anthropogenic influences continue to drive the de-oxygenation of the ocean.

3.9.4.4 Thermohaline circulation

Increased ocean stratification may also have an effect on the thermohaline circulation (THC), an oceanic current that is driven by heat and salinity gradients (Rahmstorf, 2003). Disruption to the circulation is one of the possible outcomes of climate change. A "freshening" of polar seas due to climate driven factors such as melting sea ice could have a drastic influence on the THC (Barreiro *et al.*, 2008). A collapse of the THC would bring about the largest temperature response in the North Atlantic (Vellinga and Wood, 2002), an area where deep water formation is prominent, therefore it is quite likely that deepsea benthic communities would be affected. Increasing temperature variation as a consequence of the stalling of the THC could result in exacerbating the effects of acidification and de-oxygenation. Mixing and ventilation would be reduced, possibly expanding areas of anoxic ocean and cutting off nutrient recycling, as upwelling and downwelling are disrupted, effectively starving and suffocating the deepsea benthos. It was thought that changes in the THC once brought about an abrupt 4 - 5°C warming of deep waters at the Palaeocene/Eocene boundary, but models suggested that the warming was attributable to increasing surface temperatures in areas where downwelling was occurring (Thomas *et al.*, 2003).

3.9.4.5 Ocean acidification

Ocean acidification is the lowering of the pH of the world's ocean through means of chemical reactions. The dissolution of atmospheric CO_2 is one method by which ocean acidification occurs. Since pre-industrial times the level of atmospheric CO_2 has increased from 280ppm to 380 ppm (Dupont *et al.*, 2012), with around 26% of this being absorbed by the oceans (Le Quéré *et al.,* 2009), and estimates of how much this will increase by the year 2100 range from 540 - 1200ppm (Ramirez-Llodra *et al.*, 2010; Dupont *et al.*, 2012). The increased atmospheric CO_2 will result in a lowering of the pH or the world's ocean as more CO_2 is dissolved (Figure 3.9.3). With the increase in atmospheric CO_2 from pre-industrial levels the pH of the ocean has dropped by 0.1 units and models have predicted that by 2100, over 17% of the sea floor in the North Atlantic below 500m will experience a decrease in pH of more than 0.2 units including many seamounts and deepsea canyons some of which possibly fall within marine protected areas (Gehlen *et al.*, 2014).

Acidification of the ocean will also result in major changes in the carbonate chemistry, most notably by lowering the state of the calcium compensation. This will have a detrimental effect on shell-forming (calcifying) organisms such as corals, molluscs and echinoderms (Figure 3.9.4), which all occupy deepsea benthic habitats, as well as the plankton, which contribute towards carbon flux to the sea bed. The carbonate (calcium and aragonite) saturation depth is linked to global climate as changes in acidity brought about by increased atmospheric CO_2 will alter the depths at which they occur and in turn change the carbonate chemistry of the ocean (Coxall *et al.*, 2005).

Cold water corals of the deep sea are one of the most vulnerable habitat-forming calcifiers in the North Atlantic, and reduced pH may increase carbonate dissolution and rates of bio-erosion, whilst decreasing the rate of calcification (Guinotte *et al.*, 2006; Levin *et al.,* 2014). It is estimated that 70% of the world's cold water corals will suffer from effects of ocean acidification over the next hundred years, impairing their ability to engineer habitats which are used by many other organisms, as well as having a negative impact on the ecosystem services which they provide. Maier *et al.* (2009) showed that the ability of the cold-water, reef building coral species *Lophelia pertusa* for skeletal extension was significantly reduced when the pH of water was reduced by 0.3 units compared to that of the ambient pH of the sea water from which the organisms were collected. It is therefore possible that over the next 100 years, if the pH of the ocean decreases as expected, that reef forming corals may be significantly impaired which would have a knock on effect on the organisms that exploit the habitats they create. To exacerbate this problem further, the complex interactions between the deepsea continental margin ecosystem and the biogeochemistry of the region, may result in some drivers creating responses that further alter the system by generating a feedback. Levin *et al.* (2014) gave one example whereby under-saturation of carbonate as a result of acidification, affects coral polyps in their ability to build reefs. The presence of the reef helps to buffer against decreases in pH and corresponding increases in CO_2 by dissolution of older coral and increasing alkalinity. Therefore, lowering the pH reduces the buffering capacity at a local level and thus leads to a greater decline in pH.

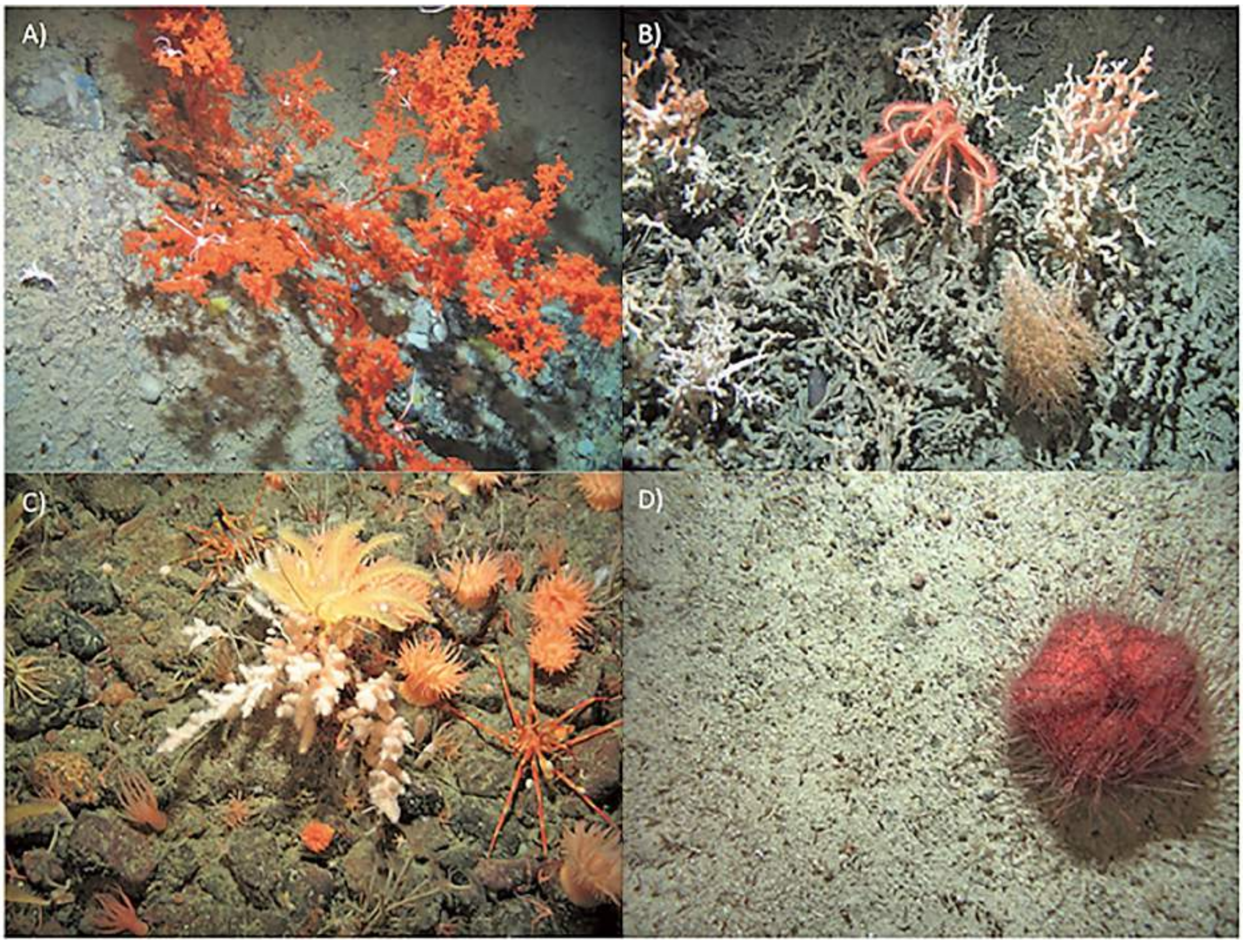

Figure 3.9.4 Some of the deepsea organisms that will be impacted by climate change, in particular by the ocean becoming warmer and more acidic. A) A colony of black coral with small crabs moving amongst the branches, B) A Brisingid seastar resting on a patch of live *Lophelia pertusa*, a cold water coral, C) Yellow crinoids found amongst anemones, brittlestars, a sea spider and a branching sponge, D) A deep water sea-urchin observed on a large expanse of gravel. © Images courtesy of Department of BIS, UK.

3.9.4.6 Nutrient supply

Surface waters service the deep sea by recycling nutrients into more usable organic matter. Increasing the stratification of the ocean, as a result of climate driven factors, will directly impact on this service and as a result will reduce the flux of organic carbon reaching the sea bed (Levin and Le Bris, 2015). Jones *et al*. (2014) illustrated that changes to the carbon supply to the deep sea may result in a ~5 % decline in biomass of benthic organisms globally in the future (2091-2100) compared with the present day (2006-2015). The predicted change in biomass is not spread evenly around the global ocean, with some areas predicted to show slight increases in biomass. However, the loss of biomass was predicted to reach almost 40% in the North-east Atlantic and 80% of the so called biodiversity hotspots, such as seamounts (Figure 3.9.5) and cold-water coral reefs, were also predicted to show a decline in biomass. Jones *et al.* (2104) also indicated that the figures for the biodiversity hotspots are likely to be underestimates due to the complex and delicate nature of processes that govern these environments; seamounts, canyons and cold-water coral reefs are all expected to suffer as a direct consequence of the reduction in organic flux from the surface due to anthropogenic global warming, especially cold-water coral reefs due to the compounding effects of ocean acidification.

Figure 3.9.5 Seamount off the Juan Fernández Islands. © Oceana / Manu San Felix.

Most life in the deepsea depends on primary production of organic carbon in the surface waters as a food supply (Hughes and Narayanaswamy, 2013). The majority of species that inhabit the deepsea benthos are deposit feeders which consume organic matter sinking from the upper ocean (Jumars and Eckman, 1983). The IPCC (2007) predict that over the next 100 years the range of global warming will be between 1.4 - 5.8°C. Such a temperature change will undoubtedly have a profound influence on surface waters and especially on the primary productivity which will be transmitted to the deep sea (Ramirez-Llodra *et al.*, 2010). Deepsea ecosystems can react quickly to changes in surface productivity. For example, Lampitt (1985) observed large fluxes of material to the deep sea floor in the Porcupine Seabight, off south-west Ireland, less than one week following the spring phytoplankton bloom. Episodic events of partially degraded phytoplankton have also been seen at several deepsea locations (Beaulieu, 2002) and have been observed to trigger short-term responses in deepsea ecosystems (Gooday, 2002). Climate oscillations in the form of both El Niño and the North Atlantic Oscillation (NAO) have also been shown to influence organic carbon flux to the deepsea bed which has a major effect on the benthic ecosystems (Smith *et al.*, 2006). Both the NAO and El Niño have an impact and influence on different functional groups of phytoplankton, and as such play a major role in the quality and quantity of carbon flux reaching the deep sea floor (Henson *et al.*, 2012). The NAO affects factors such as sea surface temperature and the ratio of diatoms to dinoflagellates in the planktonic community (Zhai *et al.*, 2013) which in turn can change the composition of the food supply to the deep sea. A decrease in organic carbon flux would have an impact on the biomass of the deepsea benthic community by reducing it, as well as impacting on the average body sizes of individuals found within these communities (Hughes and Narayanaswamy, 2013). It also has to be considered that the rising and falling of organic carbon production does not always correlate or correspond to respective increases and decreases of carbon flux to the sea bed; other factors such as currents as well as consumption by fauna living in the water column (Glover *et al.*, 2010) will alter the flux of material to the sea floor. However, as we begin to have the information to assess deepsea benthic communities over longer timescales, we can now see that there are seasonal trends in surface productivity which affect deepsea benthic communities, with higher numbers of benthic individuals being found in areas with greater flux of organic carbon to the sea bed (Glover *et al.*, 2010).

Our understanding of how populations of deepsea animals change over time was challenged by the EU-funded BENGAL programme, focusing on the Porcupine Abyssal Plain (PAP) 4850 metres deep off the south-west coast of Ireland (Billett and Rice, 2001). *Amperima rosea* (Figure 3.9.6), a small holothurian, was found in unexpectedly high levels in 1997 with more than 6,000 individuals per hectare of sea bed observed using seabed photography. This equated to an approximately 1,000-fold increase since the early 1990s (Bett *et al.*, 2001). Through analysis of trawl samples, this was shown to be a widespread event on the PAP. Contrary to what was previously thought, the populations of deepsea animals appeared to be able to change rapidly over short timescales. The research has continued at this location and has been designated as the Porcupine Abyssal Plain Sustained Observatory (PAP-SO). Further studies found that the populations declined steadily leading up to 2000, before another major increase in abundance in 2002 was observed,

Figure 3.9.6 *In situ* photographs of the small elpidiid holothurian *Amperima rosea* (E. Perrier, 1886), from time-lapse observations at the Porcupine Abyssal Plain Sustained Observatory site (48° 50' N 016° 30' W, 4850 m water depth). This species is known for its apparent 'boom-bust' population dynamics at this abyssal study site. (Image courtesy of J Durden and B Bett, National Oceanography Centre, UK; © NOC 2016).

again driven by increasing numbers of *A. rosea* (Billett *et al.*, 2010). However, it was not just limited to *A. rosea*, major changes in many other taxonomic groups were also recorded (Kalogeropoulou *et al.*, 2010; Soto *et al.*, 2010) and throughout all the size fractions of the PAP faunal community, indicating that it was environmental factors driving the variation in the populations rather than just random fluctuations (Billett *et al.*, 2010). The quantity of organic flux appears to have been the causal factor to the *"Amperima* Event". Analysis of the sediment at PAP-SO indicates that the organic input to the abyssal sea bed can lead to significant interannual changes (Lampitt *et al.*, 2010). A large deposition of organic carbon in 2001 correlated with the spike in *A. rosea* numbers observed in 2002. These results are also supported by research undertaken at another abyssal plain location, this time in the North-east Pacific, where major changes in the ecosystem were observed (Bailey *et al.*, 2006; Ruhl, 2007) and like the results at PAP were also correlated with the flux of organic carbon produced in surface waters (Ruhl and Smith, 2004). Considering this new found understanding of how variable populations are in the deep sea as a result of interannual changes in surface productivity, and the subsequent flux to the sea floor, it is clear that climate driven changes to the organic carbon supply to the deepsea benthos may be profoundly detrimental to life in these communities.

The Scottish Association for Marine Science (SAMS) is undertaking research investigating potential temporal changes in the benthic community composition at sites in the Rockall Trough, North-east Atlantic. The site is situated on the continental margin off the west coast of the UK, at bathyal depths of ~2200m. Benthic faunal samples dating back to the early 1970s are currently being examined and interannual and decadal changes in the taxonomic groups that make up the communities analysed. The preliminary results indicate that major changes in the composition of the communities have taken place. These changes have been observed by the changes in the relative abundance of the fauna collected over the time period, with some groups becoming more dominant, e.g. bivalves and a group of polychaetes. The causal factors of the changes observed, whether it is variation in the flux of organic carbon to the sea floor at the site or some form of stress and disturbance that favoured some functional groups more than others, is still unclear and further analysis is required.

3.9.5 Conclusion and recommendations

As the majority of the deep sea (~65%) is not within any one country's national jurisdiction, the responsibility for monitoring any impacts occurring within the deep ocean and thus protecting it is difficult to define (Levin and Le Bris, 2015). The United Nations Framework Convention on Climate Change (UNFCCC) governs climate law between nation states (Thorp, 2012). Ideally the UNFCCC should acknowledge the important role that the deep sea plays in influencing the global climate and thus set aside greater resources for investigating the deep sea with a means to predicting impacts on climate change (Levin and Le Bris, 2015). It is important that this is undertaken if we are to not only protect the fauna inhabiting the deep sea, but to safeguard the many resources, functions and services that the deep sea currently provides (Thurber *et al.,* 2014).

Warming, ocean acidification and de-oxygenation have been termed the deadly trio, as one or more of these processes are known to play an important role in all of the major mass extinction events that have taken place (Bijma *et al.*, 2013). Evidence points not only to all three of these processes currently occurring in the ocean, but that they are occurring at unprecedented rapid rates and over short timescales. Reducing CO_2 emissions has been suggested by many and implemented by some, however, the very nature of the deep sea will result in it continuing to experience the effects for decades, if not centuries, even after complete cessation of CO_2 emissions.

It is clear that the deepsea environment is not the stable, barren desert it was once thought to be, but instead a dynamic environment that reacts and evolves to changing conditions. As such this vast habitat is not clearly separated from the surface waters and changing atmospheric conditions, instead it is inherently connected to both of them. The deep sea acts as a buffer to global warming by absorbing and storing CO_2, and oxidizing methane seeping from frozen reserves in the sea floor. These are clear factors that would undoubtedly accelerate global warming if the deep sea were not able to undertake this important role. These anthropogenic driven climate change threaten the complex functionality of the deep-sea benthos.

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3.10 Impacts and effects of ocean warming on jellyfish

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Summary

- Representatives of gelatinous zooplankton are increasingly reported in large numbers, with more than 1000 species worldwide, including Cnidaria, Ctenophora and Thaliacea, often collectively known as “jellyfish”.
- The reasons for increasing jellyfish blooms are probably manifold, ranging from local to global. Climate change and overfishing are global phenomena, and are good candidates as primary drivers of the rise of gelatinous zooplankton, at least in some parts of the ocean.
- Current evidence suggests that sea warming is forcing temperate marine biota towards the poles, with tropicalization of temperate marine ecosystems due to community phase shifts. Climate change is also negatively affecting tropical communities, as exemplified by the increasing frequency of coral bleaching events. Gelatinous zooplankton appear to be expanding their distributions, as seen in the Mediterranean Sea with the increased presence of tropical species, likely favoured by both temperature increases and the progressive enlargement of the Suez Canal.
- There is no evidence that temperature rises are threatening tropical jellyfish species, as they are with corals, but this might be due to current lack of observations.
- Increases in temperature may broaden the reproductive periods of mid-latitude jellyfish, and improve winter survival of tropical species expanding to temperate waters, therefore boosting both alien and native outbreaks.
- Increases in temperature at high latitudes might be detrimental for indigenous species, reducing their reproductive outputs. So far, limited increases in temperature at high latitudes do not support the proliferation of warm-water, non-indigenous species.
- The resulting patterns should see a stable situation at low and high latitudes, with no tendency to gelatinous plankton blooms, whereas these phenomena should increase at mid-latitudes, but this speculation needs to be substantiated by focused studies.

Ocean warming effects	Consequences
Warming seas lead to temperature increases at tropical latitudes	Stenothermal tropical species are in distress and move towards higher latitudes, where their thermal demands are met The tropics are affected by defaunation, unless thermal tolerance evolves, after initial bottlenecks due to mass mortalities
Warming seas lead to temperature increases at high latitudes	Stenothermal boreal and polar species alter their phenology, with shorter reproductive periods, migration to deeper waters, local extinctions
Warming seas lead to temperature increases at intermediate latitudes	The species that reproduce in the summer are favoured and widen their reproductive periods, with population increases due to increased reproductive activities The species that reproduce in the winter have shorter time windows for reproduction and tend to migrate in deeper waters The arrival of tropical species, pre-adapted to the new conditions, affects the viability of the populations of indigenous species. Increasing jellyfish populations will likely produce problems to expanding human activitities in coastal areas More jellyfish stingers can lead to more frequent and significant mortalities in finfish aquaculture facilities Combined effects of recurrent hypoxic events and jellyfish proliferations might impair physiological performances of wild fish populations, too Increasing jellyfish envenomation risks in the Mediterranan Sea represent health hazards and threats leading to significant economic losses to maritime tourism
Deepening of the summer thermocline	The favourable space for species adapted to high temperatures increases both in space and time, with greater chances to develop large populations The species that are not adapted to high temperatures move deeper, below the thermocline
Increased variability of environmental conditions	Opportunistic species such as gelatinous ones, adapted to develop large populations through asexual reproduction (larval amplification) are favoured against species that require higher “predictability” of environmental conditions

3.10.1 Introduction: the rise of ocean temperature

Rising ocean temperatures are but one sign of global climate change (GCC) brought about by the excessive burning of fossil fuels and deforestation. The last IPCC Report (2014) showed that ocean warming is not a matter of debate anymore. Temperature used to be rather constant in tropical waters whereas it fluctuated seasonally at increasingly high latitudes, with warmer and cooler periods. The phenology of many non-tropical organisms is tuned to changes in temperature and photoperiod, with different species being active in the warm and cold seasons. Seasonality can also be pronounced at tropical latitudes, but is more linked to rainfall than to temperature, with an alternation between cool, wet seasons and warm, dry ones (see Boero, 1994). Temperature rises can thus favour or hinder species, according to their thermal preferences in terms of metabolic and physiological performances, altering organismal distributions and animal behaviour. Increases in sea surface temperature (SST) lead to longer periods of water stratification and to a deepening of the summer thermocline, dramatically altering the features of benthic systems, leading to extensive mass mortalities of organisms that are not able to tolerate high temperatures (Rivetti *et al.,* 2014). Warmer water masses are also less oxygenated than cool ones, and GCC therefore makes its own contribution to the spread of oxygen dead-zones, independent of inputs from cultural eutrophication. The surface layers of vertically stratified water columns are generally nutrient-poor, with food chains based on smaller rather than larger cells (Legendre and Rassoulzadegan, 1996; Parsons and Lalli, 2002). If GCC results in increased stratification, these consequences could be experienced for longer periods of time. Other effects of GCC include ocean acidification, increased sea levels and an increase in the likelihood of extreme storm events.

3.10.1.1 The rise of jellyfish

Mills (1995, 2001) was among the first to recognize a possible change in the frequency of jellyfish blooms worldwide. Since then, research on the topic has blossomed, with a steady increase in scientific contributions (summarized in Purcell *et al.,* 2001a; 2012a; Pitt and Purcell, 2009; Purcell and Angel, 2010; Brotz *et al.,* 2012; Purcell, 2012; Condon *et al.,* 2013, 2014; Gershwin, 2013; Pitt and Lucas, 2014). The causes of jellyfish blooms are manifold and many are linked to local conditions that favour episodic and rapid increases of population sizes of many species, apparently independently from each other. Since the phenomenon is increasingly recorded, however, it is reasonable to search also for global drivers. In this respect, many scientists consider that overfishing and temperature rises are global enough to explain a large part of this phenomenon, coupled with other local conditions such as eutrophication and an increase in the amount of hard substrata for polyp settlement, etc. (see Purcell *et al.,* 2007; Boero *et al.,* 2008; Richardson *et al.,* 2009; Duarte *et al.,* 2013).

This contribution focuses on the role of temperature in causing jellyfish blooms, whilst acknowledging that this is not the sole cause for this phenomenon.

3.10.2 Temperature and metabolism

A number of factors including body mass, feeding behaviour (food density) and temperature, amongst others, influence the metabolic rate of jellyfish. Temperature increases lead to increases in respiration rates of some scyphozoan and hydrozoan jellyfish (e.g. Møller and Riisgård, 2007a), and ctenophores (Lilley *et al.,* 2014), as well as the polyps of some scyphozoans (Gambill and Peck, 2014). Acclimation, at least in part (and in theory), can help jellyfish cope with the effects of temperature, and this may account for the lack of a relationship between temperature and respiration over the range 7-30°C reported in the comprehensive meta-analysis by Purcell *et al.* (2012b). These authors note that there are no studies on the specific effects of acclimation on respiration of jellyfish, and it is important to redress this issue in order to understand the metabolic implications for jellyfish in the face of both short and long term temperature change. Studies on the thermal "windows" occupied by jellyfish are few (Gambill and Peck, 2014), though a number species can readily survive in eurythermal environments spanning up to 22°C (e.g. Lilley *et al.,* 2014). Whilst such wide tolerances would permit some level of population persistence locally in the face of temperature change, as well as in novel areas following transport, temperature extremes would inevitably result in mass mortalities (e.g. Rivetti *et al.,* 2014). That said, "common garden" experiments are needed in order to establish the potential for adaptation to local conditions (Gambill and Peck, 2014). This is particularly true for the production of ephyrae through strobilation, since the presence of jellyfish blooms is based, for those species with polyp stages, on the production and survival of large quantities of young (Boero *et al.,* 2008).

Studies on adult medusae are scarce and the paradigmatic relationship between body mass and respiration is unknown for most gelatinous plankters: the investigated species are too few to allow for generalizations (see Pitt *et al.*, 2014, based on data from 21 jellyfish species including cnidarians and ctenophores). Within the paradigmatic scyphozoan *Aurelia aurita*, the mass-specific respiration rates of the different life-history stages (polyp, ephyrae, and medusae, see Figure 3.10.1) appear to be similar at similar temperatures, despite "obvious differences in morphology and activity" (Gambill and Peck, 2014). However, this finding might be not true for other species.

Mediterranean jellyfish, for example, live under thermal regimes that span the range between 12 and 28°C, with extremes that can reach 4°C in winter and over 30°C in summer (Box 3.10.1). Survival under such large thermal variations is due to the possibility of polyp formation and even encystment when environmental conditions are not suitable for medusae (Boero *et al.,* 2008). Life cycle adjustments and changes in phenology (see below), in this respect, are the obvious adaptation of jellyfish to variable thermal conditions. Coral bleaching is a result of the expulsion of symbiotic zooxanthellae from scleractinian tissues (Eakin *et al.,* 2009), which results in the eventual death of host animals. It is one of the more obvious consequences of ocean warming and it is a cause of international concern (Hoegh-Guldberg, 1999). Although a number of Medusozoa also have symbiotic zooxanthellae (e.g. *Cassiopea*, *Mastigias*, *Linuche*), and most species are similarly distributed around the tropics, understanding of jelly-bleaching is negligible.

Like carnivorous jellyfish, the respiration rates of salps and doliolids are also influenced by body size, feeding behaviour (food density) and temperature (Madin and

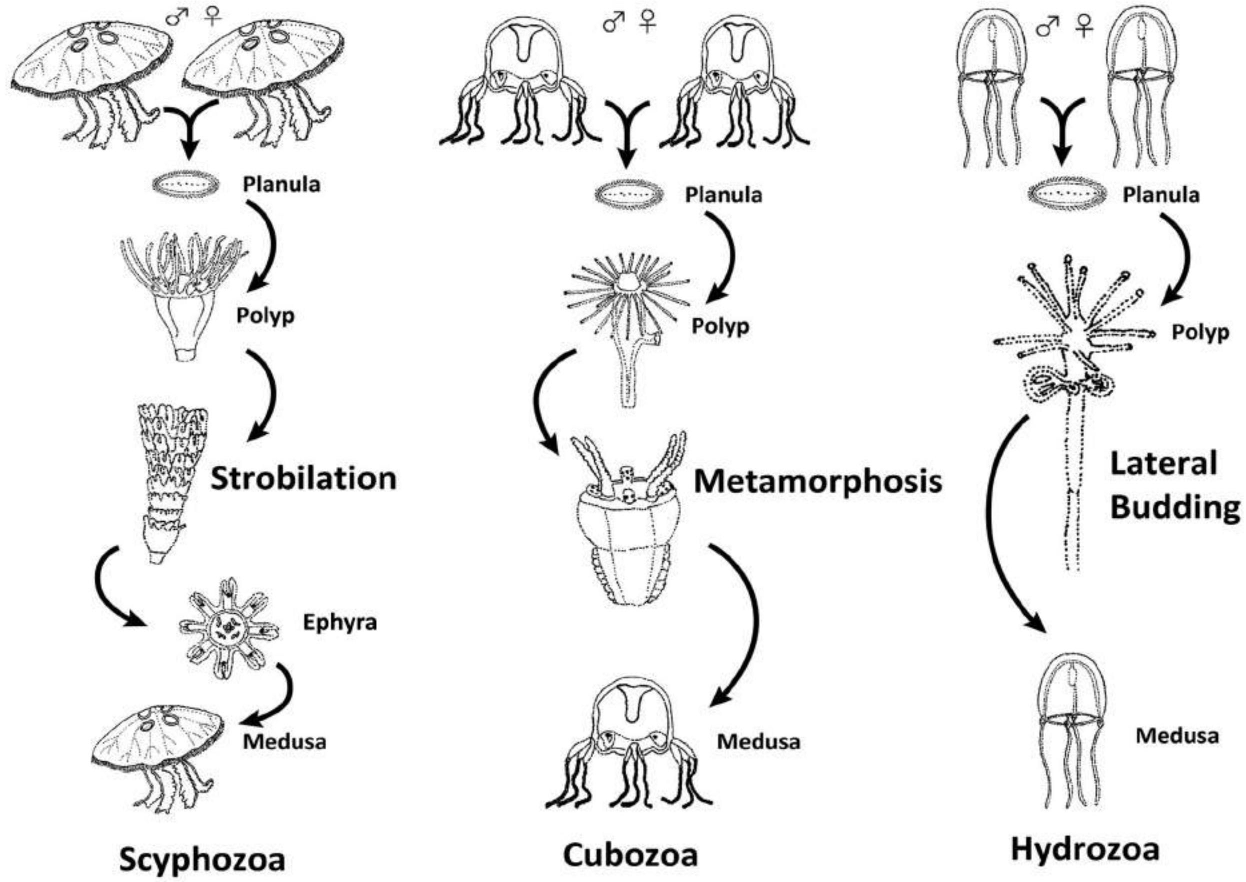

Figure 3.10.1 Main life cycle patterns in Medusozoa.

Deibel, 1998). Increases in temperature are associated with increased clearance, ingestion and growth rates (Gibson and Paffenhöfer, 2000). Weight-specific respiration rates are either independent of, or they increase with, animal size (Madin and Deibel, 1998), which the authors could not clearly explain, but suggested could be related to animal geometry or swimming activity. A similar conclusion regarding the important role of swimming activity on respiration was reached previously by Cetta *et al.* (1986), based on the fact that respiration rate was more closely linked to animal length than mass.

Harbison and Campenot (1979) studied the effects of temperature on swimming (here interpreted as a proxy for respiration) of nine salp species and observed that responses fell into one of three Categories. Category I: species such as *Pegea confederata, Cyclosalpa polae* and *Salpa cylindrica* stopped moving altogether at low temperatures; category II: species such as *Pegea socia, Cyclosalpa pinnata, C. affinis* and *Salpa maxima* displayed depressed pulsation rates at low temperatures but they did not stop moving altogether, whilst species of Category III, such as *Salpa fusiformis* and *S. aspera*, were largely insensitive to temperature changes. Harbison and Campenot (1979) correlated the species in these response categories to different environments: Type I are tropical or sub-tropical, Type II are temperate or have wide-ranging distributions, while Type III species are vertical migrators.

3.10.3 Temperature and phenology

Photoperiod and temperature are the main drivers that regulate the responses of species to seasonal cycles (phenology), especially in terms of periodic activities such as migrations or reproduction. The phenological responses of marine species to temperature change are less well documented than those of terrestrial species, though Richardson (2009) cited a number of examples whereby different zooplankton groups peaked in biomass “early”. One of these was the comb jelly *Mnemiopsis leidyi* in Narragansett Bay which now appears two months earlier than previously (Sullivan *et al.,* 2001). Conversely, Burrows *et al.* (2011) reported Puce *et al.* (2009) as the sole study demonstrating phenological changes in marine invertebrates linked to global warming. Indeed, the structure and phenology of the hydroid community in the Northern Mediterranean Sea has exhibited marked changes in species

Box 3.10.1 The Mediterranean Sea

The Mediterranean Sea is a miniaturized ocean that responds more quickly than the world ocean to environmental changes (Bianchi, 2007; Lejeusne *et al.*, 2010; Coll *et al.*, 2014; Boero, 2015). The Mediterranean, therefore, can be used as a proxy to depict a scenario that will probably become global in terms of biodiversity responses to global stresses.

Temperature increases in the Mediterranean Sea have been especially dramatic since the mid-1980s and have caused extensive mass mortalities of organisms that do not tolerate positive thermal anomalies, such as sea fans (Rivetti *et al.*, 2014). The impact of warming, thus, is negative for cold-water species whereas it is positive for tropical species or, in general, for species that are well-adapted to high temperatures. The establishment of tropical species (Galil *et al.*, 2014) counterbalances the retreat of temperate species: hundreds of tropical species have become established in the Mediterranean Sea, with a biotic change that has no counterpart in any other part of the world, leading some to define the basin as “a sea under siege” (Galil, 2000). The regional significance of temperature increases in the Mediterranean is rather obvious: temperate species show signs of distress, whereas tropical species become established and flourish (Bianchi, 2007; Boero, 2015). The number of tropical jellyfish, and their increasing abundances in the Mediterranean Sea over the last (at least 20) years exemplifies the response of jellyfish to these changes, mainly linked to temperature increases. Brotz and Pauly (2012) and Boero (2013) have reviewed the knowledge of jellyfish populations in the Mediterranean. With the most recent addition of *Cotylorhiza erythraea* (Galil *et al.*, 2016), the list of tropical scyphomedusae recently established in the Mediterranean now includes: *Rhopilema nomadica, Marivagia stellata, Cothylorhiza erythraea, Phyllorhiza punctata, Cassiopea andromeda*, and two *Aurelia* species (Scorrano *et al.* 2016). Other records of tropical species that have entered the Mediterranean Sea await confirmation, as is the case for *Cassiopea polypoides*. The arrival of non-tropical gelatinous aliens, such as the ctenophores *Mnemiopsis leidyi* and *Beroe ovata*, probably brought by ships, or the scyphozoans *Rhizostoma luteum* and *Catostylus tagi*, that entered the Mediterranean Sea through the Strait of Gibraltar, show the rapid changes of the gelatinous fauna in the basin.

The 2009 poster of the citizen science initiative on Mediterranean jellyfish (Figure 3.10.2a) covered 13 species, with only one being truly tropical (*Rhopilema nomadica*) whereas the poster of the 2016 campaign covered 21 species (Figure 3.10.2b), in many instances first reported by citizens. Among them, a new scyphozoan species, *Pelagia benovici*, has been described from the northern Adriatic Sea. This species probably reached the Gulf of Venice in ballast waters. It bloomed during the winter, but disappeared as soon as the warm season arrived. Probably, this species cannot tolerate the summer Mediterranean temperatures and became locally extinct.

The scyphozoan species that dominate the Italian seas are: *Pelagia noctiluca, Cotylorhiza punctata, Rhizostoma pulmo,* and *Aurelia* spp.; other abundant gelatinous plankters are the cubozoan *Carybdea marsupialis* and the hydrozoan *Velella velella* (Figures 3.10.3-3.10.8; Table 3.10.1).

Extensive long-term studies on the gelatinous component of the Italian marine fauna (Boero *et al.*, unpublished) shows that Mediterranean jellyfish blooms have become conspicuous since (at least) 2009. Too little is known about the thermal preferences of these species, but their population increases suggest that they are taking advantage of elevated temperatures, which probably lengthens their reproductive periods.

The increase in numbers of jellyfish observed in the Mediterranean Sea may be responsible for the “resurrection” of a species that has not been seen locally for decades. *Drymonema dalmatinum* is the largest Mediterranean scyphozoan. It is a medusivorous species that is now becoming rather frequent in the waters of the Adriatic Sea, probably due to high food availability, in the form of other jellyfish (Malej *et al.*, 2014). Apparently, the biota of the Mediterranean Sea has suffered from a process of recent jellyfication (sensu Roux *et al.*, 2013), reflecting the phenomenon that can be reconstructed from scattered observations at the global level.

Figure 3.10.2 Posters of the a) 2009 and b) 2016 Italian citizen science campaigns on jellyfish records.

composition, bathymetric distribution, and reproductive timing across a 25-year period (Boero and Fresi, 1986; Puce *et al.,* 2009). Cold-water species have either disappeared altogether or have become restricted in their bathymetric distribution to deeper areas and for shorter winter periods, whilst warm-water species (typical of the Mediterranean assemblages during summer) have expanded their temporal distributions and reproduction into the cold season. Several hydroid species reproduce sexually through a tiny medusa stage, and the periods of absence of active hydroid specimens are spent as resting hydrorhizae (Boero *et al.,* 2008).

The phenological responses of hydrozoans to global warming provide useful models to help understand the plankton dynamics of those scyphozoans and cubozoans with polyp stages. On the one hand, warm-water scyphozoans may perceive temperature increases as a trigger for ephyrae production through strobilation, and as such, are liable to lengthen the time window of medusa production. As a consequence, the presence of jellyfish in the plankton may be brought forward, leading to a probable expansion of the period when jellyfish can grow and reproduce sexually, which in turn will lead to increased polyp production, so reinforcing their presence in subsequent years. Ruiz *et al.* (2012) summarized this concept with: "medusa populations fluctuate under the simple rule the warmer the better". On the other hand, cold-water species and perhaps even cold-adapted populations, should be negatively affected by temperature increases, with negative influences on reproductive patterns: a reduced scope for asexual reproduction, including strobilation, and a shortened window for medusa growth and survival. The consistency of the polyp reservoir, in fact, is the premise for the onset of the blooms for species with a benthic stage (Boero *et al.,* 2008; Boero, 2013).

Indeed, temperature has been shown to trigger strobilation for numerous species, meaning that jellyfish blooms in temperate environments could appear earlier under regimes of temperature increases, as has been observed for several species in the Dutch Wadden Sea (van Walraven *et al.,* 2015) and the North Sea (Schlüter *et al.,* 2010), as well as for the dangerous cubozoan *Chironex fleckeri* in Australia (Jacups, 2010) and the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, U.S.A. (Sullivan *et al.,* 2001; Costello *et al.,* 2006).

Warmer waters may also result in increased reproduction for some jellyfish. For example, *Chrysaora quinquecirrha* produces more eggs in warmer waters (Purcell and Decker, 2005), and this leads to higher polyp production. Various aspects of the life cycle of *Aurelia* spp. (Figure 3.10.9) may also be influenced by warmer temperatures, including increased polyp budding, a higher proportion of strobilating polyps, increased number of strobilation cycles, and more ephyrae produced per polyp (Lucas, 2001; Purcell, 2007; Liu *et al.,*. 2009; Purcell *et al.,*. 2009; Han and Uye, 2010; Lucas *et al.,* 2012).

Similar results have also been demonstrated with *Cotylorhiza tuberculata* (Figure 3.10.10) – a species that has increased in the Mediterranean's Mar Menor – including faster planulae settlement and a higher proportion of strobilating polyps (Prieto *et al.,* 2010; Ruiz *et al.,* 2012). But temperature increases can also negatively affect cold-water species. Good conditions for the strobilation of species of *Aurelia* and *Cyanea* are in fact correlated with low temperatures in the North Sea, based on an apparent relationship with the NAO index (Lynam *et al.,* 2004). As such, "…the long-term effects of global warming might suppress *Aurelia aurita* and *Cyanea* spp. populations there" (Lynam *et al.,* 2010). This example serves to demonstrate that not all jellyfish will respond positively to warmer temperatures. Indeed, jellyfish living near their thermal maxima are expected to suffer, such as polar species that thrive in cold waters. Unfortunately, research on jellyfish in polar regions is especially scant. Of course, it is also possible that rising temperatures may also have no effect on jellyfish populations in some locations. Baumann and Schernewski (2012) report that increased temperatures do not seem to have altered the occurrence of *Aurelia aurita* in the Baltic Sea.

Warmer waters may also lead to more jellyfish through increased winter survival. For example, ephyrae of *Pelagia noctiluca* show increased mortality at lower temperatures (Rottini-Sandrini, 1982; Avian *et al.,* 1991). This species has increased in abundance in the Mediterranean Sea, potentially due to increasingly mild winters (Molinero *et al.,* 2005; Daly Yahia *et al.,* 2010). In such seasonal environments, cooling temperatures often signal the senescence of adult medusae. If critical temperatures occur later in the year, this may also increase the duration of jellyfish presence, as well as potentially prolonging the reproductive period (Canepa *et al.,* 2014; Milisenda *et al.,* 2016).

Most salp and doliolid species show seasonal patterns of abundance, and temperature has usually been correlated with both abundance and distribution (see e.g. references in Diebel (1998). Indeed, phytoplankton abundance has recently been identified through a modelling study as a key driver influencing the appearance and abundance of swarms of the salp *Thalia democratica* in the Tasman Sea (Henschke *et al.,* 2015). Increases in temperature are associated with increases in population growth rate and a reduction in generation time. In the case of the doliolid *Dolioletta gegenbauri*, there may be no change in the number of gonozooids released by phorozooids with increasing temperature (16.5 – 23.5°C), but their individual size, and hence amount of carbon released daily, does increase (Gibson and Paffenhöfer, 2002): hence, increased temperatures are associated with reduced longevity. At much higher temperatures (26.5°C), however, the gonozooids released by *D. gegenbauri* become reduced in size and effectively dysfunctional (Gibson and Paffenhöfer, 2002), implying that blooms will not persist.

Table 3.10.1 Jellyfish Citizen Science: total number of sightings and number of bloom sightings (>10 ind/m^2) of the most common jellyfish taxa along the Italian coastline (2009-2015)

	2009	2010	2011	2012	2013	2014	2015
Total N° Sightings	**303**	**1821**	**3298**	**2386**	**4544**	**1401**	**3351**
P. noctiluca	96	574	663	449	1353	404	788
R. pulmo	66	462	925	1260	1131	299	1179
C. tuberculata	36	370	665	82	681	65	421
Aurelia spp.	6	69	160	113	253	63	147
C. marsupialis	14	128	410	199	282	224	349
V .velella	19	52	9	72	94	100	82
N° Bloom Sightings	**145**	**973**	**1186**	**882**	**1928**	**652**	**1220**
P. noctiluca	55	392	274	180	665	243	354
R. pulmo	20	194	298	432	495	86	381
C. tuberculata	19	185	230	18	243	14	116
Aurelia spp.	1	46	63	30	109	28	68
C. marsupialis	7	62	125	52	75	70	120
V. velella	19	41	4	110	79	102	78

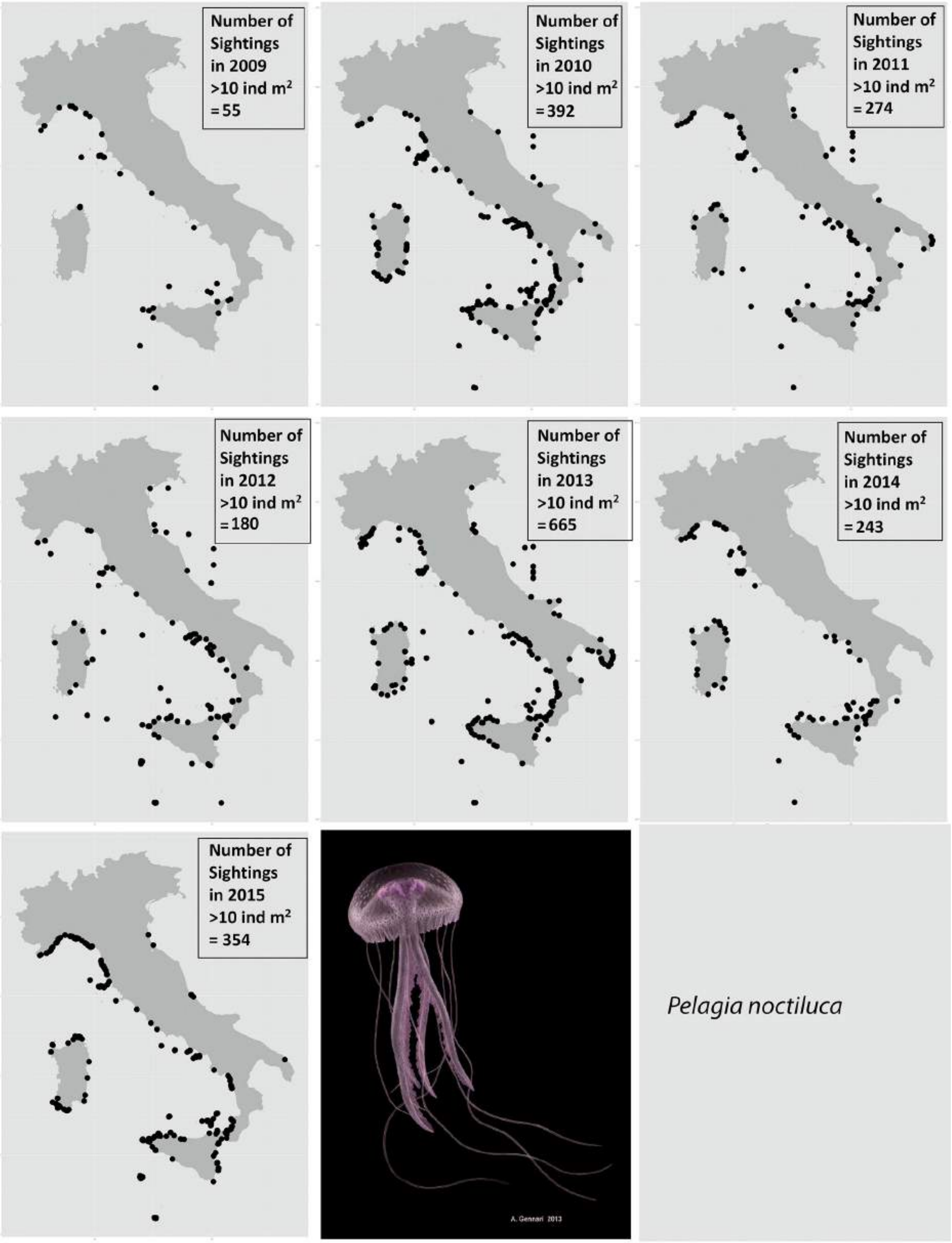

Figure 3.10.3 Maps of jellyfish distribution (*Pelagia noctiluca*) drawn by the Italian citizen science records over the 2009-2015 period.

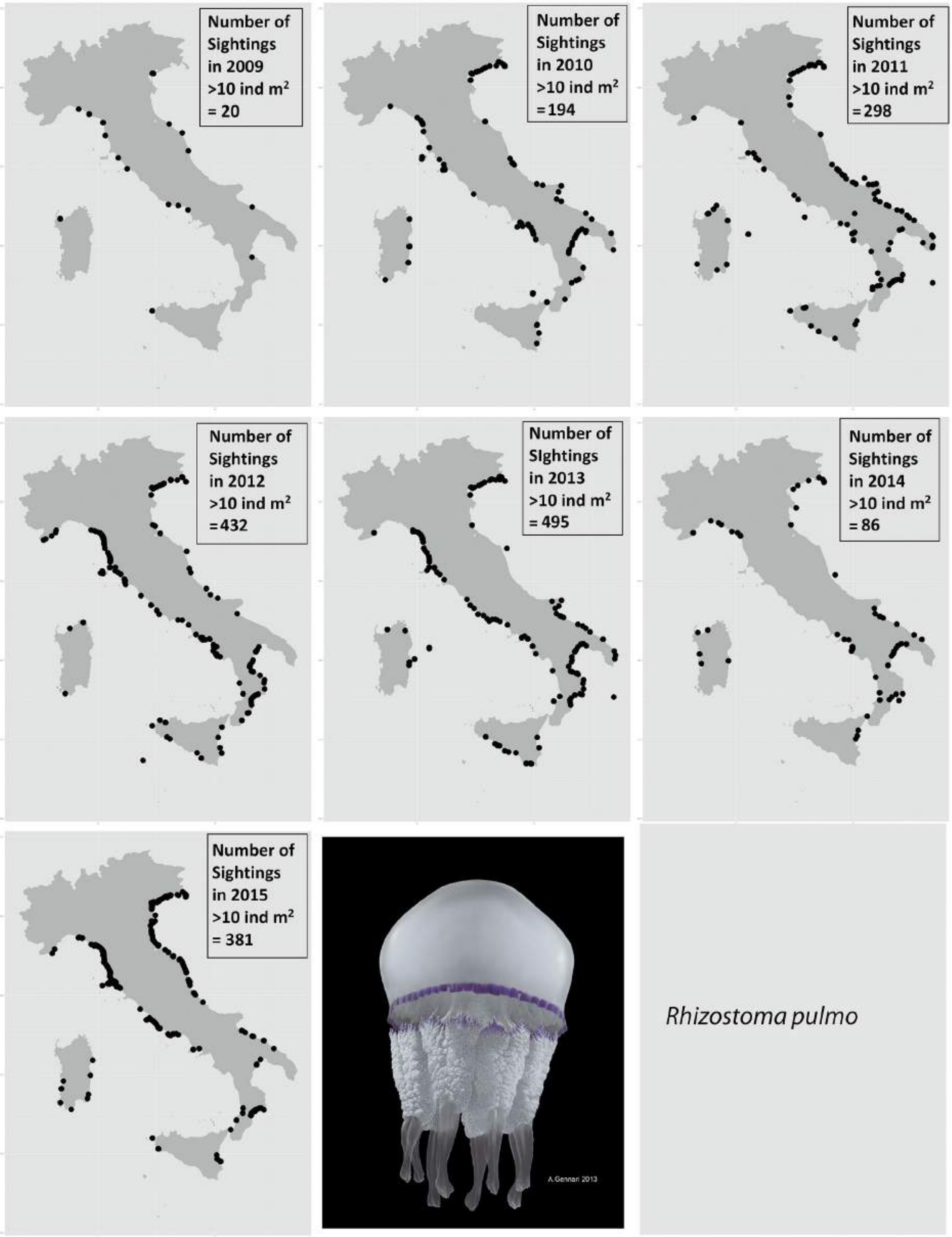

Figure 3.10.4 Maps of jellyfish distribution (*Rhizostoma pulmo*) drawn by the Italian citizen cience records over the 2009-2015 period.

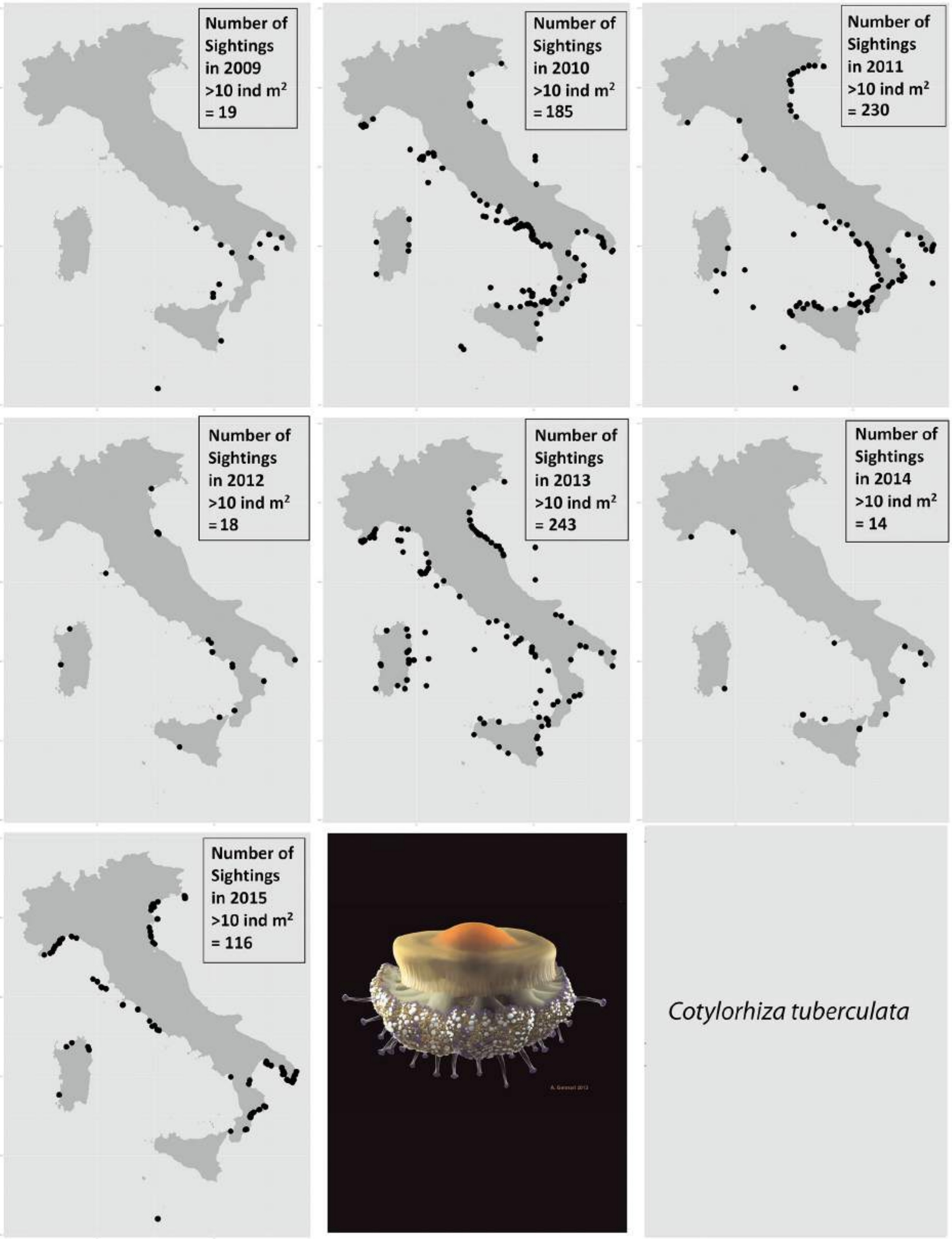

Figure 3.10.5 Maps of jellyfish distribution (*Cotylorhiza tuberculata*) drawn by the Italian citizen science records over the 2009-2015 period.

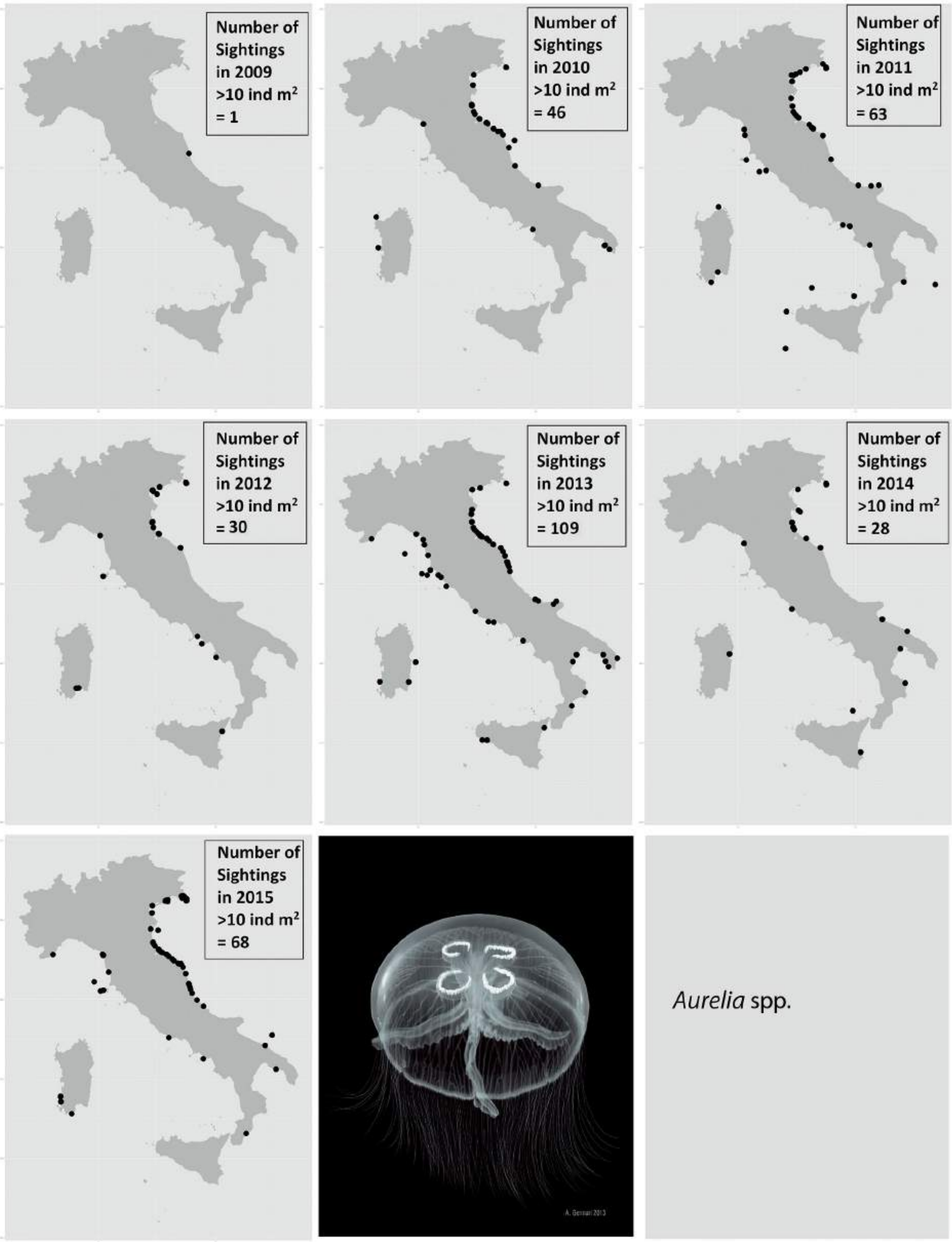

Figure 3.10.6 Maps of jellyfish distribution (*Aurelia* spp.) drawn by the Italian citizen science records over the 2009-2015 period.

Figure 3.10.7 Maps of jellyfish distribution (*Carybdea marsupialis*) drawn by the Italian citizen science records over the 2009-2015 period.

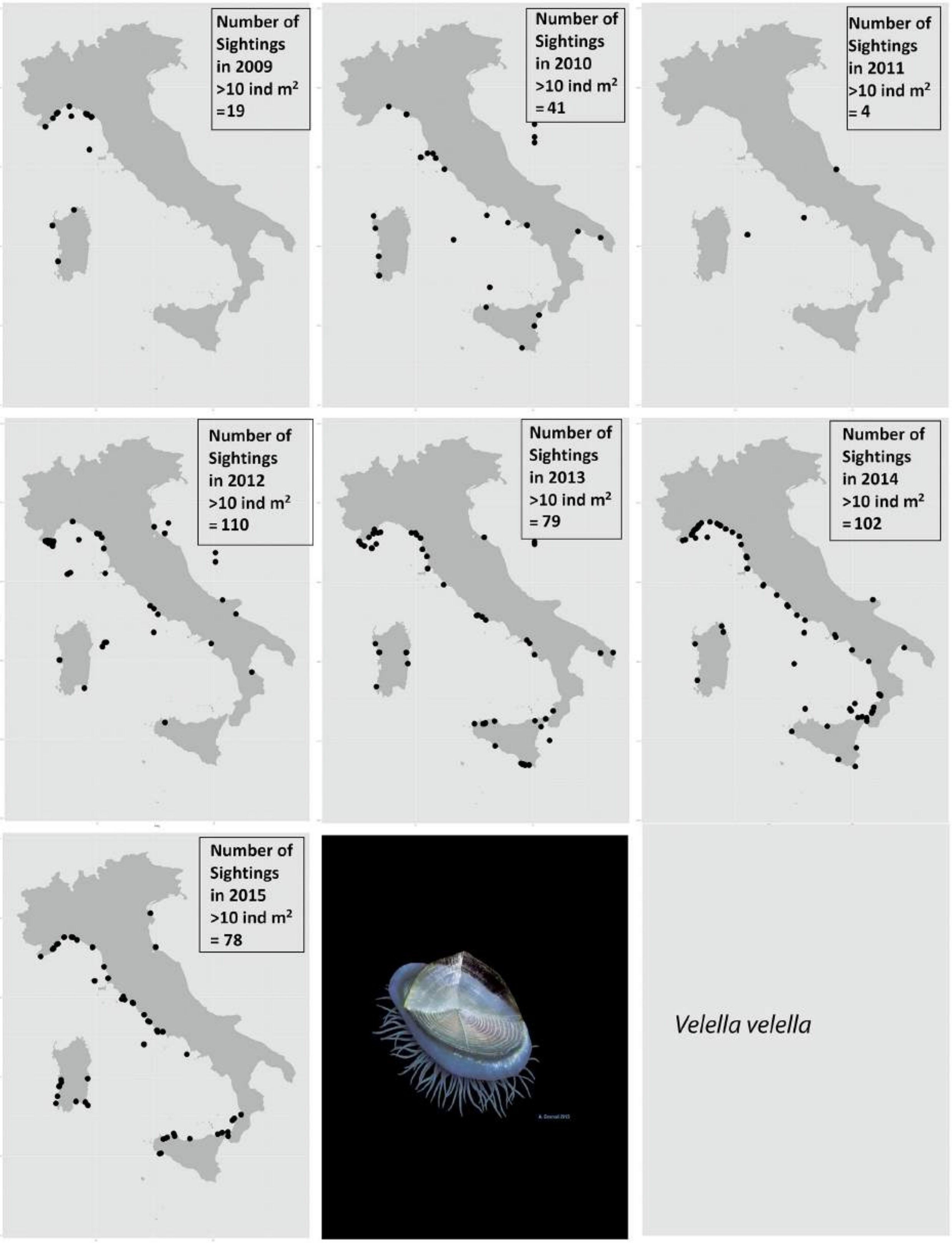

Figure 3.10.8 Maps of jellyfish distribution (*Velella velella*) drawn by the Italian citizen science records over the 2009-2015 period.

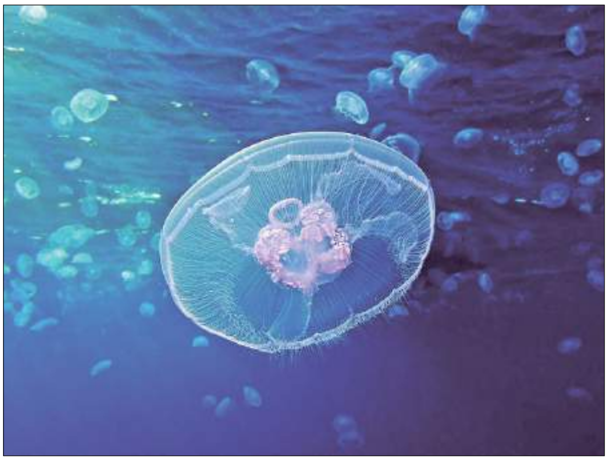

Figure 3.10.9 *Aurelia aurita.* © Alexander Vasenin.

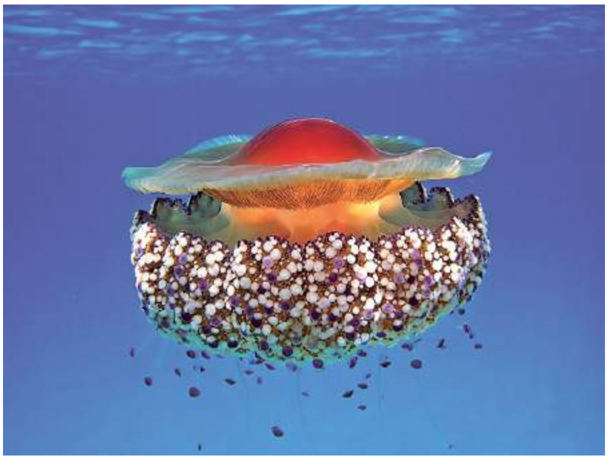

Figure 3.10.10 *Cotylorhiza tuberculata.* © Fredski2013.

3.10.4 Temperature and distribution

Warmer waters may facilitate the poleward expansion of jellyfish species that are usually restricted to a particular range of temperature. This may explain, in part, the increased blooms of the giant jellyfish *Nemopilema nomurai* in East Asian waters in recent years, as the medusae are found less often in cooler waters (Honda *et al.,* 2009; Kitajima *et al.,* 2015). Warmer temperatures, associated with less productive waters, also appear to have resulted in increased abundances of the pelagic tunicate *Salpa thomsoni* in the Southern Ocean. As the ice edge retreated due to warming, salps increased their southerly distribution, while krill (*Euphausia superba*) were negatively affected (Loeb *et al.,* 1997; Pakhomov *et al.,* 2002; Atkinson *et al.,* 2004; Lee *et al.,* 2010). Kang and Rebstock (2004) observed elevated abundances of *Doliolum nationalis* in the Northeastern Marginal Sea in the El Niño year of 1997, following their transport in the Tsushima Warm Current. By contrast, however, periods of reduced thaliacean biomass in the southern California Current over the past 50-odd years have been linked to increased water column stratification, which appears to be a feature of the environment that the cool-water, high latitude species introduced (seasonally) into the system could not cope with (Lavaniegos and Ohman, 2003, 2007; Kang and Ohman, 2014).

However, tropical jellyfish with presumably similar requirements in terms of temperature show sharp differences in invasiveness. The tropical species *Rhopilema nomadica* and *Phyllorhiza punctata* entered the Mediterranean Sea from the Suez Canal (Galil *et al.,* 1990, 2009a) and developed huge populations in the eastern Mediterranean. However, shortly after its arrival *P. punctata* rapidly extended its distribution westwards (Boero *et al.,* 2009; Keeley, 2011), while *R. nomadica* was first seen in the Central Mediterranean (Malta) in 2004 (Deidun *et al.,* 2011) and in Tunisian waters in 2008, where it is regularly spotted since 2010 during summer and autumn months (Daly Yahia *et al.*, 2013). It reached the western Mediterranean only in 2015, the hottest year ever (Koh, 2016): although still unpublished in the scientific literature, its occurrence has been documented by pictures taken during a windsurfing competition in Sardinia, near Cagliari, and reported in local newspapers (e.g. Spano, 2015). Evidently the two species reacted differently to the temperature regimes in the two basins, even though they might have originated from the same source habitat (the Red Sea). Lotan *et al.* (1994) demonstrated that temperature plays a crucial role in the life cycle of *R. nomadica* and predicted that the species would not have expanded its distribution from the warm eastern Mediterranean to the cooler western Mediterranean. Now it is likely that the recent temperature increases have allowed *R. nomadica* to reach westwards. The case of *P. punctata* and *R. nomadica* suggests that it is simplistic to expect that temperature alone will account for the distribution of species. Even if tropical species tend to expand towards higher latitudes in a period of generalized warming, not all do so in the same fashion.

Tropical species should be adapted to high temperatures, but global warming is resulting in conditions that exceed their tolerance limits. This is leading to dramatic events of coral mass mortality due to bleaching (Eakin *et al.,* 2009). Events of distress due to too high temperatures might also affect other, less conspicuous, components of marine communities that do not have the same status as corals in terms of human perception, such as jellyfish. Tropical species are usually stenothermal and do not tolerate deviations from their optimal temperature ranges. On the one hand, they do not withstand lower temperatures, and are thus restricted to the tropics but, on the other hand, they do not tolerate too high temperatures. Hence, they extend their range to higher latitudes, following their thermal niche. Species adapted to high latitudes are negatively affected by temperature increases too, as documented also for some jellyfish that strobilate in the coldest months of the year (Grondhal, 1988; Brewer and Feingold, 1991; Lucas and Williams, 1994; Lucas, 2001; Lynam *et al.,* 2004). The consequences of global warming, thus, should be of distress both for species adapted to high temperatures and for species adapted to low temperatures. These should "follow" the fulfilment of their thermal niches, changing their distributional ranges whenever possible.

The enhancement of tropical and indigenous species at mid-latitudes attracted the attention of scientists that extended the perception of the jellyfish rise to the entire globe (Richardson *et al.,* 2009), a trend that was questioned by Condon *et al.* (2012) due to uneven records of such events.

3.10.5 Jellyfish and hypoxia

As water warms, the saturation value of dissolved oxygen (DO) decreases. Thus, the oxygen demands of water-breathing organisms such as fishes and invertebrates will be increasingly difficult to meet under global warming scenarios (Pörtner and Knust, 2007; Pauly, 2010). Jellyfish also require oxygen, and are generally less abundant in hypoxic waters; however, they appear to be more tolerant of hypoxia than many other marine fauna (Purcell *et al.,* 2001b). This is in part due to their low metabolism (Rutherford and Thuesen, 2005; Thuesen *et al.,* 2005a), extremely efficient swimming (Gemmell *et al.,* 2013, 2015), and the ability of some species to store oxygen in their tissues (Thuesen *et al.,* 2005b). Laboratory and mesocosm experiments under low DO conditions confirm that jellyfish may increase predation due to a diminished prey escape response by ichthyoplankton (Breitburg *et al.,* 1997; Shoji *et al.,* 2005a), or by out-competing fish for prey (Shoji *et al.,* 2005b).

Figure 3.10.11 Dense jellyfish swarm in Gulf of Mexico. © Monty Graham, Dauphin Island Sea Lab.

Several regions around the planet appear to show increasing jellyfish populations (Figure 3.10.11) as a result of more persistent hypoxic conditions. In most of the cases listed, hypoxia is suspected to be a result of cultural eutrophication rather than oceanic warming; however, the examples demonstrate what may happen under increased hypoxia, especially as the effects of eutrophication may be exacerbated by warmer conditions.

In Japan's Seto Inland Sea, *Aurelia* populations appear to have increased in part due to hypoxia, as medusae were more abundant in areas of Hiroshima Bay with lower DO concentrations in bottom layers, compared to other zooplankton (Shoji *et al.,* 2010).

Hypoxic conditions have likely also contributed to the success of the scyphozoan *Chyrsaora quinquecirrha* and the ctenophore *Mnemiopsis leidyi* in Chesapeake Bay, U.S.A. (Breitburg *et al.,* 1997; Keister *et al.,* 2000). In the northern Gulf of Mexico, excess nutrients from the Mississippi River and numerous other estuaries result in widespread seasonal hypoxia (Rabalais *et al.,* 1994). Jellyfish in this region are monitored by a trawl programme, and the sea nettle *C. quinquecirrha* appears to have expanded into hypoxic waters in the 1990s (Graham, 2001) with the frequency of hypoxia explaining almost 60% of the variation in the catch rate (Purcell *et al.,* 2001b). Despite this correlation, there are confounding (and possibly synergistic) factors that also appear to be linked to jellyfish abundance in this ecosystem, including historical fisheries for forage fish (Robinson *et al.,* 2014). As with many areas showing increased jellyfish populations, there appears to be more than one driver at play. This is evident in the Black Sea, where invasive species, overfishing, and hypoxia due to cultural eutrophication have all likely contributed to increased jellyfish blooms (Kideys, 1994). With respect to hypoxia, it is interesting to note that in the open areas of the Black Sea, *Aurelia* planulae were found in high densities in hypoxic waters where almost no other plankters were present (Vinogradov *et al.,* 1985).

Similar to medusae, the benthic polyps of jellyfish may also have a competitive advantage over other organisms due to a tolerance for low DO concentrations. Polyps of *C. quinquecirrha* have survived and reproduced asexually during prolonged exposure to hypoxic conditions in laboratory experiments (Condon *et al.,* 2001). In Tokyo Bay, notable increases in the *Aurelia* population first occurred in the 1960s, when industrial and civic pollution resulted in increased eutrophication (Nomura and Ishimaru, 1998; Ishii, 2001; Han and Uye, 2010). The bottom layer of Tokyo Bay is now hypoxic in summer, which may reduce competition for habitat with other sessile organisms. Indeed, Ishii *et al.* (2008) found that polyps cultured from this population will grow and bud more polyps under low DO conditions. The authors note that other organisms such as mussels, barnacles, and ascidians occupy most suitable substrate in the bay, but in the hypoxic areas, jellyfish polyps are thriving. Similar mechanisms may also be at work in the Gulf of Mexico, where experiments have revealed that polyps of *Aurelia* are more tolerant of low DO conditions that the rest of the benthic fouling community (Miller and Graham, 2012).

Hypoxia may also be reinforced by jellyfish blooms, creating a positive feedback loop whereby large blooms may die and decompose, further reducing DO concentrations (West *et al.,* 2009). However, it is important to note that not all jellyfish respond to hypoxia in the same way. Many hydroids are sensitive to low DO concentrations, and hypoxia has been blamed for the reduced diversity of hydromedusae observed in the Adriatic Sea (Benović *et al.,* 1987, 2000). As Arai (2001) concludes in her review of jellyfish and eutrophication, typically the diversity of jellyfish decreases, but the biomass of select species may increase.

Experimental studies on the effects of hypoxia on thaliaceans appear to be entirely absent from the literature. Interestingly, Elliott *et al.* (2012) have noted that salps in the northern Gulf of Mexico were more abundant when hypoxic bottom waters extended higher in the water column than when deeper. These authors speculated that elevated salp abundances at these times were due either to their ability to use the hypoxic bottom waters as a refuge from predators and/or a reflection of their direct contribution to the hypoxia via faecal pellets (Elliott *et al.,* 2012).

Gomes *et al.* (2014) have recently noted massive outbreaks of a green form of the mixotrophic *Noctiluca scintillans* in the Arabian Sea in association with water undersaturated in DO. These near-surface hypoxic water blooms were associated with large populations of the salp *Pegea confoederata*, which experiments suggested could consume up to 71% of the Chl *a* and 78% of the Chl *b* (Gomes *et al.,* 2014).

3.10.6 Jellyfish and the food web of stratified water columns

It is generally understood that warm, thermally stable water columns are characterized by nutrient-depleted surface waters, lower levels of phytoplankton production, and deep chlorophyll maxima. Such surface waters tend to have complex food webs fuelled by small cells and dependent upon recycled nitrogen. While most jellyfish can eat a wide range of different plankton types, with different taxa specializing on different prey fields (Arai, 2001) depending on cnidome (e.g. Purcell, 1984) and swimming mode (Costello and Colin, 2002), feeding and growth rates vary with animal size (Purcell, 2009) as well as with prey density and type (Sullivan and Gifford, 2004; Hansson *et al.,* 2005; Møller and Riisgård, 2007b). Although relatively few studies have examined jellyfish feeding on very small prey items, Båmstedt *et al.* (2001) have shown that ephyrae of *Aurelia* grow well on a diet of the flagellate *Rhodomonas* when small, but not as they increase in size. Turk *et al.* (2008) have shown that adult *Aurelia* can have a negative impact on ciliate populations in mesocosm studies, whilst Kamiyama (2011) has shown that polyps of *Aurelia* can similarly graze on (a variety of) marine ciliates. The hydromedusa *Blackfordia virginica* also eats phytoplankton, ciliates, and POM (Morais *et al.,* 2015), and juvenile *Mnemiopsis* can thrive on a diet of phototrophic and heterotrophic dinoflagellates, ciliates, and flagellates (Sullivan and Gifford, 2004).

Thaliaceans thrive on small plankton particles of all descriptions (Madin and Deibel, 1998), and can meet their metabolic needs on submicrometre particles alone (Sutherland *et al.,* 2010). Increases in food particle size are associated with reduced clearance rates (Katechakis *et al.,* 2004), and animals can starve "in the midst of plenty" (Harbison *et al.,* 1986). They are thus ideally suited to environments dominated by the microbial food web, providing they can cope with the associated temperatures (implied by results of Lavaniegos and Ohman, 2007), though their ability to migrate vertically may buffer them to some extent.

Taken together then, at least some jellyfish can thrive in warm waters dominated by small cells. Although this appears to be particularly true for small jellyfish (Boero *et al.,* 2007), which are the types commonly to be found in stratified waters, larger animals in coastal waters can also directly access the microbial food web. This is an advantage in warm coastal lagoons subject to heavy cultural eutrophication, high concentrations of nitrogen and phosporous, low concentrations of silica, and dominated by small phytoplankton cells.

3.10.7 Ocean acidification

One of the consequences of an increase in atmospheric carbon dioxide is a reduction in oceanic pH. In the last 300 years, the pH of surface waters is estimated to have decreased by more than 0.1 pH units, and it is thought that it will drop by a further 0.3-0.5 units by the end of the century (Orr *et al.,* 2005; Mora *et al.,* 2013). A reduction in pH generally lowers the saturation state of calcium carbonate and the aragonite saturation horizon will be forced closer to the ocean's surface. Aside from the fact that this poses problems for any organism with calcified body parts, a reduction in pH will also have impacts on a range of metabolic and physiological processes as well as biogeochemical ones. Given that acidification is thought to be occurring faster now than at any time in the past 300 million years (Gattuso *et al.,* 2015), it is no wonder that ocean acidification is sometimes referred to as the "evil twin of global warming".

Jellyfish lack calcified body parts of any sort, and the statoliths within statocyts of medusozoans comprise calcium sulphate hemihydrate: jellyfish are therefore immune from decalcification. However, experiments suggest that a reduction in pH does in fact lead to smaller statoliths in the newly released meduase of cubozoans (Klein *et al.,* 2014) and in the ephyrae of scyphozoans (Winans and Purcell, 2010). That said, the reason why acidification may lead to smaller statoliths is unclear, as too are the implications on subsequent animal performance.

A reduction in pH does not appear to have any impact on the survival of the polyps of either cubozoans (Klein *et al.,* 2014) or scyphozoans (Winans and Purcell, 2010; Lesniowski *et al.,* 2015), regardless of temperature. In the case of the irukandji jellyfish *Alatina mordens*, however, growth rates may be reduced at lower pH, but this response varies slightly with temperature (Klein *et al.,* 2014).

Definitive information on the effects of pH on the growth and development of adult medusae are entirely missing at present. From CPR data, Attrill *et al.* (2007) suggested a positive link between the abundance of jellyfish and low pH in one of six areas in the North Sea, but their conclusions were challenged by other studies (Haddock, 2008; Richardson and Gibbons, 2008). At present, therefore, there are no robust data that support a link between low pH and elevated jellyfish numbers, even though, if jellyfish are more resistant to acidification than crustaceans and fish, this should result in competition release, leading to the prevalence of jellyfish over crustaceans and fish. This speculation, however, needs to be tested.

As noted previously, a number of Medusozoa have symbiotic zooxanthellae and although no experiments have been conducted to examine the relationship between pH and growth or survival of these species, evidence from other cnidarians indicates that pH, per se, has no impact on organismal photosynthesis (Doherty, 2009; Kroeker *et al.,* 2010). Indeed, it has been suggested that non-calcareous, zooxanthellate cnidarians may benefit from an increase in carbon dioxide, as zooxanthellae are considered to be usually carbon-limited (Doherty, 2009).

There is no explicit information about the response of thaliaceans to pH. That said, Chew *et al.* (2015) have noted an increase in the abundance of salps following the operations of the Kapar power plant in Malaysia, which they attributed to the ability of these organisms to tolerate elevated temperatures, reduced particle sizes and a lower pH: all environmental parameters that had changed over the same time period.

3.10.8 Trends and impacts

The impact of temperature increases has a two-fold implication according to the thermal preferences of species. Higher temperatures favour the establishment of tropical species at mid-latitudes, enhancing also indigenous species of warm-water affinity. At high latitudes these warm-water species find environments that are too cold, but are now too warm for the indigenous species. At low latitudes, tropical species are in distress due to too high temperatures.

If the trend of temperature increases continues, or even if temperatures remain stable at current levels, tropical species will continue to have opportunities to become established at mid-latitudes, where their thermal requirements can be met. The favourable abiotic conditions determined by ocean warming may also allow for the development of favourable biotic conditions for warm-water species since their possible competitors

Box 3.10.2 Potential impacts of jellyfish blooms for mariculture

Mariculture sustains nearly 30% of total value of global farmed fish (FAO, 2014), but the development of new marine aquaculture facilities is expected to increase in both coastal and offshore waters. Jellyfish may be of particular concern for marine finfish aquaculture as repeated mortality episodes of farmed fish were related to cnidarian stingers blooms over the last years, with severe economic impacts (Baxter *et al.*, 2011; Rodger *et al.*, 2011). Indeed, jellyfish may enter fish cages either intact or fragmented in parts, being washed against cage nets by currents and water turbulence. Cnidocyst discharge leads to fish tissue envenomation, local inflammatory responses, cell toxicity and histopathology, particularly skin lesions and gill damage (Bosch-Belmar *et al.*, 2016a), followed by secondary bacterial infections (Avendaño-Herrera *et al.*, 2006) and systemic reactions including physiological impairments (Marcos-Lopez, 2016). In a global warming scenario, recent experimental evidence has highlighted the interactive effects of environmental stressors and jellyfish stings (*P. noctiluca*) in the Mediterranean Sea (Bosch-Belmar *et al.*, 2016b). Higher temperatures and hypoxia synergistically increase the vulnerability of caged fish (e.g. *Dicentrarchus labrax*) to jellyfish impairing their health status (increased gill damage) and metabolic performances (increased oxygen consumption rate and critical oxygen pressure) (Figure 3.10.12), associated with relevant economic losses to aquaculture companies.

(i.e. indigenous jellyfish of cold-water affinity) are in distress under the new conditions.

Another possible trend concerns the “multiple causality” that determines jellyfish increases. The feeding opportunities determined by lack of competition and predation by fish, due to overfishing, likely favours all jellyfish species. Furthermore, cold-water species might evolve a tolerance to the higher temperatures after having been exposed to the new climatic conditions. If the genetic resources of these species allow them to express this thermal tolerance, the initial bottleneck caused by the thermal stress might become the prelude to new genetic makeups that allow for the persistence of species under the new conditions, as Boero (1994) has suggested. This is probably what happened to the temperate-water ctenophore *Mnemiopsis leydi* which, after a long period of survival in the Black Sea, invaded the Mediterranean and became established off Israel, where thermal conditions are quite different from those in the Black Sea (Galil *et al.,* 2009b).

Accordingly, these findings suggest that any increase in sea surface temperature and hypoxia in enclosed bays or coastal areas, coupled with large jellyfish blooms, might represent a severe threat increasing global change susceptibility of wild fish populations, too.

Due to the concurrent growth of the mariculture sector and increasing frequency of jellyfish blooms, negative

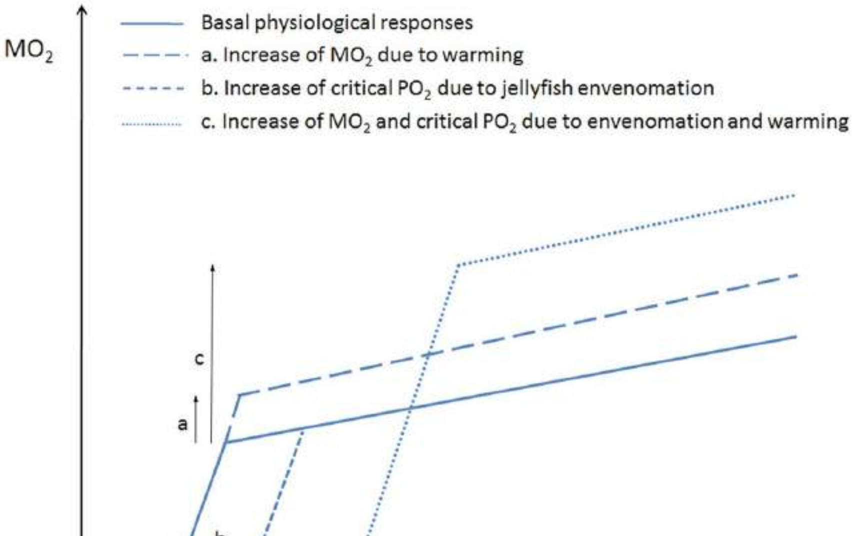

Figure 3.10.12 Theoretical model of fish physiological responses to single or combined jellyfish - ocean warming factors. Dashed lines represent the responses to single factors alone. Briefly, the rise of water temperature is mirrored by an increase of oxygen consumption rate (MO_2), but does not affect the sensitivity of fish to declining environmental oxygen tension (PO_2) (long dashed line); by contrast, jellyfish envenomation causes increased PO^{2}crit, which enhances the sensitivity to hypoxia (short dashed line). The dotted line represents the physiological response to the interaction of both factors and shows the enhanced vulnerability of fish (reproduced from Bosch *et al.,* under a Creative Commons licence).

interactions of jellyfish on farmed fish are expected to become a substantial issue in future years. Paradoxically, the expansion of marine aquaculture facilities (e.g. increasing submerged cage surfaces, pontoons, feed platform barges) determine enhanced substrate availability for jellyfish benthic stages and, in turn, have the potential to further boosting jellyfish blooms (Lo *et al.*, 2008; Purcell *et al.,* 2013).

3.10.9 Consequences

Alien jellyfish populations have implications for the wider ecosystems in which they become established, though the precise impacts and consequences will depend on the role of the species in ecosystem functioning. If blooms are formed, the consequences on human activities are often negative. The distress of jellyfish populations at low and high latitudes might have negative effects too, since these animals are part of ecosystems and play important ecological roles, also with their intermittent blooms (Piraino *et al.*, 2002; Gibbons *et al.,* 2016). Some jellyfish, in fact, might enhance fish presence, especially when occurring at medium densities, by acting as Fish Aggregating Devices (FADs), providing shelter and food to the juveniles of many fish species (Purcell and Arai, 2001). This may even be the case for *Rhopilema*, as recent unpublished observations indicate. The consequences of the presence of gelatinous zooplankton, thus depends on the ecological roles of the species in question.

3.10.10 Conclusions and recommendations

Healthy ecosystems have higher probabilities to withstand stressful situations. Jellyfish blooms have been occurring long into the past, as episodic population explosions. The persistence of such blooms, and their increasingly recorded occurrence, year after year, represents a symptom of stress that suggests a regime shift from fish-dominated to jellyfish-dominated oceans, at intermediate latitudes, and should not be underrated. Global drivers such as overfishing and climate warming, often act synergistically with more local drivers, such as the increasing availability of hard substrates suitable for polyp settlement along coastlines, or the occurrence of coastal upwelling systems (Makabe *et al.* 2014; Benedetti-Cecchi *et al.* 2015).

General recommendations can be made regarding the two primary global drivers of jellyfish blooms, namely global warming and overfishing:

1. fisheries must reduce their impacts, with a shift from industrial to artisanal practices. Many fish species eat jellyfish, and young fish juveniles and larvae (when abundant due to adult abundance), can probably outcompete jellyfish for zooplankton. The combination of more jellyfish predators and less food for jellyfish would therefore mean less jellyfish. Responsible fisheries, thus, are desirable.
2. A reduction of greenhouse gas emissions is a pre-condition to reduce global change and especially ocean warming. Tropical species are probably impacted negatively in the tropics, but are enhanced by increases in temperature at mid-latitudes, where the phenology of indigenous species is altered. Cold-water species are, instead, disadvantaged by the new conditions.

Further recommendations to reduce jellyfish populations need to be designed on case-by-case basis. Gibbons *et al.* (2016) discussed the idea of reducing jellyfish populations with jellyfish fisheries, suggesting care in putting this measure into action. Alien species surely have negative impacts on indigenous communities and should be controlled, but autochthonous species likely have very different roles in the functioning of ecosystems, and their population explosions, every once in a while, might be part of the normal ecological play. Other common-sense measures, such as reducing eutrophication should not be forgotten, though whether it is even possible or practical to reduce the amount of new hard substrata given coastal development and defences, is debatable. That does not mean, however, we should not start thinking of ways to improve environmental quality.

Surely, we must also know more about each gelatinous species and their ecological roles, before we can express judgments about their putative impacts on marine ecosystems. A further recommendation, and one emphasized by many working in the field, is thus to broaden the studies on these creatures, with special observation programmes involving task forces that can spring into action whenever a bloom is recorded, so as to understand the impacts on the rest of the ecosystem. The irregular pulses of gelatinous plankton do not synchronize with scheduled cruises with the usual bureaucratic procedures, and therefore require *ad hoc* policies of continuous observation.

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> *“Marine fishes have been responding to ocean warming in multi-faceted ways, from range shift, changes in community structure, phenology, to reduction in body size. These responses are challenging the conservation of marine fishes and add to other existing pressures from human activities.”*
>
> *“In particular, the increased likelihood of abrupt and unpredictable changes in the productive potential and migratory behaviour of exploited fish stocks may threaten to disrupt cooperative management arrangements.”*
>
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3.11 Impacts and effects of ocean warming on marine fishes

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Summary

- Marine fishes are sensitive to sea water temperature changes because their physiological performance is largely dependent on environmental temperature.
- Fishes that are tropical or polar, and fish in their early life stages are generally most sensitive to ocean warming because they have narrower temperature tolerance ranges.
- Fishes respond to ocean warming by modifying their distributions such that it offers habitats with suitable temperature for them to live. Observation so far suggest fishes have shifted their ranges by 10s to 100s of km as the ocean has warmed.
- Fish communities are altered as their component species shift their distribution under ocean warming, with an increase, outside the tropics, of warmer-water fishes through invasions and a decrease of cold-water species, while warm-water adapted species decreases in abundance in tropical areas as temperature increase. Thus, the tropics are hotspots of ocean warming-driven local extinctions.
- Ocean warming is modifying the seasonality of occurrence of biological events such as spawning and migration. This affects fish because of mismatch in the timing of availability of their prey.
- Maximum body size of fishes may decrease under ocean warming.
- Other non-climate human stressors such as fishing and pollution will interact with climate-induced changes in fish populations, increasing the sensitivity of marine fishes to climate stressors.
- The most direct way of reducing impacts from climate change on fishes is through mitigation of greenhouse gas emission. Simultaneously, climate risk-reduction measures are needed; these include reducing other non-climate human stressors, monitoring of responses of marine fish to a changing ocean, and adapting conservation measures to these responses.

Ocean warming effect	Consequences
Fishes shifting 10s to 100s of km per decade to follow habitat with suitable temperature	Species invasion and local extinction Shift in community structure, with increasing dominance of warmer-water species Disturbance of trophic interactions Shift in fishing grounds of targeted species and may increase bycatch when overlaps of distributions of targeted and non-targeted species increases Reduced effectiveness of conservation (e.g. Marine Protected Area) and fisheries management (e.g. transboundary stock management) measures
Modification of the seasonality of occurrence of biological events (i.e. phenology)	Altered spawning, migration and dispersal pattern, leading to mismatch in prey and predator occurrences and thus trophic interactions
Reduction in maximum body size	Reduced fecundity Altered trophic interactions Decreased fisheries yield
Interactions between ocean warming and other stressors	Exacerbation of the impacts listed in the above

3.11.1 Introduction

There are approximately 15,000 species of marine fishes in the ocean (Froese and Pauly, 2016). They inhabit almost all parts of the ocean from the surface water, to the deep sea, from coral reefs to seamounts (Cheung *et al.,* 2005). They are also important to the wellbeing of human society through contributing to the economy, food security and culture (see Section 4.5). In the 2000s, fish contributed over 90 million tonnes to marine fisheries catches (Pauly and Zeller, 2016), i.e. 85 % of the total marine catch. Moreover, recreational fishing accounted for catching almost 1 million tonnes of fish per year in the 2000s. In addition, marine fish are an essential part of many traditional cultures, e.g. Pacific salmon and herring for First Nations in British Columbia, Canada (Lepofsky and Caldwell, 2013), reef fishes for South Pacific Islanders (Figure 3.11.1) (Zeller *et al.,* 2015).

Figure 3.11.1 Fishing in Port Vila lagoon, Vanuatu. © Louisa Cass / AusAID.

Climate change adds to the multitude of conservation challenges facing marine fishes from human activities, notably overfishing, habitat destruction and pollution (Dulvy *et al.,* 2003; Pitcher and Cheung, 2013; Sadovy de Mitcheson *et al.,* 2013). Ocean properties have been changing because of greenhouse gas emissions from human activities since the beginning of 20th Century (Stocker *et al.,* 2013). Notably, the ocean has been warming up, becoming more acidic, less oxygenated, and having a reduced ice cover in polar areas (Gattuso *et al.,* 2015). Given the current rate of greenhouse gas emissions, these changes are projected to continue (Pörtner *et al.,* 2014). Marine fish, as water-breathing ectotherms, are physiologically and ecologically sensitive to changes in ocean properties. In addition to climate change, currently, over 550 species of marine fishes and invertebrates are listed as threatened (Critically endangered, Endangered, and Vulnerable) in the IUCN Red List. Of these species, the majority (80%) is threatened by “fishing and harvesting of aquatic resources” (IUCN, 2016). The responses of marine fish to ocean warming will add to and likely exacerbate the impacts from other human drivers.

This section aims to summarize the major effects of ocean warming on marine fishes and the implications for their conservation status. The section will focus on ocean warming as a driver of changes and its potential interactions with the carbon dioxide–related drivers such as ocean acidification. Firstly, we summarize the key mechanisms that make marine fishes vulnerable to changes in ocean properties. Secondly, we highlight the main biological and ecological responses of marine fishes to these environmental changes, and the resulting impacts on fish populations and communities. Finally, we discuss the key challenges and opportunities for conservation of marine fishes under climate change.

3.11.2 Mechanisms of climate change effects on marine fishes

The responses of marine fishes to changes in ocean temperature can be predicted from their physiology of thermal tolerance and oxygen capacity. Physiological performance of marine fishes is dependent on the their temperature preferences and tolerance limits (Pörtner and Farrell, 2008). Performance of body functions such as growth and reproduction are optimal within a certain temperature range (Figure 3.11.2). Performance decreases when temperature increases or decreases from the preferred temperature, and when temperature is beyond the temperature tolerance limits of the species, body functions are halted and survival is compromised. As body temperature, in fish, is dependent on environmental temperature, ocean warming affects the basic body functions of fish.

Different fish species and life stages can have different temperature tolerance ranges. Polar species that are adapted to the stable and cold polar environment generally have a narrower thermal window (Figure 3.11.2b). For example, some polar species e.g. Antarctic notothenioid fish have adapted to stable cold polar environments, leading to fewer red blood cells, oxygen binding proteins (Pörtner, 2002), and enzymes that are especially sensitive to temperature. Similarly, tropical species that inhabit warm waters tend to have a narrower thermal window, compared to temperate fishes that live in an environment with large seasonal temperature changes (Pauly, 2010). In addition, larval and spawning fishes have greater temperature sensitivity, rendering the early life stages of fishes more vulnerable to ocean warming.

Understanding marine organisms' thermal tolerances and the geographic pattern of climate change help explain and predict their survival and distribution under changing climate. Optimal foraging theory predicts that fishes tend to be distributed in environments that maximize their growth and reproduction. Thus, as the ocean warms, marine fishes respond, as they do in response to seasonal changes in temperature (Pauly, 2010), i.e. by shifting their distribution to maintain themselves in habitats which lie within their preferred temperature limits. Generally, fish are responsive to temperature changes throughout their range (Sunday *et al.,* 2012).

Temperature may also act indirectly on a fishes' survival and distribution by influencing phenology, dispersal, predation pressure and available food supply. Change in the distribution and abundance of prey and predators affects growth and mortality of other fishes. As temperature affects the rate of egg (Pauly and Pullin, 1988) and larval development (O'Connor *et al.,* 2007), warmer temperatures might also decrease the opportunity for predation at this phase in the life cycle. In addition, as the duration of the larval stage determines the length of time they are subjected to

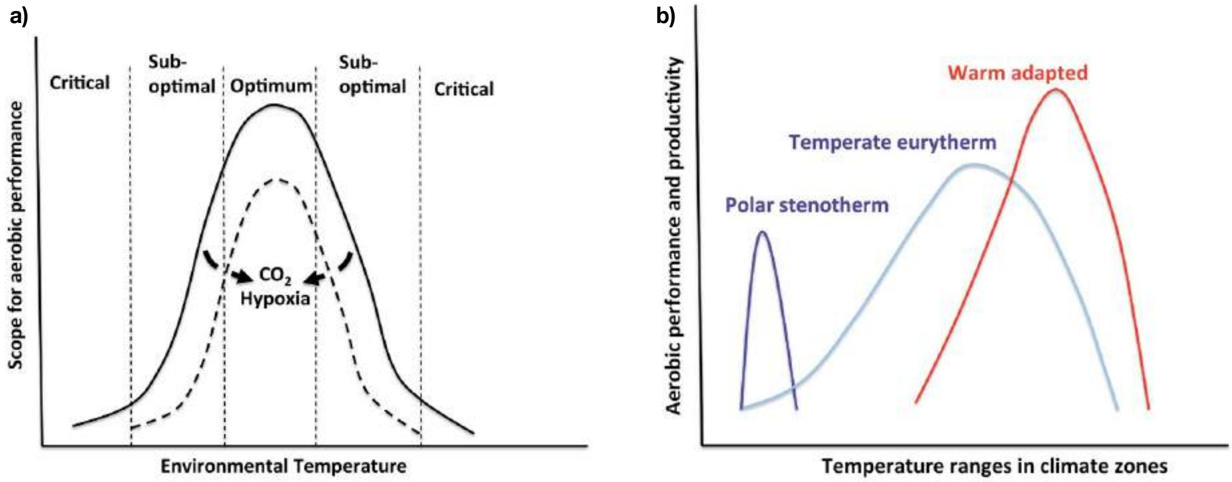

Figure 3.11.2 Relationship between temperature and physiological performance of marine water-breathing ectotherms. (a) Temperature tolerance decreases with multiple environmental stressors, and (b) temperature sensitivity is dependent on the characteristics of the environmental where organisms are adapted to (Pörtner and Knust, 2007).

Figure 3.11.3 Bigeye trevally over healthy reef in Tubbataha National Park, Philippines. © Steve De Neef.

movement by ocean currents, increased temperatures will indirectly affect population connectivity, community structure and regional to global patterns of biodiversity (O'Connor *et al.,* 2007). For example, in tropical reef systems, climate-induced increases in ocean temperature and reduced food supply will severely impact larval fishes (McLeod *et al.,* 2013). In addition, critical habitats of marine fishes, such as coral reefs (Figure 3.11.3), are extremely sensitive to ocean warming, notably through coral bleaching (see Section 3.8).

3.11.3 Observed responses of marine fishes to warming

3.11.3.1 Species range shift

Observations and theory have indicated that marine fishes frequently undergo shifts in distribution in response to changing ocean temperature. Under ocean warming, range shifts are most commonly towards higher latitudes (Perry *et al.,* 2005; Hiddink and Ter Hofstede, 2008; Poloczanska *et al.,* 2013), deeper waters (Dulvy *et al.,* 2008), and in general, following temperature velocity (Pinsky *et al.,* 2013) (Box 3.11.1). Meta-analyses of observed range shift in the last decades have shown that fishes are moving poleward, on average, at rates of 10s of km per decade (Poloczanska *et al.,* 2013) (Figure 3.11.4). Also, analysis of survey data further shows that range shifts for fishes in North American shelf seas in the last few decades are

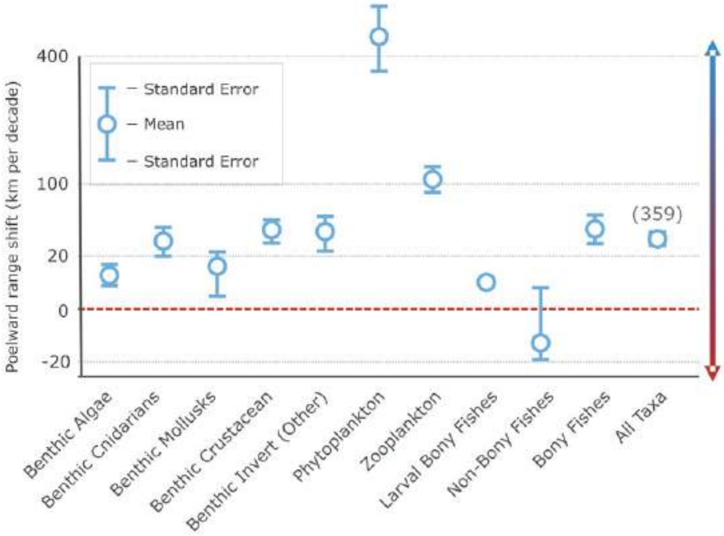

Figure 3.11.4 Meta-analysis of observed range shift for marine species (from Poloczanska *et al.,* 2013).

Box 3.11.1 Multi-facet responses of marine fishes to ocean warming: a case study in the Northeast Atlantic Ocean

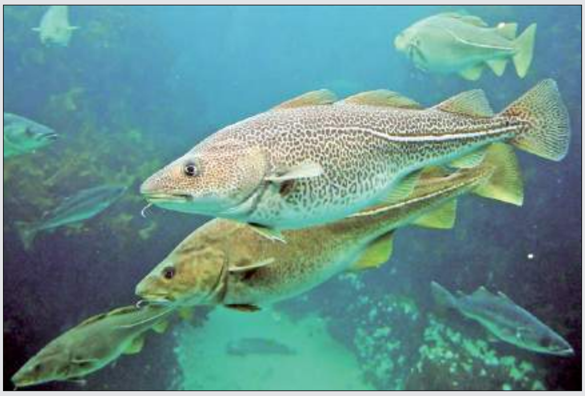

Figure 1 Atlantic Cod. © Joachim Muller.

Marine fishes in the North-east Atlantic Ocean have responded to ocean warming through changes in distributions, phenology and body size. Sea Surface Temperature (SST) in the NE Atlantic has been increasing in recent decades e.g., sea surface temperature in the North Sea and Norwegian Sea increased by 1.31°C and 0.85°C between 1982 and 2006. Amongst the 50 abundant fish species in the waters in the North-east Atlantic, 70% of the species responded to warming in the region by changing distribution and abundance between 1980 and 2008, resulting in increasing changes in species assemblages as temperature increases (Simpson *et al.,* 2011). Simultaneously, the mean temperature of catch (MTC) in the North Sea increased significantly during this period, indicating an increase in dominance of warmer water species in the fisheries catches (Cheung *et al.,* 2013a). For example, based on data since the early 20th Century, distribution of North Sea Atlantic cod (Figure 1) shifted poleward by 3.74°N and to deeper water by 54.2 m per degree Celsius of increase in SST (Engelhard *et al.,* 2014). Also, eight fish species in the North Sea show a decrease in maximum body size that is related to a 1-2°C increase in sea water temperature (Baudron *et al.,* 2014). Specifically, maximum body size of northern haddock stock was found to decrease by 29% between 1975 (average of 1973 – 1977) and 1995 (average of 1993 – 1997) (Baudron *et al.,* 2014). Moreover, increases in sea surface temperature affect the timing and magnitude of growth, recruitment and migration (Jansen and Gislason, 2011). Given continuous warming of the oceans under climate change, the trends described above will continue. For example, using a computer simulation model, 17 fishes in the North Sea are projected to continue to shift poleward at a rate of around 27 km per decade from 1905 to 2050 under a high greenhouse gas emission scenario (Jones *et al.,* 2015). These multi-facet responses of marine fishes to ocean warming may lead to impacts from species to ecosystem levels that are not yet fully understood.

in directions consistent with gradients of temperature changes (Pinsky *et al.,* 2013).

Although the biogeographical responses of fishes to ocean warming are similar, their sensitivity to temperature varies between species. The differences in sensitivity can be due to different mobility, life history stages, biological characteristics and habitats. This may limit the ability of the species to keep pace with ocean warming (Hiddink *et al.,* 2012). Also, fish species with large body size, high swimming ability, large size at settlement and pelagic spawning behaviour are also found to be more successful at colonizing temperate habitats, while habitat and food limitation during juvenile stages may constrain movement (Feary *et al.,* 2014). Genetic bottlenecks can emerge where species exhibit limited dispersal capacity due to a lack of suitable habitat, thereby preventing population connectivity, e.g., lack of gene flow between populations of corkwing wrasse, *Symphodus melops* (Figure 3.11.5), in the North Sea and Portugal (Knutsen *et al.,* 2013). In some cases, geographical and oceanographic features act as barriers to distribution shift, e.g. landmass in semi-enclosed seas such as the Mediterranean Sea (Ben Rais Lasram *et al.,* 2010) or depth in the North Sea for demersal fishes (Rutterford *et al.,* 2015).

Figure 3.11.5 Corkwing wrasse. © Pedro Silva.

3.11.3.2 Shifts in community structure

The composition of fish community will be altered as species shift their distribution under ocean warming. Generally, increase in ocean temperature results in increase in dominance of warmer water species in the fish community (Cheung *et al.,* 2013a; Stuart-Smith *et al.,* 2015). For example, on the European continental shelf, a response to warming has been demonstrated in the abundances of 72% of the 50 most common fish species inhabiting UK waters (Simpson *et al.,* 2011) (Box 3.11.1). These shifts reflect the influx of warmer-water adapted marine species to regions with colder waters that have also been observed elsewhere (Arvedlund and Kavanagh, 2009; Fodrie *et al.,* 2010). Arctic and tropical fishes have been found occupying new habitats as temperature changes. A heat wave event in western Australia was found to alter biodiversity of demersal fish, leading to a tropicalization of community structure (Wernberg *et al.,* 2013; Thomson *et al.,* 2014).

Subtropicalization of European pelagic fish communities has also been observed in the North Sea and Baltic Sea, with shifts from Atlantic herring (Figure 3.11.6a) and European sprat (1960s to 1980s) to Atlantic mackerel, Atlantic horse mackerel, European pilchard (Figure 3.11.6b), and European anchovy (1990s onwards) in response to warming, with sea surface temperature increasing at around 0.02°C yr^{-1} (Montero-Serra *et al.,* 2015), while the fish communities of the Eastern Mediterranean are increasingly dominated by fishes with warm-water affinities (Stergiou and Tsikliras, 2011; Keskin and Pauly, 2014). Global fisheries catch data, since the early 1970s are also increasingly dominated by warmer water species (Cheung *et al.,* 2013a). This is indicated by an increase in the Mean Temperature of Catch (MTC) – an indicator representing the mean temperature preference of species in annual fisheries catches weighted by their catch amount. Therefore, if catches are increasingly dominated by warmer water species, MTC increases as well. The observed changes in MTC from 1970 - 2006 are related to increase in sea surface temperature in the same period (Figure 3.11.7). However, in tropical areas, after the initial reduction in the abundance of subtropical species' catches, scope for further tropicalization of communities became limited (Figure 3.11.7).

Range shifts for fishes and invertebrates are projected to continue in the 21st Century under climate change (Cheung *et al.,* 2009; Jones and Cheung, 2015). Although in temperate climates, local extinctions may be compensated for by local invasions as species move into newly suitable habitat, thereby leading to an overall change in community structure, tropical regions may see declines in species richness as the scope for community tropicalization is reached. For example, projections of distributions for over 800 exploited fishes and invertebrates using multiple species distribution models result in a predicted average poleward latitudinal range shift of 10s to 100s km per decade under a high greenhouse gas emission scenario (Jones and Cheung, 2015). This rate of shift is consistent with observed rates of shift in the 20th Century (Poloczanska *et al.,* 2013). Such predicted distribution shifts resulted in large-scale changes in patterns of species richness through species invasions (occurring in new areas) and local extinctions (disappearing from previously occurring areas) (Figure 3.11.8). Hotspots of high local invasion are common in high latitude regions, while local extinctions are concentrated near the equator. The shifts in fish distributions may result in fish communities that are different from those previously observed (Molinos *et al.,* 2015).

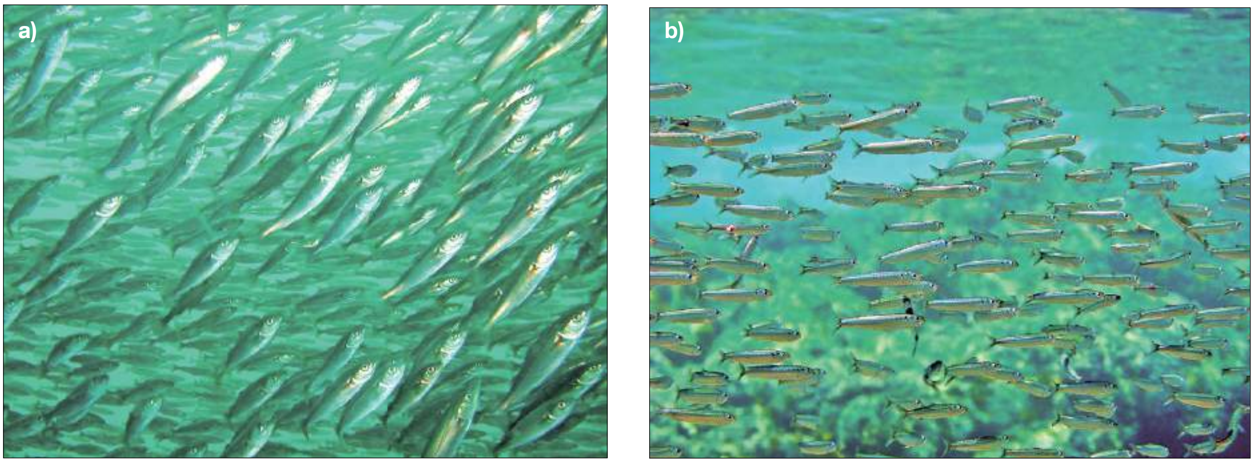

Figure 3.11.6 a) Atlantic herring. © Dirk Schories, b) European pilchard. © Alessandro Duci.

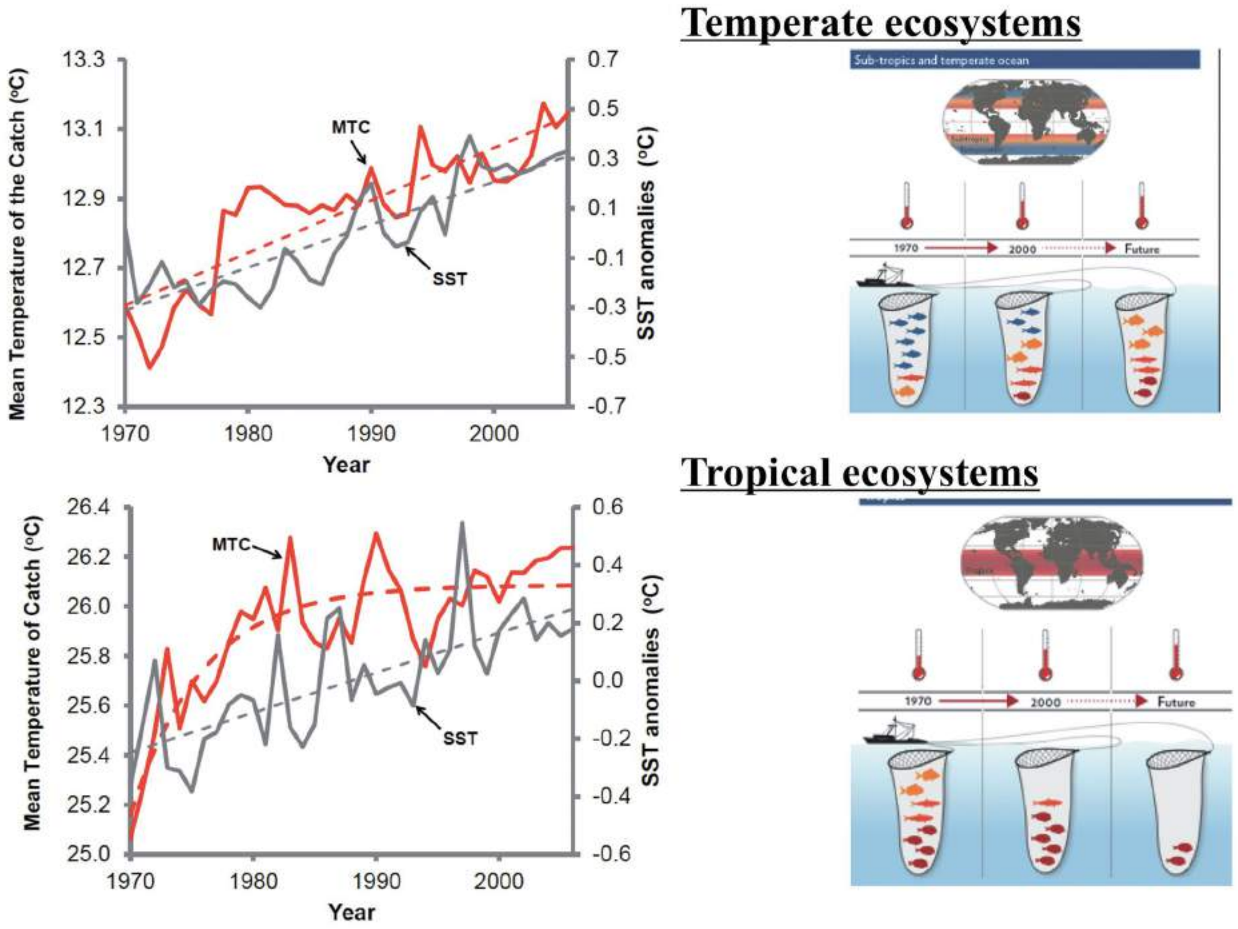

Figure 3.11.7 Average mean temperature of catch (MTC) and sea surface temperature (SST) from (upper) non-tropical and (lower) tropical large marine ecosystems (left panels). The right panels are schematic representation of hypotheses explaining the change in MTC over time (from Cheung *et al.,* 2013a).

Species range shifts can affect trophic interactions and the functioning of marine ecosystems. Species that increase in abundance may increase predation, grazing or competition with existing species. On the other hand, species may lose important food sources when prey species shift away from an ecosystem. For example, the tropicalization of temperate marine ecosystems through poleward range shifts of tropical fish grazers is shown to increase the grazing rate of temperate macroalgae (Vergés *et al.,* 2014). Such trophic impacts resulting from climate-induced range shifts are expected to affect ecosystem structure and dynamics in temperate reefs. Altered interspecific interactions between sympatric coastal fishes were observed in the Mediterranean under warmer conditions, with a cooler-water fish (e.g. rainbow wrasse, *Coris julis*; Figure 3.11.9a) being displaced by a more dominant warmer-water fish (e.g. ornate wrasse, *Thalassoma pavo*; Figure 3.11.9b) (Milazzo *et al.,* 2013). This example supports the theory that there will be 'winners' and 'losers' under climate change, with warm-adapted species outcompeting cold-adapted species in temperate marine ecosystems.

3.11.3.3 Changes in phenology

Climate change modifies phenology (i.e. periodic biological phenomena), of marine fishes so that critical phases remain synchronized with climatic alterations. For example, spawning season for 27 species in the North Sea have been shown to be negatively correlated with the mean sea surface temperature (SST) in the preceding winter (Greve *et al.,* 2005), while earlier spring migrations have also been noted (Sims *et al.,* 2001). Phenological responses are highly taxon- or species-specific, resulting from sensitivity to climatic fluctuations as well as factors such as temperature, light, or food availability (Edwards and Richardson, 2004). A meta-analysis of observed phenological shifts suggested that seasonal events of marine species advanced by an average of 4.4 days per decade during the late 20st Century (Poloczanska *et al.,* 2013). Also, larvae of 17 of the 43 species of fish species in the California Current

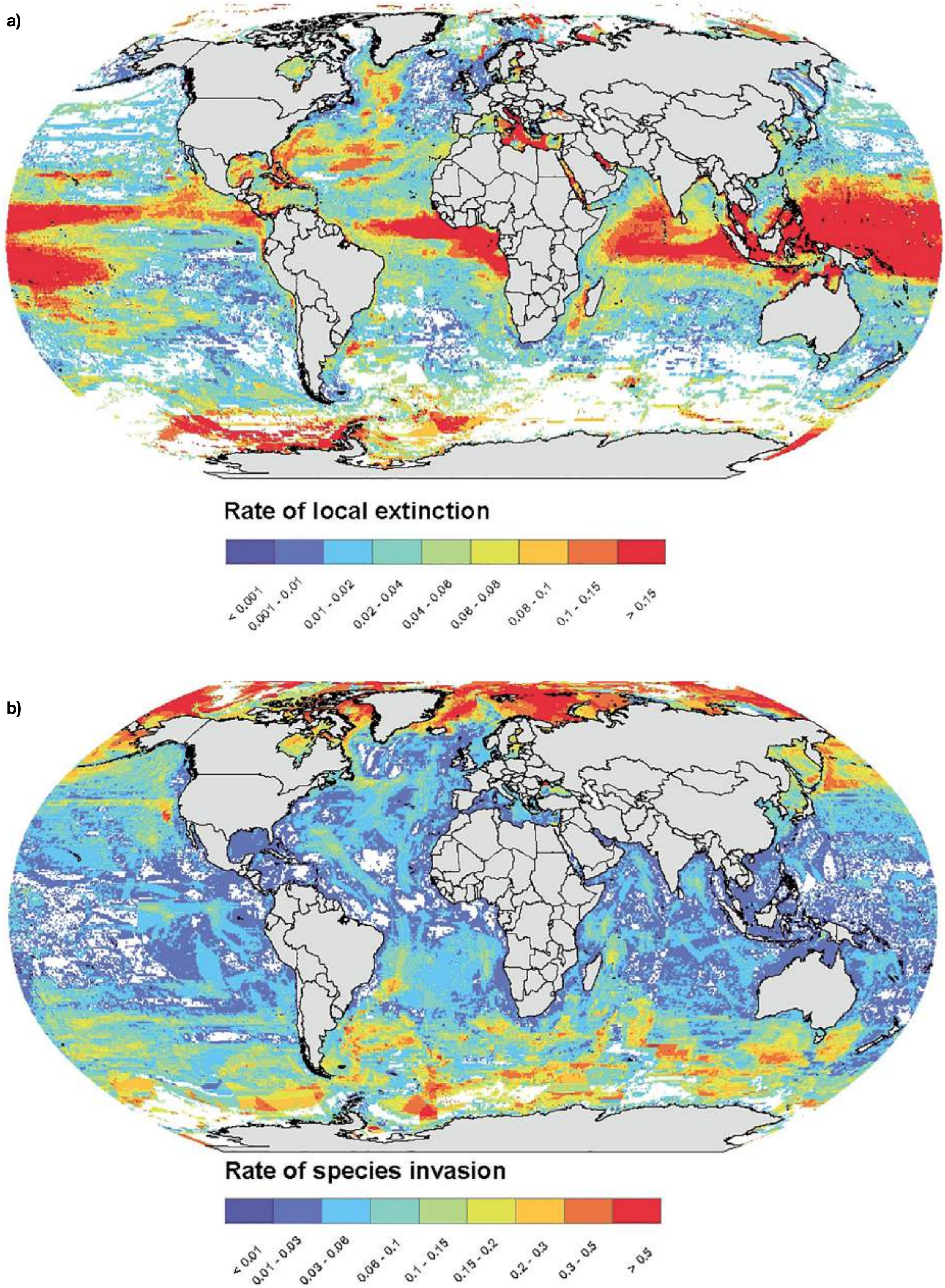

Figure 3.11.8 Projected intensity of (a) local extinction and (b) species invasion between 2000 and 2050 under the RCP 8.5 scenario (from Jones and Cheung, 2015). The unit is expressed as number of species locally extinct or invaded relative to the original species richness.

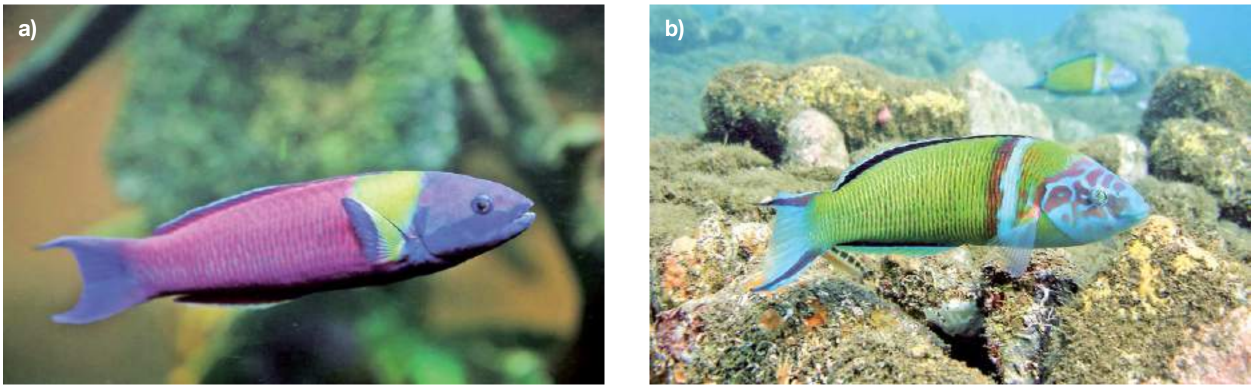

Figure 3.11.9 a) Rainbow wrasse, b) Ornate wrasse. © Gran Canaria Divers

ecosystem occurred earlier in recent decades relative to the last 58 years (Asch, 2015). However, zooplankton, being one of the main food items for these fishes, did not shift their phenology synchronously with most fishes (Asch, 2015). Such a mismatch may affect the availability of food for fishes. Altered phenology and timing of development may also lead to altered dispersal. For species whose offspring develop in the water column, for example, the duration of the larval stage will decrease with warmer temperatures. This determines the length of time larvae are subject to movement by ocean currents and thus affects the habitat that the larvae could reach (O'Connor *et al.,* 2007).

3.11.3.4 Changes in body size

Both theory and empirical observations further support the hypothesis that warming and reduced oxygen will reduce the body size of marine fishes (Pauly, 1998a) and invertebrates, such as squids (Pauly, 1998b). The preferred minimum oxygen tolerance threshold of an organism varies across species, body size, and life stage, and is highest for large organisms. As fish increase in size (weight), mass-specific oxygen demand increases more rapidly than oxygen supply which occurs via the surface of the gills (Pauly, 1998a, b). Thus, while fish reach a maximum body size when oxygen supply is balanced

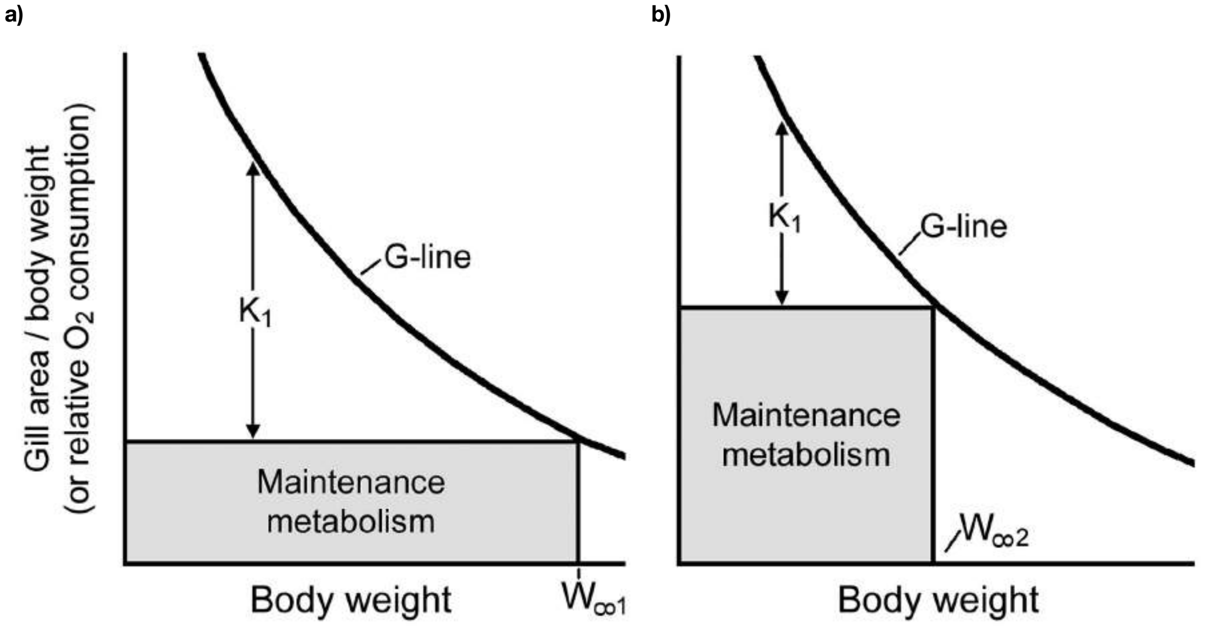

Figure 3.11.10 Diagram illustrating how maintenance metabolism determines asymptotic weight (W∞), given a 'G-line' defined by the growth of the gills relative to body weight, because, at W∞, relative gill area (and hence oxygen supply) is just enough for maintenance metabolism (shaded area); a) Fish exposed to a low level of stress (e.g. relatively low temperature, abundant oxygen, abundant food). b) Fish exposed to a higher level of stress (low dissolved oxygen concentration, high temperature, causing rapid denaturation of body protein, and/or low food density, requiring O_2 to be diverted to foraging, rather than protein synthesis). Note that food conversion efficiency and hence also the 'scope for growth' are directly related to the difference, in these graphs, between the G-line and the level of maintenance metabolism (see Pauly, 1998a,b, 2010).

by oxygen demand (Figure 3.11.10a), maximum body size decreases when temperature increases (Figure 3.11.10b). The decrease in food conversion efficiency that this implies, all else being equal, (Pauly, 2010) decreases the biomass production of fish and invertebrate populations.

Simulation model projections structured around Figure 3.11.10 suggest decreases in the maximum body size of fishes under scenarios of ocean warming and decreasing dissolved oxygen levels. Specifically, the integrated biological responses of over 600 species of marine fishes due to changes in distribution, abundance and body size were examined, based on explicit representations of ecophysiology, dispersal, distribution, and population dynamics (Cheung *et al.,* 2013b). The result was that assemblage-averaged maximum body weight is expected to shrink by 14–24% globally from 2000 to 2050 under a high-emission scenario. The projected magnitude of decrease in body size is consistent with experimental (Forster *et al.,* 2012; Cheung *et al.,* 2013b) and field observations (Baudron *et al.,* 2014) (Box 3.11.1). About half of this shrinkage is due to change in distribution and abundance, the remainder to changes in physiological performance as illustrated in Figure 3.11.10. The tropical and intermediate latitudinal areas will be heavily impacted. Decreases in growth and body size are likely to reduce the biomass production of fish populations, and hence fisheries catches, and potentially alter trophic interactions.

3.11.4 Interactions with other human drivers

The main non-climate anthropogenic stressors will interact with climate-induced changes in fish populations (Planque *et al.,* 2010), increasing the sensitivity of marine fishes to climate stressors. For example, intensive fishing leads to the depletion of large predatory species and the truncated age-structure in targeted populations, with an increased dominance of juveniles and small-bodied, fast-turnover species. Such communities tend to track changes in ocean conditions more closely (Perry *et al.,* 2010). In Tasmania, biological communities in exploited areas have been shown to be more sensitive to ocean changes relative to areas protected from fishing (Bates *et al.,* 2013). One of the most important pathways of pollution impact on marine organisms is also through nutrient enrichment from the discharge of sewage, and agricultural and industrial waste into the ocean, ultimately leading to oxygen depletion (Diaz and Rosenberg, 2008), thereby rendering marine organisms more vulnerable to ocean warming. Globally, 94% of the low oxygen "dead zones" are in areas where temperature is projected to increase by 2°C by the end of the century under the business-as-usual emissions scenario (Altieri and Gedan, 2015). Habitat degradation from other human stressors may exacerbate climate change impacts through modification of critical habitats that some fishes depend on. Depletion or local extinction of sub-populations may reduce standing genetic diversity that is important for marine fishes to adapt to the changing climate.

3.11.5 Scope for genetic adaptation

The capacity for species to acclimate or adapt to ocean warming is still uncertain, but studies have increasingly explored the feasibility and implications of genetic and phenotypic responses (Munday *et al.,* 2013). While evolutionary adaptation to ocean warming has been shown to be possible in principle (Muñoz *et al.,* 2014), evolutionary trade-offs and temporal variability make it difficult to assess the degree to which adaptation can be deemed 'successful' (Sunday *et al.,* 2014). For instance, rapid transgenerational acclimation to increases in water temperature has been exhibited by reef fish (e.g. the spiny chromis, *Acanthochromis polyacanthus*; Figure 3.11.11) (Donelson *et al.,* 2011). Although this may suggest the capacity for species to mitigate climatic stressors through epigenetics, such adaptation might come at the cost of other attributes or may be inhibited under multiple stressors (Donelson *et al.,* 2011). In particular, some forms of genetic adaptation may in fact be maladaptive (Merilä and Hendry, 2014). Also, the very existence of temperature-mediated seasonal migration in fish suggests that shifts in distributions are more likely than changes in the thermal adaptation of fish.

Figure 3.11.11 Spiny chromis. © Nikita.

3.11.6 Implications for conservation of marine fishes

Effective conservation of fish populations and ecosystems under climate change increases the resilience of ecosystems and the adaptive capacity of management systems, for example by reducing other human perturbations. While contemporary global extinction of marine fishes primarily attributable to climate change does not seem to have occurred yet, mitigating the impacts of climate change on marine fishes should be attempted, notably by reducing stresses from overfishing, habitat degradation, pollution runoff, land-use transformation, and invasive species. As such, effective implementation of ecosystem-based management that considers a much wider range of environmental and human stressors is important to conservation of marine fishes.

The reduced predictability of marine ecosystems due to climate change will make it more difficult to provide accurate assessments of the current and future status of marine fishes. Also, changing baseline oceanographic and ecological conditions may affect the effectiveness of existing conservation and management measures such as marine protected areas (Jones *et al.,* 2013). The application of adaptive management approach (Walters and Martell, 2004) through the incorporation of monitoring programmes that are designed for a changing ocean and the subsequent usage of the data to improve monitoring are thus important (Dunn *et al.,* 2016). Monitoring will include data for indicators at the pressure, state, and response levels, thereby promoting fast decision responses to changing and uncertain conditions and allowing a suite of possible responses to be maintained (Anthony *et al.,* 2015).

Marine protected areas (MPAs), for example, are a major tool to conserve marine biodiversity, and have been shown to enhance population resilience to climate-driven disturbance (Micheli *et al.,* 2012). This applies especially to large and very large MPAs, of which several have lately been declared (Boonzaier and Pauly, 2016). However, climate change-induced changes in species' distribution shifts may lead to both emigration and immigration of species from or into an MPA. This will alter the specific species assemblage being conserved, potentially losing species of conservation value and reducing the efficacy of the MPA. There is therefore a need to increase the robustness and enhance the resilience of protected areas themselves to climate change. For example, by assessing the degree of future environmental change within proposed protected areas, conservation planning that includes areas where species' range may shift to could help protect against biodiversity loss (Levy and Ban, 2012). Implementing networks of MPAs may also increase the likelihood of effectively conserving species following climate change-induced range shifts by ensuring that future potential habitats for fishes are protected (McLeod *et al.,* 2009; Gaines *et al.,* 2010).

Long-term observation data and monitoring programmes, essential to detection and attribution of the responses of marine biodiversity to climate change and ocean acidification, are limited globally. It is suggested that time-series that span at least multiple decades are needed to detect long-term trends in the ocean from natural variability (e.g. for net primary production (Henson *et al.,* 2010)). Also, analysis explicitly linking biological responses to environmental change between levels of organization (from individual to ecosystem) is also needed to provide integrated multi-scale understanding of climate change effects on marine biodiversity. The role of evolutionary and phenotypic responses to determining climate change impacts on marine biodiversity is still uncertain. The interaction of multiple anthropogenic threats, and predator-prey interactions further contribute uncertainty to predicting the likely impact of climate change on specific populations and species. For example, both fisheries and warming waters are thought to have caused a decline of sandeels (Figure 3.11.12; mainly *Ammodytes marinus*) and, in consequence, decline a breeding success of black-legged kittiwakes and common guillemots (MacDonald *et al.,* 2015) (Figures 3.11.13a,b). Disentangling the impact of these threats and projecting possible scenarios of change into the future therefore remains a challenge, despite recent advances in this area.

Figure 3.11.12 Sandeels. © Thomas Warner, DTU Aqua.

Figure 3.11.13 a) Common guillemots and razorbills, b) Black-legged kittiwakes. © John M Baxter.

Climate change may also affect the effectiveness of conservation and management, thus increasing the risk to marine fishes. In particular, the increased likelihood of abrupt and unpredictable changes in the productive potential and migratory behaviour of exploited fish stocks may threaten to disrupt cooperative management arrangements. For example, the distribution of Atlantic mackerel (*Scomber scombrus*) in the North-east Atlantic Ocean recently shifted northward, probably as a result of changing ocean conditions. The Atlantic mackerel fisheries were believed to be 'sustainable', and they were certified by the Marine Stewardship Council. However, following the species' northward shift to waters around Iceland and the Faroe Islands, these countries unilaterally increased their quota, leading to an international dispute over quota allocations with countries disputing each other's access to the straddling mackerel stock. This results in destabilization of management of the mackerel fisheries and the suspension of its Marine Stewardship Council certification (Sumaila *et al.,* 2011; Miller *et al.,* 2013). Such disputes are projected to increase as ocean warming increases with climate change.

3.11.7 Conclusions and recommendations

Marine fishes have been responding to ocean warming in multi-faceted ways, from range shift, changes in community structure, phenology, to reduction in body size. These responses are challenging the conservation of marine fishes and add to other existing pressures from human activities. The most direct way of reducing impacts from climate change is through mitigation of greenhouse gas emission. Limiting the degree of warming to less than 1.5°C, as noted as a goal in the Paris Agreement, would reduce the level of expected climate change impacts on marine fish in the 21st Century. However, climate change will continue in the next few decades, we need to reduce the resulting conservation risk on marine fish. Climate risk-reduction measures include reducing other non-climate human stressors, continuing monitoring of responses of marine fish to the changing oceans, and allowing existing conservation measures to be adaptable to these responses.

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3.11.8 References

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> *"There remains high uncertainty of how individual populations will respond to long-term rising average ocean temperatures and synergistic effects of other climate change outcomes. Oceanic tunas and billfishes may adopt new cooler subtropical areas for spawning, either replacing or in addition to existing tropical spawning sites. They may change their migration phenology, including altering the timing of spawning and truncating the spawning season."*
>
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3.12 Imapcts and effects of ocean warming on pelagic tunas

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Summary

- Many marine species are undergoing rapid shifts in geospatial and depth distributions and changes in phenology in response to ocean warming and other climate change outcomes.
- Predictions of responses of pelagic (open ocean) tunas and billfishes to long-term rising average global subsurface and sea surface temperatures have been based on evidence from model simulations and observations of responses to inter-annual and decadal cyclical climate oscillations. Simulations have accounted for potential interacting effects of ocean warming with changes in dissolved O_2 concentrations, ocean circulation patterns, ocean pH, pelagic food web structure and processes, and other climate change outcomes.
- There is high uncertainty of how individual populations will respond to rising ocean temperatures and synergistic effects of other climate change outcomes. Oceanic tunas and billfishes may adopt new cooler subtropical areas for spawning, either replacing or in addition to existing tropical spawning sites. They may alter their migration phenology, including changing the timing of spawning and truncating the spawning season. These changes may alter distributions and survival rates of larvae and young age classes, reducing recruitment and biomass in existing spawning grounds, but increasing recruitment and biomass at new spawning grounds. In order to maintain species- and age class-specific preferred habitat conditions, including optimal temperature ranges, populations may alter their foraging distributions to higher latitudes and to different longitudes, and alter their vertical depth distributions.
- Long-term trends in absolute abundance in response to ocean warming will vary by individual population. Population-specific responses will be determined by whether new spawning sites emerge, how survival rates of larvae from existing and new spawning locations change, where suitable foraging habitat occurs, the local abundance of forage species at foraging areas, and how changes in distribution affect catchability and fishing mortality rates.
- Selection for phenotypes tolerant of higher ocean temperatures at spawning and foraging habitats could occur for some populations. Warmer water temperatures, however, might increase susceptibility to overheating, reducing spawning success and recruitment. This might also reduce the likelihood of establishing new spawning and foraging areas meeting all optimal habitat conditions.
- Changes in horizontal and vertical distributions would redistribute benefits derived from tuna fisheries due to changes in the locations of fishing grounds and due to species- and stock-specific changes in catchability by surface and subsurface fishing gears.

Ocean warming effect	Consequences
Some populations may experience a range shift, moving to higher latitudes and different longitudes where they find suitable water temperatures and conditions that meet their other habitat requirements (e.g. sufficient prey, adequate dissolved O_2 levels)	Changes the availability of market species to fisheries in that overlap with the new distributions
Some populations may occupy deeper depths where they find suitable temperatures and that meet other habitat requirements (adequate O_2 concentration, ability to visually detect prey)	Reduces catchability by surface fisheries, and increases catchability by deeper fisherie
For some populations, new spawning locations may emerge in the subtropics and the timing of spawning might change	Populations that establish new spawning sites may have higher resiliency to ocean warming and other climate change outcomes Alters the distribution of young age classes which in turn would alter recruitment due to possible changes in local abundance of prey for the young tunas as well as of their predators Alters the timing of migration between foraging and spawning grounds, which would affect the availability to different fisheries
Example: Pacific Ocean skipjack tuna may shift its distribution eastward and to higher latitudes, and experience a long-term reduction in absolute biomass	Purse seine, pole-and-line and other surface fisheries in the eastern Pacific and western and central Pacific will have increased and decreased skipjack catch rates, respectively Broad changes to pelagic communities may result from the reduction in absolute biomass and range shift
Example: south Pacific Ocean albacore may shift its range south and west, a new spawning site may emerge, and total biomass may increase	Pelagic longline and other fisheries in the current range will experience reduced catch rates, while those overlapping with the new distribution will experienced higher catch rates Broad changes to pelagic communities may result from the increase in absolute biomass and range shift

3.12.1 Introduction

Many marine species have been observed to have undergone rapid shifts in distributions to higher latitudes, deeper depths or both, as well as changes in phenology (e.g. timing of migrations and spawning) modelled or inferred to be a response to increases in global average ocean temperatures (e.g. Edwards and Richardson, 2004; Perry *et al.*, 2005; Dufour *et al.*, 2010; Last *et al.*, 2011; Poloczanska *et al.*, 2013), which are projected to warm at a faster rate in the future (IPCC, 2013). Tuna resources supply the fourth most valuable globally traded fishery products and provide substantial economic revenue, employment and food security to fishing and coastal states (Gillett, 2009; Bell *et al.*, 2011; FAO, 2014). There is increasing concern over projected effects of ocean warming and other outcomes of climate change on pelagic (oceanic) ecosystems, the recruitment, biomass, distributions, and resistance and resilience to other stressors of pelagic tunas and billfishes, and concomitant effects on benefits derived from tuna fisheries (Lehodey *et al.*, 2011; Bell *et al.*, 2013a; Hobday *et al.*, 2015). This section reviews the likely effects of ocean warming on principal market species of tunas for globally traded products. First, we describe the principal market tunas, their ecology and socio-economic importance. We review the broad community- and ecosystem-level effects of selective fishery removals of pelagic apex predators, population-level responses to declining abundance, and stock status and IUCN species conservation status of the seven principal market tunas. We also review how stressors from fisheries affect tunas' resistance and resilience to ocean warming and other climate change outcomes (Brander, 2010). We conclude by describing the degree of certainty of predicted responses of market tunas to ocean warming and other climate change outcomes and identifying research priorities.

3.12.1.1 Ecological significance of tuna and tuna-like species and billfishes

The term 'tuna and tuna-like species' refers to species of the suborder Scombroidei, which is composed of the 'true' tunas and other tuna-like species (Collette *et al.*, 2001, 2006; Orrell *et al.*, 2006). There are 15 genera with 51 species currently recognized in the Scombridae (Collette *et al.*, 2001). There are seven principal market species of tunas for globally traded products: albacore (*Thunnus alalunga*), Atlantic bluefin (*T. thynnus*), bigeye (*T. obesus*), Pacific bluefin (*T. orientalis*), skipjack (*Katsuwonus pelamis*), southern bluefin (*T. maccoyii*) and yellowfin (*T. albacares*) (Majkowski, 2005). Billfishes (suborder Xiphioidei) contain four species of marlins in three genera (*Makaira, Istiompax,* and *Kajikia*), the sailfish (*Istiophorus platypterus*), and four species of spearfishes (*Tetrapturus*) in the Istiophoridae plus the swordfish (*Xiphias gladius*) in the family Xiphiidae (Collette *et al.*, 2006).The seven species of market tunas and billfishes are all pelagic. Other tunas and some tuna-like species are primarily neritic, meaning that they are found in waters primarily over continental shelves (Majkowski, 2005, 2007).

Large tunas, other Scombroidei and billfishes are at the top of the pelagic foodweb and contribute to pelagic ecosystem structure, functioning and stability (discussed in more detail in para. 3.12.1.3) (Cox *et al.*, 2002; Kitchell *et al.*, 2002; Hinke *et al.*, 2004; Ward and Myers, 2005; Polovina *et al.*, 2009; Gilman *et al.*, 2012; Polovina and Woodworth-Jefcoats, 2013; Hobday *et al.*, 2015). Market tunas are some of the largest and fastest marine fishes. They have extremely efficient metabolic systems, including a circulatory system that permits them to retain or disperse heat to achieve optimal performance, as well as tolerate a broad range of water temperatures, enabling these highly migratory species to make use of a range of oceanic habitats (Majkowski, 2005; Trenkel *et al.*, 2014). As they get larger, tunas produce more heat, enabling some species to inhabit higher latitudes and deeper waters. Tunas have strong schooling behaviour and often associate with floating objects and large marine organisms. They are highly fecund and mature at a relatively young age (Majkowski, 2005).

Skipjack and yellowfin tunas are largely tropical in distribution. Albacore and bluefin occur in temperate waters. Bigeye tuna are tropical in distribution but feed in cooler waters by feeding deeper than other tropical tunas (Collette *et al.*, 2001; Majkowski, 2007). All of the principal market tunas spawn in warm tropical waters. The three bluefin tuna species spawn in limited areas, such as Pacific bluefin tuna, which spawn in an area off Taiwan, and Atlantic bluefin which spawn in the Gulf of Mexico and western Mediterranean (Muhling *et al.*, 2011). The bluefins also have relatively short spawning periods of 1-2 months (Collette *et al.*, 2011; Muhling *et al.*, 2011). Bigeye, yellowfin, skipjack and albacore tunas, on the other hand, have extensive spawning grounds in tropical waters and long spawning seasons relative to bluefin species. Bluefin and albacore tunas make seasonal migrations between foraging grounds at higher latitudes and spawning grounds in tropical waters (Nishikawa *et al.*, 1985; Schaefer, 2001; Muhling *et al.*, 2011; Lehodey *et al.*, 2015).

3.12.1.2 Socio-economic significance

Tuna and tuna-like species have been an important food source since ancient times, and are target species of fisheries worldwide (Majkowski, 2007; Miyake *et al.*, 2010). In the 19th Century, most tuna fisheries were coastal, conducted by locally-based fleets (Majkowski, 2005, 2007). Industrial tuna fisheries began in the 1940s. Over the next few decades, fishing grounds quickly expanded as did the number of countries with large-scale coastal and distant-water tuna fleets. Demand for both canned and fresh tuna has increased rapidly, with reported landings of principal market tunas increasing from about 700,000 t in 1960 to almost 4.8 million t in 2014 (Figure 3.12.1) (SPC, 2015).

Principal market tunas and several tuna-like species are used for globally traded canned, fresh and frozen products (Figures 3.12.2, 3.12.3). The reported landings of skipjack, yellowfin, bigeye and albacore tunas is about 66% of all landed tuna and tuna-like species (FAO, 2015b). Of the principal market tunas, the three bluefin species each make up less than 1% of total global reported landings by weight (FAO, 2015b). About 82% of world tuna is consumed as canned product, and 18% as fresh product (including as *sashimi*) (Miyake, 2008). Japan consumes an estimated 78% of the fresh tuna (Miyake, 2008). By 2010, purse seine fisheries accounted for 66.5% of global reported landings, followed by longline (12.4%), pole-and-line (7.9%), troll (1.6%) and other gears (11.6%, e.g. drift gillnet, handline, traps) (FAO, 2015a).

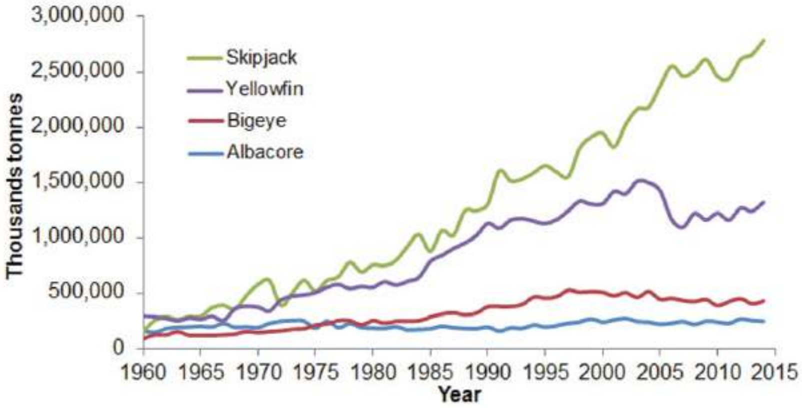

Figure 3.12.1 Global reported landings of albacore, bigeye, skipjack and yellowfin tunas, 1960-2014 (SPC, 2015).

Tuna is the fourth most valuable globally traded fishery product, accounting for ca. 8% of the $129 billion value of internationally traded fishery products (FAO, 2014). Since 2006, over half of principal market tunas have come from the western and central Pacific Ocean (SPC, 2015). Several Pacific Island Countries and territories obtain a large proportion of their gross domestic product from revenue from tuna fisheries, including fees from licensing and from granting access to foreign purse seine and longline tuna fisheries to fish in their exclusive economic zones, representing as high as 63% of total government revenue (Kiribati) (Aqorau, 2009; Gillett, 2009; Bell *et al.*, 2015; FFA, 2015). Capture and processing sectors generate additional revenue and substantial employment in the Pacific islands region (Gillett, 2009; Bell *et al.*, 2015; FFA, 2015). In 2014 the Pacific Islands Forum Fisheries Agency members (15 Pacific small islands developing states, Australia and New Zealand) obtained an estimated US$ 556 million of their combined gross domestic product from the tuna fisheries catch sector, and employed over 22,000 people in processing and various other tuna-sector related positions (FFA, 2015). Some locally-based tuna fisheries supply largely low-value fishes (smaller tunas, incidental tuna-like species) to local markets in Pacific Island Countries and territories, contributing to local food security and tourism industries (Gillett, 2009; Bell *et al.*, 2015).

Figure 3.12.2 Offloading yellowfin tuna from a Taiwanese-flagged longline vessel based in the Republic of Palau, to be exported to Japan for the sashimi market. © E. Gilman.

3.12.1.3 Trends and impacts

Of the 23 stocks of the seven principal market tuna species, nine are over-exploited. Over-exploited stocks are either over-fished (biomass is below a level estimated to produce maximum sustainable yields [MSY] or similar threshold), or over-fishing is occurring (the fishing mortality rate exceeds an MSY-based or similar reference point, indicating that the stock is not rebuilding its biomass), or both (ISSF, 2016). Most tuna stocks are under or fully exploited, dominated by skipjack, albacore and yellowfin tunas.

Of 61 Scombroidei species assessed against the IUCN Red List criteria, 13% were listed as Threatened and 7% as Near Threatened (Collette *et al.*, 2011, 2014). Pacific bluefin, southern bluefin, Atlantic bluefin, and bigeye tuna were four of the Scombroidei categorized as Threatened. The characteristics that these Threatened tunas have in common are long generational lengths, longer lived and later maturity, which when combined, results in longer time to recover from population declines (Collette *et al.*, 2011). These Threatened tuna species also have higher economic values per unit of weight relative to the other market tunas (Miyake *et al.*, 2010).

Figure 3.12.3 Handline caught bigeye and yellowfin Philippines. © Eleanor Pertridge Marine Photobank.

Except for bluefin species, which have relatively restricted spawning grounds and short spawning periods, other market tunas likely have low risks of extirpation (permanent loss of a population, local extinction) from fishery removals. This is because, for these highly fecund broadcast spawning marine fishes, there is no relationship between recruits and the abundance, biomass and egg production by adult age classes, and only at extremely low population sizes is egg production likely to be a limiting factor for recruitment (Myers *et al.*, 1999; Essington, 2010). When the biomass of a market tuna falls below the level that is estimated to produce MSY for a sufficiently long period, this could trigger decreases in supply, and increases in both value and demand, which in turn would create a larger incentive to increase fishing effort (Cinner *et al.*, 2011). Thus, market forces may drive the biomass of an over-exploited stock to a critical level if the governance system is ineffective (Gilman *et al.*, 2014a).

Some fisheries, including pelagic longline, purse seine and drift gillnet fisheries that target relatively fecund species with r-selected life history characteristics like tunas can have large impacts on incidentally caught species with K-selected life-history strategies (i.e. low fecundity, slow growth, etc.), including seabirds, sea turtles, marine mammals, elasmobranchs (sharks and rays) and some bony fishes (Hall *et al.,* 2000; Stevens *et al.,* 2000; Gilman, 2011; Croll *et al.*, 2016). There has been substantial progress in identifying effective and economically viable mitigation methods for some of these bycatch problems. However, there has been limited uptake in most fisheries in part due to management deficiencies (Gilman *et al.*, 2014b). Responses of these marine predator populations to ocean warming and other climate change outcomes are additional compounding stressors (e.g. Willis-Norton *et al.*, 2015).

Reductions in populations of scombrids and billfishes may also cause broad protracted or permanent changes to pelagic communities and ecosystems (Myers *et al.*, 1999; Essington, 2010). There is increasing understanding of these broad effects from selective fishery removals of pelagic apex predators, largely from species- and more recently size-based ecosystem trophic interaction models, and some empirical studies (Cox *et al.*, 2002; Kitchell *et al.*, 2002; Hinke *et al.*, 2004; Ward and Myers, 2005; Polovina *et al.*, 2009; Gilman *et al.*, 2012; Polovina and Woodworth-Jefcoats, 2013). Broad effects of tuna fisheries that remove large Scombroidei, which are the top of the pelagic foodweb (e.g. Collette *et al.*, 2011), include, for example, altered pelagic trophic structure and processes, where the selective removal of older age classes of a subset of species of a pelagic ecosystem apex predator guild could have cascading effects down the pelagic ecosystem food web. For example, pelagic longline selective removal of apex predators has resulted in a top-down trophic effect by releasing pressure and increasing abundance of mid-trophic level species, altering the ecosystem size structure with a decline in abundance of large-sized species of fish and increase in abundance of smaller-sized species, and possibly altering the length frequency distribution of populations subject to fishing mortality (Cox *et al.*, 2002; Kitchell *et al.*, 2002; Hinke *et al.*, 2004; Ward and Myers, 2005; Polovina *et al.*, 2009; Gilman *et al.*, 2012; Polovina and Woodworth-Jefcoats, 2013).

However, in systems with high diversity and ecological redundancy of top predators, when fishing mortality reduces a pelagic top predator species' biomass, other marine predators, including sympatric competitors that are less susceptible to capture in tuna fisheries, may functionally replace them, so that trophic cascades do not occur, with small effect on ecosystem regulation (Cox *et al.,* 2002; Kitchell *et al.,* 2002; Hinke *et al.,* 2004; Ward and Myers, 2005; Young *et al.*, 2009; Griffiths *et al.*, 2010). Instead of being controlled by top-down processes, these pelagic systems may be 'wasp-waist' systems, where high biomass mid-trophic level organisms (micronekton) exert the greatest influence on the system due to their importance as both prey (including by tunas) and predators (Olson and Watters, 2003; Griffiths *et al.*, 2010).

The selective removal of large individuals could be a driver favouring genotypes for maturation at an earlier age, smaller-size and slower-growth, potentially altering the size structure and evolutionary characteristics of affected populations (Stevens *et al.*, 2000; Ward and Myers, 2005; Zhou *et al.,* 2010).

Because tunas and possibly other pelagic apex predators drive baitfish to the surface, reducing the abundance of tunas and other subsurface predators indirectly reduces the availability of prey to seabirds (Au and Pitman, 1986; Ballance *et al.*, 1997).

As their population abundance declines, the distributions of tuna populations are predicted to respond by contracting towards the centre of their ranges, where they would maintain a stable density (Pitcher, 1995). There also could be hyperstability of relative abundance at aggregating features such as at shallow seamounts and at artificial fish aggregating devices (Gulland, 1964; Pitcher, 1995, Fonteneau *et al.*, 1999; Gaertner and Dreyfus-Leon, 2004; Morato *et al.*, 2010; Gilman *et al.*, 2012). While possible, to date, there has been no direct evidence of this occurring for tunas. For example, for western and central Pacific yellowfin tuna, greater reductions in local abundance have been observed in the tropics, the core area for this stock, where most catch and effort occurs, than at higher latitudes, the periphery of the stock's distribution (Davies *et al.*, 2014).

3.12.2 Effects and responses to ocean warming and other stressors from climate change outcomes

Several outcomes of human-induced changes to the Earth's climate resulting from modifications in the atmosphere's composition and alterations to land surfaces are likely to affect market tunas and other pelagic fishes. The atmosphere's composition is altered, for example, from the production of greenhouse gases and aerosols through the combustion of fossil fuels, biomass burning and deforestation. Alterations to the Earth's land surfaces, such as through deforestation, damming rivers, urbanization and soot covering snow alter climate, for example, by altering the surface's albedo, changing the amount of dust blown from the surface to the atmosphere, and altering the amount of water that evaporates from leaves and the soil. Human-induced climate changes include decadal and longer-term trends in ocean surface and subsurface temperature, dissolved CO_2 and O_2 concentrations, pH, ocean circulation patterns, vertical mixing, eddies, and indirect effects such as from changes in functionally linked ecosystems (Brander, 2010; Le Borgne *et al.*, 2011; Lehodey *et al.*, 2011). These outcomes of changes in climate may affect the survival of tuna larvae and subsequent recruitment and biomass, the productivity and survival of organisms in lower trophic levels that are part of tunas' food webs, larval dispersal, migration patterns, distribution, and resistance and resilience to other stressors such as fishing mortality (Brander, 2010; Le Borgne *et al.*, 2011; Lehodey *et al.*, 2011).

3.12.2.1 Ocean temperature and Scombroidei preferred habitat

Ocean surface and subsurface temperatures strongly affect the distributions and local abundance of principal market tunas and other Scombroidei. Pelagic apex predators, and in some cases sizes and sexes within species, have different pelagic habitat preferences for foraging and breeding (Hyrenbach *et al.*, 2000, 2006; Polovina *et al.*, 2004; Bailey and Thompson, 2010; Muhling *et al.*, 2011; Mitchell *et al.*, 2014; Vandeperre *et al.*, 2014). Various environmental parameters have been used to define these static and dynamic pelagic habitats. Sea surface temperature (SST), one of several dynamic environmental variables frequently used to standardize catch rates, has been observed to significantly explain species- and sex-specific catch rates of pelagic species (see review by Gilman and Hall, 2015). Individual pelagic predators, including tuna species, have disparate temperature preferences and tolerances (e.g. Lehodey *et al.*, 2011; Muhling *et al.*, 2011; Brodziak and Walsh, 2013). Larval and juvenile tunas have a narrower range of water temperatures and other environmental variables in which they can live than adults, while optimal temperatures are narrowest and warmest for spawning tunas (Lehodey *et al.*, 2011, 2015; Bromhead *et al.*, 2015).

Box 3.12.1 Population-specific predicted responses of tunas to ocean warming – three examples

As conditions become more El Niño-like, including rising ocean temperatures, in the tropical Pacific, skipjack tuna may shift its distribution eastward and to higher latitudes, and experience a reduction in absolute biomass. Subtropical south Pacific albacore may shift its range south and west, a new spawning site may emerge, and total biomass may increase. Interacting effects of climate change-caused ocean warming and eddies may disrupt successful spawning of western Atlantic bluefin, resulting in a dramatic decline in abundance and possible extirpation.

3.12.2.2 Using responses to ENSO phases to predict responses to ocean warming

Evidence of the effect of natural climate variability on tunas provides one basis for predicting responses to ocean warming from anthropogenic-caused climate change. The distribution, recruitment and biomass of tropical and temperate tunas have been observed to respond to variability resulting from natural large scale climate cycles such as inter-annual El Niño-Southern Oscillation (ENSO) (see Chapter 1 and Section 4.1) phases and longer-scale Pacific Decadal Oscillation (PDO) phases (Lehodey, 2000; Lehodey *et al.*, 1997, 2006). In the western and central Pacific Ocean, ENSO phases are associated with large scale east–west shifts in the Warm Pool and the highly productive convergence zone between the Warm Pool and 'cold tongue', altering upwelling intensity and the depth of the thermocline in different regions of the Pacific. This variability in the spatial and temporal occurrence of areas of high ocean productivity and variability in thermocline depth result in variability in the horizontal and vertical distributions (and hence variability in their availability to fisheries) and recruitment of pelagic apex predators.

For example, eastward movement of tropical skipjack and yellowfin tunas and increased recruitment have been observed, while subtropical south Pacific albacore may exhibit reduced recruitment following El Niño phases, with opposite responses following La Niña phases (Lehodey *et al.*, 1997; Lehodey, 2001; ISC, 2010). ENSO phases also affect tuna catch rates in purse seine, pole-and-line and other surface fisheries (Lehodey *et al.*, 2011). In the western Pacific Warm Pool, a shallower thermocline during El Niño phases increases the concentration of fish in the upper layer, while a deeper thermocline during La Niña phases has the opposite effect. The effect of ENSO phase on the thermocline is the opposite in the eastern equatorial Pacific. Similar effects of ENSO spatial and temporal variability in sea surface temperature, degree of vertical stratification, depth of the mixed layer, and degree of spatial concentration of preferred water temperature habitat on longline catch rates of bigeye, yellowfin and albacore tunas occur (Lu *et al.*, 1998; Briand *et al.*, 2011). There is a lag in these recruitment, biomass, and distribution responses to ENSO phases. For example, the change in skipjack average abundance occurs about eight months following an ENSO phase, and in subsequent years for adult albacore (Lehodey *et al.*, 1997, 2004; Senina *et al.*, 2008). The frequency and amplitude of ENSO varies on a multi-decadal scale due to the influence of the Pacific basin-wide Interdecadal Pacific Oscillation (IDO) and PDO, the component of the IDO in the north Pacific (e.g. Power *et al.*, 1999).

Most Earth climate model projections predict greater average warming in the eastern than the western equatorial Pacific, referred to as an 'El Niño-like' response, with continued El Niño and La Niña events (Meehl and Washington, 1996; Guilyardi, 2006; Ganachaud *et al.*, 2011). There is, however, high uncertainty in whether the frequency and strength of future El Niño and La Niña phases will change in response to climate change (Guilyardi, 2006; Lough *et al.*, 2011; Cai *et al.*, 2014; Risbey *et al.*, 2014).

3.12.2.3 Model-based predicted and observed responses

Findings from models simulating responses of some populations of Pacific tunas to climate change indicate there will be shifts in distributions and changes in absolute biomass (some increasing, others decreasing) (Box 3.12.1) (Figure 3.12.4) (Lehodey *et al.*, 2010, 2013, 2015; Nicol *et al.*, 2014). For example, model simulations of the effect of climate change scenarios predict the distribution of larvae of Pacific Ocean skipjack tuna will shift towards the eastern Pacific and to higher latitudes (Figure 3.12.4), with total biomass starting to decline after 2060 (Lehodey *et al.*, 2013). And, for comparison, model simulations for south Pacific albacore tuna

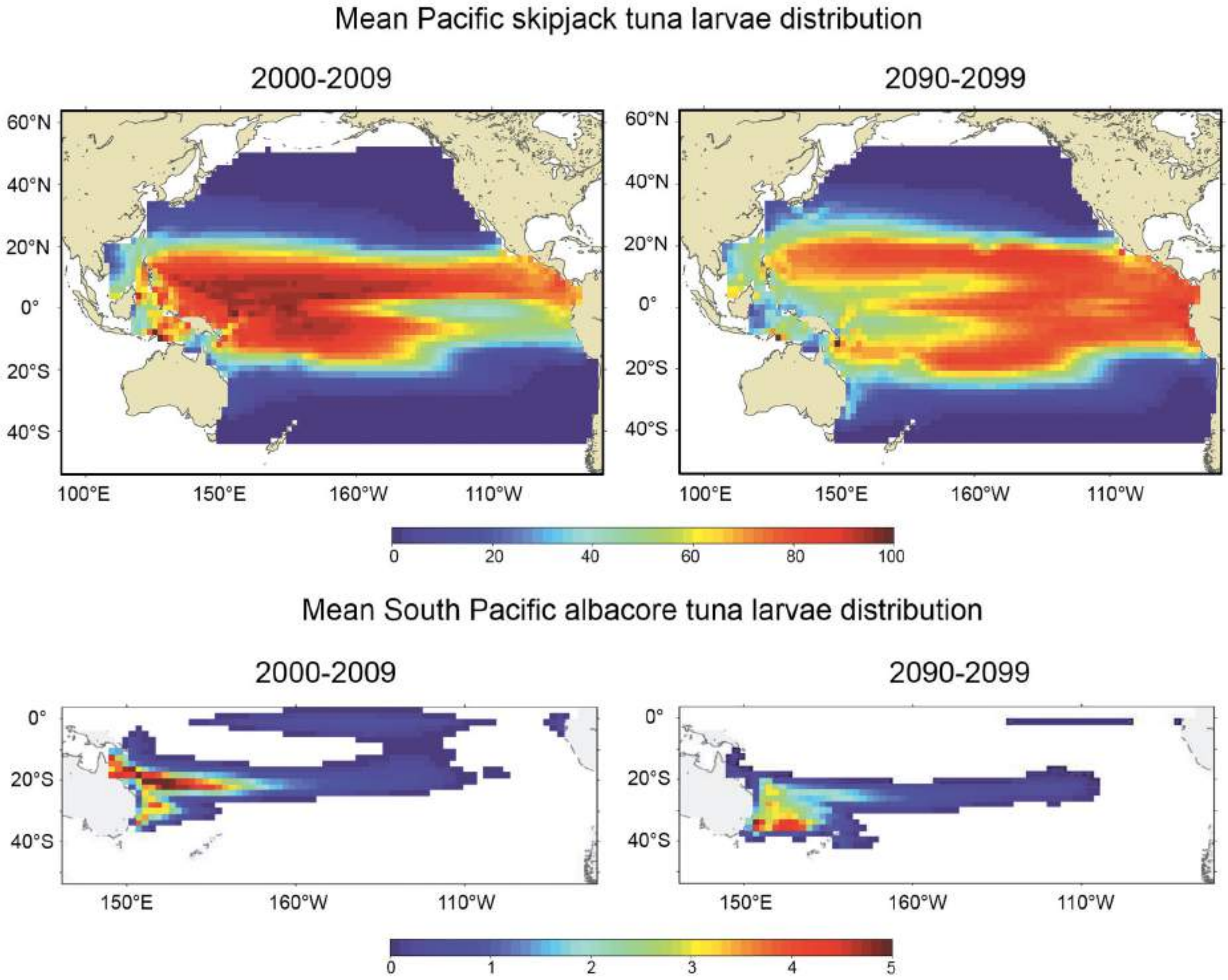

Figure 3.12.4 Model simulations of the effect of climate change on the mean spatial distributions of the density of Pacific Ocean skipjack tuna larvae (top 2 panels) and south Pacific albacore tuna larvae (bottom 2 panels) averaged over ten years at the beginning and end of the 21st Century (adapted from Lehodey *et al.,* 2013, 2015). Scales are in number of larval recruits.m $^{-2}$. For both species, the projections are based on the "business as usual" IPCC A2 scenario and using Climate model IPSL-CM4 physical forcing after correction of temperature fields and coupled to the biogeochemical model PISCES.

predict the distribution of larvae and juveniles will shift to the south closer to the Tasman Sea, while the density of individuals of these early life stages in their current core area in the Coral Sea decreases (Figure 3.12.4). Total adult biomass of south Pacific albacore is predicted to decrease and stabilize after 2035, but after 2080 when the new spawning ground in the north Tasman Sea emerges, the trend in absolute abundance is predicted to reverse (Lehodey *et al.*, 2015).

Model results also indicate there might be a decrease from the current habitat area supporting larvae and truncated spawning season for western Atlantic bluefin (Muhling *et al.*, 2011). Changes in the timing of migration from spawning to foraging grounds and in the spatial distribution of north Atlantic albacore and eastern Atlantic bluefin tunas have also been observed, possibly a response to climate change (Dufour *et al.*, 2010).

3.12.2.3.1 Effects on spawning

With rising average global subsurface and sea surface temperatures, tunas may change their spawning location and timing, which would affect the success of recruitment. Some models predict increased recruitment and biomass as a result of the formation of new spawning grounds (e.g. Lehodey *et al.*, 2015). Tunas may alter their locations for spawning from tropical to cooler subtropical areas, which in turn would alter the distribution of young age classes, altering recruitment due to possible changes in foraging success and predation of larvae and juvenile tunas (Lehodey *et al.*, 2011, 2015; Muhling *et al.*, 2011; Nicol *et al.*, 2014). Or, if tunas continue to spawn in the tropics, where warmer water temperatures might result in higher susceptibility to overheating, spawning success and thus recruitment may decline (Lehodey *et al.*, 2011, 2015).

For western Atlantic bluefin, which are already stressed by warm water temperatures at their spawning grounds in the Gulf of Mexico, ocean warming, and global climate change effects on eddies, might cause a substantial reduction or even cessation of successful spawning (Bakun, 2012). Because the dissolved O_2 demand increases with warmer temperatures for tuna to spawn, possible changes in ocean dissolved O_2 concentrations in response to climate change may narrow the temperature range of habitat suitable for spawning (Portner and Farrell, 2008; Lehodey *et al.*, 2011). Another phenological adaptation in response to ocean warming, tunas may alter their timing of spawning, and hence timing of migration between foraging and spawning grounds (Muhling *et al.*, 2011), as has been observed for young Atlantic bluefin and albacore tunas (Dufour *et al.*, 2010). Altering the season and duration of spawning could reduce larval survival due to changes in local abundance of predators and prey (Muhling *et al.*, 2011). Based on observations of variability in sensitivity to CO_2 concentrations in coral reef fishes, which might be heritable (Munday *et al.*, 2012), selection for phenotypes tolerant of higher ocean temperatures at spawning grounds could occur for some tunas, which might maintain current spawning locations but possibly at a reduced level of spawning success. This would reduce the likelihood of the phenological adaptation to new spawning areas at higher latitudes of becoming established, reducing recruitment and biomass, as predicted by one simulation run of a model for south Pacific albacore (Lehodey *et al.*, 2015).

3.12.2.3.2 Effects on foraging habitat for non-spawning tunas

Tunas, when not spawning, may respond to ocean warming by occupying new areas with suitable water temperatures and that also meet other requirements such as O_2 concentration and local abundance of prey. Tunas might alter their vertical distribution by occupying deeper depths and might alter their horizontal distribution by moving to higher latitudes and to longitudes where preferred temperatures and O_2 concentrations occur, as takes place during current El Niño phases (Lehodey *et al.*, 2011, 2015; Bell *et al.*, 2013b; Nicol *et al.*, 2014). Increased vertical structure of the water column (stratification) may restrict the depth distributions of skipjack and yellowfin tunas and billfishes that are sensitive to temperature stratification, constraining them to surface layers where SST is within tolerance ranges, affecting their access to forage species in deep water, and affecting their catchability in surface fisheries (Lehodey *et al.*, 2011; Nicol *et al.*, 2014). There is limited understanding of how prey species of oceanic tunas and billfishes will respond to ocean warming and other climate change outcomes, which in turn limits the certainty of predictions of where new tuna and billfish foraging habitat might emerge (e.g. Muhling *et al.*, 2011). For example, the micronekton that are prey for tunas may be less resilient to changes in dissolved O_2 concentrations and other physical effects of ocean warming than tunas, which might make a subset of habitat within tunas' thermal tolerance range unsuitable for foraging (LeBorgne *et al.*, 2011). Reduced O_2 concentration at depth and lower ability to visually detect prey in low light environments may reduce the suitability of deeper water habitats and prevent expanding vertical distributions by some tuna and tuna-like species, similar to the effect of increased stratification (Poisson *et al.*, 2010; Lehodey *et al.*, 2011). Subsurface changes in temperature and O_2 concentration are expected to have a larger effect on yellowfin, albacore and bigeye tunas, which have relatively wide depth distributions, than skipjack, which largely occupies surface waters (Lehodey *et al.*, 2011, 2014; Nicol *et al.*, 2014). As with the ocean warming effect on the location of spawning grounds, selection for phenotypes tolerant to higher ocean temperatures at foraging grounds could also occur for some tunas.

3.12.2.4 Individual and interacting effects of climate change outcomes on tunas

Synergistic effects of the predicted outcomes of climate change on market tunas are not well understood (Hobday *et al.*, 2015). For instance, the interacting effects of ocean warming and changes in O_2 concentrations might have a much different and larger effect on the success of tuna spawning than predicted effects from these factors individually (Portner and Farrell, 2008; Lehodey *et al.*, 2011). There may be interacting effects between ocean warming and ocean acidification, where for example, acidosis could narrow the range of optimal temperatures, narrowing new locations of optimal spawning habitat in response to ocean warming. And, possible reductions in larvae survival rates from changes in the location of suitable spawning habitat due to ocean warming may be exacerbated if reduced pH also causes a reduction in tuna larvae survival rates at low dissolved O_2 concentrations (Lehodey *et al.*, 2011; Bromhead *et al.*, 2015).

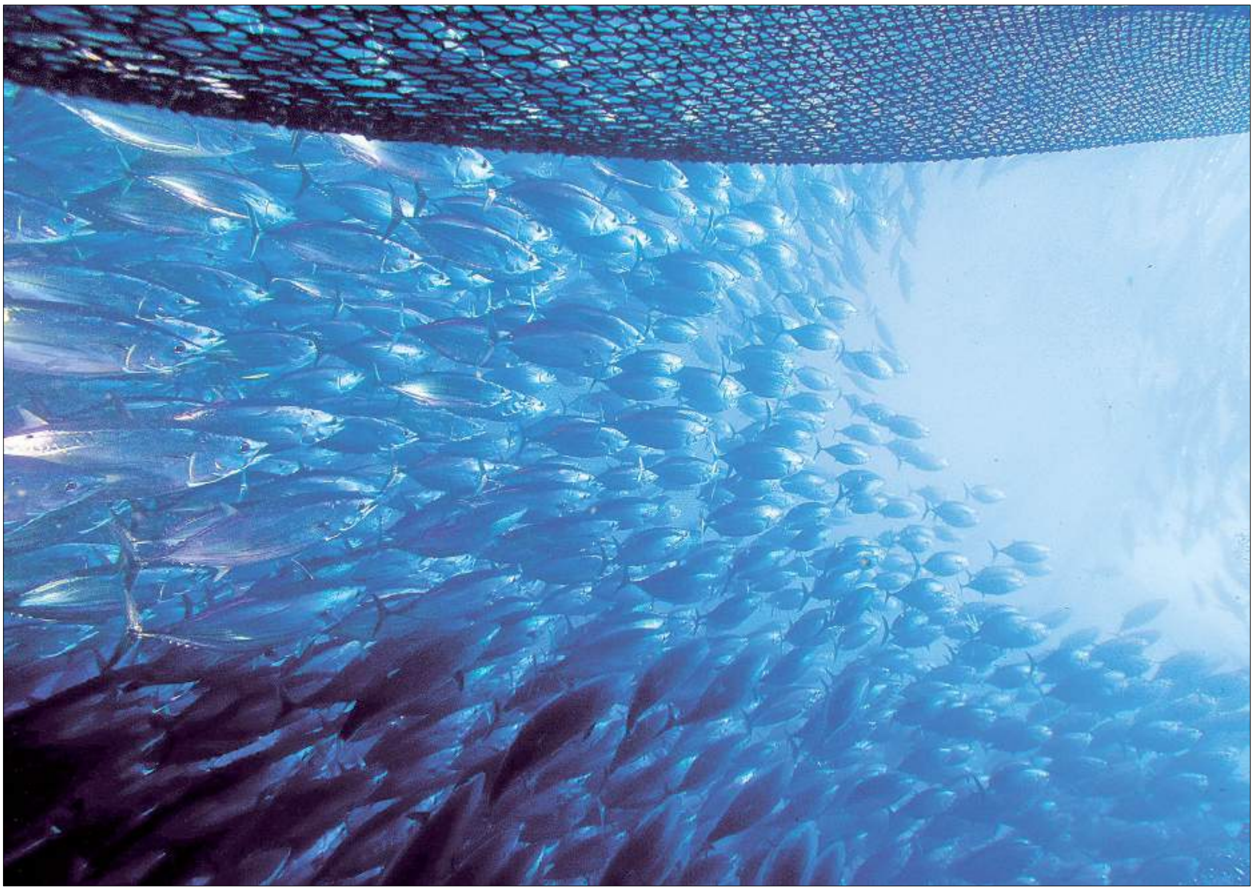

Figure 3.12.5 School of tuna in a purse seine fishing net. © Alex Hofford Greenpeace / Marine Photobank.

Effects on tunas and billfishes from other individual climate change outcomes include:

- The direction and speed of **currents** influence the locations of suitable foraging and spawning habitat for pelagic organisms, including the locations and strength of eddies, upwelling and vertical stratification and mixing of the water column. Currents in the tropics are expected to weaken, causing a decrease in the formation of eddies and increased stability of water masses (Nicol *et al.*, 2014). These changes resulting from altered ocean circulation patterns affect pelagic organisms' horizontal and vertical distributions for foraging and spawning, which in turn affects foraging success, predation and survival rates, recruitment, growth and abundance (Ganachaud *et al.*, 2011).
- **Vertical mixing of the water column**, including through eddies, wind-driven upwelling and turbulence in the mixed layer, affects the availability of nutrients for primary production at the base of tuna food webs.
- **Eddies**, in addition to affecting vertical mixing, also influence the distribution and survival rates of larvae and juveniles. Eddies retain larvae and juvenile tunas in suitable habitat that increases the probability of successful recruitment, and create suitable foraging habitat for tunas and other pelagic apex predators by concentrating their prey (Ganachaud *et al.*, 2011; Lehodey *et al.*, 2011). Bluefin tunas in particular may heavily depend on eddies to support spawning schools above a density threshold for successful reproduction (Bakun, 2012).
- **Dissolved oxygen (O_2) concentration** can affect the spawning success, growth, survival and vertical and horizontal distributions of tunas and organisms in their food webs. Organisms will not survive in areas with dissolved O_2 levels that are insufficient to meet their energy and oxidation physiological requirements, which are affected by ocean temperature (Ganachaud *et al.*, 2011; Lehodey *et al.*, 2011). Due to their broad distribution of spawning grounds, changes in O_2 concentration is not likely to affect the reproduction of albacore, bigeye, skipjack and yellowfin tunas (Lehodey *et al.*, 2011).
- **Ocean acidification** may cause tuna species and age classes with high metabolic demands to

experience physiological costs, including a reduced range of optimal temperatures, compounding adverse effects of ocean warming, and energy costs to compensate for acidosis (increased carbonic acid in body fluids) (Portner *et al.*, 2004, 2005; Lehodey *et al.*, 2011). There is evidence from one laboratory study on yellowfin tuna eggs and larvae that increased oceanic CO_2 concentrations and lower pH caused significantly reduced larvae survival, larvae size and growth, and increased time required for egg hatching (Bromhead *et al.*, 2015). Decreasing pH may affect tuna otolith formation, important for orientation, acceleration and detecting sound, particularly by tuna larvae, and thus might affect larvae survival (Fabry *et al.*, 2008; Lehodey *et al.*, 2011; Bignami *et al.*, 2013). Decreasing pH is expected to reduce sound absorption and increase sound propagation, which might affect tuna and organisms in their food webs, such as their ability to detect prey and predators (e.g. Ilyina *et al.*, 2010). Ocean acidification affects the availability of carbonate ions, affecting the abundance of some species of calcifying phytoplankton and zooplankton that are small components of lower trophic levels of tuna food webs (Ganachaud *et al.*, 2011). Based on observations in other species, tunas may also experience sub-lethal effects from reduced pH, such as reduced growth and size at age, neurological and behavioral changes and altered evolutionary characteristics of populations (Briffa *et al.*, 2012; Munday *et al.*, 2012; Nilsson *et al.*, 2012; Bromhead *et al.*, 2015).

3.12.3 Conclusions and recommendations

There remains high uncertainty of how individual populations will respond to long-term rising average ocean temperatures and synergistic effects of other climate change outcomes. Oceanic tunas and billfishes may adopt new cooler subtropical areas for spawning, either replacing or in addition to existing tropical spawning sites. They may change their migration phenology, including altering the timing of spawning and truncating the spawning season. These changes may alter distributions and reduce survival rates of larvae and young age classes, reducing recruitment and biomass in existing spawning grounds, but possibly increasing recruitment and biomass at new spawning grounds. Some populations may alter their foraging distributions to higher latitudes and to different longitudes, and alter their vertical depth distributions, in order to maintain preferred species- and age class-specific habitat conditions, including optimal temperature ranges.

Long-term trends in absolute abundance in response to ocean warming will vary by individual population. Whether a population increases or decreases in total abundance will depend, in part, on whether new spawning sites emerge, how survival rates of larvae change at existing and new spawning locations and season of spawning, where suitable foraging habitat emerges and the local abundance of forage species at foraging sites. Furthermore, changes in geospatial and depth distributions might affect fishing mortality rates due to changes in susceptibility to capture in purse seine, longline and other fishing gears. Changes in horizontal and vertical distributions will redistribute benefits derived from tuna fisheries due to changes in the locations of fishing grounds and due to species- and stock-specific changes in catchability by surface and subsurface fishing gears.

There is also high uncertainty of how the effects of ocean warming and other climate change outcomes on oceanic tunas and billfishes will affect pelagic ecosystem structure, processes and stability, and in turn how these broad changes will directly and indirectly affect the population dynamics of tunas and billfishes (Le Borgne *et al.*, 2011; Lehodey *et al.*, 2011; Nicol *et al.*, 2014). For example, effects of climate change outcomes on the productivity of lower- and mid-trophic levels in tuna food chains, as well as changes in vertical and horizontal distributions, and changes in tuna access to prey at depth due to increased stratification and decreased O_2 concentrations (Lehodey *et al.*, 2011) may test the resistance and resilience of tunas to climate change.

Improvements in the certainty of predicted responses to climate change are needed, in part, to inform decisions for achieving long-term ecologically and socio-economically sustainable tuna fisheries. Addressing large uncertainties with basin-, meso- and finer-scale climate change projections, pelagic ecosystem modelling and fundamental aspects of tuna biology and ecology will contribute to improved models of response of tunas to ocean warming and other climate change outcomes (Lehodey *et al.*, 2008, 2011; Senina *et al.*, 2008; Stock *et al.*, 2011; Dueri *et al.*, 2014; Trenkel *et al.*, 2014). For example, Lehodey *et al.* (2011) identified research on species- and life stage-specific temperature and dissolved O_2 thresholds as a priority. Recent simulations of projected climate change on primary production using a new generation Earth climate model at high resolution suggest that primary production may decrease less than previously simulated in the western warm pool (Matear *et al.*, 2015). Additionally, there is a need for improved understanding of how individual species and age classes within species are affected by and will respond to ocean warming and other climate change outcomes. Improving the understanding of potential synergistic effects of predicted climate change outcomes is a large research priority, where interacting effects may have substantially different and potentially larger effect on tunas than from the individual factors. There is a need to expand research on climate change effects on oceanic tunas and billfishes to underrepresented areas while continuing to invest in research in the Pacific Ocean, where most research has been conducted to date.

Furthermore, stressors from fisheries affect tunas' and pelagic ecosystems' resistance and resilience to ocean warming and other climate change outcomes (Brander, 2010). Tuna fleets may adjust the spatial distribution and magnitude of effort in response to changes in the abundance and distributions of different tuna stocks, as has been observed to occur in some regions in response to large scale climate cycles (Michael *et al.*, 2015). Responses of the fishing industry to changes in the abundance and distributions of market tunas resulting from climate change need to be accounted for in predicted responses of tunas to climate change. Thus, improving the certainty of predictions of ocean warming effects on tunas will require, in part, improved certainty of catch and effort data as well as predictions of the distribution of future catch and effort by the fishing industry (Lehodey *et al.*, 2011) (Figure 3.12.5).

Improvements in the certainty of predicted changes in geospatial and depth distributions and abundance of market oceanic tunas and billfishes in response to climate change will augment the capacity for making long-term management and investment decisions to achieve ecologically sustainable and commercially viable tuna fisheries and supply chains that depend on tuna products (Bell *et al.*, 2011, 2013; Lehodey *et al.*, 2011). Improved predictions will also support the identification of adaption options (Bell *et al.*, 2011; Hobday *et al.*, 2013).

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3.12.4 References

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3.13 Impacts and effects of ocean warming on seabirds

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Summary

- Seabirds throughout the world are vulnerable to increasing sea temperatures, and associated climate change such as rainfall and storminess, partly through direct effects on bird physiology, but mostly through indirect bottom-up effects, with adverse effects far more frequent than new opportunities.
- Some populations have already declined considerably due to climate change (emperor penguins declined by 50% due to reduction in adult survival related to reduced sea ice extent, rockhopper penguins at Campbell Island declined by 96% as sea temperature increased, a 70% reduction in ivory gull numbers has been attributed to increasing temperatures reducing Arctic sea ice, Arctic skua breeding numbers in Scotland declined by 74% during 1986-2011, black-legged kittiwake breeding numbers by 66% in the same period, both declines being thought due to increasing temperatures (predominantly affecting sandeel productivity).
- Modelling predicts extinction of black-legged kittiwakes in Norway within the next 10-100 years because their breeding success and survival are both reduced by increasing sea temperature.
- Some populations may redistribute polewards, but scope for redistribution is limited.
- Climate envelope models predict the near-future loss as breeding species in the British Isles of Arctic tern, Arctic skua, great skua and Leach's storm-petrel, all of which are at the southern edge of breeding range in the British Isles.

Ocean warming effects	Consequences
Warming seas affecting zooplankton community composition and food web structure	Poleward shifts of seabirds, especially in nonbreeding seasons, and large declines in populations of many seabird species in all regions of the globe
Reduced extent of sea ice	Large declines in populations of seabirds that specialize in foraging at the ice edge (e.g. emperor penguin, ivory gull, little auk)
Warming causing low latitude edge of breeding range of seabirds no longer to be suitable for breeding but creating new opportunities at the high latitude edge of breeding range	Poleward shifts of breeding distributions, but for most seabird species with greater losses at the low latitude edge than gained at the high latitude edge Extinction of some breeding colonies
Increased rainfall	Increased breeding failures of seabirds, especially of burrow-nesting species (due to burrow flooding), and increased winter mortality of cormorants
Increased storminess	Increased mortality of seabirds, especially of cormorants and alcids, and reduced breeding success of many species
Increased wind speeds	Reduced breeding success of terns, increased costs of flight for many seabirds that use flapping flight with some negative impact on population size, but reduced costs of flight for gliding seabirds that may allow those species to expand their distributions

3.13.1 Introduction

Many seabird species around the world are in decline as a consequence of a range of factors, including introduced alien mammal predators, fisheries, human exploitation, and climate change (Paleczny *et al.,* 2015). Many aspects of climate change, but especially those associated with increase in temperature, could affect seabirds directly by influencing their physiology and demography, or indirectly through impacts of climate change on other components of the ecosystem (Sydeman *et al.,* 2012; Jenouvrier, 2013). Indirect effects of increasing temperature, acting through lower trophic levels (Heath *et al.,* 2012) and so affecting seabird food supply are the main impacts of climate change on seabird populations. As long-lived homeotherms, seabirds are buffered against direct effects of increasing temperature both in terms of their physiological homeostasis and in terms of their life-history. Seabirds also have scope to learn to adapt to impacts of climate change through adjustment in their behaviour. Nevertheless, some studies have reported direct effects of climate on seabird breeding success, survival and population size, which clearly indicates that anthropogenic climate change will be likely to have the same effects. Increases in temperature not only affect seabirds directly, but also cause changes in other aspects of climate that can have profound impacts on seabirds. Increasing temperature leads to increasing storminess, with increases in wind speeds and rainfall, changes in cloud cover which can affect exposure of seabirds to solar radiation, and changes in the distribution and extent of sea-ice in polar regions, a habitat of great importance for some seabirds that specialize in feeding at the ice-edge. Examples of direct effects of climate on seabirds are listed in Table 3.13.1.

Impacts of increases in rainfall, and especially increases in heavy rain events are predicted by climate change models for many geographical areas and especially at some ocean coasts. There is particularly good evidence that burrow-nesting seabirds, such as shearwaters, puffins and some penguin species, are adversely affected by flooding of burrows caused by heavy rainfall during their breeding seasons. Increased heavy rainfall associated with temperature increase would be likely to reduce breeding success of many burrow-nesting seabirds, and in the long term could change the locations suitable for burrow-nesting seabird colonies. Kaiser and Forbes (1992) found that burrow-nesting seabirds tended to occur on islands with lower levels of rainfall, indicating that some islands are already unsuitable due to excessive risk of flooding of burrows. Thompson and Furness (1991) found that when a burrow was flooded, Manx shearwaters tended to move the next breeding season to another burrow (within the same colony), so that burrows more liable to flooding became unoccupied over time. Temperature increase could accelerate this process with breeding failure leading to birds moving to better locations within the same colony, or in extreme cases deserting the colony and moving to another location where flooding risk is lower.

A wettable plumage increases the diving efficiency of shags and other species of cormorants, but at a cost of their needing to dry the plumage on a regular basis between foraging bouts. Heavy rainfall increases mortality of European shags in winter (Table 3.13.1) and this reflects the poor waterproofing of shag plumage, requiring them to come out of the water to dry their feathers. In persistently wet weather, shags may be unable to dry their plumage, preventing them from returning to the sea to forage, and the same is likely to apply to all other species of cormorant (Figure 3.13.1).


Figure 3.13.1 European shag. © John M Baxter.

Wind directly affects seabirds by altering the energy cost of flight and in some species by affecting their foraging success. Seabirds adapted to efficient gliding flight benefit from the presence of consistent wind, reducing their flight energy costs (Furness and Bryant, 1996). Increased wind, a predicted consequence of increased temperature, can allow gliding seabirds to exploit habitat that was previously unavailable to them because of a lack of wind to permit their gliding flight. For example, wandering albatrosses have been able to expand their foraging range southwards in the Southern Ocean as a result of increased wind strength at high latitude (Weimerskirch *et al.,* 2012). In contrast, increased wind speed reduces foraging success (and probably also increases flight costs) of terns in particular, but also several other species of seabirds (Table 3.13.1), so increased wind strength may reduce habitat suitability for those species.


Figure 3.13.2 Great skua. © Robert W Furness.

Both in the Arctic and the Antarctic, some seabirds are adapted to feeding at the interface between sea and ice. Poleward shifts in this interface due to temperature increase affect the foraging costs of breeding seabirds that commute from colonies to the ice edge (Barbraud and Weimerskirch, 2001; Spencer *et al.,* 2014). Climate change may result in some breeding colonies being abandoned as the commuting costs from those sites become excessive (Table 3.13.1).

There is evidence that the low latitude breeding limit of some seabirds is determined by the air temperature or solar radiation level at the colony that these seabirds can tolerate. Great skuas are adapted to high latitude climate, but breed as far south as Scotland (Figure 3.13).

These birds show clear signs of stress when the sun shines while they are incubating, and breeding birds spend increasing time away from their territory bathing in fresh water or drinking when weather conditions are warmer or sunnier, with absence from the territory increasing risk of loss of eggs or chicks (Oswald *et al.,* 2008). Climate models suggest that great skuas and Arctic skuas may soon be lost as a breeding species in the British Isles as a direct result of warming conditions (Oswald *et al.,* 2011; Russell *et al.,* 2014). There may be a threshold temperature in this relationship, but the evidence suggests simply that warmer conditions are less suitable for the species to breed. Temperature impacts may act in combination with other factors such as food availability. Birds have to work harder when food is in short supply and that can influence both breeding success and adult survival (Davis *et al.,* 2005). Under warmer conditions, the impacts of food shortage may be magnified, whereas effects of temperature increase may be less evident if food supply is plentiful and birds have ‘spare’ time available that allows them to buffer impacts of increased temperature (Lorentsen *et al.,* 2015). So predicting the scale of warming that will lead to local extinctions of cold-adapted species at the southern limit of their breeding range is difficult.

Table 3.13.1 Examples of direct effects of climate change on seabird physiology or demography

Increased precipitation		
Seabird species	**Direct effect reported**	**Reference**
Manx shearwater	Reduced hatching success due to flooding of burrows with heavy rain in May/June	Thompson and Furness (1991)
Burrow-nesting alcids	Erosion of habitat and flooding of burrows	Kaiser and Forbes (1992)
European shag	Reduced survival during winters with higher rainfall	Frederiksen *et al.* (2008)
European shag	Shag breeding numbers were negatively related to the North Atlantic Oscillation (NAO) winter index in the previous winter. This was believed to be due to increased mortality in winter caused by high winds and rain	Bustnes *et al.* (2013)
Rockhopper penguin	Heavy rain increased chick mortality	Demongin *et al.* (2010)
Magellanic penguin	Increased rainfall reduces chick survival	Boersma and Rebstock (2014)
Adelie penguin	Increased snow precipitation reduces breeding success, especially when birds are challenged by food shortage	Chapman *et al.* (2011)
Increase in wind speed		
Seabird species	**Direct effect reported**	**Reference**
Northern fulmar	Reduced cost of flight as flight costs are especially high in calm weather in fulmars	Furness and Bryant (1996)
Terns	Reduced fishing success	Dunn (1973), Taylor (1983)
Lesser noddy	Reduced fledging success	Monticelli *et al.* (2014)
Glaucous gull	Increased feeding success at guillemot ledges	Gilchrist *et al.* (1998)
Brunnich's guillemot	Higher predation by gulls on eggs and chicks	Gilchrist *et al.* (1998)
Brunnich's guillemot	High wind speeds reduced energy gain from foraging by breeding adults	Elliott *et al.* (2014)
Kittiwake	High wind speeds reduced energy gain from foraging by breeding adults	Elliott *et al.* (2014)
Wandering albatross	Poleward shift of albatross foraging with increased winds resulting in higher breeding success	Weimerskirch *et al.* (2012)
European shag	Reduced survival during winters with increased onshore wind speed	Frederiksen *et al.* (2008)
European shag	Shag breeding numbers were negatively related to the North Atlantic Oscillation (NAO) winter index in the previous winter. This was believed to be due to increased mortality in winter caused by high winds and rain	Bustnes *et al.* (2013)
Razorbill, common guillemot, European shag, kittiwake	Increased summer storminess is likely to reduce seabird breeding success; a storm lasting 8 hrs reduced breeding success by 5 to 23% depending on nest sites used and the extent to which these provided adequate shelter	Newell *et al.* (2015)
Change in upwelling driven by changes in wind speed and direction		
Rockhopper penguin	Foraging success reduced with reduced wind-driven upwelling	Dehnhard *et al.* (2013a)

Increase in solar radiative heating and/or heat		
Great skua	More time devoted to bathing and drinking	Oswald *et al.* (2008)
Brunnich's guillemot	Increase in adult and chick mortality at nest sites	Gaston *et al.* (2002)
Change in location of ice-edge		
Emperor penguin	Emperor penguin mortality rates increased when warm sea-surface temperatures occurred in the foraging area and when annual sea-ice extent was reduced, although hatching success declined with increased sea-ice, indicating strong but contrasting effects of climate change on this species	Barbraud and Weimerskirch (2001)
Ivory gull	Migration routes and wintering areas are altered by changes in location of Arctic ice edge and may contribute to 70% decline in population of this species	Spencer *et al.* (2014)
Little auk	Migration routes and wintering areas are likely to be altered by changes in location of Arctic ice edge	Fort *et al.* (2013)
Little auk	Changes in location of summer sea ice edge relative to location of colonies may affect breeding success (likely to increase foraging costs by requiring longer commuting flights)	Gremillet *et al.* (2015)
Little auk	Melting of glaciers within foraging range of breeding birds may create foraging hotspots where fresh water and sea water mix, that could increase breeding success	Gremillet *et al.* (2015)

More studies find evidence of indirect effects of temperature increase on seabirds. Most involve bottom-up forcing through temperature-associated climate change effects on lower trophic level organisms on which seabirds depend for food, but there are also some examples of top-down effects on ecosystem structure (Table 3.13.2). Top-down impacts of climate change include climate change effects on predatory fish stocks and the alteration of food-web structure as a consequence. One of the best documented examples is the food web of the Barents Sea, where warming sea temperatures increase recruitment into the cod stock. Warming sea temperatures also affect zooplankton communities in the Barents Sea which will affect the entire ecosystem through bottom-up forcing, but the key effect of warmer temperatures is to increase reproductive output of cod, increasing the biomass of the cod stock (Box 3.13.1). Cod is a major predator of young herring and capelin, the capelin in the Barents Sea being particularly important as food for seabirds. Large decreases in seabird numbers (especially numbers of common guillemots which declined by over 90% when capelin stock collapsed in 1987, Anker-Nilssen *et al.*, 2000) have occurred as a result of fluctuating dynamics of the cod-herring-capelin system in the Barents Sea, further complicated by the impacts on each of these stocks of commercial fisheries (Table 3.13.2).

In the North Sea, many seabirds depend on lesser sandeels for food during the breeding season. Seabird breeding success is affected by the abundance of sandeels, which in turn is affected by temperature increase impacts not only on sandeel recruitment through a bottom-up process, but also through top-down impacts of predation on larval sandeels by adult

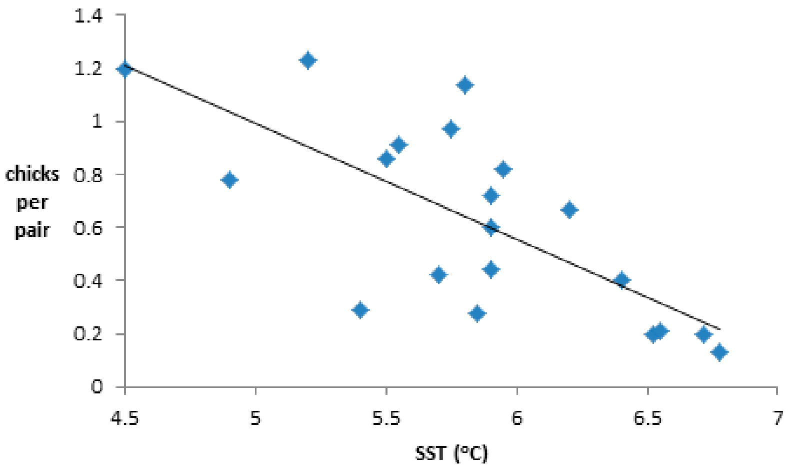

Figure 3.13.3 Relationship between annual breeding success of kittiwakes at the Isle of May, east Scotland, and sea surface temperature (SST) in the previous winter, in years when there was no commercial fishery for sandeels in the region (1983-1990 and 2003-2013). Redrawn from Frederiksen (2014).

herring and mackerel and predation on most age classes of sandeels by cod, whiting and other large predatory fish. Part of this relationship is the top-down impact of predation that is affected by temperature increase (Table 3.13.2). As with the Barents Sea, it is difficult to separate this climate change signal from impacts caused by changes in fishery management. In addition, climate variation in the North Sea is associated not only with air temperatures but also with periodic changes in ocean circulation, so that periods of warming may be followed by periods of cooling. However, a very clear example of temperature increase top down impact on seabirds is the decline in seabird numbers resulting from a climate-driven increase in pink salmon in the North Pacific associated with increased sea temperature causing higher survival of pink salmon, greatly increasing predation impact of salmon on the lower trophic level fish on which most seabirds depend (Springer and van Vliet, 2014). The influence of pink salmon on seabird demography was found to be widespread across seabird species and pervasive through different aspects of seabird demography (Box 3.13.2).

By far the largest number of studies reporting climate change impacts on seabirds report bottom-up impacts due to increasing temperature affecting the distribution and/or abundance of lower trophic level species on which seabirds depend for food. Impacts of sea temperatures, often reported as sea surface temperature (SST) have been seen for seabird populations from the tropics to the poles, one of the best examples being kittiwake breeding success in relation to sea surface temperature (Figure 3.13.4), and for seabirds of all phylogenetic and ecological types (Table 3.13.3). In most cases, increased SST reduces seabird productivity or survival (e.g. Figure 3.13.4), often with detectable adverse effects on breeding numbers. However, not all effects are negative, with a small minority of bottom-up changes to ecosystems creating improved conditions for some seabirds (Table 3.13.3).

Table 3.13.2 Examples of effects of climate change on ecosystems producing top-down impacts on seabird populations

Seabird species	Top-down driver	Reference
Common guillemot	Climate change causes top-down and bottom-up forcing of cod, herring, capelin stock interactions in the Barents Sea, altering food supply for seabirds affecting both breeding success and survival rates (Box 3.13.1).	Gjøsaeter *et al.* (2009), Stige *et al.* (2010), Bogstad *et al.* (2013), Erikstad *et al.* (2013)
Kittiwake and others	Sea temperatures affect herring recruitment and stock size. Predation by adult herring on larval sandeels at Shetland appears to be one factor influencing sandeel abundance which affects kittiwake breeding success.	Frederiksen *et al.* (2007), MacDonald *et al.* (2015)
Kittiwake	Sandeel recruitment is reduced at warmer winter sea temperatures. At Shetland, when sandeel abundance was reduced, prey switching by great skuas increased predation impact on kittiwakes and other small seabirds.	Oro and Furness (2002)
Several species, including trans-hemispheric migrants as well as breeding seabirds (see Box 3.13.2)	Bottom-up effects of climate change in the North Pacific Ocean have favoured pink salmon, which in turn exert a top-down predation on low trophic level fish species on which many seabirds depend for food. Survival of migrant seabirds and breeding success of resident seabirds decreased with increase in pink salmon abundance (Box 3.13.2).	Springer and van Vliet (2014)

Box 13.3.1 Increasing sea temperature, cod, herring and capelin stocks and fisheries in the Barents Sea, and consequences for seabirds

The Barents Sea holds very large populations of breeding seabirds, especially of common guillemots, Brunnich's guillemots, Atlantic puffins, kittiwakes, great black-backed gulls, and herring gulls (Anker-Nilssen *et al.,* 2000) (Figure 3.13.7 and 3.13.8 Guillemot and puffin). While breeding, these seabirds feed predominantly on capelin, a small, schooling, lipid-rich pelagic fish. Collapses of the Barents Sea capelin stock resulted in breeding failures, mass mortality of adult seabirds (especially of common guillemots) and abandonment of some breeding colonies (Anker-Nilssen *et al.,* 2000; Gjøsaeter *et al.,* 2009). Capelin compete with herring for zooplankton, and both these fish are important prey of cod. Although a rather simple ecosystem, interactions between sea temperature, cod, herring and capelin, and fisheries targeting each of these three major fish stocks, are complex. The temperature in the Barents Sea has increased (Gjøsaeter *et al.,* 2009; Michalsen *et al.,* 2013)). In the cool conditions of the Barents Sea, higher sea temperature leads to strongly increased production of young cod, and weakly increased production of young herring (Stige *et al.,* 2010; Bogstad *et al.,* 2013), with high production of these two stocks being synchronous during some time periods (Michalsen *et al.,* 2013), but this relationship can be affected by the level of the spawning stock. Reduced spawning stock biomass can reduce production of young even in years with favourable temperature conditions. The result can be an interaction between sea temperature and fishery mortality levels imposed on these stocks (which have at times been high). Cod will switch between herring and capelin in their diet depending on the abundance of those stocks (Stige *et al.,* 2010). High predation by cod on capelin is likely to have contributed to collapses of the capelin stock that resulted in seabird breeding failures and mortality (Stige *et al.,* 2010), although there is also evidence that seabirds can feed on 0-group cod if these are abundant, and that the abundance of this age class can therefore influence seabird population growth rate, especially if capelin abundance is low (Erikstad *et al.,* 2013). Despite the apparent simplicity of this Arctic marine ecosystem dominated by A very small number of fish species, interactions among stocks and the influences of fisheries and ocean temperature change are highly complex. There is still much uncertainty as to the relative contributions of fishing on capelin and temperature favouring high recruitment of cod and hence increasing predation on capelin, in causing the collapse of the capelin stock in 1987. Drastic reductions in capelin abundance have clearly been related to these complex interactions, and have had profound impacts on seabirds. In particular, the collapse of the capelin stock in 1987 (combined with low abundance of young cod and young herring at the same time) resulted in the death of more than 80% of the common guillemot population during winter 1987-88 (Erikstad *et al.,* 2013). This was a particularly interesting interaction because the impact on Brunnich's guillemots at the same time was apparently negligible, the interpretation being that while common guillemots are fish specialists and so were unable to survive in the Barents Sea in winter when prey fish abundance was at an extremely low level, Brunnich's guillemots can subsist on a much broader diet of zooplankton, and so were able to cope with conditions that killed most of the common guillemots (Anker-Nilssen *et al.,* 2000).

Figure 1 Atlantic puffin. © John M Baxter.

Figure 2 Herring gull. © John M Baxter.

Box 3.13.2 Increasing sea temperature, pink salmon abundance and consequences for seabirds in the North Pacific Ocean and Bering Sea

Springer and van Vliet (2014) reviewed the evidence that pink salmon abundance in the North Pacific Ocean and Bering Sea increases with warming sea temperatures, the causal mechanism for this being that pink salmon survival is higher at warmer sea temperatures. As a consequence of their high abundance in the ecosystem and predatory diet, pink salmon have a strong top-down controlling influence on the abundance of zooplankton, and hence can affect food abundance for seabirds (directly affecting food abundance for planktivorous seabirds which are abundant in this ecosystem but also affecting food abundance for omnivorous seabirds and for specialist piscivores as the last group depend on lipid-rich small pelagic fish that feed on zooplankton). Springer and van Vliet (2014) examined the connection between pink salmon abundance and seabirds, finding '*compelling evidence that pink salmon have a major influence on diets, numbers, phenology, fecundity, and/or productivity*' of 16 species of breeding seabirds (tufted puffin, horned puffin, black-legged kittiwake, red-legged kittiwake, red-faced cormorant, pelagic cormorant, parakeet auklet, least auklet, crested auklet, whiskered auklet, ancient murrelet, common guillemot, Brunnich's guillemot, glaucous-winged gull, fork-tailed storm-petrel, Leach's storm-petrel) at four major colonies in the western Bering Sea/Northern North Pacific (Buldir Island, Aiktak Island (Aleutian Islands), St George Island, St Paul Island (Pribilof Islands). From the data sets available, Springer and van Vliet (2014) ran 111 statistical tests of the null hypothesis that there was no difference in seabird demographic parameter values between years with high and low pink salmon abundance, and were able to reject that hypothesis in 50% of all tests. The rejection rate exceeded in all species the numbers that would be expected by chance alone, and '*demonstrated strong directionality and the large magnitude of effect that pink salmon have on seabirds*'.

In addition to clear impacts on breeding seabirds, Springer and van Vliet (2014) cite evidence that the temperature-determined abundance of pink salmon also affects the body condition and survival of overwintering short-tailed shearwaters, trans-equatorial migrants that spend the nonbreeding season in the North Pacific in very large numbers. Body mass and liver mass of these migrant seabirds was lower in years when pink salmon numbers were higher, and the incidence of strandings (mass mortality) of the shearwaters was two to five times higher in years of high pink salmon abundance.

Figure 1 Common guillemot. © Robert W. Furness.

Springer and van Vliet (2014) explain the high impact of pink salmon on seabirds as follows: The great interaction strength apparently derives from voracious consumption of zooplankton by pink salmon to fuel exceptionally rapid growth in spring-summer, the mass of fish increasing by 500% between March and July. Their prey are important to the structure of the plankton community on which seabirds depend either directly or through the food chain. This therefore represents a strong example of exploitative competition, with pink salmon abundance determined by sea temperature, and so seabird demography strongly influenced indirectly by sea temperature change in this Large Marine Ecosystem. The reduction in breeding success of black-legged kittiwake, for example, of 62% between years with low and with high pink salmon abundance is likely to lead to kittiwake population decline with temperature increase. Ocean temperature in the western Bering Sea has risen steadily since the 1950s, and Springer and van Vliet (2014) suggest that the impact on seabirds in this region is likely to continue to get more severe over future years.

Table 3.13.3 Examples of effects of climate change on ecosystems producing bottom-up impacts on seabird populations; rare examples where demographic response was an improvement with increased temperature are highlighted

Seabird species	Bottom-up driver	Reference
Kittiwake, common guillemot, shag	Breeding success and adult survival show negative relationships with winter sea temperature. As sandeel is the main prey species, the authors attribute this correlation to the known reduction in sandeel recruitment when sea temperature is warmer, and effects of warming on copepod species and distribution.	Anderson *et al.* (2014), Frederiksen *et al.* (2004, 2013), Burthe *et al.* (2014), Macdonald *et al.* (2015)
Little penguin	Breeding success and foraging effort were correlated with loc*al.,* regional and global climate influences. Locally, wind direction and wave height affected foraging effort, as did higher regional sea surface temperature. El Niño Southern Oscillation also affected foraging effort and breeding success, with poorer conditions during the La Niña phase. Effects were considered likely to be indirect through influences on prey (abundance or availability) rather than direct effects. Climate change is likely to increase the frequency of these adverse phases.	Berlincourt and Arnould (2015)
Lesser noddy, brown noddy, white tern, sooty tern, roseate tern	Breeding performance was reduced during the La Niña (low SST) phase of the El Niño Southern Oscillation. Climate change is likely to increase the frequency of these adverse phases.	Catry *et al.* (2013)
Little auk	Foraging activity was predominantly in marine habitat with lower SST and a flat sea bottom over the continental shelf.	Hovinen *et al.* (2014b)
Wedge-tailed shearwater and other seabirds	Prey availability to breeding seabirds decreases in direct association with within-season increases in sea-surface temperature, the mechanism being short-term horizontal and/or vertical redistribution of fish, or subsurface predators, affecting availability of prey to seabirds.	Weeks *et al.* (2013)
Manx shearwater	In summers following winters with higher SST, chick provisioning was reduced, chick growth was slower, breeding was late and adult attendance at the colony was reduced.	Riou *et al.* (2011)
Common guillemot	Climate change causes top-down and bottom-up forcing of cod, herring, capelin stock interactions in the Barents Sea, altering food supply for seabirds affecting both breeding success and survival rates.	Gjøsaeter *et al.* (2009), Stige *et al.* (2010), Bogstad *et al.* (2013), Erikstad *et al.* (2013)
29 species of seabirds at 187 North Atlantic colonies	Adult survival and recruitment of juveniles was affected by the NAO index. Seabirds with large clutch sizes show a latitude-related effect, with the NAO effect reversing sign between low and high latitude colonies. How NAO will alter as a result of climate change is uncertain.	Sandvik *et al.* (2012)
Atlantic puffin	SST in May explained 37% of variance in survival of puffins at a study colony in the Gulf of Maine.	Breton and Diamond (2014)
Southern hemisphere seabirds (meta-analysis of 47 studies >10 years duration)	Timing of breeding tends to alter with extent of sea ice in Antarctic.	Chambers *et al.* (2014)

Seabird species	Bottom-up driver	Reference
Little penguin	Warmer sea temperatures around colonies lead to earlier breeding and increased productivity.	Chambers *et al.* (2014)
Antarctic and sub-Antarctic seabirds	It seems likely that populations will relocate to breeding sites further south as lower trophic level prey species move distributions polewards with warming sea and melting ice. Populations unable to relocate, or before relocation occurs, are likely to have increased energy costs of commuting from nest sites to feeding areas. Not enough is known to make species-specific vulnerability assessments. Many seabird species in Antarctica respond negatively to increased sea temperatures, but some benefit, and effects can vary within the same species in different regions.	Constable *et al.* (2014)
Rockhopper penguin	Adult survival was highest at SST values lower than the average found over the last 40 years.	Dehnhard *et al.* (2013b)
Rockhopper penguin	Adult body mass/ body condition was higher under colder environmental conditions (positive Southern Annular Mode), suggesting that this also influences survival as shown in Dehnhard *et al.,* (2013b).	Dehnhard *et al.* (2015a, b)
Short-tailed shearwater	Breeding adults' foraging strategies differed between years with higher or lower SST, although there was no detectable impact on breeding success.	Einoder *et al.* (2013)
Wandering albatross	Early-life (up to two years old) survival was negatively related to SST, whereas recruitment rate was positively related to Southern Annular Mode and SST.	Fay *et al.* (2015)
Cory's shearwater	The Southern Oscillation Index (SOI) explained up to 66% of the variance in adult surviv*al.,* being a better predictor than number of hurricanes, so suggesting at least part of the effect is indirect through food supply. The North Atlantic Oscillation (NAO) Index explained 41% of the variance in breeding success, probably as an indirect effect on food. How these natural cycles will change as a consequence of climate change is uncertain.	Genovart *et al.* (2013)
Little auk	Survival of adults was negatively correlated with the North Atlantic Oscillation (NAO) index and local summer sea surface temperature (SST). The effects of NAO and SST were probably mediated through a change in food supply. Reproduction and growth of *Calanus* copepods, the main prey of little auks, are negatively influenced by a reduction in sea ice, reduced ice algal production, and an earlier but shorter lasting spring bloom, all of which result from an increased NAO.	Hovinen *et al.* (2014a)
Seabirds	Levels of organic contaminants and heavy metals alter with climate change impacts on marine food webs, changing the exposure of seabirds to these hazards. Changes may be inconsistent and unpredictable but deserve monitoring.	McKinney *et al.* (2015)
Lesser noddy	Birds nested later and less successfully when summer SST was higher.	Monticelli *et al.* (2014)
Rockhopper penguin	Breeding numbers decline when sea temperatures are high but increase when sea temperatures are low. The population declined by 94% from 1942 to 1984 during a period of warming conditions. Since 1996 numbers show a partial recovery, during a period of cooler conditions.	Morrison *et al.* (2015)

Seabird species	Bottom-up driver	Reference
Black-browed albatross	Adult survival was affected by SST during the breeding season, but changes affected oldest and youngest adults most. The authors suggest that intra-specific competition is most severe for old and young adults so that improved (warmer) conditions benefit those age classes.	Pardo *et al.* (2013)
Thin-billed prion	Post-breeding migrations from Falklands now tend to be poleward whereas in early 20th Century they were to lower latitude wintering areas. Suggested that this reflects changes in food distribution in a warming ocean.	Quillfeldt *et al.* (2010)
Thin-billed prion	Habitat models identified SST as an important determinant of winter distribution in the Southern Ocean of birds from two geographically distinct breeding regions.	Quillfeldt *et al.* (2015a)
Thin-billed prion, Antarctic prion and blue petrel	The non-breeding season distributions of these three ecologically similar species segregate latitudinally, SST being the most important variable separating the distributions of the species. Warming ocean conditions may not only alter their winter ranges but may cause increased inter-specific competition.	Quillfeldt *et al.* (2015b)
Kittiwake	Both survival and recruitment were related to SST. SST explained about 18% of the variance in annual population growth rate of Norwegian colonies. Dynamics of southern (Norwegian Sea) colonies were mainly affected by winter SST in the western North Atlantic wintering grounds, while dynamics of the northernmost colonies (Barents Sea) were mainly affected by autumn SST off Svalbard. Warmer conditions see faster population declines. Modelling suggested that colonies would become extinct in 10 to 100 years.	Sandvik *et al.* (2014)
Brandt's cormorant	Survival and probability of breeding were both related by a quadratic model to SST and ENSO index. Lower survival occurred at extremes of SST or ENSO index. Survival was particularly low when SST was high.	Schmidt *et al.* (2015)
Black-footed albatross, brown pelican, Cassin's auklet, California gull, Cook's petrel, Leach's storm-petrel, pink-footed shearwater, western gull, red-necked phalarope, grey phalarope, sooty shearwater, short-tailed shearwater	The spring and summer density of seabirds off southern California (all species combined) declined with climate change driven impacts in this ecosystem. The decline in seabird numbers was attributed primarily to declines in prey fish abundance caused by oceanographic change, a bottom-up forcing by climate change, although changes in krill abundance also affected seabird numbers.	Sydeman *et al.* (2014a, b, 2015a, b)
Common tern	No relationships between NAO index or Southern Oscillation and tern survival or recruitment at a colony in Germany were detected, but survival was related to primary productivity in the wintering area off Africa, as was probability of recruitment, indicating carry-over effects of environmental conditions in winter.	Szostek and Becker (2015)

Seabird species	Bottom-up driver	Reference
Common guillemot, Brunnich's guillemot, kittiwakes, red-faced cormorant	Breeding success was reduced with increased sea temperature and increased wind.	Zador *et al.* (2013)
Roseate tern	Numbers of birds breeding decreased with increasing SST. Birds nested later with increasing SST.	Ramos *et al.* (2002)

3.13.2 Definition of species and ecosystem

It is evident that climate change resulting from increasing sea temperatures may have impacts on seabirds of all phylogenetic groups and ecological types, and at all latitudes (Tables 3.13.1-3). Examples in the literature include tropical., temperate and polar seabirds, burrow-nesters as well as surface nesters or cliff nesters, seabirds that feed only at the sea surface and seabirds that feed by pursuit diving, seabirds that commute by flapping flight as well as seabirds that commute by gliding/ dynamic soaring flight, seabirds that feed almost exclusively on zooplankton as well as seabirds that feed almost exclusively on fish. Species of seabirds that are specialists, feeding on one particular prey species, or using a specialized feeding behaviour, may be more vulnerable to impacts of climate change. There are few examples of temperature increase having impacts that are detected by studies of *Larus* gull populations, as these species are generalists and opportunists which may be better able to cope with climate change effects on lower trophic levels. *Larus* gulls can switch diet and can feed on a wide range of foods, including foods with low calorific content. In contrast, climate change impacts associated with increasing temperatures have been widely reported for feeding specialists such as terns and kittiwakes.


Figure 3.13.4 Lesser black-backed gull. © John M Baxter.


Figure 3.13.5 Sooty tern. © Robert W Furness.

Although almost all of the studies cited above are with breeding populations of seabirds and focus on impacts of increasing temperature, or related climate-change effects, on breeding birds, effects of increasing temperatures may include effects outside the breeding season. With development of data loggers that can be deployed on seabirds from one breeding season to the next, allowing tracking of seabird migrations and activity budgets during winter (e.g. Frederiksen *et al.,* 2012; Lorentsen and May, 2012), we are learning a great deal about the nonbreeding ecology of seabirds, how that may be affected by increasing sea temperatures (Thompson *et al.,* 2012), and the carry-over of impacts during the nonbreeding season into subsequent breeding performance (Bogdanova *et al.,* 2011; Goutte *et al.,* 2014; Schultner *et al.,* 2014; Afan *et al.,* 2015). The existence of carry-over effects between breeding and nonbreeding seasons and vice versa (Harris *et al.,* 2000; Bogdanova *et al.,* 2011; Schultner *et al.,* 2014), shows that increases in temperature can be expected to affect the entire annual cycle of seabird ecology. The at-sea distribution of non-breeding seabirds is strongly influenced by locations of major frontal systems, which themselves are liable to move as a consequence of temperature increase in the oceans, so that seabird communities in the nonbreeding season are likely to be compressed polewards (Rodhouse, 2013; Commins *et al.,* 2014; Constable *et al.,* 2014; Santora *et al.,* 2014; Scales *et al.,* 2014).

3.13.3 Global regional significance

Seabirds throughout the world are affected by climate change associated with increasing temperature, with clear examples coming from tropical *t*emperate and polar ecosystems. Literature suggests that impacts of climate change are especially clear with seabirds that feed at the sea ice interface both in Antarctic and in Arctic ecosystems. These specialists, such as ivory gull and little auk appear to be particularly at risk of loss of critical foraging habitat within range of suitable breeding sites, and there is clear evidence of loss of the sea ice habitat from polar oceans as a consequence of warming temperatures. However, knowledge of tropical seabird ecology is much weaker than knowledge of polar seabird ecology, and so it may be unsafe to assume that tropical seabirds are at less risk; increasing temperatures in tropical oceans may be exerting comparable pressures on tropical seabirds without these being detected because both research and population monitoring of seabirds is much less extensive in tropical oceans.

Some studies indicate that climate change associated with increasing temperatures is likely to result in local extirpation of seabird populations in the near future (for example, kittiwakes from Norway, Arctic terns, Arctic skuas, great skuas, Leach's storm-petrels from British Isles). It is unclear whether populations will be able to colonize new regions where habitat may become more favourable as climate change progresses. Clearly the options for poleward redistribution of seabird populations become particularly limited at high latitudes. Seabirds have been widely used as ecological indicators of ecosystem health. That role may be compromised by impacts of climate change. However, in terms of marine ecosystem functioning, seabirds play a relatively minor role. Their consumption of lower trophic level foods is generally orders of magnitude less than the consumption by predatory fish, and so top-down forcing of ecosystems tends to be by predatory fish rather than by seabirds. Seabirds are important in terms of ecotourism in many parts of the world, and remain important as a food resource for people in several generally remote, regions.

3.13.4 Trends and impacts

Statistical analysis of relationships between climate drivers such as SST and seabird breeding success or survival can show clear relationships. For example, kittiwake breeding success at a colony in east Scotland declined from 1.2 chicks per pair at a sea temperature of 4.5°C to 0.2 chicks per pair at a sea temperature of 6.8°C (Figures 3.13.3 and 3.13.6; see Frederiksen, (2014)). The consequence of this relationship for population size is more difficult to determine. That depends on a number of uncertain relationships. Does density-dependence affect demography (Davis *et al.,* 2013; Smout *et al.,* 2013; Reiertsen *et al.,* 2014; Lorentsen *et al.,* 2015; Miles *et al.,* 2015)? To what extent is the study population part of a larger meta-population (Matthiopoulos *et al.,* 2005; Reynolds *et al.,* 2011; Ponchon *et al.,* 2015)? Do breeding numbers reflect total population size and trend or do processes such as non-breeding confound monitoring based on counts of breeding pairs at nests (Reed *et al.,* 2015)? Such questions will make the link between climate change impacts on individual demographic parameters and consequences for seabird population change a difficult one to establish (see also discussion of this in Frederiksen, (2014)).


Figure 3.13.6 Black-legged kittiwake parent and chicks. © John M Baxter.

In many large marine ecosystems, disentangling effects of climate change from effects of fisheries on the food web and seabirds is extremely difficult (Votier *et al.,* 2004; Camphuysen and Van der Meer, 2005; Garthe *et al.,* 2012; Blamey *et al.,* 2015; Collet *et al.,*


Figure 3.13.7 Rockhopper penguin. © Robert W Furness.

2015; Thomson *et al.,* 2015). Increasing temperatures and fishery impacts may even interact; seabirds may be more severely impacted by climate change under circumstances where fisheries have reduced their natural food supply. Most reported impacts of climate change have adverse effects on seabird population dynamics. Some of these have striking consequences. Modelling predicts that the kittiwake, one of the most abundant breeding seabirds in the North Atlantic, will become extinct as a breeding species in Norway between 10 and 100 years from now as a consequence of trends driven by increasing temperatures (Sandvik *et al.,* 2014). There are many quantitative assessments of climate change impacts on particular seabird populations. For example, breeding numbers of Arctic skuas in Scotland declined by 74% and kittiwake numbers declined by 66% from 1986 to 2011, trends considered to be largely due to impacts of increasing sea temperatures on their main prey, the lesser sandeel (Frederiksen *et al.,* 2005; Foster and Marrs, 2012) though possibly also influenced by sandeel fishery impacts. Rockhopper penguin (Figure 3.13.7) breeding numbers at Campbell Island have declined from 814,550 pairs in 1942 to 33,239 pairs in 2012, that change (a decline of 96%) being attributed to impacts of climate change (Morrison *et al.,* 2015).

The ivory gull population in Arctic Canada has declined by 70%, and this is attributed to climate change impacts (Spencer *et al.,* 2014) because tracking of birds from their breeding areas showed a strong dependence during the non-breeding period on ice-edge habitat. The authors conclude that the timing of formation and recession and extent of sea ice, controlled predominantly by sea temperatures, plays a large role in ivory gull distribution, migratory timing, and therefore determines the chances of survival of ivory gulls.

3.13.5 Consequences

Climate change due to increasing temperature will have more negative than positive effects on seabirds. Some local or regional populations are likely to be lost as food resources move polewards with increasing sea temperatures and become unavailable in the vicinity of traditional breeding colonies. Most seabirds are highly conservative, showing a very strong tendency to return to the same nest site every year. Many young seabirds recruit to breed in the colony where they were reared. Given the long generation time of seabirds, their ability to respond to poleward shifts in their prey may be limited (Matthiopoulos *et al.,* 2005). This is likely to lead to severe breeding failures of sensitive species at colonies which lose access to adequate prey resources (Frederiksen, 2014). The extent to which seabirds can move to new breeding sites where prey resources remain favourable, or where climate change creates new suitable habitat remains uncertain, and is likely to vary among species, for example in relation to their tendency to show breeding site fidelity and recruitment into their natal colony (Ponchon *et al.,* 2015). Climate envelope models suggest that European breeding seabirds will generally have considerably more loss of historical breeding range than gain of potential new breeding habitat (Russell *et al.,* 2014). Several seabird species breeding at the southern edge of their range within the British Isles may be lost as British breeding species; this applies especially to high-latitude adapted species such as great skua, Arctic skua, Leach's storm-petrel and Arctic tern (Russell *et al.,* 2014).

3.13.6 Conclusions and recommendations

Increasing temperature can be expected to have continuing and probably increasing impact on seabird populations globally, with widespread local or regional losses of populations. There is, therefore, a need to monitor changes in seabird populations, including monitoring of demographic parameters as well as breeding numbers, in order to inform about causes of change. Conservation efforts need to recognize the challenge of climate change for seabird populations, and should focus on measures that can be taken to enable populations to cope better with climate change impacts. Such measures would include establishment of marine protected areas for seabirds (because although marine protected areas will not alter trends in temperature, seabirds may be better able to tolerate increased temperatures if other environmental factors are benign), adjustments to fisheries management to reduce impacts of prey fish stock depletion below thresholds required by seabirds (Cury *et al.,* 2011), removal of introduced alien mammal predators from islands to facilitate seabird colonization of breeding habitat, and measures to reduce direct human impact on seabirds (such as fishery bycatch, marine pollution, and seabird hunting).

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3.13.7 References

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3.14 Impacts and effects of ocean warming on marine turtles

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Summary

- All species of marine turtles will be directly and indirectly affected by climatic change that is manifested in both ocean and nesting beach habitat changes.
- Impacts from climate change will vary geographically, temporally, and between species and populations.
- Some populations of marine turtles may already be responding to changes in climate by shifting their nesting phenology or redistributing their nesting grounds.
- Successful management of marine turtles in a changing climate will require information from long-term monitoring.

Ocean warming effects	Consequences
Increases in air and sea surface temperatures	Increase in thermal profile of nesting grounds Changes in hatchling attributes (e.g. sex ratio and size) Embryonic mortality
Altered rainfall and humidity regimes	Changes in nesting phenology and success Distributional shifts- range expansion and contraction Change in breeding capacity
Sea-level rise	Embryonic mortality Distributional shifts Loss of nesting beaches
Changes in ocean currents and stratification	Distributional shifts Range expansion and contraction Changes in abundance or distribution of food Changes in post-hatchling migrations and distribution Changes in foraging strategies, which will influence fitness and therefore reproductive capacity

* Modified table from Fuentes *et al.* (2014)

3.14.1 Introduction

Marine turtles are thought to be particularly vulnerable to climate change because they are ectotherms that rely on both oceanic and beach habitats throughout their life history (Fuentes *et al.,* 2011; Hamann *et al.,* 2013; Dudley and Porter, 2014; Hawkes *et al.,* 2014). Within these habitats, marine turtles' life history traits, behaviour, and physiology are strongly influenced by environmental factors (Standora and Spotila, 1985; Janzen, 1994). Changes in temperature and rainfall at nesting beaches can play a vital role in embryo development, hatching success, emergence rate, and hatchling sex ratio (Mrosovsky and Yntema, 1980; Fisher *et al.,* 2014). While eggs incubate, they are also vulnerable to sea-level

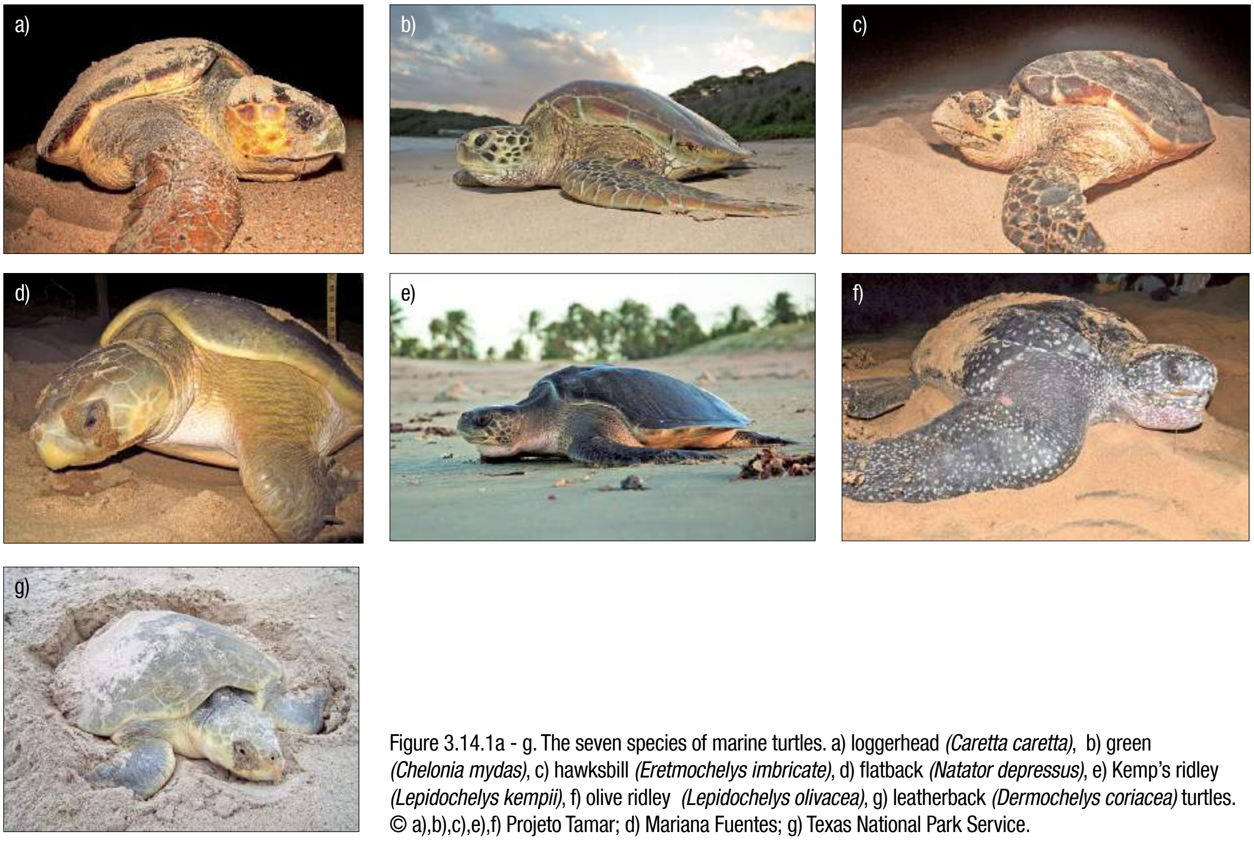

Figure 3.14.1a - g. The seven species of marine turtles. a) loggerhead *(Caretta caretta),* b) green *(Chelonia mydas)*, c) hawksbill *(Eretmochelys imbricate)*, d) flatback *(Natator depressus)*, e) Kemp's ridley *(Lepidochelys kempii)*, f) olive ridley *(Lepidochelys olivacea)*, g) leatherback *(Dermochelys coriacea)* turtles. © a),b),c),e),f) Projeto Tamar; d) Mariana Fuentes; g) Texas National Park Service.

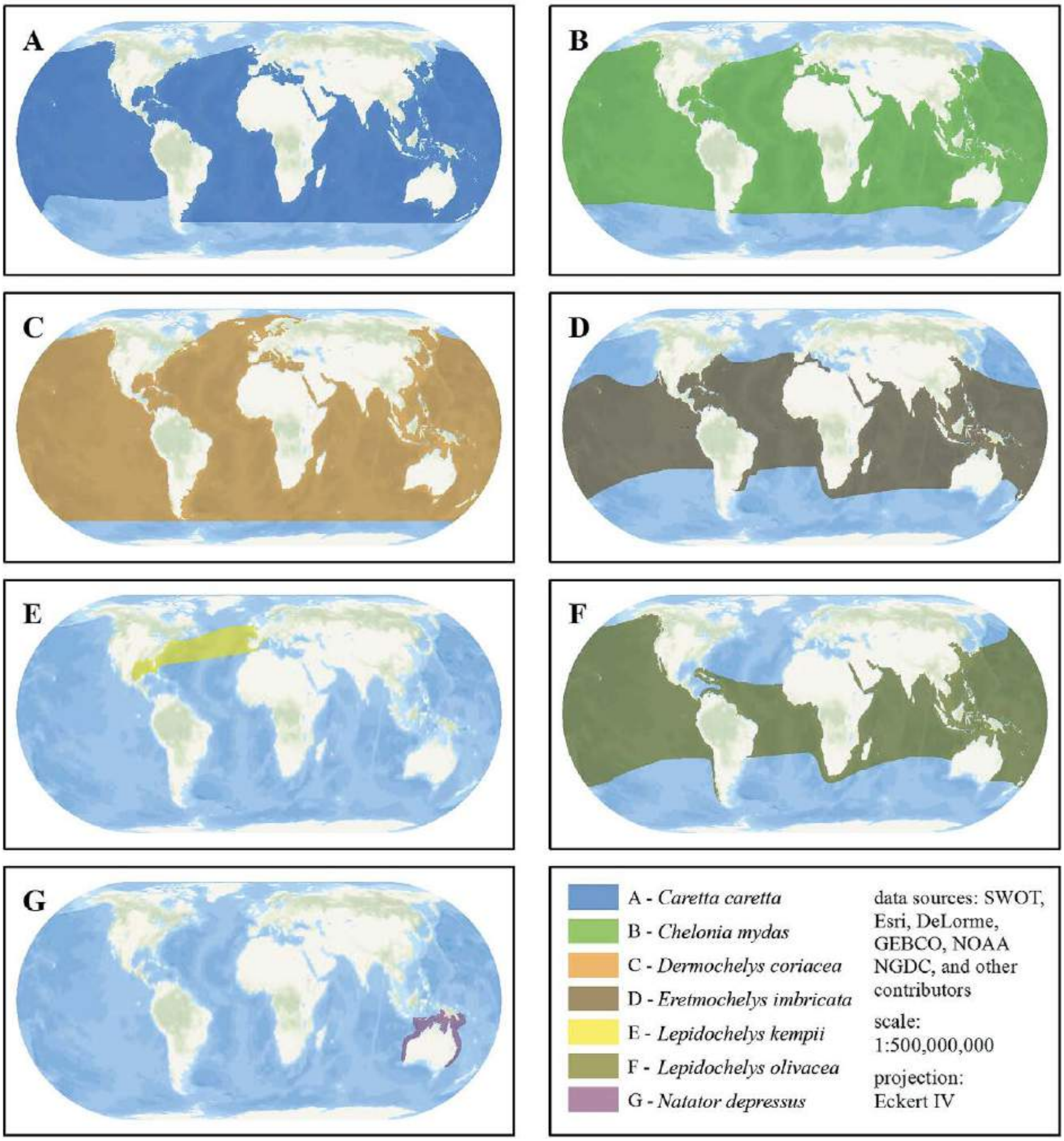

Figure 3.14.2 Global distribution of marine turtles based on maximum ranges. Figure developed by Andrew DiMatteo, CheloniData LLC.

rise and extreme events, which in the short-term can cause localized mortality of eggs and long-term loss of nesting habitat (Fish *et al.,* 2005; Van Houtan and Bass, 2007; Fuentes *et al.,* 2010a; Pike *et al.,* 2015;). In their ocean habitat, climate change may impact phenology, distribution, foraging success, and growth rates (Hamann *et al.,* 2013; Hawkes *et al.,* 2014; Bjorndal *et al.,* 2016).

Marine turtles have been around for millions of years; during this time they have endured and adapted to dramatic changes in Earth's climate (Hamann *et al.,* 2007, 2013). However, some populations of marine turtles are now depleted from past and on-going threats including fisheries bycatch, direct harvesting, egg poaching, coastal development, and pollution (Wallace *et al.,* 2011). Marine turtles are recognized internationally as species of conservation concern. On a global scale, all species, except the flatback turtle which is listed as data deficient, are classified as threatened with extinction by the IUCN (World Conservation Union) Red List of

Threatened Species (IUCN, 2015). The cumulative impact of multiple stressors on long-lived marine turtles has resulted in a major threat to their resilience and capacity to adapt to rapid climate change (Fuentes *et al.,* 2011, 2013). Concern exists on whether marine turtles can effectively respond to present day climate change given the current rapid rates of warming and the fact that they are simultaneously impacted by a wide range of anthropogenic activities (Poloczanska *et al.,* 2009; Fuentes *et al.,* 2013). Marine turtles are slow-growing, late-maturing, and long-lived and therefore only recover slowly from disturbances (Musick, 1999). Concerns prompted an increase in research on marine turtles and climate change, mostly focusing on impacts at nesting areas (Hawkes *et al.,* 2009; Hamann *et al.,* 2013). The IUCN Marine Turtle Specialist Group listed climate change among the 12 Burning Issues for marine turtle conservation (Mast *et al.,* 2004, 2005), and climate change has been highlighted as a research priority area (Hamann *et al.,* 2010; Wallace *et al.,* 2011).

3.14.2 Definition of species/ecosystem

There are seven species of marine turtles, six are in the Family Cheloniidae: the hawksbill (*Eretmochelys imbricatae*), green (*Chelonia mydas)*, flatback (*Natator depressus*), loggerhead (*Caretta caretta*), Kemp's ridley (*Lepidochelys kempii)* and olive ridley (*Lepidochelys olivacea*) turtles, and only one, the leatherback (*Dermochelys coriacea)* is in the Family Dermochelyidae (Figure 3.14.1). Marine turtles are globally distributed, inhabit nearly all oceans, and utilize coastal areas for foraging, breeding, and nesting (Wallace *et al.,* 2010) (Figure 3.14.2). Leatherbacks are the most widely distributed, with the largest northern and southern range of all marine turtle species, found in the tropical and temperate waters of the Atlantic, Pacific, and Indian Oceans, as well as the Mediterranean Sea. Hawksbill turtles are found predominantly in tropical reefs of the Indian, Pacific, and Atlantic Oceans (Wallace *et al.,* 2010); green turtles are generally found in tropical waters throughout the world (Figure 3.14.3), loggerheads are circumglobal, occurring throughout the temperate and tropical regions of the Atlantic, Pacific, and Indian Oceans; flatback turtles are only found in waters around Australia and Papua New Guinea; Kemp's ridleys are distributed throughout the Gulf of Mexico and U.S. Atlantic seaboard, from Florida to New England; and the olive ridley is globally distributed in the tropical regions of the South Atlantic, Pacific, and Indian Oceans (Wallace *et al.,* 2010).

Figure 3.14.3 Green sea turtles may swim more than 2600 kilometres between feeding sites and nesting sites. © Kaido Haagen.

Figure 3.14.4 Green turtle above sunlit seagrass bed. © Richard Wylie.

3.14.3 Global regional significance

Marine turtles fulfill important ecological roles by maintaining healthy seagrass beds (Figure 3.14.4) and coral reefs, facilitating nutrient cycling from water to land, and by providing habitat and transport of epibionts (Bjorndal, 1985; Bouchard and Bjorndal, 2000; Stachowitsch, 2014). Marine turtles are also culturally and economically valuable for many communities and economies globally in terms of eco-tourism (Tisdell and Wilson, 2001; Wilson and Tisdell, 2001; Troeng and Drew, 2004; Campbell and Smith, 2006). Thus, any reduction in, and disturbance to marine turtle populations can have ecological, cultural, and economic implications. As iconic species, marine turtles can be used to promote an understanding of the impacts of climate change on marine and coastal biodiversity, which can provide incentives for effective management and support for research and conservation (Hamann *et al.,* 2013).

3.14.4 Trends and impacts

Marine turtles will likely be affected simultaneously by multiple climatic processes (e.g. increased ocean and nesting beach temperature, precipitation change, sea-level rise, and cyclonic activity) at various temporal and geographical scales (Fuentes *et al.,* 2011; Hamann *et al.,* 2013; Hawkes *et al.,* 2014) (Figure 3.14.5). Air temperature is projected to increase globally whereas precipitation changes will vary based on location (Figure 3.14.5). Essentially, the wet areas will become wetter and the dry areas drier (IPCC, 2013). Below we discuss some of the ways that climate change may have a direct effect on marine turtles.

3.14.4.1 Ocean change

The thermal requirements of marine turtles will likely result in their distribution changing as oceans become warmer (McMahon and Hays, 2006; Pikesley *et al.,* 2015). Marine turtle distribution is strongly influenced by ocean temperature, often constrained by the 15°C isotherm (McMahon and Hays, 2006; (Hawkes *et al.,* 2007a). Shifts in the 15°C isotherm will result in marine turtles shifting their distribution (McMahon and Hays, 2006; Witt *et al.,* 2010). Indeed, poleward shifts in the distribution of leatherback and loggerhead turtles have already been observed following shifts in the 15°C isotherm (McMahon and Hays, 2006; Witt *et al.,* 2010). Similarly, it is predicted that with a rise in temperature, a progressive northward shift and overall contraction in oceanic loggerhead turtle habitat will occur in the eastern Atlantic (Pikesley *et al.,* 2015).

Alterations in ocean temperatures will not only influence the distributional range of turtles but also may impact their phenology, bioenergetics, remigration intervals, foraging success, and nesting population dynamics (Lamont and Fujisaki, 2014; Neeman *et al.,* 2015a). Responses will vary among species and populations. For example, increased temperatures at foraging grounds tend to delay leatherback nesting (Neeman *et al.,* 2015b). Conversely, warmer temperatures in months prior to the nesting season have resulted in earlier nesting for loggerhead turtles (Weishampel *et al.,* 2004; Pike *et al.,* 2006). Earlier nesting results in shorter nesting seasons for loggerhead turtles in some locations (e.g. Florida's Atlantic coast) and in extended seasons at other locations (e.g. northern Gulf of Mexico and North Carolina), with variations between different species (Weishampel *et al.,* 2004, 2010; Pike *et al.,* 2006; Lamont and Fujisaki, 2014). Earlier nesting likely reflects the conditions at foraging areas (Hays, 2000; Saba *et al.,* 2007; Sherrill-Mix *et al.,* 2008) but nesting phenology may also be related to environmental cues that signal the start of reproduction.

Marine turtles start their migration from foraging areas to distant nesting areas once they have acquired sufficient body fat (Kwan, 1994). Resource availability at foraging areas is influenced by oceanographic and climatic conditions (Broderick *et al.,* 2001), which will in turn reduce or extend the remigration interval for turtles, with poor foraging conditions resulting in longer intervals and favourable conditions leading to shorter intervals (Hatase and Tsukamoto, 2008; Suryan *et al.,* 2009). As a result temperature has been shown to be associated with the reproductive frequency of nesting turtles such that warmer/colder ocean temperatures could result in higher or lower nesting frequency depending on the species or population (Limpus and Nicholls, 1988; Saba *et al.,* 2007; Chaloupka *et al.,* 2008; Reina *et al.,* 2009; Sieg, 2011).

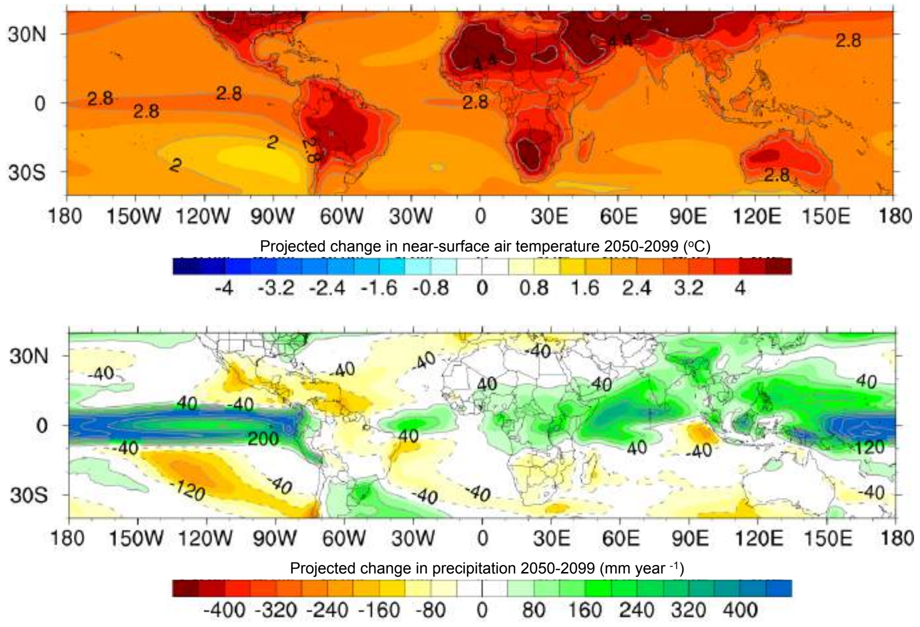

Figure 3.14.5 CMIP5 ensemble projections (37 models) of air temperature and precipitation from 2050-2099 under the IPCC RCP8.5 scenario (high-emissions scenario). The deltas were calculated for the ensemble by subtracting each climate model's historical run (1950-2005) from the RCP8.5 run (2050-2099).

The impact of ocean warming on marine ecosystem food webs is still unclear but it is likely that marine turtle foraging resources will not be immune to climate change.

3.14.4.2 Nesting beaches – sea-level rise

Ocean warming and consequent thermal expansion accounts for 30% to 55% of the 21st Century global mean sea-level rise, and will continue to contribute to predicted rises in sea level (IPCC, 2013). Much of the uncertainty in sea-level rise is due to climate model divergence in polar ice sheet change (IPCC, 2013). Sea-level rise may reduce the availability and increase inundation of marine turtle nesting areas, creating suboptimal nesting habitats (Fuentes *et al.,* 2010a; Katselidis *et al.,* 2014; Pike *et al.,* 2015). Reduction of available nesting area may amplify density-dependent issues at marine turtle nesting grounds, potentially increasing the risk of disease in nests and accidental destruction of clutches by nesting females (Bustard and Tognetti, 1969; Girondot *et al.,* 2002; Fish *et al.,* 2008). The vulnerability of marine turtle nesting grounds will vary depending on their physical characteristics, location and on their ability to shift naturally landwards in response to rises in sea level (Fish *et al.,* 2008; Katselidis *et al.,* 2014). In many coastal areas, beaches may be able to accrete, retract, and expand through natural processes. However, in areas with natural (i.e. cliffs) and artificial (i.e. beach-front development) physical barriers, landward beach recession is constrained (Fish *et al.,* 2008; Katselidis *et al.,* 2014). Small low-lying islands especially those that are not vegetated or lie on exposed reefs in areas of high tidal range, are the most vulnerable to sea-level rise (Woodroffe *et al.,* 1999; Church and White, 2006). In modelled case studies in the northern Great Barrier Reef, Australia, Florida, Greece, Hawaii, Bonaire, and Barbados it is predicted that up to 50% of nesting beaches will be lost with a 0.5 to 0.6m rise in sea level (Fish *et al.,* 2005, 2008; Baker *et al.,* 2006; Fuentes *et al.,* 2010a; Reece *et al.,* 2013; Katselidis *et al.,* 2014). Sea-level rise can also increase exposure of clutches to salt water inundation, from raised water tables and higher storm surges and waves over-topping beaches (Titus *et al.,* 1991). Saltwater inundation can directly lower egg viability and thus hatching success and may affect hatchling fitness (Patino-Martinez *et al.,* 2014; Pike *et al.,* 2015).

3.14.4.3 Nesting beaches – local climate

A strong relationship exists between ocean, local climate, and marine turtle nest temperature (Fuentes *et al.,* 2009; Girondot and Kaska, 2015), thus climate change will affect the incubation temperature and the overall nest environment of marine turtle eggs (Fuentes *et al.,* 2009). Local air temperature and precipitation play a vital role in marine turtle embryo development, hatchling success, emergence rate, and hatchling sex ratio (Limpus *et al.,* 1985; Standora and Spotila, 1985; Ackerman, 1997). While the direct impacts of air temperature on egg incubation and nest success are clearer, the impacts of precipitation are more ambiguous. Precipitation can benefit egg development and hatchling emergence (SantidriánTomillo *et al.,* 2012) due to a cooling effect on nest temperatures (Houghton *et al.,* 2007). However, excessive precipitation can also be detrimental to marine turtle clutches by causing egg suffocation, especially when eggs are developing in poorly drained sands (Kraemer and Rebecca, 1980).

Developing marine turtle embryos only successfully hatch within a relatively narrow temperature range (Howard *et al.,* 2014), such that the thermal tolerance range for development of marine turtle embryos incubated at constant temperature falls between about 25-27°C and 33-35°C (Ackerman, 1997). However, in many marine turtle populations, nest temperatures may exceed 35°C by up to several degrees (usually just prior to hatchling emergence) and eggs still hatch successfully (Howard *et al.,* 2014). Thermal tolerances are found to vary between species and populations (Howard *et al.,* 2014). For example, recent research indicates that flatback turtles may have high thermal tolerance such that flatback embryos exposed to temperatures up to 38°C within 10 days of oviposition were found to have high hatching success (Howard *et al.,* 2015). Typically, eggs incubating at higher temperatures have lower hatching success, emergence rate, and produce smaller hatchlings with higher rates of scale and morphological abnormalities and/or with reduced locomotor performance (Miller, 1985; Maulany *et al.,* 2012; Read *et al.,* 2013; Fisher *et al.,* 2014; Cavallo *et al.,* 2015). Populations that commonly nest at warmer temperatures may be more adapted to warmer temperatures (Howard *et al.,* 2014). In some cases, the offspring of females nesting on naturally hot (black sand) beaches tolerate warmer temperatures by growing larger at warm incubation temperatures when compared with the offspring of females nesting on cooler (pale sand) beaches (Weber *et al.,* 2011). Yet, there are clear upper temperature thresholds such that incubation temperatures that are too warm or too cold become lethal. It is projected that drier and warmer conditions projected for the west coast of Costa Rica, will cause a sharp decline in leatherback hatching success (from ~42% to ~18%) and in hatchling emergence (from ~76% to ~29%) between 2001 and 2100 (Santidrián Tomillo *et al.,* 2012).

This projected decrease in nest success could result in a decline in the leatherback nesting population of 7% per decade up to 2100 (Saba *et al.,* 2012). However, a global analysis of leatherback nesting beaches suggested that some regions could be more or less impacted by climate change depending on their location (i.e. temperate versus tropical) and projected change in air temperature and precipitation (Santidrián Tomillo *et al.,* 2015a).

The temperature of the incubating environment also influences the sex ratio of hatchlings because marine turtles have temperature dependent sex determination (Mrosovsky and Yntema, 1980). Warmer temperatures, above the pivotal temperature (~29°C, differs slightly within and between species, for review see Hawkes *et al.,* (2009)) — where a 1:1 sex ratio is produced — yield more females while temperatures below the pivotal temperature shift the ratio towards more males (Mrosovsky and Yntema, 1980). For leatherback turtles nesting in Playa Grande, Costa Rica, it was found that local precipitation was a stronger predictor for hatchling sex ratio (via incubation temperature measurements) than local air temperature (Sieg, 2011). Although, several studies have predicted an even higher proportion of females or a feminization of marine turtle populations as climate change progresses (Hawkes *et al.,* 2007b; Fuentes *et al.,* 2010b; Laloe *et al.,* 2014), it is still unclear how these sex ratio changes will impact turtle populations trends (but see below).

3.14.5 Consequences

Ultimately, the overall implications of climate change for marine turtles will be a reflection of their resilience to synergetic threats and ability to adapt to changing conditions and counteract projected impacts (Fuentes *et al.,* 2011, 2013). Below we discuss some of the consequences of climate change and potential adaptive responses by marine turtles.

3.14.5.1 Ocean change and sea-level rise

As a result of warming ocean temperatures, some populations of marine turtles have started to nest earlier (Weishampel *et al.,* 2004; Pike *et al.,* 2006). At some locations, earlier nesting results in shorter nesting seasons, which may result in turtles laying fewer clutches leading to reduced fecundity within seasons (Pike *et al.,* 2006). However, at other locations, extended nesting seasons have been observed as a result of warmer sea surface temperature (Limpus *et al.,* 2001; Lamont and Fujisaki, 2014). For green turtles, it has been suggested that earlier nesters are more experienced and lay more clutches (Figure 3.14.6), which will bring benefits to population growth (Limpus *et al.,* 2001). Similarly, earlier nesters are believed to have a reproductive advantage, and are able to select optimal sand conditions allowing more clutches to be incubated when such sand conditions occur during the summer (Schofield *et al.,* 2009). Indeed, earlier nesting, especially in warmer areas, may help counteract female-biases in hatchling production, as turtles nesting earlier will likely nest in cooler temperatures (Doody *et al.,* 2006). Projected changes in leatherback nesting phenology at Playa Grande, Costa Rica indicates that earlier nesting, when the air temperatures are coolest and precipitation is higher, will result in delays in climate change induced population decline by about 10–15 years (Saba *et al.,* 2012). Importantly, marine turtle populations that already nest during the cooler portion of the year may have a lower capacity of adapting through shifts in phenology (Dalleau *et al.,* 2012). Delayed nesting by leatherback turtles has been observed as a result of warmer temperatures at their foraging areas (Neeman *et al.,* 2015b) however, the consequences of later nesting on their reproductive output and population viability is still not well understood and is likely region specific. Regardless of whether nesting is earlier or later in the season, coastal managers will need to adjust the timing of their monitoring and management activities to reflect changes in nesting phenology (Weishampel *et al.,* 2010). To better understand the variability in the direction of effects of temperature on nesting phenology across species and populations, further studies are needed to explore whether additional factors affect the phenology of marine turtle populations (Neeman *et al.,* 2015b). Similarly research should also focus on understanding the implications of shifted nesting seasons for nest success, sex ratios, and hatchling dispersal (Neeman *et al.,* 2015b).

Management will also need to adjust to potential distributional shifts as a response to warmer temperatures

Figure 3.14.6 Green turtle laying eggs. © Dan Laffoley.

and sea-level rise, which will influence future nesting and foraging regions (Fuentes *et al.,* 2010a; Pike, 2013; Pikesley *et al.,* 2015). Marine turtles may start using areas that are more exposed to threats or conversely, areas that provide better foraging and incubating environments (Pike, 2013; Pikesley *et al.,* 2015). A positive example is of Kemp's ridley turtles nesting in Mexico, where it is predicted that a warming environment will render their range 6–12% more likely to occur along uninhabited stretches of coastline than current nesting beaches, suggesting that novel nesting areas will not be associated with high levels of anthropogenic disturbance (Pike, 2013). Unfortunately, most of the world's coastline is now developed (Small and Nicholls, 2003), which will hinder the capacity of marine turtles to adapt, or to encounter better or similar quality environments to colonize (Fuentes *et al.,* 2010a, 2016b) Turtles may respond to sea-level rise by shifting nesting locations further landward, up the beach; however, in doing so, will be hindered where urban development or physical barriers restrains landward beach recession (Fish *et al.,* 2005, 2008; Hawkes *et al.,* 2014; Katselidis *et al.,* 2014).

Our knowledge of whether marine turtles will be able to counteract impacts from climate change by shifting their nesting phenology or redistributing their nesting grounds is still limited and warrants further research. For the eastern Pacific leatherbacks, it has been suggested that adjusting nesting phenology or changing nesting sites may not entirely prevent potential population declines, but could offset the rate of decline (Saba *et al.,* 2012).

Although it is thought that many of the climate change related impacts to marine turtles will derive from nesting beach change (Saba *et al.,* 2012), it is still important to consider the direct effects of ocean change on their dispersal, migration, and bioenergetics. For example, climate change can impact primary production in various ways depending on the region but many Earth System Models do not agree on the direction of change from region to region (IPCC, 2013). Some marine turtle species and populations may be more flexible than others with regard to changes in the marine food web. For example, leatherback turtles exclusively feed on gelatinous zooplankton but loggerhead turtles are more omnivorous feeding on a wide variety of organisms. Therefore, one could assume that foraging specialists (i.e. leatherbacks) might be more susceptible to climate change impacts on the marine food web relative to foraging generalists (i.e. loggerheads) due to a lesser ability to switch prey type. Nevertheless, impacts will depend on how specific prey species are affected by climate change. Some organisms, such as seagrasses and macroalgae, may thrive under small increases in temperature (Koch *et al.,* 2013), resulting in positive impacts (e.g. alterations to growth rates, age at maturity and reproductive periodicity) on green turtle populations (Figure 3.14.7) (for examples see Chaloupka and Limpus, 2001; Balazs and Chaloupka, 2004). Nevertheless, in some regions, such as the Mediterranean Sea, warming temperatures are expected to negatively impact sea grass beds and the organisms that depend on sea grass bed habitat (Patel *et al*., 2016). Moreover, direct impacts of warming oceans on benthic invertebrate numbers may reduce the breeding capacity of loggerhead turtles in the Pacific Ocean (Chaloupka *et al.,* 2008). Due to the multitude of factors influencing food webs, the uncertainty of climate change impacts to regional marine food webs is still too large to make any robust projections. Similarly, our knowledge of how warming oceans may affect ocean circulation patterns and potentially cause changes in turtle dispersal, particularly among the younger age classes, and changes to the duration of oceanic life stages, is limited. Changes in the ocean and potential alterations in *Sargassum* distribution may affect early dispersal of neonate turtles. Oceanic-stage turtles are known to opportunistically remain in *Sargassum* habitats, to exploit favourable foraging and thermal niches (Mansfield *et al.,* 2014), thus changes in *Sargassum* distribution may affect dispersal and distribution of neonate turtles.

Figure 3.14.7 Green turtle on seagrass bed in Red Sea. © Nicolas Bourquin.

Ultimately, marine turtles will inhabit a warmer ocean by the end of the 21st Century; the consequential impacts to their bioenergetics, foraging success, migration, and distribution are uncertain but are not likely to be trivial. Given the biases towards research exploring the impacts of increasing temperature and sea-level rise on nesting beaches further research is necessary on the less studied life stages and oceanic habitats.

3.14.5.2 Nesting beach change

The reproductive output and consequently the recruitment and the dynamics of marine turtle populations will be affected by warmer temperatures and changing precipitation at nesting beaches (Hawkes *et al.,* 2014). Warmer temperatures may increase the production of physically weaker hatchlings (slower and smaller), but possibly with larger yolk reserves (Booth and Evans, 2011; Cavallo *et al.,* 2015). This may result in significant losses to recruitment since slower swimmers are less well equipped to escape predators and inshore retention produced by currents and wave activity (Gyuris, 2000; Booth and Evans, 2011). Nevertheless, it may be advantageous for hatchlings that are entering a food-poor environment, as larger yolk reserves may allow them to survive starvation longer than larger bodied hatchlings, which have smaller yolk reserves Ischer *et al.,* 2009; Booth and Evans, 2011).

Increased incubation temperatures will also exacerbate female biased sex ratios or produce single-sex batches of female hatchlings, potentially causing a feminization of marine turtle populations (Hawkes *et al.,* 2007b; Fuentes and Porter, 2013; Santidrián Tomillo *et al.,* 2014). No evidence to date suggests that lower proportions of male hatchlings affect reproductive success or a population's viability. In fact, among marine turtle populations, primary sex ratios are often female-biased, with sex ratios over 90% female reported at several locations (Witt *et al.,* 2010; Sieg *et al.,* 2011; Fuller *et al.,* 2013; Hays *et al.,* 2014; Marcovaldi *et al.,* 2014) with populations that have strong female bias persisting over several decades (Hays *et al.,* 2003). Female sex ratios may be compensated by the different breeding patterns of male and female turtles because males have shorter reproductive intervals than females and move between aggregations of receptive females (Hays *et al.,* 2010, 2014; Wright *et al.,* 2012; Stewart and Dutton, 2014). Therefore, the effects of projected feminization on the viability of marine turtle populations are likely to be less critical than previously suspected (Hays *et al.,* 2010, 2014). Indeed, a feminization of marine turtle populations may be beneficial in the short-term by increasing the total size of the population and reproductive output of populations (Laloe *et al.,* 2014). Nevertheless, in the long-term, the increased proportion of males may lead to reduced fecundity or female infertility, a reduction in effective population size, a loss of genetic variation, and even the potential for production of single sex cohorts (Wibbels, 2003; Mitchell *et al.,* 2010; Fuller *et al.,* 2013). The true implications of female biased populations will only be obtained when we have a better understanding of the lower viable limits of the male to female ratio (Lasala *et al.,* 2013).

Ultimately, the proportion of female hatchlings may be lower than projected since mortality is higher at female-producing temperatures due to the effect of temperature on emergence success (Santidrián Tomillo *et al.,* 2014) (Figure 3.14.8). However, as global temperature rise and incubation temperatures become higher than their thermal limits, the overall recruitment rate of marine turtles may become too low to maintain populations (Santidrián Tomillo *et al.,* 2012, 2015a). For example, a ~50–60% decline in recruitment in the eastern Pacific leatherback population is projected by the year 2100, (Santidrián Tomillo *et al.,* 2012).

Figure 3.14.8 Turtle hatchlings heading for the sea. © Carl Lundin.

Marine turtles may adapt to warmer incubating environments by shifting their nesting to cooler months and redistributing their nesting grounds (as discussed above) and changing their nest-site selection (Mitchell and Janzen, 2010; Hawkes *et al.,* 2014). Although marine turtles have the ability to adapt to changing climate over evolutionary time-scales (i.e. 10s of thousands of years), the unprecedented observed and projected rapid warming rate prevents adaptation within a short time-frame and thus forces marine turtles to rely on rapid plastic responses from individuals within populations (Hamann *et al.,* 2013). Studies should explore the ability of marine turtles to counteract future impacts, and use insights into how turtles have adapted in the contemporary period to elucidate future responses (Hamann *et al.,* 2013).

Box 3.14.1 Impacts of climate change on the largest green turtle population in the world: the Northern Great Barrier Reef green turtle population

Figure 1 Green turtle. © Ivan Conesa.

The northern Great Barrier Reef (nGBR) green turtle population is the largest green turtle population in the world (Figure Box 3.14.1), with about 41,000 females breeding annually in a typical dense nesting season (Limpus *et al.,* 2003). Nesting for this population occurs in the northern Great Barrier Reef and Torres Strait region (Limpus *et al.,* 2003). Given the ecological, economic, social and cultural value of this population there has been great concern about the potential impacts that climate change will have on the terrestrial reproductive phase of this turtle population. The work on impacts from increased temperature (from Fuentes *et al.,* 2009, 2010b) on the nGBR green turtle population predicts a feminization of annual hatchling output into the nGBR green turtle population by 2030. Predictions are bleaker for 2070, when some of the nesting grounds used by this population are predicted to experience temperatures near or above the upper thermal incubating threshold and cause a decrease of hatching success. Importantly, male producing beaches were identified, which should be protected to balance future population viability (Fuentes *et al.,* 2009, 2010b). Further impacts to the nGBR green turtle population will occur from sea-level rise (Fuentes *et al.,* 2010a), up to 34% of available nesting area across all the selected nesting grounds may be inundated as a result of predicted levels of sea-level rise. The work suggests that low sandbanks will be the most vulnerable and nesting grounds that are morphologically more stable, less vulnerable (Fuentes *et al.,* 2010a). A vulnerability assessment (Fuentes *et al.,* 2011), for this population, indicated that in the long term reducing the threats from increased temperature may provide a greater return in conservation investment than mitigating the impacts from other climatic processes (Fuentes *et al.*, 2011).

3.14.6 Conclusions and recommendations

Despite gaps in our knowledge of how marine turtles will be impacted by climate change and their responses and ability to adapt, it is apparent that they will be affected. As discussed here, the direction and magnitude of impact will vary spatially between species and populations (Figure 3.14.5). These gaps in knowledge in conjunction with uncertainties related to climate change projections and the effectiveness of strategies in reducing climate change impacts hinders the management of marine turtles as climate change progresses (Fuentes *et al.,* 2016). Until impacts are intensified and we learn more about the effectiveness and risks of potential management strategies, prioritization should be given to strategies that enhance species resilience to changing environmental conditions by mitigating other threats (Fuentes *et al.,* 2012,2013; Hill *et al.,* 2015). Several strategies, especially those mitigating the impacts of increases in temperature at nesting beaches, have been suggested. These range from habitat protection (e.g. habitat acquisition, conservation easements) and more active and direct manipulation of nests and the nesting environment (e.g. nest shading, irrigation) (Fuentes *et al.,* 2012, 2013; Wood *et al.,* 2014; Hill *et al.,* 2015; Jourdan and Fuentes, 2015). These strategies should only be implemented when long-term observations demonstrate direct changes. For effective implementation of strategies, an understanding of the system being manipulated and the population being managed is essential (Jourdan and Fuentes, 2015), highlighting the need for systematic long-term in-water and nesting monitoring programmes throughout the globe. Further, a better understanding of how human responses to climate change will affect marine turtles and their habitat is necessary to aid management. For example, sea walls have traditionally been used to protect coastal infrastructure from tides, waves and storm surges. However, these coastal armouring structures can be detrimental to beaches, reducing and/or degrading suitable nesting habitat (Mazaris *et al.,* 2009; Witherington *et al.,* 2011). This highlights the need for a better understanding of the indirect impacts of human responses to climate change and interactions with existing non-climate threats.

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3.15 Impacts and effects of ocean warming on marine mammals

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Summary

- The principal climatic influence on marine mammal species is widely acknowledged as the relationship between ocean temperature and the availability of their prey and their regional and global distributions.
- There is increasing evidence that ocean warming, in combination with other components of climate change, is already affecting marine mammals.
- Shifts in distributions, changes in the timing of migrations, some mortality events and changes in reproductive success have all been associated with climatic factors and include movements towards the poles of warmer water species and a contraction of the ranges of those typically found in colder waters.
- It is predicted that the habitats of some marine mammals – especially those dependent on riverine systems, sea-ice, shelf waters and deep sea trenches – will be reduced.
- Climate change will interact with other variables, including exposure to chemical pollution and pathogens, to synergistically impact marine mammals, and resulting population losses may be sudden.
- The speed of change will challenge conventional conservation approaches and recommendations include improving the resilience of marine mammals to other threats such as the protection of key habitats, and the development of conservation tools that allow appropriately swift and adaptive responses to changes.

Ocean warming effects	Consequences
Changes in oceanic temperature regimes	Poleward shifts of the more mobile marine mammals and other more regional changes in feeding and breeding grounds occur
Changes in location of important marine features such as upwellings and fronts and climate-change driven changes in location and intensity of human-activities	Movement of more mobile marine mammal species into new areas, and potentially into new conflicts with human activities such as fishing Changes in distribution also bring previously isolated populations into contact with the potential for enhanced disease transmission
The timing of maximum productivity at the poles shifts	A mismatch in occurrence of productivity peaks and arrival of highly migratory whales negatively impacts their reproduction
Reduced extent of sea ice	Cetaceans that live in and around the polar ice fields are affected, as are ice-breeding seals New species enter Arctic waters Some populations may be favoured (at least at first)
Climate change-driven changes in the physical and biological nature of restricted habitats	Species with restricted habitats (e.g. deep water trenches or river/estuarine systems) decline The foraging areas of sirenians are degraded and population declines follow
Increased storminess, sea-level rise and increased rainfall	Increased mortality of land-breeding seal pups and changes in fluvial regimes negatively impact some river and estuarine species

3.15.1 Introduction

There is growing effort by the scientific community to understand, monitor and predict the effects of ocean warming (and the other aspects of climate change) on marine mammals. Predictions have generally focused on climate-driven changes in physical oceanography affecting primary producers and, through 'knock-on effects', consumers at every level of marine food chains, including those marine mammals at the very top (Learmonth *et al.*, 2006; Simmonds and Isaac, 2007; Simmonds and Elliot, 2009). Very little was published on this topic before 1997 (Nunny and Simmonds, 2016) but, in some two decades, we have moved from a lack of 'predictive power' undermining our ability to predict implications (IWC, 1997), to a position where researchers are far more comfortable linking effects to change and making predictions. International conservation organizations have started to recognize both the challenge, and the improved prospects for determining response strategies, and are striving to adapt their policies accordingly. For example, the International Whaling Commission (IWC) has held a series of related workshops (IWC, 2010). The recommendations coming from the IWC process recognize the need to continue to develop more accurate models and the need to improve our understanding of the relationship between cetacean distribution and quantifiable climatic indices (such as sea surface temperature SST). In addition, the IWC has also voiced particular concerns about those species with habitats restricted through the presence of physical barriers, such as riverine species, or populations residing in 'ecological cul-de-sacs' such as bays, coves, ocean basins (e.g. northern Indian Ocean) or seas (e.g. Mediterranean Sea) with limited ability to move to mitigate localized climate warming (IWC, 2012). The IWC has also stressed the importance of long-term datasets (for examples see Leeney *et al.*, 2008; Sabatier *et al.*, 2015).

Many whale species are highly migratory and this may put them particularly at risk as they face changes to the multiple environments occupied during their migrations (Simmonds and Elliot, 2009; Ramp *et al.*, 2015). In 2014, the body charged with the conservation of migratory species, the Convention for Migratory Species (CMS), agreed a comprehensive climate change work plan (CMS, 2014). This includes the identification and promotion of "a standardized methodology for evaluating species' vulnerability to climate change" that should incorporate the whole life cycle of the species concerned, and then, the application of this vulnerability assessment to the species on the CMS appendices. The CMS work plan also calls for the identification, evaluation, prioritization and reduction of the additional impacts on migratory species resulting from changes in human behaviour due to climate change. Further illustration of the current high level of interest in this topic was provided by the Society for Marine Mammalogy Biennial Conference in December 2015. Climate change was the focus of key-note presentations and ‘evaluating how climate change will impact marine mammal stocks and distribution patterns’ was identified as a key challenge by Eileen Sobeck, Assistant Administrator for Fisheries at NOAA in her opening address (Sobeck, 2015).

These examples serve to illustrate that the context for this review is one in which the international community has now accepted that global warming is occurring and is moving to try to address it, including those bodies concerned with marine mammal conservation. The major part of this short synthesis will draw heavily on previous in-depth reviews to elaborate current understanding. Whilst marine mammals are a relatively small taxonomic group, their biomass and position in the food web makes them ecologically important and also already the focus of significant conservation concern, with 23% of species already threatened by extinction (Kaschner *et al.*, 2011). For the purposes of this section only those mammals that are highly adapted to a life in water – specifically those in the orders Cetacea (including baleen whales, toothed whales, dolphins, porpoises and beaked whales) and Sirenia (manatees and dugongs), and the sub-order of Carnivora, Pinnipedia, (seals, sea lions and walruses) - are considered. Of these animals, only the pinnipeds spend part of their life cycle out of the water, resting and breeding on ice or land and the sirenians are the only herbivores, grazing on plant material. All others feed on fish, cephalopods, bivalves or crustaceans, with some populations of a few species - such as the orca (*Orcinus orca*) (Figure 3.15.1) - feeding on other marine mammals.

The cetaceans have the greatest species diversity of the marine mammals, and are found in all sea areas, including the deep seas and some large river systems. Tables 3.15.1 and 3.15.2 list all known cetacean species and subspecies, along with their IUCN status. In addition, there are some 33 species of pinnipeds, which are found in many sea areas but with their main concentrations nearer to the poles, and six species of sirenians, which are found in warm or tropical waters. The polar bear, *Ursus maritimus*, is not specifically considered here, except where implications for it help

3.15.1 Killer whales. © Robert Pittman / NOAA.

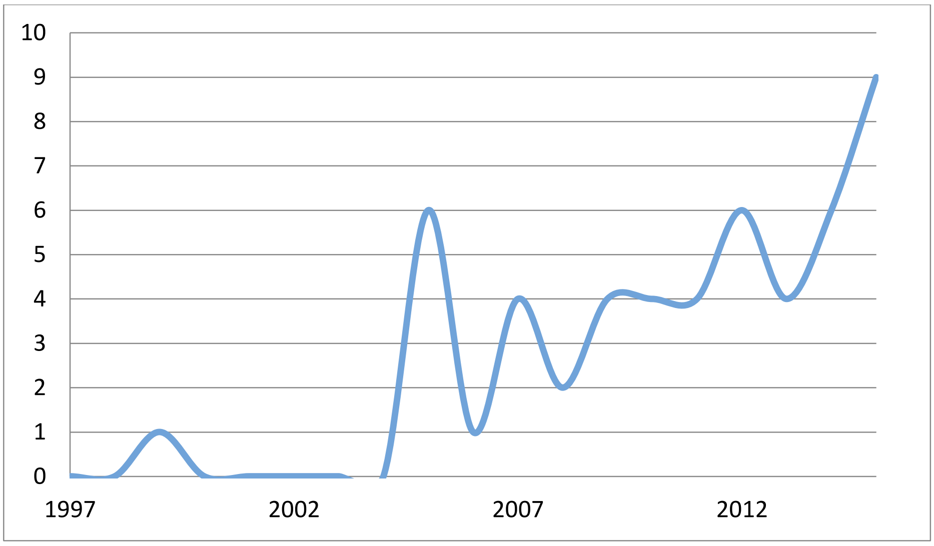

Figure 3.15.2 Number of scientific papers linking observed impacts to climate change in marine mammals 1997-2015 (N = 51).

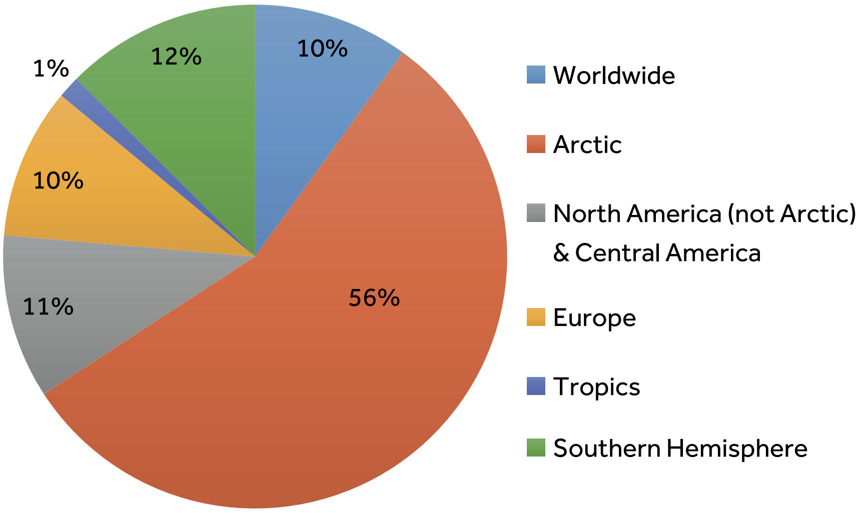

Figure 3.15.3 Regional representation of scientific papers published on marine mammals and climate change from 1997-2015, based on 352 papers drawn from database searches.

understanding of other marine mammals, but there is a substantial literature about the implications of climate change for this species.

3.15.2 Trends and impacts

3.15.2.1 General trends

Figure 3.15.2 illustrates the increase in the scientific literature that now links observed changes in marine mammal populations to climate (Nunny and Simmonds, 2016). This reflects not just a growing interest in this topic but that measurable changes are already occurring which are being attributed to a changing climate. The Arctic is a primary focus of climate studies (Figure 3.15.3) which is no surprise given the speed of change there (described below and Section 3.16). Equally marked is the apparently low level of interest and engagement in some other regions (notably the Tropics) and in certain taxa (i.e. beaked whales and river dolphins).

Few authors separate 'global warming' from 'climate change' but instead generally integrate all the effects of a changing climate when considering the implications for marine mammals. Hence a similar approach is taken here.

3.15.2.2 Drawing from expert syntheses

The distributions of marine mammals are strongly linked to temperature with some species only found at the poles, some in the tropics and others, such as blue whales (Figure 3.15.4) regularly migrating between high productivity polar feeding grounds and warmer breeding areas. The scale and breadth of the scientific literature now available, combined with the number of marine mammal species and their widely differing habitats,

Figure 3.15.4 Blue whale. © John Durban and Michael Moore (WHOI): research was conducted under Chilean permit MERI-488-FEB-2015.

makes a short review challenging and this synthesis takes particular note of several recent substantive reviews which help further identify important trends, impacts and key issues. Learmonth *et al*. (2006), for example, described the potential for warmer water species to spread and potentially increase their populations, whilst colder water species, including those with habitat restricted to the continental shelf region ('shelf-species'), could lose habitat. Such concerns were also expressed by Macleod *et al*. (2005, 2008) and Whitehead *et al*. (2008). Kaschner *et al*. (2011) took this further in a substantive modelling exercise which showed potential redistributions. Learmonth *et al*. (2006) also highlighted the vulnerability of species either associated with sea ice or which live in fresh waters and which, therefore, have restricted habitat. Table 3.15.1 shows Learmonth's predictions along with the current (i.e. 2008) IUCN categories (apart from 'data deficient' species), and which species or populations are listed on CMS appendix 1, meaning that the convention classifies them as endangered.

Table 3.15.1 Species of Cetaceans according to IUCN status (not including data deficient species) and the potential effects of Climate Change

Key: Species are grouped by IUCN status; EX – Extinct; CR – Critically Endangered; EN – Endangered; VU – Vulnerable; LR/cd – Lower Risk: conservation dependent; NT – Near Threatened; LC – Least Concern (2008 IUCN categories). CMS column gives where species is listed on Appendix 1 of the Convention for Migratory Species (CMS). CC Impact: I = Predicted increase in population; D= Predicted decrease in population; ? = unknown (Learmonth et al*, 2006).*
**Risk here refers to the conclusions of Davidson* et al*. (2012) and X shows those species which their analysis suggested were particularly at risk.*

Species/Subsp./Subpop.	Common name	Taxonomic level	CMS	CC impact	Risk*
Critically Endangered (CR) / Extinct (EX)					
Lipotes vexillifer	Baiji	species		D	X
Critically Endangered (CR)					
Balaena mysticetu	Svalbard-Barents Sea bowhead whale	subpopulation			
Balaenoptera musculus intermedia	Antarctic blue whale	subspecies			
Cephalorhynchus hectori maui	Maui's dolphin	subspecies			
Delphinapterus leucas	Cook Inlet beluga whale	subpopulation			
Eschrichtius robustus	Northwest Pacific gray whale	subpopulation			
Eubalaena australis	Chile-Peru right whale	subpopulation	1		
Eubalaena japonica	Northeast Pacific right whale	subpopulation			

Species/Subsp./Subpop.	Common name	Taxonomic level	CMS	CC impact	Risk*
Orcaella brevirostris	Ayeyarwady River I. dolphin	subpopulation			
Orcaella brevirostris	Mahakam River I. dolphin	subpopulation			
Orcaella brevirostris	Malampaya Sound I. dolphin	subpopulation			
Orcaella brevirostris	Mekong River I. dolphin	subpopulation			
Orcaella brevirostris	Songkhla Lake I. dolphin	subpopulation	1		
Phocoena phocoena	Baltic Sea harbour porpoise	subpopulation			
Phocoena sinus	Vaquita	species		D	X
Sousa chinensis	Eastern Taiwan Strait humpback dolphin	subpopulation			
Endangered (EN)					
Balaena mysticetus	Okhotsk Sea bowhead whale	subpopulation			
Balaenoptera borealis	Sei whale	species		?	X
Balaenoptera musculus	Blue whale	species	1	?	X
Balaenoptera physalus	Fin whale	species	1	?	X
Cephalorhynchus hectori	Hector's dolphin	species		D	X
Delphinus delphis	Mediterranean Common dolphin	subpopulation	1		
Eubalaena glacialis	North Atlantic right whale	species	1	?D	
Eubalaena japonica	North Pacific right whale	species	1		X
Megaptera novaeangliae	Arabian Sea humpback whale	subpopulation			
Megaptera novaeangliae	Oceania humpback whale	subpopulation			
Neophocaena phocaenoides asiaeorientalis	Yangtze finless porpoise	subspecies			
Phocoena phocoena relicta	Black Sea harbour porpoise	subspecies			
Platanista gangetica	South Asian river dolphin	species		D	X
Platanista gangetica gangetica	Ganges dolphin	subspecies	1		
Platanista gangetica minor	Indus river dolphin	subspecies			
Tursiops truncatus ponticus	Black Sea bottlenose dolphin	subspecies	1		
Vulnerable (VU)					
Balaenoptera musculus musculus	North Atlantic blue whale	subpopulation			
Delphinus delphis ponticus	Black Sea common dolphin	subspecies			
Neophocaena phocaenoides	Finless porpoise	species		?	X
Orcaella brevirostris	Irrawaddy dolphin	species		D	X
Physeter macrocephalus	Sperm whale	species	1	?	X
Pontoporia blainvillei	Franciscana	species	1	D	X
Pontoporia blainvillei Franciscana	Rio Grande do Sul/Uruguay subpopulation				
Sousa teuszii	Atlantic humpback dolphin	species	1	?	
Stenella longirostris orientalis	Eastern spinner dolphin	subspecies			
Lower Risk / conservation dependent (LR/cd)					
Balaena mysticetus bowhead whale	Bering-Beaufort-Chukchi Sea subpopulation				
Balaenoptera musculus musculus	North Pacific blue whale	subpopulation			
Near Threatened (NT)					
Cephalorhynchus eutropia	Chilean dolphin	species		?	
Delphinapterus leucas	Beluga whale	species		D	

Species/Subsp./Subpop.	Common name	Taxonomic level	CMS	CC impact	Risk*
Monodon monoceros	Narwhal	species		D	
Orcaella heinsohni	Australian snubfin dolphin	species		-	
Sousa chinensis	Indo-Pacific humpback dolphin	species		?	X
Least Concern (LC)					
Balaena mysticetus	Bowhead whale	species	1	D	
Balaenoptera acutorostrata	Common minke whale	species		?	
Delphinus delphis	Short-beaked common dolphin	species		?I	
Eschrichtius robustus	Gray whale	species		?	
Eubalaena australis	Southern right whale	species		?D	
Grampus griseus	Risso's dolphin	species		?	
Hyperoodon planifrons	Southern bottlenose whale	species		?	
Lagenodelphis hosei	Fraser's dolphin	species		?I	
Lagenorhynchus acutus	Atlantic white-sided dolphin	species		?D	
Lagenorhynchus albirostris	White-beaked dolphin	species			
Lagenorhynchus cruciger	Hourglass dolphin	species		?D	
Lagenorhynchus obliquidens	Pacific white-sided dolphin	species		?D	
Lissodelphis borealis	Northern right whale dolphin	species		?	
Megaptera novaeangliae	Humpback whale	species	1	?	
Peponocephala electra	Melon-headed whale	species		?I	
Phocoena phocoena	Harbour porpoise	species		?D	
Phocoenoides dalli	Dall's porpoise	species		?	
Stenella attenuata	Pantropical spotted dolphin	species		I	
Stenella coeruleoalba	Striped dolphin	species		?I	
Steno bredanensis	Rough-toothed dolphin	species		?	
Tursiops truncatus	Common bottlenose dolphin	species		I	
Ziphius cavirostris	Cuvier's beaked whale	species		?	
Ziphius cavirostris	Mediterranean Cuvier's beaked whale	subpopulation	1	?	

This illustrates the large number of threatened or endangered species, where climate change may be expected to make their circumstances worse. Table 3.15.2 shows the 45 cetacean species that continue to be categorized as 'data deficient' set against the same risk assessments as used in Table 3.15.1. The unclear status of so many species is itself of concern in conservation terms and undermines future action for them. Several may face population declines.

Table 3.15.2 IUCN Data Deficient (DD) species of cetaceans and potential effects of climate change

Key: CC Impact: I = Predicted increase in population; D= Predicted decrease in population; ? = unknown (Learmonth et al.*, 2006). *Risk here refers to the conclusions of Davidson* et al. *(2012) and X shows those which their analysis suggested were at risk.*

Species/Subsp./Subpop.	Common name	Taxonomic level	CC impact	Risk*
Balaenoptera bonaerensis	Antarctic minke whale	species	?	X
Balaenoptera edeni/brydei	Bryde's whale complex	species		
Balaenoptera m. brevicauda	Pygmy blue whale	subspecies		
Balaenoptera omurai	Omura's whale	species		
Berardius arnuxii	Arnoux' beaked whale	species	?	
Berardius bairdii	Baird's beaked whale	species	?	X
Caperea marginata	Pygmy right whale	species	?D	
Cephalorhynchus commersonii	Commerson's dolphin	species	D	X
Cephalorhynchus heavisidii	Heaviside's dolphin	species	?	
Delphinus capensis	Long-beaked common dolphin	species	?I	
Feresa attenuata	Pygmy killer whale	species	?I	

Species/Subsp./Subpop.	Common name	Taxonomic level	CC impact	Risk*
Globicephala macrorhynchus	Short-finned pilot whale	species	?I	
Globicephala melas	Long-finned pilot whale	species	?	
Hyperoodon ampullatus	Northern bottlenose whale	species	D	
Indopacetus pacificus	Tropical bottlenose whale	species	?	
Inia geoffrensis	Boto	species	D	X
Kogia breviceps	Pygmy sperm whale	species	I	
Kogia sima	Dwarf sperm whale	species	I	
Lagenorhynchus australis	Peale's dolphin	species	?	X
Lagenorhynchus obscurus	Dusky dolphin	species	?D	
Lissodelphis peronii	Southern right whale dolphin	species	?	
Mesoplodon bidens	Sowerby's beaked whale	species	?	
Mesoplodon bowdoini	Andrew's beaked whale	species	?	X
Mesoplodon carlhubbsi	Hubb's beaked whale	species	?	X
Mesoplodon densirostris	Blainville's beaked whale	species	?	
Mesoplodon europaeus	Gervais' beaked whale	species	?I	
Mesoplodon ginkgodens	Ginkgo-toothed beaked whale	species	?	
Mesoplodon grayi	Gray's beaked whale	species	?	
Mesoplodon hectori	Hector's beaked whale	species	?	X
Mesoplodon layardii	Strap-toothed whale	species	?	
Mesoplodon mirus	True's beaked whale	species	?I	
Mesoplodon perrini	Perrin's beaked whale	species	?	X
Mesoplodon peruvianus	Pygmy beaked whale	species	?	X
Mesoplodon stejnegeri	Stejneger's beaked whale	species	?	
Mesoplodon traversii	Spade-toothed whale	species	?I	
Orcinus orca	Killer whale	species	?	
Phocoena dioptrica	Spectacled porpoise	species	?D	
Phocoena spinipinnis	Burmeister's porpoise	species	?	
Pseudorca crassidens	False killer whale	species	?I	
Sotalia fluviatilis	Tucuxi	species	D	
Stenella clymene	Clymene dolphin	species	?	
Stenella frontalis	Atlantic spotted dolphin	species	?I	
Stenella longirostris	Spinner dolphin	species	I	
Tasmacetus shepherdi	Shepherd's beaked whale	species	?	X
Tursiops aduncus	Indo-Pacific bottlenose dolphin	species	?	

Learmonth *et al*. (2006) also considered pinnipeds and sirenians. For the Antarctic fur seal, *Arctocephalus gazella*, Galápagos fur seal, *Arctocephalus galapagoensis*, Galápagos sea lion, *Zalophus wollebaeki*, Steller sea lion, *Eumetopias jubatus*, walrus, *Odobenus rosmarus*, bearded seal, *Erignathus barbatus*, spotted seal, *Phoca largha*, ringed seal, *Pusa hispida*, Caspian seal, *Pusa caspica*, Baikal seal, *Pusa sibirica*, grey seal, *Halichoerus grypus*, ribbon seal, *Histriophoca fasciata*, harp seal, *Pagophilus groenlandicus*, hooded seal, *Cystophora cristata* and Mediterranean monk seal, *Monachus monachus*, they suggested that climate change might drive population declines. They made the same prediction for the southern elephant seal, *Mirounga leonina*, northern elephant seal, *Mirounga angustirostris*, Weddell seal, *Leptonychotes weddellii*, Ross seal, *Ommatophoca rossii* and crabeater seal, *Lobodon carcinophaga*. For the sirenians, they suggested that the West Indian manatee, *Trichechus manatus*, might increase its population but made no predictions for the other species.

Laidre *et al*. (2008) also made a comprehensive assessment of the possible consequences of climate change by applying a vulnerability index to Arctic cetaceans. In the case of the narwhal, (Figure 3.15.5) they noted that it was the most specialized of the Arctic cetaceans and highly adapted to a habitat of pack ice with only limited open water in the winter period. They commented that 'no other cetacean species occupies such dense winter sea ice cover for such a long period of time'. In total they used nine criteria to evaluate species including population size and habitat specificity. The narwhal scored the lowest of the 11 species considered and hence is potentially the most vulnerable. Simmonds and Smith (2009) trialled an extended version of this sensitivity index to consider other cetaceans and proposed a number of other potential criteria, including the predicted 'increased competition' that might result when species expand their ranges.

Risk to marine mammals was also considered by Davidson *et al*. (2012) who used 'powerful machine-learning and spatial-modelling approaches' to make their predictions. Rate of offspring production was the most important predictor of risk and the most at-risk species occur in coastal areas and in productive regions of the high seas. Some species at risk were not on the IUCN red list; for example, all the beaked whale species. This analysis also suggested that several seal species and the South American manatee (*Trichechus inunguis*), the West Indian manatee and West African manatee (*Trichechus senegalensis*) were also at risk (Figure 3.15.6).

Figure 3.15.5 Narwhal. © Paul Nicklen, SeaLegacy.

Another risk analysis was made by Schumann *et al*. (2013). They focused on the 52 marine mammal species recorded from the coasts of the Australian continent and Australia's Subantarctic islands. They systematically considered both observed and predicted impacts. Table 3.15.3 summarizes their findings.

Table 3.15.3 Summary of observed and predicted effects of climate change on marine mammals, after Schumann *et al.* (2013)

The bracketed terms 'Low-Medium', 'Low High' etc. refer to the amount of evidence and level of assessment' as determined by Schumann et al. (2013) ; Associations" refers to examples supported by one or more published works. Additional material and commentary not summarized from Schumann et al. (2013) are indicated by text in italics.

Observed Relationship (Confidence Level of Assessment)	**Associations**	**Predicted Future Change**
A. Ocean and air temperature (Low-Medium)		
I. Foraging locations and SST	6	Possible physiological response (dolphins); potential alteration in foraging behaviour (pinnipeds) *(*See also Henderson *et al.,* 2014*)*
II. Distribution shifts in response to warmer SST	2	Likely expansion of range of tropical/temperate species; cold water species range contraction; loss of habitat of shelf species may cause extinction; longer migrations; regime shift; exposure to novel pollutants and pathogens. *(*see also Azzellino *et al.,* 2008*)*
III. Effects of a reduction in sea ice	1	Blue whales may be capable of exploiting foraging areas and/or prey, but likely to be adversely affected; reproduction rates in blue whales and pinnipeds that exploit pack ice experience reduced
IV. Reproductive success in relation to SST	3	Reduced reproductive output and survival of first year pups; potential for mismatch between prey availability and critical life history stages
V. Changes in reproductive systems and success	3	Potential reduction in maternal investment and greater exposure to predation in pinnipeds; possible increase in energy expended to stay cool which may impact pup survival
VI. Disease outbreaks	1	With higher ambient temperatures, pathogens may spread more rapidly through pinniped populations especially if they are large/increasing

Observed Relationship (Confidence Level of Assessment)	Associations	Predicted Future Change
B. Frequency and severity of extreme events (Low-High)		
I. Reduction in water quality through floods	2	Unknown
II. Exposure to novel diseases through floods	1	Increase in transport of pollutants and pathogens into coastal waters
III. Storms and cyclones cause strandings	3	More frequent stranding events likely, with shallow inshore species likely to be most at risk (although species normally living close to shore may be better adapted to shallow conditions)
IV. Cyclones and flooding decimate important habitats	3	Potential effects on seagrass beds and species associated with them (i.e. dugongs)
V. Reproduction and ocean conditions	2	Reproductive success may be affected by rougher conditions (i.e. humpback and southern right whale calves may be adversely affected and seal pups drown after being washed into the ocean)
C. Ocean currents, winds and circulation (Low)		
I. Upwelling and higher coastal productivity	2	Enhanced upwelling may benefit marine mammals through more abundant prey
II. Ocean currents and upwelling improve reproductive success	1	Increased wind may bring fish prey within range (i.e. Australian fur seals in Bass Strait)
III. More frequent stranding events with increased winds	1	Coastal productivity increased which may produce more frequent strandings
D. Changing Ocean Currents (Very Low – no direct associations)		
Changes in ocean currents may affect ocean productivity	1	Changes in prey distribution and abundance expected – with ‘flow-on effects’ for marine mammals
E. Rising Sea Level (Very Low – no direct associations)		
Rising sea levels may reduce available breeding area	1	Potential reduction in breeding habitat may cause reduced reproductive output (another example could be Mediterranean monk seals breeding in caves may be vulnerable as may other seal species breeding on the sea shore)
F. Ocean acidification (Very Low – no direct associations)		
Ocean Acidification adversely affects prey of marine mammals	1-2	Impacts on Antarctic krill unclear; potential range shifts and changes in prey abundance with follow on effects for marine mammals

Recognizing the rapid rate of change in the Arctic, Laidre *et al.* (2015) highlighted the situation of 11 Arctic species: the narwhal, beluga, and bowhead whales; ringed, bearded (*Erignathus barbatus)*, spotted, ribbon, harp and hooded (*Cystophora cristata)* seals, the walrus, *Odobenus rosmarus* (Figure 3.15.7), and the polar bear. They report that in all Arctic regions, the duration of the summer (i.e. reduced ice) period has increased by 5–10 weeks, except in the Barents Sea where it has increased by >20 weeks between 1979 and 2013. For most Arctic marine mammals, trend data are absent or poor (Laidre *et a.l,* 2015). Many species are also still recovering from previous over-exploitation, which could mask any reduction in carrying capacity associated with climate-change driven habitat loss. In addition, increased biological productivity could, for an unknown period, offset potential negative impacts of sea ice loss and result in transient or longer term population increases. For example, some bowhead whale subpopulations have apparently shown positive population growth concurrent with regional sea ice loss (Laidre *et al.*, 2015) and from 1989 to 2011, the body condition of harvested BCB bowhead whales has improved during this period of reduction in sea ice (George *et al.*, 2015). By contrast, Beaufort Sea ringed seal body condition and productivity declined from 1992 to 2011 (Harwood *et al*, 2012). Laidre *et al*. (2015) concluded that the sea ice forecasts for the next 50–100 years indicate serious threats to many Arctic marine mammals. The longer periods of open water in the region also make it more attractive for oil and gas prospecting, shipping keen to exploit shorter international routes, and commercial fisheries. Reeves *et al.* (2014) noted that more than half the circumpolar range of Arctic cetaceans overlaps with known or suspected offshore oil and gas deposits and the threats associated with oil and gas development include human-generated underwater sound, ship strikes, displacement from critical habitat, and the risk of accidental or illegal discharge of oil.


Figure 3.15.6 Manatee. © Richard Wylie.


Figure 3.15.7 Walrus. © Doug Gould / Marine photobank.

Some other recent studies have also looked at particular regions. For example, Ramp *et al*. (2015) have recently shown that fin (Figure 3.15.8) and humpback whales have both shifted their date of arrival at their feeding grounds in the Gulf of St Lawrence (Canada) at a rate of more than one day per year earlier during the period 1984-2010. This meant that the two species also maintained an approximately 2-week difference in their arrival times, enabling the maintenance of temporal niche separation. Ramp *et al.* (2015) state that this trend in arrival was strongly related to earlier ice break-up and rising sea surface temperature, likely triggering earlier primary production. Whilst this shows some adaptability by the whales the authors doubt that the whales can keep pace with the rate of warming of the oceans. Similarly, in the Norwegian Sea, which is both an important migration corridor for baleen whales swimming towards northern feeding grounds and an important feeding ground for minke, humpback and fin whales, Nøttestad *et al*. (2015) reported that a reduction in minke whale abundance over the last decade and their prey species (krill and amphipods) may have shifted north. Similarly, Heide-Jorgensen *et al*. (2010) report that harbour porpoises in West Greenland may be responding to warmer waters there with longer residency times and improved body condition. Gambaiani *et al.* (2009) raise concerns for the Mediterranean including future 'trophic web mismatches' there, increased disease events and toxic algal blooms. They note that the presence of the euphausiid species *Meganyctiphanes norvegica* - the primary food of fin whales in the Mediterranean - correlates with specific hydro-biological parameters and

Figure 3.15.8 Fin whale. © Aqqa Rosing-Asvid.

that this may put them at considerable risk if conditions become unfavourable for this planktonic species.

3.15.2.3 Lessons from the distant past

There are a growing number of palaeobiological studies, especially focused on fossil and other preserved remains and ancient DNA, which consider how climate change might affect marine mammals (Nunny and Simmonds, 2016). For example, Mannino *et al.* (2015) showed that the rapid climate change that occurred around 8,200 years ago coincided with increased strandings in north-west Sicily (Italy). Similarly, Alter *et al*. (2015) have considered the palaeobiology of the gray whale, which is currently present in the Pacific but not the Atlantic. Using a combination of ancient and modern DNA, radiocarbon dating and predictive habitat modelling, they showed that dispersal between the Pacific and Atlantic was climate-dependent and occurred both during the Pleistocene, prior to the last glacial period, and the early Holocene immediately following the opening of the Bering Strait. Genetic diversity in the Atlantic declined over an extended interval that predates the period of intensive commercial whaling. This decline may have been precipitated by Holocene climate or other ecological causes. These first genetic data for Atlantic gray whales, particularly when combined with predictive habitat models for the year 2100, suggest that two remarkable recent sightings of gray whales in the Atlantic (off the coasts of Israel and South Africa) may represent the beginning of the expansion of this species' habitat.

While ancient DNA can give a useful long-term perspective on species distributions, system-wide ecological changes brought on by changing climate make it difficult to predict outcomes for most taxa (Alter *et al.*, 2015). Palaeobiological studies that show that marine mammals (and other species) have survived climate change in the past cannot be taken to indicate that today's species will adapt to the current situation given the speed of current changes.

3.15.3 Consequences

3.15.3.1 Overarching issues likely to affect many populations

The abilities of tropical and warmer water species to expand into colder regions are limited by their thermoregulatory abilities. Warming oceans and the associated effects of climate change, including the retreat of Arctic ice, are expected to change this (and, as noted above, there is evidence of this already happening). Some climate change-driven changes may be swift. Epizootics, for example, could cause rapid population crashes. Ice-dependent species and others with restricted habitats from which they cannot easily disperse to find prey or equivalent habitat, such as river dolphins and beaked whales or cetaceans resident in semi-enclosed seas (the Black Sea being an extreme example), may be most vulnerable.

Attention has tended to focus on the effects of climate change directly on animals or marine food chains, but the impacts created by climate change-driven changes in human activities may prove to be equally, or more, important. Alter *et al*. (2010) considered these 'tertiary effects' noting for example that:

- human food security problems might create a greater human reliance on marine species leading to prey depletion or even further directed takes of marine mammals;
- warming of high latitude waters may be associated with an increase in aquaculture causing increased culling of local marine mammals and local eutrophication; and
- increases in construction work in the coastal zones, rivers and estuaries - in part perhaps to help to address shifting weather patterns - may cause increased changes in habitat including fragmentation of those species associated with fresh waters.

Some changes in human activities might also have some positive effects by removing negative pressures; for example if the fishing operations causing bycatch decline or move.

The potential synergistic effects of chemical pollution, disease and climate change have recently been highlighted for polar bears, for which climate change may cause prolonged fasting and emaciation resulting in increases in tissue concentrations of persistent organic pollutants (POPs) increasing the probability for pollutant levels to exceed threshold levels for effects on health, and thus impacting on reproductive success and survival (Jenssen *et al.*, 2015). The same may apply to some other marine mammal species, noting recent increased concerns about POPs, especially PCBs, which, despite regulations and mitigation measures, continue to impact cetacean top predators in European seas (Jepson *et al.*, 2016).

Moreover, a change in environmental parameters like salinity might trigger more physiological stress and make cetaceans more susceptible to diseases or anthropogenic pressures (Learmonth *et al.*, 2006). The interplay between climatic conditions, pollution and disease in marine mammals has been a 'hot topic' for many years (e.g. Simmonds and Mayer, 1997). Van Bressem *et al*. (2009) concluded that environmental factors played a role in the emergence and pathogenicity of a range of cetacean diseases, including morbillivirus epizootics, the cause of many marine mammal mass mortalities. On this basis they suggest that inshore and estuarine species are most at risk because their habitats are often severely altered by anthropogenic factors, including climate change. Additionally, raised temperatures and eutrophication may cause increased exposure to toxic algal blooms. Figure 3.15.9 shows how some variables may interact – moving from top to bottom through physical changes, to habitat and then population-level changes.

Some species may, at least initially, be favoured, by changes in temperature and other features of their environment. Indeed, Kaschner *et al*. (2011) suggest that their modeling approach indicates that, over the course of the next 40 years, negative effects such as net range contractions may be modest for most species, while a number of species might benefit from substantial increases in optimal habitat.

3.15.3.2 Freshwater-dependent cetaceans

Freshwater-dependent cetaceans may be especially vulnerable to climate changes because of their restricted habitat, although Braulik *et al*. (2015), in their assessment of the Indus river dolphin, suggested that predicted increased rainfall might favour this species. Generally, these species can be expected to be vulnerable to changes in fluvial regimes resulting from increased or decreased rainfall and violent climatic events. Smith and Reeves (2010) comment that 'it seems unlikely that we will know enough, soon enough, to devise, much less implement, mitigation measures for preventing or moderating climate change-related impacts on freshwater-dependent cetaceans'. They recommend that key habitat characteristics related to upstream hydrology and, in the case of estuaries, tidal height and flux are identified and management attention directed towards them. Measures in such areas of particularly high conservation value, could include restriction of fishing, avoidance of water development, and encouragement of nature-oriented tourism to give local economic value to the river dolphins.

3.15.3.3 Oceanic cetaceans (temperate and tropical)

Oceanic cetaceans are largely expected to shift their distributions to adapt to changes in prey and physical conditions. However, there are important exceptions to this, including those species where new habitat cannot

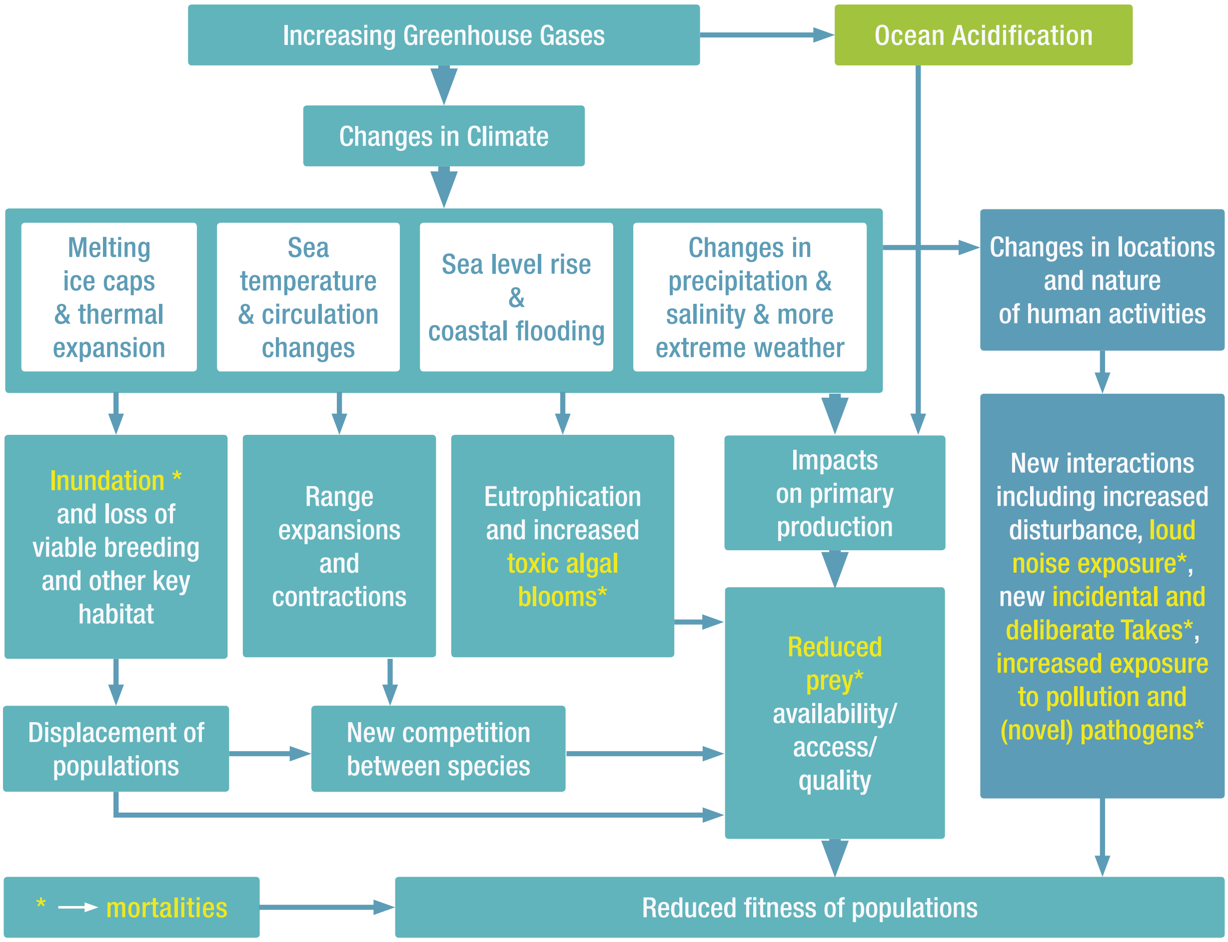

Figure 3.15.9 Some of the potential interactions between climate change and effects on marine mammal populations. *From top to bottom physical changes (inside yellow box) are linked to habitat effects and then impacts on species in the yellow boxes below. The red text and asterisks indicate where mass mortalities may occur. The blue boxes shown 'tertiary effects' – where changes in human behavior caused by climate change might be expected to impact marine mammals. The thicker blue arrows denote the stronger linkages.*

be easily accessed. Examples might include fin whales in the Mediterranean Sea and small cetaceans in the Black Sea. Furthermore, 'shelf species' in the Northern Hemisphere may not be able to find habitat if conditions push them northwards and the highly migratory species in general may be especially vulnerable because they need to find certain conditions at certain times. A mismatch between their arrival times in feeding grounds and blooms of productivity might be a particular concern, as might the loss of 'phenological cues' (environmental triggers) for migration or other key behaviour.

The situation of the critically endangered North Atlantic right whale (Figure 3.15.10) is perhaps illustrative. During the 1990s, low prey availability significantly reduced calf production and, in combination with a high mortality rate, the right whale population declined (Meyer-Gutbrod *et al.*, 2015). It is now apparent that much of the decadal variability in the population's recovery rate is driven by changes in prey availability linked to climate-associated ecosystem regime shifts. Meyer-Gutbrod *et al*. (2015) state that understanding the responses of this species to such regime shifts will be critical to developing an ecosystem-based management perspective for it and that this will not alter the importance of reducing all anthropogenic sources of mortality. Similarly, Zerbini *et al*. (2015) theorize that the habitat use of the critically endangered North Pacific right whale in the North Pacific varies because of concomitant changes in the abundance of the whale's primary copepod prey. Both right whale species are also negatively impacted by various human activities.

3.15.3.5 Oceanic cetaceans (Arctic and Antarctic species)

Potential impacts on Arctic marine mammals include loss of ice-edge habitat, entrapment in sea-ice (through rapid and atypical changes in ice conditions), enhanced competition with species moving into newly ice-free waters and enhanced interactions with human activities. The situation appears more acute in the Arctic than in

Figure 3.15.10 North Atlantic right whale. © Regina Asmutis-Silva / WDC.

the Southern Ocean but there are significant concerns there too and especially regarding loss of prey.

Laidre *et al*. (2015) made a number of important recommendations for conservation of Arctic species. In summary they called for (i) 'effective co-management' by local and governmental entities and that, given the fast pace of ecological change in the Arctic and uncertainty in how populations will respond, it will need to be flexible and adaptive; (ii) improved monitoring of Arctic marine mammals further to careful consideration of objectives; (iii) coherent species protection legislation, and they add that international agreements may be needed to protect key Arctic marine mammal habitats in some regions including the Northwest and Northeast Passages and Bering Strait (key areas of interest for shipping); and (iv) 'forward looking conservation that will include communicating accurate information to the public on topics such as regional variability in Arctic marine mammal responses to reduced ice, lack of baselines, scientific uncertainty in data, and a future Arctic ecosystem that may contain a different marine mammal species assemblage.

3.15.3.6 Deep-diving beaked whales

The habitat requirements of some beaked whales may be as restrictive as those of river dolphins. If the deep underwater canyons where they live and feed become inhospitable (perhaps if circulations and or temperatures change), how easy will it be for them to disperse to similar but still favourable habitat?

3.15.3.7 Pinnipeds (ice dependent species and others)

Species that breed or haul out on ice are expected to be negatively impacted and young pups of shore-breeding species (Figure 3.15.11) may be vulnerable to coastal inundation caused by sea-level rise and increased severe weather events (which could also affect ice and cave breeding seals) which may cause them to drown and this, in due course, may cause population level effects.

Figure 3.15.11 Atlantic grey seal – mother and pup. ©John M Baxter.

3.15.3.8 Sirenians

The situation of these warm water herbivores is somewhat different to that of the other marine mammals and, as noted, far less has been published about them with respect to climate impacts. However, their vulnerability to loss of feeding areas has already been shown in Australia (Schumann *et al.*, 2013). The seagrass which many feed on will be negatively affected if sea-level rise and storms causing increased turbidity reduce light penetration and otherwise disturb them.

3.15.4 Conclusions and recommendations

Although reduction of greenhouse gas emissions is the primary solution for mitigating long-term future warming, this phenomenon will, at best, continue for some time and we must be prepared to deal with unprecedented and rapid environmental changes and their effects on wildlife. Our current conservation tools may not be fully appropriate to this considerable new challenge. Some species and regions are better studied and monitored than others (improving our predictive powers for them) but this obviously does not mean that marine mammals elsewhere may not be significantly impacted. For example, Weir *et al*. (2014) identify increasing pressures in the Tropical Atlantic but also a significant lack of baseline studies.

As responses and plans are developed, we will have to allow for the fact that the circumstances of many marine mammal populations remain poorly known (e.g. Table 3.15.2), presenting considerable problems for their conservation. All models are enhanced by good quality long-term data sets, emphasizing the importance of long-term studies. Is there any one modelling approach or combination of approaches that we should now be investing in?

Marine mammals also offer a particular challenge because monitoring their populations (most often through ship or aircraft- based survey) is typically expensive and may compete with the costs of other more direct conservation actions. Perhaps new autonomous monitoring equipment (drones and acoustic devices) may offer a cost-effective way forward.

The IUCN as a world-leader in conservation also needs to adapt to the challenge of climate change. The integration of climate change considerations into the Red List evaluations for all marine mammals would seem sensible but as a primary driver of conservation, will the Red List process be swift enough to adapt to rapid population changes? Similarly, there is a challenge to the marine protected areas that may be established for marine mammals if those same animals then move outside of the delineated areas. Larger protected areas, the ability to rapidly change boundaries and more mobile protection may be needed.

More generally, climate change is a challenge to the concept of ‘sustainability’ as a conservation driver. The term ‘sustainability’ has increasingly replaced ‘conservation’ in the lexicon of international bodies but as conditions change – sometimes in unexpected ways – being able to safely predict that an action is sustainable Will be increasingly difficult. Returning to a more precautionary approach would appear sensible and, as marine mammals are beset by many other threats, including bycatch and pollution, this should include urgent actions to address non-climate driven threats in order to aid the resilience of marine mammal populations.

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3.16 Impacts and effects of ocean warming on Arctic ecosystems and species

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Summary

- The predictions of the changes in the Arctic are highly variable and site specific.
- The Arctic basins are likely to become more productive due to a shift from light limitation to nutrient limitation.
- As the sea ice withdraws the availability of ice-associated zooplankton and other invertebrates will be affected which will have an impact on the Arctic food chains where the polar cod is an essential link providing critical feed for seabirds and marine mammals.
- Sub-Arctic species will expand northward and compete with the Arctic species.
- Due to the reduction in sea ice it is highly likely that there will be reductions in the distribution and abundance of seals and walrus.
- Pack ice breeding seals will experience reproductive failures more frequently as their late winter/early spring breeding becomes affected, such impacts are already being observed in the Atlantic sector of the Arctic.
- Polar bears are likely to become extirpated within 50 to 70 years over most of their present range.

Ocean warming effects	Consequences
Increased temperature	Increased melting of sea ice, which will impact species and ecosystems dependent on it: seals, polar bears, walrus and endemic Arctic whales, and with the distinct risk that some of these will become extinct The Arctic ecosystem will become more productive and benthic productivity may be lost while pelagic productivity increases Increasing movement of sub-Arctic species into the Arctic Sea, with likely negative consequences to the true Arctic Sea species
Increased stratification	Will temporarily affect the productivity
Decreasing sea ice coverage	Declines in the populations of sea ice dependent animals including polar bears and seals Impacts also on walrus as these will have to breed on land and this will increase their predation over relatively smaller areas Primary productivity from phytoplankton rather than ice algae, which will decrease food availability for polar cod which will impact a number of other species feeding on the polar cod
Increasing human presence	Will affect ecosystems and biodiversity in a number of ways, due to impacts from increasing fishing, exploration and production of oil and gas, tourism, etc. which all will result in increased disturbance, pollution, etc.

3.16.1 Introduction

3.16.1.1 The physical and chemical background

Global warming since the 1970s has resulted in warming also of the Arctic Region (see for example Lawrence *et al*., 2008; Screen *et al.,* 2012; Perlwitz *et al*., 2015). There is in fact a lot of evidence indicating that the Arctic temperatures have risen more dramatically relative to those at lower latitudes. Whereas the average global warming has been estimated to be about 0.17°C per decade during the last three decades, the warming in the Arctic during the same period is estimated at some 0.60±0.07°C (Vaughan *et al.,* 2013). Hence air temperatures over the Arctic Ocean have increased 1 to 2°C since 1980. As a result of the increased temperature, areas covered with ice and snow have decreased relative to open water and snow free land. This has led to a change in albedo which is considered the main reason for the amplification of the warming in the Arctic. The rise of temperature, often referred to as Arctic Amplification (AA), is particularly pronounced in the autumn and early winter (Screen *et al.*, 2012, 2013). The reductions in sea ice are likely to continue throughout this century, and the Arctic seas may be seasonally ice-free within a few decades (Meier *et al.*, 2011) (See Figure 3.16.1).

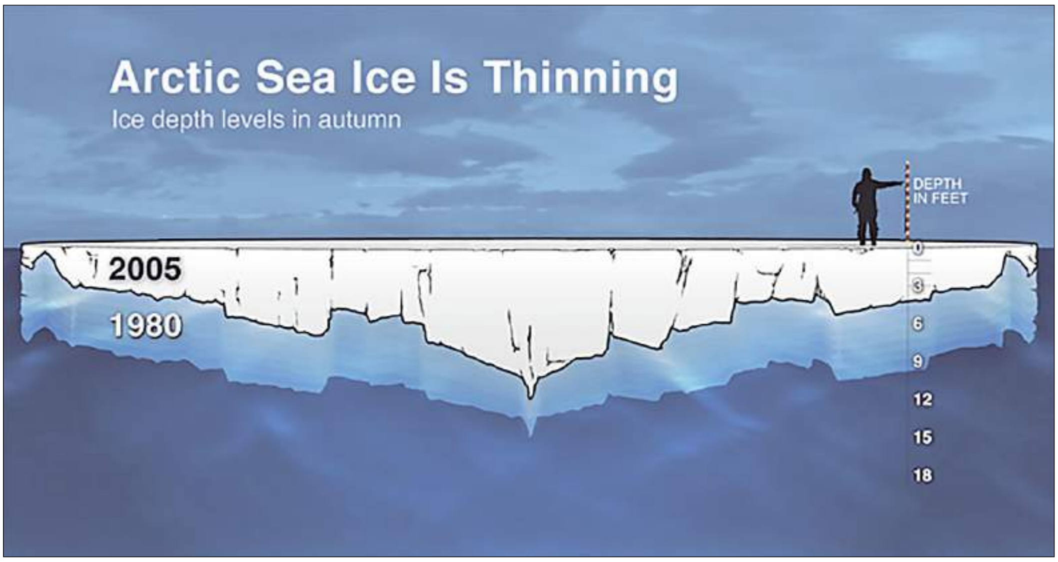


Figure 3.16.1
Arctic sea ice thinning 1980-2005 (from NASA/US Navy). For more information see: www.get2.cc51.

3.16.1.2 The melting Arctic sea ice

A very obvious sign of the Arctic warming is the disappearance of the Arctic sea ice (Figure 3.16.2). When considering the September values, during the last 60 years about 50% of the sea ice has been lost (Fetterer *et al.*,2009). Comiso and Nishio (2008) discuss a decadal ice extent reduction of -3.8±0.3% between 1980 and 2010 based on satellite passive microwave observations. Also the multi-year ice coverage is decreasing according to Kwok (2009) and based on observations for January 1st 1980-2010 from analysis of QuikSCAT time series. The analysis shows a decadal reduction of multi-year ice coverage of -0.80± 0.2x10^6 km^2. The decadal (1980-2010) reduction in ice thickness on the North Pole is -0.62m ((Vaughan *et al.* (2013) based on Kwok and Rothrock (2009), Haas *et al.* (2008), and Rothrock *et al.* (2008)) (Figure 3.16.1). However, although there is a general trend of decreasing areas covered by ice and ice thickness, there is a considerable inter-annual variability and the sea ice can grow back for several years; even decades (see Figures 3.16.3 a-c). However, as mentioned above, model simulations indicate that the Arctic seas may be seasonally ice-free within a few decades (Meier *et al.,* 2011).

3.16.1.3 The Arctic Oscillation

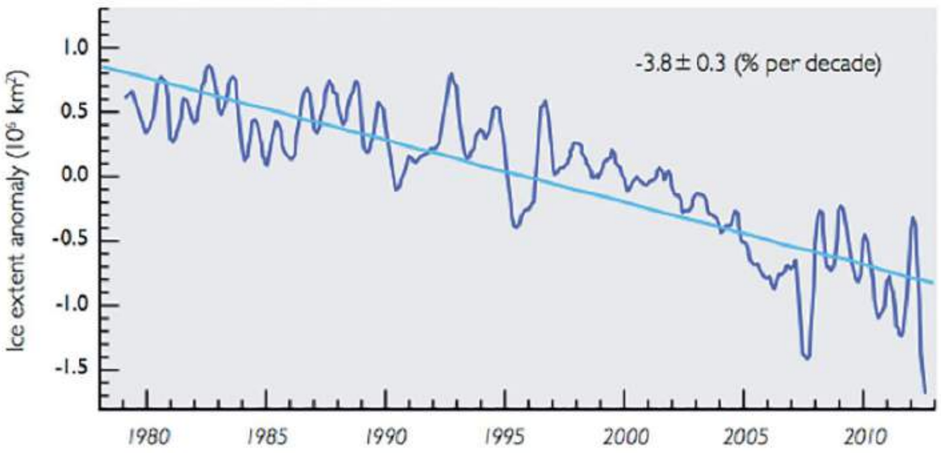
The ice covered area of the Arctic Ocean shows a clear dependent relationship to the Polar Vortex, i.e. reduced (or increased) ice coverage along the Russian coast corresponds to a more intensive (or weaker) Polar Vortex and higher (or lower) temperature (Ikeda, 2008). The atmospheric variability is explained by the Arctic Oscillation (AO) being positive (negative) with a more intense (weaker) Polar Vortex. After a distinct peak of the positive Arctic Oscillation around 1990, a decadal variation has been rather weak. The explanation for this is likely to be the anomalies in the sea ice distribution in the Pacific sector of the Arctic Basin after 1990 (Ikeda, 2008). When southerly winds push the ice away from the coastal region in summer, solar radiation effectively heats the ocean and accelerates ice melting (Kwok, 2008). This is considered to be the main explanation for the record low ice cover in 2007 and 2012 (Figure 3.16.3).

3.16.1.4 Changing albedo and increasing cloudiness

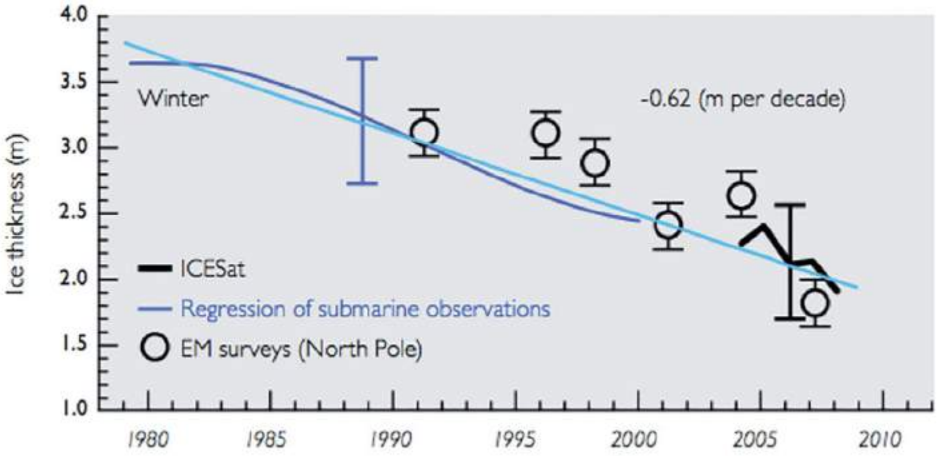
As mentioned above, the increasing melting of the sea ice is due to the changing albedo: when the ice is not there more energy is stored in the dark surface water than

Figure 3.16.2 Arctic sea ice. © Paul Nicklen, SeaLegacy.

a) **Annual ice extent**



b) **Ice thickness**



c) **Multiyear ice coverage (Jan-1)**

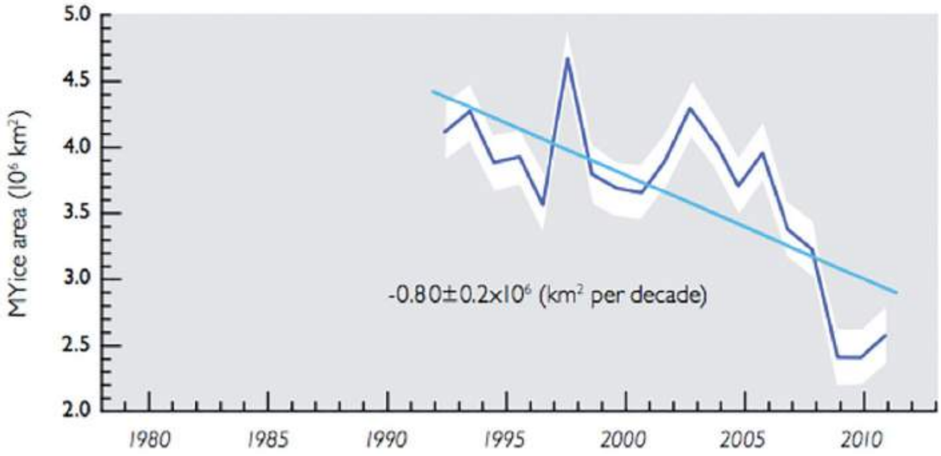


Figure 3.16.3 a) Anomalies in Arctic sea ice extent from satellite passive microwave observations (Comiso and Nishio, 2008, updated to include 2012). Modified from IPCC (2015); b) Multi-year sea ice coverage on January 1st from analysis of the QuikSCAT time series (Kwok, 2009). Modified from IPCC (2015); c) Sea ice thickness from submarine (blue), satellites (black) (Kwok and Rothrock, 2009), and in situ/electromagnetic (EM) surveys (circles) (Haas *et al.,* 2008); trend in submarine ice thickness is from multiple regression of available observations within the data release area (Rothrock *et al.,* 2008). Error bars show uncertainties in observations. Modified from IPCC (2015).

when ice is present and reflects more of the sun's rays back into the atmosphere (Comiso and Hall, 2014; Abe *et al*., 2015). Furthermore, the reduction in the albedo of the Arctic region has been exacerbated by increases in the amount of soot particles that are transported in the atmosphere to the Polar region (Kim *et al*., 2005) and that are also generated by the increasing shipping in Arctic waters. However, other factors also contribute to the increasing temperatures. There is an increase in the cloud cover, which has been observed in all seasons from observation stations in the Arctic since 1950 (Ikeda *et al*., 2003) which affects the heat-flux. Thus, both albedo and radiation are key parameters to explain the observed ice cover change.

3.16.1.5 Precipitation and input from surrounding land

An important aspect of the change in the Arctic Ocean is the influence from surrounding coastal regions. The recent increase in air temperature has resulted in increased precipitation in Alaska, Canada, Greenland, Norway and Russia which is leading to increasing volumes of fresh water in Arctic rivers. The increasing temperatures also results in melting of the permafrost (Smith *et al*., 2005; Zhang *et al.,* 2012; Price *et al*., 2013), and the increasing volumes of drainage water from these melting areas bring various particulate and dissolved organic substances, including organic carbon sequestered since the Last Glacial Maximum, as well as suspended solids into the Arctic Ocean (Shiklomanov *et al*., 2007; Wisser *et al*., 2010; Shiklomanov and Lammers, 2011). Investigations have shown that the freshwater discharge from the Mackenzie River emptying into the Beaufort Sea has increased by 25% since 2003 (Doxaran *et al*., 2015). The measurements of the concentration of suspended solids in the river plume at the mouth show an increase in particulates (terrestrial and suspended particles and organic carbon) of more than 50% in an 11 years study ending in 2009. Ocean colour satellite observations have also suggested an increase in the annual primary production in the Arctic Ocean (Arrigo *et al*., 2008, 2012)

3.16.1.6 Uptake of CO_2

The Arctic Ocean is a critical component of the global carbon cycle despite the fact that it is covered to a large extent by ice. It has been estimated that the Arctic Ocean takes up CO_2 in the order of 65 to 175 TgC y^{-1} (Bates and Mathis, 2009). These quantities correspond to 5 to 14% of the global balance of CO_2 sinks and sources. As the sea ice is decreasing the uptake of CO_2, and the corresponding reductions in pH and aragonite saturation in the Arctic Ocean water will increase (Yamamoto *et al.,* 2012). The colder waters of the Arctic naturally absorb more CO_2 than warm waters at lower latitudes, therefore the pH and the saturation levels of carbon ions, aragonite and calcium, are lower in the Arctic. If emissions of CO_2 continue at the present rate, by the end of the century the Arctic Ocean will be undersaturated in these carbon ions and therefore corrosive to unprotected shells and skeletons (Orr *et al*., 2005; Steinacher *et al*., 2009). The onset of surface undersaturation in the Arctic Ocean shows great variability between regions as a result of differences in climate change feedback factors such as the retreat of sea ice, changes in freshwater input, and changes in stratification (Popova *et al*., 2013). In addition, Arctic deep waters may receive additional CO_2 from the microbial breakdown of melting methane hydrates deposited in the Arctic Ocean seabed sediments (Biastoch *et al.,* 2011). The effects of the uptake of CO_2 in the Arctic Ocean will have fundamental impacts on species, food webs and the entire Arctic marine ecosystem.

The combined effects of the increasing temperature, reduction in ice cover, increased uptake of CO_2 and input of suspended particulate matter from surrounding terrestrial areas will certainly have an impact on the Arctic marine ecosystems.

3.16.2 The Arctic Ocean ecosystem and biodiversity

3.16.2.1 Primary production and plankton blooms

More seasonal sea ice and decreasing multi-year ice, as well as increasing open water areas will lead to more light availability for photosynthesis. Also more open water will result in more uptake of CO_2. These factors and processes should lead to increased primary productivity and an overall increase in biological productivity. There may, however, also be trends in the opposite direction. An increase in the melting of sea ice during the summer period, and increased input of fresh water from land will enhance the tendencies for stratification of the surface waters, inhibiting the upwelling of nutrient rich deeper waters. Also, an increased input of large quantities of particulate matter from Arctic rivers will at least locally result in more suspended solids in the water mass which may decrease the penetration of sunlight and consequently reduce the photosynthesis.

3.16.2.2 Plankton blooms

Investigations have revealed intensive plankton blooms occurring under the ice. In most cases these blooms have occurred under first year ice (0.5 to 1.8m thick) that has melt-water on top of the ice (e.g. in the Chukchi Sea: Arrigo *et al.,* 2012). In the Arctic summer when the sea ice melts, 60% of the surface may be covered by pools of melt water. Optical measures show that a large portion of the incident light may penetrate (more than 50% compared to around 15% under adjacent snow-free ice). Such blooms have been observed in the Barents Sea, Beaufort Sea and the Canadian Arctic archipelago (Strass and Nöthig, 1996; Fortier *et al*., 2002; Mundy *et al*., 2009).

3.16.2.3 Life in ice

The rates of natural change in the Arctic Ocean (without any anthropogenic influence in the form of climate change) are very significant and have a tremendous impact on the biodiversity, ecosystems and food webs of the Arctic Ocean. The rates of sea ice formation and decay during a season may be 1.6 and 0.9 km/h, respectively, affecting marine mammals and birds in particular. However, a range of endemic species of bacteria, unicellar animals and plants, and small multi-cellular animals are also associated with the Arctic sea ice living at the interface between the surface of the ice and the water, or in pores or tiny channels in the ice. The complex interactions between temperature, salinity, ice crystal growth pattern, and the distribution and concentration of brine results in the sea ice rather looking like a sponge, an intricate solid matrix permeated with a labyrinth of channels and pores (Figure 3.16.4). Studies of the combined total surface area of the pores and tiny channels in ice range from 0.6 to 4.0m^2 per kg ice (Krembs *et al.,* 2000). Up to 41% of this network by surface area at -2°C was covered by micro-organisms (bacteria, plants and animals). Among the many groups of animals, turbellarians, crustaceans and nematodes are common and most of the species are endemic to this very particular environment.

Furthermore, a unique fauna of several species of gammarid amphipods and copepods can be found in large numbers (up to several hundred individuals per m^2) on the underside of the ice floes (LØnne and Gulliksen, 1991; Werner, 2006). These amphipods are the food source for the polar cod, which regularly visits the underside of the ice to feed (Gradinger and Bluhm, 2004).

Sea ice also serves as feeding habitat for certain zooplankton which graze on algae on the ice and on phytoplankton associated with the ice edge (Figure 3.16.5). The zooplankton are a vital link in food webs leading to fish and seabirds as well as seals and other marine mammals. These alga and plankton are also the first links in food chains ending with the benthic community living on and in the sea bed.

Changing sea ice conditions with reduction in the extent of the sea ice will impact a number of species in the Arctic Ocean ecosystem. When the ice is melting low salinity water will be formed. With strong winds there will be mixing of the water to a certain extent, however, because of the short fetch of wind over the water between ice floes, wind mixing is minimized and lenses with nearly fresh water with salinities as low as zero will occur near the melting ice edge. The organisms that have been living in the ice and at the interface between the surface of the ice and the marine water will now be exposed to fresh water and many of them will die instantly as a result of osmotic shock. Most Arctic invertebrate species are highly specialized and non-opportunistic and many, including pelagic and benthic

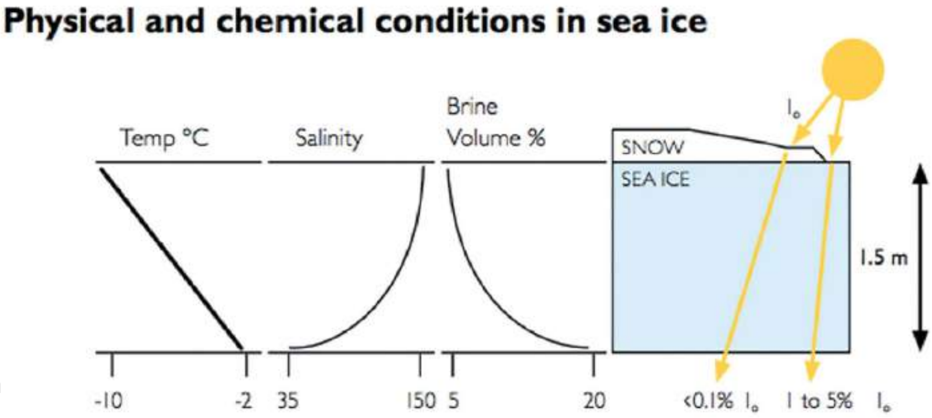


Figure 3.16.4 An illustration of the gradients of temperature, salinity, and brine volume across Arctic sea ice. The seawater under the ice is minus 1.9°C (the freezing point of seawater) and at the top of the ice is close to air temperature although snow cover will modify the temperature. The drawing shows how snow cover can significantly reduce the amount of incident irradiance (I_0). Modified from Eicken (1992).

Figure 3.16.5 Swarm of small crustaceans on underside of ice flow. © Paul Nicklen, SeaLegacy.

forms, are considered to be stenohaline, i.e. they are unable to survive outside a narrow salinity range.

3.16.2.4 Benthic invertebrates

The benthic ecosystem of the Arctic Ocean basin is restrained by the low productivity of the pelagic zone. Along the shelves the productivity is higher and here most of the approximately 5000 species of Arctic marine invertebrates that so far have been identified are found (ArcOD: www.coml.org/projects/arctic-ocean-diversity-arcod). About 350 to 400 of these occur in the Arctic deep basin. Crustaceans (shrimp, crabs), brittle stars, polychaetes and bivalve mussels can be very common in the shelf area, occurring at densities of several hundred individuals per m^2.

3.16.2.5 Arctic Ocean fish

Arctic and sub-Arctic marine waters are home to more than 400 marine and diadromous fish species. Most of the Arctic fish is demersal/benthic. The Arctic cod is the most northerly distributed gadid, occurring roughly between 60° N to the North Pole. This is a key species feeding on amphipods, euphausids, copepods and pteropods. The Arctic cod is preyed on by a range of marine mammals and marine birds. Where there are freshwater inflows into the Arctic Ocean there are a number of different species of salmonids (*Onchorynchus* spp., *Salmo* sp., *Salvelinus* spp.) which spend most of their life in the ocean but migrate into the rivers and streams for spawning. Other dominant fish families include several species of cod, eelpouts, snailfish, sculpins, perch and various flatfishes.

Although there is a significant and highly productive fishery in the Barents Sea and Bering Sea, there is little commercial fishing in the seas of the high Arctic. Therefore, there is a lack of detailed knowledge about the biodiversity and abundance of fish in these areas. Through the Arctic Ocean Diversity Census of Marine Life (ArcOD) project some progress has been made in exploring the fish fauna of the high Arctic.

3.16.2.6 Arctic marine mammals

There are 34 species of marine mammals (10 species of baleen whales, 13 species of toothed whales, 11 species of seals including walrus in addition to the polar bear and the sea otter (AMAP/CAFF, 2009)) found in the Arctic Ocean. Most of these migrate to lower Arctic latitudes or the sub-Arctic during the winter. Several of these species are very sensitive during their migration and breeding. IUCN Red List of threatened species lists 14 of these species as either endangered, vulnerable or near threatened (Table 3.16.1).

Table 3.16.1 List of threatened, vulnerable or endangered Arctic marine mammals (IUCN, 2016) and from AMAP/CAFF (2009)

Category in the Red List	Species	Latin name
Endangered	North Atlantic right whale	*Eubalaena glacialis*
Endangered	North Pacific right whale	*Eubalaena japonica*
Endangered	Blue whale	*Balaenoptera musculus*
Endangered	Fin whale	*Balaenoptera physalus*
Endangered	Sei whale	*Balaenoptera borealis*
Endangered	Sea otter	*Enhydra lutris*
Least concern	Gray whale	*Eschrichtius robustus*
Vulnerable	Sperm	*Physeter macrocephalus*
Vulnerable	Hooded seal	*Cystophora cristata*
Vulnerable	Northern fur seal	*Callorhinus ursinus*
Vulnerable	Polar bear	*Ursus maritimus*
Near Threatened	Beluga	*Delphinapterus leucas*
Near Threatened	Steller sea lion	*Eumetopias jubatus*
Near Threatened	Narwhal	*Monodon monoceros*

3.16.2.7 Birds in the Arctic/sub Arctic

About 200 species of seabirds, waterfowl and waders are found in the Arctic/sub Arctic area (AMAP/CAFF, 2009). True marine birds include auks, gulls and terns, skuas, cormorants, petrels, shearwaters, and albatrosses (Figure 3.16.6). Although some of them are found in areas covered with ice, most of these species are found in areas with open water. Some geese, ducks and swans as well as a number of waders breed in the Arctic area while others migrate through.

3.16.3 Impacts of global warming on Arctic Ocean biodiversity and ecology

3.16.3.1 Increasing human presence in the Arctic

With the warming of the Arctic there will be consequences for livelihoods of local people and increased commercial activities in the form of shipping, fishing, tourism and oil and gas related activities. Obviously, these changes will impact the Arctic ecosystem and biodiversity in the form of disturbance from the presence of humans, possibly

Figure 3.16.6 The populations of black-legged kittiwakes have decreased during least decade probably directly related to the warming of the Arctic, and in particular the disappearing sea ice and decrease in polar cod, an important food fish for the kittiwakes. © Tom Arnbom/WWF.

increased hunting, waste and pollution from ships and platforms, silt and noise from drilling on the sea bed and shipping, and air pollution from the burning of fossil fuels. In addition, there is a risk for oil spills. Reeves *et al.* (2014) reports a worrying overlap between the distribution and seasonal aggregations of some of the Arctic endemic whales, e.g. bowhead whale (Figure 3.16.7) and areas influenced by shipping or sites allocated for oil and gas development. A number of measures need to be taken to avoid disturbing the whales including re-routing of some of the shipping lanes presently in use, ship speed restrictions, temporary and/or spatial closure of particularly sensitive areas of importance to whales (such as calving and feeding areas), as well as strict regulations enforced on seismic surveys and other sources of loud noise.

3.16.3.2 Changes in Arctic food webs and food chains

The Arctic Ocean ecosystems are already being affected by the changing climate. The dynamics of the sea ice conditions are essential for a number of organisms, and decreasing sea ice coverage and more melt water on the surface of the ice will have fundamental impacts on biodiversity and food webs. Major ecosystem shifts are likely to occur as current dominant groups of organisms decrease in abundance while others increase. To forecast the results is difficult as there are not only direct effects to consider, but also indirect effects as a result of physical, biogeochemical and biological coupling. Where the stressors on the individual and the population may come from a multitude of sources the response may be additive, synergistic or antagonistic.

Some of the major changes that are already being observed in the Arctic Ocean relates to the reduction in the multi-year sea ice, more dramatic changes in the extent of seasonal ice, earlier thawing of the ice in the spring, and more melt water input into the Arctic ocean. Several of these phenomena should lead to more light input into the surface waters and therefore increased phytoplankton production which should result in a more productive pelagic system. However, there are also factors that to a certain extent may counter this increase in productivity. The melt water will reduce the salinity of the surface water which will result in stratification of the water mass separating the more nutrient-rich deeper water from the less saline and nutrient poor surface water. This will lead to lower phytoplankton productivity.

Figure 3.16.7 Two bowhead whales resting near ice flow. © Paul Nicklen, SeaLegacy.

Figure 3.16.8 Alaskan red king crab loaded into the UniSea processing plant on Amaknak Island Alaska. © Valerie Craig/ Marine Photobank.

However, this effect is likely to be short-term as wind driven turbulence will pretty soon break down the stratification.

3.16.3.3 Invasive species

The rapid environmental change of the Arctic Ocean is increasing the risk for invasive species to expand into the area. Invasive species have been identified as major factors of environmental change and is a major threat to marine systems because of their direct and indirect impacts on native ecosystems. Two species of crabs have been introduced into the Arctic and they have both exhibited invasive behaviour: the red king crab (*Paralithodes camtschaticus*) (Figure 3.16.8) (Falk-Petersen *et al.*, 2001) originally from the northern Pacific transplanted along the Russian Arctic Ocean coast, and the snow crab (*Chionoecetes opilio*) (Sundet and Bakanew, 2014) originating from Alaska and the north-western Atlantic have been found in the Barents Sea in large numbers. Both species can alter the benthic communities structure significantly opportunistically feeding on most types of epibenthic organisms resulting in reduced biodiversity and biomass.

3.16.3.4 Ecosystem shifts

Ecosystem shifts have already been observed, for example in the Bering Sea which is moving away from an ice-dominated ecosystem with bottom feeding birds and mammals as endpoints in a foodchain which depends on carbon input to the benthos from algae growing under the sea ice. Under more ice free conditions this ecosystem is turning into a system dominated by phytoplankton and pelagic fish (Grebmeier *et al.*, 2006). Other signs of major regime shifts in the Arctic Ocean are the evidence from satellite monitoring of increased phytoplankton biomass in response to more open water and a longer open water season (Arrigo *et al.,* 2008). Such regime shifts will affect the food webs and result in impacts at all levels above the first trophic level. Hence marine mammals and birds will be affected both from direct and indirect effects (see for example Cooper (2009) and Kovacs *et al.* (2011)).

3.16.3.5 Impacts on seabirds

Seabirds such as guillemots, puffins and petrels breed in large numbers during the short Arctic summer, living on the abundant food resources that become available as the sea ice melts. Based on research carried out in Canada and Norway a milder Arctic climate will affect these birds for example by altering the timing of the ice melting which will have an impact on the birds breeding success. The maximum productivity of the sea should coincide with the period when the young birds require maximum feeding. In the case of the Brunnich's guillemot in northern Hudson Bay, the ice melting has advanced about 17 days since early 1980s, but the timing of the hatching of the birds' eggs has only advanced by five days (Gaston *et al.,* 2005). As a consequence, there is now a mismatch between the peak of food supplies and the maximum food requirement. Another impact on marine birds is that the food they normally consume will change with climate change. The Arctic cod is the main fish consumed by birds as well as many marine mammals. With the melting ice and the shift from ice-benthic food chains to pelagic ones, pelagic fish such as capelin has become the dominant species. These fish have different nutritional characteristics and this together with mismatches in peak food supplies has had consequences both for adult mass and chick growth (Gaston *et al*., 2005; Mallory, 2009).

3.16.3.6 Arctic whales

The Arctic Ocean is the home of three endemic cetaceans which are characterized by their permanent presence in the Arctic, the bowhead whale, the only truly Arctic baleen whale (Figure 3.16.9), and the two toothed whales, the narwhal (Figure 3.16.10) and the beluga (Figure 3.16.11). Several other whale species enter the Arctic seasonally but only the three species mentioned are considered truly endemic. Climate change is likely to affect these whales in a number of different ways due to disruption of normal oceanographic features such as stratification, surface water temperatures and ice loss. The impacts may be due to changes in the food webs but perhaps even more important, the increased presence of humans and human activities in the Arctic in the form of increasing number of vessels and the development of hydrocarbon deposits (Reeves *et al*., 2014). The sensitivity of these whales to industrial activity has been the subject of studies in northern Alaska and Canada. They are all sensitive to noise at low (received) levels from ships, noise-generating activities such as drilling and especially seismic surveying (Reeves *et al.*, 2014). There are indications that these endemic Arctic whales are both well adapted to life in ice-infested Arctic waters and at the same time have low genetic diversity, for narwhals this is particularly low, which may make them particularly vulnerable to rapid climate change (Heide-Jorgensen, 2009).

3.16.3.7 Polar bears, seals and walruses

Signs of the impacts of Arctic Ocean warming and earlier ice break-up is the decline in condition and reproductive success of polar bears (Figure 3.16.12) in the western Hudson Bay (Regehr *et al*., 2007; Durner *et al*., 2009), similar effects have been reported from Svalbard.

Some species of seals are particularly dependent on sea-ice habitats. The ringed seal (Figure 3.16.13) is one such species and the retreating sea ice will limit this species to areas where the sea ice is predicted to remain

Figure 3.16.9 Bowhead whale in Lancaster Sound, Nunavut, Canada. © Paul Nicklen, SeaLegacy.

Figure 3.16.10 Narwhal in Admiralty Inlet, Baffin Island. © Paul Nicklen, SeaLegacy.

Figure 3.16.11 Beluga whales in Lancaster Sound, Nunavut, Canada. © Paul Nicklen, SeaLegacy.

Figure 3.16.12 Polar bears are already suffering from climate change in the Arctic Sea. It is assumed that within 50 to 70 years polar bears will have disappeared from most of their present range. © Tom Arnbom/WWF.

Figure 3.16.13 Ringed seal in ice hole. © Paul Nicklen, SeaLegacy.

Figure 3.16.14 With less sea ice the walrus is now breeding more on land. © Tom Arnbom/WWF.

longer, such as in the Canadian Arctic (Pfirman, 2009). Such compression of the range of these species will make them more vulnerable to competition for food and space. In general, a decline in the sea ice will become detrimental to ice-adapted species and advantageous to seasonal migrant species (Moore and Huntington (2008) quoted in Kovacs *et al*. (2011)). It is predicted the initial response of ice-associated seals unable to find ice habitats in traditional areas at the respective breeding times will be northward range contractions or a shift to breeding earlier in the season (Burns, 2009). However, according to Kovacs and Lydersen (2008), (quoted in Kovacs *et al*. (2009)) such a shift of the behaviour to terrestrial breeding from breeding on ice would require a remarkable degree of behavioural plasticity that has not been seen to date in regions and years where ice reductions have been rapid and major.

Also walruses (Figure 3.16.14) use sea-ice floes as resting platforms over foraging areas and substantial declines in their populations are predicted as a result of the reduction in Arctic Ocean sea ice (Jay *et al.,* 2011). Walruses are already spending more time at land-based haul-outs than on ice floes. A dramatic change in the behaviour of walruses in the Bering Strait into the Chukchi Sea have been reported (Arnbom, 2009), changes that are linked to the Arctic climate change. When walruses start to haul-out on land they overuse the nearby feeding areas. The individuals that continue to haul-out on the ice risk ending up over deep waters far from suitable feeding areas.

3.16.4 Conclusions

The predictions of the changes in the Arctic are highly variable and site specific. Obviously the depth conditions and the influence from land run off are important factors. Kovacs *et al.* (2011) summarize the biological impacts of the changes in the Arctic Ocean related to the warming and reduction of the sea ice:

- The Arctic basins are likely to become more productive due to a shift from light limitation to nutrient limitation.
- Changing sea ice and snow patterns will shift the primary production from ice algae to phytoplankton.
- As the sea ice withdraws the availability of ice-associated zooplankton and other invertebrates will be affected which will have an impact on the Arctic food chains where the polar cod is an essential link providing critical feed for seabirds and marine mammals, as well as for the Atlantic cod.
- Sub-Arctic species will expand northward and compete with the Arctic species. The decline in ice-associated species can already be observed.

Kovacs *et al*. (2011) further conclude that the current trend in reductions of the sea ice is likely to result in extinction of Arctic endemic species, a loss that will represent biodiversity losses of global significance, and reverse millions of years of evolutionary change. The expansion of the northward range of sub-Arctic species in combination with the reduction of the sea ice is likely to fundamentally impact Arctic Ocean productivity and food webs:

- Due to the reduction in sea ice it is highly likely that there will be reductions in the distribution and abundance of seals and walrus.
- Pack-ice breeding seals will experience reproductive failures more frequently as their late winter/early spring breeding becomes affected, impacts that are already observed in the Atlantic sector of the Arctic.

- Polar bears are likely to become extirpated within 50 to 70 years over most of their present range.
- Arctic endemic whales will suffer from the change in the food webs and from competition from non-endemic migrant whales, and in some regions from the potential for increased predation from killer whales (Reinhart *et al*., 2013).

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Special section - changes to Antarctic ecosystem and species

"The oceans around Antarctica are changing rapidly, with average rates of warming and freshening that greatly exceed the global mean, but with complex regional structure to the changes. "

"Management bodies in the region will need to adapt management practices to a changing future. A critical gap in capability is sustained circumpolar observations needed to assess current and future ecosystem states. "

Section 3.17 authors

3.17 Impacts and effects of ocean warming on Antarctic ecosystems and species

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Summary

- The Antarctic marine ecosystem is strongly dependent on the regional circulation and climate of the ocean, and is important because of its role in the global carbon cycle, fisheries, and for the conservation of many of the globe's iconic marine mammals, penguins and flying seabirds.
- The oceans around Antarctica are changing rapidly, with average rates of warming and freshening that greatly exceed the global mean, but with complex regional structure to the changes.
- The prognosis for the region is difficult to assess because the coupled climate models of the sort used by the IPCC perform poorly at simulating the Southern Ocean, including the sea ice environment. Nevertheless, the coupled climate models consistently predict a warming of the Southern Ocean in coming decades, along with a freshening of upper-layer water masses, and a shallowing of the surface mixed layers.
- The knowledge that is available points to a changing system that will have consequences for species and the ecosystems as a whole, largely resulting in a contraction of this ecosystem to higher latitudes.
- Management bodies in the region will need to adapt management practices to a changing future. A critical gap in capability is sustained circumpolar observations needed to assess current and future ecosystem states.

Ocean warming effects	**Consequences**
Ocean	
Increased temperature	Increased iceberg calving therefore increased scouring of shallow benthic habitats Increased rate of production Increased metabolism could cause decrease in total production if resources do not increase in the system Krill productivity in the northern part of its range is expected to decline
Increased stratification	Diatoms will benefit
Ice	
Reduced sea ice duration and cover in the future	Location-dependent increases/decreases in primary production Declines in sea ice dependent predators (Adelie penguins, crabeater seals) in areas no longer covered by sea ice. Foraging access will improve where formerly heavy pack ice becomes broken and accessible Increases in gentoo, chinstrap penguins Reduced breeding areas for emperor penguins Possible decreases in Antarctic krill (uncertain, spatially complex) Increased access of fisheries in southern areas
Response Capability	
Most rapid oceanic change on the planet; Fragmented ecosystem observations; Current coupled climate models do not represent polar regions well; Changes will differ between different sectors of the Southern Ocean	Urgency is needed in developing an integrated circumpolar capability (observations and assessments) in estimating current and future states of Antarctic marine ecosystems Management practices need to adapt rapidly to changing habitats and be tailored to the different sectors Integrated observations in each sector could provide an opportunity to test hypotheses about the key factors causing consequent changes in food webs

3.17.1 Introduction

The Southern Ocean is important in the Earth system because of its dominant role in planetary-scale ocean circulation and the global carbon cycle (IPCC, 2013). The productivity of the region also makes it important for global fisheries (Kock, 2007; Kawaguchi and Nicol, 2014). It is the region upon which many of the globe's iconic marine mammals, penguins and flying seabirds depend (Constable *et al.,* 2014b). Here we focus on that part of the Southern Ocean that is south of the Polar Front (the Antarctic Convergence) as this comprises the high latitude system often referred to as the Antarctic marine ecosystem. This part of the Southern Ocean is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Constable, 2011).

The Southern Ocean as a whole is experiencing the most rapid oceanic change on the planet (IPCC, 2013), as exemplified by average rates of warming and freshening that greatly exceed the global mean, and which extend to great depth within the ocean (Böning *et al.,* 2008). Significant complexity exists within the system, however, as illustrated by the much slower rates of change at the surface south of the Polar Front (Armour et al. 2016). The prognosis for the region is difficult to assess because the coupled climate models of the sort used by the Intergovernmental Panel on Climate Change (IPCC) perform poorly at simulating the Southern Ocean, including the sea ice environment (Meijers, 2014). This is because many of the key processes and features of the region are complex and occur at scales smaller than the models can resolve, e.g. eddies, coastal polynyas (large areas of open water within the sea ice zone), boundary currents, and dense water cascades (Meijers, 2014). Nevertheless, the coupled climate models consistently predict a warming of the Southern Ocean in coming

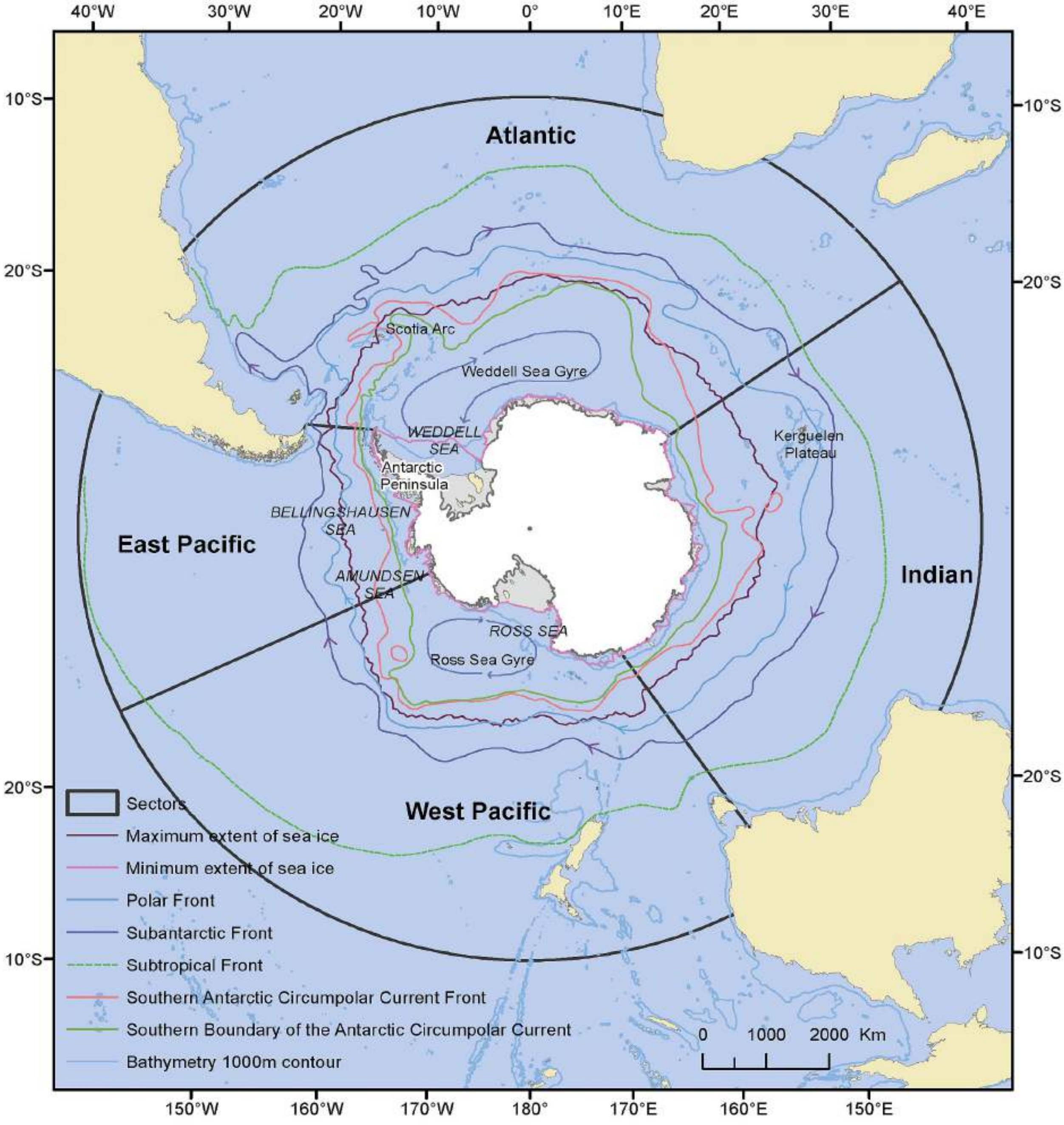

Figure 3.17.1 Major physical features of the Southern Ocean, including key locations referred to in the text; major sectors differentiating the ecosystems; minimum and maximum extent of sea ice; the Subtropical, Subantarctic and Polar fronts, Southern Boundary of the Antarctic Circumpolar Current; and the 1000 m contour (Figure 3 from (Constable *et al.,* 2014b).

decades, along with a freshening of upper-layer water masses, and a shallowing of the surface mixed layers (IPCC, 2013). Also, the knowledge that is available points to a changing system that will have consequences for species and the ecosystems as a whole and will require action by the management bodies in the region to adapt management practices to a changing future.

Drawing on recent reviews and papers since the Fifth Assessment Review of Working Group II of the Intergovernmental Panel on Climate Change (IPCC, 2014), we consider the impacts of change on Southern Ocean ecosystems. We have divided this chapter into three main sections. The first summarizes the nature of habitats and species in the Antarctic marine ecosystem and the types of changes in habitats from large-scale warming that will impact on species. The second section focuses on observed changes within four ecosystem sectors of the region. The last section considers the consequences and challenges of global warming for managing the region.

3.17.2 The Antarctic marine ecosystem

3.17.2.1 Habitats

The Antarctic marine ecosystem comprises oceanic (pelagic), geomorphological (benthic), and ice environments. It experiences a marked seasonal cycle of increasing (advancing) sea ice cover over autumn and winter and a decrease (retreat) in cover in spring and summer. Day length is very short in winter and very long in summer.

The pelagic environment is dominated by the west-to-east flow of the Antarctic Circumpolar Current (ACC) to the north (Figure 3.17.1) and an east-to-west flow of the Antarctic Coastal Current near the continent itself. The ACC is further divided by a number of ocean fronts, the temperature becoming progressively cooler as they are crossed poleward towards Antarctica. In the north, where the ACC fronts meander and develop instabilities, this is characterised by strong and active eddies, which are the oceanic equivalent of atmospheric weather systems. The Antarctic Divergence in the south is a major site globally where deep waters upwell to the surface, where they are reprocessed into different water masses and sink back into the interior of the ocean (Figure 3.17.2) (Meredith, 2016).

This overturning circulation enables major exchanges of atmospheric heat and carbon with the deep ocean reservoir. It also enables a major upwelling of macronutrients to fuel primary production in the Southern Ocean and beyond (Sarmiento *et al.,* 2004). South of the ACC, and separating it from the Antarctic continent in most of the large embayments, are large-scale gyre systems that transport water cyclonically, and which act as thermal buffers between the comparatively warm ACC and the very low temperatures that typify the Antarctic continent (Figure 3.17.1).

The benthic environment varies greatly around Antarctica (Brandt *et al.,* 2007). Intertidal and nearshore shallow water areas are scarce and mostly restricted to the Southern Ocean islands. The Antarctic continental shelf has a mean depth of about 800 m, but varies widely in extent and depth. The shelf areas around Southern Ocean islands have a depth around 200 m. The continental shelf is broken up by deeper areas, cross-shelf valleys and shallow banks. Benthic areas

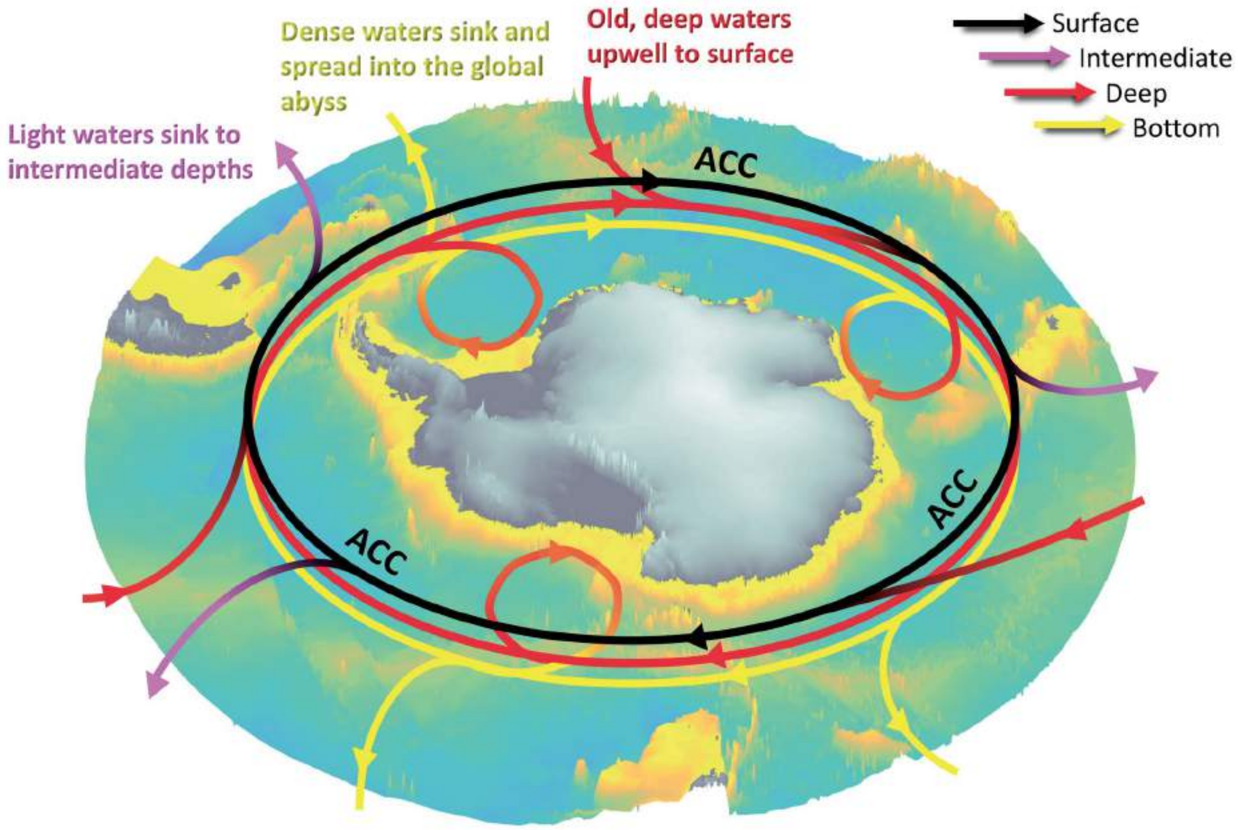

Figure 3.17.2 Schematic showing the Antarctic Circumpolar Current and the overturning circulation in the Southern Ocean (Figure xx from Meredith, 2016).

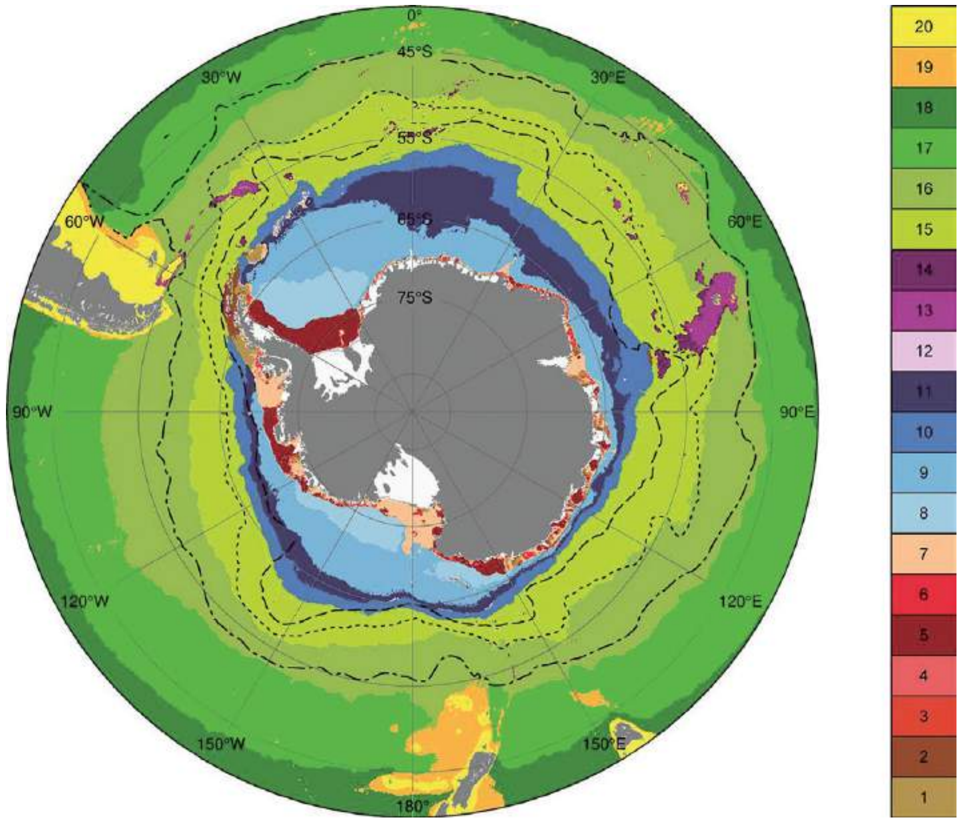

Figure 3.17.3 Pelagic regionalisation for the Southern Ocean (Map 1 from Raymond, 2014). Twenty cluster types are derived from sea surface temperature, depth and sea ice cover data layers.

shallower than around 300m are exposed to scouring by icebergs, although this may be deeper to 500-600 m near fast flowing ice sheet glacier outlets (Dowdeswell and Bamber, 2007). The continental slope descends into deep water about 4000 m deep at the abyssal plain. Banks, seamounts and plateaux rise from the abyssal plane to provide shallow habitats in the Southern Ocean while the sea floor drops deeper in trenches and fracture zones. The deep basins and trenches are characterized by soft sediment habitats with occasional hard substrata and drop stones. Hydrothermal vent habitats are linked to mid-ocean ridges and back arc basins (Rogers and Linse, 2014).

The ice environment over the continental shelf comprises areas permanently covered by ice shelves and fast ice (sea ice that remains fast against the shore or icebergs) in the south and the remainder experiencing the seasonal cycle of sea ice cover. Polynyas are important habitats within the coastal ice environment (Arrigo and van Dijken, 2003). The part of the Southern Ocean over which the sea ice advances and retreats, which includes southern parts of the ACC, is known as the marginal ice zone.

The apparent concentric circumpolar pattern of ice, pelagic and benthic habitats around Antarctica is disrupted by south-north topographies of the Antarctic Peninsula and Scotia Arc, Maud Rise, Kerguelen Plateau, and Macquarie Ridge. These cause large deviations of the ACC and the coastal current and contribute to the patterns of flow of the Weddell and Ross Gyres and smaller coastal gyres such as in Prydz Bay (Figure 3.17.1). A patchwork of pelagic and benthic habitats is therefore formed around Antarctica (Figure 3.17.3) (Douglass *et al.,* 2014; Grant *et al.,* 2006; Raymond, 2014), which, combined, give rise to four sectors where the environments have different attributes and are experiencing different types of change – West and East Pacific, Atlantic, and Indian (Figure 3.17.1) (Constable *et al.,* 2014b).

The Southern Ocean has the sparsest data coverage of any of the world's major oceans, due to its remoteness and inhospitable nature. Until recent times, oceanographic measurements were made almost exclusively from ships (e.g. Figure 3.17.4, which shows the recovery of an instrument that collects measurements of ocean temperature and salinity, and water samples from different depths). In recent years, autonomous floats and underwater gliders have expanded the scale of data collection, and reduced the exclusive reliance on research vessels for data collection. This combination of traditional and innovative data sources has shown that the Southern Ocean has warmed much faster than the global ocean as a whole, due to an imperfectly-known combination of water mass changes and shifts in the major features of the ocean circulation (Böning *et al.,* 2008). This warming has not been seen at the surface south of the Polar Front in recent years, however (Armour *et al*., 2016). Instead, a cooling has been observed, consistent with an overall moderate increase in Antarctic sea ice extent, and it has been hypothesized that the replenishment of surface waters with more invariant water from below may be a key factor in suppressing surface warming (Armour *et al.,* 2016). The changes in sea ice are also strongly regional with the West Pacific Sector (Ross Sea) showing large increases in sea ice extent while the East Pacific Sector (Amundsen-Bellingshausen-West Antarctic Peninsula) shows very strong decreases (Stammerjohn *et al.,* 2012).

The amount of water transported by the ACC has remained remarkably constant, despite a strengthening of the winds that overlie the Southern Ocean and which are known to be a major driver of ocean circulation (Böning *et al.,* 2008). The extra energy from these winds is thought to have increased the intensity of the Southern Ocean eddies (Hogg *et al.,* 2015). These eddies play a key role of determining upwelling and overturning in the Southern Ocean, and, although evidence is sparse, the overturning of the Southern Ocean is thought to have accelerated in recent decades (Waugh *et al.,* 2013), with upwelling and outgassing of old carbon from depth. However, the stability of the Southern Ocean carbon sink remains subject to great uncertainty (Le Quere *et al.,* 2007; Landschützer *et al.,* 2015), since it depends on numerous different processes that include ocean climate change, variable three-dimensional circulation, and biogeochemical phenomena, each with their own patterns of spatial and temporal change.

The influx of warm water from the ACC onto the Antarctic shelves is believed to have increased in recent decades in ecologically-important areas such as the East Pacific sector, increasing the on-shelf flow of heat, macronutrients and other biologically-relevant properties (Martinson, 2011). This influx of warm water has delivered increased heat to the undersides of the floating parts of ice sheets, most notably in the Amundsen-Bellinghausen Sea and environs, and

Figure 3.17.4 Scientists measuring the temperature of the Southern Ocean and collecting water samples from different depths close to South Georgia, during a blizzard. © Mike Meredith, British Antarctic Survey.

caused an increase in glacial ice input to the ocean in recent decades (Rye *et al.,* 2014).

The extra fresh water from ice melt has the potential to deliver increased quantities of important micronutrients, such as iron, to the ocean, but the horizontal and vertical distribution of this flux depends on ocean stratification and circulation, and hence the impact is not readily predictable.

Figure 3.17.5 Antarctic krill (*Euphausia superba*). © Russell Hopcroft/Australian Antarctic Division, 2008; Image RS34352, Image Antarctica.

3.17.2.2 Species

The Antarctic pelagic food web is dominated by Antarctic krill (Figure 3.17.5) and its predators, which are the main predators in the Antarctic. Sea ice plays a central role in the success of Antarctic krill (Kawaguchi and Nicol, 2014) (Figure 3.17.6). Antarctic krill rely mostly on large-celled phytoplankton, diatoms, for food. The diatom-krill-baleen whale food chain is the shortest in the world, making it energetically efficient. An alternative energy pathway arises from smaller phytoplankton, which are consumed by copepods and, in turn, channel the energy through a pathway of mesopelagic fish to seals and toothed whales (Murphy *et al.,* 2007b). The importance of the fish pathway is not well understood but recent analyses suggest that it may be more important in the ecosystem than originally thought (Hill *et al.,* 2012).

For benthic species, a high percentage of the deep sea species are endemic to the Southern Ocean and show regional to local patterns in contrast to the pelagic species that seem to show more circum-Antarctic distributions (De Broyer *et al.,* 2014). Energy for food webs can be gained from coastal production by benthic algae, detrital rain from surface production, or from chemosynthesis at hydrothermal vents, methane seeps and organic falls like whale carcasses

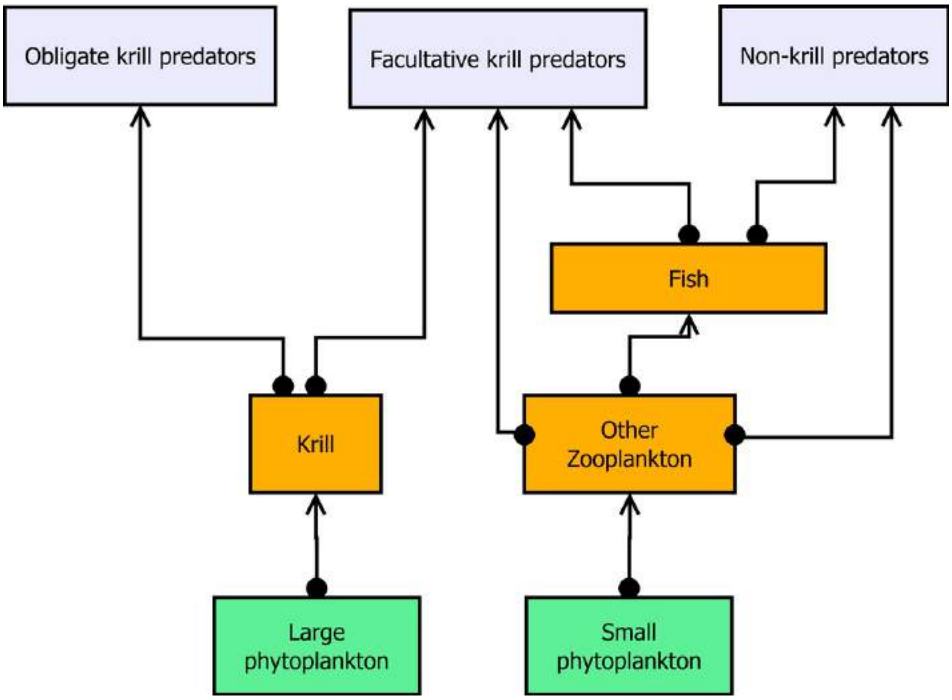

Figure 3.17.6 Alternative food webs for the Antarctic marine ecosystem (Figure 10 from Murphy *et al.,* 2007b)

Figure 3.17.7a Sea squirts in shallow water near Rothera, Antarctica. © BAS, Ali Massey; Image BAS-10009197.

Figure 3.17.7b Benthic invertebrates on the sea floor in D'Urville Sea, East Antarctica. Martin Riddle, January 2008; Image RS23140, Image Antarctica, © Australian Antarctic Division.

Figure 3.17.7c Benthic invertebrates on the sea floor in D'Urville Sea, East Antarctica, with demersal grenadiers (*Macrourus* spp.). Martin Riddle, January 2008; Image RS23151, Image Antarctica, © Australian Antarctic Division.

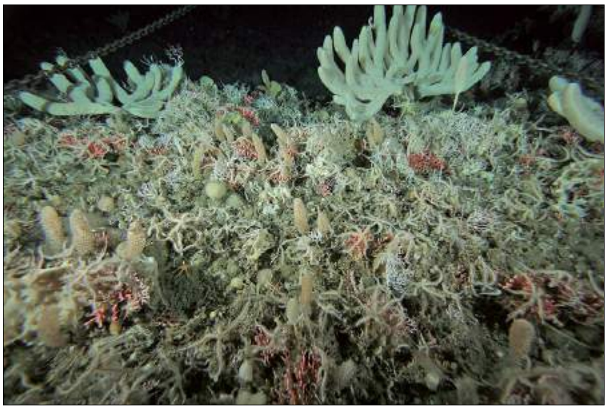

Figure 3.17.7d Benthic invertebrates on the sea floor in D'Urville Sea, East Antarctica, featuring erect sponges. Martin Riddle, January 2008; Image RS29244, Image Antarctica, © Australian Antarctic Division.

(Reid *et al.*, 2013; Gutt *et al.,* 2015). A large biomass of benthic species are habitat-forming filter feeders, such as calcifying sessile invertebrates (e.g. Bryozoa and Hydrozoa) and sponges (Gili *et al.,* 2001) as well as mobile Echinodermata (Lockhart and Jones, 2008). The benthic communities (Figure 3.17.7) display a high heterogeneity and include a variety of functional traits within the assemblages of invertebrates, like deposit feeders, grazers and predators (Gutt *et al.,* 2013a, b). Information on the benthic food web structures is scarce; only a few studies describe coastal food webs (Norkko *et al.,* 2007; Gillies *et al.,* 2013), and almost nothing is known on food web structure from shelf or deep-sea communities (Purinton *et al.,* 2008; Sumida *et al.,* 2014). Numerous fish species depend on these benthic food webs (Mintenbeck *et al.,* 2012). In contrast to the pelagic system, no long-term datasets on the turnover of benthic abundance and biomass are available, making it hard to predict the effect that changes in the pelagic system will have on the benthic system.

Increases in sea temperature and decrease in sea ice cover could have a negative effect on benthic communities in the reach of iceberg scouring (from the littoral to the continental shelf) through increased numbers of icebergs disturbing or destroying the communities (Barnes and Conlan, 2007; Gutt and Ekau, 1996; Gutt *et al.,* 1996). Simulation models of disturbance by iceberg scour of the deeper shelf communities showed high local mortality providing space for new colonization (Potts and Elith, 2006).

For the pelagic system, increased temperature will have greatest effect on lower trophic levels (phytoplankton, zooplankton, krill and fish) (Constable *et al.,* 2014b). Increased metabolism and growth rates will generally occur, increasing the rate of production. If the temperature rises too far then metabolism will require most of the energy consumed, such as may happen for Antarctic krill in the northern parts of its range (Hill *et al.,* 2013). Notably, while growth rates may increase, the total production is dependent on available resources. The productivity of the system may decline due to increased metabolic costs not being matched by increased nutrients for phytoplankton or increased food consumption by invertebrate and fish consumers, including krill.

The consequent effects on the food web arise from a number of factors related to global warming and not just temperature in isolation (Murphy *et al.,* 2012; Constable *et al.,* 2014b). Increased stratification will benefit large diatoms, which dominate over smaller phytoplankton (Sailley *et al.,* 2013; Smith *et al.*, 2014).


Figure 3.17.8 Sea ice en route to Casey. © John M Baxter.


Figure 3.17.9 Crab eater seal. © John M Baxter.


Figure 3.17.10 Group of macaroni penguins (*Eudyptes chrysolophus*) at Heard Island, Southern Ocean. © Kieran Lawton/ Australian Antarctic Division, December 2003; Image RS15656, Image Antarctica.

Changes in sea ice could give rise to a number of effects on food webs (Constable *et al.,* 2014b) (Figure 3.17.8). For example, reduced sea ice is expected to reduce suitable habitat for larval and juvenile krill, affecting their ability to find food and to shelter from predation. In contrast, reduced sea ice may increase local primary production and increase detrital rain to benthic communities. It may also impact on where sea ice dependent predators may forage. Crabeater seals are expected to forage near to sea ice (Figure 3.17.9). Similarly, emperor penguins require fast ice and ice shelf habitats for breeding. Adélie penguins forage in association with sea ice, but too much sea ice can be as detrimental to foraging success as too little sea ice (Emmerson and Southwell, 2008). Chinstrap and macaroni penguins (Figure 3.17.10) are both sub-Antarctic species that exhibit minimal affinities to sea ice, so would benefit from a decrease in sea ice cover.

Importantly, food webs may be disrupted by change in the seasonal dynamics (phenology) of the system. For example, areas with reduced sea ice are becoming exposed for the spring production earlier. Warmer temperatures cause the period of production to be shorter through faster growth rates. For land-based predators tied to colonies during breeding, this may mean that the production nearby occurs earlier than when they need it. Further, if the location of the production moves then more energy may need to be expended to forage for food, thereby reducing food returned to the young. Evidence is increasing that king penguins from subantarctic islands in the Indian sector have to forage farther to the south to obtain food for their young. As a result, their breeding success is declining.

The movement south of frontal and sea ice systems indicates that the current Antarctic marine ecosystem will contract towards the coast of Antarctica. Lower trophic levels are expected to move south with the frontal systems (Constable *et al.,* 2014b). The consequences of a warming environment for taxa constrained to subantarctic islands and shelf areas is unknown. In particular, it is unknown how the performance of these taxa will change if they are dependent on cold-water pelagic species moving further to the south (Constable *et al.,* 2014b).

3.17.3 Change in the Antarctic marine ecosystem

3.17.3.1 East Pacific

Life histories, phenologies and key population events of Antarctic marine organisms are closely tied to the advance, retreat, duration and extent of sea ice on the West Antarctic Peninsula (Ross *et al.,* 1996; Ducklow *et al.,* 2012; Steinberg *et al.,* 2012; Ducklow *et al.,* 2013). Well-known examples include the triggering of the annual spring diatom blooms by the melting of sea ice, and the arrival of penguins and other seabirds at their summer nesting sites as the ice retreats and winter snows melt, exposing bare ground for nest building and egg-laying. Western Antarctica, from the Amundsen and Bellingshausen Seas to the northern tip of the Antarctic Peninsula has been a region of rapid climate warming, especially in winter, with temperature increases of up to +7°C since 1950. Glacier retreat and reductions in the extent and duration of sea ice cover (Maksym *et al.,* 2012) have accompanied the rapid warming. Along the western side of the peninsula (WAP), extending south from Anvers Island into Marguerite Bay, sea ice duration has declined by about 90 days since the beginning of satellite detection of sea ice in 1978 (Stammerjohn *et al.,* 2008). The combination of strong connections between sea ice and key biological processes, and the rapid reductions in sea ice cover is driving changes in marine ecosystems, from the base to the top of the Antarctic food chain.

A decline in the numbers of breeding pairs of Adélie penguins nesting in the Palmer Station region (Figure 3.17.11) provided the first suggestions of ecosystem change in the region. Adélie penguins (Figure 3.17.12) are one of the main apex predators in Antarctica, along with other seabirds, seals and baleen whales. All these organisms rely on Antarctic krill as a main food source. Krill also depend critically on sea ice (Saba *et al.,* 2014). Determining whether or not krill are declining, and whether or not changes in food supply are the major factor explaining reductions in penguin numbers, are complicated and controversial questions (Trivelpiece *et al.,* 2011; Fraser *et al.,* 2013; Melbourne-Thomas *et al.,* 2013). Atkinson *et al.* (2004) concluded that Antarctic krill declined by as much as a factor of ten since the 1970s in the vast southern Atlantic and Pacific sectors of the Southern Ocean. Loeb and Santora (2015) questioned this conclusion based on a reanalysis of the same data. No change in krill abundance has been observed since 1992 in the central WAP region where the Adélie penguin declines have been most evident (Steinberg *et al.,* 2015). Easy conclusions are also complicated by the rapid *increases* in Gentoo and Chinstrap penguins in the WAP region, starting in the late 1990s (Figure 3.17.11).

More recently, significant changes have been documented for primary producers at the base of the

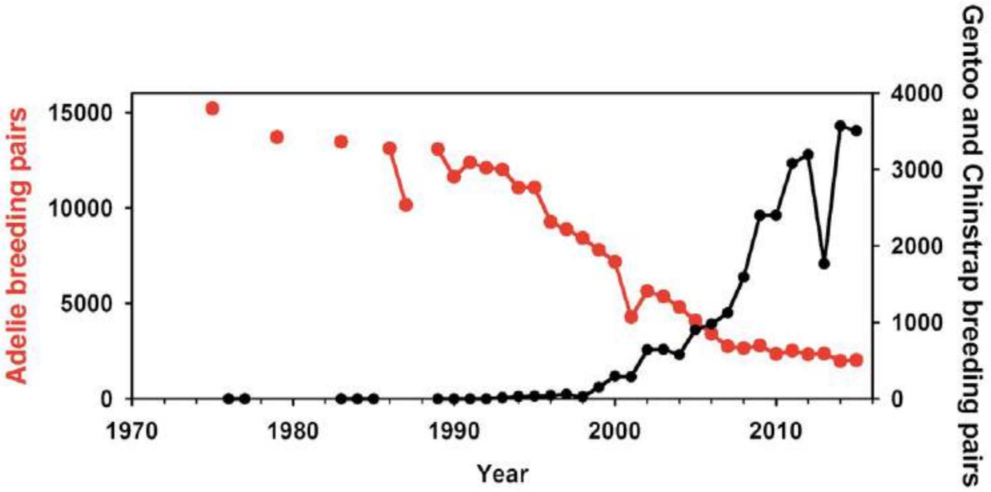

Figure 3.17.11 Penguin breeding pairs in the Palmer Station area, 1975- 2015. Absence of symbols indicates no observations were obtained. Symbols indicating zero are real observations confirming absence of established breeding pairs on nests. The declines in 1985, 2001 and 2013 are real. (recent data courtesy W. R. Fraser)

Figure 3.17.12 Fisheye view of Adelie penguins (*Pygoscelis adeliae*) at Casey Station, Antarctica. © Todor Iolovski/ Australian Antarctic Division, December 2006; Image RS5933, Image Antarctica.

food chain. In general, with the exception of the benthic chemosynthetic ecosystems, life in Antarctic seas depends on photosynthetic production of plant biomass, principally by diatoms. Diatoms, which are microscopic, single-celled phytoplankton, benefit from melting sea ice to bloom in the spring (Figure 3.17.13) (Venables *et al.,* 2013), their production sustaining krill and other large zooplankton such as pteropods (Figure 3.17.14). Two sorts of changes are occurring in phytoplankton populations as a result of declining sea ice: changes in abundance, and in the dominant types of producers (Montes-Hugo *et al.,* 2009). As expected, phytoplankton (mainly diatom) abundance has declined in the northern peninsula region, following reductions in sea ice extent (Figure 3.17.15). Interestingly, phytoplankton have increased in the south: this is because declining sea ice is exposing new areas of the ocean to sunlight for the first time, possibly for hundreds or thousands of years (Peck *et al.,* 2010). Changing sea ice and also increasing inputs of glacial meltwater are also creating conditions in coastal waters that favour phytoplankton species (cryptophytes) too small for efficient consumption by krill (Fuentes *et al*. 2016). Together, the web of dependence on sea ice is changing in many ways. These changes signal more fundamental transformations in the marine ecosystem likely to occur in the future, if the climate continues to warm.

3.17.3.2 Atlantic

There are marked habitat differences in this region, from the deep Weddell Sea regions in the south to the open water ACC regions of the Polar Front in the north, and from the restricted region of rapid flow at Drake Passage in the west to the more open waters in the east. As the ACC flows east along the Antarctic Peninsula and through Drake Passage it is deflected as it encounters the Scotia Arc, bringing polar waters northwards and influencing regional habitats. Sea ice also extends to more northern latitudes in this western region of the Atlantic sector. These interactions generate a combination of physical and chemical conditions that result in high levels of productivity across much of the western region, with lower levels farther east (Arrigo *et al.,* 2008). The annual cycle of productivity shows the generally expected seasonal progression associated with the retreat of sea ice in the spring. The extensive island regions include large areas of land and shelf, which provide extensive suitable breeding and foraging habitat for land-based breeding seabirds and marine mammals.

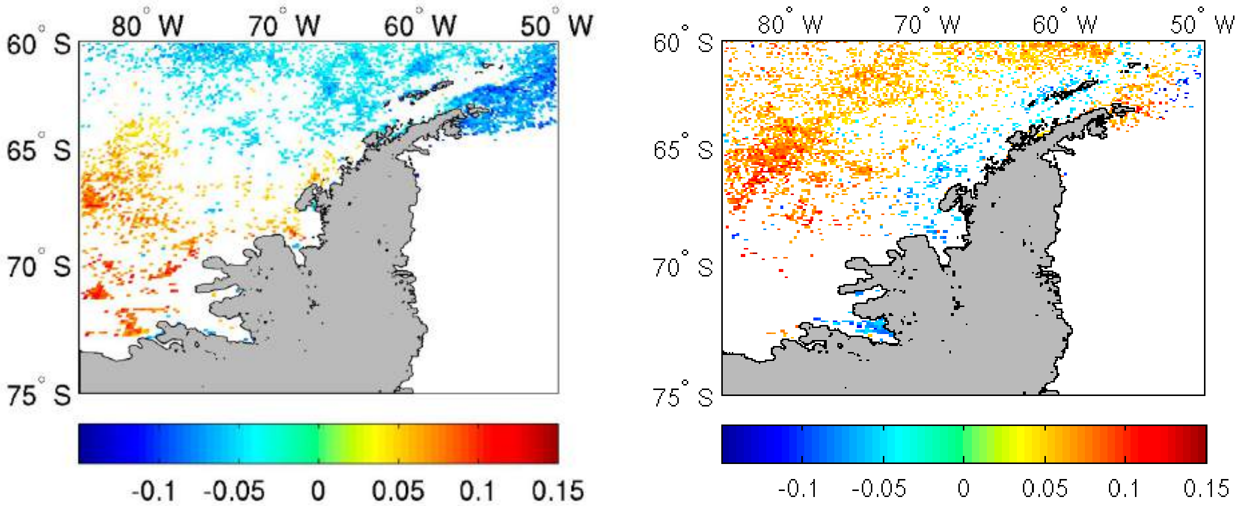

Figure 3.17.13 Trends in phytoplankton abundance (left, Chl a g m^{-2}) and cell size (right, % cells greater than 20mm) in the West Antarctic Peninsula region, 1997 - 2012. Pixels indicate trends significant at $p<0.00X$. Data derived from the MODIS-X ocean colour sensor. by Maria Kavanaugh, (WHOI)

Along with the west Antarctic Peninsula, this region shows marked interannual, sub-decadal and decadal variability, which is related to Southern Hemisphere atmospheric variability. This results in large differences between years and decades in ocean temperatures and sea-ice, which, in turn, affects the abundance of krill and the availability of krill to predators (Murphy *et al.,* 2007a, 2014; Renner *et al.,* 2012). Atkinson *et al*. (2004) indicated a decline in the abundance of krill across the South Atlantic region during the last few decades of the 20th century. A recent updated analysis indicated that the decline has not continued and a range of studies have emphasized the importance of ecosystem variability in the region (e.g. Murphy *et al.,* 2007a; Murphy *et al.,* 2014; Loeb and Santora, 2015), including krill predators, which have shown long term changes over the last few decades (Trathan *et al.,* 2007; Constable *et al.,* 2014b).

The ecosystems in the northern regions of the Scotia Sea, such as around South Georgia, are dependent on the advective movement of krill from areas farther south and west. The enhanced northward dispersal is also associated with generally cooler conditions when sea-ice extends farther north. Warmer conditions and reduced winter sea ice are expected to lead to fewer krill in more northern areas as a result of both reduced productivity and dispersal (Murphy *et al.,* 2007a, b). A model based study (Murphy *et al.,* 2007a) suggested that regional warming during the coming decades could result in the almost complete absence of krill from the more northern regions by the end of the century. That study also noted interannual and interdecadal variability that would be observed, as well as the high level of uncertainty associated with such projections; it emphasized the need for improved understanding and models. Such a regional warming would be expected to result in a general shift southwards of cold polar habitats and the increased influence of lower latitude species in more southern regions (Trathan and Agnew, 2010 ; Mackey *et al.,* 2012; Hill *et al.,* 2013) and potentially major changes in food web structure (Murphy *et al.,* 2012, 2013). The high level of interannual and decadal variability in this region indicates that caution is required in interpreting

Figure 3.17.14 A Southern Ocean pteropod (*Cio balantium*), a planktonic snail-like organism, is one type of shell forming invertebrate under threat from ocean acidification. © Russell Hopcroft/ Australian Antarctic Division, January 2008; Image RS31537, Image Antarctica.

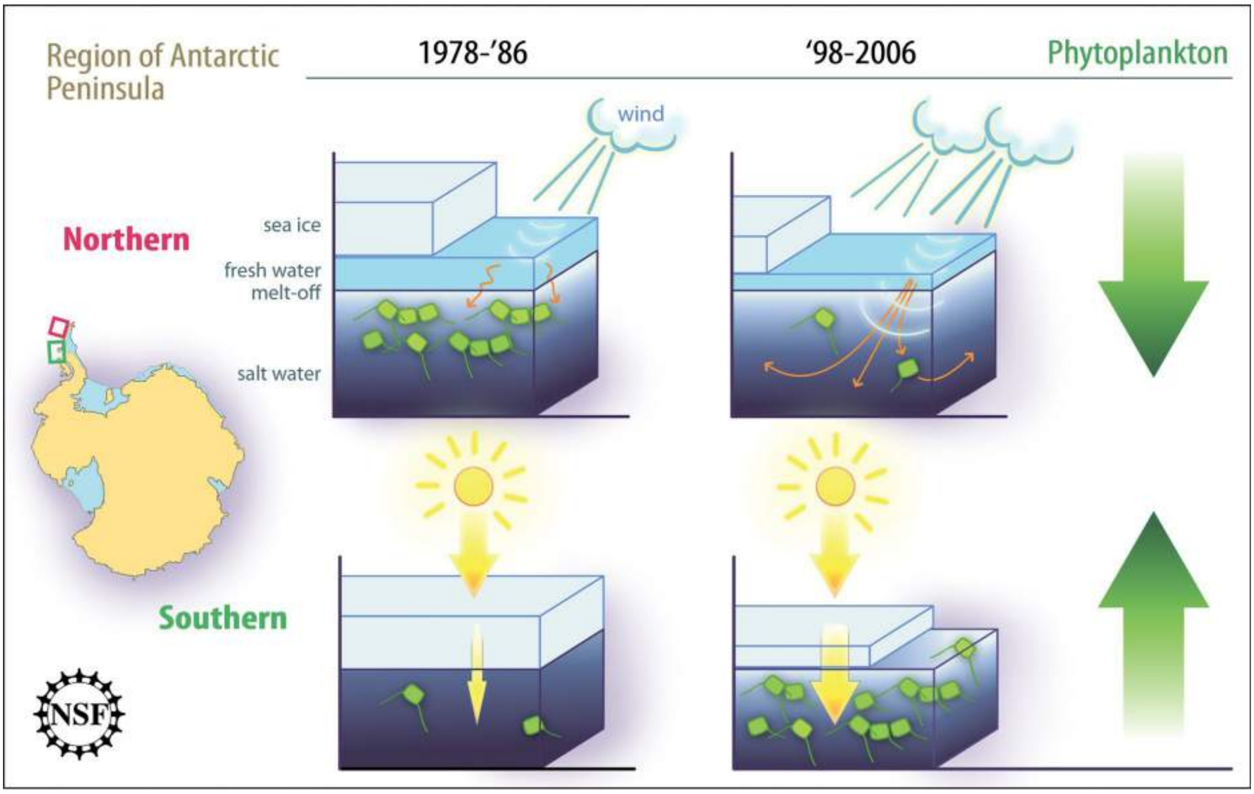

Figure 3.17.15 Cartoon illustrating causes of decreased or increased phytoplankton abundance in the north or south WAP region, respectively, between 1978 – 1986 and 1998 – 2006 (after Montes-Hugo *et al.,* 2009). In the north, reductions in sea ice cover by 1978 had already resulted in exposed (open) ocean surface, and further reductions led to decreased stratification and increased vertical mixing of plankton into deeper (darker) depths. In the south, sea ice covered the ocean surface for most or all the year, limiting light availability below the surface. Subsequent sea ice decline exposed new ocean areas for plankton growth. (Figure courtesy Zina Deretsky, NSF).

ecological effects based on short term or infrequent data series (Murphy *et al.,* 2014), and suggests that detecting future change will require observation systems with extensive spatial and temporal coverage.

In the benthic ecosystems the predicted responses to climate change will be range contractions poleward of species endemic to the Southern Ocean and range expansions southward of species able to cross the Polar Front, especially in the area of the Scotia Sea (Barnes *et al.,* 2009).

3.17.3.3 Indian

Although surveys of the ecosystem in the Indian Sector have been undertaken (Nicol *et al.,* 2000, 2010), few data are available on how the ecosystem is changing. The sector has experienced movement south of the frontal systems (Sokolov and Rintoul, 2009). Evidence so far indicates that phytoplankton and zooplankton species are likely to move south with the progression of the fronts (Constable *et al.,* 2014b). This movement south of the fronts has already been affecting king penguins (Figure 3.17.16) on subantarctic islands and this is likely to continue (Bost *et al.,* 2015).

Change in the sea ice seasonality and extent has been much more variable than experienced on the West Antarctic Peninsula and in the Ross Sea, with some local areas experiencing an increased duration of sea ice cover while other local areas experienced a decrease (Massom *et al.,* 2013). Sea ice has important consequences for Adélie penguins in the region, with the presence of fast ice adjacent to colonies causing poor foraging performance (Emmerson and Southwell,

Figure 3.17.16 King penguins (*Aptenodytes patagonicus*) on Middle Beach (Brothers Point in distance), Macquarie Island, Southern Ocean. © Robbie Kilpatrick/Australian Antarctic Division, November 2015; Image RS31770, Image Antarctica.

2008). Unlike on the Antarctic Peninsula and in the western Ross Sea, Adélie penguin populations have been increasing in East Antarctica, which is possibly a reflection that the accessibility through the sea ice has been improving even though change in the extent and duration of the pack ice has been variable throughout the sector (Southwell *et al.,* 2015).

In contrast to Adélie penguins, emperor penguins have been declining in some locations and would be expected to decline in the long term as a result of sea ice decline (Jenouvrier *et al.,* 2014) but some current declines may also be a product of migration to other sites (La Rue *et al.,* 2014).

3.17.3.4 West Pacific

The Ross Sea is an important shelf area in the Antarctic marine ecosystem with the highest productivity of the region (Arrigo *et al.,* 2008) supporting a high latitude food web with strong benthic-pelagic coupling (Pinkerton *et al.,* 2010; Smith Jr. *et al.,* 2012, 2014). The sea ice habitat has been increasing in recent decades but this may be due to winds spreading the sea ice further north, creating a more open sea ice environment throughout the area (Smith Jr. *et al.,* 2014). Few data are available on long term change of the ecosystem in this sector. Censusing of Adélie penguins along the western margins of the Ross Sea has shown a large degree of variability between colonies and over time but generally an increase in abundance at these colonies, but not to the extent observed in East Antarctica (Lyver *et al.,* 2014). There is some evidence of change in these penguin populations arising from increased access through sea ice conditions, at least in the southern Ross Sea (Whitehead *et al.,* 2015).

3.17.4 Trends and impacts

The Antarctic marine ecosystem has been changing over the last two centuries with over-exploitation of seals and whales and now their trajectories for recovery. Overlaid on this are changes due to global warming, which may arise as rapid step changes in the marine environment, such as the possible rapid reduction in the sea ice extent in the 1950s (de la Mare, 1997) and the possible shift in the pelagic ecosystem on the west Antarctic Peninsula around 1993 (Bestelmeyer *et al.,* 2011). In the recent satellite era, the changes have been more gradual and the shifts in winds are likely to be the product of the effects of ozone depletion and recovery than global warming per se. Future change is most likely to be a result of continued recovery of the ozone hole, an increasing influence of global warming and the added complication of ocean acidification (McNeil and Matear, 2008; Hauri *et al.,* 2016; McNeil and Sasse, 2016). Ocean acidification, for example, could negatively impact the reproductive performance of krill (Kawaguchi *et al.,* 2011) and benthic calcifying invertebrates. Krill may also demonstrate increased metabolism and feeding when exposed to acidifying conditions (Saba *et al.,* 2012).

A further complication in understanding the prognosis for the Antarctic marine ecosystem is the likely increase in Antarctic krill fisheries. These fisheries are currently at less than 5% of what would be regarded as a precautionary catch limit (Kawaguchi and Nicol, 2014). They are increasingly accessing areas near to the continent during winter as a result of reduced sea ice extent, with potential of concentrating in areas important to predators during that time (Kawaguchi *et al.,* 2009).

The complexity of these interactions and the poor performance of coupled climate models for the Antarctic marine ecosystem makes it difficult to forecast what may happen to this ecosystem. However, there seems little doubt that the polar ecosystem will contract towards the Antarctic continent (Hill *et al.,* 2013) and that the distribution of ice dependent species will contract with it. Current research would suggest that the krill-based system will become less productive because of reduced abundance of large diatoms, increased metabolic costs in the system, and the direct effects on reproductive performance of krill. These changes are expected to have consequent impacts on the productivity of predators (e.g. Sailley *et al.,* 2013). A major gap in knowledge is how this will affect food webs (Murphy *et al.,* 2012, 2013) and whether the system will become less productive overall, i.e. what will be the consequences for the copepod-fish-predator food chain?

3.17.5 Conclusions and recommendations

Global warming is affecting Antarctic marine ecosystems with the most likely response being a contraction of this ecosystem towards the coast of Antarctica. Change in each sector of the Southern Ocean will be influenced by the latitude of the coastline and the combined interaction of oceanography with bottom topography extending northward to the subantarctic. The expectation is that each sector will have different prognoses because of differences in the underlying oceanography and sea ice conditions, and because of potentially strong regionality in the evolving atmospheric forcing of the system.

Our understanding of the potential effects of climate change on the ecosystem come from integrated studies in the west of the Antarctic Peninsula and Scotia Arc, the former of which has exhibited the most extreme changes to date. For other regions, our knowledge is more fragmented. Also, ecosystem and coupled climate models are insufficient at present to link the available datasets for a comprehensive overview of ecosystem change and directions of change in the future. These issues pose great challenges for estimating the current circumpolar effects of climate change on the Antarctic marine ecosystem and for projecting future change.

The prognosis for the Antarctic marine ecosystem is contingent on the effects of changing sea ice on Antarctic biota. For example, will young Antarctic krill survive without sea ice? Moreover, are projections of sea ice extent and ocean warming all that is needed for projecting climate change impacts on species and ecosystems? Perhaps more account is needed of the quality of the sea ice environment and the productivity in the sea ice zone. These are known to be important factors for species such as Adélie penguins and krill. A further issue to consider is how warming will increase the metabolism of species and therefore cause a reduction in transfer of production through the food web. The outcome will be less production available to top predators unless there is an increase in the supply of nutrients to the base of the food chain. Ecosystem models will be important for assessing the consequences of the multitude of effects that are likely to arise (Murphy *et al.,* 2012; Murphy and Hofmann, 2012; Constable *et al.,* 2014b).

The changing Antarctic marine ecosystem will pose great challenges to CCAMLR. CCAMLR manages the fisheries in the region, including the krill fishery. A management strategy for the krill fishery is being developed by the Scientific Committee of CCAMLR, based on its CCAMLR Ecosystem Monitoring Programme, and aims to ensure the orderly development of the krill fishery while ensuring the fishery remains sustainable and the ecosystem is conserved. The management strategy will need to incorporate mechanisms for adjusting catch levels to take account of changes in productivity of krill and in the requirements of krill predators. In particular, assessments of the current background state of the ecosystem and the likelihood of future states are needed to help CCAMLR adapt its fisheries before problems arise in the future.

Sustained observations of species and food webs in the different sectors of the Antarctic marine ecosystem will be centrally important to not only measure the rate of change in the ecosystem, which is currently rapid, but also to identify any spatial shifts in the ecosystem as it contracts towards the Antarctic coastline and whether movement around the continent of species may occur (Constable *et al.,* 2014a*,* 2016). A concerted effort is needed to expand the current effort from the west Antarctic Peninsula and Scotia Sea to the entire region before substantially more change occurs. This could be achieved through expansion of the Southern Ocean Observing System being developed to observe change in the physics, chemistry and biology of the region (Meredith *et al.*, 2013). A first step will be to extend the biogeographic work of the International Polar Year in the Census of Antarctic Marine Life into a circumpolar benchmark of the Antarctic marine ecosystem to connect the existing datasets and establish the baseline for assessing change in the future.

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The significance of warming seas for ocean 'goods and services'

4

In this chapter we look at how changes to the dynamics of the ocean and the species and ecosystems it supports as a result of ocean warming affect some of the various benefits – the so-called goods and services – that we derive from the ocean. These range from influencing the weather through to potential changes and impacts to human health.

Within the confines of this report it was only possible to select some key benefits and indeed in compiling this chapter it was not possible to identify experts to write sections on issues such as the impacts of ocean warming recreational activities. Nevertheless, we hope that this chapter helps inform and stimulate debate and action to address the knock-on effects ocean warming present for all of us.

"Current and predicted change is having, and will continue to have, profound and probably increasing impacts on life in the ocean, the interactions between society and the ocean, and knock-on effects for life over the land through the changes in weather and climate."

"The improvement of climate model representation of the feedbacks in the climate system between the ocean and atmosphere is therefore a priority for more successful prediction."

Section 4.1 authors

4.1 Impacts and effects of ocean warming on the weather

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Summary

- The heat content of the upper 700 m of the global ocean is ~ 120×10^{21} J higher than in 1995, the equivalent of ~ 240 times the human global energy consumption in 2013.
- Since the 1990s the atmosphere in the polar regions has been warming at about twice the average rate of global warming.
- There is likely to be further major loss, and possibly the essential removal in some years, of summer Arctic sea ice in the next 5-15 years.
- The extent of Antarctic sea ice has been growing at a rate of ~1.3% per decade, although there is strong interannual variability.
- Over the last 20 years there has been a distinct change in the El Niño events, with a shift of the mean location of sea surface temperature anomalies towards the central Pacific.
- There has been an increase in the number of severe hurricanes (Saffir-Simpson scale 3-5) at a rate of ~ 25-30% per °C of global warming.
- There has been an increase in storm surges along Arctic coasts, leading to more frequent inundation of fragile coastal ecosystems.
- There have been significant increases in iceberg numbers in the ocean since the 1990s.
- There is likely to be an increase in mean global ocean temperature of 1-4°C by 2100.
- Due to increased stratification of the ocean, the global Meridional Circulation is likely to decline over the next century, although there is not a consensus as to the rate.
- Uncertainty about the future of most large-scale ocean-atmosphere teleconnections under greenhouse warming is ubiquitous.

Ocean warming effects	Consequences
Loss of Arctic sea ice	An acceleration of Arctic warming and ice loss, combined with more variable, and extreme, mid-latitude weather
Greater tropical upper ocean heat content	An increase in the number of severe tropical cyclones, with an expansion of their latitudinal range
Southern Ocean warming	A southward movement and intensification of westerly winds
Warming tropical oceans	More ecosystem stresses such as coral bleaching, but more ocean mixing beneath the stronger tropical cyclones
	Changes in climate over land, leading to changes in crop production, for example, maize yields decrease as temperatures rise
Warming polar oceans	An increase in the melting of ice sheets, particularly Greenland, an increase in iceberg calving, and a rise in sea level
Increasing freshwater supply to the ocean	A decrease in overturning and a decrease in vertical mixing reducing nutrient supply, and hence productivity, in the surface ocean

4.1.1 Introduction

The upper ocean acts as a major heat engine for the atmosphere of the planet: it absorbs solar energy that is then transferred to the atmosphere. Over much of the ocean its surface is warmer than the atmosphere above it, driving a heat flux to the atmosphere. This can be direct lower atmosphere heating via conduction (the sensible heat flux), heating throughout the troposphere via long wave radiant heating and indirect heating through evaporation of water from the ocean surface and the eventual release of its latent heat during cloud formation. This addition of heat and moisture to the atmosphere helps stimulate the formation of storms, polar lows and hurricanes but on the larger scale it modifies regional and global climate through this spatially and temporally varying addition of energy to weather patterns such as the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO).

The ocean is warming, and this has been occurring for some decades, as part of the general warming of the planet through increasing emissions of greenhouse gases. Until recently it was believed that, in terms of the global mean temperature, this upward trend in near-surface atmospheric temperature may have slowed. However, it is now likely that this was an artefact of measurements of sea surface temperature becoming more common from ocean buoys than ship intake engines, with the former tending to record cooler values than the latter (Karl *et al.,* 2015). There is very strong consistency between different methods of measuring upper ocean heat content, suggesting a consistently increasing trend over the last 20 years (Johnson *et al.,* 2015), with the heat content of the upper 700 m of the global ocean now having ~ 120×10^{21} J more energy than in 1995: this is equivalent to ~ 240 times the human global energy consumption in 2013. The ocean's impact on the atmosphere is therefore likely to be increasing over time; this section explores what could be expected and whether evidence for impacts is increasing.

4.1.2 Description of ocean warming and associated stressor impacts

4.1.2.1 Polar regions

Since the 1990s the atmosphere in the polar regions has been warming at about twice the average rate of global warming, this being greatest in the Arctic and around the Antarctic Peninsula, and called polar amplification (e.g. Overland *et al.,* 2014). This is due to several processes, called positive feedbacks, which tend to amplify the warming in high latitudes. The best known of these is probably the ice-albedo feedback, in which ice and snow that have initially melted due to warming leads to the ocean or terrestrial surface beneath darkening and so absorbing more solar energy, enhancing the warming, and accelerating the melt process. For some years the ice-albedo feedback was considered to probably be the dominant feedback in the Arctic climate system although it has long been recognized that it is augmented by other feedbacks (e.g. Hanna, 1996; Serreze and Francis, 2006). More recently, several of these have emerged as being of comparable importance. One of them, the ice-ocean heat flux feedback, arises from a rapidly warming Arctic Ocean (Timmermans, 2015). Normally, seasonal sea-ice cover acts as a highly effective insulative barrier between the relatively warmer ocean and the cold winter atmosphere. As increasingly more sea ice is removed each summer, the subsequent seasonal freeze-up is delayed and there is more and more exposed ocean (and thinner sea ice) north of Alaska each autumn. This is at a time of year when the atmosphere is cooling rapidly, increasing the temperature contrast with a still relatively warm ocean. The effect is to dramatically heat the overlying atmosphere, which can generate more local storm systems through turbulent heat convection.

Polar amplification has had profound impacts on the climatology of the high-latitude oceans and resulting effects on sea ice cover. Arctic sea ice has declined by over 13% per decade in late summer during the period of available continuous hemispheric satellite coverage since 1979, and by about 3% in late winter (Perovich *et al.,* 2014). If these trends continue, then there is the possibility that as soon as in 5-15 years little Arctic sea-ice could remain in late summer in some years (Overland and Wang, 2013).

4.1.2.2 Mid-latitude storminess

There are no clear signs of an overall increase in the frequency or intensity of mid-latitude Northern Hemisphere storminess since the late 19th Century, although shorter multi-decadal cycles are evident, e.g. with a quiet period in North Atlantic storms around the 1950s and stormy peaks around 1880-1900 and 1990 (Hanna *et al.,* 2008; Wang *et al.,* 2009). However, this does not necessarily mean there is no human-induced greenhouse warming signal modulated by the ocean, as the latter (if present) may be buried in the considerable short-term variability. The Arctic Oscillation (AO) is the main mode of atmospheric surface pressure variability between mid and high northern latitudes and is strongly related to the better-known North Atlantic Oscillation (the NAO marks south-north pressure variations in the North Atlantic region). Although the NAO became more positive between the 1960s and the 1990s, with stronger westerly winds (associated with the recent stormy peak mentioned above); this trend has subsequently been replaced by a period of pronounced variability, with some extreme negative excursions since the mid-2000s (Hanna *et al.,* 2015), which may just be natural variability but might also be related to recent Arctic sea-ice depletion (Overland *et al.,* 2015), as well as periods of positive NAO, as in the last two boreal winters.

It is unclear what will happen to mid-latitude storminess with ongoing anthropogenic ocean warming, even discounting other external forcing factors and natural (internal) variability. The tropopause (the natural thermal 'lid' of the troposphere – the lowest layer of the atmosphere in which all our weather occurs; Figure 4.1.1) is highest at the equator (about 15 km above the surface) and slopes down towards the poles (where it is about 10 km high). With increasing greenhouse-gas levels, temperatures warm at the surface and in the lower troposphere while the stratosphere (the overlying region of the atmosphere, immediately above the troposphere) cools. This effect is well observed in recent observations from the last couple of decades and is due to a denser blanket of greenhouse gases retaining more of the extra heat nearer the surface. At the same time, as seen above with reference to polar amplification of global warming, the Earth's surface, including the ocean surface, has been warming most rapidly at high latitudes. This latter change has the effect of reducing the meridional (north-south) temperature gradient, which might be expected to reduce the amount of energy available for driving mid-latitude storminess, all other factors being equal (Francis and Vavrus, 2015; Overland *et al.*, 2015). But this is just a near-surface expression of global warming. Meanwhile, in the upper troposphere at low latitudes, there is more vigorous convection due to increased latent and sensible heat fluxes under global warming, and this raises the tropopause and increases upper tropospheric temperatures near the equator (about 15 km up) while the same altitude near the poles (i.e. well within the

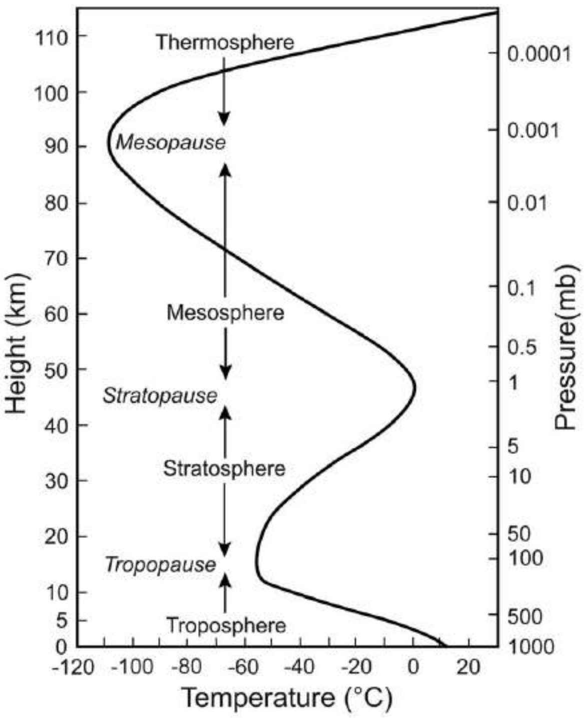

Figure 4.1.1 The zonal mean vertical profile of temperature at 45°N during summer, showing the layers in the atmosphere. Reproduced from Bigg (2003), with permission of Cambridge University Press.

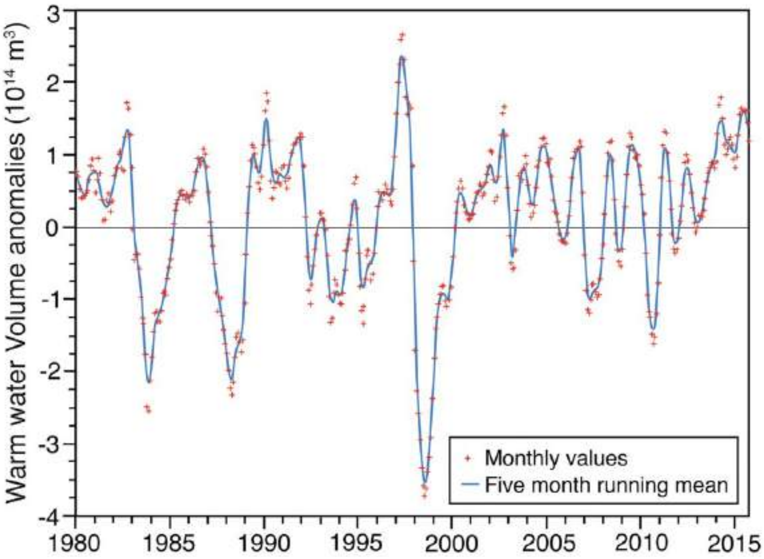

Figure 4.1.2 Time series of volume of water above 20°C in the equatorial Pacific (5°N – 5°S, 120°E – 80°W). Note the change in character in the late 1990s. Modified from http://www.pmel.noaa.gov/tao/elnino/wwv/ (last accessed 12 November 2015), provided by the TAO Project Office of NOAA/PMEL.

stratosphere at these high latitudes) significantly cools with global warming. Therefore, there is a significantly enhanced meridional temperature gradient at this higher altitude just at the same time that the north-south temperature gradient reduces near the surface (Harvey *et al.,* 2015). Thus there are two competing influences that can result in opposite changes in mid-latitude storminess under conditions of global warming. One recent model-based study (Harvey *et al.,* 2015) suggests that the near-surface meridional temperature gradient change is most important for determining changes in the wintertime North Atlantic storm track but overall this is far from certain and more work is clearly needed in understanding the multiple linkages mechanisms leading to storminess change (Barnes and Screen, 2015; Overland *et al.,* 2015).

4.1.2.3 The tropics and ENSO

Fluxes from the tropical oceans have very strong impacts on the atmosphere, not just in terms of regional or local weather changes, such as generation of hurricanes, but also in terms of basin and global scale teleconnections, such as those associated with the ENSO phenomenon. Over the last 20 years there has been a distinct change in the El Niño events, with a predominance of so called central Pacific events, where SST anomaly peaks occur in the central Pacific, compared to eastern Pacific events, where the anomalies are strongest in the eastern upwelling zone (Lee and McPhaden, 2010). This switch, and the general move towards higher ocean heat content, is well shown in Figure 4.1.2. These different types of events lead to distinctly different long range impacts such as the position and strength of temperature and precipitation anomalies over the North Pacific and North America in particular (Capotondi *et al.,* 2015), but also further afield. Thus, the preponderance of central Pacific events in recent years has led to a warm Pacific, but cooler conditions in the upwelling region along the west coast of the US; this is consistent with the recent prolonged negative state of the Pacific Decadal Oscillation (PDO) (Boulton and Lenton, 2015). The most recent strong El Niño, of 2015-16, however, was a more "normal" eastern Pacific event, and so there was a strong warm anomaly in the NE Pacific (Bond *et al.,* 2015), and a return to a positive PDO. The ENSO shift, coupled with the increased wind speeds over the tropical oceans (Mears, 2015), also has contributed to a stronger global monsoon precipitation in recent years (Wang *et al.,* 2012).

The ENSO cycle also has a strong modulating influence on tropical storm frequency and intensity in a number of regions. The warming oceans would implicitly be assumed to lead to more, and stronger, tropical storms because of the greater SST providing more sensible heat to the lower troposphere, and the increasing surface wind speeds in the tropics (Mears, 2015) leading to more evaporation – hence higher latent heat - and higher specific humidities (Willett *et al.,* 2015). Thus, the tropical atmosphere should have more energy for storm and hurricane formation. However, there is a range of ocean and atmospheric conditions necessary for hurricane formation and not all are necessarily favoured by current environmental change; indeed, predicting tropical cyclone formation rates still relies on a statistical relationship rather than a physical theory (Walsh *et al.,* 2015). For example, the tropical North Atlantic had quiet hurricane seasons for both 2013 and 2014, but for different reasons. In 2014 low hurricane numbers

Box 4.1.1 Case Study – Hurricane Catarina – the first South Atlantic hurricane

In late March 2004 the only hurricane ever observed in the South Atlantic since satellite records began in 1970 formed off the southern coast of Brazil. Unofficially known as *Catarina,* it possessed the characteristic eye wall and spiral rain band features of tropical cyclones seen elsewhere (Figure 1), had gusts reaching speeds of 195 km/hr, and its landfall led to extensive flooding and destruction of buildings. The South Atlantic is traditionally viewed as an unlikely region for hurricane formation because of its cooler sea surface temperatures, the strong vertical wind shear and the lack of a convergence zone in the atmosphere. However, in 2004 these conditions were more favourable than normal, and a low pressure system generated in the sub-tropics gained sufficient energy and convergence to result in hurricane conditions.

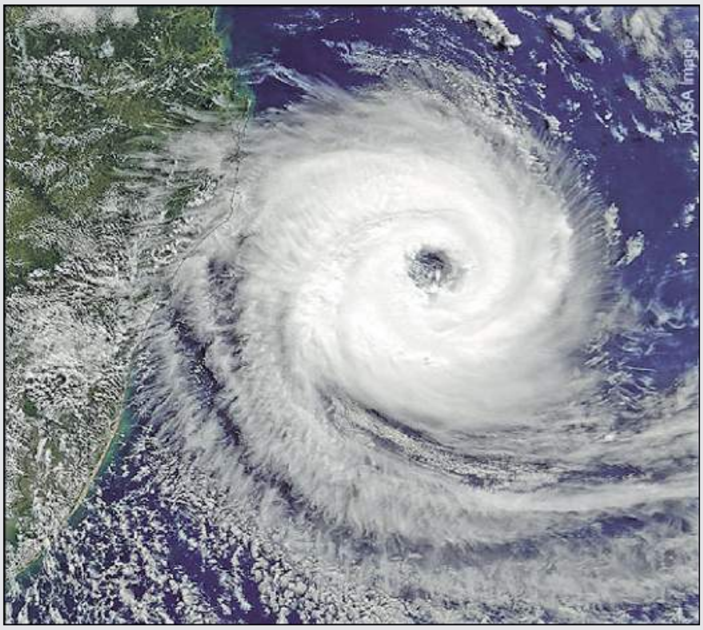

Figure 1 Image of Hurricane *Catarina* on March 26th, 2004, off SE Brazil. Image courtesy of NASA.

Sub-tropical cyclones are formed in the South Atlantic most years (Gozzo *et al.,* 2014), mostly linked to a mix of sub-tropical processes – typically cold cut-off lows combined with low level warm air advection by the subtropical high – and so not leading to hurricanes, which have typically a more tropical origin, within warm, humid and convective atmospheric conditions. The peak season for such systems is austral winter, but the conditions in the autumn (March-May) tend to be most tropical in nature. It is noteworthy that examples of more tropical storm formation have occurred in the past, such as a tropical depression that moved eastwards from Angola in 1991, showing the potential for other modes of tropical storm formation. As sea surface temperatures rise in the future, the classical condition required for hurricanes of such temperatures exceeding 26°C will begin to occur in some years, and changes to atmospheric convection related to changes in land-based heating may well make such storms a less exceptional event in the future.

were associated with the developing El Niño conditions in the Pacific, but in 2013 it was a local unfavourable thermodynamic environment that limited hurricane formation (Fogarty and Klotzbach, 2015). Despite the tendency for tropical cyclones to be favoured by warmer conditions, and for there to have been globally a more active hurricane climate since the mid-1990s (Figure 4.1.3; Kossin *et al.,* 2014), there is no trend towards more tropical storms on a regional basis over the past 20 years. This mixed story will be explored further when considering future implications.

4.1.2.4 The Southern Ocean

The Southern Hemisphere between the tropics and Antarctica is largely made up of ocean. Zonal trends in air and surface temperature tend to be lower than in the Northern Hemisphere mid-latitudes (Hartmann *et al.,* 2013). However, there is still significant atmospheric climate change which has an impact on the ocean. This is largely linked to the increase in strength of the westerly winds over the Southern Ocean over the last few decades (Hande *et al.,* 2012; Gillet and Fyfe, 2013; Zieger *et al.,* 2014). The two key differences from the Northern Hemisphere are: (1) the larger role of stratospheric ozone depletion, which causes high-altitude cooling and is considered to be the dominant source of the increasing winds over the past few decades, although with ozone recovery this effect is now beginning to reverse, and (2) the greater resilience so far of Antarctic sea-ice in the face of anthropogenic global warming. In fact, hemispheric winter sea ice coverage has grown by approximately 1.3%/decade around the Antarctic continent since the late 1970s

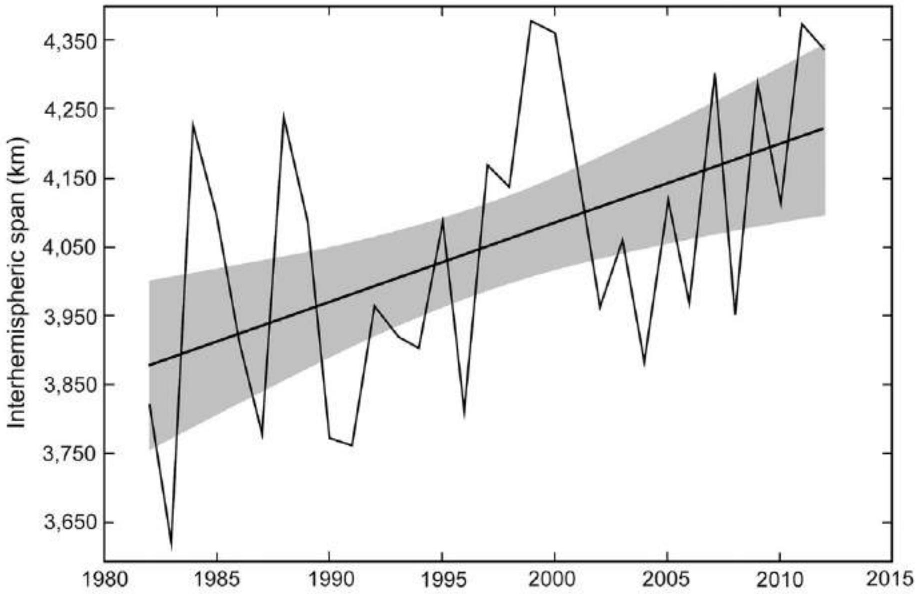

Figure 4.1.3 Variation over 1980-2012 in the width of the tropical band over which the lifetime maximum intensity of tropical cyclones are found, from best-track historical data. Shaded area shows 95% confidence limit of the trend line. Adapted from Figure 1c of Kossin *et al.* (2014).

(NSIDC, 2014), and although sea ice around the rapidly warming Antarctic Peninsula region has simultaneously undergone a rapid decline, this isn't enough to offset the overall sea ice gain. This is likely to be influenced by the huge thermal inertia of the Southern Ocean, and the latest infrared satellite temperature maps show relatively little or no net warming trends from 1981-2014 over much of the sea-ice regions surrounding Antarctica (Josefino Comiso, NASA, personal communication, 2015). There is, nevertheless, still warming at the sub-surface levels of the Antarctic Intermediate Water, because of the southward migration and intensification of the westerly winds leading to more intermediate water formation (Yasunaka and Kimoto, 2013). The anthropogenic greenhouse warming and ozone signals currently seem to be the dominant influences on Southern Ocean wind changes (Abram *et al.,* 2014). Therefore, with the caveat of all the climate-model uncertainties in being able to make reliable predictions of such complex atmospheric features, a continuation of the southward migration and intensification of the westerly winds in most seasons - or at least maintenance of current relatively stormy conditions in the mid to high Southern latitudes - seems a likely outcome for the next few decades (Thompson *et al.,* 2011).

This intensification in winds, coupled with the contraction of the storm belt towards Antarctica, is highly variable over time, but has a number of consequences. The strength of the Antarctic Circumpolar Current varies, but seems to have remained approximately of the same basic strength over the past 20 years (Meredith *et al.,* 2011). However, the oceanic eddy field has strong regional variability, with major increases in the Pacific and Indian sectors of the Southern Ocean (Hogg *et al.,* 2015). There is modulation of this signal through the interaction between the state of the Southern Ocean winds and ENSO, with the combination of El Niño with recent Southern Ocean wind strengthening enhancing the eddy field, but a La Niña not doing so (Langlais *et al.,* 2015). However, this increased oceanic eddy field will impact the strength of the southern component of the overturning circulation and carbon cycling, but also affect the winter sea ice distribution, as this is strongly modulated by wind-driven ice drift (Holland and Kwok, 2012). The winter sea ice extent has very large interannual variability, and a regional pattern of change, but, as seen, there is a trend towards a slight increase over time (Turner *et al.,* 2015). The wind strengthening also changes the Southern Ocean carbon transport (Hauck *et al.,* 2013), through enhanced export production and downward transport of carbon north of the Polar Front, while more production occurs in the upwelling zone south of the Polar Front, leading to a regional drawdown of atmospheric CO_2.

4.1.3 Ecosystem consequences

The consequences of the warming for life in the oceans are already significant. Ocean pH is already changing as a direct result of drawdown of the increased atmospheric CO_2 (Hilmi *et al.,* 2015). Species whose ranges are strongly affected by temperature have already begun to move. This involves expansion in range for some species, such as cod (*Gadus morhua*), limited

Box 4.1.2 Case Study - North Icelandic sea-surface temperature (NIceSST) as a barometer of northern North Atlantic Ocean climate change

Hanna *et al.* (2006) constructed and analysed a 119-year North Icelandic Sea-Surface Temperature (*NIceSST*) record (1883-2001) that has here been updated through March 2016 (Figure 1). It is based on the statistical merging of data from three measurement stations along, or just off, Iceland's north coast: Hraun, Raufarhöfn and the island of Grímsey. The main part of the data series comes from Grímsey. The merging procedure is needed because no one station has a complete record extending all the way back to the 1880s; however, agreement between stations is very good for the substantial periods of overlap.

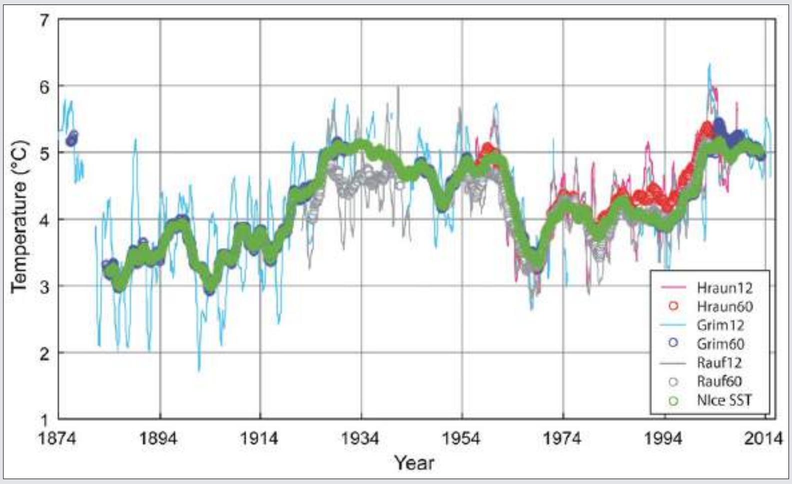

Figure 1 Total number of icebergs >5 m in diameter crossing latitude 48°Nin the NW Atlantic each year 1900-2014, as recorded by the IIP. Note that the year is defined as an ice-year, beginning in October of the year before the notional record and extending to September of the ordinal year. Reproduced from Bigg (2016), with permission of Cambridge University Press.

The *NIceSST* record provides a good representation of coastal ocean conditions around northern Iceland, where there is frequent interaction and changes between the Atlantic (Irminger) and Arctic (East Greenland and East Icelandic) currents. It is also representative of climate change and air-sea-ice interactions in a broader region of the northern North Atlantic. During particularly severe Icelandic winters, as happened most recently around 1970, sea ice is drawn to the north coast of Iceland, temporarily making its climate more continental and depressing the *NIceSST* values more than might otherwise be expected. Comparison of the *NIceSST* record with measures of Icelandic sea-ice incidence, such as the Koch ice index (Hanna *et al.*, 2004), is therefore instructive.

NIceSST shows relatively cold conditions in the late-19th Century, during the final stages of the Little Ice Age, rapid warming in the 1920s, a warm peak in the 1930s, a cold blip in about 1965-1971 that is related to the Great Salinity Anomaly – a pulse of cold fresh water that propagated around the North Atlantic – and warming since the early-mid 1990s. This latter warming is linked to the general global warming signal and was particularly pronounced from 1995-2004 but since then has plateaued – although summer 2014 saw record high air and sea-surface temperatures in northern Iceland. However, in general, *NIceSST* in the last decade of its record hovers around peak values of the previous 1930s warm peak. Long-term trends in sea-surface temperatures in Iceland (and elsewhere) tend to reflect near-surface air temperature changes logged at nearby meteorological stations.

It is unclear to what extent the relative stability of *NIceSST* since 2004 – a common feature with several other sea-surface temperature series from adjacent nearby parts of the northern North Atlantic (http://ocean.ices.dk/iroc/) – also reflects recent changes in ocean near-surface stratification and circulation that could in turn be affected by, for example, changes in precipitation, additional sea ice melt and/or changes in freshwater runoff that is influenced by precipitation and increased glacier melt. However, it is possible that the recently observed decline in the Atlantic Meridional Overturning Circulation (AMOC) (Smeed *et al.*, 2014) –although this might not be significant (Buckley and Marshall, 2016) - and/or the recent increase in Greenland atmospheric high-pressure blocking (Hanna *et al.*, 2016) – the latter tends to be linked with stronger/colder northerly and easterly winds to the east of Greenland and towards Iceland - might have suppressed ocean change in this part of the North Atlantic relative to the Arctic or sub-tropics.

The *NIceSST* data series is available from:
https://www.sheffield.ac.uk/geography/staff/hanna_edward/seasurface

by minimum temperatures, but contraction for species such as corals, which are sensitive to high temperatures. These, and other, consequences are explored more in other sections of this report. However, the changes to the weather associated with the ocean warming have also already had consequences for both marine and terrestrial species. While global hurricane numbers have not changed significantly there are now more severe hurricanes (Saffir-Simpson scale 3-5) than several decades ago (Holland and Bruyere, 2014; Vincent *et al.,* 2014), with an increase in these severe systems at a rate of ~ 25-30% per °C of global warming. This increases the risks to coastal environments in the tropics, particularly to coral reefs and coastal ecosystem stability (Ghorai and Sen, 2015). However, not all hurricane impacts are negative: the associated increased vertical mixing cools the sea surface temperature and can reduce the impact of temperature-induced coral bleaching (Carrigan and Puotinen, 2014).

Recent changes in the characteristics of El Niño events and the PDO may have been responsible for long droughts in Australia and the western USA, with the resulting stresses on all parts of the regional ecosystems, particularly river and agricultural systems (van Dijk *et al.,* 2013), but also forest fire severity (van Mantgem *et al.,* 2013).

In the Arctic the declining sea-ice extent and thickness, particularly during summer, has significant impacts on species using the ice. There is less ice for seals to haul themselves onto, and for polar bears to hunt from. The latter are experiencing extreme change in some parts of their range, particularly north of Siberia and Alaska, due to oceanic warming with consequences for polar bears throughout their life cycle (Derocher *et al.,* 2013). There are likely to be knock-on effects on the Arctic land environment through such large predators being forced to spend more time off the ice. Another impact of ocean warming and reduced sea-ice is an increase in storm surges along Arctic coasts, leading to more frequent inundation of fragile coastal ecosystems (Vermaire *et al.,* 2013).

4.1.4 Societal consequences

The consequences for society of changing weather patterns due to the warming of the oceans are considerable. They involve a mix of food and water factors, and the evolution of various types of risk. There have already been changes to precipitation patterns in a number of areas of the planet resulting from large-scale atmospheric teleconnections with ocean warming. These can be increased rainfall in some mid-latitude and monsoon areas, but decreases over various sub-tropical regions. Both will have impacts on the yields of crops over a range of important food producing areas such as Australia, North America and India. There are good correlations between wheat and maize yields with the NAO and PDO, so changes in these ocean-focused atmospheric patterns have direct implications for food production (Tian *et al.,* 2015). Similarly, increasing temperatures tend to reduce maize yields, if all other factors are held constant (Bassau *et al.,* 2014). At sea, warming temperatures will cause changes to the abundance and range of marine species used for food, leading to implications for both the billion people who depend on fish for their principal source of protein (Cury and Shin, 2015) and the fishing and aquaculture industries linked to this harvesting.

Water supplies are also impacted by these ocean-induced weather changes. Where droughts are occurring in regions that are semi-arid even in good years, often water supplies rely on a limited number of water sources. Decreases in the flows of major rivers, such as the Murray in Australia and the Colorado in the United States for example, put at risk the water needs of large human populations. In regions where storms are increasing in number or severity, flooding can be a major risk, whether inland (Schweighofer, 2014) or coastal (Vermaire *et al.,* 2013).

Risk is not just associated with food security and flooding. The increasing number of severe hurricanes poses a significant risk to economic development, housing as well as life in areas subject to landfall. While the consequences are especially severe for developing countries, such as the Philippines in Typhoon Haiyan, even developed nations such as the United States during Hurricane Sandy are still subject to major dislocation. North-west Europe faced a series of unusually severe winter storms during the 1990s (at least in the context of the previous few decades), so any changes in jet-stream activity – which are clearly related in part to ongoing climate change (Hall *et al.,* 2015) - have serious economic, societal and ecological implications for the densely-populated northern mid-latitudes. Although the 2000s onwards were marked by a generally quieter windstorm period, this more recent period saw a clustering of unusually severe winter cold-air outbreaks in both Eurasia and eastern North America that have been linked with Arctic sea-ice change and a

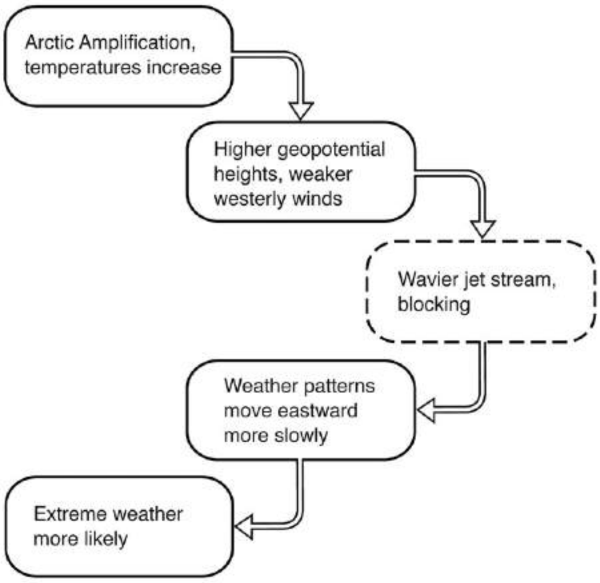

Figure 4.1.4 Hypothesized steps linking Arctic Amplification to more extreme weather events in mid-latitude Northern Hemisphere. Adapted from Overland *et al.* (2015). ©American Meteorological Society. Used with permission.

weaker and more meandering polar jet stream (Cohen *et al.,* 2014; Francis and Vavrus, 2015; Overland *et al.,* 2015; Figure 4.1.4). And, with winter NAO variability having increased significantly over the past few decades (Hanna *et al.,* 2015), the UK, for example, experienced two of its wettest and stormiest winters on record in 2013/14 and 2016 (Met Office, 2014, 2016).

In polar regions the increasing ocean temperatures are linked to greater melt and higher fluxes of icebergs from both Greenland and Antarctica (Hanna *et al.,* 2013, Bigg, 2016; Figure 4.1.5). These pose risks to the increasing use of polar waters for shipping, particularly in the Arctic. However, the melting of sea ice and the opening up of the Arctic is leading to more mineral and oil exploration, although still of a limited nature. The opening of the Arctic is also providing new, shorter, transportation routes for part of the year. These are still limited, consisting of 44 passages across the NE Passage north of Russia in 2013 (Farré *et al.,* 2014), but increasing.

4.1.5 Implications of continuing ocean temperature rise

Warming of the oceans has only been significant for a few decades, but predictions from climate model simulations of the next century, and beyond, are for this to continue, leading to changes up to 1-4°C by 2100 (Collins *et al.,* 2013). These will have consequences for the physical characteristics of the ocean, and for the weather patterns influenced by the ocean.

The most immediate consequence for the ocean of increasing atmospheric temperatures due to greenhouse warming is a direct warming of the surface waters over much of the ocean, and particularly the Arctic, where rates of change are greatest. This will increase the stratification of the ocean by making the mixed layer less dense than it is currently. Mixing between surface and deeper waters will therefore most likely become harder to initiate over large parts of the ocean. This will slow the supply of sub-surface nutrients to the surface waters, generally decreasing marine primary productivity (Mora *et al.,* 2013). However, this decline in productivity will also reduce the sequestration of atmospheric CO_2 into the ocean, providing a positive feedback on the warming. Note, however, that in the Arctic, productivity is likely to increase due to the rapid decrease in sea ice and warming of the ocean (Park *et al.,* 2015). A further consequence of making mixing more difficult is that deep water formation in the North Atlantic and Arctic is likely to decline, slowing the global meridional circulation arm deriving from the Atlantic Ocean (Collins

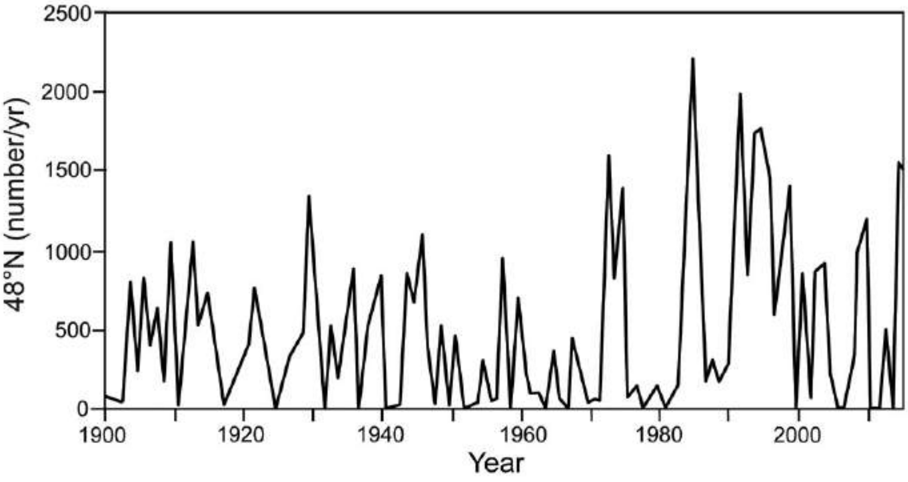

Figure 4.1.5 Total number of icebergs >5 m in diameter crossing latitude 48°N in the NW Atlantic each year 1900-2014, as recorded by the IIP. Note that the year is defined as an ice-year, beginning in October of the year before the notional record and extending to September of the ordinal year. Reproduced from Bigg (2016), with permission of Cambridge University Press.

et al., 2013). Paradoxically, this is predicted to reduce the ocean heat transport northwards in the Atlantic, slowing the rate of atmospheric, and therefore oceanic, warming over and near the North Atlantic.

In the Southern Ocean change is expected to be less dramatic because of the atmospheric isolation of the southern quarter of the globe through the strong zonal winds. Nevertheless, there is increased melting and iceberg calving in parts of West Antarctica and the Antarctic Peninsula and this is likely to continue into the future (Bigg, 2016) as atmospheric warming continues, albeit at a slower rate here. More melting will also decrease the density of the surface waters through the increased supply of fresh water. On the Antarctic Shelf this freshening will make it easier to form sea ice, perhaps increasing formation of Antarctic Bottom Water, which relies on the release of salt from near surface waters during the freezing process. However, further offshore open ocean convection is likely to decrease, as in the Northern Hemisphere.

Another possible impact of warming of the ocean is the re-creation of a relatively warm water connection between the North Pacific and North Atlantic as summer ice disappears, allowing species movement and mixing. This last happened to a substantial degree in the Pliocene, some 3 Ma, leading to a range of species becoming geographically isolated once the Arctic passage became impassable and resulting in evolution of new species. The separation of Atlantic (*Gadus morhua*) and Pacific cod (*Gadus macrocephalus*) is an example of this (Bigg *et al.,* 2008). Radical rearrangement of fisheries through species' movement and unprecedented competition is therefore possible in the longer term.

These changes to the ocean will have knock-on effects to the atmosphere above, through changing air-sea heat and moisture fluxes. Atmospheric storms of all types originating over the oceans rely on these fluxes for their basic energy supply and a likely consequence of ocean surface warming is the production of more, and more powerful, storms at many latitudes. In the tropics the area of water warmer than 26°C, an important precondition for hurricane formation, is likely to expand as well. Climate models are still not able to reproduce well tropical cyclones (Walsh *et al.,* 2015), so there is some doubt about whether the number of such storms will increase, as expected. However, it appears likely that the probability of strong hurricanes occurring is likely to increase (Vincent *et al.,* 2014), although there may be a point in the warming beyond which this trend halts (Holland and Bruyere, 2014).

There are also problems with modelling future polar jet-stream changes, and there is currently no clear consensus between studies on how mid-latitude storminess is likely to change by 2100. Gillett and Fyfe (2013) used the Coupled Model Intercomparison Project 5 (CMIP5) suite of climate-model simulations – based on 37 different models using the RCP4.5 emissions scenario - to show weak trends towards a more positive AO/NAO, which would represent generally stormier northern mid-latitudes, in all seasons by 2100. No CMIP5 model showed a significant decrease in any season. Gillett and Fyfe (2013) also noted that the more negative AO observed since 2000 is not shown in the models (when run retrospectively) – this difference reflects either model deficiency or internal variability in the AO/NAO climate system. However, Hall *et al.* (2015) also point out that other studies of model projections do show, or don't discount, a negative NAO response – with associated reduced mid-latitude storminess – to anthropogenic global warming. One such study was made by Sun *et al*. (2015) who modelled the atmospheric response of 21st Century Arctic sea-ice decline, finding a negative AO/NAO effect in winter. However, there are many other potential effects on mid-latitude storminess, for example forcing from the tropics and from the Pacific, and the level of understanding of the physical mechanisms remains insufficient to be able to make reliable projections to 2100, although for the Southern Hemisphere relatively stormy mid-high latitude conditions during the next few decades seems most likely.

It is often stated that continued warming of the tropical ocean should lead to more frequent occurrence of tropical ocean-atmosphere processes such as El Niño, as the basic state of the ocean is more conducive to such events being initiated. However, climate models are still not sufficiently good in reproducing temporal patterns of El Niño frequency for this to be certain (Capotondi *et al.,* 2015). Indeed, in the suite of climate models for the last IPCC report both increases and decreases in the frequency of such events were forecast (Christensen *et al.,* 2013). It is also unclear how links between ENSO and climate elsewhere in the tropics will change under ocean warming – modes of interaction with climate processes such as the Indian monsoon have changed over the past century and are expected to continue to do so into the future, and may even weaken (Li and Ting, 2015).

There seems little doubt that Arctic amplification of global warming will continue into the future. The increased exposure of ocean surface to the atmosphere associated with that amplification has been thought to be linked to changes in weather patterns in the mid-latitudes, specifically the Warm Ocean-Cold Continent phenomena (Overland *et al.,* 2015). However, as with other ocean-atmosphere interactions, climate models are mixed in their predicted response of the atmosphere in the future to this amplification. Change is very likely, but what its pattern and magnitude will be is currently unknown (Barnes and Polvani, 2015). This uncertainty about the future of large-scale ocean-atmosphere teleconnections under greenhouse warming is ubiquitous. As well as those already discussed, the future course and consequences of the PDO and the similar Atlantic Multi-decadal Oscillation are uncertain (Chylek *et al.,* 2014). Climate models have been giving consistent predictions of future climate change at continental to global scale for over two decades, but the detailed response of such air-sea interaction teleconnections remains uncertain.

4.1.6 Conclusions and recommendations

As the ocean warms the atmosphere above, and beyond, is being affected by this warming. Developing changes in air-sea interactions are being seen around the planet, in many cases leading to enhancement or shifting of extreme weather. This can be mid-latitude storminess, linked to changes in Arctic sea-ice, more severe hurricanes or changes to the character of El Niño events or monsoons, all linked to tropical ocean changes. These changes to the ocean, and then atmosphere, are set to continue as anthropogenic warming continues this century. More and more change to the ocean will occur, in terms of sea ice cover, stratification, the global meridional overturning circulation or the increased meltwater runoff and calving of icebergs into the ocean. Current and predicted change is having, and will continue to have, profound and probably increasing impacts on life in the ocean, the interactions between society and the ocean, and knock-on effects for life over the land through the changes in weather and climate. However, an abiding feature of predictions of the future is uncertainty, due to the failure of the range of existing climate models to reach adequate consensus on future change in processes of air-sea interaction. The improvement of climate model representation of the feedbacks in the climate system between the ocean and atmosphere is therefore a priority for more successful prediction.

The science of understanding the causes of weather and climate change linked to the ocean is also still developing. Observational networks have recently improved, and there is now an increased ability to understand the direct links between changes in the ocean and knock-on changes in the weather but the longer-term processes are still poorly understood:

- Why has the typical character of El Niño changed in recent decades?
- Why has the link between the Indian monsoon and ENSO altered?
- Why has summer Arctic sea ice cover reduced more rapidly than most model studies predicted?
- Why have the characteristics of extreme weather surrounding the North Atlantic changed recently?
- Are these processes linked to anthropogenic warming, or part of the spectrum of natural variability that we do not yet fully understand?

These are just a few of the questions that require further investigation of observational datasets, improved models and new climate modelling experiments to answer.

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4.2 Impacts and effects of ocean warming on carbon management including methane hydrates

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Summary

- Fossil fuel combustion and changes in land use patterns have measurably increased the concentration of carbon dioxide ($CO_{2)}$ in our atmosphere. This has almost certainly contributed to general rises in global temperatures observed in recent years via modifying the earth's radiation balance.
- Most of this excess heat is stored in the ocean, however, the heat capacity of the ocean coupled to the lag in transfer means that the absolute rise in temperature in the deep ocean is difficult to detect. Warming itself is concentrated in the upper ocean and in the Southern Ocean.
- The increase in CO_2 concentration in the atmosphere and subsequent warming effects would have been much larger had not around 50% of the CO_2 released to the atmosphere been taken up (roughly equally) by the ocean and the terrestrial biosphere. This ocean uptake has, however, resulted in a measureable reduction in ocean pH (the so-called ocean acidification phenomenon).
- The coupled effects of ocean warming and acidification are hard to predict but likely include: ocean deoxygenation, sea-level rise, a slowdown of ocean circulation and changes in the structure of marine ecosystems and ocean primary production. Further changes will probably include reductions in sea ice, shifts in the composition of marine ecosystems, changes in the flux of organic matter from land to sea and changes in the ocean's buffering capacity and ability to take up further carbon from the atmosphere.
- The impact of ocean acidification on different marine organisms will not be uniform, with some responding negatively, some being broadly tolerant and others responding positively.
- In pelagic ecosystems, phytoplankton cell size and taxonomic affiliation may act as determinants of how different species respond to changes in pH; for example, small phytoplankton may be unable to cope with local fluctuations in pH due to thinner diffusion boundary layers around their cells. In benthic systems, corals and other sessile organisms (e.g. bivalves) are likely to be negatively affected by the combination of warming, sea-level rise and reduced pH.
- Other direct biological effects include deoxygenation, potentially affecting denitrification, and the production of the potent greenhouse gas nitrous oxide and the transfer of organic matter from the upper ocean to the sea floor.
- Ocean circulation changes are likely to reduce the absolute rate at which carbon is biologically transferred to the ocean interior (away from contact with the atmosphere) but to increase biological carbon storage due to residence time effects.
- Sea ice changes may enhance primary production locally, potentially transforming the structure of Arctic ecosystems, however, in the long term nutrient supply may become a strong limitation to future Arctic productivity. Further consequences probably include the destabilization of tundra carbon stores with the transfer of some of this material to the ocean with unknown consequences.
- In addition, methane hydrates may become destabilized, however, direct observations of methane flares at the sea floor suggest that these do not result in significant increases in flux to the atmosphere. There has, however, been an as yet unexplained increase in surface methane concentrations.

Ocean warming effects	Consequences
Warming seawater temperatures	Change in solubility of dissolved gases: O_2 • oxygen outgassed to atmosphere • expansion of oxygen minimum zones, increased fish mortality • greater denitrification and generation of nitrous oxide, a far more powerful greenhouse gas than CO_2 • greater particle export to depth, leading to nutrient recycling and biological activity Change in solubility of dissolved gases: CO_2 • CO_2 outgassed to atmosphere, accelerating increases in atmospheric CO_2 Sea-level rise • increased flooding of coastal land and saltwater intrusion into groundwaters • increased coastal erosion and decline in mangroves / salt marshes • requirement for coastal community adaptation and infrastructure management
Increased stratification of water column (Decrease in mixing between surface and deep water masses)	Circulation change. Transport of heat from tropics to poles likely to be reduced. Reduced supply of nutrients from deep layers to surface, impacting biological activity Reduction in outgassing of natural carbon to the atmosphere, slowing atmospheric CO_2 increases. Reduction in transport of anthropogenic carbon away from surface to deep ocean leading to reduction in ocean's capacity to absorb additional CO_2 from atmosphere
Increased ocean evaporation leading to changes in rainfall patterns	Changes in flux of terrigenous carbon to ocean, with impacts on coastal and open ocean biological activity
Reduced extent of sea ice	Increased biological activity due to expanded open ocean regions and longer seasonal period for phytoplankton growth Increased stratification / decreased nutrient supply to surface to sustain biological production
Destabilization of seafloor gas hydrates through permafrost melt	Increased methane release to the atmosphere, accelerating atmospheric warming Destabilization of seafloor slopes, increasing likelihood of subsea landslides and large tidal waves (tsunamis)
Secondary effect: increased atmospheric CO_2 concentrations transfers more CO_2 to surface ocean	Ocean acidification, with possible deleterious consequences for ecosystem dynamics. Reduction in carbon export (and magnitude of biological activity). Subsequent decrease in CO_2 uptake and accelerated atmospheric CO_2 increase rates. Reduction in capacity for additional uptake of carbon from the atmosphere as carbonate stores are depleted
Warming polar oceans	An increase in the melting of ice sheets, particularly Greenland, an increase in iceberg calving, and a rise in sea level
Increasing freshwater supply to the ocean	A decrease in overturning and a decrease in vertical mixing reducing nutrient supply, and hence productivity, in the surface ocean

4.2.1 Introduction

As a greenhouse gas, CO_2 strongly absorbs outgoing radiation emitted by the cool earth, whilst letting energy emitted by the warm sun pass through the atmosphere in a near quantitative manner. The combustion of fossil fuel hydrocarbons and changes in land use practice together now add an additional ~10 PgC yr^{-1} (1 Petagram of carbon, PgC = 10^{15} grams of carbon) to the atmosphere (Hartmann *et al*., 2013; Le Quéré *et al*., 2015). These releases, have to date resulted in an increase in atmospheric CO_2 levels from around 280ppm in the pre industrial era to about 400ppm now. As a consequence, the equilibrium between incoming and outgoing radiation (which resulted in broadly stable temperatures in the recent geological past) is now being distorted and the entire planetary system warming. Of this excess heat, approximately 90% has been absorbed by the ocean and transported into the ocean interior (that part that is not in contact with the atmosphere on an annual basis) (Balmaseda *et al*., 2013) with the remainder persisting in the atmosphere. However, this warming would be much larger had the terrestrial biosphere and ocean not together absorbed around 50% of the anthropogenically produced CO_2 (Le Quéré *et al*., 2015), shared roughly equally between them. Without this, atmospheric CO_2 levels would be around 520 ppm, well in excess of the 450 ppm threshold at which it is widely considered a 2°C temperature rise and 'dangerous climate change' will occur (Rogelj *et al*., 2011).

Thus ocean processes are acting to reduce the rate at which global warming driven by anthropogenic processes is occurring. However, the associated absorption of CO_2 is also reducing ocean pH – a process known as ocean acidification (Raven *et al*., 2005; Doney *et al*., 2009; Bates *et al*., 2014). The presence within the ocean of multiple organisms who construct elements of their bodies from calcium carbonate (e.g. Wittman and Pörtner, 2013) has led to suggestions that ocean acidification will have deleterious consequences for some organisms and for the foodwebs they sustain. The warming itself also has a range of potentially important consequences, and the combination with acidification is likely to exert profound consequences on biological functioning over the next century (Pörtner and Farrell, 2008; Gruber, 2011; Hewitt *et al*., 2015). In this section we review the scale and location of heat and CO_2 uptake by the ocean, the likely consequences of these changes for biogeochemical cycling and biological processes in the ocean before finally describing the likely future evolution of the system.

4.2.2 Ocean warming and associated stressor impacts

As stated above around 90% of the extra heat now trapped within the earth system is now in the ocean (Johnson and Lyman, 2014), a consequence of the vastly higher heat capacity of the ocean relative to the atmosphere and the rapid transfer of water that has recently been in contact with the atmosphere into the deep ocean interior.

Uptake of anthropogenic heat and anthropogenic carbon (C_{ant}) show large similarities, with the Southern Ocean being the most important location (Mikaloff Fletcher *et al*., 2006; Frölicher *et al*., 2015). However, quantifying how much anthropogenic heat has been absorbed and where, is much more difficult due to the warming signal being small compared to the background bulk signal. It is only in recent years with the advent of the high-resolution Argo profiling float array (http://www.argo.ucsd.edu/) that it has been possible to establish the spatial distribution of warming. Prior to this we relied on a network of high-density observations made from research vessels, of which there is much less data over both time and space. The design of the deep Argo float array and, in particular, how it is informed by the upper ocean Argo array and the network of hydrographic sections, remains an active research topic (Johnson *et al*., 2015). Even now automated floats such as the Argo array only reliably measure the upper 2km of the ocean (whose average depth is ~3700 m), although deep Argo floats (with capabilities down to 6km+) are now being trialled (Figure 4.2.1). The combined float and research vessel based observing programmes suggest that warming is concentrated in surface waters, with important quantities in the Southern Ocean (south of 30°S) (Roemmich *et al*., 2015). An alternative strategy to estimate ocean warming is to look at the transfer (or flux) of heat into the ocean rather than temperature changes within the ocean. Such calculations are difficult because the net heat uptake represents the small difference between two very large numbers and because there are a variety of biases in the observations used to estimate heat flux between the atmosphere and the ocean.

Understanding the uptake and storage of heat is a similar problem to that of anthropogenic carbon but with some differing details. C_{ant} is essentially a passive tracer, meaning that it doesn't affect the flow of water / circulation, and its concentration only changes by dilution or air-sea interaction). Anthropogenic heat, however, does feedback onto the ocean circulation (Morrison *et al*., 2015). The ocean's ability to absorb additional carbon dioxide from the atmosphere is related to its natural background carbon levels (that would have existed pre-industrially) and how they respond to physical (temperature, salinity), chemical (alkalinity, carbonate equilibrium dynamics, pH) and biological (photosynthesis, respiration, ecosystem dynamics) factors. On timescales of days to months, as the 'natural' system changes, the capacity to accommodate additional C_{ant} varies too. These factors combine to generate substantial regional variability in

Figure 4.2.1 The aft deck of the RRS Discovery during the deployment of a deep ocean mooring that forms part of an array measuring the transport of heat northwards through the North Atlantic Ocean. November 2015. © Peter Brown, National Oceanography Centre, Southampton, UK.

the surface distribution of C_{ant} and thus the effects of the intensification of global warming in the future will be equally non-linear.

A best estimate of 155 ± 31 Pg C has been derived for the total amount of C_{ant} in the ocean for 2010 (Khatiwala *et al*., 2013), equivalent to ~45% of all fossil fuels emissions and ~30% of all human-derived CO_2 (Andres *et al*., 2012). Figure 4.2.2 shows one such estimate based on the outputs of an ocean assimilation model (Devries, 2014); this uses observations of temperature, salinity, and transient tracers (unreactive chemicals that can be used to estimate how long a water parcel has been separated form contact with the atmosphere e.g. CFC-11, radiocarbon) to constrain the ocean circulation. The largest amounts of C_{ant} are observed in the North Atlantic, where ocean heat loss causes surface waters with high levels of anthropogenic carbon to become sufficiently dense to sink to great depths away from the surface and atmospheric contact. High quantities of C_{ant} are also located in a number of rough latitudinal bands: typically, those associated with warm subtropical gyres (where favourable local chemistry allows for greater amounts of C_{ant} to be stored) or the formation regions of Antarctic Intermediate Water and Subantarctic Mode Water (that sink away from the surface to mid-depths) in the mid-latitude Southern Ocean.

A comparison of the distribution and the location of where anthropogenic carbon enters the ocean reveals certain similarities - Figure 4.2.3 shows the accumulated absorption of C_{ant} from the atmosphere since 1780derived from an ocean assimilation model (Devries, 2014). High C_{ant} uptake appears to be related to regions of high heat loss, such as the western North Atlantic (associated with the North Atlantic Current region) and the western North Pacific (Kuroshio Current region). In the Atlantic this heat loss coincides with large quantities of C_{ant} in the water column (Figure 4.2.2). In this location the ocean's overturning circulation transports warm surface waters (saturated in C_{ant}) northwards where they cool, sink, and return southwards at depth. This leads to high concentrations of C_{ant} being prevalent at all

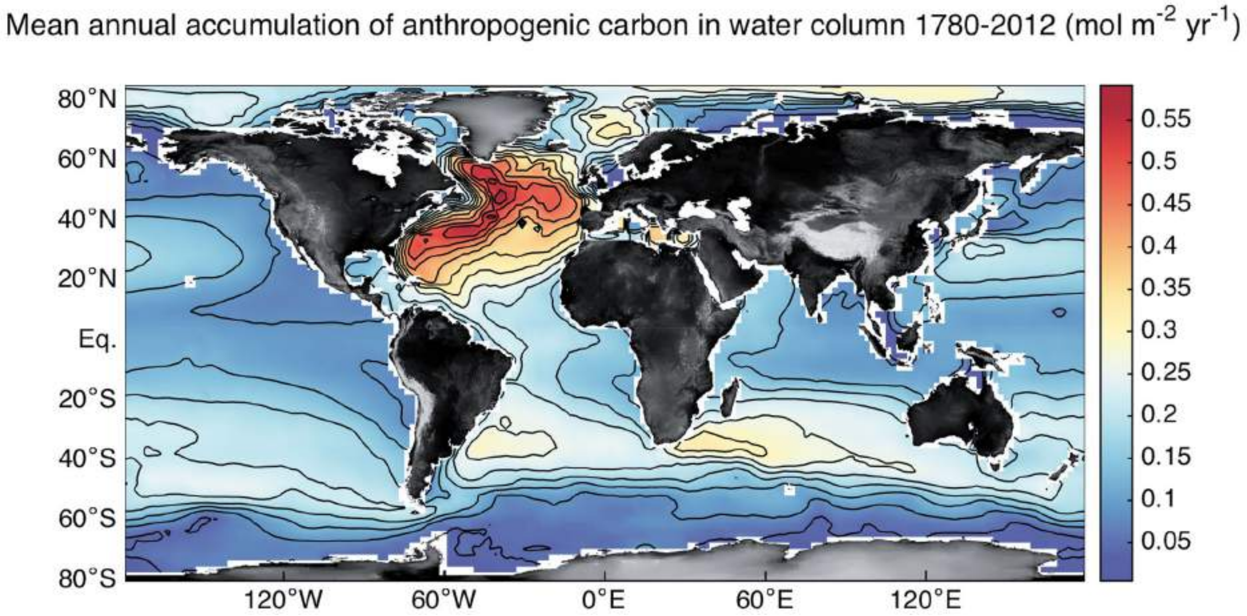

Figure 4.2.2 Estimated accumulation of anthropogenic carbon in the water column. Contours are every 0.043 mol m^{-2} yr^{-1}. Adapted from control run of ocean assimilation model of DeVries (2014).

depths down to the ocean bottom. In the North Pacific no such deep overturning circulation exists, meaning here C_{ant} absorbed is instead redistributed around the circulation gyre that extends across the full extent of the North Pacific and confined to much shallower depths (< 2000m) (Kouketsu *et al*., 2013). The most important location for C_{ant} entering the ocean, however, is the region between ~40ºS and 70ºS. This is the location of the Antarctic Circumpolar Current that travels east uninterrupted around the Antarctic continent. Here, deep waters that have not been in contact with the atmosphere for hundreds to thousands of years are brought to the surface with high natural CO_2 levels (associated with a strong biological remineralization signal) but negligible C_{ant} concentrations. Preindustrially this would have meant that large quantities of CO_2 would have been outgassed from the ocean to the atmosphere. However, now, as atmospheric CO_2 levels rise with increasing fossil-fuel based emissions, the region is converting from a net source to a net sink of CO_2. The C_{ant} absorbed here sinks to depths of 500-2000m as these recently-ventilated waters are transported northwards (Sallee *et al*., 2012) where it can then be observed in the distribution of Cant accumulation (Figure 4.2.2).

Overall, the Southern Ocean accounts for 40-50% of where C_{ant} is accumulating worldwide (Mikaloff-Fletcher *et al*., 2006). The same processes as detailed above also transfer anthropogenic heat into the ocean and the Southern Ocean is thought to be even more important globally. Models and observations suggest that between 67 and 98% of global heat gain is occurring south of 30ºS (Frölicher *et al*., 2015; Roemmich *et al*., 2015). It is the unique regional ocean circulation that drives this behaviour: a combination of cold waters coming to the surface from depth before warming and sinking again further to the north, and to the south, strong heat loss creating waters dense enough to sink to the ocean bottom. Together with the intense mixing and eddy activity created from the strong eastward flow of the water currents, heat and carbon can be carried away from the surface and contact with the atmosphere (Dufour *et al*., 2015; Frölicher *et al*., 2015). However, these same unique ocean circulation features are also the most susceptible to change due to ocean warming effects.

4.2.3 Societal consequences

The effects of these various changes on the marine system are likely to be diverse and include both those driven directly or indirectly by the change in heat/ absorption of carbon (changed temperature, deoxygenation, slower circulation, reductions in primary production, ocean acidification impacts on organisms) and those caused by the general planetary warming (sea-level rise, loss of sea ice, increased terrestrial organic matter fluxes to the ocean).

We now discuss a range of possible elements of ocean functioning which are likely to be impacted by current or

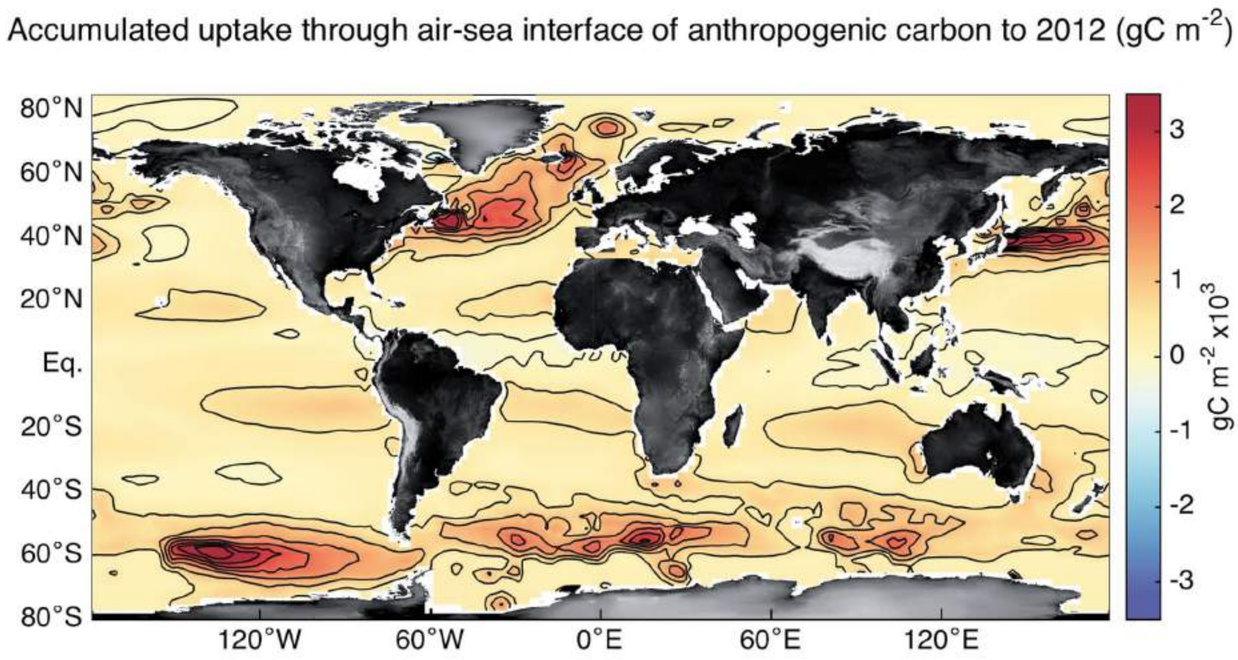

Figure 4.2.3 Accumulated air-to-sea flux of anthropogenic carbon from 1780 to 2012, calculated using outputs of control run of ocean assimilation model of DeVries (2014).

forthcoming change. Important considerations include the absolute sensitivity of individual processes to stress, the ability of the system to evolve, the ability to acclimate, the ways in which stressors interact synergistically and the extent to which systems are pushed up to and beyond the range of natural variability. Over recent years a vast amount of research into the effects of multiple stressors operating in isolation or synergistically has been undertaken.

4.2.3.1 Deoxygenation

Ocean deoxygenation is occurring now, partly as a direct consequence of the warming (that makes oxygen less soluble in warmer waters and which is ongoing) and partly as a consequence of the reduced circulation rates (that decrease the transport of oxygen into the subsurface ocean from the atmosphere) (Keeling *et al*., 2010). The latter appears to be happening as predicted by state-of-the-art IPCC class models although not quite at the same rate. Reduced oxygen levels have been observed in much of the ocean (e.g. the Mauritanian upwelling by west Africa, the Benguela upwelling by south-west Africa, the Arabian Sea, the Peruvian upwelling, the equatorial Pacific, Ulloa *et al*., 2012) and it seems likely that these areas will expand. Aside from the direct consequences of these zones expanding (fish mortality, species shift, etc.) there are at least two important consequences of these expansions which have the capacity to impact on ocean functioning in a major way.

The first results from the fact that, where oxygen levels become sufficiently low, the respiration of organic matter is undertaken by specialized bacteria using nitrate as the terminal electron acceptor rather than oxygen (Ulloa *et al*., (2012)). Such 'denitrification' removes fixed nitrogen from the oceans, a key component of biological production that would potentially be limited if bio-available nitrogen were not produced via nitrogen fixation. However, a product of the complex set of metabolic pathways in the nitrogen cycle that becomes activated under low oxygen conditions is nitrous oxide. Nitrous oxide is a potent greenhouse gas (approximately 260-300 times more powerful than CO_2 over 100 years) whose flux from the ocean to the atmosphere is increasing. Thus any expansion of low oxygen regions clearly has the potential to intensify this flux.

The second results from evidence that suggests that in regions where oxygen becomes low, a greater fraction of sinking material reaches the deep ocean. The reasons for this are unclear, with at least six hypotheses being present in the literature (Keil *et al*., 2015). One possibility is that the organisms that ordinarily degrade this sinking material (and fragment it into smaller, slower-sinking particles) cannot survive in low oxygen waters and are hence prevented from intercepting this flux. Alternatively, the rate at which this material is degraded is reduced due to it being respired via nitrate, which is present at low concentrations compared to oxygen. The depth at which material is recycled is an important control over air sea CO_2 partitioning (Kwon *et al*., 2009); any expansion of anoxic regions and the recycling depth therefore has the possibility of affecting the ocean's biological capacity to remove carbon dioxide from the atmosphere, and by extension longer-term climate impacts.

4.2.3.2 Sea-level rise

It is widely acknowledged that a likely consequence of ongoing environmental change is an increase in sea level. Anthropogenically-forced ocean thermal expansion and ice sheet melting, along with a much smaller contribution from changes in land-water storage, have led to a global sea-level rise of 3.3 ± 0.4 mm yr^{-1} over the last two decades (Cazenave *et al*., 2014). Projections indicate that under a moderate climate change scenario a further global mean rise of 0.54 ± 0.19 m is predicted by the end of the century (Slangen *et al*., 2014), although significant regional variability will exist (Carson *et al*., 2016). A number of physical impacts will accompany this, including increased flooding of coastal land (and saltwater intrusion into groundwaters), a growth in coastal erosion rates, and a decline in mangroves and saltmarshes (Nicholls and Casenave, 2010). These will have direct and indirect socio-economic costs, including a necessity for greater coastal community adaptation and infrastructure management (Hill, 2015). Low-lying regions and densely-populated deltas will be particularly at risk in the coming years.

4.2.3.3 Circulation change

Warming will have significant effects on ocean circulation. Currently dense water formation (whereby waters sink to the ocean bottom) in polar regions is compensated for by upwelling (water transport to the surface from deep) in subpolar regions and at the equator. It is likely that this general pattern will be maintained but slow down (Rahmstorf *et al*., 2015). A consequence will be that the redistribution of heat from the tropics to the poles that it mediates will reduce, in addition to a likely reduction in biological production as the supply of new nutrients from deeper waters that sustains it, itself reduces (Laufkötter *et al*., 2015a). A reduction in the amount of particulate carbon that sinks from the surface to deeper waters (the sinking flux) could result, and with it the biological contribution to removing CO_2 from the atmosphere. Model projections suggest a ~ 20 % decrease in global sinking flux (Cabré *et al*., 2014; Fu *et al*., 2015), but with large regional differences. The North Atlantic and oligotrophic (nutrient-limited) gyres are predicted to experience the strongest declines of 30-40%, while the sinking flux may actually increase in the Arctic and high latitude Southern Ocean (Laufkötter *et al*., 2015b). However, any reductions in biological carbon flux are not likely to reduce the amount of carbon stored biologically in the ocean interior (and by extension, transfer it to the atmosphere). Instead, they will be compensated for by the reduced upwelling of deep waters to the surface where they would ordinarily outgas CO_2 to the atmosphere due to their high carbon concentrations (Cox *et al*., 2000). The reduction in biological carbon flux to the interior will, however, have consequences for food supply to the deep ocean (Jones *et al*., 2013).

4.2.3.4 Supply of terrestrial carbon to the ocean

Terrestrial soils contain 1500-2400 Pg of organic carbon, approximately double the amount stored in ocean waters and at least four times the amount of fossil-fuel carbon combusted to date (Ciais *et al*., 2013). Globally rivers receive ~0.9 Pg of terrigenous organic carbon each year and export approximately half of this to the sea (Cole *et al*., 2007).

A variety of processes influence the flux of terrigenous organic carbon into inland waterways, including land use change, increased and more variable precipitation, precipitation chemistry, warming and CO_2-enhanced DOC production (Tranvik and Jansson, 2002; Freeman *et al*., 2004; Monteith *et al*., 2007; Butman *et al*., 2015; Smith *et al*., 2015). The individual and interactive effects of these processes on the export of terrigenous organic carbon to the ocean and its fate therein are not fully understood (Lehmann and Kleber, 2015). This is in part because different soil types (which are subject to different combinations of the aforementioned processes) produce and release organic matter that has different biochemical characteristics that are more or less favourable to different types of degradation. For example, peatland produces coloured dissolved organic matter that is typically degraded abiotically via photolysis, whereas agricultural soil produces organic matter that is readily amenable to biological degradation (Berggren and del Giorgio, 2015). Improved understanding of the fate of terrigenous organic matter in aquatic ecosystems is crucial for the development of Earth System Models that are used to predict the future climate (Burd *et al*., 2016).

4.2.3.5 *Ocean acidification*

Due to the presence of dissolved carbonate in sea water, the absorption of CO_2 from the atmosphere has a much smaller effect on pH than would otherwise be the case in its absence (Zeebe and Wolf-Gladrow, 2001). This is the 'buffering capacity' of the ocean, but its long-term effect becomes limited as carbonate is depleted. Thus, as the ocean continues to absorb anthropogenic CO_2 and ocean acidification increases, its capacity to absorb more will decline (Thomas *et al*., 2007), a reduction that will be further exasperated by a warming ocean. Direct effects of ocean acidification on plankton are currently unknown. However, research has highlighted species-specific effects (e.g. Flynn *et al*., 2012; Gibbs *et al*., 2013; Meyer and Riebesell, 2015; Richier *et al*., in prep.), the importance of co-varying ocean properties (e.g. temperature, nutrients or food availability) (e.g. Poulton *et al*., 2014; Mayor *et al*., 2015) and changes in how an organism's intrinsic growth and metabolic rate respond to elevated CO_2 concentrations (e.g. Lohbeck *et al*., 2012). Unifying concepts bringing together organism physiology, evolutionary history and ecological theory promise to consolidate the diverse experimental and observational data that currently exist (e.g. Bach *et al*., 2015; Gaylord *et al*., 2015).

4.2.3.6 *Sea ice loss*

One demonstrable effect of ocean warming is the loss of multi-year sea ice in the Arctic, and expansion of the marginal ice zone where ice is only present for part of the year. The implications of this changing habitat for primary production and changes to the subsequent material flows through Arctic ecosystems are poorly understood. From 1998 to 2012 there has been a 30% increase in Arctic Ocean primary production, due in part to the reduced extent of sea ice and a longer seasonal period for phytoplankton growth (Arrigo and van Dijken, 2015). However, what happens into the future is unclear as increased warming and ice-melt in the Arctic may increase stratification and reduce nutrient supply to the surface. A strong seasonal nutrient limitation may characterize a future ice-free Arctic Ocean (e.g. Lawrence *et al*., 2015; Yool *et al*., 2015).

4.2.3.7 *Escape of seafloor gas hydrates*

Methane (CH_4) is also an important greenhouse gas (approximately 34 times more powerful than CO_2 over 100 years) with an atmospheric half-life of 10 years (Prinn *et al.,* 1995). Concentrations in the atmosphere have been steadily increasing with post-industrial human population growth (IPCC, 2014), although there are many natural sources of methane (living organisms, rotting vegetation, and geological sources – both petrogenic and biogenic, Riedel *et al*. (2010)), on land and in the ocean. In the marine context, seafloor methane is in the form of solid methane hydrates. These exist as an ice-like solid made of methane and water molecules, and are stable under high pressures and low temperatures, and are found in deep waters on continental margins and slopes. They are attracting particular attention as hydrates lock methane in place beneath the ocean floor. However, these are susceptible to destabilization leading to methane release (Maslin *et al.,* 2004; Westbrook *et al.,* 2009).

Petrogenic methane is derived from the chemical decomposition (cracking) of hydrocarbon deposits at several kilometres depth within the Earth's crust, themselves the remnants of living organisms from the deep geological past that have been buried by the build-up of sediments over millions of years. Biogenic methane, however, is generated within the upper 10s of metres beneath the sea floor by microbes digesting organic matter laid down in relatively modern sediment, and it is these that are probably the dominant source of methane in seafloor hydrates (Riedel *et al.*, 2010). Both petrogenic and biogenic methane can migrate upwards to the seafloor surface through buoyant forces (either permeating through sediments or through fissures) and give rise to seafloor features such as vents and pockmarks where the methane escapes into the water column. With methane present, methane hydrates can form in water depths greater than about 300 m on continental margins and down to several 100s of metres beneath the sea floor where the geothermal gradient determines the depth of the hydrate stability field (Kvenvolden, 1993). Evidence for methane (and natural CO_2) gas escape at the sea floor is found on continental margins around the world, including shelf seas, where organic matter is prevalent in marine sediments transported from land. Global estimates of seafloor methane gas are sketchy, but estimates for seafloor hydrates range between 2×10^{16} m^3 (Kvenvolden, 1988) and 1×10^{15} m^3 (Milkov *et al*., 2003). This is comparable to known reserves of conventional natural gas, and hence they are potentially a very important component in future climate change predictions. To date, constraints on seafloor methane and methane hydrates are poorly known and are not

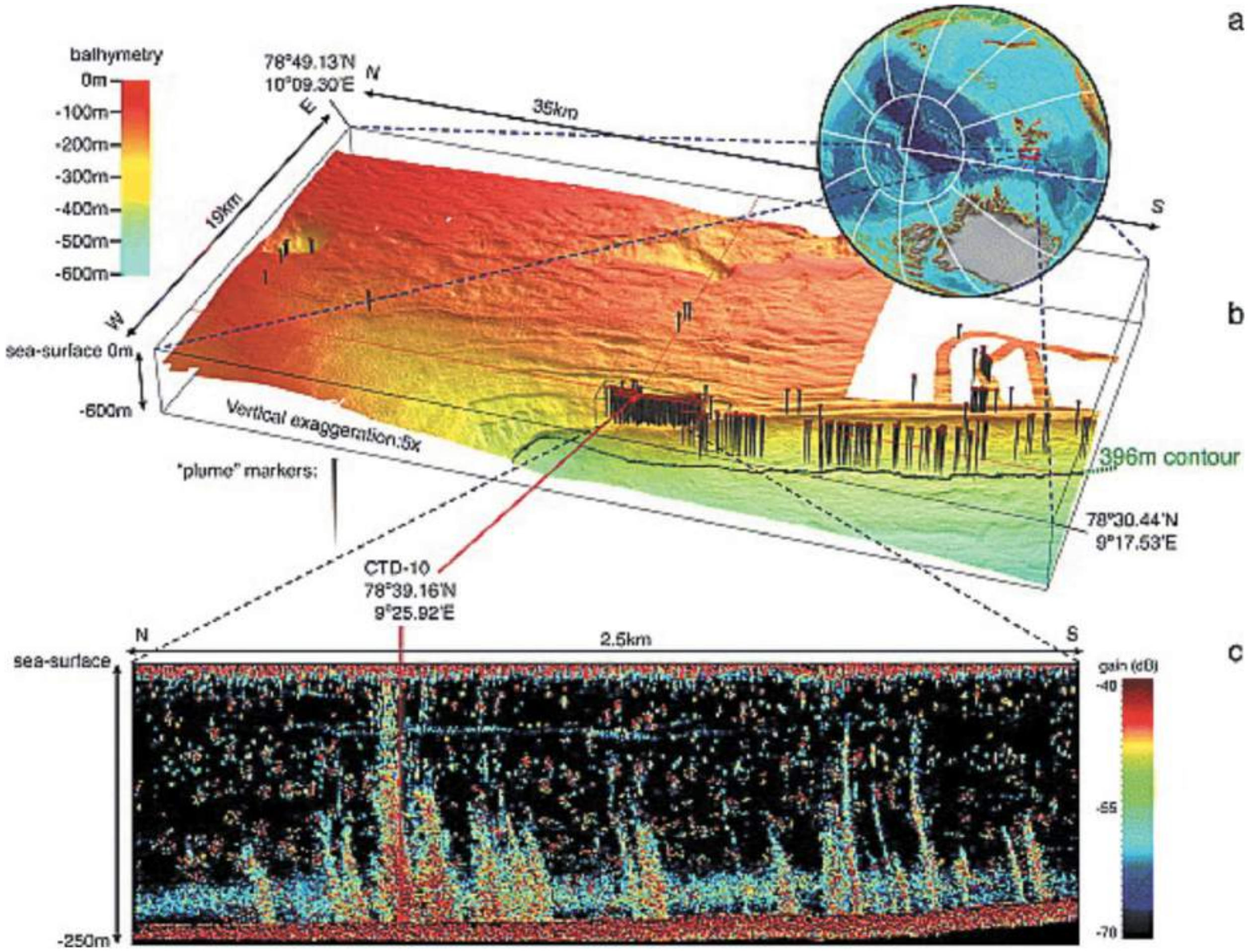

Figure 4.2.4 from Westbrook *et al.* (2009). (a) Location of survey area west of Svalbard; IBCAO bathymetry (Jakobsson *et al.*, 2008). (b) Positions of plumes acoustically imaged with the EK60 sonar, depicted by "pins", superimposed on perspective view of the bathymetry of part of the area of plume occurrence. Bathymetry is from EM120 multibeam survey of cruise JR211 gridded at 20-m resolution, combined with high-resolution survey data from the Norwegian Hydrographic Service for the shallower-than-200-m part of the map. The 396-m isobath is the expected landward limit of the GHSZ. (c) Part of record from an EK60 acoustic survey from JR211, showing examples of observed plumes. Amplitude of acoustic response is given by the colour of the "bubbles". All plumes show a deflection towards the north caused by the West Svalbard Current. The sea bed, at around 240-m depth, is shown by the strong (red) response. The position of CTD cast 10 is indicated by vertical red arrow.

factored into Earth system models of the oceans (IPCC, 2014), a major knowledge gap. Also, scientists suggest that significant volumes of methane could be released into the water column as seafloor hydrates dissociate in rapidly warming polar regions over the next 100 years (Westbrook *et al*., 2009).

Methane released from seafloor hydrate dissociation and methane vents in deep waters will mostly dissolve in the water column affecting ocean acidification. Seafloor methane released in shallow shelf seas, however, will mostly find its way into the atmosphere. An example of the latter is the huge Arctic area in the Siberian and Laptev seas where sub-sea permafrost is melting and releasing methane, in addition to permafrost melt on adjoining landmasses (Shakova *et al.,* 2010). Recent research has focused on the fate of seafloor methane hydrates in the Arctic, a region of the world that is changing most noticeably in response to global warming, such as the melting of sea ice. Studies show that bottom water temperatures off shore of Svalbard (an Arctic island group) have increased by 1°C in the last 30 years and geophysical surveys have shown evidence for possible seafloor hydrate dissociation (melting) and release of methane gas into the water column (see Figure 4.2.4) (Westbrook, 2009). A further possible consequence of seafloor hydrate dissociation is the destabilization of slopes leading to landslides on the sea floor that could generate large tidal waves (tsunamis). Indeed, a large seafloor landslide offshore of Norway about 8000 years ago produced a tidal wave that washed up beach sediments on the coast of

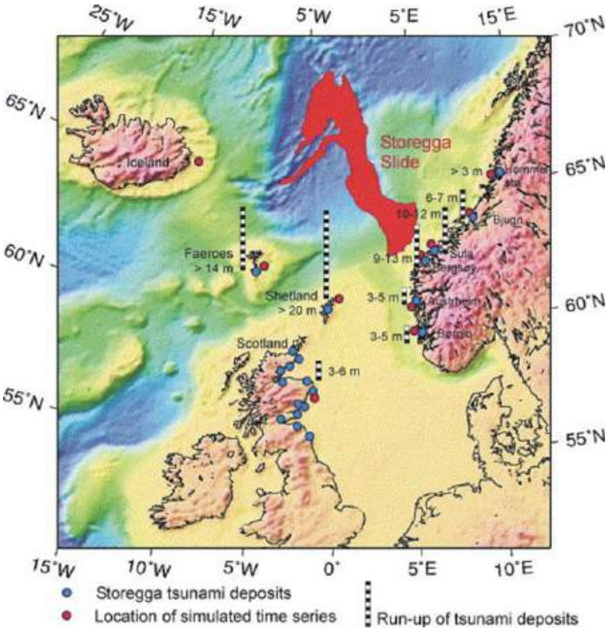

Figure 4.2.5 Showing the extent of the Storegga slide (red) dated at c. 8k years ago, location of coastal tsunamis deposits and simulation time series (blue and red dots respectively), and run up distances (black and white bars) (after Talling *et al.,* 2014).

Scotland (Dawson *et al.*, 1988). If such an event were to happen today, this would certainly affect coastal populations in North West Europe (Figure 4.2.5) (Talling *et al.,* 2014). However, the possible link between seafloor landslides and hydrate dissociation is still poorly understood.

4.2.4 Implications of continuing ocean temperature rise

Currently, the extent to which C_{ant} is absorbed from the atmosphere is determined by how long surface waters are in contact with the atmosphere and the chemical buffer capacity of the sea water to absorb additional CO_2. While the former is determined by both large-scale and regional ocean circulation, the latter is dependent on local chemistry (particularly alkalinity) and processes that impact it, such as temperature changes. The buffer capacity can be quantified by calculating the Revelle Factor (RF). This describes how seawater carbon levels respond to a given change in atmospheric CO_2 concentrations, with lower values indicating a higher buffer capacity (more anthropogenic carbon can be absorbed from the atmosphere). Typical modern day values of RF range from 8 to 17 (Figure 4.2.6), with subtropical waters being able to hold higher concentrations of anthropogenic carbon than those waters towards the poles. As additional carbon is absorbed, the buffering capabilities of the water declines (local RF values increase). This reduces its ability for further carbon uptake, a scenario explored in Figure 4.2.7.

Under IPCC climate scenario RCP 8.5 ('business as usual'), an annual average warming of 3.81 ± 1.10°C compared to 1980 levels is predicted by the end of this

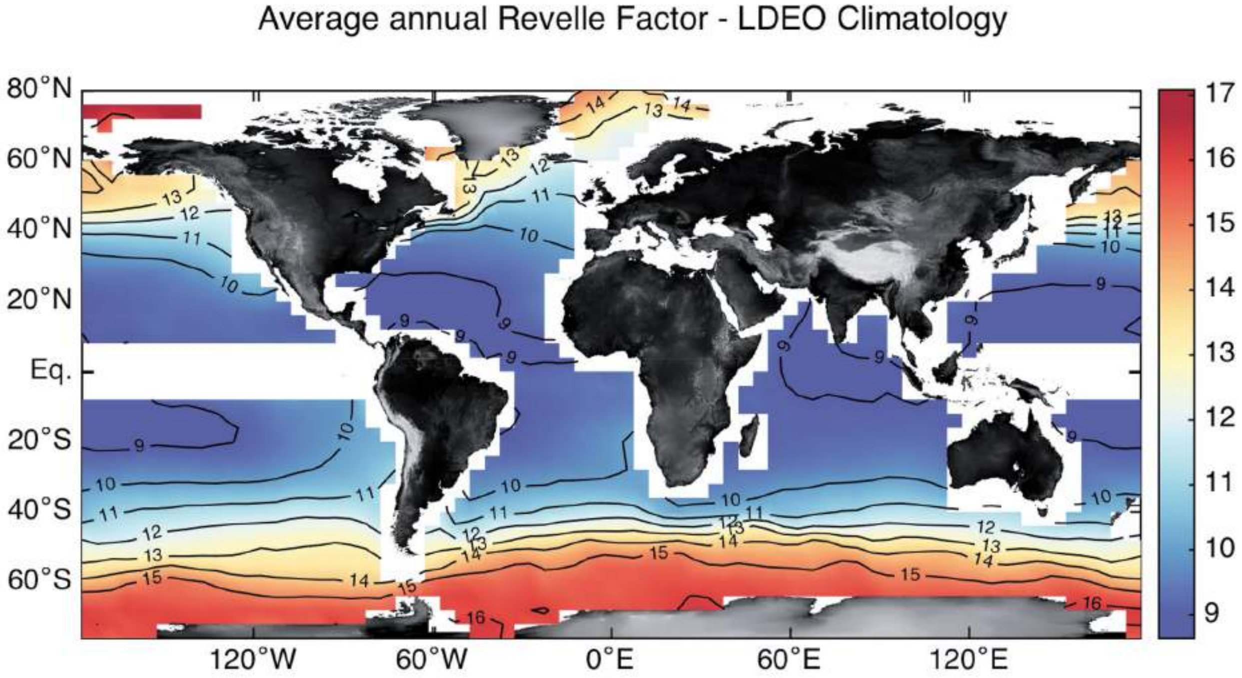

Figure 4.2.6 Annual average of Revelle Factor – this describes the capacity of the surface ocean to absorb additional carbon dioxide from the atmosphere, with low values representing a greater buffering capacity for anthropogenic CO_2 calculated using carbon data from Lamont-Doherty carbon climatology (Takahashi *et al.,* 2014). Data from the equatorial Pacific region have been omitted due to the large degree of interannual variation observed here.

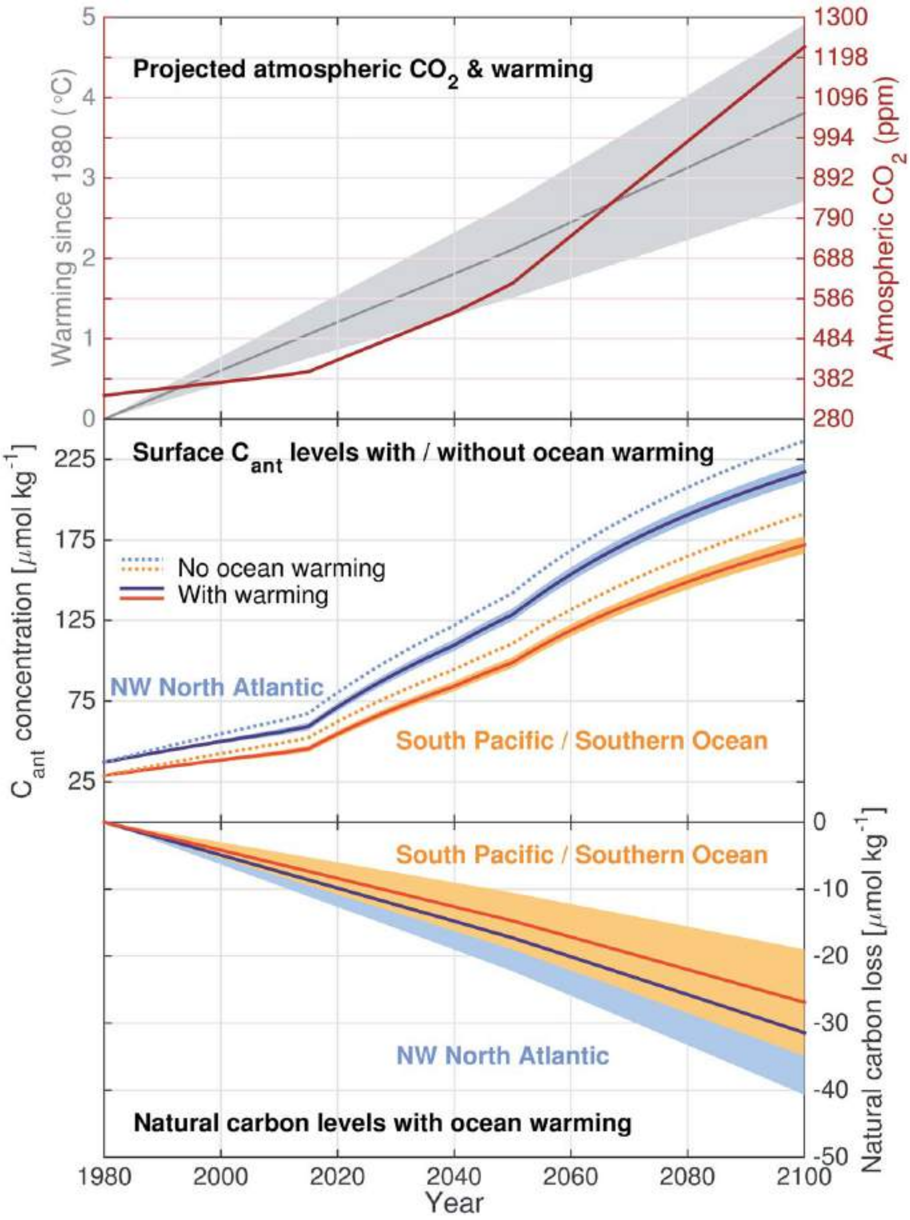

Figure 4.2.7 Projected effects of continued atmospheric CO_2 increases and associated warming. Top: expected atmospheric carbon concentrations (red) and average global temperature increase for IPCC RCP8.5 climate scenario (warming of + 3.81 ± 1.10 °C by 2100 compared to 1980) (IPCC, 2014). Middle: Projected surface ocean anthropogenic carbon concentrations for two locations (NW North Atlantic and South Pacific sector of the Southern Ocean) both with (solid line, and shaded area for warming uncertainty) and without (dashed lines) the effects of warming waters. Bottom: Projected effect on natural carbon levels of surface seawaters due to ocean warming. Initial carbon data from Lamont-Doherty carbon climatology (Takahashi *et al.*, 2014).

century, largely precipitated by atmospheric CO_2 levels reaching 1225 parts per million (more than four times their pre-industrial level) by 2100 (upper panel). The ocean responds by absorbing increasing quantities of carbon, causing surface water anthropogenic carbon concentrations to increase (middle panel). Higher levels are observed in the North Atlantic compared to the Southern Ocean due to their respective RF values, and both initially track the atmospheric change. However, as ocean surface carbon concentrations increase (and RF values rise) their capacity for additional uptake is reduced. This leads to surface water C_{ant} increase rates to slow down and more CO_2 remaining in the atmosphere. If warming is also included in this projection, then even less anthropogenic carbon will be absorbed from the atmosphere. The dynamics of the seawater carbonate system dictate that overall, colder waters can hold higher concentrations of carbon than warmer waters 9 Zeebe and Wolf-Gladrow, (2001). Thus rising seawater temperatures will see natural carbon increasingly outgassed into the atmosphere as CO_2 solubility decreases (Figure 4.2.7 bottom panel). This trend will cause the atmospheric accumulation rate to accelerate further. In this context, ocean warming is a positive climate feedback, increasing atmospheric CO_2 levels but by primarily impacting the ocean's natural carbon system.

In addition to effects on solubility, further feedbacks on anthropogenic carbon uptake are expected from rising temperatures (Sabine and Tanhua, 2010; Tanhua *et al*., 2013). The impacts, however, are difficult to quantify affecting both physical and biological carbon systems and not necessarily with the same sign. For instance, greater ocean stratification (through heat content changes / an acceleration in the hydrological cycle caused by intensified evaporation/precipitation, greater sea-ice melt) will slow the ventilation of waters depleted in anthropogenic carbon (and thus C_{ant} uptake) and the supply of nutrients to the surface (and thus biological carbon uptake). However, it will also reduce the upwelling rate of waters high in natural carbon (and thus outgassing to the atmosphere). Ocean circulation changes could similarly impact the oceanic carbon system, shortening or lengthening timescales for air-sea gas exchange, the rate-limiting step for CO_2 uptake.

4.2.5 Conclusions and recommendations

Changes in the marine environment driven by increases in atmospheric CO_2 are likely to have profound and broad reaching effects on many aspects of marine carbon cycling with important societal consequences. Sea-level rise (caused by thermal expansion and increased glacial water runoff) will increase the risk of coastal erosion and flooding, and cause decline in mangrove and salt marsh extent (and the large carbon stocks they harbour). Dissolved gases such as oxygen and carbon dioxide will become less soluble in warming waters; this will lead directly to increases in the extent of oxygen minimum zones and denitrification rates, and also the movement of both CO_2 and nitrous oxide (both powerful greenhouse gases) from the ocean to the atmosphere. Warmer surface waters will increase ocean stratification and the magnitude of their mixing with deeper waters. While this will reduce the transport of waters high in CO_2 to the surface (and thus CO_2 outgassing), it will also reduce surface nutrient supply and the biological activity it sustains (that would ordinarily cause the uptake of CO_2). Warming waters are also leading to melting permafrost, that destabilizes seafloor gas hydrates and leads to an increased release of methane to the water column above (and inevitably into the atmosphere). In addition, the destabilization will lead to an increased risk of seafloor landslides and the likelihood of large tidal waves (tsunamis). Secondary impacts of ocean warming relate to the increasing carbon concentrations of surface waters that accompany it. While the uptake of carbon by the ocean is currently slowing the accumulation of CO_2 in the atmosphere, this will not continue indefinitely as its buffering capacity reduces. Simultaneously, ocean acidification will impact the chemical pathways and ecosystem dynamics currently enable ocean biology to drive carbon uptake from the atmosphere.

Considerable mitigation measures, through emissions reductions and technological development, will be necessary to minimize the impacts on the carbon system and the global climate system as a whole, although a large degree of future change is already locked into the system (Mathesius *et al*., 2015). Similarly, coping and adaptation strategies must be developed for future possible changes related to elevated levels of greenhouse gases. Substantial research efforts are needed to investigate how physical forcings, marine biogeochemistry and ecosystems and ocean circulation current interconnect, and how ocean warming is impacting now and into the future. This requires a mixture of coordinated studies over a range of scales, from laboratory experiments to large-scale monitoring schemes and modelling programs.

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> *“Climate change has had, and is likely to have a mostly negative effect on the capacity of reefs and vegetation to protect coasts from erosion and storm damage.”*
>
> *Section 4.3 author*

4.3 Impacts and effects of ocean warming on the protection of coasts by habitat-forming species

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Summary

- Coastal areas have warmed 35% faster than open ocean areas since 1960 and are more susceptible to direct impacts from warming, sea-level rise, changes in storms and increased land runoff than any other ocean realms.
- Vegetation and reef-building species form habitats in shallow water that protect coastlines from erosion and sea-level rise by reducing the height of waves, reducing current flow and stabilizing sediments.
- Coral reefs (240,000km^2 globally) are suffering from the continued effects of high-temperature-induced coral bleaching, with mortality in 2016 up to 85% in parts of the Great Barrier Reef and 22% mortality overall, the highest since the El Niño/Southern Oscillation event of 1997-1998.
- Mangroves (~130,000km^2) are expected to lose 10-15% of their area due to climate change by 2100, but the greatest current threat is from logging with 1-2% area lost per year, likely to dwarf the effects of climate over the same period.
- Saltmarshes (37,000km^2), seagrasses (288,000km^2) and kelp beds all have similar coastal protective effects, but face different threats, with saltmarshes losing most from coastal development, and seagrasses and kelp beds from negative effects of increased temperatures at warm geographical range edges.
- Increased dissolved CO_2 in the ocean has a positive effect of on the productivity of non-calcifying attached vegetation (+22%), but most effects of acidification on species associated with these coastal habitats such as calcifying algae and shellfish are negative.

Ocean warming effects	Consequences
Warming seas affecting community composition and resulting protective effects of coastal habitats	Changes in relative proportions of cold-water and warm-water species, each with potentially different effectiveness as protectors of coasts
Warming causing low latitude edge of habitat forming species to retreat but creating new suitable areas at the high latitude edge of species ranges	Poleward shifts of distributions inducing total loss of temperate-only habitats (such as kelps) at equator-ward margins Expansion of tropical corals into subtropical areas, but potential losses in tropics during thermal extremes
Increased storminess	Capacity of coastal habitats to protect from storms may be overcome, and damage to such habitats further reduces their effectiveness in reducing wave heights and erosion effects
Increased wind speeds	General increases in coastal wave heights increase importance of coastal habitats as offering protection from wave damage

4.3.1 Introduction

Climate change effects on marine species are wide ranging, affecting rates of calcification, population dynamics, the distribution of species and the habitats they may create, and the timing of seasonal events (Poloczanska *et al.,* 2016). Observed effects of climate change are mostly in line with simple expectations of shifts in distributions polewards towards cooler conditions in areas where oceans have warmed, and spring seasonal events are happening earlier as the same temperatures occur earlier in the year (Poloczanska *et al.,* 2013). The recent Fifth Assessment report by the Intergovernmental Panel on Climate Change (IPCC) of observed and expected changes in ocean life in relation to climate, (Hoegh-Guldberg *et al.,* 2014), summarizes these changes and the causes and consequences for the ecosystem services that the ocean provides (Olsson *et al.,* 2014), with the particular effects on coasts and coastal habitats (Wong *et al.,* 2014).

Ocean temperatures warmed by 0.075°C/decade between 1960 and 2009 (Burrows *et al.,* 2011), a change mostly attributed to anthropogenic climate change (Rosenzweig *et al.,* 2008). Sea areas adjacent to coasts warmed 35% faster (0.092°C/decade) than open ocean areas (0.068°C/decade, Figure 4.3.1), putting coastal areas more at risk of the consequences of climate-driven change in ecosystems. Climate change is not only the increase in temperature. Observed changes, and those anticipated by climate models, include changes in sea level (Church *et al.,* 2013) and changes in ocean pH (Orr *et al.,* 2005). Changes have also been seen and projected in regional seasonal storminess (with some increases, in the Northeast Atlantic in winter, and declines elsewhere (Hartmann *et al.,* 2013), albeit

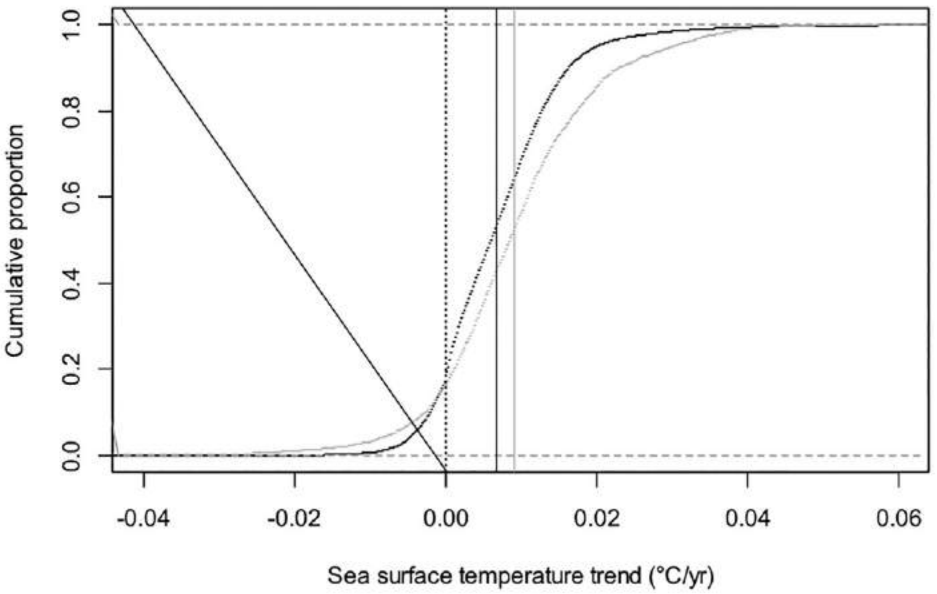

Figure 4.3.1 Rates of change in sea surface temperature between 1960 and 2009 from the Hadley Centre compiled sea surface temperature dataset (HadISST v1.1, Rayner *et al.* 2003). Change in coastal areas (grey lines) versus open ocean areas (black line) shown by the cumulative proportion of ocean areas (1° latitude/longitude areas). Coastal areas have warmed 35% faster than open ocean areas, as shown by the solid vertical lines through the means for coasts (grey) and open ocean (black). Coasts also show more variable rates of change, with more areas showing greater cooling and warming than the open ocean.

with low confidence in future projections (Church *et al.,* 2013)), with associated increases in precipitation and land runoff, particularly in the wet tropics (Collins *et al.,* 2013). These elements of climate change act separately and in combination to threaten the protective ecosystem services that coastal habitats provide (Wong *et al.,* 2014). Coasts, in particular, will bear the brunt of the effects of changes in sea level. While there is much evidence that coastal ecosystems can cope with rapid changes in sea level, particularly through recent glacial cycles, the pace of sea-level rise anticipated for the next 100 years (2.1-3.5 mm/yr, or 18-29 cm from 2016 to 2100; Church *et al.,* 2013) may exceed the resilience of coastal habitats to track the changing coastlines. A consequence may be the total loss of a habitat, such as the drowning of coral reefs (Hoegh-Guldberg *et al.,* 2007), a phenomenon last seen during rapid post glacial sea-level rise due to collapsing ice sheets and meltwater release (Blanchon and Shaw, 1995).

4.3.2 Coastal protection offered by reefs and marine vegetation

Coastal habitats created by vegetation and reef-building organisms play important roles in reducing the negative effects of waves, storm surges, floods and tsunamis on coastal land, reducing erosion, and damage to land and property along coastlines, as well as supporting a much greater richness of species than comparable areas lacking these structuring species, such as kelp, (Burrows, 2012). The global extent of these habitats can be seen from the areas in each EEZ of coastal countries (Figure 4.3.2, from data in Halpern *et al.,* 2012). Tropical and subtropical countries are those most protected by mangroves, coral reefs and seagrasses, with saltmarshes more prevalent in temperate countries and globally distributed rocky reefs providing the substratum for the kelp forests found largely in temperate regions (Steneck *et al.,* 2002; Steneck and Johnson, 2013).

4.3.2.1 Coral reefs

Coral reefs have a considerable protective role as barrier reefs around islands and along continental coastlines (Hoegh-Guldberg *et al.,* 2007) (Figure 4.3.3). The protective role of reefs is usually only revealed when reefs are degraded or lost. Mortality of coral causes an increase in local wave action (Sheppard *et al.,* 2005), leading to significant costs where alternative structures need to be built to replace the lost protection offered (in Moberg and Folke, 1999). Estimates of the global extent of corals vary with values ranging among 108,000 km^2 (Andréfouët *et al.,* 2006), 284,000km^2 (Spalding *et al.,* 2001), and 238,000 km^2 (Table 4.3.1, from Halpern *et al.,* 2012).

Effects on coral reefs of temperature increases associated with climate change are immediately visible,

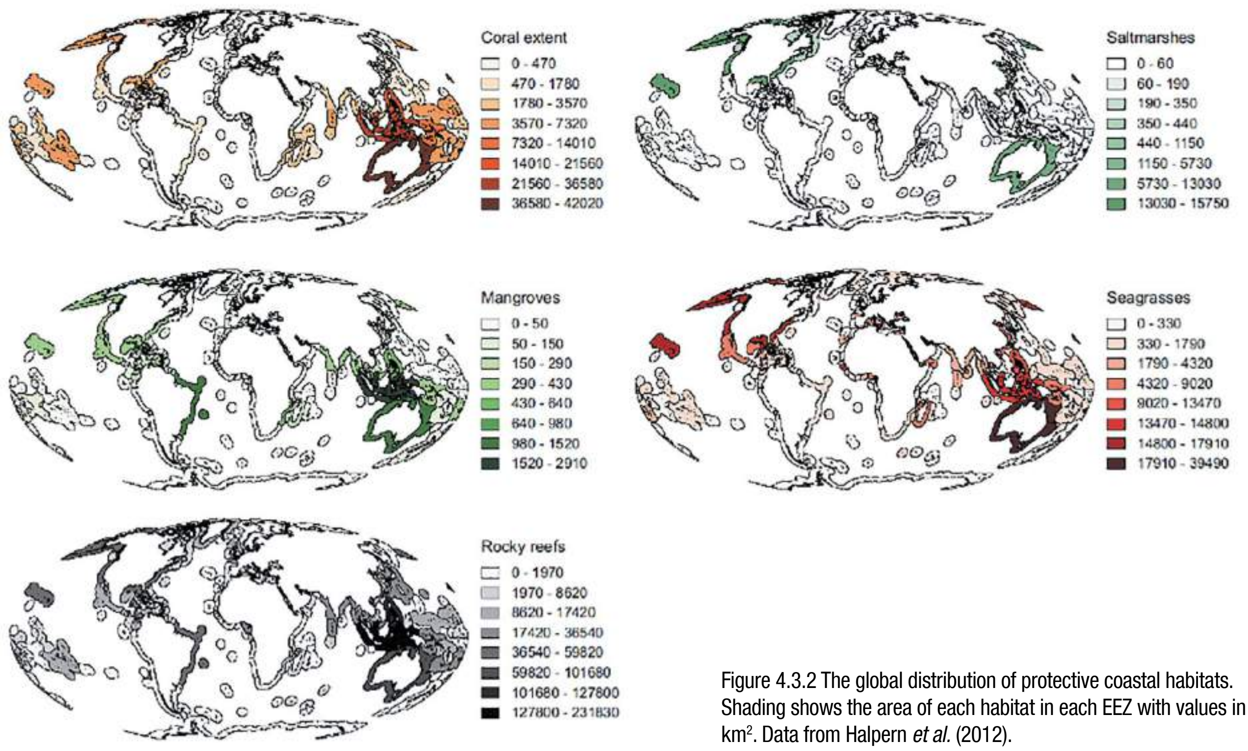

Figure 4.3.2 The global distribution of protective coastal habitats. Shading shows the area of each habitat in each EEZ with values in km^2. Data from Halpern *et al.* (2012).

Table 4.3.1 Total extent of coastal protection habitat across EEZs of coastal countries.

	Global extent (km^2)
Coral reefs	238000
Mangroves	15000
Rocky reef	1323000
Saltmarsh	37000
Seagrass	288000

through the rapid changes in appearance of reefs during hot periods. Warming events cause bleaching in corals (Kleypas *et al.,* 2008), the expulsion of photosynthetic zooxanthellae, and such events are associated with mass mortalities (Eakin *et al.,* 2010; Section 3.8) (Figure 4.3.4). Bleaching events tend to occur in El Niño-Southern Oscillation (ENSO) years, such as in 1997-1998. The thermal stress associated with heating is evident from satellite data, allowing the duration and intensity of high temperature events to be combined into useful indices. Patterns in these indices are useful predictors of the times and places where coral bleaching occurs (Selig *et al.,* 2010); with 2016 hving seen one of the most damaging years for coral bleaching yet recorded, with extreme heat stress across large parts of the Great Barrier Reef in Australia (http://www.coralreefwatch.noaa.gov/satellite/bleaching5km/index.php), and high levels of mortality, up to 85% in some areas and 22% across the whole of the reef (Australian Institute of Marine Science (AIMS), 2016). Warming can also have a positive effect on coral along their poleward range margins, where regions previously too cold for coral may now be amenable to their growth. Coral species have advanced in these conditions in Western Australia and Japan (Greenstein and Pandolfi, 2008; Yamano *et al.,* 2011). Such expansions are counteracted by retreats in equatorial water (Kiessling *et al.,* 2012). Where effects have been determined, ocean acidification and warming tend to act synergistically on corals, increasing mortality and decreasing calcification (Reynaud *et al.,* 2003). This has consequences for rates of erosion and accretion, and is likely to shift the balance in favour of losses while increasing the likelihood of damage through breakage (Andersson and Gledhill, 2013).

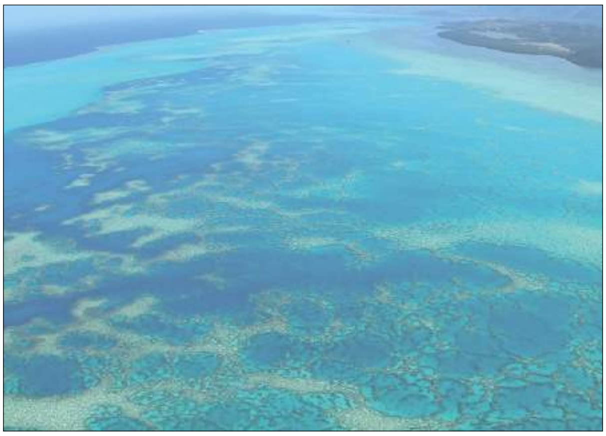
Figure 4.3.3 Fringing reefs provide protection to low lying islands. © Dan Laffoley / IUCN.


Figure 4.3.4 Coral bleaching. Coral dying and dead at Lizard Island GBR. © Ocean Agency (http://www.theoceanagency.org/). [from https://www.theguardian.com/environment/2016/jun/07/the-great-barrier-reef-a-catastrophe-laid-bare],

4.3.2.2 Mangroves

The global extent of mangroves at 160 000km^2 (Bouillon *et al.,* 2009) (also estimated at 132,000 km^2, Giri *et al.,* 2011) is thought to have been reduced to 50% of the original area by over-harvesting, development on coastlines and environmental change through pollution and salinity change (Bouillon *et al.,* 2009) (Figure 4.3.5). As with other coastal vegetated habitats, their main protective function is the attenuation of waves, reducing flow and causing sediment accumulation. The 2004 SE Asian tsunami highlighted their potential role in protection against tsunami flows, with evidence suggesting that mangrove forests over 100m wide did reduce flows but did not significantly reduce the human death toll (Alongi, 2008). The 1-2% per year rate of loss from logging currently outstrips the estimated 10-15% loss from climate change by 2100 (Alongi, 2008), so climate change itself is unlikely to account for the biggest future change in the protection offered by coastal mangroves. That said, sea-level rise may pose the biggest climate-related threat to mangroves (Gilman *et al.,* 2008), with rates of sediment accumulation in many areas not keeping pace with rises in sea level, particularly around Pacific islands.

The IPCC AR5 WG2 report on the regional context for climate change impacts (Hewitson *et al.,* 2014) uses mangrove restoration in some countries (Vietnam,

Figure 4.3.5 Mangrove forest in New Caledonia. © Dan Laffoley/IUCN.

Djibouti, Brazil) as an example of how climate adaptation might help reduce vulnerability and increase resilience to floods and storms. Once restored, mangrove forests can reduce wave height and lessen further erosion of the coasts.

4.3.2.3 Seagrass beds

Seagrasses are similar to coral reefs in global extent (estimated at 288,000km^2, Table 1, Halpern *et al.,* 2012), but reports of the total area of seagrasses vary widely from 177,000 km^2 (Waycott *et al.,* 2009) through 300,000km^2 (Kennedy and Björk, 2009) to 600,000km^2 (Duarte, 2002) for reasons that are unclear. Where changes have been measured, most seagrass areas are in decline, with 29% of the area of seagrasses lost over the last 127 years (Waycott *et al.,* 2009). Like mangroves, much of these losses have been through coastal development (Lotze *et al.,* 2006; Orth *et al.,* 2006) and further human development along coasts may be greater threat to seagrasses than the direct effects of climate change. The reported rapid rate of loss of seagrasses at 7% a year has led to four European species being included in the IUCN Red List (IUCN Red List, 2014).

Seagrasses are important for carbon production and storage, storing up to 15% of the ocean's carbon (Kennedy and Björk, 2009), and supporting local foodwebs. Seagrasses also stabilize sediments (Orth *et al.,* 2006), while their role in coastal protection is similar to that of other submerged vegetation in reducing waves (Ondiviela *et al.,* 2014), with consequential effects on erosion. Direct threats from climate change to the protection offered by seagrasses are varied (Ondiviela *et al.,* 2014), and may depend on the location within ranges, but increased mortality of species such as *Posidonia oceanica* (Figure 4.3.6) has been seen in relation to a 3°C increase in sensitive areas (Marba and Duarte, 2010). Not all effects of climate change on these species are negative: a synthesis of experimental studies (Kroeker *et al.,* 2013) suggests that increased dissolved CO$_2$ associated with ocean acidification increases rates of photosynthesis and productivity of seagrasses.

Figure 4.3.6 *Posidonia oceanica.* © Iñaki Relanzón /TLM.

Figure 4.3.7 Saltmarsh at Carrabelle in Florida. © Stephen L Tabone/stabone.com.

4.3.2.4 Saltmarshes

Like other coastal biogenic habitats, saltmarshes (Figure 4.3.7) protect coasts by reducing the height of waves (Möller *et al.,* 1999; Möller and Spencer, 2002), especially important during storm surges (Möller *et al.,* 2014). Plant diversity on saltmarshes has a strong effect on the erodibility of saltmarsh sediments (Ford *et al.,* 2016). The role of vegetation in saltmarshes in protecting against erosion is not simple, acting more indirectly through modification of the dynamics of sediment transport and accumulation, and the protective effect may be more useful against slow change such as sea-level rise but less so against breaking waves at the edges of a marsh (Feagin *et al.,* 2009). Nonetheless, in developed areas, re-creation and active management of saltmarshes can help with the problem of 'coastal squeeze' and potentially reduce the need for man-made coastal defences. Saltmarshes are likely to migrate inland as sea levels rise (Wong *et al.,* 2014), and careful managed realignment of coastal defences may ensure that the extent of these habitats are maintained (Wolanski and Elliott, 2015).

4.3.2.5 Kelp beds

Evidence that kelp beds provide protection from waves is sparse, despite this being invoked as an important ecosystem service for kelp beds by alleviating the effects of storms (Smale *et al.,* 2013; Angus and Rennie, 2014). Waves do become smaller in the presence of kelp beds (Mork, 1996; Løvas and Tørum, 2001), but in one study kelp did not have a significant effect on the rate of erosion of sand dunes (Løvas and Tørum, 2001). Kelp beds may have the most protective effect where rocky reefs immediately offshore protect soft coastlines, such as on the western coast of the Outer Hebrides, in Scotland (Angus and Rennie, 2014), where beach-cast material has long been used as fertilizer in adjacent agricultural land (Orr, 2013). Very large plants, such as the giant kelp, may even slow coastal currents (Jackson and Winant, 1983) and thereby have an influence on coastal sediment dynamics.

Globally, declines in kelp populations and associated communities are more often reported than increases, such as the losses of giant kelp *Macrocystis pyrifera* (Figure 4.3.8) in Australia (Wernberg *et al.,* 2011) and the smaller laminarian species *Saccorhiza polyschides* in retreat near its southern limit in Spain (Fernández, 2011). These changes can be rapid, such as the distribution shift and declines following the anomalous short term high temperature event in Western Australia in 2011 (Wernberg *et al.,* 2013). Most climate-related changes in kelp populations may be through reduction of the abundance of habitat-forming species at their trailing equatorward range edges. The functionality of such systems may also change with species compositional change as cold-water species are replaced by warm-water ones. As kelp forests in Europe approach their southern-most limits on the Atlantic coasts of France and Spain, the dominant kelp species of open coasts, *Laminaria hyperborea* (S. limit mid Portugal) (Kain, 1979; Lüning, 1990), is gradually replaced by the warm-water *Laminaria ochroleuca* (S. limit Morocco) in the southern part of its range (Smale *et al.,* 2014). The effects of changing community composition on the delivery of protective functions of the coastal ecosystem is likely to depend on the identity of the species being lost or gained. Different kelp species are likely to have different effects on wave attenuation, depending on the size of adult plants and associated communities of epiphytes: the southern *L. ochroleuca* has much fewer epiphytes than *L. hyperborea* for example and thereby likely to have a lesser wave attenuating effect (Figure 4.3.9). Different kelp species around the UK have quite different preferences for wave exposure (Burrows, 2012), with *Laminaria hyperborea* found in the most extremely wave-exposed habitats, giving way to other species in more sheltered environments. Loss of *Laminaria hyperborea* from the southern end of its geographical range may be more important for coastal protection than the loss of kelps from more sheltered habitats, and this pattern may be repeated in other parts of the world.

Figure 4.3.8 Giant kelp, *Macrocystis pyrifera.* © Claire Fackler, CINMS, NOAA. - NOAA Photo Library: sanc0063, Public Domain, https://commons.wikimedia.org/w/index.php?curid=17972018.

Where storms are expected to increase, impacts on kelp forests change the complexity of food webs within them, first increasing their complexity and then decreasing with further increases in storm intensity and

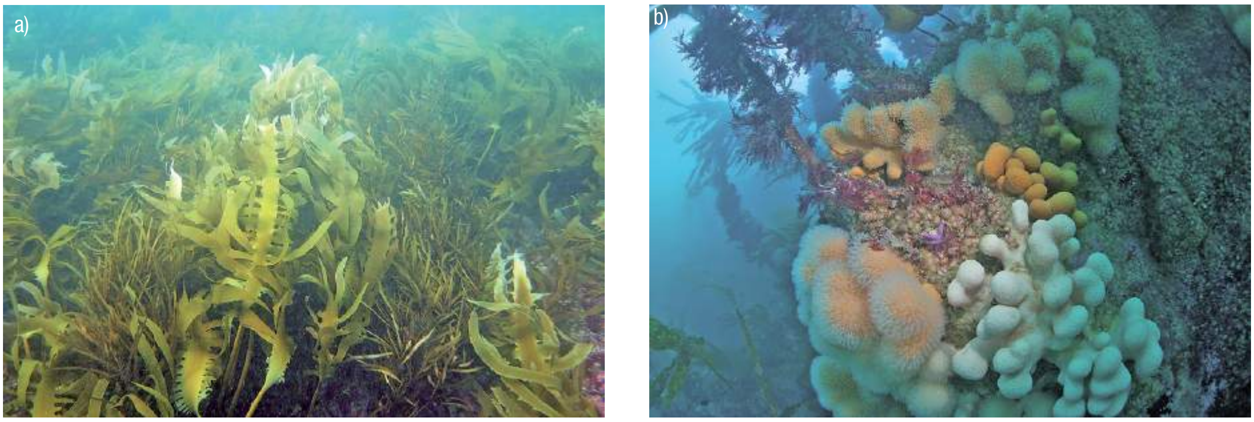

Figure 4.3.9 a) *Laminaria ochroleuca.* © Saspotato; b) *Laminaria hyperborea* with heavy epiphytes growing on stypes. © SNH.

frequency (Byrnes *et al.,* 2011). Loss of kelp plants following storms combined with extreme high water levels have been implicated in increasing the severity of a storm in western Scotland that resulted in loss of life (Angus and Rennie, 2014).

Among mostly negative effects on coastal systems, ocean acidification may benefit the structuring species in kelp forests. Where effects on macroalgae of increased dissolved CO_2 have been measured, these have been generally positive (Kroeker *et al.,* 2013), with an average 22% increase in growth. That said, kelp forests often have extensive populations of subcanopy calcifying algae, whose rates of photosynthesis (-28%) and abundance (-80%) are strongly compromised by acidification (Kroeker *et al.,* 2013). Calcifying algae may be completely replaced by diatoms in Arctic regions, as aragonite saturation falls and reduces their ability to perform calcification, while in warmer waters the effects of increasing temperatures are likely to outweigh any positive effects of acidification, leading to kelps disappearing completely (Brodie *et al.,* 2014)

4.3.3 Societal consequences

The implications of continuing ocean temperature rise for human populations are far-reaching, from the direct inundation of coastal communities in poor and rich countries alike, through the climate-mediated loss of economically important habitats and fisheries, to the loss of coastal protection by fringing habitats (the focus of this review). Such habitat loss has impacts at a local level: loss of mangroves increasing the impacts of urban flooding in Lagos, Nigeria was chosen by the IPCC WG2 as an example of how climate change effects on ecological systems may impact livelihoods and poverty (Olsson *et al.,* 2014).

4.3.4 Conclusions

Climate change has had, and is likely to continue to have a mostly negative effect on the capacity of reefs and vegetation to protect coasts from erosion and storm damage. Ongoing removal of these habitats by human development along coastlines further diminishes the benefits for coastal protection, and significantly increases the costs of protecting coasts through the increased need for engineering structures to protect people, buildings and coastal infrastructure such as transport links. The usefulness of habitats as protectors of the coast is not well enough understood in terms of their ability to reduce erosion and wave damage, and even the area of such habitats is not well known, as the widely varying estimates for global extents of the same habitat show here. Better indicators of the state of habitats and their functioning as protectors of coasts, globally-resolved updatable fine-scale maps of the extents of these protective habitats (such as those used in Halpern *et al.,* 2012), measurements and projections of losses and gains in habitats, and increased understanding of the effects of losses are all need for a clearer picture of how climate impacts on coastal biogenic habitats will affect coastal societies.

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4.4 Impacts and effects of ocean warming on marine phytoplankton and harmful algal blooms

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Summary

- Global climate change is altering the abundance, distribution and species composition of phytoplankton at the base of marine food chains. Climate change adds a new level of uncertainty to seafood security and safety for an ever growing human population.
- Emerging phytoplankton climate responses include: (1) range expansion of warm-water at the expense of cold-water species; (2) changes in abundance and seasonal bloom window; (3) increased cellular toxin content of harmful algal bloom species; and (4) secondary effects for marine food webs, when individual zooplankton and fish grazers are differentially impacted by climate change.
- Developing predictive capability has been frustrated by: contradictory species and especially strain-specific responses; lack of insights into evolutionary adaptation and how harmful algal species interact with the broader phytoplankton and zooplankton grazer communities; and scarcity of sustained biological data streams. Unexplored factor interactions may underpin differing climate responses by different geographic ocean provinces.
- To progress phytoplankton climate science, we need better science including agreement on 'best practices' experimental protocols, use of biological reference organisms and climate 'hot-spot' observer sites. We also need better data streams through more investment in global observation systems and improved ocean sensor capabilities. Finally, we need better integrated and coordinated research communities in order to define management options and better forecast risks to human health and seafood security.

Ocean warming effect	Consequences
Alteration of abundance, distribution and species composition of phytoplankton	Largely unpredictable alterations in marine food webs leading to edible fish
Phenological mismatch between phytoplankton and zooplankton or fish grazer responses	Risk for seafood security
Appearance of harmful algal blooms in currently poorly managed areas	Risk for seafood safety
Ecosystems disturbed by pollution or climate change are more prone to invasive species	Risk for marine biodiversity
Reduced phytoplankton growth	Reduced net CO_2 uptake could accelerate global warming
Perplexing complexity of predicting multi-factorial phytoplankton climate responses	We need better science, better data streams, better integrated research communities

4.4.1 Introduction

Microscopic unicellular planktonic algae form the basis, either directly or indirectly, of all marine food webs leading to edible fish. Through the process of photosynthesis these microscopic floating plants provide 50% of the oxygen humans breathe and constitute a major consumer of anthropogenically produced atmospheric CO_2. Small but numerous, if all the microalgal cells in the world oceans could be packed in a plank, 386,000 km long, 7 cm thick, and 30 cm wide, it would stretch from the Earth to the Moon (Andersen, 2005). The ability of the ocean to act as a sink for anthropogenic CO_2 relies on the conversion of this gas by phytoplankton into particulate organic matter and subsequent partial loss to the deep ocean (tne so-called biological pump). Any reduction in net ocean CO_2 uptake caused by shifts in ocean circulation or reduced phytoplankton growth in surface waters could lead to an acceleration in the rate of increase in atmospheric CO_2 and global warming. Increased recognition of phytoplankton as a climate driver is well demonstrated by commercial interests exploring options such as ocean fertilization to combat anthropogenic climate change (Glibert *et al.,* 2008). Whilst temperature is a key factor of ocean climate, climate change is multifactorial also covering changes in water column stratification, light penetration, carbonate chemistry (ocean acidification) and nutrient availability (Figure 4.4.1).

Climate on the Earth has been constantly changing, over scales of both millions of years (glacial to interglacial periods) and including short-term oscillations of tens of years (El Niño Southern Oscillation, North Atlantic

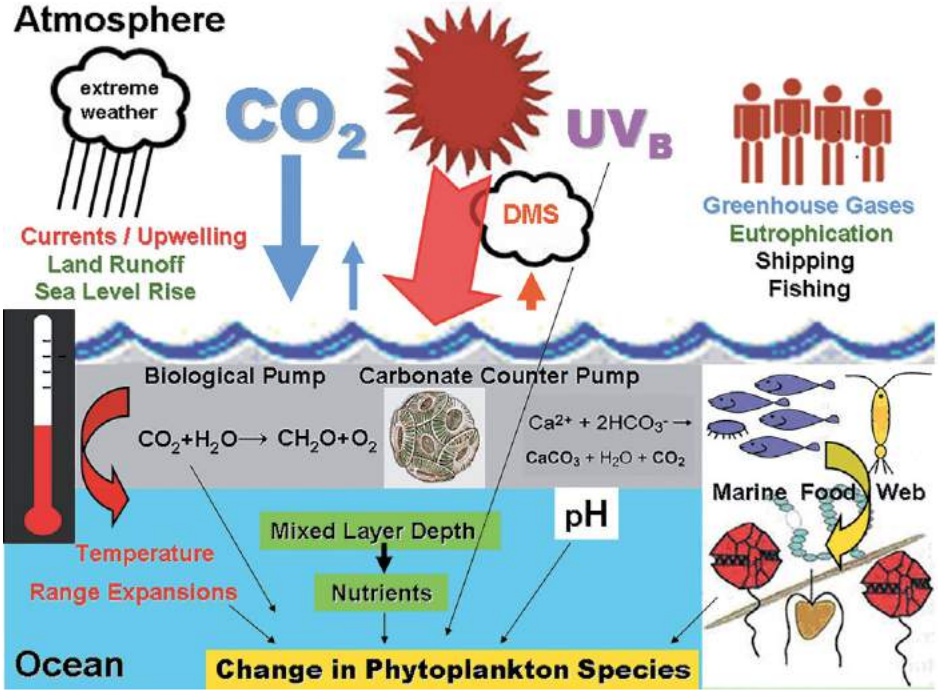


Figure 4.4.1 Climate change is multifactorial. Ocean warming, water column stratification, and associated changes in light penetration (increased ultraviolet exposure), nutrient availability, but also carbonate chemistry (pH) all drive changes in phytoplankton species composition. Human population pressures on the marine environment through nutrient pollution, ship ballast water introduction of invasive species, and marine food web alteration from overfishing represent additional stressors (adopted from Hallegraeff, 2010).

Oscillation). The Earth's climate in the distant past has at times been subject to much higher ultraviolet-B levels and CO_2 concentrations than seen at present. The first photosynthetic cyanobacteria evolved 3.5 billion years ago at CO_2 levels 1,000x those of the present, followed by green algae 1,000 million years ago (500x present) and dinoflagellates 330–400 mya (8x present), whereas more recently evolved diatoms and golden-brown flagellates operated under comparatively low CO_2 environments (2–3x present) (Beardall and Raven, 2004). During the past 800,000 years, atmospheric CO_2 has fluctuated between 180 ppm in glacial and 300 ppm in interglacial periods, but in the past 200 years, this has increased from 280 ppm to 400 ppm at present, with values of 750–1,000 ppm predicted by 2100. In the past 1,000 years, the Earth has gone through episodes warmer than present, such as the medieval warm period AD 550–1300, and colder than now, such as the little ice age AD 1300–1900. Global temperatures in the past 20–30 years have increased significantly with a further rise of 2–4°C predicted over the next 100 years (IPCC, 2014). From a geological perspective, there is nothing remarkable about the magnitude of climate change being experienced now, however, there exists no precedence for the much (>10x) faster pace of change (occurring over hundreds not millions of years) and that it starts from a warmer baseline.

Because of their short generation times and longevity, many phytoplankton are expected to respond rapidly to current climate change. However, our knowledge of the potential of marine microalgae to adapt is very limited. Collins and Bell (2004) grew the freshwater green alga *Chlamydomonas* over 1,000 generations at almost 3x present atmospheric CO_2 concentration. The cells acclimated to the change but did not show any genetic mutations that could be described as adaptation. Lohbeck *et al*. (2012) exposed *Emiliania huxleyi* coccolithophorid cultures founded by single or multiple clones to increased concentrations of CO_2 in 500 generation selection experiments. Compared with populations kept at ambient CO_2 partial pressure, those selected at increased partial pressure exhibited higher growth rates suggestive of adaptive evolution. It should not be underestimated that microbial life in the ocean has had 3.5 billion years to evolve, thus representing an enormous genetic diversity and physiological plasticity (Read *et al.,* 2015). While changes in distribution, performance and genetic diversity of individual species are to be expected, complete extinction of microalgal species is unlikely.

Responding to the predictions from IPCC physico-chemical climate models, over the past 15 years phytoplankton climate science has progressed from single-factor to multi-stressor single-species lab and multi-species mesocosm manipulation experiments, to tentative predictive modelling. Key environmental factors identified include: increased temperature, enhanced surface stratification (affecting nutrient and light availability), elevated CO_2 (stimulating photosynthesis and driving 'ocean acidification' biogeochemistry), and increased extreme precipitation and storm events. Not all trophic levels are responding to the same extent, and where zooplankton or fish grazers are differentially impacted by ocean warming, this may have cascading impacts on the structure of marine food webs. While the collapse of the North Atlantic cod fishery has been widely attributed to overfishing, an underlying climate-driven regime shift in its preferred zooplankton prey is also thought to have played a key role (Engelhard *et al*., 2014).

4.4.2 The formidable challenge of predicting phytoplankton community responses

While considerable progress has been made in understanding of the physics of climate change, understanding the impacts on biological communities is in its infancy. There will be winners and losers from climate change, but predicting how individual species will respond poses a formidable challenge. Increasing temperature, enhanced surface stratification, alteration of ocean currents, intensification or weakening of local nutrient upwelling, stimulation of photosynthesis by elevated CO_2, ocean acidification, and increased frequency of heavy precipitation and storm events causing changes in land runoff and micronutrient availability may all produce contradictory species- or even strain-specific responses (Figure 4.4.1). Complex factor interactions exist (e.g. Feng *et al.,* 2008) and eco-physiological experiments rarely take into account genetic strain diversity (Langer *et al.,* 2009; Kremp *et al.,* 2012; Müller *et al.,* 2015) and physiological plasticity. To conduct ecologically realistic climate change scenario experiments thus increasingly calls for complex multi-factorial experiments using multiple strains, complemented with mathematical modelling to extrapolate the results to unevenly changing global oceans scenarios (Bopp *et al*., 2013; Glibert *et al*., 2014; Dutkiewicz *et al*. 2015; Boyd *et al*., 2016) (Figure 4.4.2).

An undoubted key driver for future phytoplankton changes in open ocean environments will be increasing

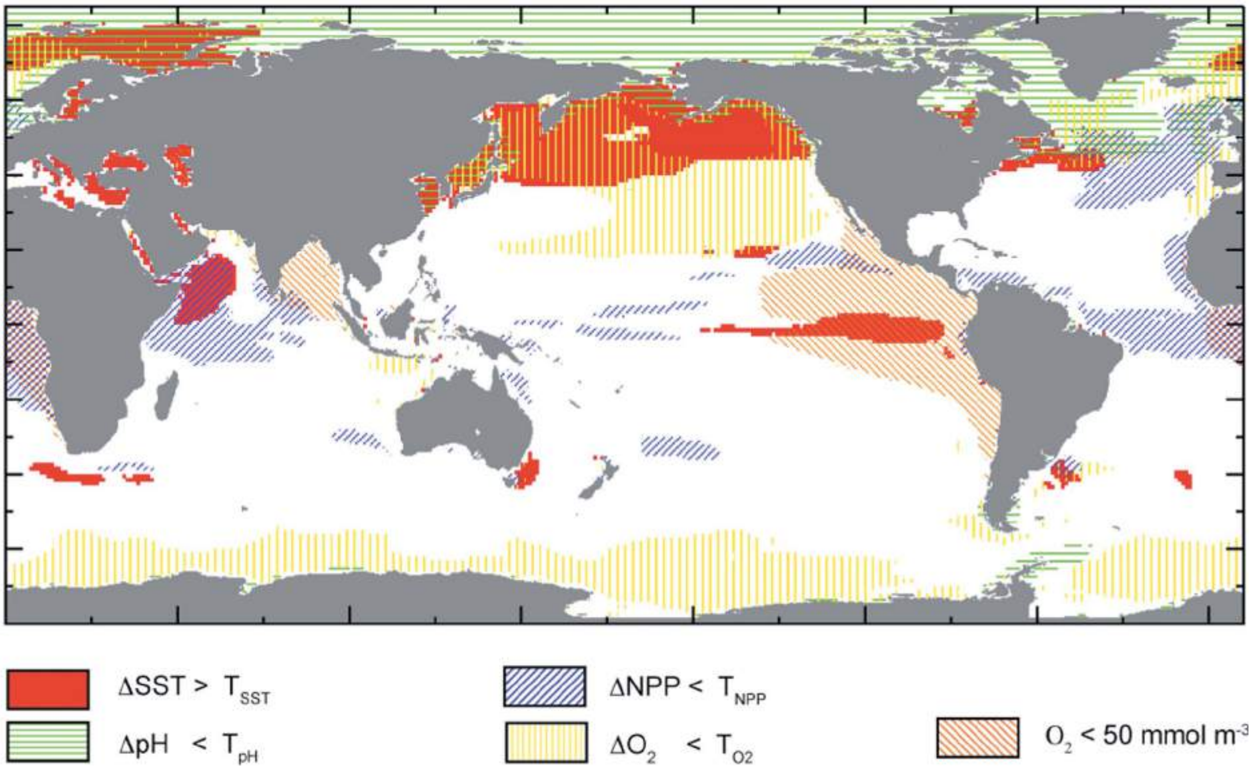


Figure 4.4.2 Different ocean regions change at different rates. Global hotspots in terms of temperature change (red), ocean acidification (green), nutrient alterations (blue) and lowered oxygenation (yellow and orange) are indicated. Adopted from Bopp *et al.* (2013) based on RCP8.5 model predictions comparing 2090s with 1990s.

sea surface temperature and enhanced water column stratification (shallowing of the mixed layer). This may lead to more rapid depletion of surface nutrients, a decrease in replenishment from deep nutrient-rich waters and therefore reduced phytoplankton biomass ('oligotrophication'; Behrenfeld *et al*., 2006). By contrast, in high-latitude regions with relatively deep mixing and sufficient nutrients, decreasing mixing depth can result in higher phytoplankton biomass because of increased light availability (Doney, 2006). Cyanobacteria can dominate both marine and freshwater ecosystems under higher temperature, notably when combined with eutrophication (O'Neil *et al*., 2012).

Extreme weather events such as heavy rainfall (nutrients from land runoff), hurricanes and dust storms are well-known to impact on marine phytoplankton. Winds influence the supply of iron to the surface ocean through aeolian transport of dust from land to sea, contributing micronutrients such as iron which stimulate algal blooms such as *Karenia brevis* off Florida (Walsh and Steidinger, 2001). An Australian dust storm on the other hand triggered massive microbial rafts of potentially pathogenic *Aspergillus* fungi covering an ocean area 25 time the surface of Great Britain (Hallegraeff *et al.,* 2014).

It is widely predicted that increasing CO_2 will lead to ocean acidification, a decrease in ocean pH (from 8.1 down to 7.7 by 2100) and associated changes in carbonate chemistry. Most harmful algal bloom species tested lack carbon concentrating mechanisms and hence they may benefit from increased atmospheric CO_2. While initial attention focused on potentially adverse impacts of ocean acidification on calcifying organisms such as the coccolithophore *Emiliania huxleyi* (Riebesell *et al*., 2000), a much greater impact may derive from how ocean acidification will alter availability of micronutrients such as iron (Shi *et al*., 2010). Dominance and community structure of harmful bloom dinoflagellates can be profoundly altered by changing pCO_2, and both toxic dinoflagellates (*Alexandrium catenella, Karlodinium veneficum*) and toxic diatoms (*Pseudo-nitzschia multiseries*) have been shown to produce higher cellular toxin concentrations under near-future levels of ocean acidification (Fu *et al*., 2010, 2012; Sun *et al*., 2011; Tatters *et al*., 2013).

4.4.3 Algal blooms: the good and the bad

Under favourable environmental conditions of light, temperature, salinity, water column stability and nutrients, algal populations of only a few cells can quickly multiply into dense blooms containing millions of cells per litre which can discolour the sea water (sometimes referred to as 'red tides'). Most plankton blooms appear to be beneficial to human society in that they drive food chains leading to commercial fisheries as well as serve as a sink for anthropogenically produced $CO_{2.}$ Ocean fertilization experiments suggest that at various times in the Earth's history, proliferation of algal blooms which gobbled up carbon dioxide and sank to the bottom of the sea, taking greenhouse gas with them, may thus have contributed to a cooling of climate (Watson *et al*., 2000). Under exceptional conditions algae may become so densely concentrated that they deplete the oxygen in the water upon their demise. This can cause indiscriminate kills of fish and invertebrates in sheltered bays. Prolonged low oxygen conditions, such as those caused by excessive nutrient pollution from human activities into coastal waters, can lead to oxygen dead zones that fail to support marine life. An essentially different phenomenon is the production by certain species of dinoflagellates, diatoms and cyanobacteria of potent neurological toxins which can find their way through fish and shellfish to humans. When humans eat seafood contaminated by these microalgal toxins, they may suffer a variety of gastro-intestinal and neurological illnesses, including Paralytic, Diarrhetic, Amnesic, or Neurotoxic Shellfish Poisoning and Ciguatera Fish Poisoning. Human drinking water supplies can be contaminated by cyanobacterial toxins. Algal bloom species show a perplexing diversity of biomass and toxicity patterns, ranging from species that can cause toxicity problems even at very low cell concentrations, to species which are basically non-toxic but whose nuisance value derives from their high biomass production. In addition to trying to predict how global phytoplankton abundance may respond, special attention has focused on the behaviour of so-called harmful algal blooms (Hallegraeff, 2010; Wells *et al*., 2015). Persistent near-monospecific algal blooms have sometimes been referred to as ecosystem disruptive algal blooms (EDABs), in which toxic or unpalatable algal species disrupt grazing of phytoplankton by zooplankton and thus diminish nutrient supply via

Harmful algal blooms, ocean warming and economic loss.

Harmful algal blooms that discolour the water, kill fish and contaminate seafood with biotoxins are highly visible expressions of phytoplankton community alterations. These events cause severe economic losses through damage to tourism, biodiversity, aquaculture and fisheries. Some algal blooms are completely natural and seasonally recurrent phenomena, but others may reflect responses to nutrient pollution, loss of zooplankton grazer control or reflect ship ballast water or climate-driven range expansions. Multifactorial climate change is adding a new level of uncertainty to seafood security and seafood safety. Recent examples include:

Figure 1 Red-tide dinoflagellate *Noctiluca* slick around salmon farm cages. © Gustaaf M Hallegraeff.

The red-tide dinoflagellate *Noctiluca* in the period 1860-1950 was only known from Sydney where it has been responsible for tourist beach closures (e.g. on famous Sydney Bondi Beach), from 1980-1993 it expanded along the New South Wales coast in response to eutrophication, and during 1994-2005 the changing East Australian Current drove a range extension down to Tasmania (34°S) where it threatened to smother salmon farms with 4m thick pink slicks (Figure 1).

The largest ever reported algal blooms and aquaculture fish kills in Chile in 2016 causing US$ 800M losses were associated with an unusually strong El Niño pattern.

A major outbreak of Paralytic Shellfish Poisoning in 2012 and 2015 along 200km of coastline of Tasmania, Australia, leading to closures of mussel, oyster, scallop, abalone and rock lobster industries and four human hospitalizations, occurred in this same area not previously known to be at risk. When a Tasmanian shipment of blue mussels was tested by Japanese import authorities to be contaminated with dinoflagellate toxins, this triggered a global product recall and loss to the local economy of AU$ 23M (Campbell *et al*., 2012).

recycling. Ecosystems disturbed by pollution or climate change are considered more prone to ballast water or climate-driven invasions than mature stable ecosystems (Stachowicz *et al.,* 2002). Temperature perturbations could perhaps create a niche for such species?

Harmful algal blooms in a strict sense are completely natural phenomena which have occurred throughout recorded history (e.g. Captain Vancouver's crew in 1793 suffering from Paralytic Shellfish Poisoning). Whereas in the past three decades unexpected new algal bloom phenomena have often been attributed to nutrient pollution, increasingly novel algal bloom episodes are now circumstantially linked to climate change. There is no doubt that the growing interest in using coastal waters for aquaculture is leading to a greater awareness of toxic algal species. People responsible for deciding quotas for pollutant loadings of coastal waters, or for managing agriculture and deforestation, should be made aware that one probable outcome of allowing polluting chemicals to seep into the environment will be an increase in harmful algal blooms. In countries which pride themselves on having disease- and pollution-free aquaculture, every effort should be made to quarantine sensitive aquaculture areas against the unintentional introduction of non-indigenous harmful algal species. Nor can any aquaculture industry afford not to monitor for an increasing number of harmful algal species in water and for an increasing number of algal toxins in seafood products, using increasingly sophisticated analytical techniques.

4.4.4 Algal bloom range extensions and climate change

Temperature influences motility, cyst germination, nutrient uptake, photosynthesis, growth rates and many other physiological processes. Temperature defines the geographic distribution of many species and their responses to climate change. Shifting temperature means and extremes alter habitat and cause changes in abundance through local extinctions and latitudinal expansions or shifts. Vulnerability is thought to be greatest in polar organisms due to their narrow temperature ranges and in tropical species living close to upper thermal limits.

The Paralytic Shellfish Toxin-producing dinoflagellate *Pyrodinium bahamense* is presently confined to tropical, mangrove-fringed coastal waters of the Atlantic and Indo-West Pacific. In the Philippines alone, *Pyrodinium* has been responsible for more than 2000 human illnesses and 100 deaths resulting from the consumption of contaminated shellfish as well as sardines and anchovies. A survey of cyst fossils (named *Polysphaeridium zoharyii*) going back to the warmer Eocene 50 million years ago indicates a much wider range of distribution in the past. For example, in the Australasian region at present, the alga is not found farther south than Papua New Guinea but, some 100,000 years ago in the Pleistocene, the alga ranged as far south as Sydney Harbour (McMinn, 1989) There is concern that, with increased greenhouse warming of the oceans, this species may one day return to Australian waters.

Ciguatera caused by the benthic dinoflagellate species complex *Gambierdiscus toxicus* is a tropical fish food poisoning syndrome well-known in coral reef areas in the Caribbean, Australia, and especially French Polynesia. From 1960 to 1984, >24,000 patients were reported from this area, which is more than six times the average for the Pacific as a whole. Whereas, in a strict sense, this is a completely natural phenomenon, from being a rare disease two centuries ago, ciguatera has now reached epidemic proportions in French Polynesia. Evidence is accumulating that reef disturbance by hurricanes, military and tourist developments, as well as coral bleaching (linked to global warming) and coral damage due to ocean acidification are increasing the risk of ciguatera. An apparent range expansion of *Gambierdiscus* has been reported in the Mediterranean and the Canary Islands, the Caribbean and West Indies (Tester *et al*., 2010). The 2.5-3.5°C projected increase in sea surface temperature in the Caribbean is estimated to increase the incidence of ciguatera fish poisonings over the coming century by 200-400% (Gingold *et al*., 2014).

Noctiluca is another example of a red-tide dinoflagellate species that appears to have been increasing globally in the past two decades (Harrison *et al*., 2011). Although in some regions this may be, at least in part, a function of increasing observations and awareness, in other regions such as south-east Asia this appears to reflect a real change in plankton dynamics associated with eutrophication and climate change. While not harmful to humans, this heterotrophic dinoflagellate is a voracious predator on phytoplankton, zooplankton and even fish eggs. *Noctiluca* has sometimes been interpreted as a coastal or offshore manifestation of eutrophication, since an increase in nutrients provides an increase in phytoplankton, its main food supply as a grazer. Red *Noctiluca* has dramatically increased along the east coast of Australia (McLeod *et al.,* 2012). Initially it

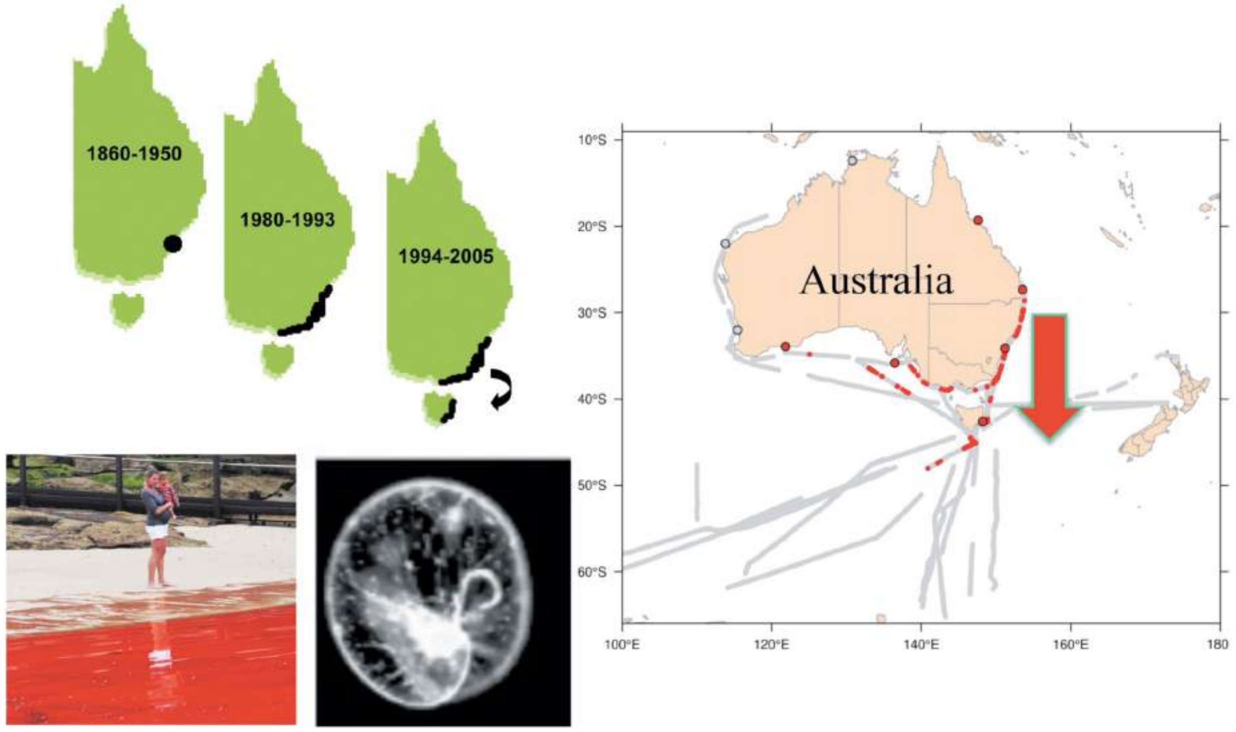


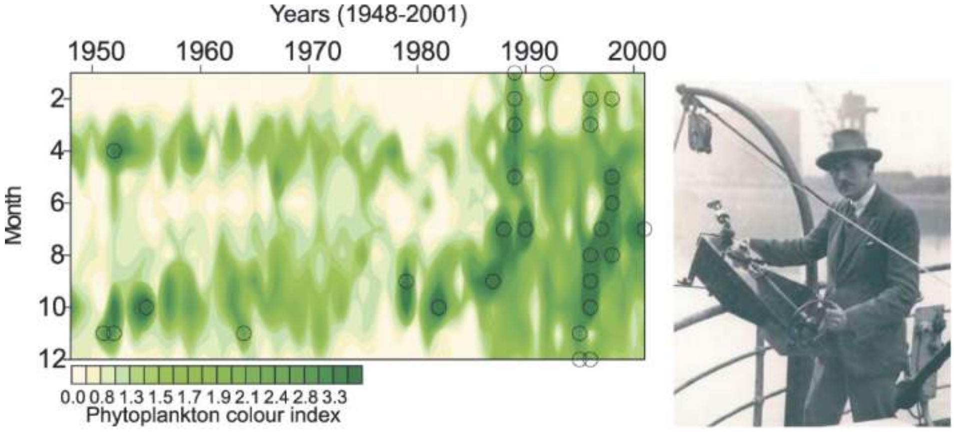
Figure 4.4.3 Dramatic Australia-wide range expansion of the red-tide dinoflagellate *Noctiluca scintillans* (insets), in the periods 1860-1950 (only known from Sydney Harbour), 1980-1993 (expanding along New South Wales coast in response to eutrophication), 1994-2005 (East Australian Current driven range extension) and 2008-2013 (moving into the Southern Ocean; arrow). In addition to its nuisance value for tourism and fish farm operations, *Noctiluca*'s voracious phagotrophic feeding behaviour may disturb marine food web structure. Updated after McLeod *et al.* (2012).

was only known from Sydney, before in 1980-1993 expanding along the New South Wales coast, but during 1994-2005 it exhibited a range extension down to Tasmania (34°S) (Figure 4.4.3). Green *Noctiluca* (containing photosynthetic green flagellate symbionts) has expanded in the last decade into the northern Arabian Sea where winter phytoplankton blooms previously comprised mainly diatoms, but now have been replaced by green *Noctiluca.* This latter organism combines carbon fixation with ingestion of prey to the detriment of regional fisheries and the long-term health of an ecosystem supporting coastal fisheries serving a population of 120 million people.

4.4.5 Lessons from the fossil record, long-term plankton records and decadal scale climate events

The ecosystem response to natural climate variability in the past provides a glimpse into the climate-induced changes of the near future. Important lessons can be drawn from the dinoflagellate cyst fossil record (Dale, 2001) and from the few long-term data sets available (such

Figure 4.4.4 Long-term monthly values of "phytoplankton chlorophyll colour" in the central North Sea from 1948 to 2001, measured via 50 years of Continuous Plankton Recorder surveys towed behind merchant ships (inset on the right). Circles denote > 2SD above the long-term monthly mean. Note an apparent regime shift in 1989 towards earlier and more abundant spring and autumn phytoplankton blooms (adopted from Edwards, 2004, with permission).



as the Continuous Plankton Recorder surveys; Edwards and Richardson, 2004; Richardson and Schoeman, 2004). Data from the Continuous Plankton Recorder in the North-east Atlantic confirm that warming from 1960 to 1995 enhanced phytoplankton growth. In response to transient warming, phytoplankton distribution in the North Atlantic shifted poleward by hundreds of km per decade since the 1950s. Phenology of plankton in the North Atlantic was also affected, with seasonal timing of phytoplankton blooms now occurring up to 4-5 weeks earlier in the North Sea in response to regional climate warming (Figure 4.4.4), Moore *et al.* (2008) predict longer-lasting *Alexandrium catenella* blooms in Puget Sound under future climate change scenarios, and a poleward expansion and increase in abundance of coccolithophore blooms of *E. huxleyi* has been claimed for both Northern and Southern Hemispheres (Winter *et al*., 2014).

4.4.6 Mitigation of the likely impact on seafood safety

The greatest problems for human society are posed by being confronted with a new level of uncertainty for seafood security and safety for an ever growing human population. While, for example, ciguatera contamination would be expected and monitored for in tropical coral reef fish, with the apparent range extension of the causative benthic dinoflagellate into warm-temperate seagrass beds of South-eastern Australia (Kohli *et al.,* 2015) other coastal fisheries unexpectedly could be at risk. Similarly, incidences of increased surface stratification in estuaries or heavy precipitation or extreme storm events are all warning signs that call for increased vigilance of monitoring seafood products for algal biotoxins even in areas not currently known to be at risk. An unusually warm El Niño year in 2015 in Eastern Pacific coastal waters, representative of what can be expected more of in future, generated unprecedented toxic algal bloom events (Kudela, 2015). Only with improved global ocean observation systems, such as improved and expanded ocean sensor capabilities (e.g. argo floats, ocean gliders, coastal moorings and coastal radar, multi-wavelength and variable fluorometers, *in situ* imaging devices and optical sensors) in support of integrated satellite-derived "ocean colour" maps and expanded biological and biogeochemical observations (continuous plankton recorder, eco-genomics) can we expect to define management options, forecast ocean-related risks to human health and safety, and shed light on the impact of climate variability on marine life and humans in general. Following the lead of physical oceanographers who operate globally well integrated research programmes, biological oceanographers need to learn to collaborate better in order to achieve global aims. It is pleasing to see that a number of national (e.g. the US NSTC Joint Subcommittee on Ocean Science and Technology Ocean Observatories Initiative (OOI), the Australian Integrated Marine Observing System (IMOS)) and international programmes (e.g. the Intergovernmental Oceanographic Commission of UNESCO's GEOHAB, IOC Global HAB status reports initiative) are actively pursuing these ambitious goals.

Acknowledgements

Our understanding of climate driven impacts on phytoplankton communities and processes is continuously increasing. This section represents an update on an earlier review in *Journal of Phycology* 2010, and benefited from my attendance at the April 2013 IOC-UNESCO GEOHAB meeting in Paris, May 2015 IOC-ICES-PICES-SCOR Symposium on HABs and Climate Change in Götheborg, Sweden, and May 2016 Symposium on the Ocean in a high-CO_2 world in Hobart, Australia.

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4.5 Impacts and effects of ocean warming on the contributions of fisheries and aquaculture to food security

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Summary

- Fisheries and aquaculture play a vital but often poorly acknowledged role in global food security. Together, fisheries and aquaculture provide 4.3 billion people with ~15% of their average per capita intake of animal protein. By 2050, an additional 75 million tonnes of fish will be needed to help feed more than 9 billion people.
- The recent revolution in aquaculture, and continued improvements to management of capture fisheries, have potential to provide the additional fish required. However, warming of the world's ocean could disrupt these important initiatives.
- Ocean warming will result in 'winners' and 'losers. Changes in distributions of fish stocks as species seek their optimal temperatures, and as the habitats on which they depend are altered by higher water temperatures, will result in decreases in fisheries production in some countries and increases in others. Similarly, the prime locations for mariculture are expected to be altered by ocean warming, resulting in changes in yield patterns among countries.
- The effects of ocean warming on the contributions of marine fisheries and mariculture to food security should not be considered in isolation from those of other drivers. Rapid population growth, fish exports and poor fisheries management also affect availability of fish in many developing countries. These drivers often create a gap between how much fish is needed for good nutrition and local fish harvests. The main effects of ocean warming are to alter (increase or decrease) the gap.
- Changes to the gap due to ocean warming are expected to be greatest in tropical and subtropical countries. Adaptations are needed to minimize, and to fill, the gap.
- Adaptations to minimize the gap include reducing the impact of local stressors on fish habitats through improved integrated coastal management and marine spatial planning; keeping production of fisheries within sustainable bounds using the most appropriate management measures for the national context and a climate-informed ecosystem approach; and improving supply chains.
- The most important adaptation for filling the gap will be the expansion of environmentally sustainable mariculture (and freshwater aquaculture). However, for some developing countries, the most practical adaptations for filling the gap will be re-allocating some of the catch of large and small pelagic fish taken by industrial fleets to small-scale fishers, and/or arranging for industrial fleets to land more of their catch in local ports.

Ocean warming effect	**Consequences**
Total production of fish from capture fisheries has levelled off at about 90 million tonnes per year	Aquaculture now supplies the remainder of the ~130 million tonnes of fish used directly for food
An additional 75 million tonnes of fish will be needed to help feed more than nine billion people by 2050	Continued improvements to fisheries management will be needed but expanded aquaculture production will be required to meet most of the demand
Ocean warming is expected to increase progressively due to continued greenhouse gas emissions	The plans to optimize production from marine fisheries and to expand mariculture are likely to be affected by ocean warming
Distributions of fish stocks will change as fish species seek their optimal ocean temperatures	Marine fisheries production will increase in some countries and decrease in others
Prime locations for mariculture will change as the ocean warms	Countries will become more or less suitable for mariculture and patterns of yields among countries will change
Rapid population growth, fish exports and poor fisheries management are reducing availability of fish per capita in many developing countries	A gap is emerging between how much fish is needed for good nutrition and how much fish is available locally
Ocean warming will widen this gap in some countries and reduce it in others	Practical adaptations are needed to minimize, and to fill, the gap

4.5.1 Introduction

Fisheries and aquaculture play a vital but often poorly acknowledged role in global food and nutrition security (Béné *et al.,* 2015, 2016). The ~130 million tonnes of fish[1] currently produced from marine and freshwater capture fisheries and aquaculture used directly for human consumption (Figure 4.5.1) provide 4.3 billion people with about 15% of their average per capita intake of animal protein (HLPE, 2014). Furthermore, about 10% of the world's population – predominantly from developing and emergent countries – rely heavily on fisheries and aquaculture for the income needed to buy food (Allison *et al.,* 2013; HLPE, 2014).

In recent decades, total production from capture fisheries has levelled off at about 90 million tonnes per year, with about 75% used directly for food (Figure 4.5.1), because most marine resources are now fully exploited, and in some cases over-exploited (FAO, 2014a). Rapid development of aquaculture has met the remainder of the demand (FAO, 2014a). In fact, the rate at which aquaculture has increased has enabled global fish supply to outpace population growth, and the supply of other sources of animal protein (De Silva, 2012a; FAO, 2014a; Youn *et al.,* 2014). Although capture fisheries will always need to be an important source of fish, particularly in developing countries (Hall *et al.,* 2013), most of the expected future demand for fish will have to come from aquaculture (Merino *et al.,* 2012; FAO, 2014a). Rice and Garcia (2011) provide a potent example of estimated future demand – they calculate that an additional 75 million tonnes of fish will be required to provide more than 9 billion people with 20% of their dietary protein requirements by 2050.

There is optimism that continued improvements in aquaculture related to feed formulation, feeding technologies, farm management and selective breeding can supply the future needs for fish (FAO, 2014a). A particularly beneficial development is the reduced dependence on fish meal for feeds, which decouples marine fisheries and aquaculture production, paving the way for more wild fish to be used directly for human consumption. There is also the prospect that total sustainable production from capture fisheries could increase by up to ~20% with improved management (OECD-FAO, 2013; Costello *et al.,* 2016). Similarly, there is a view that fish production from inland capture fisheries is under-estimated (Beard *et al.,* 2011; Bartley *et al.,* 2015) and that there is scope for freshwater fish resources to make significant additions to supplies of food fish (Youn *et al.,* 2014), particularly among rural communities in developing countries. On the other hand, failure to address the many factors that affect the production of capture fisheries, including habitat

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[1] Fish is used here in the broad sense and includes finfish, shellfish (invertebrates), sharks and rays

degradation, over-capacity and a range of socio-economic drivers (Gillett and Cartwright, 2010; Hall, 2011), could reduce present-day harvests from the wild and widen the gap to be filled by aquaculture.

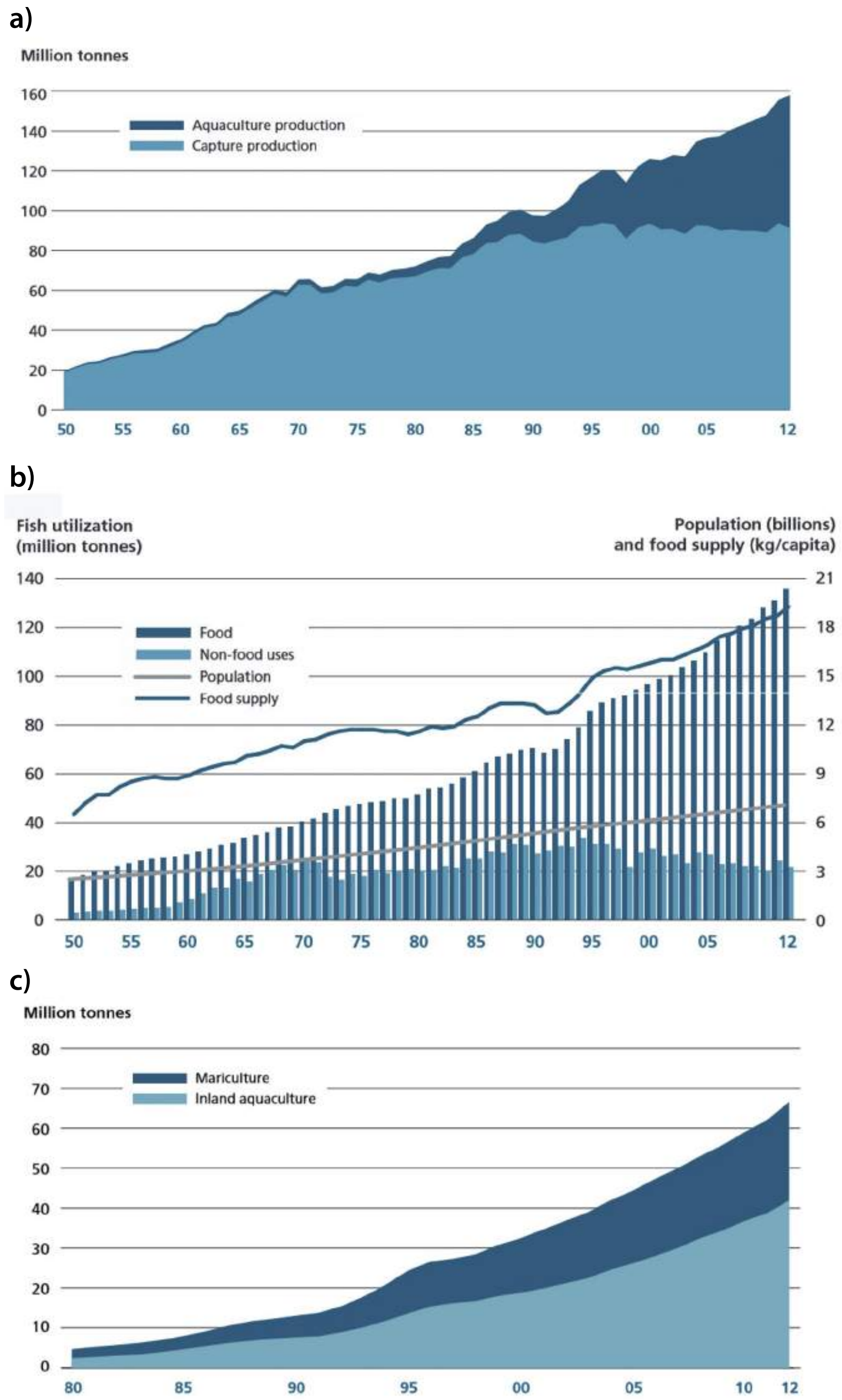

Figure 4.5.1 a) World capture fisheries and aquaculture production, 1950–2012; b) world fish utilization and supply, 1950–2012; and c) global inland aquaculture and mariculture production, 1980–2012 (source: FAO, 2014a).

Climate change poses an additional risk to the initiatives underway to supply more than 200 million tonnes of fish for human consumption by 2050. The best laid plans for better management of capture fisheries and technical improvements in aquaculture could be affected by changes to the environment beyond the control of managers. One of the main consequences of increased greenhouse gas (GHG) emissions – warming of the world's ocean – has the potential to disrupt these plans. Because 87% of capture fisheries production (FAO, 2014a), and 47% of aquaculture production (FAO, 2016), comes from marine and coastal (hereafter marine) waters, any such disruptions are expected to have a significant effect on global seafood production. The potential effects may be even more significant because there are limits to the expansion of inland aquaculture (which currently accounts for 90% of finfish aquaculture production) due to foreshadowed restrictions on availability of fresh water (FAO, 2014a). This means that a greater percentage of the additional 75 million tonnes of fish needed by 2050 will have to come from marine aquaculture (hereafter 'mariculture').

Here, we review assessments of the projected effects of ocean warming on the contribution of marine fisheries and mariculture to food security and livelihoods. We focus mainly on developing country regions because they have the greatest dependency on fish for nutrition (Bell *et al.,* 2009; Davies *et al.,* 2009 ; Kawarazuka and Béné, 2011; Wanyonyi *et al.,* 2011; Lam *et al.,* 2012; Barnes-Mauthe *et al.,* 2013; FAO, 2014a; Portner *et al.,* 2014). This is not to say that the effects of ocean warming are insignificant for fisheries in developed countries. They are significant, as demonstrated by several studies from the North Atlantic and North Pacific (e.g. Cheung *et al*., 2012; Hollowed *et al*., 2013; Colburn *et al*., 2016; Hare *et al*., 2016), and by our summary of global assessments of the effects of ocean warming on marine fisheries (para 4.5.5). Alterations in fish catch from developed countries, such as Japan and those in the EU and North America, due to ocean warming can also be expected to have impacts on food security in the developing country regions by influencing exports to developed countries.

We begin with a brief summary of the expected effects of ocean warming on marine fish species and ecosystems, report the projected effects of such changes on the production of marine fisheries and mariculture, and conclude with the implications and practical adaptations to minimize the risks and capitalize on the opportunities.

Our analysis is limited to ocean warming and does not consider the effects of ocean acidification on production from marine fisheries and mariculture; such effects are discussed by Hilmi *et al.* (2015) and have been shown to vary with taxa and region. The effects of global warming on inland aquaculture in general have been assessed by De Silva and Soto (2009) and De Silva (2012b); specific cases have also been considered by Phan *et al.* (2009), Nguyen *et al.* (2014, 2015) and Li *et al.* (2016), for example.

We found winners and losers. Projected changes in the distribution and abundance of species, primary productivity supporting marine fisheries, and environmental conditions suitable for mariculture and proliferation of parasites, pests and diseases, indicate that fish production is likely to increase in some countries/regions and decrease in others (Harvell *et al.,* 1999; Allison *et al.,* 2009; Barange *et al.,* 2014; FAO, 2014a; Hoegh-Guldberg *et al.,* 2014).

4.5.2 Effects of ocean warming on marine species and ecosystems

Although some fish species can respond to the warming of the ocean described in Sections 3.11 and 3.12 by adjusting *in situ* (Maggini *et al.,* 2011), the most widely documented impacts of climate change on species supporting marine fisheries are shifts in distributions to areas of preferred temperature (Last *et al.,* 2011; Pinsky *et al.,* 2013; Jung *et al.,* 2014). Such range shifts are due largely to the direct effects of changes in temperature on the physiology and behaviour of species (Pörtner, 2001; Pörtner and Farrell, 2008; Pratchett *et al.,* 2010; Section 3.11) (Figure 4.5.2). In particular, changes in temperature can have significant effects on the timing of reproduction and development duration (phenology) and, therefore, dispersal of eggs or larvae. Temperature changes also affect individuals and populations through altered rates of metabolism, consumption and assimilation (Buckley, 2013). In addition, changes in ocean temperature affect the size and hence productivity of species (Cheung *et al.,* 2013a), which may require changes in management (Audzijonyte *et al.,* 2013, 2014, 2016).

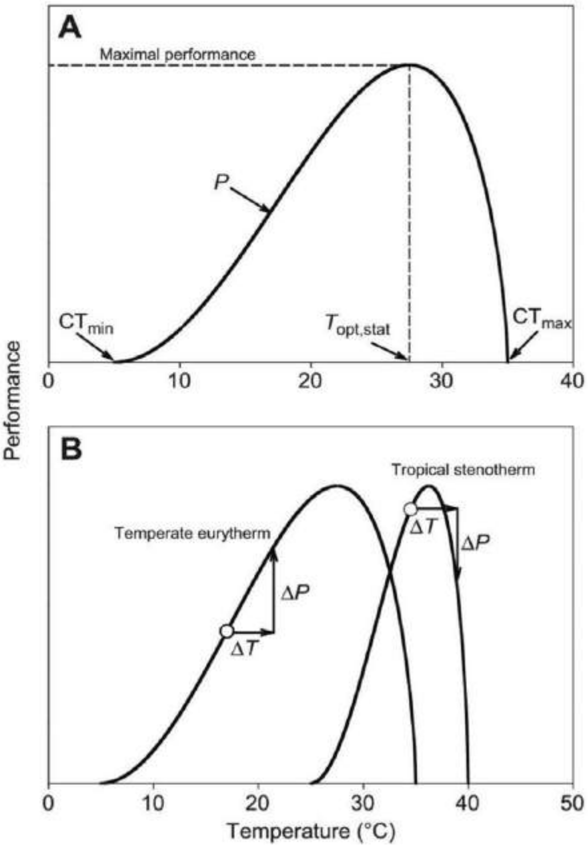

Figure 4.5.2 (A) Thermal performance curves typically have a characteristic, unimodal shape exemplified by performance as a function of body temperature. Often the reaction norm's peak is shifted to the right of centre, such that performance increases relatively slowly up to T_{opt}, but decreases rapidly above T_{opt}. Although performance curves are generally modelled as functions, performance is typically only measured at a small number (4–8) of discrete temperatures in empirical studies. (B) A given increase in temperature (ΔT) results in an increase in nominal performance (ΔP) for a temperate fish and shellfish species, but the same temperature increase results in a decrease in nominal performance for a tropical species capable of living or surviving within a narrow temperature range (source: Dowd *et al.,* 2015).

In general, marine species are 'tracking' ocean warming by moving towards the poles, resulting in range extensions at poleward boundaries of their distributions (analogous to species invasions) and range contractions at equatorward boundaries (analogous to local species extinctions) (Chen *et al.,* 2011; Poloczanska *et al.,* 2013; Bates *et al.,* 2014; Section 3.11). These changes in distribution are evident in waters surrounding all continents, and for a wide range of marine organisms, e.g. phytoplankton (Thompson *et al.,* 2009, 2015; Section 3.2), seaweeds (Wernberg *et al.,* 2011; Nicastro *et al.,* 2013; Section 3.3), invertebrates (Pitt *et al.,* 2010; Chen *et al.,* 2011) and fish (Cheung 2008, 2010; Last *et al.,* 2011; Sunday *et al.,* 2015; Sections 3.11 and 3.12).

Ocean warming can also have indirect effects on fisheries production by altering primary productivity (Le Borgne *et al.,* 2011; Blanchard *et al.,* 2012; Barange *et al.,* 2014) and the benthic habitats that support fisheries (Hoegh-Guldberg *et al.,* 2011; Waycott *et al.,* 2011). Ocean warming can increase stratification of the water column (Ganachaud *et al.,* 2011; Hoegh-Guldberg *et al.,* 2014), reducing upwelling and the availability of nutrients required for the growth of phytoplankton at the base of the food webs supporting fisheries (Le Borgne *et al.,* 2011). The contributions of some benthic habitats to fisheries production are particularly vulnerable to ocean warming. In particular, the corals that provide habitat for fish and invertebrates in many tropical developing countries are being adversely affected by bleaching due to elevated sea surface temperature (SST) (Pratchett *et al.,* 2008; Hoegh-Guldberg *et al.,* 2011, 2014; Ainsworth *et al.,* 2016; Section 3.8).

Changes in distribution, phenology and abundance of marine species related to the direct and indirect effects of ocean warming can have significant impacts on the structure and function of ecosystems (Tylinakias *et al.,* 2008, Johnson *et al.,* 2011; Marzloff *et al.,* 2016). Where shifts in the distributions or abundances of species occur at different times and rates (Sunday *et al.,* 2012, 2015; Pecl *et al.,* 2014), links between species can be broken allowing, for example, some species to escape from predators and exploit a wider range of environments (Jaeschke *et al.,* 2012; Section 3.11).

4.5.3 Effects on fish supply

Changes in the production of marine fisheries and mariculture due to the direct and indirect effects of ocean warming need to be considered together with other factors affecting the supply of fish (Gillett and Cartwright, 2010; Bell *et al.,* 2011a; Hall *et al*., 2011). In many developing countries, rapid population growth is driving a gap between sustainable fish harvests and the amount of fish needed to contribute to good nutrition (see para. 4.5.3.1). The effects of ocean warming have the potential to widen or reduce this gap. In other developing countries, trade policies that result in the majority of fish being exported limit local supplies of fish and overshadow the expected effects of ocean warming on availability of fish per capita (Delgado *et al*., 2003; Béné and Heck, 2005; Hobday *et al.,* 2015). Fisheries management approaches can also have a profound effect on fish supply and the effects of poor management are likely to exceed the effects of ocean warming for many years to come.

Below, we summarize the importance of fish to food security and livelihoods, and the expected effects of projected ocean warming on marine fisheries, in five developing country regions. Several of these projections rely on model forecasts, which remain susceptible to some uncertainty and bias (Cheung *et al*., 2016b). Therefore, a measure of caution is needed in applying percentage projected changes to fish catch derived from these models. We also summarize the expected effects of ocean warming on mariculture worldwide and the key findings from several global assessments of the effects on marine fisheries.

4.5.3.1 Pacific Islands

Traditionally, Pacific Island coastal communities have had some of the highest rates of fish consumption in the world (3-4 times the global average) and relied on fish to provide 50-90% of their dietary animal protein (Bell *et al.,* 2009). Much of this fish has come from subsistence coastal fisheries based on coral reefs (Dalzell *et al.,* 1996; Pratchett *et al.,* 2011). Rapid population growth in several Pacific Island countries is expected to alter this situation. By 2035, population growth alone will reduce the availability of fish per capita below the 35 kg of fish per person per year recommended for good nutrition of Pacific Island people (SPC, 2008; Bell *et al*., 2009). The direct effects of increased SST on fish metabolism projected to occur under a high GHG emissions scenario, and the indirect effects of ocean warming on the quality of coral reef fish habitats as a result of increased coral bleaching and ocean acidification, are expected to reduce production by ~20% by 2050 and exacerbate this situation (Bell *et al.,* 2011b, 2013; Pratchett *et al.,* 2011).

Table 4.5.1 Estimates of coastal fisheries production based on coral reef area for selected Pacific Island countries, the amount of fish needed for food in 2020 and 2035, and expected surplus (+) or deficit (-) in fish supply, relative to the recommended 35 kg per person per year or traditionally higher levels of fish consumption, for each country for each period. The quantities of tuna needed to fill the gap in fish supply and the percentage of average national tuna catch required to provide this tuna in 2020 and 2035 is also shown (after Bell *et al.,* 2015a).

Country	Coastal fish production (tonnes.y^{-1})[a]	Fish needed for food (tonnes)[b]		Surplus (+)/ deficit (-) coastal fish (tonnes)[c]		Tuna needed for food (tonnes)		Average tuna catch (tonnes)[d]	Percentage of average tuna catch required[e]	
		2020	2035	2020	2035	2020	2035		2020	2035
PNG[f]	98,760[g]	117,000	169,100	-18,200	-73,800	18,200	63,200[h]	597,657	3.0	10.6
Solomon Is[i]	27,610[j]	25,400	35,600	2,210	-7,990	0	7,990	144,454	0	5.5
Kiribati[k,l]	12,960	10,900	13,400	2,060	-890	4,900	6,370	330,177	1.5	1.9
Nauru[k]	130m	700	800	-570	-670	570	670	99,033	0.6	0.7

a Based on median estimates of sustainable fish harvests of 3 tonnes per km^2 (Newton *et al.,* 2007)

b Based on estimates in supplementary material for Bell *et al.* (2015a)

c Calculations for 2035 include a 2-5% reduction in the production of coastal fisheries due to the effects of climate change (Pratchett *et al.,* 2011)

d Based on the 5-year average total tuna catch (all gear types) for the period 2009-2013, rounded to the nearest tonne.

e Assumes that all tuna will come from industrial fishing within the EEZ and does not allow for catches from nearshore FADs, the contribution of bycatch, or the effects of climate change on tuna catch (Bell *et al.,* 2013)

f Fish needed for food based on providing different quantities per capita for the urban, coastal/riverine and inland populations of PNG (see Bell *et al.,* 2015a)

g Includes 17,500 tonnes of freshwater fish.

h Allows for freshwater pond aquaculture to supply 1 kg of fish per person per year by 2035 (Bell *et al.,* 2011b), reducing the overall deficit in fish of 73,800 tonnes to 63,200 tonnes

i Fish needed for food based on recommended fish consumption of 35 kg per person per year (see Bell *et al.,* 2015a)

j Includes 2000 tonnes of freshwater fish

k Fish needed for food based on recent, traditional levels of fish consumption for rural and/or urban populations (Bell *et al.,* 2009)

l National average incidence of ciguatera fish poisoning, renders several species of coral reef fish unfit for human consumption at some locations

m Based on reconstructions of catches of coastal fish by the 'Sea around us' project, University of British Columbia

The rich tuna resources of the region provide a potential solution. Allocation of a relatively small percentage of the tuna catch from the exclusive economic zones of Pacific Island countries would provide the additional fish required (Bell *et al.,* 2015a) (Table 4.5.1). However, the effects of ocean warming under a high GHG emissions scenario will make this solution easier to apply in some countries than in others. Preliminary modelling of the effects of the most abundant tuna species in the region, skipjack tuna *Katsuwonas pelamis* (Figure 4.5.3), indicates that there is likely to be an eastward shift in the relative abundance of this important fish species (Bell *et al.,* 2013; Lehodey *et al.,* 2013) (Figure 4.5.4). Over time, it should be easier for coastal communities in Kiribati, Cook Islands and French Polynesia in the central and eastern Western and Central Pacific Ocean (WCPO) to catch tuna than it is for coastal communities in the western WCPO, e.g. in Papua New Guinea (PNG) and Federated States of Micronesia. However, there will still be large (albeit reduced) quantities of tuna available in the western WCPO in the future for both export and domestic food security (Figure 4.5.4).

Figure 4.5.3 Women selling skipjack tuna caught by small-scale fishers around Tarawa Atoll, Kiribati. © Johann Bell.

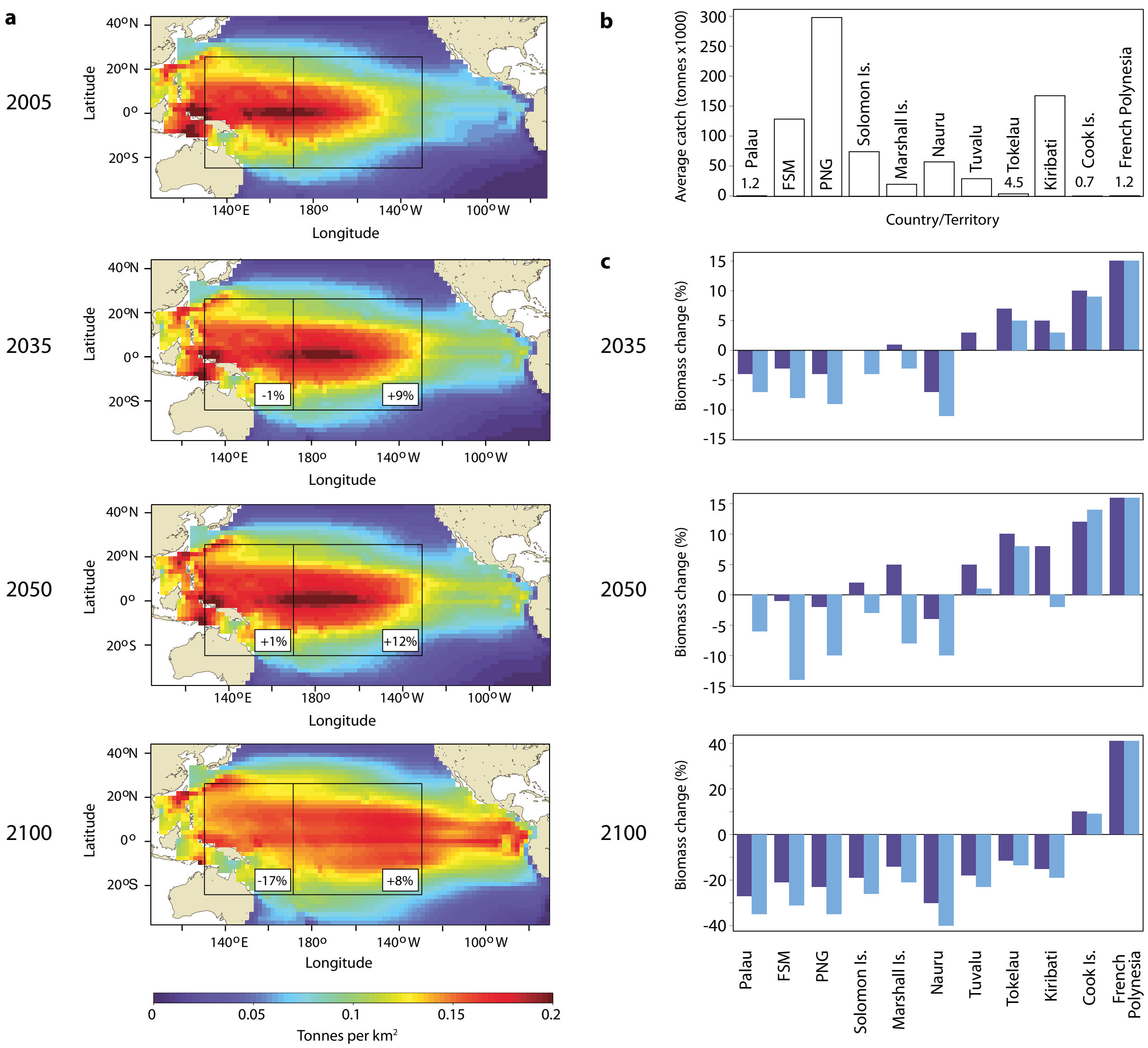

Figure 4.5.4 Projected distributions of skipjack tuna biomass across the tropical Pacific Ocean under the IPCC SRES A2 emissions scenario. (a) Simulations for 2005, 2035, 2050 and 2100 derived from the SEAPODYM model (Lehodey *et al.,* 2013), including projected average percentage changes for the boxed areas east and west of 170°E. (b) Recent average annual catches of skipjack tuna (2000–2010) from exclusive economic zones of selected Pacific Island countries and territories; FSM = Federated States of Micronesia, PNG = Papua New Guinea. (c) Estimated changes in biomass relative to virgin stock levels (dark blue), and incorporating fishing effort 1.5 times greater than the average for 1990–1999 (light blue), for 2035, 2050 and 2100 (source: Bell *et al.,* 2013).

4.5.3.2 South-east Asia

Based on the 'Sea Around Us[2]' catch data (Pauly and Zeller, 2016), total marine fisheries catch in South-east Asia increased from around 2.5 million tonnes per year in the 1950s to more than 25 million tonnes in the 1990s. Catches have since stabilized at around that level, with a decreasing trend in the last decade.

The increase in marine and freshwater fish catch, and in the production from freshwater aquaculture and mariculture, has enabled per capita fish consumption in South-east Asia to increase from ~13 to 32 kg per person per year since 1961 (FAO, 2012). As a result, present-day fish consumption in the region is well in excess of the global average of ~19 kg per person per year (FAO, 2014a). Nevertheless, many fish stocks in the region have been over-exploited, with resource abundance at the end of the 20th Century being 5-30% relative to the level in the 1950s (Silvestre *et al.,* 2003). Correspondingly, marine fisheries in the South China Sea area are now characterized by high numbers of fishing vessels and collectively employ millions of people (Table 4.5.2).

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[2] www.seaaroundus.org

Table 4.5.2 Summary of approximate number of fishing vessels and the number of people employed in marine and coastal fisheries (from 2000–2012, depending on data availability), together with estimated landed value in 2012, in selected countries/areas in the South China Sea (SCS) (source: Dyck and Sumaila, 2010; ; Sumaila and Cheung, 2015)

Country/Area	No. fishing vessels	No. people employed	Landed value (USD x 1000)
China - northern SCS	92,300	648,800	9,807,035
Hong Kong	4,000	8,800	296,774
Indonesia	76,800	320,000	1,084,985
Malaysia - east coast, Sabah, Sarawak	24,600	56,000	1,219,133
Philippines –regions NCR, CAR, I, III, IV	117,000	627,000	817,335
Taiwan	231,600	271,600	2,731,292
Thailand	58,100	168,700	1,286,627
Vietnam	129,500	540,000	4,384,180

Maintaining the significant contribution of marine fisheries and mariculture to per capita fish consumption and livelihoods in South-east Asia will be a formidable challenge as the ocean continues to warm. It will depend greatly on future GHG emissions and the level of effective fisheries management (Sumaila and Cheung, 2015). Under a high 'business as usual' emissions scenario (RCP8.5), harvests from marine fisheries in South-east Asia are projected to decrease by 10% to >30% by 2050 relative to 1970-2000, depending on the country (Figure 4.5.5) (Cheung *et al.,* 2016a). The reduced harvests are expected to be driven by local extinctions as species change their distributions in response to the increases in water temperature. Overall, loss of more than 20% of the original fish species richness in South-east Asia is projected by 2050 (Jones and Cheung, 2015).

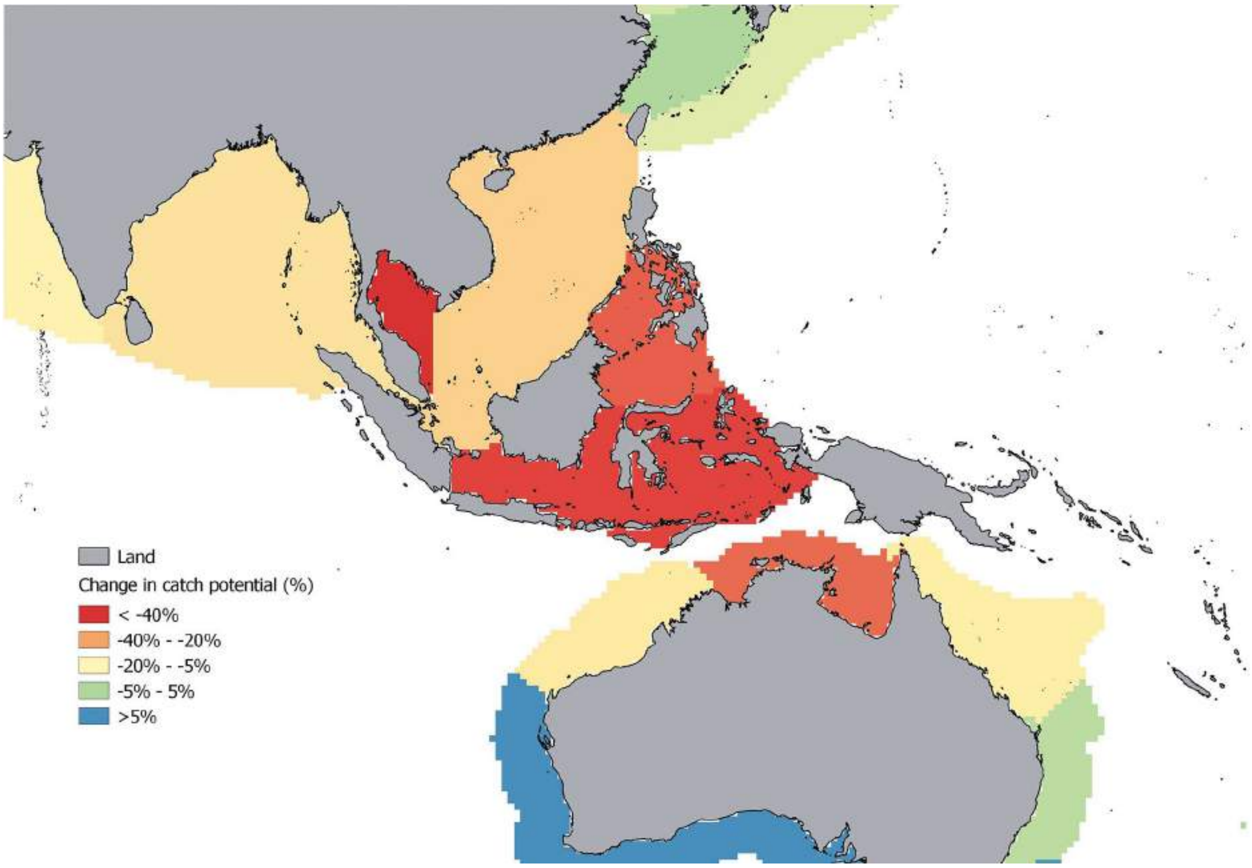


Figure 4.5.5 Multi-model ensemble projections of mean percentage changes in potential fish catch from South-east Asia by 2050, relative to recent catch levels (1971–2000), under the RCP 8.5 emissions scenario (source: Cheung *et al.,* 2016a).

Under-performing fisheries management in the region will exacerbate the impact of climate change. For example, a recent assessment of the effects of a business as usual emissions scenario combined with status quo levels of fisheries exploitation in the South China Sea, using trophodynamic models, projected that the biomass of several groups of fish species (including groupers, sharks, threadfin breams and croakers) could decrease by 50% or more (Sumaila and Cheung, 2015). On the other hand, a low GHG emissions scenario can reduce the impacts from climate change and ocean acidification on the marine ecosystem. Simultaneously, substantial reduction of fishing will rebuild over-exploited fish stocks. Both of these measures would be expected to have a positive impact on the biomass of most stocks. However, reducing effort would result in lower catches for several of the main species while stocks are rebuilt, creating an even wider gap in fish supply to be filled by mariculture (and freshwater aquaculture) (see Para. 4.5.4).

4.5.3.3 East Africa and Western Indian Ocean

The high population density in coastal and small island developing states in East Africa and the Western Indian Ocean (WIO) relative to coral reef area (Table 4.5.3), coupled with poverty-driven dependence on fishing for food and cash, has caused degradation of these important fish habitats through over-harvesting and destructive fishing (Wells *et al.,* 2007; Wafar *et al.,* 2011; Samoilys *et al.,* 2015). As a result, fisheries based on coral reefs now only make a modest contribution to per capita fish consumption, typically less than 5 kg per year, for communities living within 25 km of the coast (Table 4.5.3). Seychelles and Mayotte are the exceptions. By 2030, coral reefs will provide even less fish per person due to predicted population growth. Ocean warming, which has caused widespread coral mortality (Obura, 2005; Ateweberhan *et al.,* 2011) and reduced productivity of coral reef fisheries (Graham *et al.,* 2007) in the WIO, is exacerbating the situation. Consequently, small-scale fishers in the region are being encouraged to transfer more of their effort offshore to tuna and other oceanic fish species. Because tuna and other oceanic species fall within the mandate of the Indian Ocean Tuna Commission, increased access to some of these fish stocks, e.g. yellowfin tuna, by small-scale fishers

Table 4.5.3 Estimated availability of coral reef fish per capita (kg) in 2015 and 2030 for coastal populations in countries from East African and the Western Indian Ocean.

Country	**Coral reef area (km^2)^a**	**Estimated reef fish production (tonnes yr^{-1})^b**	**Total human population in 2015^c**	**2015**		**2030**	
				Population within 25 km of coast^d	**Reef fish per capita (within 25 km of coast) (kg/person/yr)**	**Population within 25 km of coast^e**	**Reef fish per capita (within 25 km of coast) (kg/person/yr)**
Somalia	710	4,260	10,787,000	3,290,035	1.29	5,030,365	0.85
Kenya	1724	10,344	46,050,000	2,809,050	3.68	3,990,132	2.59
Tanzania	3580	21,480*	53,470,000	7,271,920	2.95	11,278,072	1.90
Mozambique	1860	11,160	27,978,000	9,148,806	1.22	13,549,245	0.82
Madagascar	2230	13,380	24,235,000	5,622,520	2.38	8,342,720	1.60
Seychelles	1690	10,140	96,000	96,000	105.63	101,000	100.40
Comoros	430	2,580	788,000	788,000	3.27	1,081,000	2.39
Mayotte (France)	985	5,910	240,000	240,000	24.63	344,000	17.18
La Reunion (France)	18.6	112	861,000	861,000	0.13	947,000	0.12
Mauritius	870	5,220	1,273,000	1,273,000	4.10	1,310,000	3.98

* Likely to be an over-estimate because large areas of Tanzania's reefs have been destroyed by dynamite fishing (Wells, 2009; Slade and Kalangahe, 2015); a = sources: UNEP (2009) except Kenya (Samoilys *et al.,* in press), Reunion (Nicet *et al.,* 2015); Mayotte (Andréfouë *et al.,* 2009); b = calculated as total coral reef area in km x 6 tonnes (based on 6.09 tonnes km^{-2} yr^{-1} for Kenya in 2006 (Samoilys *et al.,* in press); c = UN World Population Prospects: 2015 Revision Vol. 1; d = source: UNEP (2009); e = UN World Population Prospects: 2015 Revision Vol. 1.

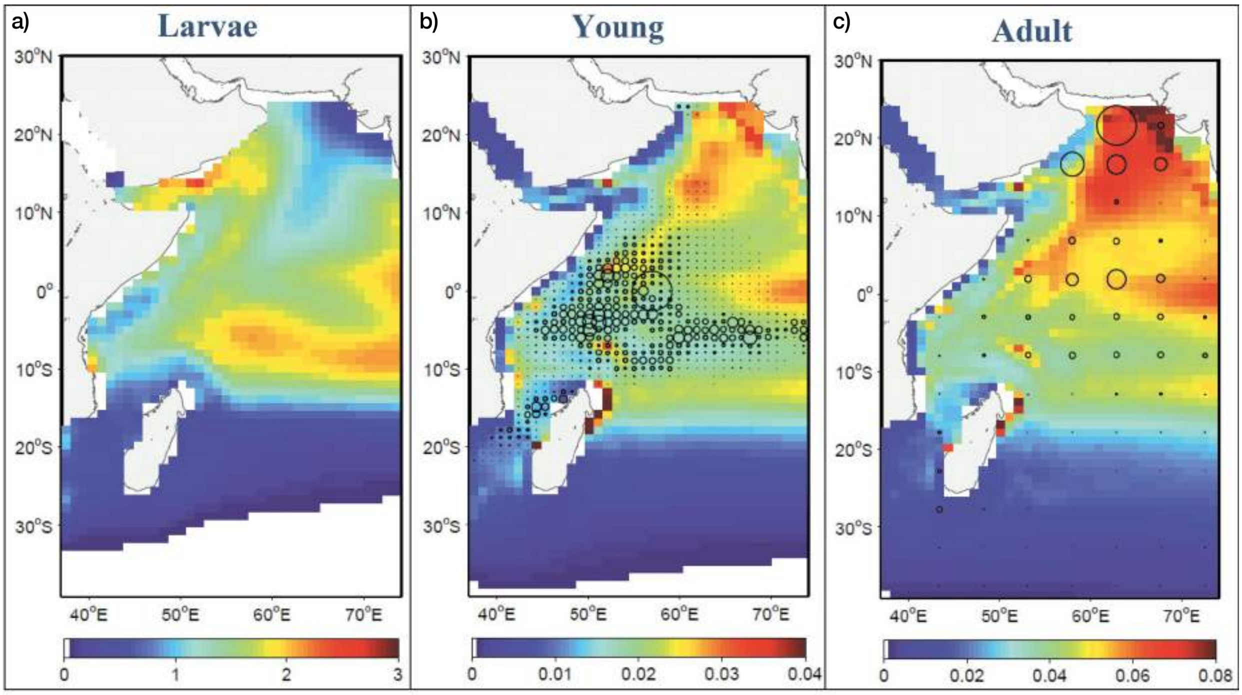


Figure 4.5.6 Reconstruction of the history of yellowfin tuna dynamics and fisheries in the Western Indian Ocean using the SEAPODYM model and results presented in Senina *et al.* (2015). The panels show the average spatial distribution of yellowfin tuna density for three different life history stages: a) larvae, b)young fish caught by purse seine, and c) adults caught by longline. The locations of catches of young fish made by purse seine are shown with circles on panel b) (largest circle radius corresponds to a catch of 200 tonnes) and the locations of catches of adults by longline are shown with circles on panel c) (largest circle radius corresponds to a catch of 10 tonnes).

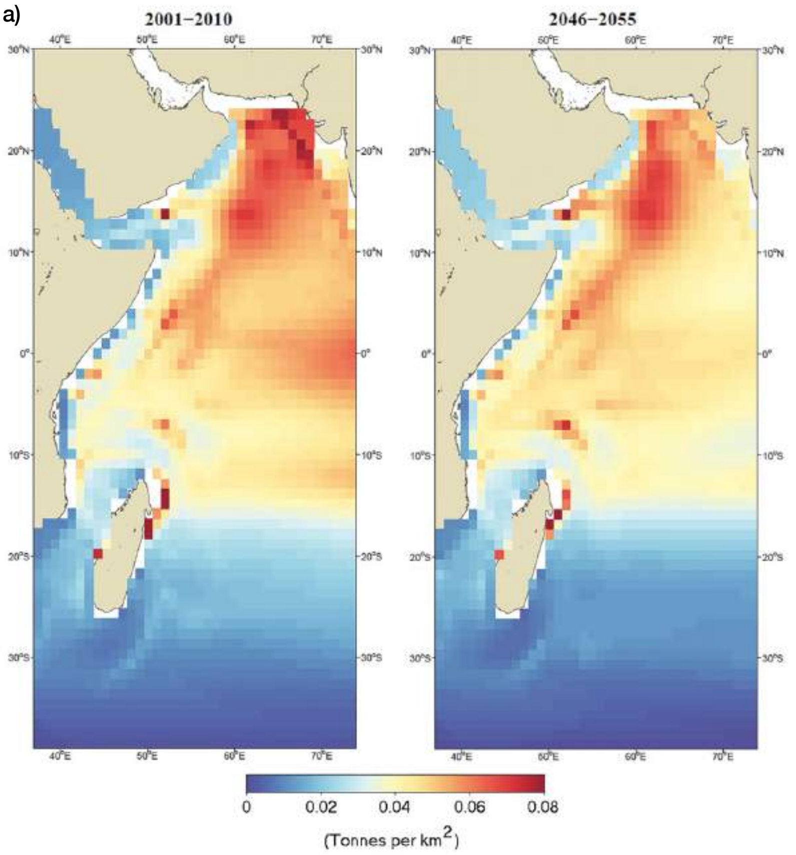
will need to be accommodated through reallocation of a proportion of the catch of industrial fleets so that no net increase in catch occurs. However, some oceanic fish species in the WIO, such as skipjack tuna and kawakawa tuna, are not currently overfished and not subject to overfishing (IOTC, 2015).

Ocean warming is likely to affect this recommended adaptation to some extent. For example, preliminary modelling of the effects of higher water temperatures on yellowfin tuna, one of the large pelagic fish species commonly caught by small-scale fishers in the WIO (Herrera and Pierre, 2010; Kaplan *et al.,* 2014), indicates that substantial changes in the distribution and abundance of this species are likely to occur in the future (Senina *et al.,* 2015). Relatively good confidence can be placed in these projections because the SEAPODYM model (Lehodey *et al.,* 2008) used for the simulations predicts the historical catch of yellowfin tuna in the main fishing grounds well (Figure 4.5.7).

The modelling indicates that stronger stratification will occur in the upper water column, leading to reduced production of phytoplankton, zooplankton and micronekton in the food web that supports yellowfin tuna in tropical regions of the WIO. The simulations show that distribution of larval yellowfin tuna is likely to become less dense in the equatorial region and increase in the western Arabian Sea by the middle of the century. These changes are driven by a favourable increase in water temperature in the western Arabian Sea and an unfavourable and strong decrease in phytoplankton (primary production) in the equatorial region. By 2050, the density of adult yellowfin tuna is projected to decrease throughout the WIO, with the greatest decreases occurring from Kenya southward (Figure 4.5.6). Simulations at a higher resolution are now needed to confirm the results from the preliminary modelling.

4.5.3.4 West Africa

Although annual per capita fish consumption in most countries in West Africa is lower than the global average (Table 4.5.4), several nations in the region have a relatively high dependence on fish and fisheries for food and income due to the scarcity of other sources of animal protein (Brashares *et al.,* 2004; Smith *et al.,* 2010). Fish is also an important source of the essential micronutrients and vitamins missing from local staples (rice, maize and cassava), in particular, iron, iodine, zinc, calcium and vitamins A and B (Roos *et al.,* 2007; Kawarazuka, 2010; Golden *et al.*, 2016).



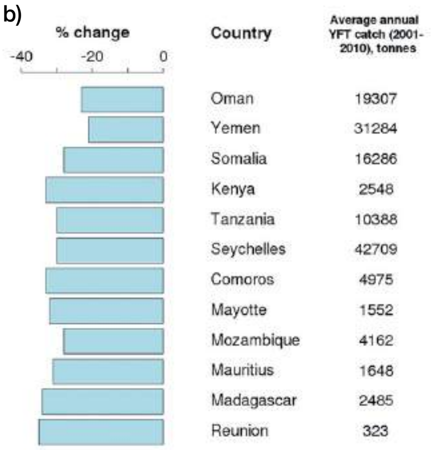


Figure 4.5.7 a) Projected changes in distribution of adult yellowfin tuna biomass in the western Indian Ocean between 2005 and 2050 for a 'business as usual' high emissions scenario (IPCC RCP8.5) using SEAPODYM and the IPSL Earth model forcing simulations (source: Senina *et al.,* 2015); b) estimated changes in biomass relative to original unfished stock levels between 2005 and 2050, and estimated average catch of yellowfin tuna (YFT) for the exclusive economic zones of selected countries in East Africa/Western Indian Ocean. Catch data were obtained from the Indian Ocean Tuna Commission and combine both industrial catches from the geo-referenced catch-and-effort dataset and artisanal catches from the nominal catches dataset (see http://iotc.org/documents/all-ce-files and http://iotc.org/documents/nominal-catch-species-and-gear-vessel-flag-reporting-country, respectively, for an explanation of possible errors involved in combining these datasets).

Table 4.5.4 Estimated annual average per capita food fish supply in West African countries (2007–2011), together with the average volume of fish taken by distant water fishing nations (DWFNs) licensed to fish in a nation's exclusive economic zone, and volume of fish exported, per year.

Country	Fish supply (kg/capita/year)[a]	Fish caught by DWFNs (tonnes)[b]	Fish exports (tonnes)[c]
Sierra Leone	33.2	34, 900	5,600
Gambia	28.9	63,900	3,300
Ghana	26.5	1,700	22,400
Senegal	25.2	281,000	108,200
Côte d'Ivoire	17.5	91,500	40,600
Nigeria	16.0	17,000	22,700
Cape Verde	11.1	3,300	14,500
Guinea	9.4	555,300	7,600
Mauritania	9.2	1,640,200	149,700
Togo	6.8	33,000	1,500
Benin	3.6	3,500	600
Liberia	3.2	71,400	100
Guinea Bissau	1.8	198,600	4,400

[a] based on fish food supply data (source: FAO, 2015)

[b] annual average catch between 2006 and 2010 extracted from the Sea Around Us catch reconstruction database (www.seaaroundus.org)

[c] source: FAO (2016) (http://www.fao.org/fishery/statistics/global-commodities-production/query/en)

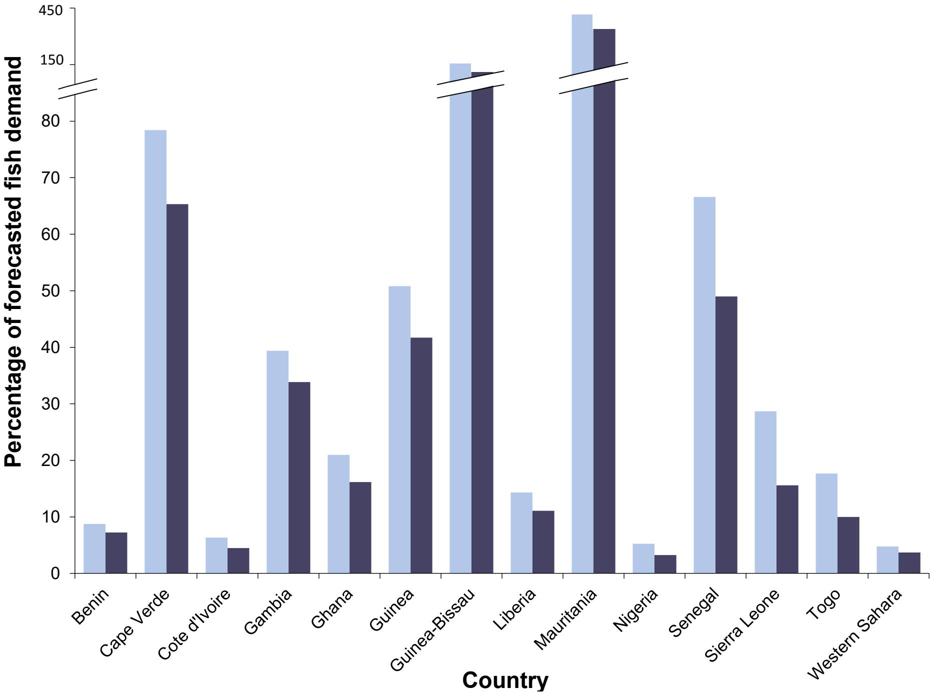


Figure 4.5.8 Percentage of forecasted fish demand expected to be supplied by catches from the wild in West African countries by the 2050s under a high emissions scenario (SRES A1B) (dark blue) and assuming that emissions can be reduced to the year 2000 level (light blue). Future fish demand was estimated using current per capita fish consumption and projected national population growth (United Nations, 2009).

Some countries in the region gain government revenue from licensing distant water fishing nations (DWFNs) targeting small pelagic fish, squid and cuttlefish within their exclusive economic zones, or from exporting substantial quantities of fish (Table 4.5.4). Although revenues from licences and exports can boost purchasing power to buy food, there is concern that the focus on revenue has been at the expense of long-term economic development and food security (Trouillet *et al.,* 2011; Belhabib *et al.,* 2013, 2014).

Population growth is expected to result in a significant increase in demand for fish in West Africa. For example, twice as much fish will be needed by Benin and Liberia by 2050 (Lam *et al.,* 2012). Regrettably, present-day fisheries management, trade and distribution practices will not be able to deliver the fish required in the future (Delgado *et al.*, 2003, Béné and Heck, 2005). Modelling also indicates that there will be a shortfall in fish supply for all countries in West Africa due to climate change by 2050 (Lam *et al*., 2012).

Figure 4.5.9 Fishermen in Cape Verde off the western coast of the African continent. © Dyhia Belhabib.

Continued high GHG emissions are expected to increase the gap further (Figure 4.5.8) (Lam *et al.,* 2012), with the largest differences between forecasted demand for fish and projected fish catch occurring in Benin, Côte d'Ivoire, Nigeria and Western Sahara. Across the region, the potential reduction in total annual landings by the 2050s under a high emissions scenario is estimated to be 670,000 tonnes (i.e. a reduction of 26% compared to current levels) (Lam *et al.,* 2012). For the EEZs of the six countries located closest to the equator (Ghana, Côte d'Ivoire, Liberia, Togo, Nigeria and Sierra Leone), catches are projected to be reduced by around 50%. The projected decreases are due to the expected shifts in distribution of fish species in response to higher water temperatures, and a decrease in net primary productivity in the tropical region by the 2050s (Sarmiento *et al.,* 2004; Bopp *et al.,* 2013).

Reduced future landings of fish in West Africa are not only expected to have implications for food security, they will affect the economies of countries that are highly dependent on fish exports, such as Mauritania and Senegal. In this region, narrowing the gap in the fish needed for local food security and reducing the burden involved in importing fish will depend on rebuilding overfished or depleted stocks, reducing post-harvest losses and ensuring that a sufficient proportion of the region's rich small pelagic fish resources are allocated for local consumption (FAO, 2014a). It will also depend on increasing the currently low capacity of fishing communities (Belhabib *et al.,* 2016) to adapt to climate change (Figure 4.5.9).

4.5.3.5 Central and South America

Consumption of fish is relatively low in several Latin American countries (Flores, 2014) due to ready access to other animal protein and cultural preferences (Table 4.5.5). However, the region makes a substantial contribution to the global supply of fish, and the supply of fish meal for mariculture, freshwater aquaculture and animal husbandry (Gasalla and Castro, 2016). Overall, the wide variety of marine fisheries in the region, which range from the world's largest fishery (Peruvian anchovy) to squid fisheries in both the Pacific and Atlantic Oceans, to numerous small-scale coastal fishing activities, have yielded annual catches exceeding 10 million tonnes for several decades (FAO, 2016).

Harvests from the large fisheries in Peru and Chile, and fisheries in Brazil and Argentina, vary significantly from year to year, however, due to the profound effects of the El Niño Southern Oscillation (ENSO) (Bakun, 1993;

Table 4.5.5 Recent population, total fish catch and patterns of per capita fish consumption for selected countries in Latin America (source: FAO, 2014a; Flores, 2014).

Country	Population in 2012 (million)	Total fish catch in 2012 (tonnes)	National fish consumption (person^{-1} yr^{-1}) (kg)	Trend in fish consumption
Argentina	41,900,000	7380,00	5.0	Stable
Brazil	198,700,000	842,900	11.2	+ 6 kg in 10 years
Chile	17,460,000	2,572,881	6.4	Stable
Colombia	47,700,000	75,651	6.1	+2.1 kg in 6 years
Guyana	800,000	3,900	34.0	Stable
Honduras	7,930,000	8,300	3.5	Increasing
Mexico	120,800,000	1,581,579	13.2	Stable
Nicaragua	5,920,000	33,850	7.5	Stable
Panama	3,840,000	176,649	25	Stable
Perú	28,990,000	4,807,923	19.0	Increasing
Uruguay	3,400,000	76,162	6.0	Stable
Venezuela	29,950,000	213, 069	6.5	Increasing

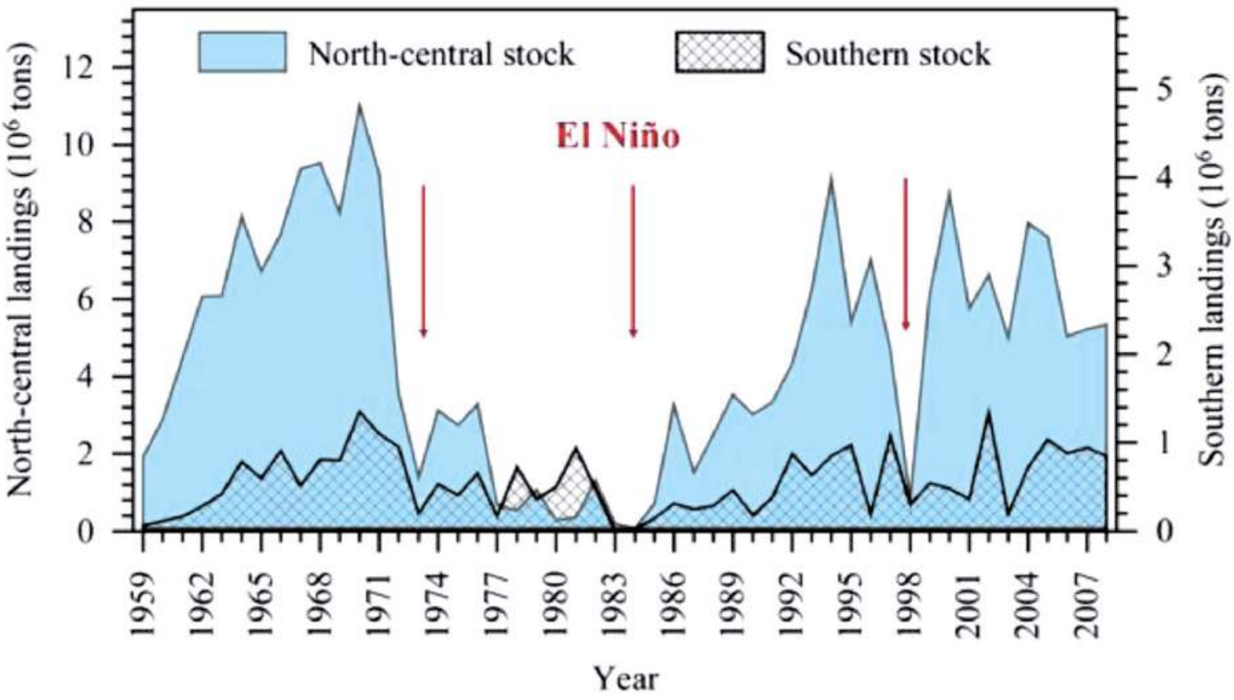


Figure 4.5.10 North-central and southern stock Peruvian anchovy landings between 1959 and 2008 in relation to El Niño events (source: IMARPE).

Sharp and McLain, 1993; Garcia *et al.,* 2004). This is illustrated best by the effects of ENSO on the production of Peruvian anchovy: catches fall dramatically during El Niño events when weakening of the south-east trade winds limits the upwelling of the nutrient-rich waters required to support a high biomass of this species, but increase dramatically when strong upwelling recommences under La Niña conditions (Daw *et al.,* 2009; Arias Schreiber *et al.,* 2011) (Figure 4.5.10). It remains to be seen whether ocean warming will change the effects of La Niña events on the Peruvian anchovy fishery and the strength of the upwelling involved. It is interesting to note, however, that Barange *et al.* (2014) project declines in fish production in Peru based on a model incorporating upwelling systems. Maximizing the sustainable benefits of this globally significant fishery will continue to depend on applying the various strategies identified to cope with great variation in abundance due to climatic variability (Arias Schreiber *et al.,* 2011).

In contrast, ocean warming and the knock-on effects on ocean circulation and stratification on primary production (Hoegh-Guldberg *et al.,* 2014) are expected to disrupt fishing patterns for a variety of other marine fisheries in the region. The effects of ocean warming are expected to be particularly strong in South Brazil and Uruguay (Popova *et al.,* 2016). Elsewhere, the impacts of ocean warming are expected to be mixed. For example, catches of 10 of the top 12 fish species caught in Mexico are projected to decline by 2050 under a high GHG emissions scenario (Sumaila *et al.,* 2014); landings by small-scale fisheries are projected to decrease in tropical areas as species move poleward in response to thermal stress (Cheung *et al.,* 2010) and sea-level rise reduces the extent of coastal fish nursery habitats (Costa *et al.,* 1994; Canziani *et al.,* 1998); Pacific and Atlantic sardines are expected to continue to move into cooler and deeper waters (Gasalla, 2012; Silva *et al.,* 2015); skipjack tuna are likely to be more abundant in the Inter-American Sea and other productive oceanic areas (Muhling *et al.,* 2015); and jumbo squid are expected to continue to be caught more commonly by Peruvian and Chilean small-scale fisheries (Rodhouse *et al.,* 2014).

The mixed responses of species to ocean warming in Central and South America will result in advantages for some countries and disadvantages for others. Artisanal fishers in Latin America dependent on coastal fish species for food and income are likely to suffer hardship where species move poleward, because the restricted mobility of fishers will prevent them from operating further afield to target the usual stocks. In other locations, there may be enhanced opportunities for livelihoods through creation of more sport fishing enterprises targeting increased abundances of species of interest to anglers.

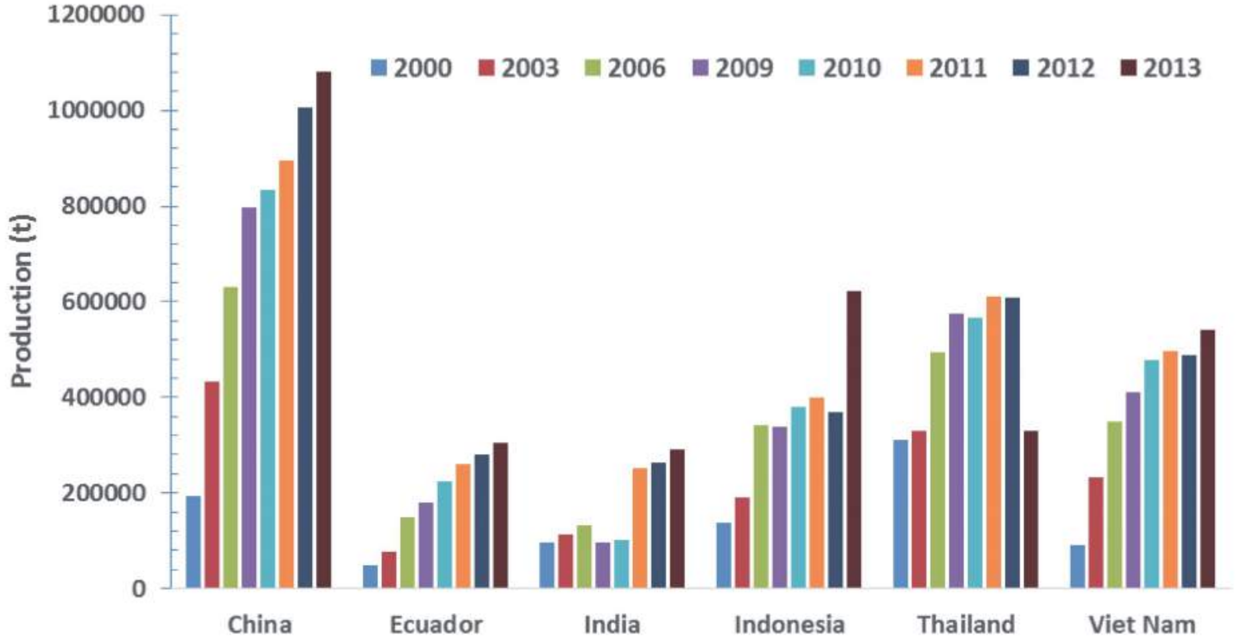


Figure 4.5.11 Trends in shrimp production, in selected years, in major producing countries from 2000 onwards (source: FAO, 2014b).

4.5.4 Effects on mariculture

For the past two decades, most mariculture production has occurred in the tropics and sub-tropics and been dominated by seaweed and molluscs (De Silva and Soto, 2009; FAO, 2014a). Substantial shrimp farming also occurs in tropical and subtropical coastal and estuarine areas (Ahmed and Diana, 2015) (Figure 4.5.11), supplying >70% of shrimp marketed globally (Benzie, 2009) (Figure 4.5.12). However, all shrimp culture depends on feeds containing fish meal.

The rapid development of aquaculture during recent decades is expected to continue, and will need to provide most of the increasing demand for fish (FAO, 2014a) (Figure 4.5.13). It remains to be seen whether more finfish will be produced through mariculture in the future – at present, only 10% of farmed finfish production occurs in coastal waters (FAO, 2016). Expansion of finfish aquaculture in fresh water will become increasingly difficult unless environmentally sustainable cage culture can be accommodated

Figure 4.5.12 Harvesting shrimp (*Penaeus monodon*), Chilaw, Sri Lanka. © Sena De Silva.

Figure 4.5.13 Intensive finfish cage culture in Xinqua Bay, Hainan Island, China. © Sena De Silva.

in water bodies impounded for other purposes – a process that has already begun in some developing countries (Abery *et al.,* 2005; Blow and Leonard, 2007; De Silva and Phillips, 2007). But mariculture of finfish also faces limitations because low-cost farming methods are largely restricted to sheltered coastal areas. Although technology and computer simulations exist for offshore expansion of mariculture by anchoring large sea cages in open ocean areas (Duarte *et al.,* 2009), such developments are often likely to be beyond the financial resources of developing nations, which have the greatest needs for fish. Nevertheless, it is perhaps inevitable that the proportion of farmed finfish produced by mariculture will need to increase.

Recent assessments indicate that ocean warming can be expected to affect plans to expand mariculture both directly and indirectly (De Silva and Soto, 2009; De Silva, 2012b). The main direct impacts are likely to be caused by alterations in the suitability of areas for growing particular species, driven by higher water temperature.

Fish mariculture in temperate regions, where much of the present-day production occurs (Halwart *et al.,* 2007), is expected to be affected negatively by ocean warming. Salmon farming and the emerging culture of cod *Gadus morhua* need to operate within a relatively narrow range of temperatures for optimal performance. Temperatures >17 ºC would be detrimental to salmon and cod farming because feed intake drops and feed utilization efficacy is reduced above this threshold (Anon., 2008).

Changes are also expected to occur in prime locations for farming tropical and sub-tropical marine finfish, such as groupers, snappers and cobia, as water temperatures increase. Where temperatures begin to exceed the thermal optima for these species, mariculture operations will need to move to higher latitudes.

The effects of a warmer ocean, manifested through changes in current patterns, and in salinity, run-off of nutrients and dispersal of pollutants resulting from higher rainfall, are also likely to reduce the productivity of other mariculture operations in tropical areas. For example, abrupt changes in salinity and alteration of coastal currents can be expected to affect recruitment of wild post-larvae collected for grow-out (World Bank, 2000; Ahmed *et al.,* 2013).

One of the main indirect effects of ocean warming on mariculture is expected to be more frequent disease outbreaks arising from redistribution of existing pathogens and increased virulence of previously dormant pathogens (Harvell *et al.,* 1999; Mennerat, 2010; Altizer *et al.,* 2013; Leung and Bates, 2013; Chadag, 2014) (Table 4.5.6). The recent effects of early mortality syndrome on shrimp farming (FAO, 2013) provide another insight into the economic losses that can occur as a result of mariculture diseases. The incidence of ice–ice disease during farming of seaweed *Kappaphycus alvarezii* (‘cottonii’) and *Eucheuma denticulatum* (‘spinosum’) has also increased recently in north-east Sulawesi, Indonesia (Aslan *et al.,* 2015). Factors that predispose seaweed to this disease include changes in temperature, salinity, light intensity, and colonization by bacteria, fungi and epiphytes (Largo *et al.,* 1995a,b; Largo, 2002; Solis and Draeger, 2010).

Another indirect threat to mariculture from warmer, more nutrient-rich, coastal waters is that the frequency of harmful

Table 4.5.6 Aquatic diseases prevalent in tropical countries and their relationship with some of the key elements of climate change (source: Mohan, 2015)

Disease	**Description and sensitivity to climate change**
Infection with *Aphanomyces invadans* (Epizootic Ulcerative Syndrome-EUS)	Fish fungal disease. Seasonal disease of wild and farmed freshwater and estuarine fish; grows best at 20-30 C; salinity over 2 ppt can stop the spread, 97 species of fish confirmed to be susceptible; no data available on vectors; transmission horizontal; outbreaks normally associated with cooler months of the year and after rainfall.
Koi herpes virus disease (KHVD)	Fish viral disease. Reported both in tropics and temperate regions; common carp and varieties of this species like koi are most susceptible; disease pattern influenced by temperature; occurring between 16 and 25°C.
Viral Encephalopathy and Retinopathy (VER)	Fish viral disease. Serious disease of mainly marine fishes; reported from more than 50 species; water most important abiotic vector; reported in both tropics and temperate regions; outbreaks related to water temperature.
White Spot Disease (WSD)	Shrimp viral disease. Wide host range, especially decapod crustaceans, in marine, brackish and freshwater systems; horizontal and vertical transmission, outbreaks induced by rapid changes in salinity; temperature has profound influence on disease outbreaks with temperatures of 16-30°C conducive for outbreaks; stocking in cold season is one of the predisposing factors of WSD outbreaks.
Infectious Myonecrosis	Shrimp viral disease. Temperature and salinity effects are considered to be predisposing factors to disease outbreaks
White tail disease	Viral disease of freshwater prawn. Penaeid shrimp and aquatic insects are vectors; rapid change in salinity, temperature and pH are predisposing factors to disease outbreak.
Shrimp AHPND	Emerging bacterial disease of shrimp. Caused by pathogenic strain of *Vibrio parahaemolyticus*; reported from Asia and Latin America; nutrient loading and water quality as predisposing factors.
Fish ectoparasites like protozoans, flukes, crustaceans (*Argulus*, *Lernaea*)	Life cycle and larval development influenced by water temperature.
Streptococcus infection in fishes	Diverse host range; higher temperatures (>30°C) predisposes fishes like tilapia to outbreaks of *Streptococcus* infection.

algal blooms (HABs) could increase (Peperzak, 2003; Edwards *et al.,* 2006; Al-Azri *et al.*, 2015). HABs pose a threat to human health through consumption of filter-feeding molluscs, resulting in what is commonly called 'shellfish poisoning'. The effects of HABs can also be expected to dislocate local benefits from mariculture, e.g. employment.

Possible shortages in the supply of fish used to make the fish meal and fish oil ingredients in mariculture feeds (De Silva and Soto, 2009) is one potential indirect impact not expected to unduly disrupt the expansion of marine fish farming. Recent modelling suggests that technological developments should reduce the dependence of mariculture on fish meal (Merino *et al.,* 2012; Barange *et al.,* 2014).

4.5.5 Global assessments for marine capture fisheries

Recent assessments of the future status of marine fish stocks include not only studies examining the projected effects of climate change but also those focusing on the possible effects of improvements in management. For example, Costello *et al.* (2016) examined more than 4,700 fisheries worldwide, representing 78% of reported global fish catch, and concluded that: 1) the median fishery is in poor health; 2) only 32% of fisheries are in good biological condition; 3) applying sound management reforms could generate annual increases in global catch exceeding 16 million tonnes; and 4) appropriate reforms could result in rapid recovery, with the median fishery taking less than 10 years to reach target levels. In short, common-sense reforms to fishery management could improve overall fish abundance and increase food security and profits. However, as useful as such assessments are, the proposed improvements in management may be of limited value unless they also integrate the likely effects of climate change from global assessments, like those described below (Schindler and Hilborn, 2015).

Global assessments of future fish production that include climate change as a driving factor, confirm the patterns from the five developing country regions – there will be winners and losers (Weatherdon *et al.,* 2016). Thus, the scope for increased catches outlined by Costello *et al.* (2016) can be expected to vary among locations. As a general rule, global assessments project losses of fish species and decreased fisheries production in tropical areas and increases in higher latitude temperate areas (Allison *et al.,* 2009; Cochrane *et al.,* 2009; Cheung *et al.,* 2011; Blanchard *et al.,* 2012; Barange *et al.,* 2014; Jones and Cheung, 2015). However, differences occur among assessments, depending on the modelling approach used, when projections are downscaled to regional or national levels, highlighting differing uncertainties among models. For example, Barange *et al.* (2014) project a different pattern of winners and losers among West African countries than those described in para. 4.5.3.4. Use of ensemble modelling approaches promises to help reduce such inconsistencies and quantify the uncertainties relating to projections of fisheries production due to climate change and, ultimately, help build confidence in using these projections for policy discussion (Jones *et al.,* 2012; Jones and Cheung, 2015; Cheung *et al.,* 2016b). For example, the Fisheries and Marine Ecosystem Model Intercomparison Project (FISH-MIP) seeks to collate global research efforts to compare global and regional projections of living marine resources and fisheries. It aims to standardize model inputs, where possible, and compare outputs from multiple models to assess climate and fisheries impacts on marine ecosystems and the services that they provide.

4.5.6 Implications for food security

From the evidence summarized above, there is every reason to believe that ocean warming will reduce or redistribute the benefits of marine fisheries and mariculture in those regions of the world with a high dependence on fisheries for food security and livelihoods (Figure 4.5.14).

All four dimensions of the contributions of marine fisheries and mariculture to food security will be affected (Cochrane *et al.,* 2009). The *availability* of fish will vary as a result of changes in fish habitats, fish stocks and the distributions of species. The *stability* of supply will be altered by changes in seasonality, increased variance in ecosystem productivity and increased variability in catches. *Access* to fish will be affected by changes in opportunities to derive livelihoods from marine fisheries and mariculture, *utilization* of fish will be affected because some communities will need to adjust to species not consumed traditionally, and increased prevalence of aquatic diseases and HAB are likely to render some fish production inedible more frequently.

The effects on food security are likely to be greatest in tropical and subtropical countries where the largest reductions in fisheries production are generally expected to occur. However, as profound as the effects of ocean warming on productivity of marine fisheries are likely to be in many of these countries, population growth and

Figure 4.5.14 Fishers sorting their nets near Honiara, Solomon Islands. © Johann Bell.

the quality of resource management will probably have a much greater influence on availability of fish per capita for the next few decades (Para. 4.5.3). This implies that governments must identify effective ways of minimizing and filling the gap between the amount of fish readily available and the quantities of fish required for good nutrition of national populations.

4.5.7 Recommended adaptations

The main adaptations to reduce the gap in supply of fish for food security involve instituting better management of fish habitats and fish stocks (Figure 4.5.15), and improving supply chains. To fill the gap, governments will need to ensure that mariculture (and freshwater aquaculture) continue to develop in environmentally

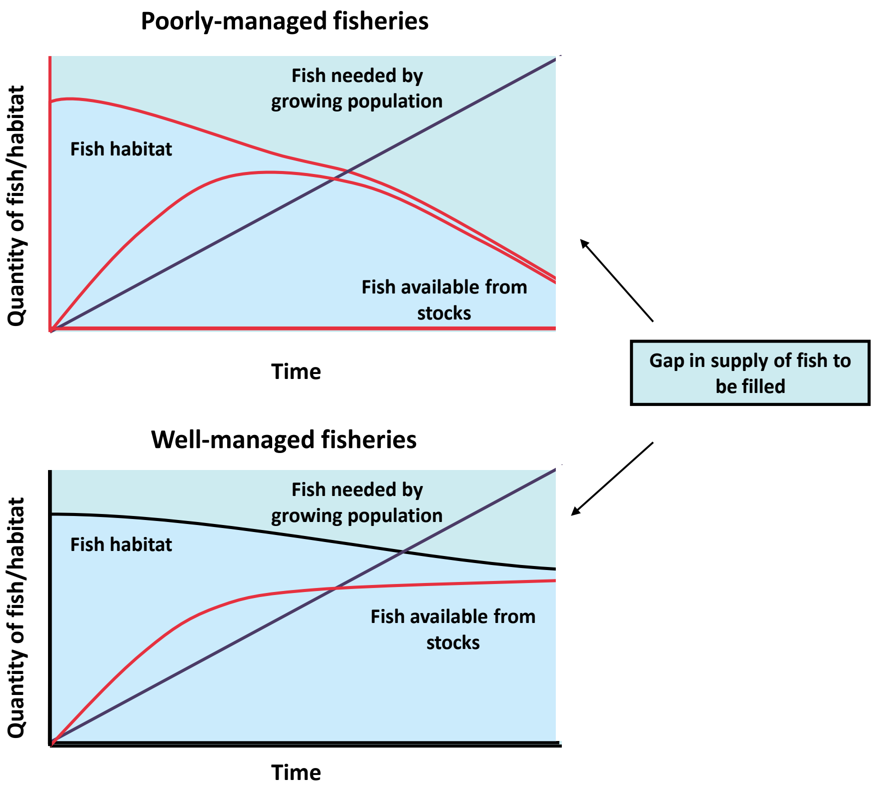


Figure 4.5.15 The importance of managing fish habitats and fish stocks well to minimize the gap between the fish required for good nutrition of populations and sustainable harvests of fish (source: Bell *et al.*, 2011b).

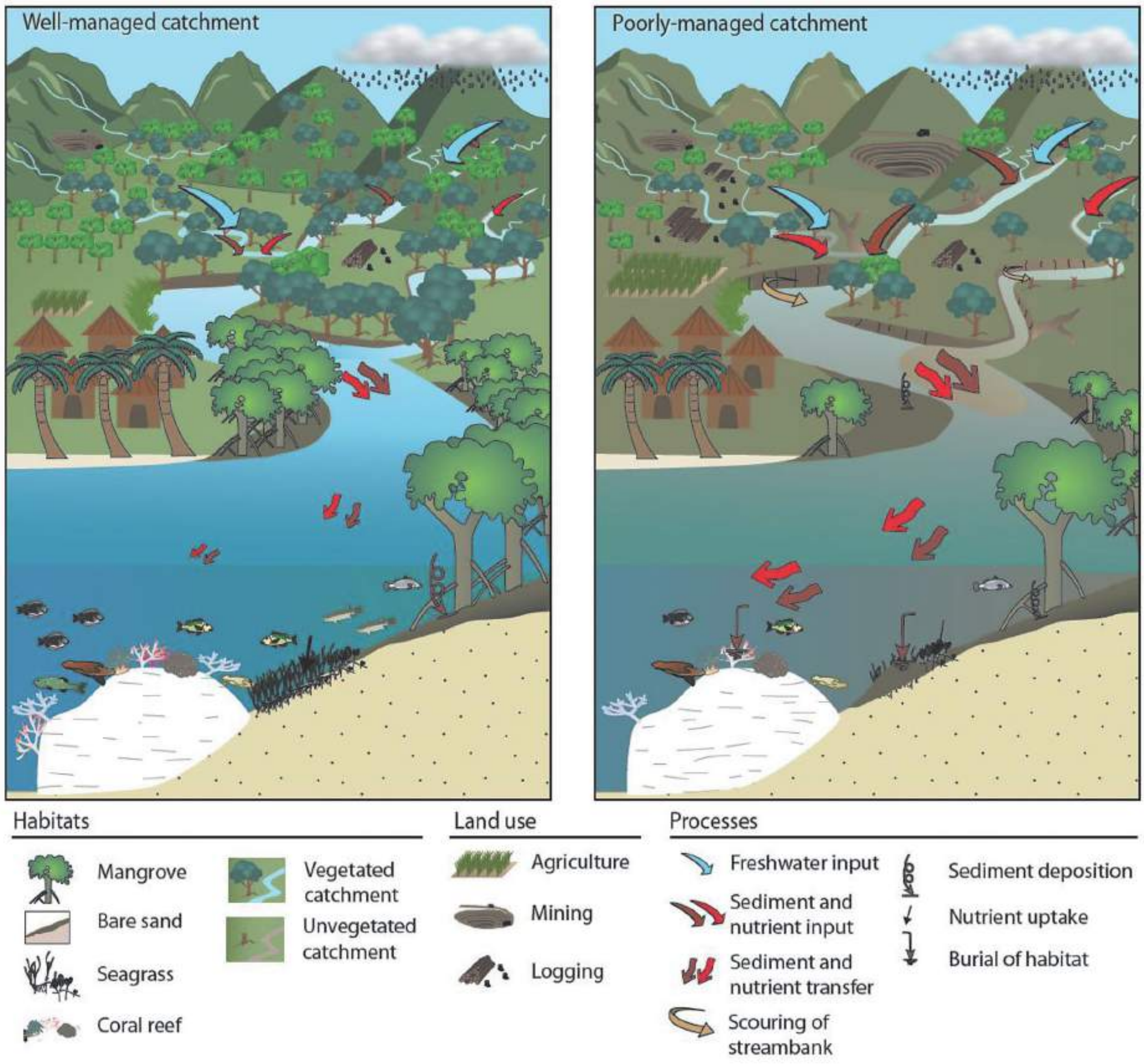


Figure 4.5.16 Differences in the quality of coastal fish habitats when catchments are managed well or managed poorly (source: Bell *et al.,* 2011c).

sustainable ways (De Silva and Soto, 2009; De Silva, 2012b; Hall *et al.,* 2011; FAO, 2014a) and, where necessary, reallocate some of the fish normally traded (either as exports or through sale of licences to DWFNs) to domestic consumption.

4.5.7.1 Adaptations to reduce the gap

Where they are currently weak, improvements in the following two broad categories of management will help to reduce the gap by optimizing fisheries production.

1. Reducing the impact of local stressors on fish habitats. For example, restoring catchment vegetation to minimize the effects of run-off of sediments and nutrients on coral reefs, mangroves and seagrasses (Figure 4.5.16). The need for such integrated coastal management and marine spatial planning is widely recognized (Sale *et al.,* 2014), and may extend to constructing artificial habitats to increase the capacity of coastal environments for fish recruitment. Integrated coastal management is now imperative to reduce the negative effects of coastal development on fisheries production and the incidence of HABs.
2. Keeping production of fisheries within sustainable bounds using the most appropriate management measures for the national context and an ecosystem approach that integrates the effects of climate change (Heenan *et al.,* 2015; Samoilys *et al.,* 2015). For many developing countries, this will depend on primary fisheries management

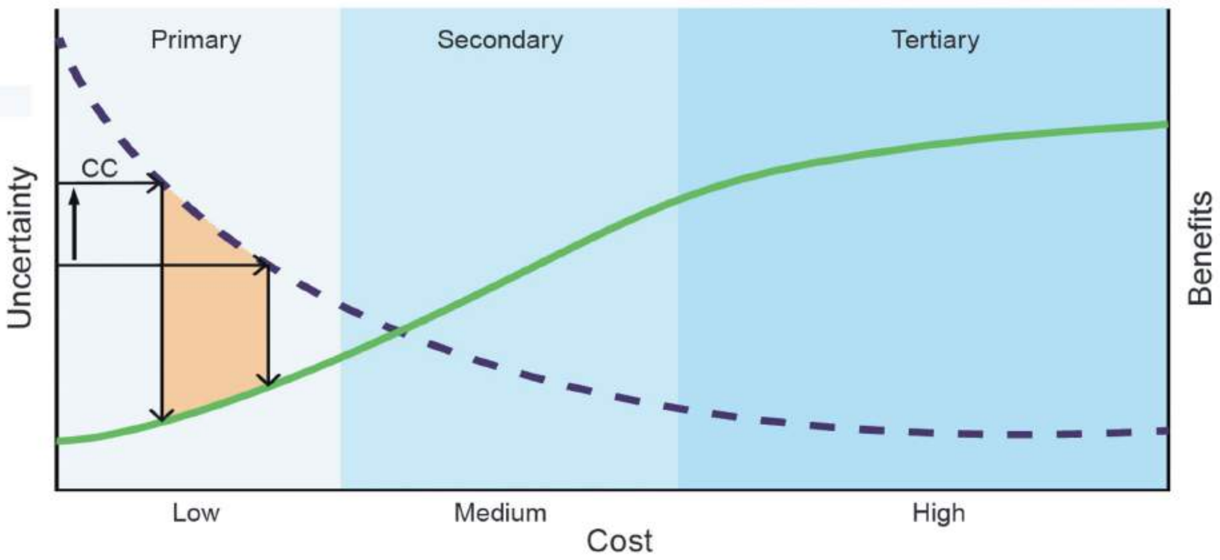


Figure 4.5.17 General relationship between potential benefits from fisheries (green line), and uncertainty in information for management (blue line), as functions of costs, for primary, secondary and tertiary fisheries management (source: Cochrane *et al.,* 2011 and Bell *et al.,* 2011c). The reduction in benefits under primary fisheries management as a result of the increased uncertainty caused by ocean warming and other features of climate change (CC) is indicated by the orange shading.

(Cochrane *et al.,* 2011)[3], which will need to become progressively more precautionary as the ocean continues to warm (Figure 4.5.17) and be well enforced (Samoilys *et al.,* in press). Climate-informed, primary fisheries management will involve raising awareness of the alterations in fish distribution and abundance due to ocean warming and diversifying fishing practices to take catches representative of the changes in relative abundance of species (Cheung *et al.,* 2013b). For coral reef fisheries, herbivorous fish species are expected to comprise a higher proportion of the catch in the future (Pratchett *et al.,* 2011). However, harvesting of herbivorous fish will need to be restrained to ensure they remain plentiful enough to help remove the algae that inhibit the survival and growth of corals (Bellwood *et al.,* 2004).

Improvements to supply chains, from beginning to end, can also help fill the gap by making fishing more efficient and reducing waste. Environmental forecasting of the best times to fish (and the onset of extreme events) via mobile phone networks can reduce travel/search times for small-scale fishers and enhance diversification of livelihoods into farming activities when fish are harder to catch. Mobile phones can also be used to assess market conditions to optimize income and arrange the timing of transport to markets. Improving fish handling, by providing better access to ice, for example, will increase the time that catches remain fit for human consumption.

4.5.7.2 Adaptations to fill the gap

Increasing environmentally sustainable mariculture (and freshwater aquaculture) is one of the most important adaptations to the effects of ocean warming on the availability of fish for food security. The following steps will be particularly important:

- improving national capacity by providing the necessary technical knowledge, extension services and incentives to scale-up the production of juvenile fish for grow-out and increase the number of fish farms;
- continuing the research needed to develop suitable feeds for marine finfish with minimal fish meal and fish oil content, including exploration of the best ways to incorporate fish processing waste into feeds;
- commencing more genetic improvement programmes to build the resilience of domesticated species to higher SST and pathogens expected to be favoured by ocean warming;

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[3] Primary fisheries management recognizes the need to use simple harvest controls, such as size limits, closed seasons and areas, gear restrictions and protection of spawning aggregations. In many cases it can be applied most effectively through community-based approaches (Govan *et al.*, 2008; SPC, 2010; Rocliffe *et al.*, 2014). Secondary and tertiary fisheries management require greater investments in stock assessments to reduce uncertainty about the economic benefits that can be gained from more accurate and precise estimates of sustainable harvests.

- exploring the scope for domestication of additional marine fish species (preferably omnivores) with promising attributes for hatchery rearing, tolerance of higher temperatures and rapid growth in culture systems;
- promoting the capture and culture of wild-caught post-larvae of species that have high post-settlement mortality but good survival in culture (Hair *et al.,* 2002), provided such harvests do not have adverse effects on recruitment to capture fisheries;
- encouraging stock enhancement of coastal species where it has been demonstrated that release of culture juveniles adds value to other forms of management (Bell *et al.,* 2005b; Lorenzen *et al.,* 2010); and
- growing-out bycatch species, as done in India (pers. comm. S. Shyam, CMFRI), in ways that address risks of overfishing as a result of this practice.

Despite the great need to increase aquaculture production (Merino *et al.,* 2012), for several developing countries the most practical ways of filling the gap in fish supply will be increasing access to large and small pelagic fish presently caught mainly by industrial fleets. Options available to governments include:

- Assisting small-scale coastal fishers to transfer some of their fishing effort to pelagic fish by equipping them to fish safely and effectively further from shore and expanding the use of nearshore fish aggregating devices (Bell *et al.,* 2015b) (Figure 4.5.18). Such investments not only increase access to fish now, they will help communities adapt to the negative effects of ocean warming on the productivity of fisheries associated with coral reefs (Bell *et al.,* 2013). Even where tuna are projected to decline within EEZs as the ocean warms (Para. 4.5.2), tuna are still expected to be abundant enough to make these adaptations effective.
- Implementing policies that: 1) ensure that industrial fishing operations do not have negative effects on small-scale fishers, 2) require industrial fleets to land bycatch, and target species if necessary, at major ports to provide urban communities with low-cost fish, and 3) facilitate the development of small and medium enterprises to distribute fish to urban and peri-urban areas (Bell *et al.,* 2015a). In many cases, the fish to be retained for local food security can be offloaded during routine transhipping operations and may only be a small proportion of the total industrial catch. For example, only 3% of the tuna catch in Papua New Guinea would be needed for coastal and urban communities to have access to the recommended quantities of fish for good nutrition by 2020 (Table 4.5.1). Although reallocation of a small percentage of the recommended tuna from the waters of PNG for direct domestic consumption is likely to result in a small economic loss, the benefits to public health are expected to be substantial (Golden *et al*., 2016). Quantifying this trade-off will assist governments to implement the best food security policies for adapting to the effects of ocean warming on fisheries resources.

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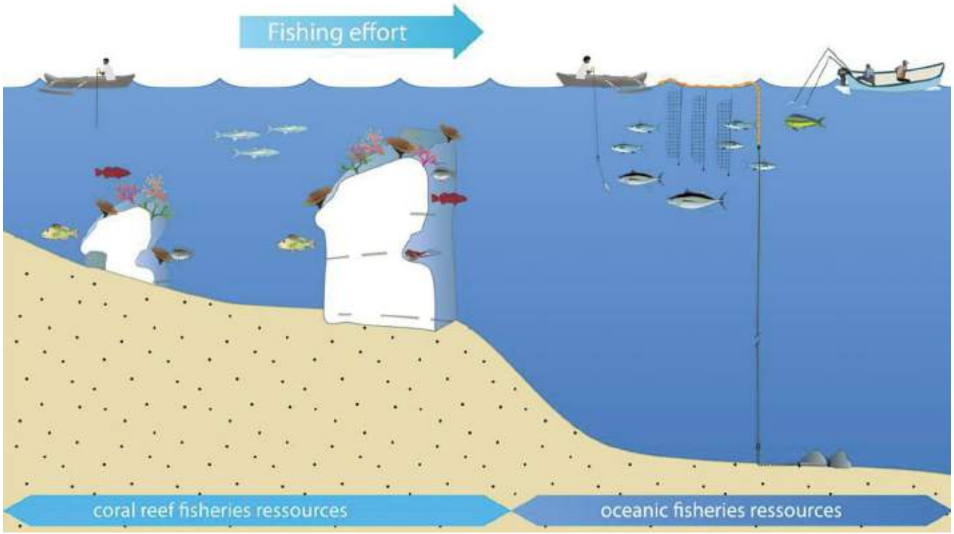

Figure 4.5.18 Nearshore fish aggregating devices allow some coastal fishing effort to be transferred to pelagic (oceanic) fisheries resources (source: SPC, 2014). (However, managers should ensure that no net increase in the overall catch of oceanic fisheries resources occurs by reducing industrial catches to cater for the needs of small-scale fishers).

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"As rates of poleward range shifts in marine systems are happening between 1.5 and 5 times faster in open marine systems than on land, it is possible that where a pathogen survives in marine conditions this could provide the quickest route for its spread to new regions."

"There is a worrying lack of detailed experiments of thermal limits on survival, reproduction and growth of pathogenic organisms and their carriers. Such depth of understanding is essential to more rigorously link observed changes in disease incidence with anthropogenic climate change, and to confidently project changes into the future."

Section 4.6 authors

4.6 Impacts and effects of ocean warming on human health (disease)

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Summary

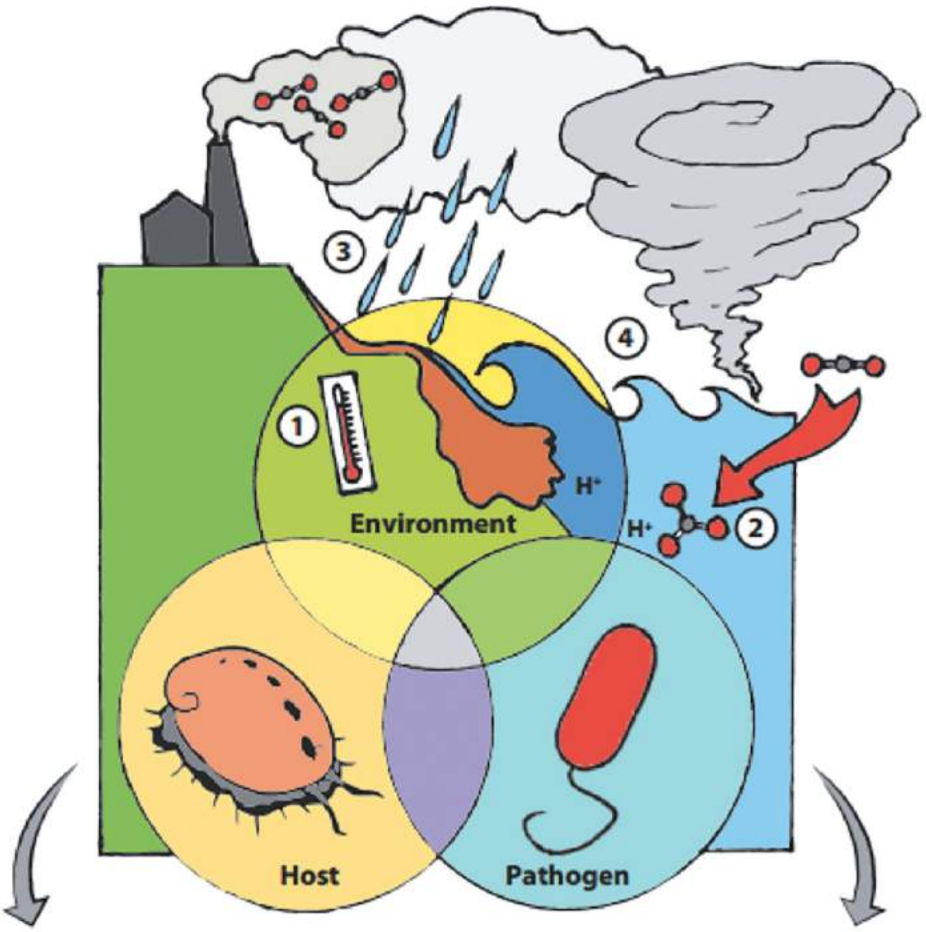
- Billions of people live connected to the sea, so potentially are influenced by changes to disease dynamics associated with marine systems.
- There is emerging evidence that climate change has caused increases in diseases among many wild populations of plants and animals in terrestrial and marine systems, in the latter generally linked to changes in sea surface temperature.
- In coldest temperate and boreal regions, increases in minimum temperature rather than maximum temperatures could be critical for increased pathogen survival, and thus allow emergence of warm-water diseases into historically cool seas.
- There are early signs that human health is already being impacted by enhanced survival and spread of tropical diseases with increasing temperatures, particularly pathogenic species of bacteria in the genus *Vibrio* (one of which causes cholera) and Harmful Algal Bloom species that cause a variety of neurological illnesses (such as Ciguatera).
- However, studies on the impacts of climate change on human diseases mediated by marine systems are primarily correlations between sea surface temperature (SST) and disease incidence. There is a worrying lack of detailed experiments of thermal limits on survival, reproduction and growth of pathogenic organisms and their carriers. Such depth of understanding is essential to more rigorously link observed changes in disease incidence with anthropogenic climate change, and to confidently project changes into the future.
- As rates of poleward range shifts in marine systems are happening between 1.5 and 5 times faster in open marine systems than on land, it is possible that where a pathogen survives in marine conditions this could provide the quickest route for its spread to new regions. Models of spread of human disease would be improved by inclusion of possible marine-mediated shifts in geographic ranges of disease organisms and their vectors or reservoirs.
- From a purely ocean's perspective, human disease risk is most likely to be affected by changes in disease incidence for marine animals that are part of our diet, allowing for direct transmission of the pathogen to humans, or for infections of wounds exposed during recreational (e.g. bathing) activities.

Ocean warming effects	Consequences
Higher maximum SST	Increased risk of harmful *Vibrio* bacteria outbreaks and harmful algal blooms in moderately warm waters (e.g. southern temperate zones such as the southern USA and continental Europe) Possible decreased risk of *Vibrio* and harmful algal outbreaks in warmest tropical waters
Higher minimum SST	Increased risk of harmful *Vibrio* bacteria outbreaks in moderately cold waters (e.g. northern temperate and boreal zones such as northern USA and Alaska, Canada, the UK and Norway)
Increased acidity	Indications that at least one species of diatom increases toxicity under more acid conditions Altered species compositions, effects currently unclear
Earlier spring warming and extended warm spring/ summer periods	May promote earlier, more prolonged and denser phytoplankton blooms Directly promote harmful algal blooms and indirectly promote *Vibrio* outbreaks
Geographic shifts in seasonal and annual temperature bands (particularly poleward shifts of warm waters)	Promotes poleward shifts of the ranges of species that are either directly pathogenic to humans, produce disease-causing toxins, or cause disease outbreaks in commercial seafood with resulting decreased harvests Risk of diseases currently associated with warm waters is increasing in historically cold-water regions Risk is further increased by emergence of such "tropical" diseases in "temperate" countries that lack appropriate experience to recognize and treat many of these diseases

4.6.1 Introduction

Given that 44% of the current global population live near the coast and 8 out of 10 of the world's largest cities are coastal (Nganyi *et al.,* 2010), billions of people are influenced by the planet's coastal seas. There are a range of mechanisms where climate change can influence the ocean and, thus, directly or indirectly affect human health and welfare. Sea- level rise and increased frequencies and severities of storms can, for example, cause potentially catastrophic coastal inundation and damage, with major loss of life and social structure. Rising sea levels can result in saline incursion to freshwater systems and groundwater, reducing potable water for drinking and irrigation. Geographic shifts in fish distributions, through changes in both seawater temperature and strength and trajectories of major ocean currents, can directly impact food supply. These impacts have been highlighted in several major reports (e.g. multiple chapters in the IPCC Fifth Assessment Reports), and will be covered elsewhere within the current Report. The focus of this section is on a relatively less recognized impact of climate change: on how a warming ocean can influence human health through changes in the geographic locations and risk of transmission of pathogens and biologically-produced toxins from the marine environment.

Evidence suggests that observed warming could affect many vector-borne diseases through a range of mechanisms such as altering disease, vector, or reservoir's distributions, or by increasing outbreak probability and risk of disease transmission (Figure 4.6.1) (Loevinsohn, 1994; Epstein, 2000; Gubler *et al*., 2001; Kovats *et al*., 2003; WHO, 2004; Lloret *et al.,* 2016). Links between disease outbreaks and climate variability vary strongly by region, but overall global patterns are apparent: of 17 common communicable human diseases, 12 (71%) were weakly to strongly affected by changes in rainfall and temperature (Kovats *et al*., 2003). Practically all of these cases are, however, associated with terrestrial or freshwater systems. There are numerous studies linking climate variability in



Changes in host	Climate factor	Changes in pathogen
• Increased susceptibility • Change in behavior • Invasions • Range shifts	①	• Increased activity • Change in virulence • New emergence • Invasions • Range shifts
• Increased susceptibility (?) • Change in larval survival/recruitment • Change in behavior • Reductions in diversity (?)	② $2-$ H^+ H^+	• Change in virulence • Change in abundance
• Increased susceptibility • Nutrient stress • Salinity stress • Contaminant stress	③	• New emergence • Change in virulence • Invasions • Range shifts • Increased nutrients
• Increased susceptibility • Physical injury	④	• New emergence • Invasions • Range shifts • Mixing/resuspension of particles

Figure 4.6.1 Cartoon of the inter-relationships among climate change variables and host-pathogen interactions. 1) Increased temperatures, 2) increased atmospheric CO_2 causing acidification, 3) Changes in amounts and patterns of precipitation (particularly through their effects on coastal salinity), and 4) increases in frequencies and intensities of storms and cyclones. (Reprinted with permission from Figure 1 in Burge *et al.* (2014).

coastal systems to increases in vector-borne diseases of humans, but these are typically indirect effects of sea surface temperature (SST) variability on terrestrial climate, which in turn affects disease prevalence and transmission by terrestrial vectors and reservoirs, such as mosquitos and sand flies (Andersen *et al.,* 2015), or freshwater animals, such as snails (Zhou *et al.,* 2008). For example, increases in coastal temperatures, rainfall and humidity have been documented to increase risk of malaria, dengue, leishmaniosis, chikungunya, schistosomiasis and non-specific diarrhoea in coastal human populations (Wong *et al.,* 2014).

The potential for climate-related spread of human diseases through marine systems is less reported, and has received comparatively little attention. A recent review by Burge *et al.* (2014) provided evidence for increases in infectious diseases in marine organisms world-wide. However, human impacts were only cited twice, and both of those studies relate to the well-known effects of certain *Vibrio* spp. causing food poisoning. A recent review of seafood safety suggested early signs of emergence of "tropical" human diseases into historically temperate seas (Lloret *et al.,* 2016), but rigorous linkages with anthropogenic climate change (driving both ocean warming and acidification) remain elusive. Marine systems, like freshwater systems, also have the possibility of disease transmission through wounds encountering infected water. In this section, we summarize what is known about how a warming ocean may impact human health through the spread or propagation of diseases and/or their reservoirs via these various means.

4.6.2 Changes in the geography of diseases

It is now very clear that anthropogenic climate change has already substantially altered the geographic distributions and timing of seasonal events (phenology) of a wide diversity of wild plants and animals (Parmesan and Yohe, 2003; Root *et al.,* 2003; Parmesan, 2006; Rosenzweig *et al.,* 2008; Poloczanska *et al.,* 2013). Global analyses of some 4,000 species have estimated that between half and two-thirds of wild species have shown significant long-term changes consistent with local or regional warming trends (Parmesan and Hanley, 2015). Observed responses include earlier spring phenologies, poleward and upward range shifts of individual wild species, as well as extinctions of individual populations. Impacts have been detected in all studied taxonomic groups (plant, vertebrate and invertebrate), and in terrestrial, freshwater and marine systems.

Of particular interest with respect to human health risk is the advance into the temperate zone of historically tropical species (Parmesan, 2006; Poloczanska *et al.,* 2013). A recent study by Guernier *et al.* (2004) showed that the global distributions of key human pathogens (bacteria, viruses, protozoa, fungi and other parasites) follows the same latitudinal diversity gradient as most animals and plants. Higher species richness of pathogens in the tropics was related to climatic variables. Laboratory experiments with pathogens showed that, as with large-bodied organisms, many can only develop within particular temperature limits, and often have a quite narrow temperature range for optimal growth (MacDonald, 1957; Patz *et al*., 2001; WHO, 2004). This set of studies suggests that general global warming could drive the expansion of pathogens into historically cold regions with increasing temperatures (i.e. cold-temperate and boreal regions), but may also result in a reduced prevalence in the warmest parts of the historical ranges of these diseases. The best projections of future geography of human disease come from terrestrial systems, where decades of detailed experimental work has refined our understanding of the specific thermal limits and optimum for survival, growth, reproduction and transmission of various human diseases, such as malaria, shown in Figure 4.6.2 (Rogers and Randolf, 2000). This depth of experimental knowledge is largely lacking for diseases associated within the marine realm, making modelling future risk difficult, with high uncertainty in projected outcomes.

Sixty-two percent of human pathogens use wild animals as hosts (Cleveland *et al*., 2001), suggesting that changes in disease dynamics in wild animals could also affect human disease risk. The geographic distributions of vector-borne diseases are often limited by the climatic tolerance of their vectors and reservoirs, as well as by biological restrictions that limit the survival and incubation of the infective agent in the vector population. Moderate (10-50 km) to substantial (>1000 km) poleward range shifts have been detected in thousands of insects, birds and mammals over the past 30 to 130 years (Parmesan and Yohe, 2003; Parmesan, 2006; Poloczanska *et al.,* 2013). Some species in each of these groups act may as vectors or reservoirs of human diseases - either directly as the host of the disease, or indirectly by harbouring the host. In summary, there is an emerging consensus that anthropogenic climate change is likely to drive advances of 'tropical' microbial species, including those that cause human diseases, into cold-temperate zones historically free of these diseases (Smith *et al.,* 2014;

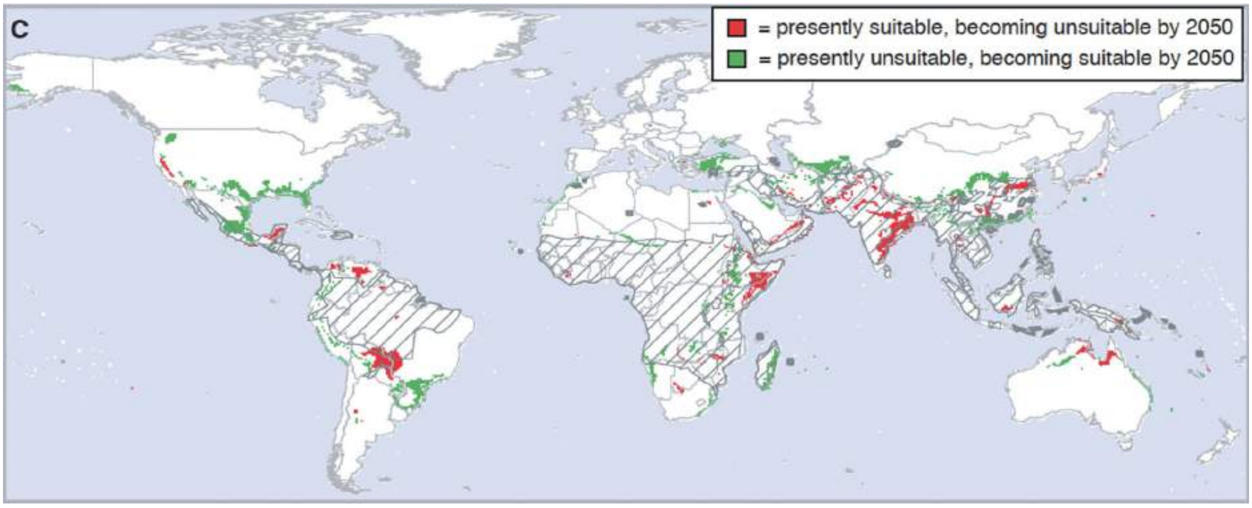


Figure 4.6.2 A summary of projected changes in the distribution of malaria incidence in humans by 2050 from modelling the climate space of current malaria incidence. This best model used three climate variables: temperature, precipitation and saturation vapour pressure. Grey hatching represents the areas global malaria incidence as of 2000. Red areas indicate areas where malaria is currently present but expected to disappear by 2050. Green areas indicate areas where malaria is currently absent but expected to appear by 2050. (Reprinted with permission from Figure 1c in Rogers and Randolf (2000).

WHO, 2015; Berdelet *et al.,* 2016). As it is now clear that latitudinal movement of species is happening between 1.5 and 5 times faster in open marine systems than on land (Burrows *et al.,* 2011), it is possible that where a pathogen survives in marine conditions this could provide the quickest route for its spread to new regions.

4.6.3 Water-borne diseases, food and wounds

From a purely ocean perspective, human disease risk is most likely to be affected by changes in disease incidence for marine animals that are (1) part of our diet, allowing for direct transmission of the pathogens or toxins to humans, or (2) present at recreational sites, allowing for direct infections of exposed wounds. There are two major sources of marine-related human illness: species of bacteria in the genus *Vibrio* and toxins manufactured by certain algae. While it is also possible to contract viruses and other parasites from seafood, *Vibrio* bacteria and algal toxins are by far the most common causes of disease.

4.6.3.1 Vibrio bacteria and climate change

Many marine-based human pathogens are sensitive to sea temperature variability. For example, in the Gulf of Mexico, incidence of the *Vibrio vulnificus* bacteria in oysters rises dramatically with sea temperature. The human impact is severe, as 30% to 48% of people die after contracting this bacterium (Shapiro *et al.,* 1998). In one study, 60% of the variation in *V. vulnificus* concentrations in oysters in the Gulf of Mexico was explained by temperature (Motes *et al*., 1998). In another study, 89% of human contraction of *V. vulnificus* came from eating oysters harvested in waters with mean annual temperatures > 22°C, and disease incidence rose sharply during summer months (Shapiro *et al*., 1998). In the North Sea, there was an unequivocal positive relationship between *Vibrio* numbers and annual sea surface temperature, established by DNA analyses of formalin-fixed samples collected over a 44-year period (Vezzulli *et al*., 2012). Kaspar and Tamplin (1993) showed (in culturing experiments) that *V. vulnificus* preferred temperatures between 13-22°C, but survived poorly below 8.5°C, indicating that for the coldest temperate regions increases in minimum temperature rather than maximum temperatures could be critical for increased pathogen survival.

However, even with its high latitude geography, the shallow Baltic Sea allows for substantial warming in summer, reaching temperatures >16°C, well above the minimum necessary for *Vibrio* survival. Baker-Austin *et al.* (2013) documented an association between *Vibrio* spp. outbreaks and recent increases in sea temperatures coupled with decreased salinity. Mean SST in July had risen from around 16°C in the late 1800s to around 18°C in the past decade. While several *Vibrio* species were present, *Vibrio vulnificus* was the most lethal. Baker-Austin *et al.* (2013) concluded that *Vibrio*-related illnesses about doubled for every degree C increase in maximum water temperature. Thus, once above a minimum survival temperature in these normally cold waters (as the Baltic is in summer), *Vibrio* infection rate was more closely related to maximum temperatures.

There are other indications of a recent emergence of novel *Vibrio* infections in historically *Vibrio*-free regions. Alaska experienced its first outbreak of *Vibrio* poisoning in 2004, being not only one of the largest outbreaks in U.S. history, but occurring 1,000 km further north than any other incident of human poisoning by *Vibrio parahaemolyticus* from oysters (McLaughlin *et al.,* 2005). The authors related this outbreak to rising SST: the oyster farm had experienced a significant rise in mean water temperature of 0.21°C per year since 1997. The year of the outbreak (2004) was the only year in which summer water temperatures did not drop below 15°C (the putative threshold for humans falling ill after consumption). In Israel, temperatures soared to record highs in summer 1996. This was followed by an unprecedented outbreak of *Vibrio vulnificus* infections of market handlers of fish farmed in inland salt-water ponds (Paz *et al.,* 2007). Infection rates were highly correlated with air temperatures over the next three (also warm) years, and fish handlers continue to this day to be at high risk of infection, even though *Vibrio* poisoning was absent prior to 1996 (Paz *et al.,* 2007). These could be the result either of recent northward range shifts in one or more species, or of endemic species that have recently increased reproduction and, hence, achieved higher population numbers that would lead to higher infection rates.

Vibrio spp., as well as biotoxins from harmful algal blooms (see below), can also be directly transmitted via contaminated water into open wounds of bathers (reviewed by Young, 2016). Indeed, most of the cases of recent *Vibrio* disease in humans in the Baltic have been related to wound infections (Baker-Austin *et al.,* 2013). *V. cholerae* (that causes the disease cholera) is also tolerant of low salinity, allowing it to grow to high numbers in rivers and ground water used for drinking (Colwell, 1996).

For some *Vibrio* species, basic biology is reasonably documented and supports the likely spread of *Vibrio* due to climate change. For example, when environmental conditions are not conducive to reproduction, *V. cholerae* can live in a viable but quiescent state and become pathogenic when conditions become more favourable. Experiments with *Vibrio fluvialis* in seawater microcosms showed strains survived as culturable bacteria for at least 1 year (Amel *et al.,* 2008), but were able to resuscitate to the culturable state after up to 6 years of incubation in marine sediments. A diversity of marine life can also serve as reservoirs, with *V. cholerae* having been found living in the mucosa of many shellfish and in crustacean zooplankton, and subsequently found in fish which have fed on plankton hosts. *V. cholerae* has also been found in aquatic vegetation, such as water hyacinth and in blue-green bacteria (Colwell, 1996).

Broad correlations between outbreaks of human cholera in coastal areas and coastal SST have been found in a range of studies (Portner *et al.,* 2014; Smith *et al.,* 2014; Wong *et al.,* 2014). However, positive correlations have also been found with other factors such as salinity (driven by sea and river levels as well as rainfall), nutrient levels, and concentrations of phytoplankton and cyanobacteria (Kaspar and Tamplin, 1993; Jutla *et al.,* 2011; Smith *et al.,* 2014). Correlational analyses showed strong repeated patterns in which extreme warm water temperatures cause algal blooms which then promote rapid increases in zooplankton abundances and hence also in their associated *V. cholerae* bacteria. A single copepod has been found to contain 10,000 *V. cholera* individuals. Analyses of long term data sets from Peru and Bangladesh (from 18 years up to 70 years) show that cholera has only recently become associated with El Niño events, perhaps in concert with rising human inputs of nutrients from agriculture (Pascual *et al.,* 2000; Rodó *et al.,* 2002; Jutla *et al.,* 2011).

Thus, there is compelling evidence for links between climate variability, climate change (e.g. via increases in strength of El Niño events), native plankton dynamics, bacterial dynamics in the wild, and cholera disease epidemics (Smith *et al.,* 2014). Although even for this relatively well-studied disease, we do not have a sufficiently deep understanding of how it responds to the many environmental changes that humans are driving to be confident in projections of risk into the future. Evidence from the Baltic, however, provides a strong suggestion that warming of coastal waters, perhaps in particular elevations in minimum temperature, provides a mechanism for disease spread into cold-temperate or even boreal zones, via the marine realm, in response to anthropogenic climate change.

4.6.3.2 Harmful algal blooms and climate change

Another source of food poisoning from seafood is caused by toxins produced by certain types of algae that, during periods of high population increases create "harmful algal blooms" (HABs), that lead to accumulation of high quantities of these toxins in fish and shellfish. About 100 species have been implicated in causing human diseases, and may be comprised of dinoflagellates or diatoms or cyanobacteria that produce a variety of toxins with neurological effects or that damage vital organs (Portner *et al.,* 2014; Smith *et al.,* 2014; Wong *et al.,* 2014; Berdalet *et al.,* 2016). There are a variety of products produced by different algal species. The names of the resulting diseases speak to the variety of symptoms caused: diarrhetic and azaspiracid shellfish poisoning (gastric distress including diarrhoea and vomiting, non-fatal), neurotoxic shellfish poisoning (multiple neurological symptoms including slurred speech, vertigo and muscle pain, non-fatal), amnesic shellfish poisoning (memory loss, brain damage, occasional death), paralytic shellfish poisoning (common in puffer fish, causing paralysis and often death) (Isbister and Kiernan, 2005; Berdalet *et al.,* 2016)

One of the most common diseases from HABs is ciguatera fish poisoning (Marques *et al.,* 2010; Berdalet *et al.,* 2016). Ciguatera causes moderate to severe gastric and neurological impacts that can last years (Isbister and Kiernan, 2005) and can reach levels lethal to humans (Hamilton *et al.,* 2010). Recent cases from the Indian Ocean report additional symptoms, including hallucinations, nightmares and depression (Isbister and Kiernan, 2005). Ciguatera poisoning in humans has been highly correlated with SST of fishing grounds (Hales *et al.,* 1999). A more detailed analysis was made possible by a long-term database on fish poisoning between 1973 and 1996 in the Pacific (Llewellyn *et al.,* 2010). Llewellyn and colleagues, examining spatial correlations between SST and ciguatura poisoning, found suggestions not only for a lower temperature limit, but also for an upper temperature limit (Figure 4.6.3). Numbers of ciguatura cases were highest in areas with average SSTs from 27° to 29°C, whilst cases were absent in areas below 23°C. Conversely, oceanic regions that are typically very hot in summer (up to 35°C), such as the Indo-Pacific warm pool, the Red Sea and the Arab Sea, had almost no ciguatura cases (both in the time period of this study, 1986-1996, and historically). These patterns indicate that ciguatera poisoning may increase during initial ocean warming, but may then decline again as temperatures rise further above their optimal limits for growth (Llewellyn *et al.,* 2010). As with most other marine diseases, further experimental research is needed to determine these thermal limits quantitatively. Little is known about the basic temperature limits for reproduction, nor for peak (optimal) growth and reproduction that is likely to lead to high densities, and hence high transmission rates.

Furthermore, harmful algal blooms can be stimulated by a complexity of processes beyond SST that are also being altered by anthropogenic climate change, including changes in upwelling, temperature gradients (stratification), and seasonal cycles of the various algal species involved (Hallengraeff, 2010; Fu *et al.,* 2012; Portner *et al.,* 2014; Berdalet *et al.,* 2016). A particularly long-term dataset (>40 years) from the Continuous Plankton Recorder Survey highlighted yet another complexity, that of the interaction of SST with nutrient inputs from human activities. Edwards *et al.* (2006) documented a pronounced increase in abundances of phytoplankton, dinoflagellates and diatoms in the North Sea coincident with a temperature regime shift to a warmer state in the 1980s. There were concurrent increases in frequencies of harmful algal blooms in some areas of the North Sea, though notably not across the whole of the North Atlantic, suggesting an additional role of nutrient inputs in promoting blooms (Edwards *et al.,* 2006). However, a further analysis of North Sea data, that included river inputs, concluded that the notable increase in productivity across the North Sea was independent of geographic variation of nutrient input, but strongly related to areas of increased temperature and reduced turbidity (McQuatters-Gollop *et al*., 2007). Thus the role of nutrients is still unclear. It is possible that a warming ocean may well result in increased phytoplankton production (potentially including harmful species) under a variety of nutrient regimes, not only where inputs are highest.

A third group of toxins are from cyanobacteria ("blue-green algae"). Experimental studies have documented that toxic strains of cyanobacteria benefit more from warmer temperatures than do non-toxic strains, suggesting a greater proliferations of toxic cyanobacteria with rising SSTs (Davis *et al.,* 2009). Rising CO_2 has also been experimentally shown to increase toxicity of a particularly harmful diatom, *Pseudo-nitzschia fraudulenta*, that causes potentially lethal amnesic shellfish poisoning (Tatters *et al.,* 2012).

These groups of toxins are particularly insidious. They have no taste nor smell, are not deactivated by cooking, and there are no antidotes (Isbister and Kiernan, 2005; Berdalet *et al.,* 2016). While in general not enough is understood about the basic ecological processes and how they interact to be able to quantitatively predict future risk with anthropogenic climate change, a trend towards increased risk is expected (Hallengraeff, 2010; Fu *et al.,* 2012; Smith *et al.,* 2014; Wong *et al.,* 2014).

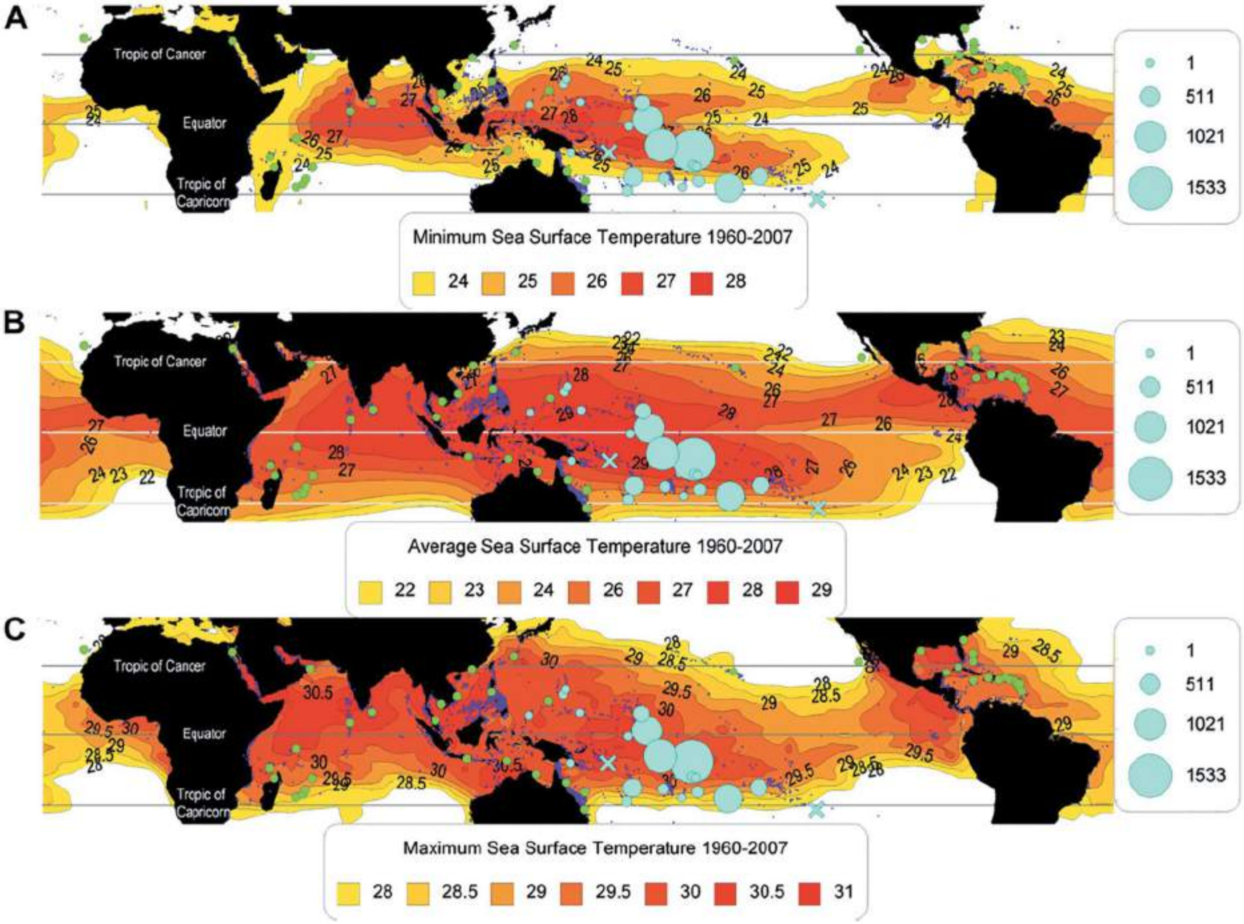


Figure 4.6.3 Global distribution of ciguatera and ciguateric fish relative to (A) minimum, (B) average and (C) maximum sea surface temperatures for the period 1960–2007 from the HadISST dataset. Light blue circles depict annual case rate of fish poisoning from the SPEHIS dataset (1988–1996) with circle size indicating the case rate as per the legend to the right. The two light blue crosses indicate the Solomon Islands and Pitcairn Island where zero cases of ciguatera were recorded in the SPEHIS dataset. Small green circles indicate reported locations of ciguatera or capture of ciguateric fish from the primary scientific literature as well as quality testing reports for various major fish markets (e.g. Japan, Hong Kong). Blue dots locate coral reefs obtained from the Worldfish Center Reefbase (www.reefbase.org).
(Reprinted with permission from Figure 1 in Llewellyn (2010).

This concern has prompted new research into improving monitoring and testing techniques, and developing a deeper understanding of algal bloom dynamics and drivers should lead to better predictive capacity (Erdner *et al.,* 2008; Fu *et al.,* 2012; Moore *et al.,* 2013).

4.6.3.3 Food availability, disease and climate change

Diseases of animals we eat may not infect humans, but can still impact human well-being by reducing abundances of human food resources (see Section 4.5). There is emerging evidence that climate change has also caused increases in diseases among many wild populations of plants and animals in terrestrial (Daszak *et al.,* 2000), as well as marine systems (Harvell *et al.,* 1999; Burge *et al.,* 2014). In a single year (1991), the oyster parasite *Perkinsus marinus* extended its range northward from Chesapeake Bay to Maine - a 500 km shift. Censuses from 1949 to 1990 showed a stable distribution of the parasite from the Gulf of Mexico to its northern boundary at Chesapeake Bay. The rapid expansion in 1991 has been linked to above-average winter temperatures rather than human-driven introduction or genetic change (Ford, 1996). This parasite causes high mortality when established, resulting in substantially reduced oyster harvests.

4.6.4 Conclusions and recommendations

Active management approaches that have been most successful in reducing human risk of disease from freshwater or vector-borne diseases are not applicable to marine systems (e.g. pesticide-impregnated bed-netting to reduce disease transmission from mosquitos and sand flies). The best way to reduce human risk of marine-mediated disease is to improve early detection of toxin and disease outbreaks. This would allow local communities and the commercial seafood industry to reduce exposure through short-term alteration of behaviours (e.g. temporary bans on swimming) and consumption patterns (e.g. temporary bans on marketing suspect species). There is therefore a need for increased frequency and better efficiency of monitoring techniques for bio-toxins and disease outbreaks in species destined for human consumption, particularly important in densely settled coastal regions and for developing nations that currently lack appropriate monitoring and testing capacity.

For some seafood, post-harvest processing, such as flash-freezing, pasteurization or exposure to very saline water has been shown to decrease bacterial counts to non-harmful levels (Burge *et al.,* 2014). Post-harvest sterilization techniques should become routine in areas with high counts of *Vibrio* present in fish and shellfish, or where measured SSTs indicate optimal conditions for harmful *Vibrio* spp.

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Conclusions and recommendations

5

Whether ocean warming affects a particular group of organisms, alters the structures of ecosystems such as coral reefs, changes the very essence of environmental conditions, or indeed influences weather, it impacts on everyone to some degree as we are an ocean planet. It has profound implications not just for ecosystems but also for the significant number of coastal communities and valuable economies that depend on a healthy ocean. This report describes ocean warming and its consequences by building on the IPCC's more recent reports, and adding in new information published since then, as well as highlighting lesser known consequences of ocean warming on species, ecosystems and services to ensure greater awareness and scrutiny of them in the future. Over 25% of the peer reviewed science used in this report – some 550 papers - has been published since the IPCC's last assessment in 2013. Despite greater recognition being given in climate discussions, such as at COP21 in Paris, we hope that this report will keep up awareness that the scale and nature of changes and problems in the ocean continue to grow. Urgent action by the international community, not just agreements, is what is now needed. The longer it takes to properly embed the ocean at the core of such agreements and take action at a global level, the greater the likelihood that the progressive and growing changes to the ocean described in this report will challenge food and human security, geopolitics and development at a global scale. During the production of this volume, IPCC has announced that it will prepare a special report on climate change and oceans and the cryosphere. We hope that this contribution on ocean warming will help that process and shape further thinking on the scale and consequences of climate change in our seas.

In this report we have focused on the facts. Leading scientists from around the world were invited to join with colleagues to contribute individual chapters and sections. Each was subject to peer review and tells in the scientist's own words the scale and nature of changes being driven by ocean warming, often in association with other stressors such as ocean acidification and deoxygenation. The report demonstrates the origin, scale and nature of ocean warming from a wide variety of aspects. In so doing, it describes the impacts on better known ecosystems such as seagrasses and coral reefs, and regions such as the Arctic and Antarctic, but has expanded that view to many other aspects - ranging from the smallest micro-organisms to the biggest whales. The ocean has been a vital moderating influence on the scale of global warming up to now having absorbed a significant amount of the excess heat and CO_2 produced as a result of the burning of fossil fuels. This regulating function happens at the cost of profound alterations of the ocean's physics and chemistry, especially leading to ocean warming and acidification, and consequently sea-level rise.

The evidence presented by scientists in this report show the costs these alterations are now having to species, ecosystems and people. These costs can be summarized as widespread, progressive and of significant concern. This report, as a result, contains repeated calls and warnings about the need for dramatic reductions in the amount of CO_2 we are emitting. It notes that even with dramatic cuts it will be 50 years before warming will flatten out due to the multi-decadal lag in the climate system. Due to the very nature of the deep sea, the effects will continue to be experienced there for decades, if not centuries, even if a complete cessation of CO_2 emissions were possible. When we step back, as we have tried to do with this report, and look at the overall consequences of our business-as-usual activities, it is clear that we are locking ourselves into an increasingly difficult future for us and generations to come.

Even the challenging reduction targets set by COP21 in Paris are not in fact, if met, a return to hospitable conditions where everything would be fine. As Chapter 2 and subsequent sections in Chapters 3 and 4 detail they actually represent a 'minimum ambition' to prevent dangerous anthropogenic interference with the climate system. Achieving the 'minimum ambition' will already bring major changes in the functioning and resources of the ocean as we know them. Exacerbating an already concerning situation is the fact that the absorptive role of the ocean is also predicted to decline in the 21st Century, suggesting that the physics and chemistry of the ocean will be significantly different by 2100. As atmospheric CO_2 continues to increase as a result of our activities, the solutions (i.e. mitigate, protect, repair, adapt) become fewer and less effective, thus decreasing the long-term ability of humankind to cope with the changes in the ocean that are now being observed.

We have known about global warming for about 120 years, since Svante Arrhenius's work[11], and ocean warming from Rossby's work[12] in the 1950s. It is clear though that the heat and carbon management roles of the ocean have only been properly recognized in the international debate on climate change in the last decade or so, and afforded their proper significance by the scientific community within the last few years.

More than 93% of the enhanced heating since the 1970s due to the greenhouse effect and other human activities has been absorbed by the ocean, and data show a sustained and accelerating upward trend in ocean warming. 2015 was recently analysed to have been the warmest year within the 136-year of extended reconstructed sea surface temperature records, and the fourth such record-breaking year since 2005.

Exploration of the opening Chapters, and the sections in Chapter 3 on different groups of marine species and ecosystems, show that ocean warming is happening and is not just a two-dimensional sea surface phenomenon. Analysis of ocean heat content estimates that approximately two thirds of the excess heat thus far absorbed by the ocean has been taken up by the upper ocean in the surface to 700m depth layer with one third absorbed into the deep ocean below 700m depth. By absorbing a disproportionate amount of heat from global warming and by taking up the rapidly increasing emissions of carbon dioxide, the ocean has shielded the world from even more rapid changes in climate. Carbon dioxide – one of the main greenhouse gases, the root cause of ocean warming – is also causing ocean acidification. As Chapter 4 shows, temperature, ocean acidification and deoxygenation, which together are driving responses in species and ecosystems, are having an impact on the benefits derived from the ocean in the form of 'goods and services'. As many authors have commented, the scale, nature and problems associated with ocean warming are progressive and based on our current understanding getting worse. The rates of increase in both temperature and CO_2 are of grave concern and emphasize the urgent need to stem further warming by dramatically reducing CO_2 emissions from our activities.

What is perhaps striking is the scale, nature and complexity of the responses that are now being seen, and the attendant uncertainties in making detailed predictions about these in the future. Marked biological manifestations of the impacts from ocean warming and other stressors in the ocean have taken the form of changes in biogeographical, phenological, biodiversity, community size changes, and species abundance changes as well as whole ecological regime shifts. Such regime shifts often interfere, or are predicted to interfere, with the benefits we depend on from the ocean. More precise interactions, such as the relative importance of direct physiological effects and indirect effects through other abiotic pathways and species

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[11] http://www.lenntech.com/greenhouse-effect/global-warming-history.htm

[12] https://www.aip.org/history/climate/oceans.htm#M_13_

interactions remain largely unknown. Multiple stressors (warming, acidification and oxygen reductions) interact cumulatively and exposure to one stressor (such as warming) can affect the tolerance of a species to another stressor. There is a worrying lack of detailed experiments of thermal limits on survival, reproduction and growth of pathogenic organisms and their carriers that are being favoured by ocean warming. The problem is that we know ocean warming is driving change in the ocean – this is well documented. The speed of change in the ocean, such as the poleward range shifts in marine systems, is happening between 1.5 and 5 times faster than on land. Such range shifts are potentially irreversible with great impacts on ecosystems – but the consequences of these changes, decades down the line, are far less clear.

Whilst rising CO_2 levels and increasing warming can occasionally have positive effects, the overwhelming evidence and predictions shown in this report are for a cocktail of negative effects, which we are only just starting to understand, but about which we know enough to be very concerned. The warning signs are clear to see. These range from the persistence of jellyfish blooms and their increasing frequency of occurrence, year after year, through to the current prevalence of bleaching of coral reefs around the world, but also the increasing confidence of predictions that all coral reefs will be so affected by 2050, unless we change our ways, and quickly. Ocean warming and climate change are ultimately contributing to global homogenization of biodiversity, as vulnerable species become extinct and "non-native" species from different biogeographic regions spread, overlap, and become established across the world's ocean. Predictions are for a decrease of biodiversity in warm-water regions, but as much as a 300% increase in polar regions. Biomass losses in deep sea areas in the north-east Atlantic for example may reach 40%, and for biodiversity hotspots, such as seamounts, even 80%.

Overall, ocean primary production is expected to continue to change, however, the global patterns of these changes are difficult to project, but regional evidence suggests that carbon cycling and storage will be fundamentally altered in some specific coastal situations, e.g. saltmarshes and mangroves. Existing projections suggest an increase in productivity in high latitude systems like the Arctic and Southern Ocean and a decrease in productivity in the tropics and mid-latitudes. Ocean warming is causing the expansion of zones experiencing oxygen deficiency, with important consequences for biogeochemical cycling and an increased role for the microbial world, and especially bacteria, archaea and viruses, at the expense of eukaryotes which are generally more sensitive to reduced oxygen levels. This will likely make the already dominant role of microbes in the functioning of the marine ecosystems even more pronounced in a scenario of a warming ocean. Declines in the amount of oxygen will make the demands of water-breathing organisms, such as fishes and invertebrates, increasingly difficult to meet under global warming scenarios, and will stimulate the production of nitrous oxide which is a potent greenhouse gas approximately 310 times more powerful than CO_2. It also has one of the longest atmosphere lifetimes of the greenhouse gases, lasting for up to 150 years. There is evidence that the flux of nitrous oxide from the ocean to the atmosphere is increasing.

All these changes and predictions for the future matter from moral, social, ecological and economic perspectives. The value of our relationship with the ocean sometimes seems difficult to cost, but is the ultimate relationship that enables life to exist on Earth. Estimates of worth vary but range from the services value of seaweeds at US$30,000 $ha^{-1}yr^{-1}$ through to US$5-10 trillion yr^{-1} for the services provided by rocky shores. In terms of economic losses, where this is quantified, it runs from millions to trillions of dollars a year. For example, the current tourism costs associated with the loss of corals from warming and acidification have been estimated as high as US$12 billion per year, with annual estimated costs from the loss of reef ecosystem services rising to US$1 trillion by 2100, directly and indirectly affecting many of the benefits we have so far taken for granted.

Alongside the high economic impacts from recent extreme storm event impacts, other *single* event economic losses related to ocean warming impacts already run from the tens to hundreds of million dollars. A major outbreak of Paralytic Shellfish Poisoning in 2012 and 2015 along 200km of coastline of Tasmania triggered a global product recall and loss to the local economy of AU$ 23million. A single coral bleaching event in South-east Asia suggested an economic loss of services to dive tourists in the order of US$49-74 million for the six-month period during and following bleaching, whilst more recently the 2016 unusually strong El Niño pattern triggered the largest ever reported algal blooms and aquaculture fish kills in Chile causing losses of US$ 800million.

There are also early signs that human health is already being impacted by enhanced survival and spread of tropical diseases with increasing temperatures, particularly pathogenic species of bacteria in the genus Vibrio (one of which causes cholera) and harmful algal bloom species that cause a variety of neurological illnesses (such as Ciguatera). From a purely ocean perspective, human disease risk is most likely to be affected by changes in disease incidence for marine animals that are part of our diet, allowing for direct transmission of the pathogen to humans, or for infections of wounds exposed during recreational (e.g. bathing) activities.

There is already a fundamental concern for the economic effects and consequences ocean warming will have on global fisheries and aquaculture. Together they play a vital but often poorly acknowledged role in global food security, providing 4.3 billion people with ~15% of their average per capita intake of animal protein. By 2050, an additional 75 million tonnes of fish will be needed to help feed more than 9 billion people, but warming of the world's ocean could disrupt these important initiatives with projected decreases in fisheries production in some countries and increases in others. Similarly, the prime locations for mariculture are expected to be altered by ocean warming, resulting in changes in yield patterns among countries.

The costs of this for countries could be high as we know key species are vulnerable to ocean warming impacts, such as tuna, and they account for 8% of the $129 billion value of internationally traded fishery products. Rapid population growth, fish exports and poor fisheries management also affect availability of fish in many developing countries. These drivers often create a gap between how much fish is needed for good nutrition and local fish harvests. The main effects of ocean warming will be to alter (increase or decrease) the gap, with the greatest changes expected in tropical and subtropical countries. Closing this gap will require the expansion of environmentally sustainable mariculture (and freshwater aquaculture), or even re-allocating some of the catch of large and small pelagic fish taken by industrial fleets to small-scale fishers, and/or arranging for industrial fleets to land more of their catch in local ports. From the community perspective, the greatest human losses will likely fall upon those people who rely upon the ocean for day-to-day subsistence – typically in these poorest coastal nations.

With issues of such importance at stake, we need to vastly improve the science and knowledge available as we move forward into an increasingly compromised ocean world. This is a common conclusion of many scientists across many sections in Chapter 3. As the global community through action, or sadly and probably inaction, increasingly commits itself to a high carbon future, knowledge of ocean warming and biological interactions will become invaluable in working out how we cope with the impacts and changes that become evident and prevalent, and impact and alter our way of life.

With the realization that ocean ecosystems are vulnerable to human threats such as overfishing, climate change, eutrophication, habitat destruction, pollution and species introductions there is an increasing imperative to observe ocean biology in a more integrated fashion in order to provide the long-term baselines needed for management actions and research. Historical datasets will need to be maintained and where possible expanded into new areas of the world's ocean where there are little or no sustained observations, including the open and the deep ocean and seabed Area. Many new international research initiatives such as Global Earth Observation System of Systems (GEOSS) and Group on Earth Observations Biodiversity Observation Network (GEOBON) are being set up to address these issues and monitor these changes. Future biological monitoring of these open-ocean ecosystems, through an integrated and sustained observational approach, will be essential in understanding the continuing impacts of ocean warming and other stressors on oceanic systems.

Improvements in ecosystem and coupled climate models are needed to provide a comprehensive overview of ecosystem change and directions of change in the future. A repeated problem in this respect is being able to resolve sufficient detail to make models more applicable at the regional scale. Inadequacies in such systems already pose great challenges, for example, for estimating effects of climate change on the Antarctic marine ecosystem and for projecting future change. This is a widespread problem as there is a failure of the range of existing climate models to reach adequate consensus on future change in processes of air-sea interaction. Such uncertainty is an abiding feature of predictions of the future, and is why the improvement of climate model representation of the feedbacks in the climate system between the ocean and atmosphere is therefore a priority for more successful prediction.

More comprehensive observations may allow us through international collaboration to mitigate and adaptively manage some of their more detrimental impacts. More studies are needed in this respect. The impacts of ocean warming and other stressors will drive a new paradigm in ecological restoration towards active management and restoration. This will increasingly drive approaches from just 'protect' towards more active intervention to recover or restore, with a focus on sustaining resistance or increasing resilience in natural systems and their services, and increasing adaptive capacity. Increasing human interventions on the ecologically-sensitive design of artificial structures may become increasingly important as natural habitats are "squeezed" by sea-level rise. The viability of reducing impacts of warming by managing additional local stressors such as eutrophication, pollution and commercial and overfishing needs more investigation, but is clearly already a part of the strategy to sustain ocean benefits moving forwards. The rationale being that the more ecosystems are impacted, the less they will be resilient to gradual and on-set change. Blue skies research should also explore issues such as opportunities for maintaining ecological functions through species replacements or boosting resilience of cool-adapted populations through assisted *a priori* breeding with warm-adapted populations. Alongside this are simple needs such as good resolution maps of the distribution worldwide of ecosystems, habitats and species to put all such observations, plans, and actions into operation. It is perhaps surprising to many that we have yet to successfully complete even this most basic of steps. None of this however should detract from the urgency or need to reduce global CO_2 emissions which lies centrally at the heart of what the international community must achieve.

There are a number of overall recommendations that can be made in light of the evidence presented in this report:

1. **Recognition of impact severity**. There is a need to much better recognize the unequivocal scientific evidence that shows impacts on key marine and coastal organisms, ecosystems, and services are already detectable, and that high to very high risks of impact are to be expected by 2100, even under the low emissions scenario (RCP2.6). These impacts will occur across all latitudes, making this a global concern beyond the usual North/South divide.

2. **Concerted joined-up global policy action for ocean protection.** There is a need to join up action across global conventions and agreement on climate change and environmental protection. Action must be taken in light of these findings on ocean warming to accelerate and dramatically scale-up area-based, effective, and full protection of marine ecosystems, and to implement much better sustainability measures across the entire ocean. Similarly, species assessment and advice, such as IUCN's Red List, must ensure that ocean warming impacts are fully integrated into assessments, findings and actions.

3. **Ensure comprehensive protection and management**. There is a need to ensure that we very rapidly fill gaps in protective regimes, such as protecting the High Seas and the seabed Area – the ocean and sea floor beyond the jurisdiction of any single country – under a new Implementing Agreement under the Law of the Sea, as well as expanding global convention to actually be 'global' – such as expanding the World Heritage Convention to take action across the High Seas and seabed Area.

4. **Updated risk assessments**. A re-evaluation will be needed on the risks that impacts from ocean warming and other stressors pose to humanity, to the viability of the very species and ecosystems involved, and to the provisioning of goods and services we derive from them. As documented in this report vast change is underway and will be locked in for many decades – there is an urgency to determine what risk this holds for now and for the future so we can mitigate, plan and adapt accordingly.

5. **Updated economic analysis.** New and updated economic analysis is needed on the scale, nature and effects of impacts from ocean warming and other stressors. This is both in terms of the severity of impacts that are being felt, and are being predicted, but also on how such impacts may affect regional economies as high worth services are affected (e.g. coral reefs, kelp forests, mangroves, seagrass, etc.) and the distribution of valued assets diminish or increase (e.g. economically valuable species such as tuna, krill, etc.).

6. **Closing gaps in fundamental science and capability needs**. There is a need to rapidly assess the science, observing and modelling capacity and needs in light of the widespread changes happening from ocean warming and other stressors. This report has repeatedly highlighted fundamental and massive gaps in our understanding that already compromise even our basic ability to understand and predict with any confidence what changes already underway may mean to our wellbeing. Whilst some of the ocean warming-related science and capability needs right now may not sit easily against other priorities for governments, as the planet changes we may regret the day we didn't take action on them early enough to give us the essential data we will need in the future.

7. **Achieving rapid and substantial cuts in greenhouse gases.** Greenhouse gas mitigation at the global scale is the overarching solution that will determine the future of all other solutions (protect, repair, adapt). As a result, rapid and substantial reductions of greenhouse gas emissions are required. Through the implementation of the Paris Agreement under the UNFCCC, Parties should now put forward rapid and substantial reductions of greenhouse gases, and consider ocean impacts in the so-called "nationally determined contributions" (NDCs) outlining national best efforts towards a sustainable low carbon future. The concerns among the scientific community is that as atmospheric CO_2 increases, the options for the ocean (i.e. mitigate, protect, repair, adapt) become fewer and less effective. Time is not on our side and delays in taking action on greenhouse gas reductions close off future prospects that could otherwise help us cope with changes and impacts.

To conclude, the evidence in this report shows a complex story of change in the ocean, change that is underway, is often already locked in for future decades, and is beginning to impact on all our lives whether it is obvious or not. This is no longer a single story of challenges to coral reefs, but stories of changes across species and at ecosystem scales, and across geographies and the entire world. It is pervasive change, driven by ocean warming and other stressors that are already operating across scales and in ways we only barely understand. It is critical that we sit up and recognize these issues and act, or we will be poorly prepared, if at all, for an uncertain changing future.

The ocean lies at the heart of the climate system and so must now lie at the heart of climate discussions. We have perhaps become distracted by our daily issues on land, and have been ignoring the impact climate has been having on by far and away the majority of the living space on the planet – the ocean. A relevant architecture must now be developed to put the ocean at the heart of climate discussions. The scale and nature of impacts we are seeing are already running way ahead of what we know, and importantly, what we are apparently capable of acting on. Adaptation action is already needed to evolve short- and long-term management strategies for the ocean. This most likely will require increased levels of support and investment. Finally, and most critical, is the need to address atmospheric CO_2 and achieve rapid and significant reductions in what we emit. To do otherwise will be to 'sleepwalk ourselves into a nightmare', where no level of conservation action in the future will be enough to override the impacts in order to save many of the ocean's species, ecosystems and benefits we currently rely on and take for granted.

About IUCN

IUCN is a membership Union uniquely composed of both government and civil society organisations. It provides public, private and non-governmental organisations with the knowledge and tools that enable human progress, economic development and nature conservation to take place together.

Created in 1948, IUCN is now the world's largest and most diverse environmental network, harnessing the knowledge, resources and reach of more than 1,300 Member organisations and some 16,000 experts. It is a leading provider of conservation data, assessments and analysis. Its broad membership enables IUCN to fill the role of incubator and trusted repository of best practices, tools and international standards.

IUCN provides a neutral space in which diverse stakeholders including governments, NGOs, scientists, businesses, local communities, indigenous peoples organisations and others can work together to forge and implement solutions to environmental challenges and achieve sustainable development.

Working with many partners and supporters, IUCN implements a large and diverse portfolio of conservation projects worldwide. Combining the latest science with the traditional knowledge of local communities, these projects work to reverse habitat loss, restore ecosystems and improve people's well-being.

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