



THE VALUE OF OFFSHORE MARINE PROTECTED AREAS FOR OPEN OCEAN HABITATS AND SPECIES



Marine and Coastal Biodiversity Management
in Pacific Island Countries



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The MACBIO project supports partner countries in collecting and analyzing spatial data on different forms of current and future marine resource use, establishing a baseline for national sustainable development planning.

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THE VALUE OF OFFSHORE MARINE PROTECTED AREAS FOR OPEN OCEAN HABITATS AND SPECIES

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EXECUTIVE SUMMARY

This paper reviews the value of, especially, no-take marine protected areas (MPAs), specifically for protecting offshore areas. It describes open ocean habitats and explores the question of whether offshore MPAs can be effective in helping to ensure the future of the open ocean's pelagic and benthic habitats and species including large, wide-ranging and migratory fauna that inhabit all depths of the ocean.

The open ocean is defined here as areas beyond the 80-metre bathymetric contour, beyond shallow fringing and continental shelf reef-associated habitats, including the whole water column and seabed, and geomorphic features such as seamounts and pinnacles that rise directly from the deep sea. Long considered invulnerable, open ocean ecosystems are under increasing pressure from human activities, including industrial scale fishing, bycatch of non-target species, noise, pollution and litter associated with shipping (including cruise shipping), marine debris, non-renewable resource extraction and climate change.

No-take MPAs are the best conservation tools available to protect marine species and habitats and to conserve marine biodiversity. Offshore MPAs are an effective, affordable, simple and equitable tool to conserve oceanic habitats and communities, including highly mobile and migratory species.

Recent scientific findings support the assertion that offshore species and habitats benefit from offshore MPAs, because:

- The open ocean, far from being featureless, has distinctive and interlinked bathymetric layers, biogeographic regions within each layer that may or may not overlap, and distinctive hydrodynamic (e.g. eddies, currents, fronts, vertical boundaries) and geomorphic features (e.g. seamounts, trenches, islands) that can be mapped and characterised.
- Pelagic species are not uniformly distributed, but tend to aggregate around bathymetric and hydrographic features that are predictable in space and time. Even species identified as highly migratory display predictable movement patterns where the majority (70-90 %) of the population moves no farther than 600 kilometres (km).
- Protecting even a part of species' ranges or life cycles, especially critical habitat areas which function as important feeding or breeding grounds, reduces overall population decline. Partial protection works best in a coordinated approach; for example, implementing a combination of no-take MPAs and areas of limited fishing effort or gear restrictions.

Critics of offshore MPAs have focused on three major assumptions. In this review, we find each assumption to be incorrect. We respond, in detail, to each assumption by synthesising the most recent research addressing the issues raised. In summary:

Size: Offshore MPAs have to be very large to encompass an adequate portion of pelagic species' home ranges.

This assumption is flawed. Firstly, offshore MPAs are not always aiming to protect just pelagic species and, in fact, when they are, strategically placed and/or multiple, smaller MPAs encompassing an adequate proportion of home ranges (now understood to be smaller, on average, than generally thought) can have significant, positive impact upon pelagic species.

Fisheries management: There is some scepticism about the use of offshore MPAs as a fisheries management tool, with concerns about displaced fishing effort.

Best practice fisheries management requires application of many different management tools, which ideally includes a range of MPAs. This has already been shown to work, and displaced fishing effort is often offset by "spillover" of adult and larval target species from populations inside MPAs as they recover from fishing pressure.

Governance: There is concern that arranging governance and enforcement, both within a country's exclusive economic zone (EEZ) and across boundaries, is too challenging.

Remote sensing and satellite technologies are already being used within Pacific Island countries to an increasing degree with increasing sophistication to address multiple maritime compliance issues (e.g. to do with tuna and other offshore fishing, border protection, smuggling, shipping safety). These technologies can be harnessed to support compliance with any offshore MPAs.

Offshore MPAs are most effective when established in combination with other management arrangements, including non-spatial tools such as catch or bycatch limits in fisheries, limited entry systems for mining or fisheries, or ballast water and discharge regulations for shipping, effective maritime compliance regimes, policies supporting a scientific approach to adaptive management, and performance monitoring and evaluation protocols.

No-take MPAs, both inshore and offshore, reduce human pressure and help protect the ecosystem services our marine environment provides. They represent our best chance to preserve populations, biodiversity, habitat and food web integrity, and give species and habitats a buffer to withstand and recover from the large-scale, pervasive and unpredictable effects of climate change. As well as pelagic habitats, offshore MPAs also protect deep-sea benthic and demersal ecosystems that are linked to the entire vertical pelagic realm above them. Larger-scale MPAs have greater capacity to protect greater diversity, larger habitats, and entire trophic webs and ecological processes. Nations are responding to the evidence that open ocean no-take MPAs work by implementing them within and beyond their boundaries, including some which are very large. Globally, there are now 10 no-take MPAs larger than 100,000km², and the number is growing. Other types of MPAs can be part of an MPA network that will encourage the sustainable use of marine resources. With sufficient capacity support, the establishment and management of offshore MPAs is well within the capabilities of Pacific governments and will help them maintain the ocean ecosystem goods and services that benefit their people.



1 INTRODUCTION

The open ocean, long considered invulnerable, is under increasing pressure from human impacts (Halpern et al., 2008; Ramirez-Llodra et al., 2011; Verity et al., 2002). Here we define the open ocean as the areas seaward of the 80-metre bathymetric contour, beyond shallow fringing and continental shelf reef associated habitats, including the whole water column and seabed, and geomorphic features such as seamounts and pinnacles that rise directly from the deep sea (Ban et al., 2014). We chose the 80-metre bathymetric contour because this generally excludes continental shelf environments.

As coastal fisheries become depleted, and technological improvements allow fishing vessels to venture further offshore and into deeper waters, pelagic fish stocks and deep-water ecosystems are more at risk of overexploitation than ever before (Baum et al., 2003; Huvenne et al., 2016). Eighteen years ago, researchers already reported that “almost 70 percent of fished stocks are listed as ‘fully fished, overfished, depleted, or recovering’” (Boersma and Parrish, 1999). Numerous heavily exploited species are now of conservation concern, including tuna, billfish and sharks (Collette et al., 2011; Ferretti et al., 2010). For instance, almost all sharks recorded by Baum *et al.* (2003) underwent a 50 percent decline over the 15 years of their study.

Currently, all tuna stocks – even widely distributed and fecund species - are considered fully exploited or overfished (Passfield and Gilman, 2010). In the open ocean, overfishing affects species ranges, ecological linkages, community composition and trophic functioning in both the horizontal and vertical dimensions (Roberts, 2002; Worm and Tittensor, 2011). The relatively low productivity, weaker governance and data deficiency of the open ocean makes it likely that much of the fishing activity targeting pelagic species is unsustainable (Norse et al., 2012). Other threats to the open ocean are the issues of bycatch of non-target species, noise, pollution and litter associated with shipping (including cruise shipping), non-renewable resource extraction and climate change (Ban et al., 2014).

Marine protected areas (MPAs), are defined here as “*a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values*” (Day et al., 2012). No-take MPAs, where all extraction is prohibited, are considered the best conservation tools available to protect marine species and habitats from exploitation and damage, and to conserve marine biodiversity and build resilience to other impacts (Costello, 2014; Graham et al., 2011). They can also help maintain or restore native species diversity, habitat diversity and heterogeneity, keystone species, connectivity and important ecological processes (Green et al., 2013). The capacity for well-designed no-take MPAs to meet their objectives (Foley et al., 2010) is increasingly well-documented, especially the benefits to populations of exploited species (Babcock et al., 2010; Edgar et al., 2008; Graham et al., 2011; Halpern and Warner, 2002; Tancell et al., 2016). When species diversity is protected, rates of resource collapse decrease and recovery potential and ecosystem stability increase, sometimes exponentially (Ferretti et al., 2010; Worm and Tittensor, 2011). Protection of exploited species and their habitats by reducing factors such as extraction and pollution makes ecosystems more resilient and therefore better able to withstand the effects of climate change. (Hughes et al., 2010; Mumby and Hastings, 2008; Worm et al., 2006). Also, sustaining marine ecosystems means maintaining the ecosystem goods and services that they provide (Hoegh-Guldberg et al., 2015). However, their application to open ocean environments is being challenged due to the dynamic nature of oceanic habitats, the lesser knowledge about offshore pelagic and benthic communities, the mobile nature of larger species that inhabit the open ocean, physical and biological complexity in both the horizontal and vertical planes of the ocean, and issues related to design, enforcement and governance, especially in the case of the “high seas”, or areas beyond national jurisdiction (Ban et al., 2014; Game et al., 2009; NOAA, 2017). Indeed, some studies have found no effect of small no-take MPAs on some pelagic species (Santana-Garcon et al., 2014).

This report, for the first time, reviews all current knowledge and issues pertaining to MPAs in the open ocean. It considers the arguments raised against their implementation and synthesises information to address the issues that may make spatial protection in the open ocean challenging. We explore the characteristics of open ocean ecosystems and species, review emerging research methods, and discuss possible answers to the question: Do no-take MPAs work for open ocean pelagic and benthic habitats and species, including migratory species?



2 THE CASE FOR OFFSHORE MPAS

There are significant gaps in knowledge about the effectiveness of no-take MPAs in protecting offshore pelagic and benthic habitats and species (Claudet et al., 2010; Dunne et al., 2014; Palumbi, 2004), but knowledge gaps are a common obstacle in marine environments, and can be overcome with robust design principles (Fernandes et al., 2005). Increasing evidence suggests that no-take MPAs can benefit open ocean habitats and communities, including highly mobile and migratory species (Koldewey et al., 2010; Mills and Carlton, 1998). And, obviously, larger no-take MPAs bring more benefits than smaller MPAs (Edgar et al., 2014; Santana-Garcon et al., 2014).

Arguments such as high cost, difficulty of implementation and enforcement and low chance of success have been used to deter governments from implementing them (Hilborn, 2016; Kaplan et al., 2010). Nevertheless, in recent years, governments consider that the benefits outweigh the costs of large no-take MPAs as evidenced by the growth in number of large-scale MPAs, including on the high seas (O’Leary et al., 2012); there are now 10 MPAs larger than 100,000 km² (Leenhardt et al., 2013) (Figure 1). For offshore pelagic and benthic species and habitats, including highly migratory species and poorly understood planktonic, nektonic and sub-surface community assemblages, however, there is still a need to gather empirical evidence of the effectiveness of fixed-area MPAs (Kaplan et al., 2014, 2010; Palumbi, 2004).

Positive, measurable no-take MPA effects on pelagic species exist (Baum et al., 2003; Claudet et al., 2010; Jensen et al., 2010; Worm et al., 2003), including for large migratory species such as marine mammals, large predators (Beare et al., 2010; Hooker and Gerber, 2004; Jensen et al., 2010; Roberts and Sargant, 2002) and seabirds (Young et al., 2015). Offshore MPAs can be used to protect highly mobile and migratory species at highly vulnerable stages of their life cycles by encompassing seasonal breeding or feeding grounds, other aggregation areas or key parts of their migratory routes (Hooker and Gerber, 2004; Louzao et al., 2006; Palumbi, 2004; Young et al., 2015) and all habitats critical to the survival of the species (critical habitats). Spawning aggregations in particular are increasingly shown to be temporally predictable, and therefore both vulnerable to exploitation and responsive to protection (Gell and Roberts, 2002; Pears et al., 2006; Roberts and Sargant, 2002).

Protecting vulnerable areas such as breeding or spawning grounds can result in a greater source of larvae or young to the exploited part of the population, resulting in improved breeding success and lower mortality overall, as well as more sustainable fisheries (Harrison et al., 2012; Lauck et al., 1998). Some researchers have suggested that protecting at least 30-50 percent of a species’ total habitat would afford it adequate protection (Clark, 1996; Lauck et al., 1998), while others argue that for species that undertake extensive migrations, spatial protection must be coupled with strict harvest quotas (Gerber et al., 2003). Furthermore, any spatial protection that aims to encompass biologically significant parts of large species’ life cycles is highly likely to also protect highly abundant and diverse communities of smaller pelagic species (Hyrenbach et al., 2000).

Large-scale offshore MPAs have the capacity to protect greater diversity, larger habitats, entire trophic webs and ecological processes (Maxwell et al., 2014). As well as pelagic habitats, offshore MPAs would protect deep-sea benthic and demersal ecosystems that are closely linked to the entire vertical pelagic realm above them, but remain poorly understood and are at risk from activities such as trawling, oil and mineral exploration, and sea dumping (Davies et al., 2007; Huvenne et al., 2016; Norse, 2005; Williams et al., 2010). Protecting entire bioregions¹ can preserve pathways of horizontal and vertical connectivity without the need for the more complex conservation planning usually needed to establish an MPA network (Green et al., 2013; Jones et al., 2007).

Globally, the success of MPAs increases when they are no-take, well-enforced, old, large, and naturally isolated by physical features (Edgar et al., 2014). Because of the vast extent and three-dimensional nature of oceanic ecosystems and the increased understanding of their value, no-take MPAs in the open ocean are rapidly expanding in the planet’s “last frontier of conservation management” (Game et al., 2009; Micheli et al., 2004; Pala, 2009). However, before the question of whether offshore MPAs truly work is addressed, it is important to consider the particular characteristics of open ocean habitats and species.

¹ A marine bioregion is defined as an area of the marine environment whose limits are defined by the geographical distribution of biophysical attributes and ecological systems; the groups of animals and plants, and the physical features within a biological region (or bioregion) are relatively distinct from the surrounding biological regions (or bioregions) (adapted from ANZECC, 1996).

VERY LARGE MARINE PROTECTED AREAS

> 100,000 km²



28 MPAs totaling

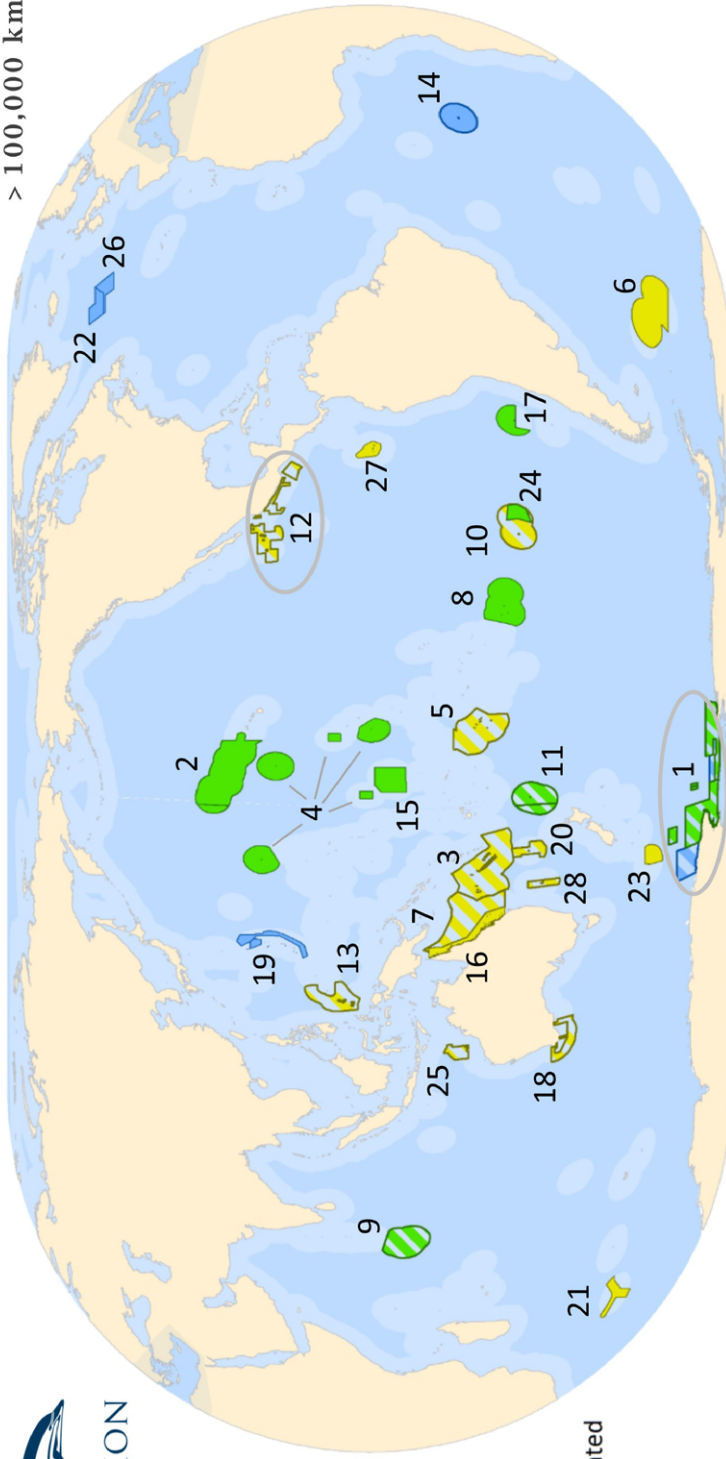
4.4% of the total ocean area

■ No-take Marine Reserve

■ Multi-zoned (with some No-take) Marine Protected Area

■ Other Marine Protected Area

Officially designated, unimplemented



- | | | |
|---|---|---|
| 1 Ross Sea Protected Area* 1,549,000 km ² (CCAMLR, 2016) | 15 Phoenix Islands Protected Area 408,250 km ² (Kiribati, 2006) | 22 Charlie Gibbs North High Seas Area 178,651 km ² (OSPAR, 2010) |
| 2 Papahānaumokuākea Marine Nat'l Monument 1,508,870 km ² (USA, 2006, 2016) | 16 Great Barrier Reef Marine Park 345,400 km ² (Australia, 1975) | 23 Macquarie Island Marine Reserves 162,000 km ² (Australia, 1999) |
| 3 Natural Park of the Coral Sea* 1,368,806 km ² (France, 2014) | 17 Nazca-Desventuradas Marine Park 297,518 km ² (Chile, 2015) | 24 Motu Motiro Hiva Marine Park 150,000 km ² (Chile, 2010) |
| 4 Pacific Remote Islands Marine Nat'l Monument 1,270,000 km ² (USA, 2009, 2014) | 18 South-west Corner Commonwealth Marine Reserve* 271,898 km ² (Australia, 2012) | 25 Argo-Rowley Terrace Commonwealth Marine Reserve* 146,099 km ² (Australia, 2012) |
| 5 Marae Moana - Cook Islands Marine Park* 1,065,000 km ² (Cook Islands, 2012) | 19 Marianas Trench Marine Nat'l Monument 246,608 km ² (USA, 2009) | 26 Charlie Gibbs South High Seas Area 145,420 km ² (OSPAR, 2010) |
| 6 South Georgia & South Sandwich Islands Marine Protected Area 1,000,700 km ² (UK, 2010) | 20 Norfolk Commonwealth Marine Reserve* 188,433 km ² (Australia, 2012) | 27 Galapagos Marine Reserve 133,000 km ² (Ecuador, 1998) |
| 7 Coral Sea Commonwealth Marine Reserve* 989,842 km ² (Australia, 2012) | 21 Prince Edward Islands Marine Protected Area 180,000 km ² (South Africa, 2009) | 28 Lord Howe Commonwealth Marine Reserve* 110,149 km ² (Australia, 2012) |
| 8 Pitcairn Islands Marine Reserve 834,334 km ² (UK, 2015) | 9 Chagos Protected Area 545,000 km ² (UK, 2010) <i>Status Uncertain</i> | |
| 9 Easter Island Marine Park* 631,368 km ² (Chile, 2015) | 10 Kermadec Ocean Sanctuary* 620,000 km ² (New Zealand, 2015) | |
| 11 Pacific Remote Islands Marine Nat'l Monument 1,270,000 km ² (USA, 2009, 2014) | 12 Pacific Mexicano Profundo* 577,800 km ² (Mexico, 2016) | |
| 12 Palau National Marine Sanctuary 500,000 km ² (Palau, 2015) | 13 Palau National Marine Sanctuary 500,000 km ² (Palau, 2015) | |
| 14 St Helena Marine Protection Zone 445,000 km ² (UK 2016) | | |

6 Jan 2017

CCAMLR—Convention of Antarctic Marine Living Resources OSPAR—Commission from the Oslo and Paris Conventions

FIGURE 1. Size and position of "Very Large Marine Protected Areas" (> 100,000 km²) As of January 2017.

From http://www.mpatlas.org/media/filer_public/10/33/10334e01-1583-47d6-a286-16491cedac93/vlmpa_jan2017.jpg

3 DEFINING OPEN-OCEAN HABITATS

Open ocean habitats are not homogeneous, as sometimes thought, but, rather, include a diverse range of relatively well-defined and stable pelagic, demersal and benthic habitats.

3.1 SPATIAL PATTERNS

For the purposes of marine planning, the open ocean differs from coastal or shallow habitats in the following major ways: 1) the bulk of species are planktonic, nektonic or sub-surface pelagic organisms; they tend to be widely distributed and are difficult to sample and map; 2) many oceanic species at higher trophic levels, and of conservation significance, are widely distributed, often migratory and wide-ranging; 3) the sizes and boundaries of biogeographical domains (patterns of co-occurrence of species, habitats and ecosystem processes) vary significantly both by geographic location (latitude and longitude) and by depth; 4) habitat types range from ephemeral (e.g. surface frontal systems) to hyper-stable (e.g. deep sea); and 5) linkages occur in both the vertical and horizontal dimensions (Ban et al., 2014). In the open ocean, vertical and horizontal linkages are critical in the transfer of physical (e.g., energy, heat), chemical (e.g., oxygen, nutrients) and biological (e.g., sinking detritus or “marine snow”, diel vertical migrations, migratory species) elements that support ecological structure and function” (Graf, 1989; Rex et al., 2006; Ban et al., 2014). In this sense, assemblages within each ocean layer interact with those above and below them, as well as those within horizontally adjacent areas.

The view that the deep ocean is physically and biologically homogeneous at depth is slowly being dispelled (Benoit-Bird et al., 2016). As knowledge about the open ocean increases, there are ways in which we can identify consistent patterns. There are features that are relatively stable, or appear regularly, in space and time, that can be mapped. This includes topographic features such as seamounts, rises, shelf breaks, canyons, ridges and trenches and their associated benthic habitats.

There are persistent, recurring hydrographic features such as currents, fronts, eddies and upwellings that can influence pelagic habitats at all depths (not just at the surface or at the bottom) and aggregate marine life into distinct communities or “hotspots” of productivity or biodiversity (Figure 2).

The deep open ocean varies dramatically in physical (especially light, temperature and pressure) and biological/ecological characteristics with depth. The ocean has at least five major layers: an epipelagic/photoc zone, mesopelagic/mesophotic zone, bathypelagic zone, abyssopelagic and hadal zone (Figure 2) each comprising a pelagic and, if bathymetry allows, a benthic component. The layers are interconnected vertically through the downward drift of marine snow, the vertical migrations of many species that feed closer to the surface at night, and the deep-diving behavior of some pelagic predators (Herring, 2002; Howey et al., 2016).

EPIPELAGIC OR PHOTIC ZONE. In the first 200m of open ocean, planktonic primary producers receive enough light for photosynthesis, and therefore form the basis of the food web. A complex food web has evolved around phytoplankton, zooplankton, planktivores of increasing size, and large oceanic apex predators. Hotspots of pelagic productivity, driven by seafloor topography, currents, fronts, eddies and upwelling, occur in this zone. Benthic communities in this zone are supported by coral and rocky reefs, islands and pinnacles rising from deeper zones.

MESPELAGIC OR MESOPHOTIC ZONE. From 200 to 1,000m, primary production is replaced by sinking organic matter (marine snow), including plankton, as the primary food source. Consumers either scavenge marine snow or sinking carcasses, or prey on each other. Similar assemblages exist as in the photic zone, but different species occur, such as copepods (free-swimming crustaceans) and siphonophores (free-swimming corals, hydroids and true jellyfish). Some siphonophores are the longest animals in the world; individuals can grow to 40 metres (www.siphonophores.org).

There is enough light for organisms to distinguish cycles of night and day, and the main thermocline occurs here (Sutton et al., 2008). Species are often pigmented red or transparent to evade predators in the low light. Below this zone, temperature tends to be relatively stable between +4 and -1°C. Oxygen minimum zones, with very low dissolved oxygen concentrations, can occur in this depth range. Many mesopelagic organisms (e.g. lanternfish, jellyfish, crustaceans) undertake vertical migrations to feed in shallower waters at night. Vertical connectivity between the photic and mesopelagic zones is bidirectional; many species of commercial value and conservation interest that frequent the photic zone (manta rays, sharks, toothed whales, tunas) regularly dive to at least these depths to feed (Howey et al., 2016; Jaine et al., 2014; Papastamatiou et al., 2015; Perez et al., 2017; Rodríguez-Cabello et al., 2016).

In the deeper half of the mesopelagic zone (500–1,000 m), it is estimated that up to 90% of deep-sea fish, 65% of decapod species, all but one species of euphausiid, 20–30% of copepods and most ostracods are bioluminescent (Herring, 2002). Benthic mesophotic communities include corals and fishes on the slopes of seamounts, which attract pelagic species.

BATHYPELAGIC ZONE. Between 1,000 and 4,000m there is no sunlight penetration, and conditions in any one location are relatively stable and uniform (Baker et al., 2007). Hydrostatic pressure continues to increase with depth. Organisms are adapted to the pressure and darkness, and pelagic diversity can be very high, including taxa such as fish (eg. anglerfish, hatchetfish and dragonfish), crustaceans, mollusks and jellyfish (Davoren, 2013). Adaptations include dark or black pigmentation, small eyes, bristles or other structures to aid buoyancy and bioluminescence.

The primary food source in this layer and those below is marine snow (Bochdansky et al., 2017). Changes in the availability of marine snow caused, for example, by changes in surface conditions, drive the temporal dynamics of biological processes and food webs (Rowe, 2013).

Hydrothermal vents are concentrated on the seafloor at this depth, forming rich and unique chemosynthetic communities. The seafloor tends to be covered in fine mud that has been found to host interstitial life. Benthic communities in this zone tend to be sparse and concentrated around fallen whale carcasses and other food sources, vents and seeps, seamount slopes and other topographic features. Where these communities do occur, they are characterized by high biomass, diversity and endemism, with strong cold-water characteristics (Sayre et al., 2017).

ABYSSOPELAGIC ZONE. From 4,000 to 6,000m is an area of immense pressure and very low temperature, inhabited primarily by decapods (e.g. deep-water swimming crabs and squat lobsters) and, in the deepest waters, by mysid shrimp. Hydrothermal vents can be found on the seafloor in this zone. The seafloor tends to be covered in fine mud. Benthic communities in this zone tend to be sparse and concentrated around fallen whale carcasses and other food sources, vents and seeps, seamount slopes and other topographic features (Smith et al., 2008).

HADAL ZONE. This habitat occurs in ocean trenches, below 6,000m, to a maximum depth of ~11,000m in the deepest parts of the ocean, the Marianas and Tonga Trenches. Jellyfish and viperfish are typical pelagic organisms, and benthic habitats can support patchy but rich assemblages. The seafloor tends to be covered in fine mud. Benthic communities in this zone, as with other ocean zones, tend to be concentrated around fallen whale carcasses and other food sources, vents and seeps, the sides of trenches and other topographic features (Smith et al., 2008).

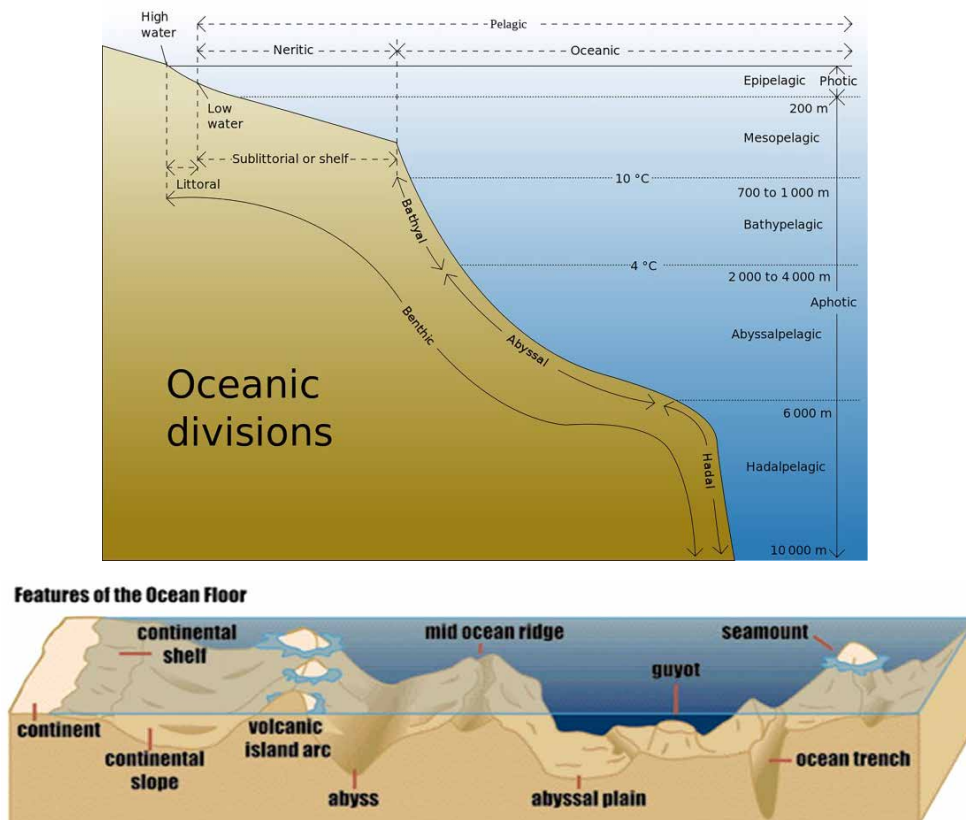


FIGURE 2. Schematic diagrams of oceanic zones and important topographic features.

Within each zone there are horizontal changes in physical and biological characteristics with latitude and longitude, at various spatial scales. These horizontal patterns may overlap vertically; these combinations create a three-dimensional mosaic of relatively stable habitats that support distinct pelagic assemblages. It is therefore possible to biogeographically classify the open ocean using physical, taxonomic, physiognomic and ecological geography dimensions.

3.2 BIOGEOGRAPHIC CLASSIFICATIONS

A very broad, global biogeographic classification of the open ocean exists, with 30 large-scale pelagic provinces, 38 benthic provinces based on depth (bathyal, abyssal and hadal) and 10 hydrothermal vent provinces, combining taxonomic, ecological and biophysical data (Figure 3, UNESCO, 2009).

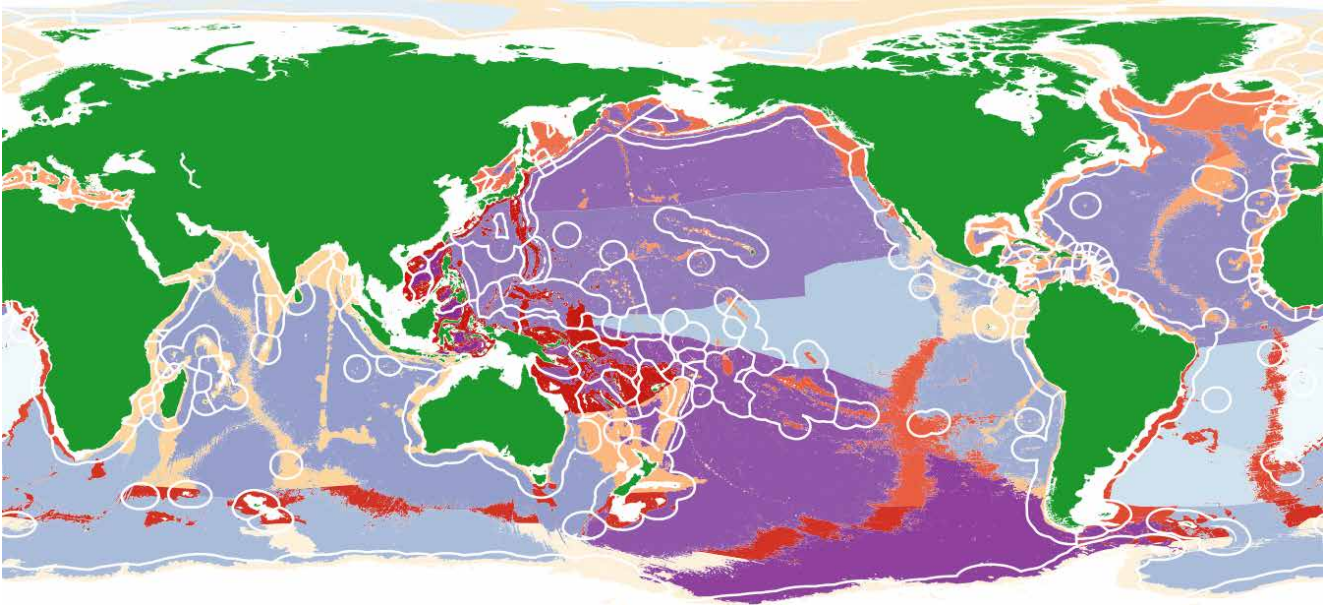


FIGURE 3. One example of a marine bioregional classification (UNESCO 2009; Watling et al 2013)

This is just one example; others include work by Spalding et al (2007) and Longhurst (2010); more recently, environmental data has been used to create three-dimensional maps of the ocean, resulting in a comprehensive set of 37 distinct volumetric region units, called ecological marine units (EMUs) (Sayre et al., 2017).

Horizontal structure within the photic surface layer has also been expressed biogeographically using the distribution of tuna and billfish communities (Reygondeau et al., 2012). It was found that tuna and billfish species form nine well-defined communities across the global ocean, each inhabiting a region with specific environmental conditions that were used to define biogeochemical provinces. A strong relationship exists between these highly mobile species and the physical and chemical characteristics of the global ocean, despite their high tolerance for a wide range of environmental conditions (Reygondeau et al., 2012).

A bioregionalisation of the ocean's mesopelagic zone (200–1,000m) was also recently developed, using information from the deep scattering layers (a biomass-rich layer of marine animals, found between 300 and 460m deep, thick enough to reflect sound waves), resulting in 10 distinct biogeographic provinces (Proud et al., 2017).

The biogeography of benthic bathyal fauna can be characterised into latitudinal bands (O'Hara et al., 2011). The bathyal ophiuroid fauna recorded by a number of separate expeditions was found to be distributed in three broad latitudinal bands, with adjacent faunas forming transitional ecoclines rather than biogeographical breaks. The spatial patterns were similar to those observed in shallow water, despite the order-of-magnitude reduction in the variability of environmental parameters at bathyal depths.

These classifications demonstrate both that there is a diversity of life within our oceans across horizontal as well as vertical planes, with a degree of predictable stability in that diversity.

These classifications are, however, too broad for use in national spatial planning efforts because, largely, the biogeographic provinces described encompass entire countries' Exclusive Economic Zones (EEZs). But the general approach and data usage are useful for potential application on a finer scale and have recently been applied by Wendt et al (in prep) to define 465 deep-water bioregions across the Southwest Pacific at a scale useful for national management efforts.

3.3 EMERGING RESEARCH AND METHODS

Identifying biogeographic boundaries, species distributions and special or unique areas in the open ocean is challenging, and has typically relied on environmental patterns that can be sampled remotely; new ideas and methods can significantly augment the ability to identify and define open ocean habitats.

Pelagic predator hotspots can help identify areas of increased production or biological activity where there are no other obvious signs marking aggregations in deeper waters (Davoren, 2013; Louzao et al., 2017). Using deep-diving pelagic predators as a guide, Benoit-Bird et al. (2016) described the spatial distribution of prey aggregations, and found that animals deep in the water column (from 600 to 1200m) are horizontally heterogeneous at scales from 10m to 50km. They used oceanographic profiles, trawl nets and active acoustic measurements to study pelagic assemblages along mid-water transects in the mesopelagic and bathypelagic zones. A number of horizontal physical patterns were observed at depth, including variations in fluorescence, scattering, and clarity.

Deep biomass can be successfully predicted from satellite-derived data on surface productivity (Vereschchaka et al., 2016). In the Mediterranean, Craig et al. (2010) found that surface chlorophyll concentrations correlated with the density of bioluminescent organisms in the mesopelagic layer, at depths of 500-1,000m. Because such a large proportion of deep-sea planktonic organisms are bioluminescent, they surmised that this would be a good proxy for overall biomass at depth.

Mesopelagic zooplankton abundance and biomass were tightly coupled to surface production over time scales of 10s of days. Species distribution modelling of well-known species has recently been used to explore species' mesopelagic and bathypelagic horizontal ranges, and distribution patterns for two common deep-water eels were found to correlate well with surface and bottom environmental variables such as oxygen, calcite and silicate concentrations (DeVaney, 2016).

Where pelagic assemblages are associated with deep-sea topographic features, the assemblage composition may be horizontally consistent over a large area, such as the bathypelagic assemblage associated with the northern Mid-Atlantic Ridge (Sutton et al., 2008).

A combination of Lagrangian analysis of remote sensing and biologging can be used to track the temporal and spatial variability of dynamic oceanographic features such as ecologically important fronts, and can help to explore possible trends associated with climate variability (Della Pella et al., 2017).

Louzao et al. (2017) used stable isotope analysis of deep-dwelling fishes to detect oceanic fronts at the surface. They found that isotopic latitudinal gradients were explained by pelagic oceanographic conditions along the study area, specifically indicating the presence of ecotone or biophysical transition zone.

Surface productivity effectively translates into the availability of marine snow, which links deeper assemblages with surface waters (Graf, 1989). The density and composition of marine snow also drives differences in deep pelagic communities, with distinct microbial assemblages attracted to different types of marine snow, and different species again present where marine snow density is low or absent (Bochdansky et al., 2017). Different microbial communities may attract different species of scavengers, leading to spatially delineated areas, especially under the more permanent surface features. It is possible that the distribution of detritus in the euphotic layer could, in the future, be used to predict boundaries of different community types in the bathypelagic layer. Seasonality or other forms of temporal variability in the availability of marine snow create more subtle, but measurable, temporal dynamics in the biological processes and food webs of the deep ocean (Rowe, 2013).

The vertical structure of physical variables (temperature and salinity) does not necessarily overlap across the horizontal bathymetric layers, and this can sometimes be reflected in the assemblage structure. For example, horizontal variability in chaetognath community composition in the Andaman Sea above the thermocline did not match the patterns found from the thermocline down to 500m (Nair and Gireesh, 2010). Vereschchaka et al. (2016) measured zooplankton assemblage composition and biomass at depths between ~2000 and 6000m and identified 300 taxa dominated by crustaceans, with latitudinal and longitudinal changes in community structure.

4 PREDICTABILITY OF BATHYMETRIC AND HYDROGRAPHIC FEATURES

There are persistent and predictable bathymetric and hydrographic features in the open ocean that can be located and mapped (Belkin et al., 2009; Harris et al., 2014; Hyrenbach et al., 2000; Miller and Christodoulou, 2014) (Table 1). Hyrenbach et al. (2000) distinguished between three types of distinctive oceanic features: 1) static systems, defined by topographic features; 2) persistent hydrographic features, such as currents and frontal systems; and 3) ephemeral habitats, shaped by wind- or current-driven upwellings and eddies.

All three types of features are known to enhance primary productivity and attract aggregations of marine life of all trophic levels at various depths, and may be identified by making use of sophisticated real-time satellite imagery (Game et al., 2009) or by analysing the foraging distribution of higher predators (Hyrenbach et al., 2000).

Seabed geomorphology features such as shelf breaks, canyons and seamounts provide benthic habitat for sessile and demersal species throughout all the depth layers, and alter the water flow above them, usually creating nutrient-rich upwellings and causing highly productive plankton blooms or swarms of planktonic and nektonic organisms (Genin, 2004; Sansón and Provenzale, 2009).

The biophysical processes that explain this include 'trophic focussing', where vertically migrating zooplankton is trapped; 'trophic subsidy' from enhanced horizontal fluxes of planktonic prey (Genin, 2004); enhanced productivity from upwelling of nutrient rich water to the euphotic zone along the side of the seamounts (White and Mohn, 2004); or from trapping the deep scattering layer (DSL) and diverting it to shallower water (Allain et al., 2006).

Some compelling information about the value of seamounts to pelagic species comes from fishers that target seamounts when fishing for tuna and other pelagic species. Interviews with Pacific Island fishers revealed that they spend an average of 40% of their time fishing near seamounts, and that the influence of seamounts on the catch rate of target species ranges to approximately 20km from the seamount (Passfield and Gilman, 2010). This information is valuable in the context of spatial planning for pelagic species, especially when setting boundaries to include seamounts.

While much is made of the importance of seamounts to pelagic species, the feeding of predators around seamounts must also affect seamount ecology (Passfield and Gilman, 2010). Some tuna aggregations, for example, may be present at an individual seamount for up to a period of weeks or months (Sibert et al., 2000).

Similarly, in bathypelagic fish assemblages that are directly associated with ridge systems, trophic linkages are likely to be bi-directional (Sutton et al., 2008). The trophic influence of pelagic species on demersal and benthic communities may be largely indirect, such as large, mobile pelagic species preying on demersal species, or on the predators of benthic prey (Allain et al., 2006). There is also an ontogenetic link between pelagic and benthic seamount habitats: most seamount benthic species have a pelagic stage, usually as juveniles (Allain et al., 2006). For instance, the armorhead (*Pseudopentaceros wheeleri*) is believed to have a pelagic stage from 1.5-2.5 years before recruiting to the seamount benthos (Boehlert and Sasaki, 1988).

Cold water corals and coral mounds can also have enhanced biodiversity, providing micro- to meso-scale habitats for pelagic organisms (Roberts et al., 2009). Turbulent water flow in the lee of islands and emergent reefs also serves to retain the planktonic food sources of pelagic fish (Rissik and Suthers, 2000). These features have been shown to act as highly effective natural aggregation devices for tuna and other migratory species, primarily for feeding (Hyrenbach et al., 2000; Morato et al., 2010), but also for breeding (Hearn et al., 2010). In terms of benthic-pelagic linkages, seamounts, ridges and open ocean islands provide a direct link between the photic zone and deep-sea habitats, influencing the diversity, density and behaviour of benthic and pelagic biota (Sutton et al., 2008).

Hydrodynamic features such as eddies, currents, upwellings, downwellings, oxygen minimum or maximum zones, and fronts are areas of high productivity or hydrodynamic structure, attracting aggregations of pelagic species that comprise entire food webs (Palacios et al., 2006; Yen et al., 2006). Temperature fronts, or water mass boundaries, are well-known as biological hot spots and migration corridors (Miller and Christodoulou, 2014). Predictable mesoscale (10s– 100s km) hydrodynamic features are particularly significant for attracting pelagic species, and can easily be identified and mapped with remote sensing technology (Scales et al., 2014).

The dynamic nature of these features fuelled an argument against spatial closures (Alpine and Hobday, 2007), but many of these features are predictable in space and time and can be tracked remotely (Game et al., 2009; Maxwell et al., 2011), even in the deeper layers. For instance, there is a known permanent oxygen minimum zone in the mesopelagic zone of the eastern tropical North Atlantic (Hauss et al., 2016). Pelagic hotspots can be identified and defined through electronic tagging studies, which provide information on species aggregations and interactions, or through remote sensing of characteristics (e.g., size, life span, seasonality, persistence) of observable ocean features that could affect biological productivity and animal distributions (Palacios et al., 2006).

Metrics for mapping pelagic biodiversity include: diversity measures for individual system components such as phytoplankton, zooplankton and fish; satellite Earth observation surrogate measures (thermal fronts, sea surface temperature (SST) and ocean colour); and indicators such as pelagic megafauna (e.g. basking sharks, cetaceans), seabirds and pelagic fish spawning areas (Jackson et al., 2009). For instance, tracking seabirds can aid marine spatial planning by highlighting areas of frequent use, which are typically highly productive and therefore attract other pelagic species (Tancell et al., 2016). Miller and Christodoulou (2014) mapped oceanic and shelf-sea fronts (boundaries of water masses of different temperatures) as a proxy for pelagic biodiversity during spatial planning for the establishment of MPAs in UK waters.

Building upon this generic understanding of the three-dimensional diversity of the ocean's pelagic and benthic systems, Wendt et al (in prep), have used 30 environmental data layers (including data at depth, e.g. bathymetry, temperature, salinity, P, Si, dissolved oxygen) to describe 465 deep-water bioregions across the SW Pacific.

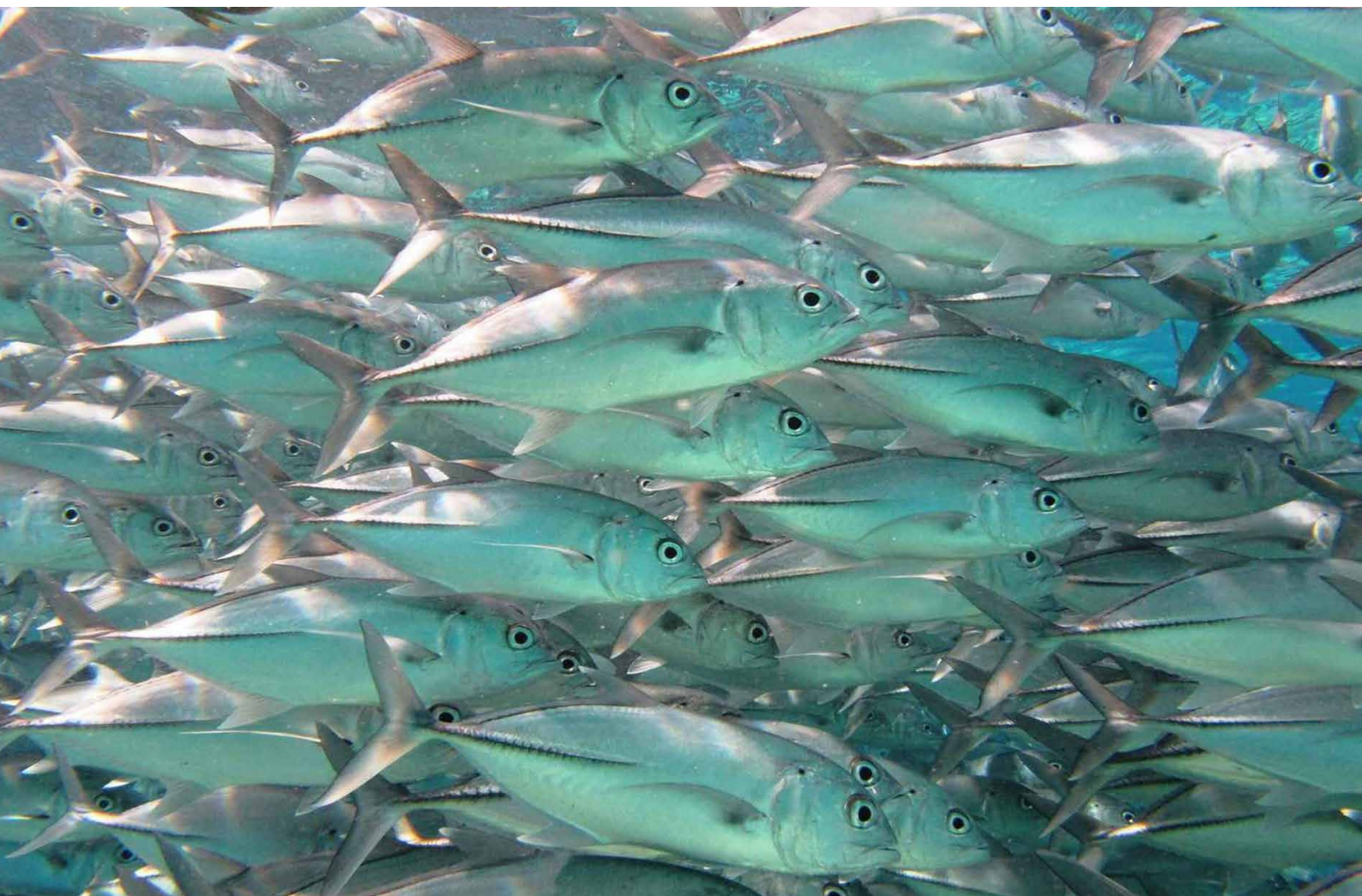


TABLE 1. Characteristics of some open ocean features that define them as different habitats

| TYPE | FEATURE | CHARACTERISTICS | KEY SOURCES |
|--------------|---|--|--|
| Topographic | Seamounts (and similar undersea elevations), ridges | Seamounts are “large isolated elevation(s), greater than 1,000m in relief above the sea floor, characteristically of conical form. Ridges are defined as “elongated narrow elevation(s) of varying complexity having steep sides, often separating basin features”. Seamounts and ridges have steep slopes which can cause the upward movement of nutrients from the deep ocean (upwellings) and create hotspots of pelagic productivity and biodiversity, attracting deepwater and pelagic species such as tuna, deep-water snapper, sharks, whales and dolphins. | (Harris et al., 2014; IHO, 2008; Morato and Clark, 2007) |
| | Canyons, trenches | Submarine canyons are steep-walled valleys with V-shaped cross sections. A trench is a long, narrow, usually very deep and asymmetrical depression of the sea floor, with relatively steep sides. Ocean trenches are the deepest parts of the ocean, commonly 6 to 10 km in depth. The steep walls of these features tend to create upwellings that support high productivity and biodiversity. Deep-diving pelagic species tend to congregate in the waters above these depressions to feed. | (IHO, 2008; Shephard, 1964) |
| | Shelf breaks | Shelf breaks are where the continental slope begins at the seaward edge of the continental shelf. Shelf breaks can form fronts in the waters above them, and tend to be highly productive pelagic habitats. | Belkin et al. (2009) |
| | Reefs, islands | Oceanic reefs and isolated islands can form as rises and pinnacles from the deep seabed and break the ocean surface. In their wake, there are often turbulent areas and eddies that entrain plankton and attract larger pelagic species. The deep slopes off the islands and reefs support rich benthic communities that are often habitat for feeding and breeding. | (Rissik and Suthers, 2000) |
| Hydrographic | Eddies | Eddies are vortex-like circulations of water, usually spinning off major currents, and can occur at various scales. Mesoscale eddies tend to be predictable, and can revolve in cyclonic or anti-cyclonic directions. Anticyclonic eddies accumulate organic matter within their cores and exhibit elevated microbial respiration and heterotrophic production. Cyclonic eddies enhance nutrient inputs to the surface ocean increasing new production and chlorophyll concentration. Current estimates suggest that ~50% of the global new primary production may be caused by eddy-induced nutrient fluxes. | Baltar et al. (2010) |
| | Fronts | A front is a narrow zone of abrupt change in water properties (salinity, temperature, nutrients, etc.) that separates broader areas with different water masses or different vertical structure. They can be a few metres or many thousands of km long. Most fronts are almost stationary and seasonally persistent. The vertical extent varies from a few meters to more than 1 km, with major fronts reaching depths exceeding 4 km. Major thermohaline fronts are associated with fronts in other properties, such as nutrients, ocean colour, chlorophyll, and turbidity. Convergences of surface waters towards fronts contribute to elevated primary production known as “hot spots” of marine life, from phytoplankton to apex predators, and serve as spawning, nursing and feeding areas for fish, sea birds, and marine mammals, with high biodiversity. The surface convergence can also lead to concentrations of pollutants, thus endangering species frequenting the fronts. | Belkin et al. (2009) |
| | Upwellings and downwellings | Upwelling is a process in which deep, cold water rises toward the surface, usually bringing nutrients from deeper pelagic layers and from the benthos to the upper layers. Downwelling is sinking of accumulated high density material beneath lower density material, such as colder or saline water beneath warmer or fresher water. Downwelling occurs warm surface water spins clockwise, creating surface convergence and pushing surface water downwards. | Saldivar-Lucio et al. (2016) |
| | Currents | Ocean currents are continuous, directed horizontal movement of seawater generated by forces such as breaking waves, wind, the Coriolis effect, cabbeling, temperature and salinity differences. Depth contours, shoreline configurations, and interactions with other currents influence a current’s direction and strength. Ocean currents can flow for large distances, and together, create the global conveyor belt which plays a dominant role in determining the climate of many of the Earth’s regions. They connect distant regions of the planet and transport water masses, migrating species, nutrients, pollution, debris, larvae and other components of the ocean. | Roemmich (2007) |



5 DO NO-TAKE MPAS WORK FOR OPEN OCEAN PELAGIC AND BENTHIC HABITATS AND SPECIES, INCLUDING MIGRATORY SPECIES?

A number of issues specific to offshore MPAs have been raised by critics to deter governments from implementing them (Table 2). Together, these issues are fuelled by three primary assumptions:

- **SIZE:** Offshore MPAs are aiming only to protected large migratory pelagic species and have to be very large to encompass an adequate portion of pelagic species' home ranges;
- **FISHERIES MANAGEMENT:** There is some scepticism about the use of offshore MPAs as a fisheries management tool, with concerns about efficacy and displaced fishing effort; and
- **GOVERNANCE:** There is concern that arranging governance and enforcement in the open ocean of a country's EEZ is too challenging.

Increasingly, these assumptions have fallen in the face of emerging knowledge and innovative solutions that highlight the benefits and possibilities offered by offshore MPAs (Table 2). In the following sections, we review the literature on characteristics of the open ocean and its inhabitants as they pertain to the question of offshore MPA efficacy.



TABLE 2. Summary table of issues, raised by critics of offshore MPAs for the protection of pelagic species, with explanations and proposed solutions. Table reproduced and extended from Game *et al.* (2009).

| ISSUE | | ASSUMPTION | SOLUTIONS AND COUNTER-ARGUMENTS |
|-----------------------------|--|---|---|
| Size | Many pelagic species are highly mobile, often covering thousands of kilometres annually. | Offshore MPAs mainly (or only) aim to protect large migratory pelagic species. Spatial protection is either impossible across whole ranges or for all life-history stages for large, pelagic species, or the area required for conservation management would be unreasonably large. | Offshore MPAs can be put in place to achieve multiple objectives, not just the protection of large, migratory pelagic species. Many threats to pelagic organisms are either site specific or cumulative, and can be reduced through spatial protection (Hooker and Gerber 2004). In addition, many organisms either show site fidelity or have relatively small and defined areas of critical habitat within their range or life histories (Hyrenbach <i>et al.</i> 2006, Louzao <i>et al.</i> 2006). The willingness and capacity of nations to establish large-scale offshore MPAs is increasing; there are already 10 MPAs >240,000 km ² (Toonen <i>et al.</i> , 2013). |
| | The pelagic ocean is characterized by physical processes that are dynamic in space and time. | The environment is too dynamic to be represented in static MPAs. Mobile MPAs would be too difficult to enforce. | Many important pelagic features are either spatially or temporally predictable, so static or dynamic MPAs need to be designed accordingly (Alpine and Hobday, 2007). Large-scale MPAs would have a high likelihood of including dynamic features (Toonen <i>et al.</i> , 2013). For features with less predictability, mobile fisheries closures have been effectively implemented off eastern Australia based on near real-time predictions of pelagic habitat (Hobday and Hartmann 2006). Governance issues are also addressed below. |
| Fisheries | Closing areas to fishing will increase fishing pressure in a smaller area | The “displacement effect” will deplete target populations in the remaining fished area | No-take MPAs can benefit target species into adjacent fisheries, both through the emigration of adults and juveniles and the export of propagules (Babcock <i>et al.</i> , 2010; Halpern <i>et al.</i> , 2010; Harrison <i>et al.</i> , 2012; Russ, 2002). This “spillover” effect must be integrated into analyses of displaced fishing effort as must the effectiveness of other fisheries management tools. The ecosystem service and biodiversity benefits gained from protection outweigh the minimal negative impacts upon according to economic impact assessments E.g.- the protection of 20 percent of the high seas may lead to the loss of only 1.8 percent of the current global reported marine fisheries catch (Sumaila, 2005). |
| | | Regulations or moratoria on gears or catch are more appropriate for limiting incidental capture of threatened pelagic fauna. | Although catch and gear regulations are an important component of pelagic conservation, they have so far proved inadequate in protecting many target and bycatch species. Offshore MPA can supplement other fisheries management tools. (Pauly <i>et al.</i> 2002). |
| Governance, design and cost | The open ocean is generally data-poor compared with terrestrial or coastal systems. | Lack of data on the complexities of deep ocean ecosystems limits the selection and design of offshore MPAs. | Widespread data sets, especially time-series data on remotely sensed physical and biological features (e.g., chlorophyll), are more abundant than commonly perceived (e.g. there are 70 available in the Pacific) and are useful for offshore MPA selection. In contrast to fisheries catch limits, the selection of offshore MPAs does not have to rely on full understanding of ecosystem functions. New methods and techniques for research and monitoring in the deep sea are advancing rapidly (e.g. Bouchet and Meeuwig, 2015). |
| | Use of the open ocean is generally difficult and expensive to observe, and it is therefore challenging to enforce regulations. | Offshore MPAs will be too difficult and expensive to enforce, especially in developing nations. | Widespread adoption of satellite VMSs, satellite technology and financial support for this in developing nations is already improving remote maritime surveillance and compliance. |
| | Offshore MPAs might need to extend outside a country’s EEZ. | Beyond national jurisdictions there is no legal basis for MPAs. | Numerous existing international and regional agreements can be exercised to regulate offshore MPAs in the high seas (Koldewey <i>et al.</i> 2010). Offshore MPAs might need to extend outside a country’s EEZ but should still be declared within the EEZ as a basis on which to make the claim for a high seas extension, or creation of a new offshore MPA in a neighbouring EEZ. |

5.1 HIGHLY MOBILE SPECIES

5.1.1 Movement habits of pelagic species

Migratory and highly mobile taxa make up only a small part of the open ocean's fauna, and yet they remain at the centre of the discussion about the adequacy of offshore MPAs. Before addressing the concerns about the adequacy of offshore MPAs for protecting these mobile species, it is important to consider that the bulk of pelagic biodiversity and abundance is made up of innumerable smaller pelagic species with relatively sedentary lifestyles, and that these species would also be protected within offshore MPAs (Sutton et al., 2008). In fact, it is estimated that the biomass of small deep-dwelling pelagic fishes is two to three orders of magnitude greater than the total global fisheries landings (Sutton et al., 2008). Broad diversity patterns of planktonic, nektonic and higher-order pelagic organisms tends to overlap, peaking at latitudes between 20 and 30° N or S (Trebilco et al., 2011). Diversity and biomass also vary vertically, and vertical connectivity occurs through most bathymetric layers (Sutton, 2013).

In practical terms, larger species can act as “umbrella” species which are being used to guide the identification of areas with greater overall biomass and biodiversity in the open ocean (Trebilco et al., 2011). A key argument against offshore MPAs is that they would need to be very large to adequately protect migratory species (Kaplan et al., 2010)(Table 2), some of which have been documented to travel >2000 km (Block et al., 2011). Kaplan et al. (2010) argue that the tropical skipjack tuna (*Katsuwonus pelamis*) does not undertake consistent feeding or breeding migrations, making it difficult to establish an offshore MPA for its protection in the right place. Similarly, the population of whale sharks protected by the Ningaloo Marine Park is in decline, due to intensifying threats elsewhere along its range (Bradshaw et al., 2008). Witt et al. (2011) tracked leatherback turtles and suggested that these species are so wide-ranging that at least 11 nations would need to be involved in their protection in the south Atlantic, and most of their range is outside national jurisdictions and therefore even more complex to protect.

However, others argue that it is not necessary to protect a species' entire range to benefit the population, and that positive results occur from protecting a species' preferred habitat during vulnerable life stages such as breeding or nesting, which tend to be predictable (Alpine and Hobday, 2007; Hamilton et al., 2015; Sibert and Hampton, 2003). A modelling study showed that because highly mobile species are often also the most heavily exploited, they are most likely to benefit from no-take MPAs (Micheli et al., 2004). Partial protection for migratory species has been shown to help protect populations (de Juan and Leonart, 2010; Pauly et al., 2002). The arguments against offshore MPAs are losing traction as the number of very large MPAs increases and evidence of their success is starting to emerge (Figure 1, Table 4).

In fisheries management, the phrase “highly migratory” can be derived from the long-range movements of a few individuals within a population, rather than those population as a whole (Grewe et al., 2015), with studies of individual tuna mobility demonstrating they would benefit from national-level closures (Robinson et al., 2016; Sibert and Hampton, 2003). There are species with subpopulations that demonstrate varying levels of sedentarism, referred to as “behavioural polymorphism” (Gruess et al., 2011). Even long-range migrants have preferences for certain combinations of physical variables such as temperature and oxygen concentrations (Carlisle et al., 2017), often staying within ‘high-use’ areas where those variables serve to concentrate prey (Eckert, 2006).

Species with the ability to undertake migrations of more than 1,000 nautical miles tend to move between 400-600 nautical miles on average (Table 3). For example, the lifetime displacement of skipjack tunas is 420-470 nm, and 20% less for yellowfin tuna (Sibert and Hampton, 2002), both distances being much less the maximum recorded distance travelled by an individual of the species. While this may take them across EEZ boundaries, there is a high likelihood that they may spend at least 50 percent of their time inside any given large MPA or network of MPAs (Sheppard, 2010), effectively complying with the guidelines set up by Clark (1996) and Lauck *et al.* (1998) for adequate protection. Furthermore, recent genetic research has found that the establishment of no-take MPAs is followed by evolutionary selection for individuals with decreased movement rates within decades (Mee et al., 2017). This was found especially true in areas with higher fishing pressure, even in tunas and sharks (Mee et al., 2017).

The evolution of decreased movement can, in turn, augment the efficacy of marine reserves, especially for species with short generation times, such as skipjack tuna (Mee et al., 2017). Sibert and Hampton (2003) state that while international arrangements are ideal, protection of tuna stocks within an individual country's EEZ is also highly effective. Furthermore, regional arrangements among neighbouring nations are likely to be sufficient to cover the range of many species (Sibert and Hampton, 2002).

5.1.2 Predictability of migratory or mobile species

Even highly migratory or mobile species have been found to travel and rest or aggregate along predictable pathways and locations defined by topographic or oceanographic features (Morreale et al., 1996; Scales et al., 2014). In fact, the predictability of movements and aggregations of terrestrial migratory species has already been applied to the protection of migratory species on land and is considered viable in the open ocean (Norse, 2005).

Unlike terrestrial and coral reef systems, where hotspots are defined in terms of biodiversity, many pelagic hotspots occur in areas of high chlorophyll concentration where highly mobile species spend time foraging, and are typically defined in terms of species richness, biomass or abundance (Reese et al., 2011). A study on dispersal and connectivity in deep-sea organisms, undertaken on the assumption that distances must be larger at depth, and with the implication that offshore MPAs would need to be much larger, found instead that predictability was comparable to shallow-water organisms (Baco et al., 2016).

The tendency for pelagic species to aggregate in predictable seasons and areas of ocean has made those at the top of the food web highly exploitable, and predicting the location of aggregations of commercially valuable species has been important in fisheries oceanography (Alpine and Hobday, 2007).

TABLE 3. Recorded movement distances for species caught by the Western and Central Pacific Ocean fisheries, either as target or bycatch species, and additional species of conservation significance.

| SPECIES | MOVEMENT DISTANCE | REFERENCE |
|----------------------------|--|--|
| Yellowfin tuna | 34 tunas tagged in the Coral Sea and recaptured, most along the New South Wales (NSW) coast within 200 nautical miles (nm) of release; longest straight-line distance between release and recapture was 569 nm after 9 months. 273 tunas tagged by game fishers, most recaptured within the Australian Fishing Zone less than 600 nm from release. Most tunas tagged by the Australian Commonwealth Scientific and Research Organization (CSIRO) in the Coral Sea were caught close to the release area. | Hampton and Gunn (1998) |
| | Median lifetime displacement of 336-376 nm, mostly northeast into EEZs of other Pacific Island nations. | Sibert and Hampton (2003) |
| | Average distance travelled for all individuals recaptured from 2006 to 2008 was 247 nm. | Industry & Investment (I&I) NSW (2009) |
| | Tagged individuals at liberty for 93-1773, of which 95% did not travel further than 810 nm from the release point. | Schaefer et al. (2014) |
| | Two tagged individuals made long-range movements (>4,000 km), but the vast majority were recaptured near their point of release, and within the same EEZ. | Itano and Holland (2000) |
| Bigeye tuna | Most tuna tagged by CSIRO in the Coral Sea were caught close to the release area. | Hampton and Gunn (1998) |
| | 90% of tuna captured within 150 nm of tagging location. | Clear <i>et al.</i> (2005) |
| Albacore tuna | Two individuals tagged and recaptured: one moved 302 nm, the other 1,727 nm. | I&I NSW (2009) |
| | Average distance travelled was 859.25 km. | Cosgrove <i>et al.</i> (2010) |
| Skipjack tuna | Median lifetime displacement ranges from 420 to 470 nm. | Sibert and Hampton (2003) |
| Broadbill swordfish | Median movement of tagged fish was 744 km. | Sedberry and Loefer (2001) |
| | Average distance travelled during 193 days was 30 ± 43 km. | Sepulveda <i>et al.</i> (2010) |
| Striped marlin | 90% of 360 tagged individuals were recaptured less than 1,000 km from the tagging location. | Jensen <i>et al.</i> (2010) |
| | Mean straight-line distance per fish was 921 ± 264 km. | Holdsworth <i>et al.</i> (2009) |
| | Average distance of 280 nm. | Squire Jr. (1974) |
| | The majority of striped marlin released off Australia have a mean displacement of less than 200 nm (after six to nine months). | Bromhead <i>et al.</i> (2004) |
| | Average distance travelled for all individuals recaptured from 2006 to 2008 was 214.2 nm. | I&I NSW (2009) |

| SPECIES | MOVEMENT DISTANCE | REFERENCE |
|----------------------------------|--|---------------------------------|
| Black marlin | Average short-term movement of five tagged marlin was 277.4 nm. | Gunn <i>et al.</i> (2003) |
| | Average distance travelled for all individuals recaptured from 2006 to 2008 was 727.5 nm. | I&I NSW (2009) |
| Sailfish | Average distance travelled for all individuals recaptured from 2006 to 2008 was 38.6 nm. | I&I NSW (2009) |
| Dolphinfish | Move distances of up to 440 km. | Kingsford and Defries (1999) |
| | Average distance travelled for all individuals recaptured from 2006 to 2008 was 112.6 nm. | I&I NSW (2009) |
| Wahoo | Can move more than 1,000 km. | Theisen <i>et al.</i> (2008) |
| Shortfin mako shark | Move between ocean basins, enough to cause a lack of genetic differentiation. | Schrey and Heist (2003) |
| | Approximately 75% of the makos travelled less than 500 nm from their original tagging location with a mean distance of 398. | Kohler <i>et al.</i> (2002) |
| | Average distance for seven juveniles tracked between six and 45 hours was 55 km. | Sepulveda <i>et al.</i> (2004) |
| | Average distance travelled for all individuals recaptured from 2006 to 2008 was 571 nm. | I&I NSW (2009) |
| | Tagged off eastern Australia, stayed within the region. | Stevens <i>et al.</i> (2010) |
| Blue shark | 82% of recaptured blue sharks travelled less than 1,000 km. | Queiroz <i>et al.</i> (2005) |
| | More than 75% of the blue sharks travelled less than 1,000 nm from their original tagging location with a mean distance of 463 nm. | Kohler <i>et al.</i> (2002) |
| | Average distance travelled for all individuals recaptured from 2006 to 2008 was 697 nm. | I&I NSW (2009) |
| | Tagged off eastern Australia, stayed within the region. | Stevens <i>et al.</i> (2010) |
| Porbeagle shark | More than 90% of tagged porbeagles travelled less than 500 nm from their original tagging location, with a mean distance of 234. | Kohler <i>et al.</i> (2002) |
| Thresher shark | Tagged off eastern Australia, stayed within the region. | Stevens <i>et al.</i> (2010) |
| Tiger shark | In a satellite tracking study, receivers detected inter-island movements by 6 (40%) tiger sharks with straight-line distances ranging from 106 to 318 km. | Holland <i>et al.</i> (1999) |
| Rough-toothed dolphins | Genetic differentiation shows that dolphins remain close to individual oceanic islands. | Albertson <i>et al.</i> (2017) |
| Humpback whales | Tagged whales travelled an average of 3116 km in between 19 and 45 days. | Rosenbaum <i>et al.</i> (2014) |
| Seabirds | 50% travelled under 1000 km for foraging; almost 100% less than 2000 km. | Weimerskirch (2007) |
| Wandering albatross | Wandering albatrosses travelled up to thousands of kilometres from the colony during incubation (mean: 1176 km, range: 61–3381) and brooding (mean 450 km, range: 88–1800). During the brooding period, adults made shorter trips (mean: 72 h, range: 5–286) compared to the incubation period (mean: 251 h, range: 63–559). | Louzao <i>et al.</i> (2011) |
| Black-browed albatross | Mean foraging ranges were between 969 and 4,557 km, depending on breeding stage. | Huin (2002) |
| Buller's albatross | The birds, tagged in the Snares island group south of New Zealand, had a dual strategy of short trips (mean duration 1.3 days, mean foraging range 129 km) and long trips to southern New Zealand (9.6 days, 871 km) or Tasmania (22.0 days, 1918 km). | Stahl and Sagar (2006) |
| White-chinned petrels | Individuals birds could travel >2000 km, but most chick-rearing trips were, on average, only 610 km from the colony. | Phillips <i>et al.</i> (2006) |
| Leatherback turtles | Tagged 46 female leatherback turtles, 12,095 tracking days between 2004 or 2007, with a mean track duration of 263 days, a distance of 8,070 km, and a travel speed of 37.7 km per day. | Shillinger <i>et al.</i> (2008) |
| | Tagged turtles travelled across the Atlantic but there were several key high-use foraging areas. | Eckert (2006) |
| | Tagged turtles in the Atlantic dispersed between 1079 and 7563 km from nesting beaches. | Witt <i>et al.</i> (2011) |
| | Tagged turtles in South Africa: half travelled 1000s of kms, but the other half remained within 500km. | Robinson <i>et al.</i> (2016) |
| Multiple deep-sea species | Estimates of dispersal distance ranged from 0.24 km to 2,028 km with a geometric mean of 33.2 km. | Baco <i>et al.</i> (2016) |

5.2 POPULATION DYNAMICS AND GENETICS

It is becoming clear that some highly exploited tuna populations can no longer be managed as single, ocean-wide stocks, and that the ranges of genetically different subpopulations of each species must be taken into account during management including spatial planning (Albertson et al., 2017; Grewe et al., 2015). The discrete populations are likely to be reproductively isolated units (Ward et al., 1994), so their response to both exploitation and protection will be different, depending on their relative productivities and levels of fishing mortality (Grewe et al., 2015).

Determining the range of a genetic stock or population of organisms, versus the range of an entire species or tagged individuals, can be challenging, but it is especially important in the case of exploited species (e.g. tuna) or species of conservation interest (e.g. whales). Identification of population structure and boundaries can be used to delineate fisheries management units, but also in spatial planning for offshore MPAs (Aguila et al., 2015).

Where populations are homogeneous globally or within oceans (Chiang et al., 2006; Laconcha et al., 2015; Veríssimo et al., 2017), genetic research can identify the critical spawning areas for each broad region (Albaina et al., 2013). Recent genetic techniques can also detect where subspecies may be more connected than previously thought (Malder et al., 2017). For example, genetic research in the Philippines and the Bismarck Sea indicates that yellowfin tuna, previously believed to be of a single stock in the Pacific Ocean, is composed of at least three genetically distinct populations (Aguila et al., 2015; Grewe et al., 2015). Skipjack tuna has long been known to exist as two genetically distinct subpopulations in the western Pacific; the boundary between the migratory ranges is at the Tasman Front (Fujino, 1976). Rough-toothed dolphins tend to stay close to oceanic islands, to the point of being genetically different between island groups (Albertson et al., 2017).

Given the predictability in migration pathways and important areas in many oceanic species, and given that important areas for one species or population are often also important for others (“hotspots”), finding such areas is becoming easier even in offshore habitats (Hyrenbach et al., 2000). Given the home ranges or movement distances captured in many tagging studies (Table 3), and that protecting ~50% of a species’ range can benefit the whole population (

Table 4), it is feasible to surmise that a network of no-take areas of between 150 and 500 km in diameter would be adequate to benefit many pelagic species. For the highly migratory striped marlin (*Kajikia audax*), reduction in fishing pressure over a small part of its range has already resulted in measurable improvement (Jensen et al., 2010).

5.3 EXISTING EVIDENCE OF OFFSHORE MPA BENEFITS

The limited data from relatively new large MPAs means that some of the evidence of their positive effects for large pelagic species comes from modelling or fisheries studies (Table 4) (Alpine and Hobday, 2007; Baum et al., 2003); effects on entire food webs and lower trophic groups are not generally studied.

Compelling proof comes from what is termed an “unintended experiment”: fisheries catch data were compiled after a large area of the North Sea (575,000 km²) had been closed to fishing during the six years of World War II (Beare et al., 2010). This study showed conclusively both increased abundance in pelagic (including migratory) species and larger proportions of older fish. In a more recent study, the protection of billfish from longlining in a part of their range off Baja California resulted in an overall population increase of up to 22 percent (Jensen et al., 2010). The recovery of whales following the combination of reduced whaling and the establishment of large whale sanctuaries also highlights the benefits of offshore MPAs that cover only parts of species’ ranges (Clapham et al., 1999; Richards, 2009). More recent reviews and meta-analyses have found increasing empirical evidence that highly mobile and large-bodied species exploited by fisheries tend to benefit from offshore MPAs of varying size (Claudet et al., 2010). Habitat use by seabirds can shed light on highly productive areas that can be prioritised for conservation, as shown by seabird tracking studies (Tancell et al., 2016).

TABLE 4. Summary of studies predicting offshore MPA effects for mobile and migratory pelagic species, using a variety of methods.

| SOURCE | TYPE OF STUDY | LOCATION | SPECIES | SUMMARY OF FINDINGS |
|--------------------------------|----------------------|----------------------|---|---|
| Clark (1996) | Opinion piece | Global | All exploited species | Offshore MPAs need to include up to 50% of a population or home range in order to protect a species from overfishing. Fisheries management not considered. |
| Lauck <i>et al.</i> (1998) | Modelling | Hypothetical | Hypothetical | Offshore MPAs need to include up to 50% of a population or home range in order to protect a species from overfishing. Fisheries management not considered. |
| Roberts and Sargent (2002) | Modelling | Hypothetical | Hypothetical migratory fish | Protecting important aggregation areas has a disproportionate effect on entire populations of highly mobile and migratory species. |
| Baum <i>et al.</i> (2003) | Modelling | Northwest Atlantic | Sharks | Priority areas for shark conservation are highlighted. Population benefits for sharks with fishing closures of different areas are modelled. Offshore MPAs coupled with reductions in fishing effort have positive effects on sharks and other large pelagic predators. |
| Gell and Roberts (2002) | Review | Global | All species | Highlights reversal of notion that mobile species cannot be protected by offshore MPAs. Even for highly mobile species, a portion of the population may remain within a small home range. Protecting migration bottlenecks, nurseries, spawning or feeding aggregation sites can benefit even highly migratory species. |
| Worm <i>et al.</i> (2003) | Modelling | Northwest Atlantic | Pelagic species, primarily predators | Identifies pelagic diversity hot spots associated with productivity and habitat features. Protecting hot spots from fishing has large benefits for pelagic populations. Identifies pelagic predator diversity hot spot in Great Barrier Reef/ Coral Sea area. |
| Willis <i>et al.</i> (2003) | Empirical, modelling | Northern New Zealand | Snapper (<i>Pagrus auratus</i>) | Density and size of snapper increase inside offshore MPAs, despite its high mobility. |
| Hooker and Gerber (2004) | Opinion piece | Global | Predators and megafauna | Offshore MPAs are beneficial for protecting predators and other megafauna (e.g., cetaceans, seabirds). Present tools and approaches for enhancing offshore MPA effectiveness. |
| Micheli <i>et al.</i> (2004) | Meta-analysis | Global | All species | Highly mobile species benefit from offshore MPA protection. |
| Palumbi (2004) | Review | Global | All species | Shows positive, neutral or negative impacts of offshore MPAs depending on certain factors and states, "If fishing effort is not displaced, then the impact of MPAs on highly migratory species is similar to the effect of decreasing fishing effort by the same percentage as the percent area dedicated to MPAs." |
| Hyrenbach <i>et al.</i> (2006) | Empirical | Central California | Black-footed albatross (<i>Phoebastria nigripes</i>) | Show the benefit of protecting albatross foraging grounds, even though these comprise only a part of their overall range. |
| Louzao <i>et al.</i> (2006) | Empirical, modelling | Balearic Islands | Balearic shearwater (<i>Puffinus mauretanicus</i>) | Marine zoning measures can benefit populations of far-ranging seabirds by extending protective measures beyond their breeding colonies and into their foraging range. |
| Alpine and Hobday (2007) | Modelling | Eastern Australia | Pelagic, migratory and other species targeted by fisheries or of conservation concern | Quantified the area requirements of pelagic protected area networks to protect pelagic species (target and non-target). Area requirements ranged from 7 to 26% of the East Australian region for adequate protection of pelagics. |

| SOURCE | TYPE OF STUDY | LOCATION | SPECIES | SUMMARY OF FINDINGS |
|-------------------------------------|----------------------|-------------------------------------|--|---|
| Pichegru <i>et al.</i> (2009) | Empirical | Benguela upwelling region | Cape gannets (<i>Morus capensis</i>) and African penguins (<i>Spheniscus demersus</i>) | Measured overlap between seabird feeding and commercial fishing grounds. No-take MPAs in bird-feeding hot spots is likely to increase the birds' breeding success. |
| Beare <i>et al.</i> (2010) | Empirical | North Sea | North Sea gadoids | Large North Sea area unfished during World War II. Large benefits to exploited fish, including migratory species. Older fish benefit fastest and in greatest proportion, creating a "Mexican wave" in numbers of subsequent generations. |
| Claudet <i>et al.</i> (2010) | Meta-analysis | European marine reserves | Fish | Density and size of species targeted by fisheries increase inside no-take MPAs, even highly mobile species. |
| De Juan and Leonart (2010) | Modelling | Mediterranean | All pelagic species | Identifies habitats critical to pelagic species in the Mediterranean. Results suggest offshore MPAs can help protect pelagic species. |
| Jensen <i>et al.</i> (2010) | Empirical | Baja California | Striped marlin (<i>Kajikia audax</i>) | Temporary closures of Mexico's EEZ to long-lining (1977–1980, 1984–1985) caused increase in striped marlin, despite its range extending outside the closed area. |
| Koldewey <i>et al.</i> (2010) | Review | Global | All species | Evidence that even partial protection of highly mobile and migratory species is beneficial. "Highly migratory" species may be based on long-range movements of a few individuals, while most of the population remains within a home range. |
| Young <i>et al.</i> (2015) | Empirical, modelling | Central Pacific | Boobies (<i>Sula sula</i> , <i>Sula dactylatra</i> , <i>Sula leucogaster</i>) | More than 85% of these wide-ranging species' foraging time was spent inside two offshore MPAs |
| Witt <i>et al.</i> (2011) | Empirical | South Atlantic | Leatherback turtles (<i>Dermochelys coriacea</i>) | Tagged individuals travelled between 2,190 and 7,348 km, mostly in the high seas. However, certain groups were restricted to regions of elevated chlorophyll content |
| Shillinger <i>et al.</i> (2008) | Empirical | | | Tagged 46 female leatherback turtles, 12,095 tracking days between 2004 and 2007, with a mean track duration of 263 days, a distance of 8,070 km, and a travel speed of 37.7 km per day. |
| Tancell <i>et al.</i> (2016) | Empirical | South Georgia | Albatrosses and large petrels | 86% of the area used most intensely year-round by these highly migratory birds when breeding at South Georgia fell within a region currently managed by the CCAMLR ¹ . |
| Santana-Garcon <i>et al.</i> (2014) | Empirical | Houtman-Abrolhos, Western Australia | Pelagic fishes | MPA of 22.3 km ² had no effect on pelagic fish species. |
| Yen <i>et al.</i> (2006) | Empirical | California Current System | Seabirds | Shearwaters, fulmar, and red-necked phalarope were positively associated with persistent hydrographic features, black-footed albatross, red phalarope, and Leach's storm petrel had a weaker association, and Cook's petrel had none. |
| Maxwell <i>et al.</i> (2011) | Empirical | Congo and Gabon coastlines | Olive ridley sea turtles (<i>Lepidochelys olivacea</i>) | Turtles remained within a 30km radius from the original nesting site before departing for foraging grounds. Only 44.6% of high-density turtle areas were found within the current park of 900 km ² . The proposed transboundary park would incorporate 97.6% of high-density areas |
| Williams <i>et al.</i> (2009) | Empirical | British Columbia | Killer whales (<i>Orcinus orca</i>) | Whales showed strong preference for the reserve over adjacent waters. The area comprises ~0.001% of the whales' range, but an overall average of 6.5% of the population was present each day |
| Huvenne <i>et al.</i> (2016) | Empirical | Scotland | Deep cold-water coral mounds | Offshore no-take MPA adequately protected intact coral communities, but severely damaged areas failed to recover. |

To summarise, the assumption that the sole purpose of offshore MPAs would be to benefit targeted, pelagic fish is flawed, and most offshore MPAs have broader goals (Davies et al., 2017). Aside from this, most of the open ocean's inhabitants are not very mobile and comprise small planktonic and nektonic fishes and invertebrates with more sedentary lifestyles (Sutton et al., 2008). The idea that all large pelagic animals are highly mobile comes from data collected about the maximum distance travelled by one or a few individuals of a species, which is not necessarily reflective of all or even the average mobility of the whole population (Sibert and Hampton, 2003). In addition, many species use predictable movement pathways and breeding, feeding and resting areas in the ocean that can be tracked, mapped and protected (Hyrenbach et al. 2006, Louzao et al., 2011). Some estimates suggest that, even if not targeting aggregation areas, then including 30-50% of a species' range within an MPA should have a positive effect on the whole population (Sibert and Hampton 2002).

5.4 ECONOMIC CONSIDERATIONS OF OFFSHORE MPAS

Fishers are typically opposed to the establishment of MPAs that overlap with their fishing grounds because of the perceived loss of revenue (Blyth-Skyrme et al., 2006; Nelson and Bradner, 2010), even though it has been shown that fishing yield can be sustained (Hastings and Botsford, 2003). Closure of large areas to fishing may lead to displacement of fishing effort that will cause overexploitation elsewhere, especially if there is no other fisheries management in place (Baum et al., 2003; Worm et al., 2003). For instance, in a modelling study of the northwest Atlantic, the closure of an area with low to intermediate existing fishing pressure displaced fishing effort to areas of higher species diversity and increased the catch rate of most by-catch shark species (Baum et al., 2003). This is an undesirable outcome from both a fisheries and conservation perspective. In contrast, an economic impact assessment of fisheries closure in the high seas concluded that overall losses would be minimal in comparison with the ecosystem service and biodiversity benefits gained from such protection – and that the offshore MPAs would protect more than just a few large species (Sumaila, 2005). It was calculated that the closure of 20 percent of the high seas may lead to the loss of only 1.8 percent of the current global reported marine fisheries catch (Sumaila, 2005).

Often the displaced fishing effort can be offset, however, by “spillover” of larvae and adults from the no-take areas to adjacent areas open to fishing, especially if other fisheries management tools are in place (Abesamis et al., 2006; Goni et al., 2010; Halpern et al., 2010; Harrison et al., 2012; Mee et al., 2017; Russ, 2002). No-take MPAs can export target species into adjacent fisheries, both through the emigration of adults and juveniles and the export of propagules (Abesamis et al., 2006; Babcock et al., 2010; Gell and Roberts, 2002; Goni et al., 2010; Harrison et al., 2012). This “spillover” effect must be integrated into analyses of displaced fishing effort, as must the effectiveness of other fisheries management tools.

5.5 GOVERNANCE AND ENFORCEMENT OF OFFSHORE MPAS

Where an offshore MPA is placed entirely within a nation's EEZ, concerns are focused on governance issues such as the logistics and costs of management (Ban et al., 2014; Maxwell et al., 2014). Lessons from existing large, multiple-use MPAs can offer both insights to the type of surveillance and enforcement required which is now already being applied in the Pacific (e.g. VMS), and a cautionary tale of the effects of ineffective enforcement (Ayling and Choat, 2008; Emslie et al., 2015; Harrison et al., 2012; Williamson et al., 2004).

There is still much to be learned about the enforcement of offshore MPAs. In remote oceanic areas, large offshore MPAs are easier to police than multi-use parks or even networks of smaller no-take MPA (Sheppard 2010), and a recent analysis found that larger MPAs cost less to manage per unit area than smaller ones (Ban et al. 2009). Surveillance in a vast and remote area may be challenging, but there is increasing sophistication in vessel-monitoring systems (VMSs) and satellite technology (Game et al., 2009) both of which are already being applied in the Pacific (see http://www.ffa.int/vessel_registration, <https://www.wcpfc.int/vessel-monitoring-system>). Additionally, there are existing arrangements and infrastructure that may be used for management activities and compliance monitoring (Ban et al. 2009) including in the Pacific where regional cooperation with regard to tuna management and enforcement offers opportunities for low cost expansion to monitoring of offshore MPAs (see also Table 2).

5.6 OFFSHORE MPA MANAGEMENT

There is emerging literature on multiple-use MPA management in the open ocean (e.g. Maxwell et al., 2014; Wedding et al., 2016), with practical suggestions such as:

- structured decision making and multi-criteria decision analysis for setting management objectives and actions,
- the use of geospatial technologies in all aspects of offshore MPA implementation, management and enforcement,
- cost-effective strategies for performance monitoring of complex pelagic interactions and wide-ranging species, including priority setting and tiers of monitoring importance linked to funding levels,
- techniques to increase compliance within offshore MPAs, such as participatory monitoring,
- focusing on enforcement across the large scales of offshore MPAs, such as setting enforcement priorities across multiple jurisdictions (e.g. to do with fishing, shipping, border protection, smuggling, environmental protection), and
- using techniques such as international enforcement partnerships and enforcement technologies.

Ban et al. (2014) proposed the integration of three elements: marine spatial planning and the establishment of offshore MPAs; the precautionary approach; and adaptive management, with the following four considerations: 1) including non-spatial tools such as catch or bycatch limits in fisheries, limited entry systems for mining or fisheries, or ballast water and discharge regulations for shipping; 2) considerations of the coupling between benthic and pelagic ecosystems; 3) the development of supporting policy for a scientific approach to adaptive management; and 4) performance and compliance monitoring and evaluation protocols.

Currently, existing large offshore MPAs include at least 10% of the range of 26.9% of species assessed in a recent study; the remaining 73.1% of species fell short of these global targets within large MPAs (Davies et al., 2017). This is thought to be because, so far, very large MPAs have been placed mostly in remote areas to avoid interfering with commercial interests, rather than systematically designed to adequately include species' ranges (Leenhardt et al., 2013). The need to design offshore MPAs according to robust design principles is clear (Davies et al., 2017).

A key lesson to be learned from the Great Barrier Reef Marine Park is the importance of applying pragmatic design principles within data-poor systems, which include almost all marine ecosystems. Effective design principles provide clear requirements for replication, minimum amounts, minimum size, spacing, ecological representativeness and the protection of known special, unique and vulnerable sites, (Fernandes et al., 2005). Development of design principles for offshore MPAs are in their infancy, but emerging knowledge can be applied to the development of guidelines.

6 CONCLUSIONS

Ample scientific evidence now exists for the use of MPAs to protect the open ocean ecosystem and its services, including to help maintain the populations of migratory and highly mobile pelagic species. Recent research demonstrates that large pelagic species targeted by fisheries benefit from open ocean MPAs, because:

Protecting a part of species' ranges or life cycles, especially critical habitat areas which function as important feeding or breeding grounds, can cause a decrease in overall population mortality;

Pelagic species are not uniformly distributed, but tend to aggregate around bathymetric and hydrographic features that are predictable in space and time, making the most beneficial design of offshore MPAs possible; and

Species identified as "highly migratory" display movement patterns where the majority (70 to 90 percent) of the population moves no farther than 600 km.

The protection of highly mobile and migratory species in offshore MPAs would automatically include the innumerable species making up the lower trophic levels, throughout all the interconnected vertical layers of ocean below the surface; they can essentially act as "umbrella species".

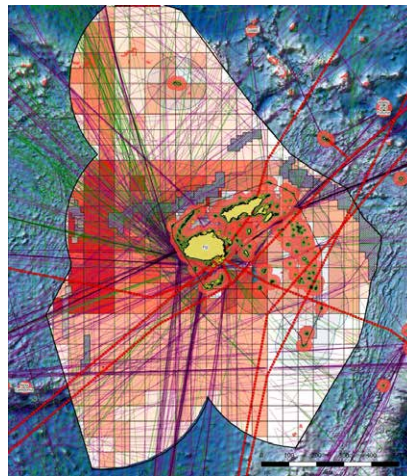
Importantly, however, much of the open ocean's community of animals does not comprise targeted, highly migratory, large pelagic species. The ocean's biomass is made up primarily of small planktonic and nektonic species that form abundant and diverse communities. And due to the vertical coupling of habitats, and the relative stability and predictability of the diverse open ocean systems, the protection offered by offshore MPAs is likely to benefit a wide range of resident, oceanic organisms, including those not yet identified.

There is a degree of difficulty associated with arranging governance and enforcement in the open ocean, and more beyond one country's EEZ. However, Pacific Island countries and others are already embracing relatively cost-effective remote technologies and multi-jurisdictional alliances to optimise compliance efforts. Obviously, it will be most effective for offshore MPAs to achieve their ecological and economic objectives if in combination with other management arrangements, which will also require effective governance and enforcement programs.

Advances in open ocean research have allowed for the mapping of topographic features, stable and ephemeral hydrodynamic features, and the boundaries of biological hotspots and biogeographic regions. There is greater understanding of the ocean's three-dimensional complexity and an ever-increasing willingness of nations to establish large-scale MPAs (multiple use and no-take). Ultimately, no-take MPAs are the best tool available, as they reduce human pressure, represent our best chance to preserve populations, biodiversity, habitat and food web integrity, and give species and habitats a buffer to withstand and recover from the large-scale, pervasive and unpredictable effects of climate change.

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