

Climate change and the future for coral reef fishes

Philip L Munday^{1,2}, Geoffrey P Jones^{1,2}, Morgan S Pratchett¹ & Ashley J Williams³

¹ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Qld 4811, Australia; ²School of Marine and Tropical Biology, James Cook University, Townsville, Qld 4811, Australia; ³Fishing and Fisheries Research Centre, School of Earth and Environmental Sciences, James Cook University, Townsville, Qld 4811, Australia

Abstract

Climate change will impact coral-reef fishes through effects on individual performance, trophic linkages, recruitment dynamics, population connectivity and other ecosystem processes. The most immediate impacts will be a loss of diversity and changes to fish community composition as a result of coral bleaching. Coral-dependent fishes suffer the most rapid population declines as coral is lost; however, many other species will exhibit long-term declines due to loss of settlement habitat and erosion of habitat structural complexity. Increased ocean temperature will affect the physiological performance and behaviour of coral reef fishes, especially during their early life history. Small temperature increases might favour larval development, but this could be counteracted by negative effects on adult reproduction. Already variable recruitment will become even more unpredictable. This will make optimal harvest strategies for coral reef fisheries more difficult to determine and populations more susceptible to overfishing. A substantial number of species could exhibit range shifts, with implications for extinction risk of small-range species near the margins of reef development. There are critical gaps in our knowledge of how climate change will affect tropical marine fishes. Predictions are often based on temperate examples, which may be inappropriate for tropical species. Improved projections of how ocean currents and primary productivity will change are needed to better predict how reef fish population dynamics and connectivity patterns will change. Finally, the potential for adaptation to climate change needs more attention. Many coral reef fishes have geographical ranges spanning a wide temperature gradient and some have short generation times. These characteristics are conducive to acclimation or local adaptation to climate change and provide hope that the more resilient species will persist if immediate action is taken to stabilize Earth's climate.

Correspondence:

Philip L Munday, ARC Centre of Excellence for Coral Reef Studies, and School of Marine and Tropical Biology, James Cook University, Townsville, Qld 4811, Australia
Tel/Fax: +61 7 47815341
E-mail: philip.munday@jcu.edu.au

Received 27 Nov 2007
Accepted 28 Feb 2008

Keywords Climate change adaptation, community structure, global warming, habitat loss, population dynamics, range shifts

Introduction	262
Sensitivity of reef fishes to predicted climate changes	263
Sea surface temperature	264
Ocean acidification	267
Ocean circulation	268
Cyclones and extreme weather	268
Sea level rise	269

Impact of climate change on populations and communities	269
Life-history traits	269
Recruitment and population dynamics	269
Population connectivity	270
Habitat loss and community structure	271
Geographic ranges	273
Interactions with other stressors	274
Adaptation to climate change	275
Coral reef fisheries	275
The future	276
Future ecology	277
Future evolution	277
Future management	278
Future science	278
Acknowledgements	279
References	279

Introduction

Climate change is expected to have serious consequences for Earth's ecological systems, resulting in an overall loss of diversity, disruptions to ecosystem processes and a reduction in the ecological goods and services provided to human societies (Thomas *et al.* 2004; Lovejoy and Hannah 2005). Shifts in plant and animal distributions, changes to population abundances, adjustments to the timing of seasonal activities, increased prevalence of disease and the spread of invasive species have already been linked to climate change (Harvell *et al.* 2002; Walther *et al.* 2002; Parmesan and Yohe 2003; Root *et al.* 2003; Parmesan 2006). Impacts such as these are expected to become more pervasive as the climate changes rapidly over the next 50–100 years (Intergovernmental Panel on Climate Change (IPCC) 2007a).

Coral reefs are particularly susceptible to rapid climate change because exposure to maximum ocean temperatures just a few degrees above the long-term average at any location can cause corals to become stressed, bleach and die (Hoegh-Guldberg 1999). Repeated episodes of mass coral bleaching since 1970 have already caused a decline in coral cover at a global scale (Wilkinson 2002; Gardner *et al.* 2003; Hughes *et al.* 2003) and this trend is expected to continue as ocean temperatures increase further over the coming decades (Hoegh-Guldberg 1999; Donner *et al.* 2005). Coral reefs are also threatened by ocean acidification, which reduces the ability of scleractinian corals to form carbonate skeletons (Feely *et al.* 2004; Kleypas *et al.* 2006). Ocean acidification will

compromise the reef-building capacity of corals and could see some reefs enter a state of net erosion by the end of this century (Guinotte *et al.* 2003). Coral reefs are among the most diverse ecosystems on Earth and continued loss of coral cover and the erosion of the complex habitat structure associated with healthy coral reefs is expected to have significant consequences for a vast number of reef-associated species, although these consequences are only just beginning to be understood (Munday and Holbrook 2006; Hoegh-Guldberg *et al.* 2007; Munday *et al.* 2007; Pratchett *et al.* 2008, in press). Changes to ocean temperature, pH, ocean currents and extreme weather events that will accompany climate change will have additional impacts on reef-associated species through effects on individual performance, trophic linkages, recruitment dynamics, connectivity between populations and other key ecosystem processes.

Over 4000 species of teleost fishes are associated with coral reefs (Lieske and Myers 1994; Allen 2007), yet how they will be affected by climate change has received remarkably little attention (Roessig *et al.* 2004; Harley *et al.* 2006). The impacts of climate change will vary among life stages, with the larval and reproductive stage expected to be most vulnerable. Most coral reef fishes have a life cycle that includes a pelagic larval stage lasting for a few weeks to months (Leis 1991). When they are sufficiently well developed, the larvae settle to the reef and become part of the reef-based population. Patterns of larval survival and dispersal play a key role in the dynamics of reef fish populations (Doherty 1991;

Caley *et al.* 1996) and the ecological and genetic connectivity between populations (Sale 1991; Cowen 2002). Larval reef fishes are highly sensitive to environmental conditions (Leis and McCormick 2002) and any effects of climate change on the number of larvae produced, or their growth, survival and dispersal patterns, could have significant consequences for adult populations.

Changes to the composition and structure of coral reef habitats are expected to have further significant consequences for fish populations and communities (Pratchett *et al.* 2008). The loss of coral from bleaching has already caused significant declines in the diversity and abundances of reef fishes in some places (Jones *et al.* 2004; Wilson *et al.* 2006) and this effect will be magnified if the structural complexity of reefs declines following bleaching events (Graham *et al.* 2006). The effects of coral bleaching and ocean acidification are additional to existing disturbances that kill live coral, such as outbreaks of crown of thorns starfish or pollution from terrestrial run-off. We expect that the on-going degradation of coral reef habitat as a result of climate change will result in impoverished reef fish communities.

Changes to fish populations and communities could have important feedbacks to other parts of the reef ecosystem and to human societies. Fishes have a significant presence in all major feeding groups and are important for energy transfer throughout the reef system (Depczynski *et al.* 2007). They are the dominant large predators on reefs and their presence influences the community structure and abundance of smaller species (Hixon 1991; Jones 1991; Almany and Webster 2004). Some reef fishes, such as grazing herbivorous fishes have key functional roles, preventing the growth of macroalgae that might otherwise smother corals (Steneck 1988; McCook *et al.* 2001; Bellwood *et al.* 2004; Hughes *et al.* 2007). Other species facilitate the settlement of corals by removing sediment and fine algae from the substratum (Steneck 1997). Reef fishes also have high social and economic value. They are the basis for subsistence and artisanal lifestyles of coastal communities in many tropical countries and they also support significant commercial fisheries (Russ 1991; Polunin and Roberts 1996; McClanahan *et al.* 2005; Sadovy 2005). Coral reefs also generate significant tourism revenue for some countries (Cesar *et al.* 2003). For example, Australia's Great Barrier Reef is responsible for over \$5 billion per annum in tourism revenue (Access Economics 2007). Clearly, significant impacts of

climate change on populations and communities of coral reef fishes could have far-reaching ramifications for coral reef ecosystems and for the human societies that depend on them.

In this review, we assess and predict the likely impacts of climate change on populations and communities of coral fishes. We first examine the sensitivity of marine fishes to changes in the physical environment and consider how predicted changes in the ocean climate will affect the growth, survival, behaviour and reproductive success of individuals. We then consider how these effects could influence life histories, population dynamics, community structure and the geographical distributions of coral reef fishes. We also explore the potential for adaptation of coral reef fishes to rapid climate change. Finally, we examine the potential consequences for coral reef fisheries and consider how climate change might interact with other anthropogenic stresses to affect reef fish populations.

There are critical gaps in our understanding of how the tropical ocean will change over the coming century, especially at regional and local scales. There are even larger gaps in our understanding of how rapid changes in the ocean climate will affect reef fishes at the individual, population and community levels. These knowledge gaps introduce a high level of uncertainty to many of our assessments. Nevertheless, our synthesis identifies areas of major concern regarding the possible effects of climate change on coral reef fishes and highlights critical issues for future research.

Sensitivity of reef fishes to predicted climate changes

The ocean and the atmosphere act as a linked system, with changes in one part of the system having feedback to the other. Both the atmosphere and the oceans are getting warmer due to the enhanced greenhouse effect caused by the accumulation of carbon dioxide and other greenhouse gases in the atmosphere (IPCC 2007b). The ocean is an enormous reservoir of heat, with the top few metres storing a similar amount of heat as the entire atmosphere (Houghton 2004). Additional heat contained within the oceans is redistributed around the globe via major circulation patterns. Changes in ocean temperature in turn influence wind stress, which is a major driver of ocean circulation. Ocean temperature also influences the evaporation of water vapour into the atmosphere, with consequences

Table 1 Predicted impacts of climate change on populations and communities of coral reef fishes and the level of certainty associated with these predictions.

Impact	Drivers	Details	Certainty
Reduction in local diversity and changes to community composition	Loss of coral cover and erosion of reef structural complexity	Loss of coral-dependent species and declines in abundance of species that prefer to settle near live coral. Further declines in abundances of a broad suite of species as habitat structure erodes. Generalist planktivores, small herbivores and rubble dwellers will tend to be favoured.	High
Geographic range shifts	Increased ocean temperature	Species distributions will shift to match the position of preferred temperature gradients. Some low-latitude species will expand ranges towards higher latitudes. Some high-latitude species will contract ranges towards margins of reef development. Increased extinction risk of small range, coral-dependent species near margins of reef development.	High
Reduced pelagic duration	Increased ocean temperature	Small increases in water temperature will tend to accelerate larval development and competency to settle. Larger increases in temperature may be detrimental.	High
Life-history modification	Increased ocean temperature	On average, populations will have individuals that tend to be shorter lived, reach shorter maximum sizes and mature earlier.	Moderate-high
Shift of breeding season	Increased ocean temperature	Breeding will commence earlier. Populations may breed longer at higher latitudes.	Moderate
Reproductive decline	Increased ocean temperature	Bimodal breeding seasons could develop at low latitudes.	Moderate
More extremes in recruitment	Increased ocean temperature and/or changes in ocean circulation and productivity	Low-latitude species and species that do not shift the timing of breeding will experience reduced reproductive performance. A mismatch between timing of reproduction and optimum conditions for larvae could develop.	Moderate
Reduced productivity	Increased ocean temperature and/or changes in ocean circulation	Shorter pelagic durations and faster larval growth will tend to increase survival during the larval stage. However, higher metabolic rates will increase the risk of starvation where food supply is patchy or unpredictable. Highly variable and unpredictable – some locations may tend to have better recruitment and others poorer recruitment.	Low
Reduced connectivity	Habitat loss and increased ocean temperature	Less nutrient enrichment due to increased stratification of surface waters in combination with higher metabolic demands of consumers could reduce productivity at higher trophic levels. Planktonic food chains will be less productive at higher temperatures. Highly variable and unpredictable – productivity may increase at some locations.	Low
Reduced population genetic diversity	Increased ocean temperature and habitat loss	Increased habitat fragmentation and smaller population sizes will reduce population connectivity. Reduced pelagic larval durations and earlier reef-seeking behaviour might tend to reduce the average scale of larval dispersal.	Low
Reduced performance	Ocean acidification	Strong selection favouring temperature-tolerant genotypes and reduced populations sizes from habitat degradation will reduce local genetic diversity.	Low
		More dissolved CO ₂ and lower pH could increase metabolic demands, especially of larval fishes. Potential problems for otolith development.	Low

High-certainty predictions are well supported by empirical observations and experimentation. Moderate-certainty predictions have some empirical or experimental support, but are not conclusive. Low-certainty predictions are speculative and lack good supportive evidence.

McDonald 1997). Fishes are particularly sensitive to temperature during their early life history. Across a wide range of fish species, embryonic development rate increases nearly threefold for every 10 °C increase in temperature (Rombough 1997), although it is not known if this rate holds for tropical reef fishes. After hatching, increased temperature tends to increase larval growth rate, decrease the age at metamorphosis and increase swimming ability (McCormick and Molony 1995; Benoît *et al.* 2000; Hunt von Herbing 2002; Meekan *et al.* 2003). In a recent experimental analysis, Green and Fisher (2004) showed that larval duration of the red-and-black anemonefish (*Amphiprion melanopus*, Pomacentridae) was 25% shorter, growth rate was higher and swimming ability enhanced at 28 °C compared with that at 25 °C. Similarly, Sponaugle *et al.* (2007) found a strong correlation between water temperature, growth rates and larval duration of the bluehead wrasse (*Thalassoma bifasciatum*, Labridae). Cohorts recruiting during periods of warmer water exhibited faster growth and shorter larval durations. Consequently, it appears that small increases in water temperature will generally hasten the developmental rate of larval reef fishes and decrease their larval duration, provided that ambient temperatures do not exceed optimum levels for growth and development, and the larvae can consume sufficient additional food to support the increased energetic demand of developing at a higher temperature.

Although increased temperature may accelerate growth and development, it may also increase mortality rates. Pre-hatching mortality of Ambon damselfish (*Pomacentrus amboinensis*, Pomacentridae) embryos was higher at 31 °C compared with that at 29 °C and larvae survived for a shorter period of time on their endogenous yolk-sac resources at the higher temperature (Gagliano *et al.* 2007). This indicates that even relatively small increase in temperature could have a negative effect on the total number of larvae reaching settlement. Very little is known about the effects of abnormally high temperatures on the interactions between growth, development and survival of early life-history stages of reef fishes and this is a serious gap in our knowledge.

Reproduction of tropical reef fishes appears to be highly sensitive to temperature fluctuations (Pankhurst and Porter 2003). Increased temperature could have either a positive or negative effect on reproductive output, depending on whether or

not populations are currently close to their thermal optimum for reproduction. Ruttenberg *et al.* (2005) found that mass-specific egg production of white-tailed damselfish (*Stegastes beebei*, Pomacentridae) in the Galápagos Islands declined rapidly from a peak near 25 °C to very low rates at 20 and 27 °C. This indicates that a temperature increase of just a few degrees Celsius could significantly depress reproductive success in fish populations that are near their thermal optimum, unless they shift the timing of reproduction.

Fishes on equatorial coral reefs often breed throughout much of the year (Srinivasan and Jones 2006) and reproductive success in these populations could be seriously compromised if higher temperatures in future mean that the thermal optimum for reproduction is exceeded for large parts of the year. Breeding tends to be more seasonal at higher latitudes (Robertson 1991; Srinivasan and Jones 2006) and is often associated with increasing water temperature in spring (Colin 1992; Danilowicz 1995; Sadovy 1996; Samoily 1997; Hilder and Pankhurst 2003). The upward trend in water temperature may be sufficient to trigger breeding in many species, but others may require a threshold temperature to be reached before they breed. For example, coral trout at several locations on the Great Barrier Reef appear to commence spawning when the sea temperature reaches approximately 26 °C (Samoily 1997; Frisch *et al.* 2007; D. Williamson, personal communication). Increased ocean temperatures could cause an earlier start to the breeding season for species with temperature thresholds for reproduction, and possibly a longer breeding season if thermal limits for reproduction are not exceeded. Alternatively, a split breeding season might develop, with reproduction occurring either side of the summer maximum (Fig. 2).

Although some species probably use temperature to cue breeding, other species may use photoperiod or a combination of photoperiod and temperature to start the breeding season (Pankhurst and Porter 2003). These species would suffer the greatest impacts of increased temperature on reproduction because they are less likely to adjust the timing of reproduction to suit the thermal environment. Reproductive success could be seriously compromised if higher water temperatures: (i) cause egg production to be impaired (Van Der Kraak and Pankhurst 1997); (ii) increase embryonic mortality (Gagliano *et al.* 2007); or (iii) lead to a mismatch between the timing of breeding (set by photoperiod)

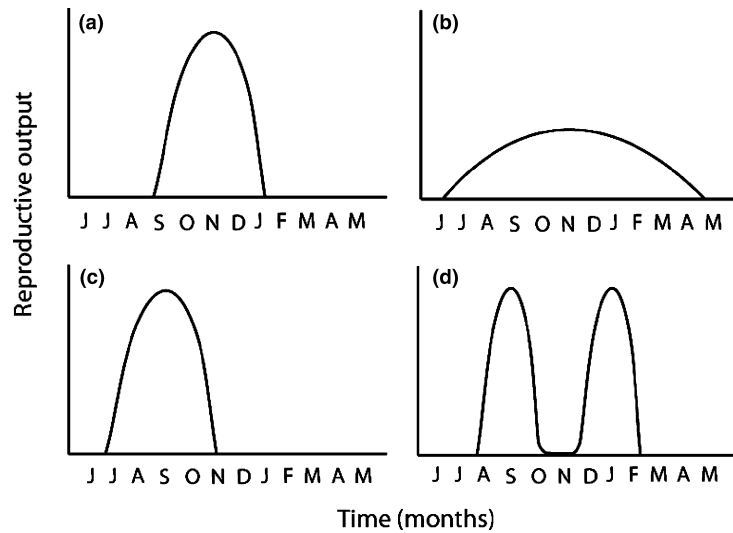


Figure 2 Possible alternate breeding scenarios at higher sea temperatures: (a) conceptual current-day breeding season, (b) longer breeding season with lower effort, similar to that currently seen in lower latitude populations (c) earlier start to breeding season, (d) bimodal breeding season.

and the optimal conditions in the plankton for survival and dispersal of larvae (set by temperature) (Edwards and Richardson 2004).

Ocean acidification

The amount of carbon dioxide (CO_2) dissolved in the ocean increases as atmospheric partial pressure of CO_2 increases. Additional CO_2 reacts with water to form carbonic acid, which through a series of reactions leads to a decline in pH and a shift in the carbonate–bicarbonate ion balance (Feely *et al.* 2004). Atmospheric CO_2 concentrations have increased from an estimated 280 p.p.m. in pre-industrial times to approximately 380 p.p.m. today (IPCC 2007b). Depending on emission scenarios, CO_2 concentrations are predicted to reach 540–979 p.p.m. by the end of the century (IPCC 2007b) and this will cause the average ocean pH to drop 0.4–0.5 points compared with pre-industrial levels (Royal Society 2005). This would make the ocean more acidic than at any time in the past 400 000 years (Feely *et al.* 2004). The effects that increased levels of dissolved CO_2 and reduced pH will have on reef fishes remain highly speculative because very little research has been conducted on this issue.

The acidification of lakes by atmospheric pollutants has caused significant reductions in the growth rate, reproductive success and survival of some freshwater fishes (Jackson and Harvey 1995). Although the decrease in ocean pH as a result of climate change is not expected to be as severe as

that caused by acid pollution in freshwater lakes, the impact of reducing pH through elevated CO_2 levels appear to be more dramatic than an equivalent reduction in pH by the direct addition of acids (Ishimatsu *et al.* 2004). Furthermore, coral reef fishes have evolved in a relatively stable pH environment, and therefore, may tend to be more sensitive to pH changes than freshwater fishes. Consequently, there is at least room for concern that reduced pH could have negative effects on coral reef fishes. Fish embryos and young larvae are more sensitive to pH changes than are juveniles and adults (Brown and Sadler 1989), therefore, effects of acidification are most likely to be detected at these early life stages. Eggs of pelagic spawning fishes might be more susceptible to pH changes than those of demersal spawners because they are released directly into ocean waters where pH remains relatively stable over the nocturnal–diurnal cycles. By contrast, pH fluctuations can occur close to the reef substratum due to daytime consumption of CO_2 by algae and night-time release of CO_2 by all reef organisms. For this reason, eggs of benthic spawners may have a greater tolerance to pH fluctuations.

Increased levels of dissolved CO_2 not only acidify the ocean, but they also act to decrease the pH of animal tissue (Pörtner *et al.* 2004). In fishes, the internal pH level is controlled by the exchange of ions, mostly across the gills, and small changes in internal or external pH can be readily compensated (Claiborne *et al.* 2002). Although this compensatory mechanism is not detrimental in the short

term, ultimately it might have some physiological costs, especially for species or life stages with high metabolic demands (Pörtner *et al.* 2004) and when compounded by higher metabolic demands at elevated temperatures (Pörtner and Langenbuch 2005). Larval reef fishes have exceptionally high oxygen demands (Nilsson *et al.* 2007) and are more likely to be challenged by changes in pH than are post-settlement fish.

Ocean acidification is expected to have serious consequences for calcifying organisms, such as corals, because it reduces the availability of carbonate ions (Feely *et al.* 2004; Kleyvas *et al.* 2006). Skeletal growth in juvenile and adult fishes is unlikely to be impacted because these life stages have precise control over their internal ionic environment. However, changes in the carbonate ion balance might be sufficient to retard skeletal or otolith (ear bone) development during embryonic or larval stages. Experiments have shown that skeletal calcification of some invertebrate larvae is reduced at CO₂ concentrations within those predicted to exist by 2100 (Shirayama and Thornton 2005). Whether these levels will affect the skeletal or otolith development of larval fish is currently unknown, but should be a priority area for research because disruption to the development of these structures could have significant effects on the swimming and feeding efficiency of larvae or their ability to orient towards the sound of reefs or other relevant signals.

Ocean circulation

Climate change will almost certainly influence ocean circulation and upwelling; however, the changes are expected to differ greatly among regions and locations, and the magnitude of change at any location is difficult to predict (Bindoff *et al.* 2007; Steinberg 2007). Nevertheless, some broad trends have been suggested. Increased thermal stratification of the ocean surface layer is expected, reducing the input of nutrients from cooler waters below the thermocline (Bindoff *et al.* 2007; Poloczanska *et al.* 2007). Increased heat content of the ocean and changes to wind fields may tend to increase the strength of some ocean currents. For example, the South Equatorial Current, which is a major oceanographic driver on the Great Barrier Reef, is expected to increase in strength over the next 50 years (Cai *et al.* 2005; Poloczanska *et al.* 2007). Surface currents might also tend to increase

in strength due to the increased thermal stability of the shallow surface zone (Steinberg 2007), although this effect could be counteracted by changes in the strength or direction of surface winds at some locations.

Changes to current patterns could impact fishes in several ways. First, local and meso-scale currents often play an important role in the dispersal patterns of larval fishes (James *et al.* 2002; Suthers *et al.* 2004; Sponaugle *et al.* 2005; Cowen *et al.* 2006). Any changes in the strength or direction of these currents could influence larval transport among reefs. Second, nutrient supply influences the production and distribution of plankton (Hays *et al.* 2005; McKinnon *et al.* 2007), which is food for larval fishes and planktivorous adults. Changes to primary and secondary productivity brought about by change to oceanographic circulation could influence the growth and survival of larval fishes (Searcy and Sponaugle 2000; Sponaugle and Pinkard 2004; Meekan *et al.* 2006) and the growth and reproductive success of planktivorous adults, such as caesionids and many pomacentrids, and acanthurids.

Cyclones and extreme weather

The frequency of intense cyclones is predicted to increase as a result of climate change (Webster *et al.* 2005; IPCC 2007b). Whether the total number or locations of tropical cyclones will change is uncertain. More extreme droughts and floods are predicted in a warmer world, and consequently, the extremes of rainfall and river flow are expected to become more common over the next 100 years (Lough 2007). More extreme rainfall patterns will lead to greater variability in patterns of nutrient enrichment to coastal waters, with possible consequences for the quality and quantity of planktonic food available to larval and adult coral reef fishes in nearshore waters (Hays *et al.* 2005; McKinnon *et al.* 2007).

Tropical cyclones often cause a temporary decline in the abundance of some fishes on impacted reefs (Halford *et al.* 2004) due to the loss of critical habitat or food for certain species (Wilson *et al.* 2006). Recovery of the fish populations occurs as the benthic habitat recovers over a period of years to decades (Halford *et al.* 2004). Stronger cyclones will increase the disturbance regime experienced by reef communities, with increased impacts on fish communities at local scales. A more troubling conse-

quence of increased cyclone intensity is the interaction with other disturbances, such as coral bleaching, that also decrease coral cover and degrade habitat structure. The cumulative effect of an increasing number of disturbances on the physical structure of reefs has the potential to systematically degrade reef fish communities.

Sea level rise

Sea level is rising due to thermal expansion of the oceans and additional contributions of water from melting glaciers and continental ice sheets. Average sea level has risen nearly 20 cm since 1870 and is predicted to rise at least another 30–40 cm by 2100 (Church and White 2006; IPCC 2007b). Sea level rise will be far greater if melting of ice sheets and glaciers accelerates dramatically, as has been suggested by some recent studies (Velicogna and Wahr 2006). It is unlikely that coral reef fishes will be seriously affected by a vertical sea level rise of <1 m. Many species can be found across a range of depths, either within or among reefs, and most experience daily tidal fluctuations in depths greater than that predicted to occur from sea level rise. Even for those species with narrow depth distributions, reef structure and profile are probably more important than sea level height in setting their depth distributions. Inundation of coastal environments might have consequences for the small number of coral reef species that inhabit estuaries, mangroves and sea-grass beds as juveniles and migrate to reefs later in life (Sheaves 1995).

Impact of climate change on populations and communities

Life-history traits

Life-history traits of reef fishes can differ markedly between populations and much of this variability appears to be influenced by complex interactions between temperature, density, food availability and mortality rates (Gust *et al.* 2001; Meekan *et al.* 2001; Choat and Robertson 2002; Robertson *et al.* 2005; Ruttenberg *et al.* 2005). Within-species variations in maximum size and age have been correlated with temperature at geographical (Choat and Robertson 2002; Robertson *et al.* 2005) and local scales (Ruttenberg *et al.* 2005). In general, individuals tend to reach smaller maximum sizes and have shorter lives in warmer environments, although

there are exceptions to this pattern (Williams *et al.* 2003). Therefore, we might expect life histories within local populations to shift towards smaller maximum size and reduced maximum longevity as temperature increases. Average age or size at maturation of fishes is often correlated with maximum age or size (Beverton 1992); so, we also expect that size or age at maturation will tend to decrease if life histories shift towards smaller maximum size and younger average age at higher temperatures. These shifts would be observed as long-term trends in mean values for particular populations.

Increased temperature might be expected to increase growth rate within populations, but will only do so if individuals can consume more food at higher temperatures to compensate for increased metabolic rate (Jobling 1997). Some reef fishes exhibit an inverse relationship between growth rate and temperature across their geographic ranges (Choat and Robertson 2002; Robertson *et al.* 2005), which contrasts with the evidence for increased growth rate at higher temperatures for larval fishes (Wilson and Meekan 2002; Meekan *et al.* 2003; Sponaugle *et al.* 2007), and suggests that adult growth is often food limited. The effect of increased sea temperatures on the growth of reef-based individuals is difficult to predict and will depend on interactions between temperature, metabolic rate, food availability and nutritional quality and population density.

Reef fishes exhibit considerable variation in life-history traits among habitats. On the Great Barrier Reef, for example, parrotfishes on the outer reef grow slower, have higher mortality rates, reach smaller maximum sizes and change sex earlier than individuals of the same species living just 10–20 km away on the midshelf (Gust *et al.* 2002; Gust 2004). Consequently, expected changes to life-history traits are not expected to be large compared to natural variation that already exists among populations occupying different habitats.

Recruitment and population dynamics

Recruitment to reef fish populations is often highly variable and many populations exhibit significant variation in their age structure that can be linked to variation in the magnitude of recruitment pulses (Doherty 1991). Warmer conditions (within the range currently experienced by reef fishes) generally appear to enhance recruitment. For example, good

recruitment to bicolour damselfish (*Stegastes partitus*, Pomacentridae) populations in San Blas has been correlated with higher water temperatures and favourable winds (Wilson and Meekan 2002). Strong year classes of several damselfishes in the Galápagos Islands were correlated with warm El Niño events (Meekan *et al.* 2001) and synchronized increases in the population size of damselfish species on the Great Barrier Reef often follow warm El Niño conditions (Cheal *et al.* 2007). There is increasing evidence that the survival of larval coral reef fishes is linked to growth rate, with individuals from strong recruitment pulses often exhibiting higher growth rates during the larval period than those from weak recruitment pulses (Searcy and Sponaugle 2000; Bergenius *et al.* 2002; Wilson and Meekan 2002; Meekan *et al.* 2003). Furthermore, numerous studies have found a positive correlation between larval growth rate and ocean temperature (McCormick and Molony 1995; Wilson and Meekan 2002; Meekan *et al.* 2003; Sponaugle *et al.* 2007). All these observations suggests that small increases in temperature might tend to have a favourable influence on recruitment, although these benefits could be counteracted by reduced egg production and increased egg mortality at higher temperatures, thereby reducing the number of larvae entering the pelagic phase in the first place.

Warmer conditions tend to increase the developmental rates of larval fishes and reduce the time to metamorphosis (McCormick and Molony 1995; Benoît *et al.* 2000; Green and Fisher 2004). Larval mortality rates are typically very high; so, even a small reduction in larval duration might have a positive influence on the magnitude of recruitment (O'Connor *et al.* 2007). However, additional energy must be consumed by larval fishes to maintain higher metabolic rates at higher temperatures and to sustain increased growth. Although there is little evidence that larval fishes are food limited (Leis 1991), copepods and other food resources favoured by larval fishes are not uniformly distributed (Suthers *et al.* 2004; Meekan *et al.* 2006) and higher energetic demands at higher temperatures mean that larvae have a greater chance of starving before encountering favourable patches of food. Furthermore, climate change will probably cause greater fluctuations in the quality and quantity of planktonic food resources for larval fish (Edwards and Richardson 2004; McKinnon *et al.* 2007). Consequently, we expect that warmer sea temperatures will increase the spatial and temporal vari-

ation in larval supply to reefs, and thus cause greater variability in recruitment to reef-based populations – there will be more good recruitment events and more recruitment failures.

Recruitment at higher temperatures will tend to be enhanced at times or locations where larvae have reliable food supplies, but will be negatively affected at times or locations where food is less abundant or difficult to locate. Upwelling and convergence zones generate abundant food resources for larval fishes (Suthers *et al.* 2004; Meekan *et al.* 2006). Larval survival and recruitment may generally be improved at these locations, provided climate change does not affect patterns of primary and secondary productivity. At other locations, the condition of larvae at settlement appears to be dependent on less predictable encounters with oceanographic features (Sponaugle and Pinkard 2004). Recruitment will probably become more variable at these locations. Larger increases in water temperature could lead to widespread recruitment failure due to reproductive failure of adults.

Population connectivity

Currents and tides potentially play an important role in the retention and dispersal of larval fishes (Cowen 2002; James *et al.* 2002; Burgess *et al.* 2007). Any changes to circulation patterns as a result of climate change could have fundamental effects on the spatial and temporal patterns of larval supply to individual reefs and the degree of connectivity among reefs. Additionally, increased sea temperatures could modify connectivity between reefs through effects on larval development and behaviour. Larval swimming ability develops through ontogeny (Fisher *et al.* 2000) and late-stage larvae of many reef fish species are capable of swimming long distances (Stobutski and Bellwood 1997). They can also orient to reefs using a range of sensory mechanisms (Kingsford *et al.* 2002; Montgomery *et al.* 2006). Theoretical models predict that the spatial scale of larval dispersal is highly sensitive to the ontogenetic timing of reef-seeking behaviour and active swimming ability (Armsworth 2000; Cowen *et al.* 2006). Increased temperature tends to accelerate larval development and enhance swimming ability (Benoît *et al.* 2000; Hunt von Herbing 2002; Green and Fisher 2004). Therefore, the average scale of dispersal between reefs might be reduced due to earlier reef-seeking ability and improved swimming ability in warmer condi-

tions, although this remains highly speculative, and would be difficult to detect because of the interacting effects of currents on dispersal patterns and the prospect of more variable larval survival and recruitment at higher temperatures.

Habitat loss and community structure

The frequency of coral bleaching is predicted to increase as sea temperatures rise (Hoegh-Guldberg 1999; Hughes *et al.* 2003). Repeated bleaching will change the composition of benthic reef communities and lead to fundamental shifts in the composition of the associated fish communities. Declines in live coral cover, changes in the species composition of those corals remaining and a loss of habitat complexity will all combine to decrease the diversity and abundance of reef fish assemblages and alter their species composition (Pratchett *et al.* 2008) (Fig. 3).

Approximately 10% of coral reef fishes can be classified as coral dependent (Pratchett *et al.* 2008) and these species are the ones most immediately affected by coral loss (Kokita and Nakazono 2000; Spalding and Jarvis 2002; Halford *et al.* 2004;

Munday 2004; Bellwood *et al.* 2006; Pratchett *et al.* 2006). Coral-dependent species include obligate coral dwellers (Munday *et al.* 1997; Gardiner and Jones 2005), corallivores (Pratchett 2005) and species that always settle into live coral (Booth and Wellington 1998; Öhman *et al.* 1998; Holbrook *et al.* 2000). Some reef fish families are more reliant on corals than others, with a higher proportion of species in diverse reef fish families such as butterflyfish (Chaetodontidae), cardinalfish (Apogonidae) and gobies (Gobiidae) directly at risk from loss of corals (Pratchett *et al.* 2008). Many of these fish–coral relationships are species specific and so the magnitude of the threat depends on the susceptibility of particular coral species to bleaching, combined with the degree of coral specialization of the fish species (Munday 2004; Feary *et al.* 2007a). Declines in coral cover nearly always cause corresponding declines in the abundances of coral-dependent species (Wilson *et al.* 2006), but specialist species that inhabit or consume just one or a few coral species often suffer the greatest declines because they are unable to use alternative coral resources as their preferred corals decline in abundance (Munday 2004; Pratchett *et al.* 2008).

Community responses to loss of coral cover can extend to a greater range of coral reef fishes than the 10% of species that are directly coral dependent. Seventy-five per cent of fish species declined in abundance, with 50% of species declining by more than 50%, following a severe loss of live coral on coastal reefs in Papua New Guinea, and only a relatively small number of species increased in abundance (Jones *et al.* 2004). This response to a severe loss of coral cover does not appear to be particularly unusual. In a recent meta-analysis of studies that monitored fish assemblages following disturbances to coral communities, Wilson *et al.* (2006) found that an average of 62% of the fish species investigated declined in abundance following a loss of at least 10% coral cover. Declines in abundance were the greatest among coral dwellers and coral feeders; however, some invertebrate feeders and planktivores also declined in abundance.

Many reef fishes prefer to settle near live coral even if adults are not coral dependent (Jones *et al.* 2004; Feary *et al.* 2007b). This may explain why a broader range of species exhibit a response to large-scale coral loss than would be predicted based on adult habitat associations alone (Booth and Beretta 2002). Jones *et al.* (2004) estimated that 65% of fish

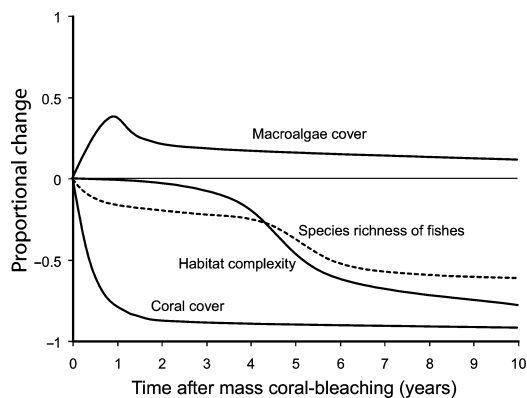


Figure 3 Conceptual diagram of changes in key attributes of coral reef habitats (solid lines) and fish communities (dashed line) following severe coral bleaching. Initially, species richness of local coral reef fish assemblages declines due to the loss of species that are strongly dependent on live coral. In habitats where coral contribute most of the topographic complexity, the collapse of dead coral skeletons over a period of several years will greatly reduce habitat complexity, causing a further decline in species richness. If coral communities do not recover (as illustrated) over 50% of species may ultimately be lost due to the combination of declines in habitat complexity and delayed effects of coral loss.

species on the reefs they studied preferentially settle in or near live coral. Moreover, the proportional decline in abundance of each species was correlated with their proportional use of live coral at settlement. This suggests that loss of suitable habitat for new settlers, and a suppression of cues that encourage settlement, are likely to be responsible for declines in abundance of a variety of species following significant coral loss.

The structural complexity of the reef usually declines after coral bleaching due to erosion of the dead coral skeletons, and because many of the corals most susceptible to coral bleaching are also the ones with the highest structural complexity (Marshall and Baird 2000). Reefs with high structural complexity support more individuals and more species of fishes than reefs with low structural complexity (Jones 1991; Syms and Jones 2000; Garpe *et al.* 2006; Graham *et al.* 2006). Therefore, we expect to observe a decline in the diversity and abundance of the associated fish communities as the increased frequency of coral bleaching causes an overall decline in the structural complexity of coral reefs. Herbivores often increase in abundance following a loss of coral cover (Wilson *et al.* 2006), presumably because more area becomes available for algal growth. However, even these species ultimately decline when habitat structure is lost (Sano *et al.* 1987; Garpe *et al.* 2006). The only species likely to benefit from coral loss and reef degradation are small generalist species and herbivores that live in areas of low relief and rubble, such as various gobies, blennies, eels and some damselfishes (Syms and Jones 2000; Bellwood *et al.* 2006; Glynn 2006, Feary *et al.* 2007a).

The full impacts of coral loss on adult populations may take years to eventuate, even for coral-dependent species. Adults are often able to persist for a considerable time following a loss of preferred coral resources (Pratchett *et al.* 2006) and recruitment failures may take some time to affect adult population sizes, especially in long-lived species (Graham *et al.* 2007). Rather than immediate responses to coral loss, populations of many reef fishes will exhibit a slow and insidious decline due to increased attrition of adults and reduced replenishment by recruits over many years. Loss of coral can have serious effects on the growth (Kokita and Nakazono 2000) and body condition (Pratchett *et al.* 2004) of corallivorous species, which will probably flow on to the reproductive success of the population. Similarly, use of alternative coral hosts can have

dramatic effects on the growth and longevity of coral-dwelling fishes (Munday 2001), with potentially serious implications for reproductive success (Fig. 4). Therefore, the negative effects of habitat loss on the survival of adults and the availability of substratum for the settlement of new recruits are likely to be reinforced by a decline in adult reproductive performance.

Reef fish communities have considerable resilience to disturbance and can recover from cyclones and bleaching events over years to decades, provided that benthic habitat recovers (Halford *et al.* 2004). However, even where coral cover has returned, recovery of the fish communities may be incomplete if a different suite of coral species dominate the new assemblage (Berumen and Pratchett 2006). The consequences of habitat loss on reef fish communities will depend on the frequency and intensity of bleaching events, com-

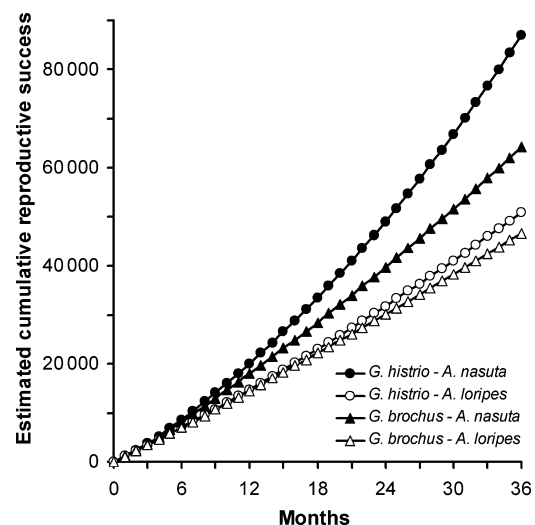


Figure 4 Estimated cumulative reproductive success for two species of coral-dwelling gobies (*Gobiodon histrio* and *Gobiodon brochus*, Gobiidae) inhabiting two different coral habitats (*Acropora nasuta* and *Acropora loripes*, Acroporidae). Differential loss of *A. nasuta* colonies from coral bleaching would have a negative effect on the reproductive success of both goby species because estimated reproductive success over an average goby's lifetime is lower when inhabiting *A. loripes* compared with *A. nasuta* for both goby species. Calculations were based on age-based growth rates of gobies in each species of coral from Munday (2001), a maximum body size of 49 mm for *G. brochus* and 62 mm for *G. histrio* (P.L. Munday, unpublished data) and using the size-fecundity relationships for coral-dwelling gobies reported by Kuwamura *et al.* (1993).

bined with the impacts of other disturbances, relative to the potential for the reefs and their associated fish communities to rebound.

Geographic ranges

Range shifts correlated with higher than average oceanic temperatures have been observed in temperate marine fishes (Holbrook *et al.* 1997; Parker and Dixon 1998; Perry *et al.* 2005). Similar responses should be expected for coral reef fishes as average sea surface temperatures increase. How geographic ranges will change and the consequences this will have on species persistence depends to a large degree on existing latitudinal distributions and temperature tolerances. Some coral reef fishes currently have ranges that span the latitudinal extent of coral reefs, others have ranges centred near the equator, and others only occur near the high-latitude edges of coral reef development (Jones *et al.* 2002; Allen 2007). Range shift scenarios differ for these different geographic distributions.

Geographic ranges are well known for species from the families Chaetodontidae and Pomacanthidae and these species serve to illustrate a range of possible outcomes. A large proportion of species in both families have ranges that span the latitudinal extent of coral reefs (Table 2) and these species have limited potential for range shifts (Fig. 5a) although populations may decline in low latitude waters if thermal tolerances are exceeded. Less than one-quarter of the species have ranges centred near the equator, but do not reach higher latitudes (Table 2). Many of these species might expand their ranges into higher latitudes as sea temperatures increase (Fig. 5b). A slightly smaller number of species have

mid-latitude ranges (Table 2) that might tend to contract towards higher latitudes (Fig. 5c). Finally, nearly one-quarter of species have small ranges near the high-latitude margins of reef development (Table 2). Many of these small-range species could experience dangerous range contractions as sea temperatures increase (Fig. 5d). Of course, whether a species shifts its range, or not, as temperature increases will depend on its thermal tolerance in relation to the current-day range (Pörtner and Knust 2007), the potential for acclimation and local adaptation, interactions with other species at the range boundary, dispersal capacity and the availability of suitable habitat outside the existing range.

The latitudinal range of coral reefs is not expected to expand significantly in response to increasing sea temperatures (Hoegh-Guldberg 2005) and although some fishes found on coral reefs also occur on rocky reefs at higher latitudes, the majority of coral reef species are unlikely to persist in non-reef areas, even if temperatures become more favourable at higher latitudes. Consequently, species that already have small ranges near the limits of coral reef growth will experience further range contractions that would ultimately increase their risk of extinction from other impacts. Areas of high endemism associated with isolated island groups, such as the Hawaiian Islands (Allen 2007), are likely to experience multiple extinctions as isolation restricts the potential for range shifts.

The ability of tropical species to establish permanent populations at higher latitudes will depend on their degree of dependence on coral reefs for food, shelter and reproduction, their tolerance to lower minimum temperatures in winter, and competition from established sub-tropical and temperate water species. Some species of fishes common on coral

Table 2 Current-day latitudinal distributions and potential range shifts due to increased sea surface temperature for species of Chaetodontidae and Pomacanthidae.

Existing distribution	Possible range shift	Family		
		Chaetodontidae	Pomacanthidae	Total
Pan-latitudinal	Limited range change	45	28	73
Equatorial	Range expansion	23	18	41
Mid-latitude	Range contraction	20	14	34
Small range at margin of reef development	Range contraction and/or population decline	33	23	56

Possible range shifts are based on the geographical ranges described in Allen *et al.* (1998) and assume that the preferred thermal environment is found near the middle of the current-day range.

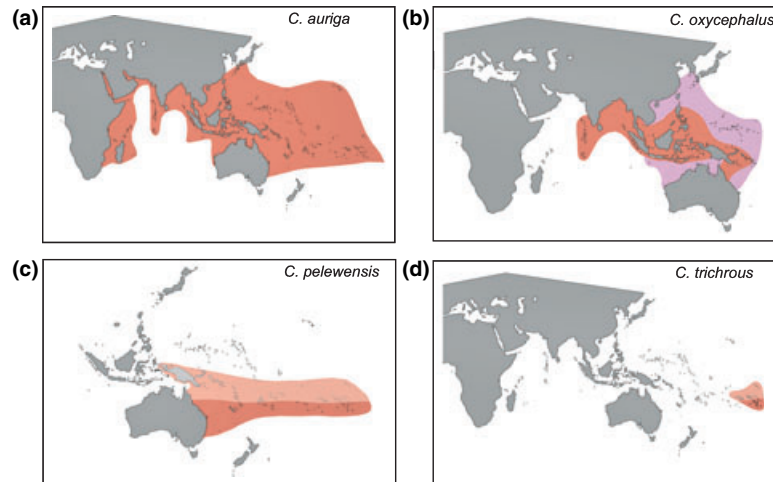


Figure 5 Examples of potential range shifts that could occur among species of butterflyfishes (*Chaetodon*, Chaetodontidae) as sea temperatures increase. Orange shading represents existing range, purple represents possible range expansion and faded orange represents possible range contraction. (a) Existing geographical range spanning the latitudinal extent of coral reef development – range shift unlikely to occur. (b) Existing geographical range centred near the equator and not extending to the latitudinal extent of coral reef development – range expansion possible. (c) Existing geographical range centred near mid-latitudes, often reaching the latitudinal extent of coral reef development – range contraction likely. (d) Existing small range near the latitudinal extent of coral reef development – range contraction leading to serious reduction in area is possible. Species selected for illustrative purposes only.

reefs already have populations beyond the latitudinal extent of coral reefs (Randall *et al.* 1997) and these species will probably expand their southern range limits as sea temperatures increase. However, the appearance of entire communities of coral reef fishes at higher latitudes than current distributions is highly unlikely.

Interactions with other stressors

Climate change will interact with other anthropogenic stressors to compound the problem of reef degradation. Destructive fishing practices and terrestrial pollution (especially elevated sedimentation) have degraded coral reefs in many parts of the world (Birkeland 1997; Burke *et al.* 2002; Wilkinson 2002) and will continue to be chronic stresses for reefs near large human populations. Elevated sedimentation, in particular, can increase coral mortality from bleaching and reduce the capacity of reefs to recover after mass bleaching (Fabricius 2005; Hoegh-Guldberg *et al.* 2007). The combined effect on reef fishes would be an acceleration of the changes to community structure and abundance described above due to habitat degradation.

Overfishing is a serious problem on coral reefs in many parts of the world (Sadovy 2005; Berkes *et al.* 2006; Newton *et al.* 2007) and some reef fish populations are already greatly depleted, even before they face the challenges of climate change. Overfishing of herbivorous fishes is particularly problematic because it can potentially lead to the proliferation of algae and a regime shift to an alternative stable state were corals are less dominant (Hughes *et al.* 2003; Bellwood *et al.* 2004; Mumby *et al.* 2006a; Hoegh-Guldberg *et al.* 2007). A regime shift on coral reefs would almost certainly cause a loss of fish diversity, especially among coral-dependent species, and a shift towards communities containing fewer specialist and more generalist species (Munday 2004; Bellwood *et al.* 2006; Wilson *et al.* 2006). Unfortunately, the combined effects of overfishing and climate change impacts on herbivorous fishes may make undesirable phase shifts more likely. Although some herbivorous fishes tend to increase in abundance immediately after a coral bleaching event, they usually decline below their original numbers once habitat structure is eroded (Sano *et al.* 1987; Garpe *et al.* 2006). A decline in herbivore numbers would increase the probability of regime shifts to algal-dominated reefs,

and could reduce the potential for recovery because even healthy herbivore populations do not always control a rapid proliferation of macroalgae (Ledlie *et al.* 2007).

Adaptation to climate change

Heritable changes in life-history characteristics that are consistent with climate change predictions have been detected in a number of terrestrial animals (Bradshaw and Holzapfel 2006; Skelly *et al.* 2007). In each case, the phenotypic change corresponds to an increase in fitness under the new climate regime, indicating that genetic adaptation to climate change is already underway in some animal populations. Some acclimation and adaptation to climate change will almost certainly occur in reef fish populations; however, the extent will vary greatly among species, depending on their current ranges, temperature tolerances, genetic connectivity with other populations and generation times.

Species with geographic ranges already spanning large temperature gradients have the greatest potential for acclimation and adaptation because they must either have considerable plasticity in thermal tolerance, or be locally adapted to the temperature gradient. This means there should be some potential to accommodate increases in sea temperatures by individual acclimation or gene flow from low-latitude populations. There is evidence for strong genetic connectivity among populations of coral reef fishes in some regions, such as the Great Barrier Reef in Australia (Doherty *et al.* 1995; Messmer *et al.* 2005; Bay *et al.* 2006). Consequently, high-latitude populations in these locations might already contain some tolerance to higher temperatures due to regular genetic input from lower latitude populations. Furthermore, as sea temperatures increase, gene flow from low-latitude populations might assist high-latitude populations in adapting to the new conditions. More isolated populations, such as those inhabiting island groups in the central Pacific or Indian Oceans, have lower levels of genetic connectivity to other populations (Planes 2002), which greatly reduces the potential for local adaptation to increasing ocean temperature by transfer of favourable genotypes.

To a large degree, the potential for genetic adaptation will depend on generation time. Some coral reef fishes have very short generation times that should favour rapid local adaptation. For example, many goby species are annuals (Depczynski and

Bellwood 2005; Hernaman and Munday 2005), which means there is the opportunity for selection to occur over 50–100 generations before the end of the century. Other coral reef fishes are long lived, but still tend to mature within a few years, e.g. 2–4 years in some acanthurids that can live 30–40 years (Choat and Robertson 2002). The relatively short generation times of these species should provide some potential for local adaptation to climate change. Yet other species are both long lived and late maturing, e.g. 9–10 years in some serranids and lutjanids (Pears *et al.* 2006; Marriott *et al.* 2007). There is little potential for local adaptation of these species, unless there is considerable genetic input from populations already adapted to warmer waters.

Although some acclimation or adaptation to increased temperature seems possible, especially for species with short generation times, there is little prospect of adaptation to habitat degradation. As discussed above, some reef fishes depend on live coral at one or more critical life stages and many more require complex habitat structure to escape predators (Beukers and Jones 1997; Syms and Jones 2000; Almany 2004). Significant declines in fish diversity following large-scale loss of live coral (Wilson *et al.* 2006) and further declines following loss of habitat structure (Graham *et al.* 2006) indicate that many species are unable to persist once their habitat has seriously degraded. There is little prospect of genetic adaptation under these circumstances. Habitat degradation will also retard adaptation to other climate change impacts (e.g. increased temperature) by reducing genetic variability within populations (decreased population size) and by reducing genetic connectivity between populations (smaller and more patchily distributed populations).

Coral reef fisheries

Total global fisheries yield from coral reefs is estimated to be worth at least US\$5 billion annually and many millions of people in tropical countries are directly dependent on food harvested from local reefs (Cesar *et al.* 2003, Sadovy 2005). Most coral reef fisheries exploit multiple species (Polunin and Roberts 1996), and although diverse multi-species fisheries are likely to be more resilient to environmental change than highly specialized fisheries (Worm *et al.* 2006), this depends on specific vulnerabilities of target species and assuming there are

not other major impacts that influence overall diversity and productivity. A serious concern is that many of the fisheries that provide food and livelihoods for millions are already over-exploited (Newton *et al.* 2007; Hoegh-Guldberg *et al.* 2007) and, therefore, have little resilience to additional impacts from climate change.

Numerous studies have demonstrated a strong link between climatic fluctuations, such as El Niño and La Niña events, and the distribution or productivity of exploited fish populations (Lehodey *et al.* 1997; O'Brien *et al.* 2000; Worm *et al.* 2005; Ottersen *et al.* 2006). However, these impacts tend to be species specific (Lehodey *et al.* 2003), making it difficult to predict the magnitude and direction of changes in fisheries productivity arising from environmental change. The consensus is that while some fisheries target species will be negatively impacted by climate change, others may benefit (McLean *et al.* 2001). Importantly, the coral reef fish species that are most vulnerable to environmental change (e.g. small bodied, restricted range and highly specialized coral-dependent species) are not generally targeted by coral reef fisheries (Pratchett *et al.* 2008). Perhaps this is why there is currently little evidence for changes in the size, composition or total value of landings from reef-based fisheries following severe episodes of climate-induced coral bleaching (McClanahan *et al.* 2002; Grandcourt and Cesar 2003). However, it is also possible that effects of environmental change and coral bleaching on fisheries target species are delayed due to lag effects from recruitment failure, and not yet apparent (Graham *et al.* 2007). Lag effects will make climate change impacts difficult to detect, and difficult to separate from the effects of fishing, but nonetheless important in the long term.

Changes to primary productivity brought about by climate change could affect biomass at all trophic levels. For example, slower growth appears to have occurred in benthic populations of three species of herbivorous damselfishes during warm El Niño conditions in the Galápagos Islands (Meekan *et al.* 1999). The green and red algae preferred by these damselfishes was largely replaced by brown algae of lower nutritional value during the warm period, probably causing a food shortage that curtailed growth rates. Similarly, climate-induced changes to plankton communities could affect the growth and abundance of planktivorous fishes, with flow-on effects to larger predatory species that are favoured by fishers (Fig. 1). Predictions about how trophic

structure and biomass might be affected on coral reefs are difficult, because the net impact of climate change on tropical marine productivity is uncertain and is likely to vary greatly from place to place – there might be positive effects on biomass in some locations and negative effects in others (Gregg *et al.* 2003; Steinberg 2007). However, more generally, we expect an overall decline in biomass at higher trophic levels as a result of a general decline in primary productivity caused by increased thermal stratification of the water column and reduced nutrient input from cooler, deeper waters, combined with increased metabolic rates of most organisms at higher ocean temperatures (Bopp *et al.* 2001, 2005; Loukos *et al.* 2003; Hobday *et al.* 2006). Reduced productivity would add further pressure to coral reef fisheries that are already over-exploited (Newton *et al.* 2007).

Most coral reef species of commercial importance are broadly distributed and their geographical distributions might not be significantly affected by climate change in the short-to-medium term, but there are clear exceptions. The sweetlip emperor (*Lethrinus miniatus*, Lethrinidae), an important commercial and recreational fisheries species, has a restricted anti-equatorial distribution with an apparent upper thermal limit of about 28°C (Williams *et al.* 2003). On the Great Barrier Reef, sweetlip emperor are restricted to south of 18°S where the impact of climate change on water temperature is predicted to be the greatest (Lough 2007). The distribution of this species will probably shift south as water temperature increases, potentially causing a shift in fishing effort and reducing fisheries productivity.

The future

Climate change will undoubtedly be the major factor determining the future of most coral reef fishes, impacting on them through all life stages and through a variety of mechanisms. Recent ecological advances provide some capacity for predicting the future, but great uncertainty remains (Table 1). Some of the impacts of climate change on coral reef fish are predictable and are in fact already in progress (e.g. effects of habitat degradation). Other impacts are much less certain for a variety of reasons, including uncertainty in climate change projections, poor understanding of the responses likely to accompany changes to environmental factors at individual, population

and community levels, and the complexity of interactions that can occur between different physical and biological factors that will be affected by climate change. However, what is certain is that without immediate action to limit further global warming, the future is bleak for many reef-associated species.

Future ecology

The most immediate and identifiable impacts of climate change on coral reef fishes will be changes in community composition and loss of biodiversity as a result of coral bleaching. There is now sufficient evidence to indicate that large-scale declines in coral cover will have serious consequences for the diversity and abundance of reef fish assemblages. Coral-dependent fishes suffer the most rapid declines in abundance as coral cover is lost. Many other species will exhibit longer term declines in abundance, due to loss of settlement habitat and the erosion of reef architecture and structural complexity that are essential for recruitment and survival. Some species, such as territorial herbivores and invertebrate feeders, may initially increase in abundance as coral cover declines, but even these species will decrease in abundance if habitat structure erodes. Declines in species richness and abundance will be highly patchy, and interspersed with cycles of recovery, but the overall trend will be negative if climate change continues to cause severe and repeated impacts on the composition and physical structure of the reef benthos. The only species likely to benefit are some generalist planktivores, small herbivores and rubble dwellers.

The different impacts of climate will interact with each other and with other threats and stresses to coral reefs, potentially leading to synergistic or cumulative effects that compound the problem. For example, increased bleaching and ocean acidification will have cumulative effects on the degradation of coral reef habitat. These impacts could interact with overfishing and compound the effects of terrestrial pollution to further degrade benthic communities, or even cause a regime shift from coral- to algal-dominated reefs. Dramatic phase shifts in the benthic habitat would, in turn, further affect the composition of reef fish communities.

Range expansions and contractions will occur as ocean temperature increases. Some coral reef fish species will extend their distribution limits as temperature increases. A similar number of species

will probably experience range contractions. Of greatest concern are small-range species currently living near the margins of coral reef distributions, which will face an increased risk of extinction as their ranges contract.

Increased temperature will probably cause a shift in life-history traits of local populations, although these changes will be relatively small compared with the natural variation already exhibited by many species across their geographic ranges. The most likely response to rising temperatures will be a shift in life-history traits in high-latitude populations to more closely match those currently seen in low-latitude populations.

Recruitment may tend to be enhanced by small increases in temperatures, but will become more variable where food supply for larvae is spatially or temporally unpredictable. Temperature changes at the upper range of climate change predictions are likely to have serious consequences for the reproductive performance of adults, potentially leading to complete reproductive failure and subsequent population collapse.

Major ecological processes, such as predation, competition and herbivory will be affected by shifts in the relative abundances of species in local assemblages. The strength of predator-prey and competitive interactions could also be altered by the reduction in habitat structure (Beukers and Jones 1997; Holbrook and Schmitt 2002; Almany 2004) and greater variability in the number of individuals recruiting to local populations (Caley *et al.* 1996). How changes in the relative strength of predation and competition will affect fish communities, and the function of coral reef ecosystems as a whole, remains largely unknown. Alteration of benthic habitat structure could favour some herbivorous fishes over others. Whether the species favoured are the ones that consume macroalgae will have important consequences for the ability of reefs to resist phase shifts (Hughes *et al.* 2007; Ledlie *et al.* 2007). However, even if key herbivores remain, coral reefs are not guaranteed to return to a coral dominated state after a disturbance if other stresses limit coral recruitment and recovery (McClanahan 2008).

Future evolution

Some fish species may acclimatize to increased sea temperatures as a result of existing phenotypic plasticity in their populations. Connectivity between

populations should also promote some genetic adaptation to increased temperature by gene flow from extant populations residing in warmer locations. Local adaptation to climate change will be most evident in small, short-lived species, where selection can operate over a large number of generations. Larger species, with long generation times, have little potential for local genetic adaptation to rapid climate change. A serious concern for all reef fishes is that habitat loss could have a negative effect on the potential for adaptation to environmental change, because smaller and more fragmented populations will have less genetic variability for selection to act upon and will be less effective in spreading favourable genotypes. Small-range species near the latitudinal margins of reef development and species living on isolated island groups are mostly at risk because they cannot move to more favourable locations as environmental conditions change and because their isolation will restrict the exchange of genes from other populations that might otherwise help them adapt to climate change.

Future management

First and foremost, there is a critical need to control and reduce greenhouse gas emissions to give at least the more resilient component of the coral reef fish fauna a long-term future. Management strategies that target other human impacts, such as over-exploitation and poor water quality, may help to minimize the shorter term impacts by increasing the resilience of reef ecosystems (Hughes *et al.* 2003). Given the evidence for the top-down control of coral reefs, maintaining healthy predator and herbivore fish populations may provide a certain amount of resilience to climatically induced changes. Marine protected areas, while not a 'cure-all' solution to the problems faced by coral reefs, may contribute to reef resilience by protecting exploited, ecologically important species (Mumby *et al.* 2006a,b). However, as the majority of small reef fish species are not exploited, protected areas offer reef fish biodiversity limited protection from extrinsic disturbances such as climate change (Boersma and Parrish 1999; Jones *et al.* 2004, 2007; Aronson and Precht 2006). A rapid reduction in greenhouse gas emissions, leading to a stabilization of global temperatures and ocean pH, is the only viable, long-term solution to the climate change crisis facing coral reefs.

Climate change is likely to increase the risk of fisheries collapses. The predicted increase in recruitment variability will make optimal harvest strategies more difficult to determine and fisheries may become more susceptible to overfishing during episodes of low recruitment. Incorporating larger 'safety margins' into harvest levels could provide some insurance from greater variability in population fluctuations and uncertainty about other climate change impacts. In some cases, lower harvest rates will need to be considered because of the possibility that reduced planktonic productivity and loss of benthic shelter will lead to a reduction in food supply for larger predatory species that are favoured by most commercial fisheries. More generally, incorporating climate change scenarios and the range of potential effects on fish populations into stock assessments and management strategy evaluations is essential for sustainable management of coral reef fisheries in future.

Future science

Much more research is required before we can predict the full ramifications of climate change on coral reef fishes and develop more and better strategies for minimizing the loss of biodiversity. More information is required on the effects that changes in the physical environment will have on the function and behaviour of reef fishes, because much of the available data on how fishes respond to changes in temperature comes from temperate species and these results might not be directly applicable to tropical marine fishes. Improved projections of how ocean currents and primary productivity will change at regional and local scales are sorely needed, as these projections are critical for predicting how individual performance, population dynamics and connectivity pattern will change over the coming century. More information is needed on the habitat requirements of reef fishes, especially around the time of settlement. Many reef fishes are closely associated with live coral habitat at the time of settlement, even if adults are not. Understanding the habitat requirements of fishes throughout their life will enable more precise predictions to be made about the long-term consequences of declining coral cover for reef fish assemblages.

Finally, more attention needs to be given to the potential for acclimation and adaptation of reef fishes to a changing climate. Ultimately, it is the

potential for species to adapt that will determine whether tolerance limits can keep pace with the changing environment. If global action can reduce the rate of climate change to bring it in line with the potential rate of adaptation of many species, and at the same time prevent irreversible damage to the coral reef habitat, there is at least a glimmer of hope on an otherwise bleak horizon.

Acknowledgements

We thank Gerald Allen for data and maps of the geographical distribution of butterflyfishes, Marian Wong for assisting with the figures and Gerald Allen, Howard Choat, Ove Hoegh-Guldberg, Terry Hughes, Johanna Johnson, Jeff Leis, Janice Lough, Laurence McCook, David McKinnon, Mike Kingsford, Paul Marshall, Serge Planes, Peter Sale, Marcus Sheaves, Maya Srinivasan and David Williamson for discussions, comments and support that have helped in the development of this manuscript.

References

- Access Economics (2007) Measuring the economic and financial value of the Great Barrier Reef Marine Park 2005/6. Report by Access Economics Pty Limited for the Great Barrier Reef Marine Park Authority. Great Barrier Reef Marine Park Authority, Townsville, Qld. 84 pp.
- Allen, G.R. (2007) Conservation hotspots of biodiversity and endemism for Indo-Pacific coral reef fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems*. DOI: 10.1002/aqc.880.
- Allen, G.R., Steene, R. and Allen, M. (1998) *Angelfishes and Butterflyfishes*. Odyssey, Perth.
- Almany, G.R. (2004) Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos* **106**, 275–284.
- Almany, G.R. and Webster, M.S. (2004) Odd species out as predators reduce diversity of coral-reef fishes. *Ecology* **85**, 2933–2937.
- Armsworth, P.R. (2000) Modeling the swimming response of late stage larval reef fish to different stimuli. *Marine Ecology Progress Series* **195**, 231–247.
- Aronson, R.B. and Precht, W.F. (2006) Conservation, precaution, and Caribbean reefs. *Coral Reefs* **25**, 441–450.
- Bay, L.K., Crozier, R.H. and Caley, M.J. (2006) The relationship between population and genetic structure and pelagic larval duration in coral reef fishes on the Great Barrier Reef. *Marine Biology* **149**, 1247–1256.
- Bellwood, D.R., Hughes, T.P., Folke, C. and Nystrom, C. (2004) Confronting the coral reef crisis. *Nature* **429**, 827–833.
- Bellwood, D.R., Hoey, A.S., Ackerman, J.L. and Depczynski, M. (2006) Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology* **12**, 1587–1594.
- Benoit, H.P., Pepin, P. and Brown, J.A. (2000) Patterns of metamorphic age and length in marine fishes, from individuals to taxa. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 856–869.
- Bergenius, M.A.J., Meekan, M.G., Robertson, D.R. and McCormick, M.I. (2002) Larval growth predicts the recruitment success of a coral reef fish. *Oecologia* **131**, 152–155.
- Berkes, F., Hughes, T.P., Steneck, R.S. et al. (2006) Globalization, roving bandits, and marine resources. *Science* **311**, 1557–1558.
- Berumen, M.L. and Pratchett, M.S. (2006) Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. *Coral Reefs* **25**, 647–653.
- Beukers, J.S. and Jones, G.P. (1997) Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* **114**, 50–59.
- Beverton, R.J.H. (1992) Patterns of reproductive strategy parameters in some marine teleost fishes. *Journal of Fish Biology* **41**, 137–160.
- Bindoff, N.L., Willebrand, J., Artale, V. et al. (2007) Observation, oceanic climate change and sea level. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller). Cambridge University Press, Cambridge, UK, pp. 385–432.
- Birkeland, C. (1997) *Life and Death of Coral Reefs*. Chapman & Hall, New York.
- Boersma, P.D. and Parrish, J.K. (1999) Limiting abuse: marine protected areas, a limited solution. *Ecological Economics* **31**, 287–304.
- Booth, D.J. and Beretta, G.A. (2002) Changes in a fish assemblage after a coral bleaching event. *Marine Ecology Progress Series* **245**, 205–212.
- Booth, D.J. and Wellington, G. (1998) Settlement preferences in coral reef fishes: effects on patterns of adult and juvenile distributions, individual fitness and population structure. *Australian Journal of Ecology* **23**, 274–279.
- Bopp, L., Monfray, P., Aumont, O. et al. (2001) Potential impacts of climate change on marine export production. *Global Biogeochemical Cycles* **15**, 81–99.
- Bopp, L., Aumont, O., Cadule, P., Alvain, S. and Gehlen, M. (2005) Response of diatoms distribution to global warming and potential implications: a global model study. *Geophysical Research Letters* **32**, L19606.
- Bradshaw, W.E. and Holzapfel, C.M. (2006) Evolutionary response to rapid climate change. *Science* **312**, 1477–1478.

- Brown, D.J.A. and Sadler, K. (1989) Fish survival in acid waters. In: *Acid Toxicity and Aquatic Animals* (eds R. Morris, E.W. Taylor, D.J.A. Brown and J.A. Brown). Cambridge University Press, Cambridge, pp. 31–44.
- Burgess, S.C., Kingsford, M.J. and Black, M.P. (2007) Influence of tidal eddies and wind on the distribution of presettlement fishes around One Tree Island, Great Barrier Reef. *Marine Ecology Progress Series* **341**, 233–242.
- Burke, L., Selig, E. and Spalding, M. (2002) *Reefs and Risk in Southeast Asia*. World Resources Institute, Washington, DC.
- Cai, W., Shi, G., Cowan, T., Bi, T. and Ribbe, J. (2005) The response of the Southern Annular Mode, the East Australian Current, and the southern mid-latitude ocean circulation to global warming. *Geophysical Research Letters* **32**, L23706. DOI: 10.1029/2005GL024701.
- Caldiera, K. and Wickett, M.E. (2003) Anthropogenic carbon and ocean pH. *Science* **425**, 365.
- Caley, M.J., Carr, M.H., Hixon, M.A. et al. (1996) Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* **27**, 477–500.
- Cesar, H., Burke, L. and Pet-Soede, L. (2003) *The Economics of Worldwide Coral Reef Degradation*. Cesar Environmental Economics Consulting, the Netherlands.
- Cheal, A.J., Delean, S., Sweatman, H. and Thompson, A.A. (2007) Spatial synchrony in coral reef fish populations and the influence of climate. *Ecology* **88**, 158–169.
- Choat, J.H. and Robertson, D.R. (2002) Age-based studies. In: *Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem* (ed. P.F. Sale). Academic Press, San Diego, CA, pp. 57–80.
- Church, J.A. and White, N.J. (2006) A 20th century acceleration in global sea level rise. *Geophysical Research Letters* **33**, L01602. DOI: 10.1029/2005GL024826.
- Claiborne, J.B., Edwards, S.L. and Morrison-Shetlar, A.I. (2002) Acid-base regulation in fishes: cellular and molecular mechanisms. *Journal of Experimental Zoology* **293**, 302–319.
- Colin, P.L. (1992) Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. *Environmental Biology of Fishes* **34**, 357–377.
- Cowen, R. (2002) Larval dispersal and retention and consequences for population connectivity. In: *Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem* (ed. P.F. Sale). Academic Press, San Diego, CA, pp. 149–170.
- Cowen, R.K., Paris, C.B. and Srinivasan, A. (2006) Scaling of connectivity in marine populations. *Science* **311**, 522–527.
- Danilowicz, B.S. (1995) The role of temperature in spawning of the damselfish *Dascyllus albisella*. *Bulletin of Marine Science* **57**, 624–636.
- Depczynski, M. and Bellwood, D.R. (2005) Shortest recorded vertebrate lifespan found in a coral reef fish. *Current Biology* **15**, 288–289.
- Depczynski, M., Fulton, C.J., Marnane, M.J. and Bellwood, D.R. (2007) Life history patterns shape energy allocation among fishes on coral reefs. *Oecologia* **153**, 111–120.
- Doherty, P. (1991) Spatial and temporal patterns in recruitment. In: *The Ecology of Fishes on Coral Reefs* (ed. P.F. Sale). Academic Press, San Diego, CA, pp. 261–293.
- Doherty, P.J., Planes, S. and Mather, P. (1995) Gene flow and larval duration in seven species of fish from the Great Barrier Reef. *Ecology* **76**, 2373–2391.
- Donner, S.D., Skirving, W.J., Little, C.M., Oppenheimer, M. and Hoegh-Guldberg, O. (2005) Global assessment of coral bleaching and required rates of adaptation under climate change. *Global Change Biology* **11**, 1–15.
- Edwards, M. and Richardson, A.J. (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**, 881–884.
- Fabricius, K.E. (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* **50**, 125–146.
- Feary, D.A., Almany, G.R., Jones, G.P. and McCormick, M.I. (2007a) Coral degradation and the structure of tropical reef fish communities. *Marine Ecology Progress Series* **333**, 243–248.
- Feary, D.A., Almany, G.R., McCormick, M.I. and Jones, G.P. (2007b) Habitat choice, recruitment and the response of coral reef fishes to coral degradation. *Oecologia* **153**, 727–737.
- Feely, R.A., Sabine, C.L., Lee, K., Berelson, W., Kleypas, J., Fabry, V.J. and Millero, F.J. (2004) Impact of Anthropogenic CO₂ on the CaCO₃ system in the oceans. *Science* **305**, 362–366.
- Fisher, R., Bellwood, D.R. and Job, S. (2000) The development of swimming abilities in reef fish larvae. *Marine Ecology Progress Series* **202**, 404–421.
- Frisch, A.J., McCormick, M.I. and Pankhurst, N.W. (2007) Reproductive periodicity and steroid hormone profiles in the sex-changing coral-reef fish, *Plectropomus leopardus*. *Coral Reefs* **26**, 189–197.
- Gagliano, M., McCormick, M.I. and Meekan, M.G. (2007) Temperature-induced shifts in selective pressure at a critical developmental transition. *Oecologia* **152**, 219–225.
- Gardiner, N.M. and Jones, G.P. (2005) Habitat specialisation and overlap in a guild of coral reef cardinal fishes (Apogonidae). *Marine Ecology Progress Series* **305**, 163–175.
- Gardner, T.A., Côté, I.M., Gill, J.A. et al. (2003) Long-term region-wide declines in Caribbean corals. *Science* **301**, 958–960.
- Garpe, K.C., Yahya, S.A.S., Lindahl, U. and Öhman, M.C. (2006) Long-term effects of the 1998 coral bleaching event on reef fish assemblages. *Marine Ecology Progress Series* **315**, 237–247.
- Glynn, P.W. (2006) Fish utilization of simulated coral reef frameworks versus eroded rubble substrates off Panama,

- eastern Pacific. In: *Proceedings of 10th International Coral Reef Symposium, Okinawa, 28 June to 2 July 2006* (eds Y. Suzuki, T. Nakamori, M. Hidaka et al.). International Coral Reef Society 2004, Okinawa, pp. 250–256.
- Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Bijoux, J.P. and Robinson, J. (2006) Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences, USA* **103**, 8425–8429.
- Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Robinson, J., Bijoux, J.P. and Daw, T.M. (2007) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conservation Biology* **21**, 1291–1300.
- Grandcourt, E.M. and Cesar, H.S.J. (2003) The bio-economic impact of mass coral mortality on the coastal reef fisheries of the Seychelles. *Fisheries Research* **60**, 539–550.
- Green, B.S. and Fisher, R. (2004) Temperature influences swimming speed, growth and larval duration in coral reef fish larvae. *Journal of Experimental Marine Biology and Ecology* **299**, 115–132.
- Gregg, W.W., Conkright, M.E., Ginoux, P., O'Reilly, J.E. and Casey, N.W. (2003) Ocean production and climate: global decadal changes. *Geophysical Research Letters* **30**. DOI: 10.1029/2003GL016889.
- Guinotte, J.M., Buddemeier, R.W. and Kleypass, J.A. (2003) Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin. *Coral Reefs* **22**, 551–558.
- Gust, N. (2004) Variation in the population biology of protogynous coral reef fishes over tens of kilometers. *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 205–218.
- Gust, N., Choat, J.H. and McCormick, M.I. (2001) Spatial variability in reef fish distribution, abundance, size and biomass: a multi-scale analysis. *Marine Ecology Progress Series* **214**, 237–251.
- Gust, N., Choat, J.H. and Ackerman, J.L. (2002) Demographic plasticity in tropical reef fishes. *Marine Biology* **140**, 1039–1051.
- Halford, A., Cheal, A.J., Ryan, D. and Williams, D.M. (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef, Australia. *Ecology* **85**, 1892–1905.
- Harley, C.D.G., Hughes, A.R., Hultgren, K.M. et al. (2006) The impacts of climate change in coastal marine systems. *Ecology Letters* **9**, 228–241.
- Harvell, C.D., Mitchell, C.E., Ward, J.R. et al. (2002) Climate warming and disease risks for terrestrial and marine biota. *Science* **296**, 2158–2162.
- Hays, G.C., Richardson, A.J. and Robinson, C. (2005) Climate change and marine plankton. *Trends in Ecology and Evolution* **20**, 337–344.
- Hernaman, V. and Munday, P. (2005) Life-history characteristics of coral reef gobies. I. Growth and life-span. *Marine Ecology Progress Series* **290**, 207–221.
- Hilder, M.L. and Pankhurst, N.W. (2003) Evidence that temperature changes cues reproductive development in the spiny damselfish, *Acanthochromis polyacanthus*. *Environmental Biology of Fishes* **66**, 187–196.
- Hixon, M.A. (1991) Predation as a process structuring coral reef fish communities. In: *The Ecology of Fishes on Coral Reefs* (ed. P.F. Sale). Academic Press, San Diego, CA, pp. 475–508.
- Hobday, A.J., Okey, T., Poloczanska, E.S., Kunz, T.J. and Richardson, A.J. (2006) Executive summary: impacts of climate change on Australian marine life. Report to the Australian Greenhouse Office, 36 pp.
- Hoegh-Guldberg, O. (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* **50**, 839–866.
- Hoegh-Guldberg, O. (2005) Climate change and marine ecosystems. In: *Climate Change and Biodiversity* (eds T.E. Lovejoy and L. Hannah). Yale University Press, New Haven, CT, pp. 256–273.
- Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J. et al. (2007) Coral reefs under rapid climate change and ocean acidification. *Science* **318**, 1737–1742.
- Holbrook, S.J. and Schmitt, R.J. (2002) Competition for shelter space causes density dependent predation mortality in damselfishes. *Ecology* **83**, 2855–2868.
- Holbrook, S.J., Russell, S.J. and Stephens, J.S. (1997) Changes in an assemblage of temperate reef fishes associated with a climate shift. *Ecological Applications* **7**, 1299–1310.
- Holbrook, S.J., Forrester, G.E. and Schmitt, R.J. (2000) Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. *Oecologia* **122**, 109–120.
- Houghton, J. (2004) *Global Warming: The Complete Briefing*, 3rd edn. Cambridge University Press, Cambridge.
- Hughes, T.P., Baird, A.H., Bellwood, D.R. et al. (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* **301**, 929–933.
- Hughes, T.P., Rodrigues, M.J., Bellwood, D.R. et al. (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* **17**, 360–365.
- Hunt von Herbing, I. (2002) Effects of temperature on larval fish swimming performance: the importance of physics to physiology. *Journal of Fish Biology* **61**, 865–876.
- IPCC (Intergovernmental Panel on Climate Change) (2007a) Summary for Policymakers. In: *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds M.L. Parry, O.F. Canziani, J.P. Paluttilof, P.J. van der Linden and G.E. Hanson). Cambridge University Press, Cambridge, UK, pp. 7–12.
- IPCC (Intergovernmental Panel on Climate Change) (2007b) Summary for Policymakers. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working*

- Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (eds S. Solomon, D. Qin, M. Manning *et al.*). Cambridge University Press, Cambridge, UK, pp. 1–18.
- Ishimatsu, A., Kikkawa, T., Hayashi, M., Lee, K. and Kita, J. (2004) Effects of CO₂ on marine fish: larvae and adults. *Journal of Oceanography* **60**, 731–741.
- Jackson, D.A. and Harvey, H.H. (1995) Gradual reduction and extinction of fish populations in acid lakes. *Water, Air & Soil Pollution* **85**, 389–394.
- James, M.K., Armsworth, P.R., Mason, L.B. and Bode, L. (2002) The structure of reef fish metapopulations: modelling larval dispersal and retention patterns. *Proceedings of the Royal Society of London B* **269**, 2079–2086.
- Jobling, M. (1997) Temperature and growth: modulation of growth rate via temperature change. In: *Global Warming: Implications for Freshwater and Marine Fish* (eds C.M. Wood and D.G. McDonald). Cambridge University Press, Cambridge, pp. 225–253.
- Jones, G.P. (1991) Post-recruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In: *The Ecology of Fishes on Coral Reefs* (ed. P.F. Sale). Academic Press, San Diego, CA, pp. 294–328.
- Jones, G.P., Caley, M.J. and Munday, P.L. (2002) Rarity in coral reef fish communities. In: *Coral reef fishes: dynamics and diversity in a complex ecosystem* (ed. P.F. Sale). Academic Press, San Diego, CA, pp. 81–101.
- Jones, G.P., McCormick, M.I., Srinivasan, M. and Eagle, J.V. (2004) Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences, USA* **101**, 8251–8253.
- Jones, G.P., Srinivasan, M. and Almany, G.R. (2007) Population connectivity and conservation of marine biodiversity. *Oceanography* **20**, 100–111.
- Kingsford, M.J., Leis, J.M., Shanks, A., Lindeman, K.C., Morgan, S.G. and Pineda, J. (2002) Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science* **70**, 309–340.
- Kleypas, J.A., Feely, R.A., Fabry, V.J., Langdon, C., Sabine, C.L. and Robbins, L.L. (2006) *Impacts of Ocean Acidification on Coral Reefs and Other Marine Calcifiers: A Guide for Future Research*. Workshop held on 18–20 April 2005, St Petersburg, FL, sponsored by NSF, NOAA, and the US Geological Survey 88 pp.
- Kleypas, J.A., Danabasoglu, G. and Lough, J.M. (2008) Potential role of the ocean thermostat in determining regional differences in coral reef bleaching events. *Geophysical Research Letters* **35**, L03613. DOI: 10.1029/2007GL032257.
- Kokita, T. and Nakazono, A. (2000) Rapid response of an obligately corallivorous filefish *Oxymonacanthus longirostris* (Monacanthidae) to a mass coral bleaching event. *Coral Reefs* **20**, 155–158.
- Kuwamura, T., Yogo, Y. and Nakashima, Y. (1993) Size-assortative monogamy and paternal egg care in a coral goby *Paragobiodon echinocephalus*. *Ethology* **95**, 65–75.
- Ledlie, M.H., Graham, N.A.J., Bythell, J.C. *et al.* (2007) Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs* **26**, 641–653.
- Lehodey, P., Bertignac, M., Hampton, J., Lewis, A. and Picaut, J. (1997) El Niño Southern Oscillation and tuna in the western Pacific. *Nature* **389**, 715–718.
- Lehodey, P., Chai, F. and Hampton, J. (2003) Modelling climate-related variability of tuna populations from a coupled ocean-biogeochemical-population dynamics model. *Fisheries Oceanography* **12**, 483–494.
- Leis, J.M. (1991) The pelagic stage of reef fishes: the larval biology of coral reef fishes. In: *The Ecology of Fishes on Coral Reefs* (ed. P.F. Sale). Academic Press, San Diego, CA, pp. 183–230.
- Leis, J.M. and McCormick, M.I. (2002) The biology, behaviour and ecology of the pelagic, larval stage of coral reef fishes. In: *Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem* (ed. P.F. Sale). Academic Press, San Diego, CA, pp. 171–199.
- Lieske, E. and Myers, R. (1994) *Coral Reef Fishes: Indo-Pacific and Caribbean*. HarperCollins, London.
- Lough, J. (2007) Climate and climate change on the Great Barrier Reef. In: *Climate Change and the Great Barrier Reef* (eds J.E. Johnson and P.A. Marshall). Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Townsville, Qld, pp. 15–50.
- Loukos, H., Monfray, P., Bopp, L. and Lehodey, P. (2003) Potential changes in skipjack tuna (*Katsuwonus pelamis*) habitat from a global warming scenario: modelling approach and preliminary results. *Fisheries Oceanography* **12**, 474–482.
- Lovejoy, T.E. and Hannah, L. (2005) *Climate Change and Biodiversity*. Yale University Press, New Haven, CT.
- Marriott, R.J., Mapstone, B.D. and Begg, G.A. (2007) Age-specific demographic parameters, and their implications for management of the red bass, *Lutjanus bohar* (Forsskal, 1775): a large, long-lived reef fish. *Fisheries Research* **83**, 204–215.
- Marshall, P.A. and Baird, A.H. (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* **19**, 155–163.
- McClanahan, T.R. (2008) Response of coral reef benthos and herbivory to fishery closure management and the 1998 ENSO disturbance. *Oecologia* **155**, 169–177.
- McClanahan, T.R., Maina, J. and Pet-Soede, L. (2002) Effects of the 1998 coral mortality event on Kenyan coral reefs and fisheries. *Ambio* **31**, 543–550.
- McClanahan, T.R., Mwaguni, S. and Muthiga, N.A. (2005) Management of the Kenyan coast. *Ocean and Coastal Management* **48**, 901–931.
- McCook, L.J., Jompa, J. and Diaz-Pulido, G. (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* **19**, 400–417.
- McCormick, M.I. and Molony, B.W. (1995) Influence of water temperature during the larval stage on size, age

- and body condition of a tropical reef fish at settlement. *Marine Ecology Progress Series* **118**, 59–68.
- McKinnon, A.D., Richardson, A.J., Burford, M.E. and Furnas, M.J. (2007) Vulnerability of Great Barrier Reef plankton to climate change. In: *Climate Change and the Great Barrier Reef* (eds J.E. Johnson and P.A. Marshall). Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Townsville, Qld, pp. 121–152.
- McLean, R.F., Tsyban, A., Burkett, V. et al. (2001) Coastal zones and marine ecosystems. In: *Climate Change 2001: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (eds J.J. McCarthy, O.F. Canziani, N.A. Leary, D.J. Dokken and K.S. White). Cambridge University Press, Cambridge, pp. 343–379.
- Meekan, M.G., Wellington, G.M. and Axe, L. (1999) El Niño–Southern Oscillation events produce checks in the otoliths of coral reef fishes in the Galapagos Archipelago. *Bulletin of Marine Science* **64**, 383–390.
- Meekan, M.G., Ackerman, J.L. and Wellington, G.M. (2001) Demography and age structures of coral reef damselfishes in the tropical eastern Pacific Ocean. *Marine Ecology Progress Series* **212**, 223–232.
- Meekan, M.G., Carleton, J.H., McKinnon, A.D., Flynn, K. and Furnas, M. (2003) What determines the growth of tropical reef fish larvae in the plankton: food or temperature? *Marine Ecology Progress Series* **256**, 193–204.
- Meekan, M.G., Carleton, J.H., Steinberg, C.R. et al. (2006) Turbulent mixing and mesoscale distributions of late-stage fish larvae on the NW Shelf of Western Australia. *Fisheries Oceanography* **15**, 44–59.
- Messmer, V., vanHerwerden, L., Munday, P.L. and Jones, G.P. (2005) Phylogeography of colour polymorphism in the coral reef fish *Pseudochromis fuscus* from Papua New Guinea and the Great Barrier Reef. *Coral Reefs* **24**, 392–402.
- Montgomery, J.C., Jeffs, A., Simpson, S.D., Meekan, M. and Tindle, C. (2006) Sound as an orientation cue for the pelagic larvae of reef fishes and decapod crustacean. *Advances in Marine Biology* **51**, 143–196.
- Mora, C. and Ospina, A.F. (2001) Tolerance to high temperatures and potential impact of sea warming on reef fishes of Gorgona Island (tropical Eastern Pacific). *Marine Biology* **139**, 765–769.
- Mumby, P.J., Dahlgren, C.P., Harborne, A.R. et al. (2006a) Fishing, trophic cascades and the process of grazing on coral reefs. *Science* **311**, 98–101.
- Mumby, P.J., Harborne, A.R., Williams, J. et al. (2006b) Trophic cascade facilitates coral recruitment in a marine reserve. *Proceedings of the National Academy of Sciences, USA* **104**, 8362–8367.
- Munday, P.L. (2001) Fitness consequences of habitat selection and competition among coral-dwelling fish. *Oecologia* **128**, 585–593.
- Munday, P.L. (2004) Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biology* **10**, 1642–1647.
- Munday, P.L. and Holbrook, S.J. (2006) Changing coral communities: what are the consequences for reef fishes? In: *Proceedings of 10th International Coral Reef Symposium, Okinawa, 28 June to 2 July 2004* (eds Y. Suzuki, T. Nakamori, M. Hidaka et al.). International Coral Reef Society 2004, Okinawa, pp. 214–215.
- Munday, P.L., Jones, G.P. and Caley, M.J. (1997) Habitat specialisation and the distribution and abundance of coral-dwelling gobies. *Marine Ecology Progress Series* **152**, 227–239.
- Munday, P.L., Jones, G.P., Sheaves, M., Williams, A.J. and Goby, G. (2007) Vulnerability of fishes of the Great Barrier Reef to climate change. In: *Climate Change and the Great Barrier Reef* (eds J.E. Johnson and P.A. Marshall). Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Townsville, Qld, pp. 357–391.
- Newton, K., Côté, I.M., Pilling, G.M., Jennings, S. and Dulvy, N.K. (2007) Current and future sustainability of island coral reef fisheries. *Current Biology* **17**, 655–658.
- Nilsson, G.E., Ostlund-Nilsson, S., Penfold, R. and Grutter, A.S. (2007) From record performance to hypoxia tolerance: respiratory transition in damselfish larvae settling on a coral reef. *Proceeding of the Royal Society, London B* **274**, 79–85.
- O'Brien, C.M., Fox, C.J., Planque, B. and Casey, J. (2000) Fisheries: climate variability and North Sea cod. *Nature* **404**, 142.
- O'Connor, M.I., Bruno, J.F., Gaines, S.D. et al. (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences, USA* **104**, 1266–1271.
- Öhman, M.C., Munday, P.L., Jones, G.P. and Caley, M.J. (1998) Settlement strategies and distribution patterns of coral-reef fishes. *Journal of Experimental Marine Biology and Ecology* **225**, 219–238.
- Ottersen, G., Hjermann, D.Ø. and Stenseth, N.C. (2006) Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fisheries Oceanography* **15**, 230–243.
- Pankhurst, N.W. and Porter, M.J.R. (2003) Cold and dark or warm and light: variations on the theme of environmental control of reproduction. *Fish Physiology and Biochemistry* **28**, 385–389.
- Parker R.O. Jr and Dixon, R.L. (1998) Changes in a North Carolina reef fish community after 15 years of intense fishing – global warming implications. *Transactions of the American Fisheries Society* **127**, 908–920.
- Parnesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology and Systematics* **37**, 637–669.

- Parmesan, C. and Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42.
- Pears, R.J., Choat, J.H., Mapstone, B.D. and Begg, G.A. (2006) Demography of a large grouper, *Epinephelus fuscoguttatus*, from Australia's Great Barrier Reef: implications for fishery management. *Marine Ecology Progress Series* **307**, 259–272.
- Perry, A.L.L., Ellis, P.J. and Reynolds, J.D. (2005) Climate change and distribution shifts in marine fishes. *Science* **308**, 1912–1915.
- Planes, S. (2002) Biogeography and larval dispersal inferred from population genetic analysis. In: *Coral reef fishes: dynamics and diversity in a complex ecosystem* (ed. P.F. Sale). Academic Press, San Diego, CA, pp. 201–220.
- Poloczanska, E.S., Babcock, R.C., Butler, A. et al. (2007) Climate change and Australian marine life. *Oceanography and Marine Biology: An Annual Review* **45**, 407–478.
- Polunin, N.V.C. and Roberts, C.M. (1996) *Reef Fisheries*. Chapman & Hall, London.
- Pörtner, H.O. and Knust, R. (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* **315**, 95–97.
- Pörtner, H.O. and Langenbuch, M. (2005) Synergistic effects of temperature extremes, hypoxia, and increases in CO₂ on marine animals: from Earth history to global change. *Journal of Geophysical Research* **110**, C09S10. DOI: 10.1029/2004JC002561.
- Pörtner, H.O., Langenbuch, M. and Reipschlag, A. (2004) Biological impact of elevated ocean CO₂ concentrations: lessons from animal physiology and earth history. *Journal of Oceanography* **60**, 705–718.
- Pratchett, M.S. (2005) Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef. *Marine Biology* **148**, 373–382.
- Pratchett, M.S., Wilson, S.K., Berumen, M.L. and McCormick, M.I. (2004) Sublethal effects of coral bleaching on an obligate coral feeding butterflyfish. *Coral Reefs* **23**, 352–356.
- Pratchett, M.S., Wilson, S.K. and Baird, A.H. (2006) Declines in the abundance of *Chaetodon* butterflyfishes (Chaetodontidae) following extensive coral depletion. *Journal of Fish Biology* **69**, 1269–1280.
- Pratchett, M.S., Munday, P.L., Wilson, S.K. et al. (2008) Effects of climate-induced coral bleaching on coral-reef fishes: ecological and economic consequences. *Oceanography and Marine Biology: An Annual Review* **46**, 251–296.
- Pratchett, M.S., Wilson, S.K., Graham, N.A.J., Munday, P.L., Jones, G.P. and Polunin, N.V.C. (in press) Coral bleaching and consequences for mobile reef organisms: past, present and uncertain future. In: *Coral Bleaching: Patterns, Processes, Causes and Consequences* (eds M. Van Oppen and J. Lough). Springer, Hiedelberg (in press).
- Randall, J.E., Allen, G.R. and Steene, R.C. (1997) *Fishes of the Great Barrier Reef and Coral Sea*. University of Hawaii Press, Honolulu, HI.
- Robertson, D.R. (1991) The role of adult biology in the timing of spawning of tropical reef fishes. In: *The Ecology of Fishes on Coral Reefs* (ed. P.F. Sale). Academic Press, San Diego, CA, pp. 356–386.
- Robertson, D.R., Ackerman, J.L., Choat, J.H., Posada, J.M. and Pitt, J. (2005) Ocean surgeon fish *Acanthurus bahianus*. I. The geography of demography. *Marine Ecology Progress Series* **295**, 229–244.
- Roessig, J.M., Woodley, C.M., Cech, J.J. and Hansen, L.J. (2004) Effects of global climate change on marine and estuarine fishes and fisheries. *Reviews in Fish Biology and Fisheries* **14**, 251–275.
- Rombough, P.J. (1997) The effects of temperature on embryonic and larval development. In: *Global Warming: Implications for Freshwater and Marine Fish* (eds C.M. Wood and D.G. McDonald). Cambridge University Press, Cambridge, pp. 177–223.
- Root, T.L., Hall, K.R., Schnelders, S.H., Rosenzweig, C. and Pounds, A. (2003) Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60.
- Royal Society (2005) *Ocean acidification due to increasing atmospheric carbon dioxide*. The Royal Society, London.
- Russ, G.R. (1991) Coral reef fisheries: effects and yields. In: *The Ecology of Fishes on Coral Reefs* (ed. P.F. Sale). Academic Press, San Diego, CA, pp. 601–635.
- Ruttenberg, B.I., Haupt, A.J., Chiriboga, A.I. and Warner, R.R. (2005) Patterns, causes and consequences of regional variation in the ecology and life history of a reef fish. *Oecologia* **145**, 394–403.
- Sadovy, Y. (1996) Reproduction of reef fisheries species. In: *Reef Fisheries* (eds N.V.C. Polunin and C.M. Roberts). Chapman & Hall, London, pp. 15–59.
- Sadovy, Y. (2005) Trouble on the reef: the imperative for managing vulnerable and valuable fisheries. *Fish and Fisheries* **6**, 167–185.
- Sale, P.F. (1991) Reef fish communities: open nonequilibrium systems. In: *The Ecology of Fishes on Coral Reefs* (ed. P.F. Sale). Academic Press, San Diego, CA, pp. 564–598.
- Samoilys, M.A. (1997) Periodicity of spawning aggregations of coral trout *Plectropomus leopardus* (Pisces: Serranidae) on the northern Great Barrier Reef. *Marine Ecology Progress Series* **160**, 149–159.
- Sano, M., Shimizu, M. and Nose, Y. (1987) Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation on reef fish communities at Iriomote Island, Japan. *Marine Ecology Progress Series* **37**, 191–199.
- Searcy, S.P. and Sponaugle, S. (2000) Variable larval growth in a coral reef fish. *Marine Ecology Progress Series* **206**, 213–226.
- Sheaves, M.J. (1995) Large lutjanid and serranid fishes in tropical estuaries: are they adults or juveniles? *Marine Ecology Progress Series* **129**, 31–40.

- Shirayama, Y. and Thornton, H. (2005) Effects of increased atmospheric CO₂ on shallow water marine benthos. *Journal of Geophysical Research* **110**, C9.
- Skelly, D.K., Joseph, L.N., Possingham, H.P. et al. (2007) Evolutionary responses to climate change. *Conservation Biology* **21**, 1353–1355.
- Spalding, M.D. and Jarvis, G.E. (2002) The impact of the 1998 coral mortality on reef fish communities in the Seychelles. *Marine Pollution Bulletin* **44**, 309–321.
- Sponaugle, S. and Pinkard, D.P. (2004) Impact of variable pelagic environments on natural larval growth and recruitment of a reef fish. *Journal of Fish Biology* **64**, 34–54.
- Sponaugle, S., Lee, T.N., Kourafalou, V. and Pinkard, D.P. (2005) Florida Current frontal eddies and the settlement of coral reef fishes. *Limnology and Oceanography* **50**, 1033–1048.
- Sponaugle, S., Grorud-Colvert, K. and Pinkard, D. (2007) Temperature-mediated variation in early life history traits and recruitment success of the coral reef fish *Thalassoma bifasciatum* in the Florida Keys. *Marine Ecology Progress Series* **308**, 1–15.
- Srinivasan, M. and Jones, G.P. (2006) Extended breeding and recruitment periods of fishes on a low latitude coral reef. *Coral Reefs* **25**, 673–682.
- Steinberg, C. (2007) Impacts of climate change on the physical oceanography of the Great Barrier Reef. In: *Climate Change and the Great Barrier Reef* (eds J.E. Johnson and P.A. Marshall). Great Barrier Reef Marine Park Authority and Australian Greenhouse Office, Townsville, Qld, pp. 51–74.
- Steneck, R.S. (1988) Herbivory on coral reefs: a synthesis. In: *Proceedings of the Sixth International Coral Reef Symposium, Townsville, 8–12 August 1988* (eds J.H. Choat and O. Bellwood). Organizing Committee of the 6th International Coral Reef Symposium, Townsville, Qld, pp. 37–49.
- Steneck, R.S. (1997) Crustose corallines, other algal functional groups, herbivores and sediments: complex interactions among reef productivity gradients. In: *Proceedings of the Eighth International Coral Reef Symposium, Panama, 24–29 June 1997* (eds H.A. Lessios and I.G. Macintyre). Smithsonian Tropical Research Institute, Balboa, pp. 695–700.
- Stobutski, I.C. and Bellwood, D.R. (1997) Sustained swimming abilities of the late pelagic stages of coral reef fishes. *Marine Ecology Progress Series* **149**, 35–41.
- Suthers, I.M., Taggart, C.T., Kelley, D., Rissik, D. and Middleton, J.H. (2004) Entrainment and advection in an island's tidal wake, as revealed by light attenuation, zooplankton, and ichthyoplankton. *Limnology and Oceanography* **49**, 283–296.
- Syms, C. and Jones, G.P. (2000) Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology* **81**, 2714–2729.
- Thomas, C.D., Cameron, A., Green, R.E. et al. (2004) Extinction risk from climate change. *Nature* **427**, 145–148.
- Van Der Kraak, G. and Pankhurst, N.W. (1997) Temperature effects on the reproductive performance of fish. In: *Global Warming: Implications for Freshwater and Marine Fish* (eds C.M. Wood and D.G. McDonald). Cambridge University Press, Cambridge, pp. 159–176.
- Velicogna, I. and Wahr, R. (2006) Acceleration of Greenland ice mass loss in spring 2004. *Nature* **443**, 329–331.
- Walther, G.R., Convey, P.E., Menzel, A. et al. (2002) Ecological responses to recent climate change. *Nature* **416**, 389–395.
- Webster, P.J., Holland, G.J., Curry, J.A. and Chang, H.R. (2005) Changes in tropical cyclone number and intensity in a warming environment. *Science* **309**, 844–1846.
- Wilkinson, C. (2002) Executive summary: status of coral reefs of the world 2002. In: *Status of Coral Reefs of the World 2002* (ed. C. Wilkinson). Australian Institute of Marine Science, Townsville, Qld, pp. 7–31.
- Williams, A.J., Davies, C.R., Mapstone, B.D. and Russ, G.R. (2003) Scales of spatial variation in demography of a large coral reef fish: an exception to the typical model? *Fisheries Bulletin* **101**, 673–683.
- Wilson, D.T. and Meekan, M.G. (2002) Growth-related advantages for survival to the point of replenishment in the coral reef fish *Stegastes partitus* (Pomacentridae). *Marine Ecology Progress Series* **231**, 247–260.
- Wilson, S.K., Graham, N.A.J., Pratchett, M.S., Jones, G.P. and Polunin, N.V.C. (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology* **12**, 2220–2234.
- Wood, C.M. and McDonald, D.G. (1997) *Global Warming: Implications for Freshwater and Marine Fish*. Cambridge University Press, Cambridge.
- Worm, B., Sandow, M., Oschlies, A., Lotze, H.K. and Myers, R.A. (2005) Global patterns of predator diversity in the open oceans. *Science* **309**, 1365–1369.
- Worm, B., Barbier, E.B., Beaumont, N. et al. (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science* **314**, 787–790.