Chapter 9
Coral Bleaching and Consequences for Motile Reef Organisms: Past, Present and Uncertain Future Effects

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9.1 Introduction

While coral reefs are subject to a wide range of anthropogenic and natural disturbances, sustained and ongoing climate change is rapidly emerging as the single greatest threat to these important ecosystems (Hughes et al. 2003; West and Salm 2003; Munday et al. 2007). The potential effects of climate change on coral reef ecosystems are numerous, but the most devastating effects to date have been large-scale and severe episodes of coral bleaching (Smith and Buddemeier 1992; Goreau et al. 2000; Chap. 3). The global significance of coral bleaching was most evident in 1997–1998, when high sea surface temperatures resulted in severe coral bleaching and high mortality (up to 99% coral mortality) in over 50 countries throughout the world (Chaps. 3, 8). Increasing frequency and severity of mass-bleaching events are clearly linked to climate change (Walther et al. 2002; Hughes et al. 2003) and the longer-term future is potentially catastrophic, not just for corals, but for coral reefs as a whole.

There are no other ecosystems in which the major habitat-forming organisms have been functioning so close to their upper thermal limit. Corals are the fundamental building blocks of coral reefs, providing a spatial diversity of habitats and a three-dimensional structure that supports an exceptional diversity of reef animals. Recent research clearly demonstrates that coral decline has had profound effects on reef fishes and other reef-associated organisms (Sin 1999a; Caley et al. 2001; Jones et al. 2004; Idjadi and Edmunds 2006; Wilson et al. 2006; Munday et al. 2007). Moreover, changes in the composition of coral assemblages, which may occur following severe or recurrent disturbances (Chap. 8), lead to changes in the composition of reef-associated faunas (e.g. Berumen and Pratchett 2006), with potentially major implications for coral reef biodiversity and ecosystem function (Bellwood et al. 2004; Jones et al. 2004).

Studies on the effects of bleaching on motile reef organisms were mostly initiated after the 1997–1998 bleaching event (e.g. Graham et al. 2006; Pratchett et al. 2006), limiting the understanding of long-term impacts (>8 years) of climate-induced coral bleaching. In addition, coral reef environments are commonly exposed to multiple disturbances, making it difficult to identify the role or importance of any one factor (e.g. Jones et al. 2004; Pratchett et al. 2006). Different kinds of disturbances

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Ecological Studies 205,

(e.g. climate-induced coral bleaching, severe tropical storms, coral disease) may have a range of impacts on coral reefs, but most disturbances are detrimental for corals. Climate change itself will also impact on coral reefs in a multitude of ways. For example, it will cause increasingly frequent and severe episodes of coral bleaching and may also lead to an increasing frequency of severe tropical storms (Webster et al. 2005; Chap. 1). Despite the limitations of short-term studies and the complexities of multiple disturbances, it is important that we assemble the available information on the impacts of coral bleaching, to recognise the future scale of degradation that could occur to coral reefs and develop appropriate responses.

Much of the current knowledge of the indirect effects of coral bleaching relates to changes in the abundance of coral reef fishes immediately following bleaching events (Table 9.1). At least one-quarter of extant fish species are associated with coral reefs (Spalding et al. 2001) and fishes are the most conspicuous, diverse, and well studied group of motile reef organisms. Many coral reef fishes depend on the coral reef habitat for vital resources such as food, shelter, and living space (Jones and Syms 1998). Not surprisingly, many species (up to 75%) exhibit significant declines in abundance following extensive coral depletion (Jones et al. 2004), while a small number of non-coral specialists may actually increase in abundance. The specific effects of coral depletion on coral reef fishes depend on the scale at which fishes interact with benthic habitats, as well as the spatial extent of disturbances. Coral reef fishes are generally resilient to localised disturbances (within or among individual reefs) because depleted populations can be quickly replenished from other unaffected populations (Sale 1991). However, the spatial extent of habitat degradation from climate-induced coral bleaching is immense and may ultimately threaten many species with small geographic ranges (Munday 2004). To fully comprehend the impacts of habitat disturbance on fishes we need to understand both their specific habitat requirements and the ways in which different disturbances affect the biological and physical structure of the substratum.

In this chapter, we review the effects of climate-induced coral bleaching on motile reef organisms, including fishes and motile invertebrates. These effects range from declines in the physiological condition and reproductive output of individuals to declines in biodiversity and the potential for global extinction. Coral-bleaching events represent acute large-scale disturbances, often resulting in extensive coral mortality followed by gradual degradation of the reef framework (Garpe et al. 2006; Graham et al. 2006; Chap. 8). By considering different time-scales, we can distinguish the immediate effects of coral bleaching associated with a reduction or loss of live coral tissue (<3 years) from medium-term changes in the biological and physical structure of reef habitats (3–10 years) and extrapolate these to give a longer-term (>10 year) prognosis for the fate of coral reef ecosystems. The short-term effects of coral mortality (<3 years) are mainly restricted to those species that feed, shelter or recruit on live corals (Wilson et al. 2006). Even so, strongly coral-dependent species may exhibit a range of responses, including altered patterns of resource use, mass migration to coral-rich habitats, recruitment failure and/or localised extinction. These effects may be further magnified following changes in the biological and physical structure of reef habitats, which may occur 3–10 years following extensive coral death (Graham et al. 2006). Most importantly, extensive coral mortality ultimately leads to a decline in structural complexity through the gradual erosion of dead coral skeletons. Structural complexity provided by coral skeletons moderates key biological processes of competition and predation (Beukers and Jones 1997) and exerts a much stronger influence on the abundance and diversity of motile reef organisms than loss of coral cover alone. The few studies which have explored the effects of coral depletion over this time-scale (Jones et al. 2004; Garpe et al. 2006; Graham et al. 2006) clearly demonstrate the far-reaching consequences of coral death and reef degradation on motile reef organisms. It is also

Table 9.1 Published studies on effects of increased temperature and bleaching-induced coral mortality on motile reef organisms. These studies are mostly conducted over very short time-frames (<3 years post-bleaching) and mainly focus on coral reef fishes. *GBR* Great Barrier Reef

Location	No. years post-bleaching	No. species considered (families)	Source
Coral reef fishes			
Cocos Island, Costa Rica	3	1	Guzmán and Cortés 1992
Panama	1	1	Glynn 1985
Eastern Pacific	4	1	Guzmán & Robertson 1989
Moorea, French Polynesia	1	135 (27)	Adjeroud et al. 2002
One Tree Island, GBR, Australia	2	13 (1)	Booth and Beretta 2002
Kimbe Bay, PNG	3	538 (20)	Jones et al. 2004
Kimbe Bay, PNG	5	6 (1)	Munday 2004
Trunk Reef, GBR, Australia	<1	1	Pratchett et al. 2004
Trunk Reef, GBR, Australia	3	15 (1)	Pratchett et al. 2006
Palm Island, GBR, Australia	<1	144 (12)	Thompson and Malcolm 1999
Orpheus Island, GBR, Australia	6	36	Bellwood et al. 2006
Okinawa, Southern Japan	1	1	Kokita and Nakazono 2001
Okinawa, Southern Japan	<1	1	Tsuchiya 1999
Ishigaki Island, Japan	1	110 (19)	Shibuno et al. 1999
Iriomote Island, Japan	2	55	Sano 2004
Chagos	3	203 (29)	Sheppard et al. 2002
Seychelles	7	134 (16)	Graham et al. 2006
Seychelles	1	44 (14)	Spalding and Jarvis 2002
Tanzania	6	91	Garpe et al. 2006
Tutia Reef, Tanzania	<1	84	Lindahl et al. 2001
Kenya	3	(13)	McClanahan et al. 2002a, b
Arabian Gulf, Dubai	3	103	Riegl 2002
Coral reef invertebrates			
Bahia, Brazil	2	24	Attrill et al. 2004
Cocos Island, Costa Rica	3	2 (2)	Guzmán and Cortéz 1992
Panama	1	2 (2)	Glynn 1985
Panama	<1	2 (1)	Glynn et al. 1985
Okinawa, Southern Japan	<1	4 (1)	Tsuchiya et al. 1992
Okinawa, Southern Japan	<1	9 (3)	Tsuchiya 1999
Kenya	3	(2)	McClanahan et al. 2002

likely that extremely severe and/or large-scale bleaching events will have even longer-lasting effects on coral reef ecosystems (over time-frames >10 years), especially given that the frequency and intensity of coral bleaching is expected to increase (Donner et al. 2005; Chap. 10).

9.2 Short-Term Effects (up to 3 Years)

Extensive coral depletion, whether caused by climate-induced coral bleaching or other disturbances, can have pronounced effects on motile reef organisms (e.g. Kaufman 1983; Lassig 1983; Dawson-Shepherd et al. 1992; Jones et al. 2004; Wilson et al. 2006). Most notably, coral depletion is related to rapid and pronounced declines in the abundance of coral reef species that directly depend on scleractinian corals for food (Williams 1986; Kokita and Nakazono 2001; Pratchett et al. 2006), habitat (Tsuchiya et al. 1992; Munday et al. 1997; Munday 2004), and recruitment (Booth and Beretta 2002; Jones et al. 2004; Srinivasan 2007). Effects of coral depletion on strongly coral-dependent species are, nonetheless, highly variable. For example, Munday (2004) found that changes in the abundance of six species of obligate coral-dwelling gobies (*Gobiodon* spp.) following a severe loss of coral habitat ranged from 50% to 100%, depending on their degree of habitat specialisation. Among strongly coral-dependent species, specific responses depend upon: (1) the extent to which populations are limited by the availability of live coral, (2) their versatility in use of alternate resources, and (3) the degree to which sub-lethal responses mitigate or delay declines in abundance (Pratchett et al. 2004; Wilson et al. 2006).

9.2.1 Coral Dependence and Ecological Versatility

There are a diversity of reef-associated species that rely directly on live coral, many of which are very small and often go unnoticed (Munday and Jones 1998; Bellwood et al. 2006). On the Great Barrier Reef (GBR), Jones et al. (2004) and Munday et al. (2007) estimated that 9–10% (107 in ~1220 species) of coral reef fishes specifically rely on live coral for food or shelter and cannot persist on reefs devoid of coral. Similar proportions of motile reef invertebrates are also reliant on corals. For example, 30% of species of decapod crustaceans found on coral reefs often live in or on corals (A. Díaz-Ruíz, personal communication) and 9–10% of these species (mainly *Alpheus* shrimps and xanthid crabs) specifically rely on live corals for food and shelter (Garth 1964; Knudsen 1967; Debelius 2001). Among coral reef fishes, the most diverse and abundant group of fishes that rely on corals are the suite of fishes that live or shelter within branching corals, including damselfishes, gobies, and velvetfishes (Munday et al. 2007). Coral depletion leads to rapid and severe declines in the abundance of these fishes (e.g. Booth and Beretta 2002; Munday 2004), with noticeable effects on biodiversity (Jones et al. 2004; Wilson et al. 2006). In the extreme, reefs comprised entirely of rubble and no live coral have 30–50% less species than reefs with moderate levels of coral cover, due mostly to a lack of coral-dependent species (Sano et al. 1987; Glynn 2006; Graham et al. 2006).

Among motile reef organisms that use corals for food or shelter there is considerable variability in the degree to which they depend on coral; and there are large differences in their responses to coral loss. Coral-feeding butterflyfishes, for example, can be divided into: (1) obligate coral feeders, which feed almost exclusively on live coral, (2) facultative coral feeders, for which corals constitute 20–70% of their diet, and (3) putative non-coral feeders, which are rarely seen to feed on corals (Harmelin-Vivien and Bouchon-Navaro 1983; Pratchett 2005). As would be expected, facultative and non-coral feeders are typically much less affected by declines in live coral, compared with obligate coral-feeding butterflyfishes (Pratchett et al. 2006). However, even among obligate coral-feeding species there are major differences in susceptibility to disturbance, attributable to differences in their degree of dietary specialisation (Pratchett et al. 2006). If species use a wide range of different corals, including some corals that are resistant to disturbance, then they will be relatively unaffected during all but very severe declines in coral cover (Gardiner and Jones 2005). In contrast, highly specialised species that rely on corals highly sensitive to bleaching will be significantly affected. All corals are susceptible to bleaching at some level, but certain genera, such as *Pocillopora*, *Stylophora*, and *Acropora*, are particularly prone to bleaching (Marshall and Baird 2000) and quickly die once bleached (Baird and Marshall 2002; McClanahan et al. 2004). Ironically, it is these corals that are most frequently used by both coral-dwelling and coral-feeding organisms (Munday et al. 1997; Sin 1999b; Vytopil and Willis 2001; Pratchett 2005; Feary et al. 2007; Srinivasan 2007; Fig. 9.1). Some other bleaching-resistant corals, such as branching *Porites* spp., also provide a habitat for fishes and invertebrates, but they tend to be occupied by less-specialised species that use a wide range of different corals (Gardiner and Jones 2005; Hixon and Jones 2005; Brooks et al. 2007).

Overall, there is considerable overlap in the primary coral preferences of coral-dwelling and coral-feeding species, though they do vary in their degree of specialisation (Munday 2004; Gardiner and Jones 2005; Pratchett 2005). For example, in the northern GBR, all species of coral-feeding butterflyfishes have the greatest feeding preference for *Acropora hyacinthus* and/or *Pocillopora damicornis* (Pratchett 2007), but these butterflyfishes consume from 11 to 49 coral taxa (Pratchett 2005). Highly versatile species may escape the full effects of resource depletion by using alternate resources, whereas highly specialised species are severely affected by any reductions in their specific resources, possibly leading to extinction (e.g. Munday 2004). Generalist coral-feeding species may alter their dietary composition in response to changes in prey availability (Pratchett et al. 2004; Berumen et al. 2005) but, even so, these species eventually succumb to extensive coral depletion (Pratchett et al. 2006).

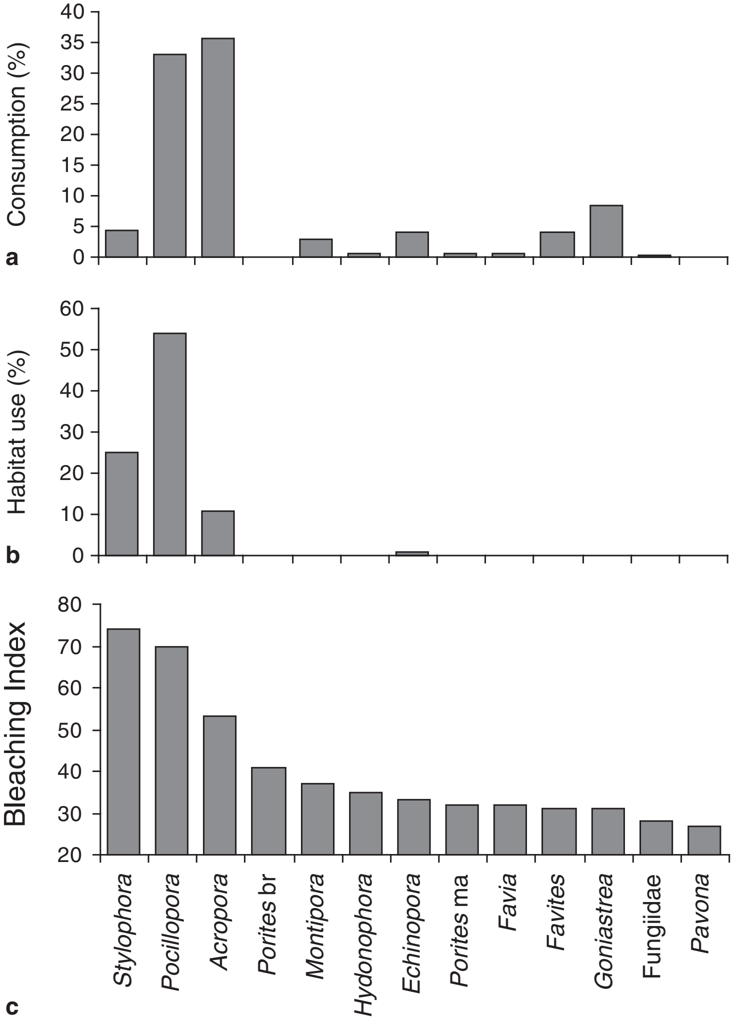

Fig. 9.1 Patterns of percent coral use by: **a** a coral-feeding butterflyfish (*Chaetodon plebius*) and **b** a coral-dwelling damselfish (*Dascyllus aruanus*; Pratchett, unpublished data) compared with: **c** bleaching susceptibility of different coral types (genera plus growth forms: *br* branching, *ma* massive) on the Great Barrier Reef (McClanahan et al. 2004)

9.2.2 Sub-Lethal Effects of Coral Depletion

Even where there is no immediate change in the abundance of motile organisms, coral depletion may still have significant and lasting deleterious effects. For example, reductions in live coral may limit settlement and recruitment for species that are otherwise unaffected by coral depletion (Bouchan-Navaro et al. 1985; Booth and Beretta 2002; Jones et al. 2004; Srinivasan 2007). Pratchett et al. (2004) showed that there was no immediate change in the abundance of *Chaetodon lunulatus* following severe coral bleaching, but this species did exhibit immediate and significant declines in physiological condition. Corallivorous organisms may partially compensate for initial depletion of prey resources by switching prey (Pratchett et al. 2004) or increasing their home ranges (Tricas 1989; Kokita and Nakazano 2001; Samways 2005). These changes in behaviour may allow corallivorous species to persist in the short term, but reduced access to preferred coral prey is likely to reduce energetic intake (Berumen et al. 2005), with implications for growth, reproductive output, and ultimately survivorship (Kokita and Nakazano 2001; Pratchett et al. 2004).

Even species that do not typically feed on scleractinian corals may be adversely affected by declines in coral abundance due to associated reductions in the production of coral propagules. Mass spawning of corals provides a large seasonal pulse of high-energy prey consumed by many different fishes and motile invertebrates, thereby representing a huge injection of energy into coral reef ecosystems (Pratchett et al. 2001; McCormick 2003). Any consumers capable of capturing and digesting coral propagules have been shown to amass considerable lipid stores following coral spawning (Pratchett et al. 2001). This may significantly enhance individual fitness, principally increasing larval quality through maternal effects (McCormick 2003). Further, the timing of mass spawning by corals at some locations (notably the GBR) immediately precedes the major reproductive period for coral reef fishes (Thresher 1984; Claydon 2004). Consequently, widespread reductions in coral cover and associated reductions in the abundance of coral propagules may have small, but potentially significant, effects on the quality and survivorship of larval fishes and the reproductive output of those species that regularly consume coral propagules.

9.3 Medium-Term Effects (3–10 Years)

Although the consequences of bleaching for fishes and motile invertebrate communities in the months and initial years after bleaching events are well documented, there is little information on how bleaching may affect these communities over longer time periods. Following disturbance it can take 5–10 years for coral cover to return to pre-disturbance levels (e.g. Halford et al. 2004; Gardner et al. 2005) or for the reef framework to collapse (e.g. Sheppard et al. 2002). During this period, the reef status lies somewhere between fully recovered, where coral cover has returned to pre-bleaching levels, and a full phase shift, where coral has been replaced by macroalgae and the reef framework may have been seriously eroded. Here we consider the implications of these alternative scenarios for motile fauna.

9.3.1 Recovery Scenario

Recovery of coral communities in the aftermath of severe bleaching is dependent on a number of interacting factors. The severity and spatial extent of the initial coral loss dictates the ability of surviving corals to reproduce and reseed affected areas

(Riegl and Piller 2003; Graham et al. 2006). Isolated reefs are much more sensitive to declines in viability of local populations, whereas well connected reefs, such as those along continental margins or large archipelagos, may have greater scope for sourcing corals from upstream (Ayre and Hughes 2004). If source populations are available to promote recruitment, coral recovery is dependent on the availability of reef substrate suitable for settlement. Here local populations of herbivores play a key role in cropping algae and maintaining the benthos in a suitable state for coral recovery (Bellwood et al. 2004; Mumby et al. 2006; Hughes et al. 2007). In such a scenario, and if other synergistic disturbances do not hinder recovery, coral cover can be regained within 5–10 years (Halford et al. 2004).

Although total coral cover can return to pre-bleaching levels within 10 years, community re-assembly may take much longer; and increased frequency and severity of bleaching is likely to lead to communities dominated by a specific subset of corals that are bleaching-resistant (Arthur et al. 2005). Changes in the relative abundance of different corals then favours different motile reef organisms, leading to changes in the dominance and community structure of these assemblages. For example, Berumen and Pratchett (2006) showed that the relative abundance of different coral-feeding butterflyfishes was altered following a shift in the coral community, instigated by an *Acanthaster* outbreak. When *Acanthaster*-resilient corals proliferated, butterflyfishes that predominantly fed on these corals became the dominant species (Berumen and Pratchett 2006). Similar changes in coral and fish communities will be expected following coral bleaching events, due to marked differences in the susceptibilities of corals to climate-induced coral bleaching. Importantly, the corals that are most susceptible to bleaching (e.g. *Acropora* spp.) are an integral component of reef complexity, their skeletons providing refuge for many species that do not necessarily associate with live coral. If branching corals are replaced by encrusting and massive growth forms, habitat complexity will decline, ultimately reducing the abundance and diversity of fauna reliant on branching corals for shelter.

Disruption of reef-associated communities at the time of bleaching may also change motile species composition, even if the coral communities fully recover. Removal of dominant fish and invertebrate species provides space for new recruits and, as larval supply is stochastic (Doherty 1991), recruitment patterns and subsequent communities will vary. Pre-emption of space by new species might retard the recolonisation of some previous residents, although competitive hierarchies can eventually re-instate species as they gradually recruit back to the reef. This process appears to be particularly important for habitat and feeding specialists (Munday et al. 2001). The re-introduction of specialist species will, however, be dependent on the presence of their preferred coral species.

9.3.2 Reef Collapse

If the coral does not recover, physical and biological forces can lead to erosion of the reef framework and a reduction in structural complexity (Glynn 1997;

Sheppard et al. 2002). Not all reefs are equally susceptible to collapse. In some environments, such as highly exposed reef fronts, corals contribute little to topographic complexity. Also, reefs vary in the amount of time it takes to break down, due to differences in:

- The composition of the initial benthic assemblage, because certain corals (mostly branching), and possibly other reef-building organisms, are much more susceptible to collapse than others (Glynn 1997)
- The degree of exposure to strong wave action, which determines the relative contribution of erect and fragile coral forms to coral composition (Madin and Connolly 2006) and may influence recruitment
- The stability and strength of the underlying ancient reef framework
- The abundance of bioeroders, such as excavating parrotfishes (Bellwood et al. 2003) and urchins (McClanahan and Shafir 1990)
- The successive occurrence of large-scale physical disturbances, such as severe tropical storms

Consequently, different reefs may be in varying degrees of decay from the same disturbance (Graham et al. 2006) and the time-frame to collapse may vary from 3 years to decades (Sheppard et al. 2002; Garpe et al. 2006).

Where the physical structure of benthic reef habitats remains unchanged, but coral cover has not recovered, the species richness, taxonomic breadth, and abundance of the fish community may be largely unchanged (Bellwood et al. 2006; Garpe et al. 2006; Graham et al. 2006). Nonetheless, community composition may have changed markedly, favouring species with generalist life history traits (Bellwood et al. 2006). However, long-term declines in coral cover may result in a loss of fish biodiversity, local extinctions, and dramatic shifts in species composition (Jones et al. 2004; Munday 2004; Berumen and Pratchett 2006; Pratchett et al. 2006). In Kimbe Bay, Papua New Guinea, Jones et al. (2004) estimated that up to 65% of reef fishes require live coral at settlement and the majority of these declined in abundance following a 6-year period of coral decline. Initial declines are expected to be greatest among smaller-bodied species, but smaller size classes within all species may no longer survive to replace adult fishes. Many of these species are long-lived (Choat and Robertson 2002) and thus there may be a lagged response whereby the full effects of bleaching take decades to be realised as adults die and are not replaced (Graham et al. 2007).

Various experimental and correlative studies have highlighted the importance of habitat complexity to diversity, abundance and biomass of motile reef organisms (Luckhurst and Luckhurst 1978; Sano et al. 1987; Grigg 1994; Syms and Jones 2000; Dulvy et al. 2002; Idjadi and Edmunds 2006; Wilson et al. 2007). This suggests that, if the physical matrix of a reef collapses following bleaching, it may result in more substantial impacts than coral loss alone, leading to significant reductions in abundance of many groups, reduced taxonomic distinctness, declines in species richness, and increased community dispersion (Garpe et al. 2006; Graham et al. 2006). Reductions in diversity and abundance may also extend to key functional groups of herbivorous fishes (Graham et al. 2006), directly affecting the recovery potential of the entire ecosystem (Bellwood et al. 2004). Several studies of the short-term impacts of bleaching suggest that herbivores initially increase in abundance (Wilson et al. 2006) and that continued increases, associated with greater algal cover, may be expected to create the space necessary to facilitate coral recovery (Bellwood et al. 2004). However, in extreme cases, a negative feedback may occur, whereby increased herbivory increases bioerosion and, in turn, reduces habitat complexity, resulting in reduced herbivore diversity and abundance (Graham et al. 2006); bioerosion may be especially enhanced in nutrient-enriched coastal environments (Chazottes et al. 2002; Carreiro-Silva et al. 2005). The ecological mechanisms behind negative impacts to fish assemblages when the physical structure of the reef framework collapses are likely linked to the key structuring processes of predation (Hixon 1991), competition (Jones 1991), and recruitment (Doherty 1991).

In terms of recruitment, many reef organisms settle directly among the branches of live corals, presumably because they provide good refuge from predators (Booth and Wellington 1998; Booth and Beretta 2002; Jones et al. 2004). However, the preferred settlement habitat (e.g. among coral species, between living corals vs dead but intact coral skeletons) varies among species (Öhman et al. 1998) and the importance of physical structure in settlement is not yet clear. Where the habitat is complex, the influence of predation may be reduced, increasing the survival of smaller, motile reef organisms (Dulvy et al. 2002; Jones and McCormick 2002; Hixon and Jones 2005; Lee 2006). It is likely, therefore, that competition for refugia could be intense (Hixon and Jones 2005), resulting in less aggressive individuals occupying unfavourable territories and being more susceptible to predation (Holbrook and Schmitt 2002). Reef fishes tend to use refuge holes most appropriate for their body size (Hixon and Beets 1993; Beukers and Jones 1997; Friedlander and Parish 1998). Thus the scale of structural complexity, or the reduction of it, will likely influence the size of fishes that are able to escape predation. Almany (2004) demonstrated that there is a complex interplay between habitat complexity, predation, and competition in determining the early post-settlement survival of common damselfishes, but any decline in structural complexity of reef habitats is likely to be detrimental for the abundance and diversity of motile reef organisms.

9.3.3 Phase-Shifts to Macroalgal-Dominated Systems

Coral mortality following bleaching events provides space on the reef for rapid colonisation by turf-forming algae (Diaz-Pulido and McCook 2002). On reefs where herbivorous fishes and/or urchins are abundant, algal assemblages may remain as cropped turf forms for several years after the bleaching event (Aronson et al. 2002; Arthur et al. 2005). However, if grazing pressure is low, fleshy macroalgae can develop within months of coral depletion (Ostrander et al. 2000; McClanahan et al. 2001; Diaz-Pulido and McCook 2002), limiting the future recovery of coral assemblages (Hughes et al. 2007) and potentially bringing about a phase shift from coral- to macroalgal-dominated reefs. Excess nutrients will further increase the likelihood of habitat degradation by enhancing algal growth, suppressing coral recruitment, and supporting increased densities of bio-eroding organisms (Fabricius 2005).

Shifts from coral- to macroalgal-dominated states will have broad consequences for motile reef fauna. Species that feed, shelter or recruit to live corals will not occur on algal-dominated reefs (Jones et al. 2004). Some species, such as the spiny lobster (*Panulirus argus*) and Nassau grouper (*Epinephalus striatus*), shelter within macroalgal habitats as juveniles (Marx and Herrnkind 1985; Dahlgren and Eggleston 2000) and their abundance may increase when macroalgae proliferate. However, the adult habitat on coral reefs must be preserved if the densities of these animals are to be maintained. Algae also provide a habitat for invertebrate crypto-fauna, with areas of greater algal biomass harbouring a greater abundance of invertebrates (Zeller 1988; Dulvy et al. 2002), which may attract invertebrate predators. Similarly, some fishes, such as *Naso unicornis* and *Kyphosus vaigiensis*, feed primarily on macroalgae (Choat et al. 2002) and may be attracted to reefs where macroalgae are prominent. Macroalgae do not, however, provide structural complexity and reef stability to the same extent as corals and the overall abundance and diversity of motile reef organisms on algal-dominated reefs is much lower, compared with coral-dominated reefs (Sano 2001).

9.4 Long-Term Effects (>10 Years)

Long-term studies (>10 years duration) on the indirect effects of climate-induced coral bleaching have not been conducted due to the relatively recent (mostly since 1998) emergence of bleaching as a global threat to coral reef ecosystems. However, extremely severe and/or large-scale bleaching events will have longer-term effects on coral reef ecosystems (Graham et al. 2007), especially given that the frequency and intensity of coral bleaching are expected to increase (Donner et al. 2005; Chap. 10) and recovery at some locations may be very slow. Changes in ocean chemistry and acidification are also expected to weaken coral skeletons (making them more susceptible to increasingly severe and frequent tropical storms) and reduce reef accretion (Hughes at al. 2003), leading to dramatic changes in the physical and biological structure of coral reef environments. It is inevitable that changes in coral communities and coral reef habitats will have significant impacts on motile reef organisms, including many effects that have not yet been considered. Aside from widespread habitat degradation, increases in temperature will have direct impacts on coral reef organisms because most species are ectotherms, for which cellular and metabolic activities are strongly dependent on ambient temperature. Motile reef organisms are as much dependent on, as they are critical to, the ecosystem function of coral reef environments. Direct or indirect effects of climate change and coral bleaching on motile reef organisms may, therefore, undermine the resilience of coral reef ecosystems, which will have significant ecological and economic ramifications (Bellwood et al. 2004; Worm et al. 2006).

9.4.1 Direct Effects of Climate Change on Motile Reef Organisms

In addition to indirect effects of habitat modification, future increases in ocean temperatures are expected to have direct effects on the whole-organism function, life history, and behaviour of coral reef animals, with concomitant effects on their distribution and abundance (Munday et al. 2007). Geographic range shifts are one of the most frequent and readily observed consequences of climate change for species in a wide range of ecosystems (Walther et al. 2002; Parmesan and Yohe 2003; Perry et al. 2005). As average ocean temperature increases, the geographic ranges of some coral reef animals will shift or expand (Victor et al. 2001), but the ranges of species already living near the present limits of coral reef development will probably contract.

Increasing ocean temperatures are likely to have greatest effects on reproductive output and early life history stages. The reproductive performance of marine ectotherms is strongly influenced by temperature (Van der Kraak and Pankhurst 1997). Although increased temperature may extend the breeding season of some species, it might lead to reduced or bimodal breeding seasons for species already reproducing near their upper thermal limits. The larval stage of marine organisms is also particularly sensitive to ambient temperature. Warmer temperatures can increase growth and development, thereby decreasing larval pelagic duration (Green and Fisher 2003; Bryars and Havenhand 2006), which may lead to higher recruitment (Wilson and Meekan 2002; Meekan et al. 2003) and increased larval survival (Searcy and Sponaugle 2000; Bergenius et al. 2002). However, increased growth and developmental rates will only occur if there is sufficient food and metabolic demands are greater at higher temperatures (Jobling 1997). Ultimately, the number of larvae recruiting to reef populations, and their physiological condition, will depend on complex interactions between temperature, developmental rates, food supply, and ocean currents, all of which are likely to be influenced by global warming.

Acclimatisation to temperature increases occurs in many marine animals (Hawkins 1996), although this capacity is limited for species already living near their thermal limits (Stillman 2003). Local adaptation to increased temperature is also possible, through gene flow from populations already living at higher temperatures and directional selection on existing genetic variability. The rapid generation times of many small fishes and invertebrates (Depzynsky and Bellwood 2005; Hernaman and Munday 2005) could aid local genetic adaptation to increased temperature. However, many other motile reef organisms are very long-lived (e.g. Choat and Robertson 2002) and local adaptation in these species will require much longer time-frames. The consequences of strong genetic selection to increased temperature are unknown, but could include a genetic bottleneck that reduces the capacity of motile reef organisms to adapt to other environmental changes, such as the ongoing degradation of their reef habitat. Direct effects of climate change on coral reef organisms will be more important as ocean temperatures continue to increase, but for now, indirect effects of coral bleaching and habitat degradation are having the greatest impacts on population size and fitness of non-coral organisms.

9.4.2 Impacts on Fisheries and Direct Economic Costs of Coral Bleaching

Climate-induced coral bleaching clearly has significant and far-reaching ecological impacts on coral reef ecosystems, but it also has a significant economic impact. Climate change has had, and will continue to have, profound impacts on the world's fisheries yields (McLean et al. 2001). In the past, the productivity of most fisheries has been strongly linked to major climatic events, such as El Niño and La Niña events, resulting from changes in regional productivity with changing ocean temperature and circulation patterns. On coral reefs, the most pressing and immediate impacts on fisheries yields are likely to arise from flow-on effects of climate-induced coral-bleaching. Independent of existing pressures on fisheries stocks (Worm et al. 2006), declines in productivity and habitat availability from coral loss may lead to declines in the abundance of primary consumers which, in turn, will have impacts extending to higher trophic levels, larger predators, and important fisheries species such as coral trout and snappers (Munday et al. 2007). Currently, there is little evidence that fisheries catches have actually declined after mass coral bleaching, but it is very difficult to detect any short-term changes in fisheries yields in the face of changing fishing pressure (McClanahan et al. 2002; Grandcourt and Cesar 2003). Direct observation of the population structure of fishery target species has, however, revealed marked declines in the abundance of smaller fishes following bleaching (Graham et al. 2007). This suggests that climate-induced coral bleaching has impaired population replenishment, such that some fished populations are destined to decline. Long-term degradation of physical reef structure will inevitably affect abundances, catch rates and compositions of coral reef fishes, with significant implications for human populations and nations that rely on exploitation of these species. Socio-economic consequences of fisheries collapse may be minor where there are alternative (e.g. pelagic) resources or fishing grounds, but in some areas long-term impacts of bleaching on fishers are expected to be substantial (Graham et al. 2007). The state of reef coral and fish communities also affects tourists' perceptions (e.g. Shafer and Inglis 2000; Williams and Polunin 2000), reducing the likelihood of tourists returning to the same location (Uyarra et al. 2005). In many places, especially developed nations, the value of fishes and reefs to tourism is far greater than fishing (Pet-Soede et al. 1999). Climate-induced coral depletion is likely to have significant and possibly irreversible consequences for both tourism and fishing industries (Worm et al. 2006).

9.5 Conclusions

Coral reefs are unique ecosystems in that they harbour an exceptional diversity of motile species. Many of these species have a close association with the coral communities which form the reef framework and contribute to its complex physical structure. While further research on patterns of resource use for coral reef organisms is essential, effects of coral bleaching and associated coral loss clearly extend beyond those species traditionally thought to have specific reliance on corals for food and shelter (e.g. butterflyfishes, damselfishes, gobies). Without corals, tropical reefs will support a very limited diversity of motile reef organisms, mostly highly generalist species that associate with rubble and algal substrates (Jones et al. 2004). Corals and coral reef environments are not expected to disappear completely, but there are likely to be shifts in community structure towards bleaching-resistant species (Hughes et al. 2003; McClanahan et al. 2004), which are less structurally complex and rarely used by coral-dwelling or coral-feeding species (McClanahan et al. 2004). Without intervention and effective management, coral reef habitats may become dominated by highly undesirable yet resilient coral assemblages.

Assemblages of reef-associated animals can recover following disturbances, provided that the benthic communities themselves recover (Halford et al. 2004) which are, in turn, dependent upon an intact fauna of functionally important motile species (Hughes et al. 2007). Resilience and the potential for coral reef ecosystems to recover from past disturbances depends on a range of factors. These include the spatial scale and intensity of disturbances, the temporal pattern of disturbances, whether these disturbances have unique, common, or interacting effects, the availability of reservoir populations for the replenishment of degraded populations, and the functional integrity of the system. By actively reducing or managing these interacting factors we will be best placed to limit, or at least retard, the devastating cumulative impacts of coral bleaching on coral reef communities. This requires an explicit and unequivocal decision to manage reefs to maximise their resilience. Reef stressors that can be directly managed, such as sediment runoff and poor water quality, must be limited or reduced as a matter of urgency (Hughes et al. 2003). Similarly, fishing pressure, especially on important functional groups, must be controlled to maintain functional integrity of reef systems (Bellwood et al. 2004; Marshall and Schuttenberg 2006). In overfished areas it will be necessary introduce measures to restore populations. Marine protected areas are valuable tools because they provide a degree of protection against the impacts of exploitation and a reproductive reservoir for the recovery of impacted populations. We should also encourage the protection of resilient reefs in areas less susceptible to bleaching as a source of population replenishment for nearby reefs that are damaged by bleaching (Salm et al. 2006). This integrated management for reef resilience in conjunction with immediate steps to reduce atmospheric greenhouse gas concentrations is critical for the future of coral reefs.

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