Chapter 11
Effects of Coral Bleaching and Coral Loss on the Structure and Function of Reef Fish Assemblages

M. S. Pratchett, C. A. Thompson, A. S. Hoey, P. F. Cowman, and S. K. Wilson

11.1 Introduction

Mass coral bleaching, caused by elevated ocean temperatures, has now emerged as a major, if not the single most important, contributor to elevated rates of coral mortality (Hughes et al. 2017; Chaps. 3, 4, and 13), greatly accelerating the degradation of coral reef ecosystems throughout the world. Coral reefs have been subject to increasing anthropogenic disturbances and threats throughout the last few decades (if not centuries), resulting in sustained declines in the cover or abundance of scleractinian corals and corresponding shifts in the structure of reef habitats (Hughes et al. 2003; Alvarez-Filip et al. 2011). Climate change (specifically resulting in coral bleaching) is almost always considered, along with a variety of other more localised anthropogenic disturbances and threats, as a key contributor to sustained and ongoing coral loss (e.g. De'ath et al. 2012). However, mass coral bleaching has previously been considered to be a relatively minor, though emerging and increasingly important, contributor to coral loss, especially relative to other major disturbances such as severe tropical storms and outbreaks of coral predators (Pratchett et al. 2011a; De'ath et al. 2012). The extent and severity of the latest (2014–2017)

M. S. Pratchett (✉) · A. S. Hoey · P. F. Cowman
ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, Australia
e-mail: morgan.pratchett@jcu.edu.au

C. A. Thompson
College of Science and Engineering and ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, Australia

S. K. Wilson
Marine Science Program, Government of Western Australia Department of Biodiversity, Conservation and Attractions, Kensington, WA, Australia

Oceans Institute, University of Western Australia, Crawley, WA, Australia

global bleaching event (Hughes et al. 2017, 2018), as well as successive years of severe bleaching in many locations, have firmly heralded in an era where global climate change is the foremost threat to coral reef ecosystems.

What makes coral reef ecosystems particularly vulnerable to climate change is that reef-building (scleractinian) corals are both very sensitive to elevated temperatures (Jokiel and Coles 1990; Smith and Buddemeier 1992; Chaps. 2 and 9) and fundamental to the structure and function of coral reefs (Bellwood et al. 2004; Pratchett et al. 2015a). Scleractinian corals are the building blocks of coral reefs, not only contributing to reef accretion (Pratchett et al. 2015a) but also forming complex habitats which support a high diversity of fishes (Coker et al. 2014) and other reef-associated organisms (Stella et al. 2011). The importance of scleractinian corals is particularly apparent given marked declines in the abundance and diversity of coral reef fishes following acute and extensive coral loss (Jones et al. 2004; Wilson et al. 2006; Munday et al. 2008; Pratchett et al. 2008a; Cheal et al. 2017) caused by severe tropical storms (hurricanes, typhoons and tropical cyclones), outbreaks of coral predators and mass coral bleaching. Such effects are particularly pronounced when coral cover falls below 10% (Wilson et al. 2006; Holbrook et al. 2008), suggesting that $\geq$10% coral cover is necessary to maintain ecological functions that support diverse assemblages of coral reef fishes.

Many coral reef fishes rely on scleractinian corals for food (Cole et al. 2008), habitat (Coker et al. 2014) and/or settlement (Jones et al. 2004; Coker et al. 2012). However, the range of coral reef fishes that decline in abundance following extensive coral depletion (60–75%) far exceeds that which are known to have an explicit and direct reliance on scleractinian corals (Jones et al. 2004; Graham et al. 2007; Pratchett et al. 2011b; Cheal et al. 2017). The broadscale ecosystem consequences of extensive coral loss suggest that we have overlooked some important ecological benefits of coral-rich habitats for reef fishes (e.g. Dixson et al. 2014; Pratchett et al. 2015b). For example, extensive coral depletion may effectively remove major odour cues that are used by reef fishes and corals to orientate towards and settle within coral reef habitats (Dixson et al. 2014). The effects of coral loss on the biodiversity and abundance of reef-associated organisms may also be compounded by declines in topographic complexity (Syms and Jones 2000; Wilson et al. 2006; Graham et al. 2009; Coker et al. 2012), which occurs due to erosion and decomposition of dead coral skeletons (Sheppard et al. 2002) and disproportionate loss of key habitat-forming corals (Graham et al. 2006; Alvarez-Filip et al. 2011). Importantly, high levels of structural complexity increase habitat area and moderate key ecological interactions (e.g. competition and predation) contributing to increased species packing, as well as facilitating coexistence of large numbers of diverse species (Gratwicke and Speight 2005).

In this chapter, we revisit the effects of mass coral bleaching (and associated changes in the structure of tropical reef habitats) on the structure and function of reef fish assemblages. In particular, this chapter will investigate the ecological and economic consequences of declines in the abundance of fishes, based on the selectivity of effects within and among different functional groups, as well as testing for compensatory dynamics necessary to maintain key ecological functions

following species declines or losses (Houlahan et al. 2007). It is well established that extensive coral depletion (whether caused by mass coral bleaching, tropical cyclones or outbreaks of invertebrate corallivores) results in significant declines in abundance across a broad range of reef fishes (Pratchett et al. 2011b) and overall declines in diversity of fish assemblages (Wilson et al. 2006). However, it is still not known whether far-reaching declines in the abundance of coral reef fishes will compromise ecological functions and especially those functions that are fundamental in maintaining ecosystem resilience (Bellwood et al. 2003; Hoey and Bellwood 2009). Importantly, net declines in the abundance or performance of ecologically important reef fishes may lead to feedbacks that inhibit recovery and reassembly of coral-dominated habitats (Graham et al. 2015) and/or further exacerbate the degradation of coral reef environments (Hoey and Bellwood 2011).

The extent to which declines in the abundance and diversity of fishes will cause ecological functions to be lost or compromised depends on the number of species that can perform a particular function (i.e. *functional redundancy*) as well as variation in responses to environmental perturbations among functionally equivalent fishes (i.e. *response diversity*) (Elmqvist et al. 2003). Some fishes, particularly herbivorous or generalist species, actually exhibit increases in abundance following extensive coral loss (Jones et al. 2004; Bellwood et al. 2006; Pratchett et al. 2008a; Halford and Caley 2009; Cheal et al. 2017). Intuitively, species that are ecologically equivalent would be equally or similarly affected by perturbations that lead to loss of habitat complexity or resource depletion. For example, extensive coral depletion will lead to declines in coral prey across all species of corallivores, though different species may be more or less affected depending on their degree of dietary specialisation (Pratchett et al. 2008a). Functionally equivalent species may also differ in the extent to which they are adversely affected by small-scale or patchy habitat disturbances based on differences in the scales at which they associate with reef habitats (Nash et al. 2016). To maintain ecosystem function, however, significant declines in the abundance of key ecological species must be offset by compensatory increases in the abundance of species that can perform, or contribute to, the same function, though compensatory dynamics are rarely observed in most ecosystems (Houlahan et al. 2007). To explicitly test for response diversity and compensatory dynamics among reef fishes, data were compiled from a variety of studies that have looked at species-specific declines in abundance of fishes before and then 1–7 years after distinct episodes of coral loss, following Pratchett et al. (2011b). While we were primarily interested in the effects of coral depletion caused by climate-induced coral bleaching, data were taken from all studies that have explored changes in the abundance of fishes following acute episodes of coral loss, regardless of the cause. Each species of fish was independently assigned one of four primary functional groups based on their trophic function (i.e. carnivores, omnivores, corallivores and herbivores). Species were subsequently assigned to secondary functional groups based on feeding mode, diet and behaviour to reflect their role in ecosystem processes and/or differential sources of their prey. Response diversity and compensatory dynamics were then assessed based on the distribution of responses (changes in abundance) for fishes within 19 distinct functional or trophic groups.

11.2   Coral Bleaching and Changes in the Structure of Reef Habitats

Coral reefs are among the most vulnerable ecosystems to global climate change (Walther et al. 2002), owing to the magnitude and severity of habitat loss that occurs during severe mass bleaching episodes (Hughes et al. 2017, 2018). The scale and magnitude of coral loss caused by pantropical mass bleaching events eclipse all other major acute disturbances (e.g. tropical cyclones, outbreaks of coral predators and coral disease) that have contributed to coral declines around the world. Generally, it is the cumulative effects of multiple discrete disturbances, which may or may not be increasing in incidence, that have caused coral declines in major reef regions (Gardner et al. 2003; De'ath et al. 2012). These disturbances tend to occur at the scale of individual reefs or reef clusters. However, large-scale mass bleaching is unequivocally linked to sustained increases in global sea surface temperatures (Heron et al. 2016), which may be compounded by ocean-scale climatic features (e.g. El Niño events). In 1998, for example, mass coral bleaching was reported on coral reefs throughout the Indo-Pacific and in the Caribbean (Wilkinson 2000) and killed 75–99% of corals across the worst affected regions (Goreau et al. 2000; Graham et al. 2006). This event contributed greatly to increased recognition of climate change as a significant threat to coral reef ecosystems (Hoegh-Guldberg 1999) and motivated many of the foremost studies on ecosystem effects of severe coral bleaching and coral loss (Graham et al. 2006, 2008). Graham et al. (2008) surveyed fish assemblages at 66 sites across the western Indian Ocean in the aftermath of the 1998 bleaching and assessed changes in the size structure and taxonomic composition of fish assemblages by comparing results with surveys conducted prior to the bleaching (in 1990–1998). The key finding from this study was that spatial management arrangements provided no protection against mass coral bleaching and subsequent effects of coral loss on reef fish assemblages. It was also apparent that mass coral bleaching had disproportionate impacts on small-bodied (<20 cm total length) reef fishes (Graham et al. 2008). Beyond that, the effects of the 1998 bleaching event (on both coral and fish assemblages) were highly variable (Graham et al. 2008), requiring much greater consideration of the specific changes to coral reef habitats that are caused by mass coral bleaching. It is also important to realise that mass coral bleaching was even more widespread in 2014–2017 than in 1998 (Hughes et al. 2017, 2018), though the impacts of these latest pantropical bleaching events are yet to be fully realised.

11.2.1   Bleaching Selectivity and Changes in Coral Composition

The specific effects of mass coral bleaching on coral reef fishes will depend on the magnitude (extent and severity) and selectivity of coral loss. All scleractinian corals

are susceptible to bleaching at some level, but certain genera, such as *Stylophora*, *Pocillopora*, *Acropora* and *Montipora*, tend to be much more susceptible, based on the proportion of colonies and species that bleach (McClanahan et al. 2004; Hoey et al. 2016) and are also more likely to die once bleached (Baird and Marshall 2002). The selectivity of mass coral bleaching declines with increasing severity (Hughes et al. 2017), whereby there are very few corals that can withstand prolonged exposure to extreme temperatures. During moderate bleaching events, however, bleaching and mortality may be restricted to a few specific coral taxa (Baird and Marshall 2002). For the most part, it is branching corals that tend to exhibit higher rates of bleaching and mortality (Baker et al. 2008), though it is unknown whether this reflects a taxonomic bias in coral morphology (McCowan et al. 2012) or inherent physiological properties of massive or robust corals that increase resistance and resilience to coral bleaching (Loya et al. 2001). Taxonomic differences in susceptibility to bleaching can vary spatially and temporally (Guest et al. 2012; Pratchett et al. 2013), depending on depth and habitat, the recent thermal history, hydrodynamics and endosymbiont associations. Moreover, increasing incidence of coral bleaching will not necessarily favour those coral species that are most resistant to bleaching (Hughes et al. 2003; Baker et al. 2008). Rather, directional shifts in the composition of coral assemblages will depend on both rates of colony-level mortality due to bleaching (relative to normal background rates of whole colony mortality) and the differential recovery capacity of species. Importantly, corals with rapid growth and high rates of population turnover may be relatively unaffected by recurrent bleaching (Linares et al. 2011), compared to slow-growing coral species that invest significant energy in maintenance and persistence.

Declines in the species richness of coral assemblages can directly impact on diversity of fish assemblages (Messmer et al. 2011), though there are specific coral taxa that are particularly important in providing food and habitat resources and also make disproportionate contributions to topographic complexity of reef habitats (Coker et al. 2012). Corals vary in the extent to which they provide effective habitat for reef fishes mainly due to differences in gross morphology (e.g. branching versus encrusting or massive colonies), though some specialist coral-dwelling fishes only occupy very specific corals and clearly distinguish within or among coral species (Munday 2001; Messmer et al. 2011; Noonan et al. 2012). The corals that are most important in providing habitat for highly specialised coral-dwelling fishes (including digitate *Acropora*, *Stylophora* and *Pocillopora* corals; Coker et al. 2014) are particularly susceptible to coral bleaching. Some of the more bleaching-resistant corals, such as branching *Porites* spp., are also important in providing habitat for a wide range of fishes (Richardson et al. 2017), but they tend to be occupied by less-specialised species that use a wide range of different corals (Gardiner and Jones 2005; Coker et al. 2014). Coral specialists are, by definition, expected to have a much stronger reliance on live corals and are more vulnerable to any changes in coral availability (Munday 2004; Pratchett et al. 2012). Given the close association of many specialist reef fishes with *Acropora* and *Pocillopora* corals, selective depletion of these corals may be just as devastating as a wholesale loss of scleractinian corals, affecting both the availability of preferred habitats and topographic complexity.

Even if these corals are generally resilient to recurrent bleaching, temporary declines in the availability of critical habitats may have devastating effects for fishes that are directly reliant on specific coral hosts (Munday 2004).

11.2.2 Coral Loss and Increasing Predominance of Alternative Habitat-Forming Taxa

While moderate bleaching is likely to cause directional shifts in the structure of coral assemblages (described above), severe episodes of mass bleaching affect a significant proportion of scleractinian corals (Hughes et al. 2017) and are likely to lead to extensive and widespread declines in coral cover. Such reductions in the abundance or cover of corals within shallow reef environments are often accompanied by increases in abundance of other alternative habitat-forming organisms, such as macroalgae (Hughes et al. 2010), though this depends on the specific environmental settings and relevant constraints on macroalgal growth and coral dynamics (Chong-Seng et al. 2014). Accordingly, there have been documented increases in the abundance of herbivorous fishes following widespread coral loss and concomitant increases in cover and biomass of macroalgae (Jones et al. 2004; Pratchett et al. 2008a; Cheal et al. 2017). In some instances, high densities of herbivores can prevent proliferation of macroalgae even after extensive coral depletion. However, fisheries exploitation has reduced the abundance of herbivorous fishes in many reef regions, compromising their capacity to respond to increasing cover and growth of macroalgae (Rasher et al. 2013). Once established, shifts from coral to macroalgal dominance may be reinforced by reduction in grazing and increased production of algal propagules (Hoey and Bellwood 2011) as well as constraints on recovery and replenishment of coral assemblages (Hughes et al. 2007). Moreover, the estimated biomass of herbivorous fishes needed to promote recovery of coral-dominated habitats (>180 kg per hectare) is much greater than what is required to prevent the initial proliferation of macroalgae and exceeds the estimated biomass of herbivorous fishes in most reef regions (Hoey et al. 2016).

Fundamental shifts in the dominant habitat-forming biota within tropical reef environments will significantly affect the behaviour, abundance and composition of coral reef fishes. While there are some species of reef-associated fishes that will benefit from increased cover and biomass of macroalgae (Dahlgren and Eggleston 2000; Wilson et al. 2010, 2017), fishes that feed, shelter or recruit to live corals are likely to disappear from reefs dominated by macroalgae (Jones et al. 2004). Importantly, macroalgae do not provide the same level of habitat structure and complexity as scleractinian corals, and the overall abundance and diversity of fishes on algal-dominated reefs are much lower, compared with coral-dominated habitats (Sano 2001). In the Seychelles, Graham et al. (2015) showed that the biomass of herbivorous fishes was highest on reefs with high levels of underlying structural complexity and this, in turn, was a major determinant of whether reefs recovered (rather than

undergoing a regime shift to macroalgae) following the 1998 mass coral bleaching. While data on overall biomass of fishes was not presented for coral- versus macroalgae-dominated reefs (Graham et al. 2015), restoration of the functional integrity of reefs that recovered will likely have significant ecological and economic benefits, such as increased contribution to local fisheries production.

11.2.3 Coral Loss Versus Declines in Topographic Complexity

Mass coral bleaching is categorised (along with outbreaks of coral predators and coral diseases) as a *biological* or *nonstructural* disturbance (Wilson et al. 2006) whereby corals are killed without directly modifying their physical structure, at least in the short term. *Physical* or *structural* disturbances (e.g. tropical cyclones), meanwhile, cause immediate reductions in both live coral cover and topographic complexity of the reef framework by dislodging and/or breaking apart coral skeletons (e.g. Madin and Connolly 2006). *Structural* disturbances are generally thought to have much more pronounced and far-reaching effects on reef fishes compared to biological disturbances, because coral loss is compounded by declines in structural complexity (Wilson et al. 2006) and it is sometimes difficult to identify the independent contributions of coral loss versus topographic collapse (Pratchett et al. 2008a; Graham and Nash 2013). In at least some cases, coral loss appears to have greater influence on abundance of fishes than declines in structural complexity (Komyakova et al. 2013), while loss of coral diversity is the foremost driver of declines in diversity of reef fishes (Messmer et al. 2011; Holbrook et al. 2015). Moreover, extensive coral depletion can lead to declines in structural complexity, regardless of whether it is caused by biological or physical disturbances; coral colonies that have died due to bleaching (or other biological disturbances) are immediately subject to physical and biological forces that cause skeletal erosion and decomposition (Glynn 1997; Sheppard et al. 2002; Ferrari et al. 2017a), leading to inevitable, though sometimes protracted, declines in structural complexity (e.g. Sano et al. 1987). There are, however, instances where habitat complexity is provided by underlying substrate rugosity and is independent of coral loss (Pratchett et al. 2008a; Emslie et al. 2014), which may actually buffer fish assemblages during periods of coral loss.

The timing and sequence of decomposition and structural collapse of dead coral skeletons have only rarely been explicitly studied, but it is increasingly apparent that this is a gradual and ongoing process (Ferrari et al. 2017a), rather than an acute and delayed effect of coral mortality. Notably, delayed declines in the abundance and diversity of fishes, which may be apparent >3 years after extensive coral depletion (Pratchett et al. 2008a), have been at least partly attributed to lags in declines in topographic complexity following extensive coral mortality (Graham et al. 2006). The extent to which coral reef habitats are actually vulnerable to structural collapse

also varies, depending on the extent to which coral assemblages are dominated by branching species, variation in the structural integrity of corals (even among different branching species), localised differences in the factors that promote physical and biological erosion and the relative contribution of contemporary coral growth versus underlying reef structure to topographic complexity (Pratchett et al. 2008a; Cheal et al. 2017).

11.3 Declines in Abundance of Reef Fishes and Loss of Biodiversity and Function

Much of the current understanding regarding the effects of mass coral bleaching on coral reef fishes comes from studies that have documented species-specific changes in abundance of fishes before and after specific bleaching events (e.g. Graham et al. 2008). While the results of such studies are dependent on the specific timing of surveys and especially the time elapsed following mass coral bleaching (Pratchett et al. 2009), the magnitude of species losses is broadly comparable to the effects of coral depletion caused by tropical cyclones, outbreaks of crown-of-thorns starfish and experimentally imposed disturbances (Fig. 11.1). Where coral mortality was
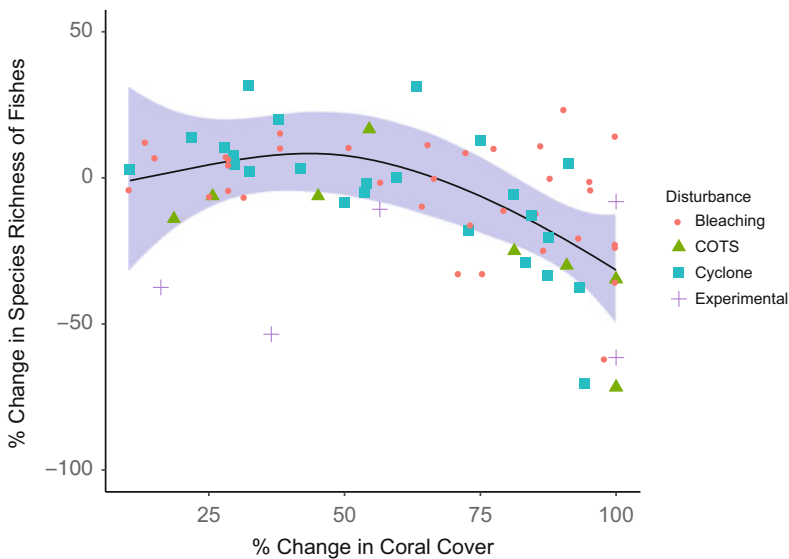

Fig. 11.1 Effects of coral loss on biodiversity (species richness) of coral reef fishes. The relationship between change in species richness (%) is plotted against increasing declines (%) in local coral cover, based on data extracted from 30 independent studies, categorised according to the major (but not exclusive) cause of localised coral loss. Confidence intervals (~95%) for the general additive model were calculated using a continuous set of predictor variables ($n = 1000$), with the MGCV package in R

>60%, the number of species recorded along belt transects or within point counts generally declined, although there was considerable variation among studies, with some documenting limited or even positive changes in diversity of fishes when coral mortality was >80%. Notably, extreme levels of species loss (60% decline in species richness) occurred following near-complete coral loss, regardless of what caused this coral mortality. However, moderate levels of coral loss had limited or positive effects on the local diversity of reef fishes (Fig. 11.1) which may reflect increases in the abundance and diversity of generalist fishes following initial loss of corals and corresponding increases in habitat heterogeneity (Wilson et al. 2006). It is important, however, to consider species-specific responses of fishes to mass coral bleaching, to understand which species are affected and potential impacts on ecosystem function and fisheries production (e.g. Brandl et al. 2016).

11.3.1   Interspecific Variation in Vulnerability to Coral Bleaching and Depletion

Fishes vary in their responses to habitat perturbations (and potential resource depletion) due to varying levels of ecological specialisation and differential reliance on specific resources (e.g. coral prey), their capacity to use alternative habitats or resources following changes in resource availability, their distribution relative to areas of major impacts and variation in the scales at which they associate with coral reef habitats (Pratchett et al. 2011b). The main group of fishes that consistently exhibit pronounced and often very rapid declines in abundance following localised coral depletion are obligate coral-feeding fishes (Wilson et al. 2006, 2014; Emslie et al. 2011; Fig. 11.2). Declines in the abundance of coral-feeding fishes are directly attributable to prey depletion and subsequent starvation, reflected in initial declines in their physiological condition (Pratchett et al. 2004). Coral-feeding fishes are initially attracted to bleached, diseased or injured corals, though they will preferentially feed on healthy (unbleached corals) in the longer term (McIlwain and Jones 1997; Cole et al. 2009). This suggests that the nutritional quality of corals declines soon after they bleach. The eventual mortality of bleached corals will then further constrain prey availability for obligate coral-feeding fishes. Accordingly, virtually all corallivorous fishes (including soft-coral feeders) exhibit significant declines in abundance, probably reflecting high rates of mortality, as opposed to movement among habitats, following localised coral depletion (Emslie et al. 2011; Wilson et al. 2014; Fig. 11.2). While localised declines in the abundance of these fishes may result from movement, the potential to find more suitable habitats is likely to be very limited, especially given the spatial extent of major mass bleaching events (e.g. Hughes et al. 2017). Even if fishes are able to find relatively undisturbed reef environments, high levels of aggression among coral specialists (e.g. coral-feeding butterflyfishes, Blowes et al. 2013) are likely to constrain the invasion of new habitats by displaced individuals. Moreover, individual fishes are likely to persist
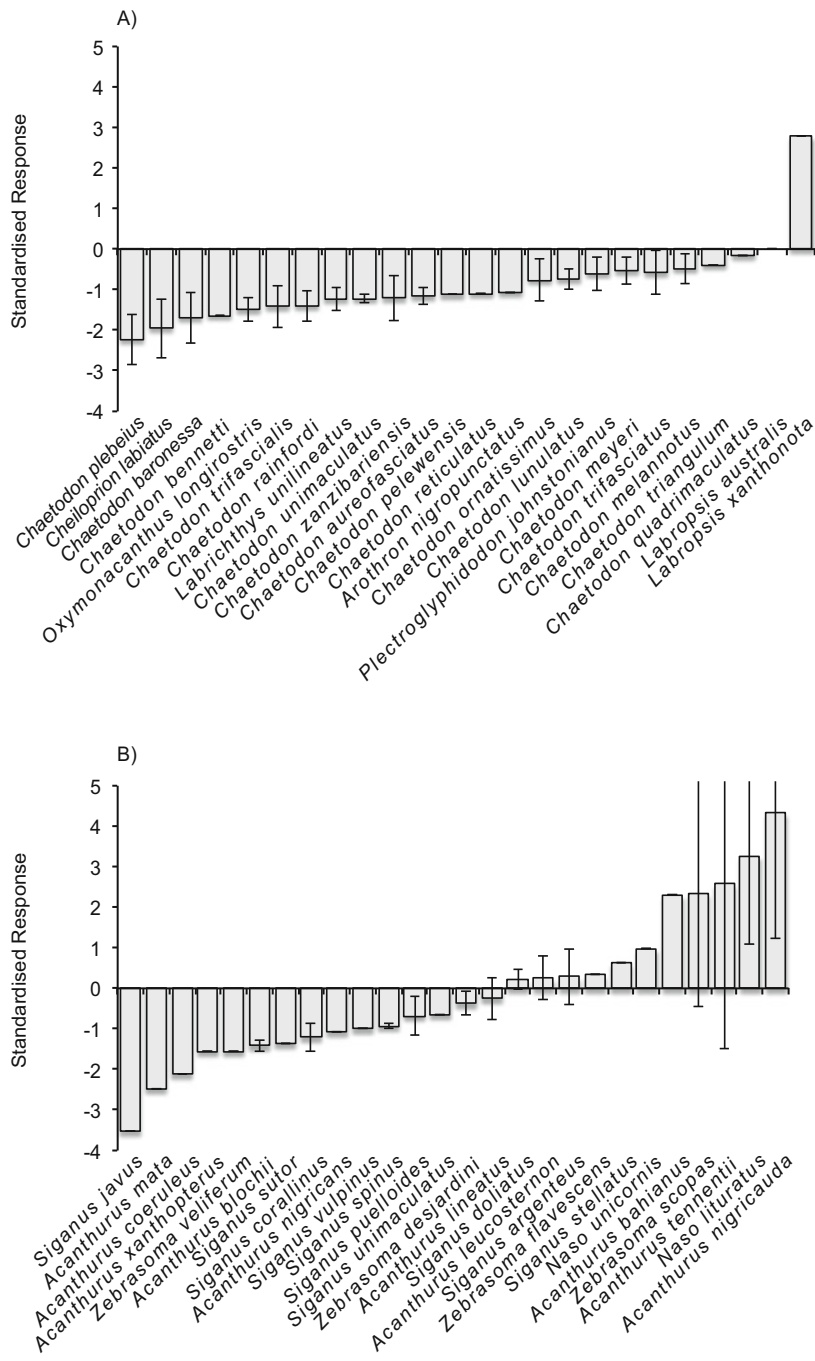
Fig. 11.2 Standardised responses of (**a**) obligate corallivores and (**b**) croppers and browsers to significant (>10%) declines in coral cover. Species-specific responses are calculated based on their proportional decline in abundance divided by proportional declines in live coral cover and averaged across multiple studies, where possible. Standard errors are calculated based on variation in responses among studies

within their established home ranges for some time after corals have bleached and died (Pratchett et al. 2004), which would further limit their ability to ultimately outcompete conspecifics and invade new habitats.

For fishes with an explicit and direct reliance on corals (e.g. for food and habitat), declines in abundance are often disproportionate to levels of local coral depletion. For example, *Chaetodon trifascialis* is often locally extirpated following relatively low (e.g. 14%) levels of coral depletion. The standardised response (which explicitly accounts for proportional coral loss) for *C. trifascialis* is, therefore, as low as −5. Such disproportionate declines in the abundance of these fishes reflect high selectivity in coral use as well as the sensitivity of preferred coral species to mass coral bleaching and other major disturbances. *Chaetodon trifascialis* is among the most highly specialised of coral reef fishes (Pratchett 2014), feeding almost exclusively on tabulate *Acropora* as well as a few other select species (e.g. *Acropora florida*). Accordingly, declines in the abundance of *C. trifascialis* relate to declines in the abundance of their major prey (tabulate *Acropora*), rather than overall declines in live coral cover. Other relatively specialised corallivores (*C. plebeius*, *C. baronessa* and *Oxymonacanthus longirostris*) also exhibit disproportionate declines in abundance following significant (>10%) reductions in local coral cover (Fig. 11.2). The only corallivorous fish that has been seen to increase in abundance following coral depletion is *Labropsis xanthonota*, for which densities of recruits actually increased (albeit from very low densities) following mass coral bleaching in Chagos (Graham et al. 2008).

Concern about the loss of key functional groups on coral reefs mostly centres around herbivorous fishes, largely due to their role in preventing and potentially reversing macroalgal overgrowth (Hughes et al. 2007; Hoey and Bellwood 2011). While all herbivorous fishes ostensibly consume and remove algae, they perform different and complimentary roles in helping reefs to resist shifts to alternate states and reassemble following disturbances. Specific differences in the feeding mode of herbivorous fishes, as well as variation in body size, group size and home ranges, suggest that each and every species of herbivorous fish may have a subtly different role in preventing or reversing proliferation of macroalgae following extensive coral depletion (Mouillot et al. 2014). Certainly, there are some individual species that contribute disproportionately to specific functions. For example, overfishing of the excavating parrotfish, *Bolbometopon muricatum*, has resulted in a near total loss of external bioerosion on several Indo-Pacific reefs (Bellwood et al. 2003, 2012) even though there are several other excavating species on these reefs. In many regions, fisheries exploitation represents the foremost threat to herbivorous fishes (Graham et al. 2011), though it is also apparent that at least some herbivorous fishes decline in abundance following extensive coral depletion (Fig. 11.2). While some herbivorous fishes do increase in abundance following coral depletion, presumably responding to increases in the areal extent and/or productivity of algae, these responses are not consistent either within or among species. Most notably, there are several species of acanthurids (e.g. *Acanthurus lineatus* and *A. tennenti*) that have exhibited contrasting responses (increases versus decreases in abundance) to coral loss in different studies conducted at different locations. Moreover, apparent declines in

the abundance of several species of croppers and browsers (Fig. 11.2) are based on results from just one study location. Such vagaries in responses of herbivorous fishes to changes in resource availability may reflect the role of irregular larval supply and recruitment in facilitating population increases. However, rapid increases in the abundance of some fishes almost certainly reflect the aggregation and movement of fishes into degraded reef habitats (Hart et al. 1996), which may also be constrained by local densities and distributions of fishes.

11.3.2   Loss of Biodiversity and Function

The extent to which declines in the abundance of fishes will constrain key ecological functions depends on the functional identity of component species and the variation in responses to coral loss among species that contribute to similar functions. For fishes that are directly reliant on corals for food, it is to be expected that entire functional groups will respond similarly to the localised depletion of scleractinian corals (e.g. Pratchett et al. 2011b). However, the responses of other groups are much less clear. For herbivorous fishes, several studies have reported increases in the abundance of specific species or groups following large-scale reductions in coral cover (e.g. Adam et al. 2011; Gilmour et al. 2013), and previous meta-analyses have shown that the majority of species that respond positively to coral loss are herbivorous fishes, though such effects may be relatively short-lived (Wilson et al. 2006; Pratchett et al. 2008a). As discussed previously, increases in the abundance of herbivorous fishes are generally attributed to increased cover and availability of turfing algae, which rapidly colonise dead coral skeletons (Mumby and Steneck 2008). When large numbers of corals die, there may also be a significant, though temporary, input of nutrients that actually increase algal productivity and growth. However, beneficial effects of increased food availability following the loss of live corals may be more than offset by declines in the availability of preferred settlement habitats and increased intensity of competition and predation within degraded reef habitats.

Comparisons of the standardised responses to coral loss for each of 19 distinct functional (or trophic) groups show that while there was considerable variation in the response of individual species within each group, the net effect is a decline in abundance for 18 of the 19 functional groups examined (Fig. 11.3). The only exception was the macroalgal browsers (*Naso* spp. and *Siganus* spp.) that show a net positive response to coral loss. Interestingly, these browsing fishes do not associate with live coral or structurally complex areas at settlement, instead settling to areas of coral rubble (e.g. *Naso unicornis*, Doherty et al. 2004) or dense macroalgae, predominantly *Sargassum* (*Siganus* spp., Hoey et al. 2013; Evans et al. 2014). This, coupled with the increased availability of algal resources following coral mortality (e.g. Diaz-Pulido and McCook 2002), suggests these species are not reliant on live coral and may actually prosper in habitats with depauperate coral cover.
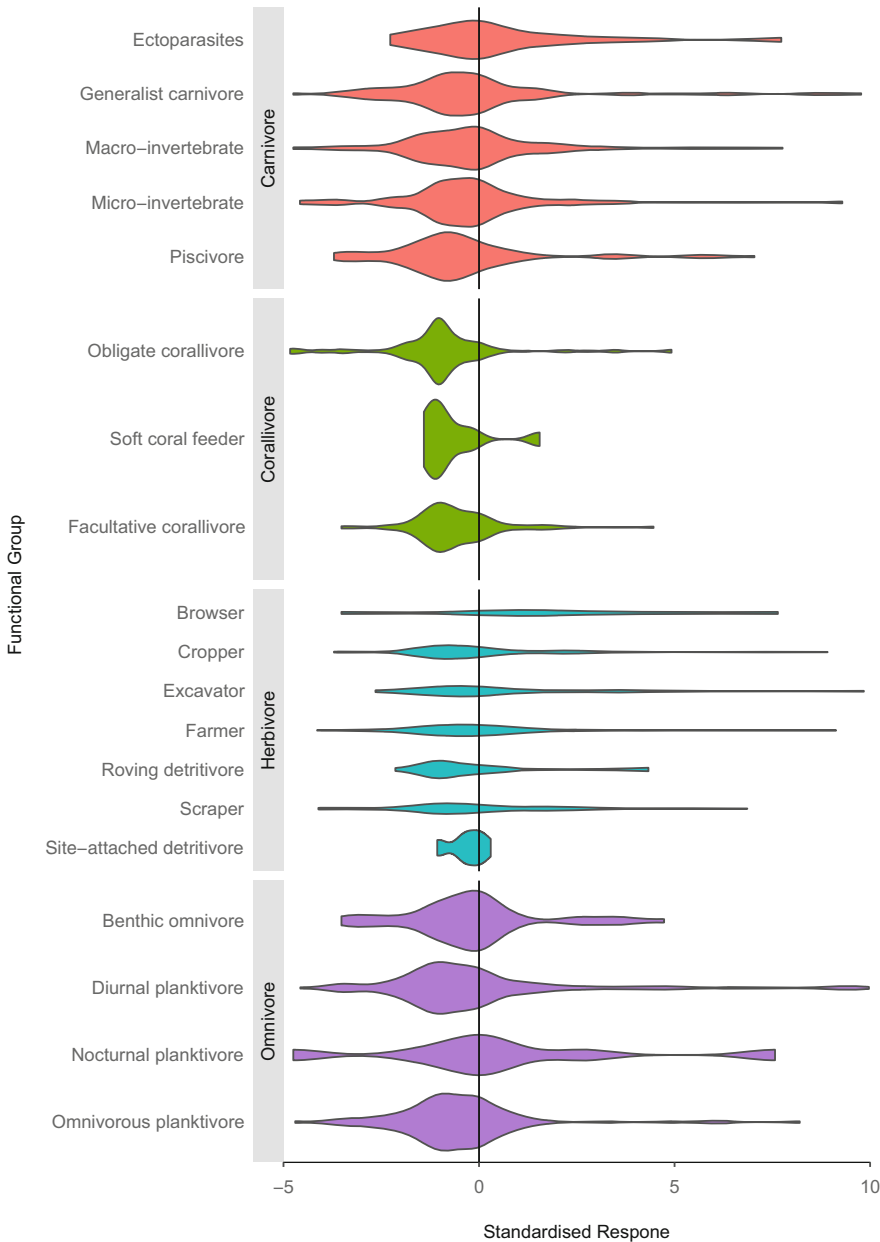
Fig. 11.3 Variation in standardised responses to coral loss (proportional change in the abundance of individual species divided by proportional declines in in local coral cover) for 19 functional (trophic) groups of reef fishes. Responses are predominantly negative showing the broad range of fishes that decline in abundance following coral loss

Although the net response of most functional groups to coral loss was negative, there was considerable variation among species within each group. This variation likely reflects differences in the intensity and/or nature of the disturbance, the temporal scale over which the changes were quantified and the longevity of the species and the reliance of individual species on live coral for settlement, food and/or shelter. For example, many scraping and excavating parrotfishes settle to macroalgal (Green 1998) or mangrove habitat (Dorenbosch et al. 2006), yet other species, such as the bumphead parrotfish *Bolbometopon muricatum*, settle to branching *Acropora* (Hamilton et al. 2017). The reliance of *B. muricatum* on live coral at settlement is of particular concern as, when present, it overwhelmingly dominates the process of external bioerosion on reefs (Bellwood et al. 2003, 2012), and as such the loss of corals could undermine this ecological process. Similarly, differences in settlement habitat are evident within other function groups. For example, the piscivorous coral trout *Plectropomus leopardus* settles to rubble habitats (Light and Jones 1997), while the congener *P. maculatus* settles to branching *Acropora* (Wen et al. 2013). Predicting the effects of coral loss on the functional composition of reef fish assemblages is complex. Despite some fishes appearing to be largely unaffected by coral loss (Emslie et al. 2017) or even thriving following coral loss (e.g. Adam et al. 2011), the net effect of extensive coral depletion on almost all functional groups is negative (Fig. 11.3). Although changes in the abundance do not account for differences in the functional contribution of individual species, the prevalence of negative impacts suggests ongoing coral loss is likely to compromise the functioning and productivity of coral reefs, especially given cumulative effects of multiple disturbances (Brandl et al. 2016).

11.3.3   Effects of Coral Reef Degradation on Tropical Fisheries Production

Coral reef ecosystems are a major contributor to tropical coastal fisheries production, with coral reef fishes accounting for up to 65% of coastal fisheries production in the tropical Pacific (Bell et al. 2013). Coral reef fisheries typically target multiple species across almost all trophic levels, including piscivores, invertivores and herbivores (Dalzell et al. 1996). Differential effects of coral bleaching and depletion across major functional groups are, therefore, expected to cause changes in catch composition, if not declines in overall fisheries production. Cheung et al. (2013) showed that there have been marked shifts in catch composition for tropical fisheries from the 1970s to 2006. These changes are related to changing thermal regimes, differential thermal sensitivities of tropical fishes and increasing redistribution of fishes to match changing climatic envelopes (Cheung et al. 2010). However, significant and widespread habitat degradation due to increasing incidence and severity of mass coral bleaching will also have consequences for coral reef fish and fisheries (Pratchett et al. 2011c; Bell et al. 2013). By 2100, the combined effects of habitat

degradation and ocean warming, together with ocean acidification, are projected to cause a 20–50% decline in sustainable fisheries production of demersal fishes from tropical coastal environments across Pacific island countries and territories (Pratchett et al. 2011c). These projected declines are mostly linked to ongoing habitat loss across coral reef, seagrass and mangrove habitats, though the projected rates of habitat loss (e.g. 50% decline in mean coral cover by 2035) may have been overly conservative given the habitat loss that is likely to have occurred during recent pantropical mass coral bleaching events. Projected declines in coral reef fisheries productivity caused by climate change could equate to losses of up to US$8.4 billion per annum by the year 2100 (Speers et al. 2016). Given the increasing demand for fish with significant increases in human population across tropical island nations, the degradation of coral habitats from bleaching poses a major threat to future food security (Bell et al. 2017).

The specific effects of coral bleaching on fisheries species and production remain equivocal (Brander 2007; Cinner et al. 2013), given difficulties in discerning climatic signals against background fluctuations in catch and effort (McClanahan et al. 2002; Grandcourt and Cesar 2003). Graham et al. (2007) found declines in the size structure of fisheries target species following extensive mass bleaching in the Seychelles. It is also clear that extensive coral depletion, especially when combined with declines in topographic complexity, can impact on the abundance of large-bodied reef fishes and fisheries target species (Pratchett et al. 2011c, 2017). Most fishes that associate with live coral are small-bodied (Coker et al. 2014) and are not typically targeted by fishers. Reduced abundance of these small-bodied fish can, however, impact on prey availability for larger piscivorous species (Wen et al. 2016). For example, reduced abundance of coral-dwelling planktivores following bleaching resulted in an increased benthic, rather than pelagic, isotopic signature in the barred-cheek coral trout, *Plectropomus maculatus* (Hempson et al. 2017a). This shift in dietary composition was also associated with declines in individual condition, potentially attributable to declines in resource availability within degraded reef systems (Hempson et al. 2017b). This may explain why densities of these *P. maculatus* covary with fluctuations in live coral cover (Williamson et al. 2014), though coral habitats are also important for growth and survival of newly settled individuals (Wen et al. 2013) which feed on benthic invertebrates that are generally more prevalent in the presence of live corals.

Previous studies (and meta-analyses) on the susceptibility of reef fishes to coral depletion and changes in the structure of reef habitats emphasised the vulnerability of small-bodied species (Wilson et al. 2006; Graham et al. 2008), which often have closer association with benthic habitats and explicitly utilise complex habitats to moderate exposure to predators. However, more recent analyses show that species with large body size are equally vulnerable to coral depletion and reef degradation as their smaller-bodied counterparts (Pratchett et al. 2014), though there may be significant lags in the time required for such declines to become apparent. The mean and modal standardised responses to coral loss for all groups of carnivorous fishes, which include many large-bodied piscivores and macro-invertebrate feeders, were negative (Fig. 11.3). The mechanistic basis for such declines is likely to be

complex and vary among species. However, high coral cover and topographic complexity may be critical to the feeding success of many ambush predators, such as groupers (Kerry and Bellwood 2012). Some larger-bodied fisheries species (e.g. *Bolbometopon muricatum*) may also rely on specific corals or coral-rich habitats for settlement (Rogers et al. 2014; Hamilton et al. 2017), even though adults are only loosely associated with coral habitats, which would explain why extensive coral depletion results in protracted declines in the abundance of these species. The overall importance of corals (cf. algae or other reef habitats) for inducing settlement or promoting survival of newly settled fishes is still largely unknown (but may have been greatly underappreciated, Jones et al. 2004), as habitat requirements for many juvenile coral reef fish are yet to be established (Wilson et al. 2010).

Dramatic shifts in the species composition, abundance and biomass of reef fishes are likely to occur following shifts from coral- to macroalgae-dominated systems (Chong-Seng et al. 2014; Graham et al. 2015; Ainsworth and Mumby 2015), which may become increasingly common following severe mass coral bleaching and will have obvious connotations for fisheries production. Most notably, the abundance of many traditional fisheries species is suppressed on reefs dominated by macroalgae (Ainsworth and Mumby 2015). There are, however, other fishes that are very abundant on reefs with high cover of macroalgae (Graham et al. 2014), which might still sustain high fisheries productivity, albeit based on a different suite of species (Ainsworth and Mumby 2015). Exploring new fishing opportunities and adapting to changes in resource availability may help to close the gap between productivity of coral reef fisheries and increasing fisheries demands in tropical island countries (Bell et al. 2017). Embracing such changes must, however, take account of the ecological importance of some fishes and balance the needs for fisheries production versus contributions of fishes to ecosystem function. If, for example, fisheries capitalise on the increased abundance of herbivorous fish that can occur following mass coral bleaching (Wilson et al. 2006; Pratchett et al. 2008a), this may undermine the capacity for recovery and reassembly of coral-dominated habitats (Bozec et al. 2016).

11.4 Changes in the Behaviour and Fitness of Reef Fishes

While there are many studies that have documented changes in the abundance and diversity of fishes on reefs affected by coral bleaching and coral loss (Graham et al. 2008), sublethal effects of such disturbances have often been overlooked. However, fishes may respond to coral bleaching and coral loss in ways other than absolute changes in their local abundance (Table 11.1). These differences in feeding rates and diet, physiological condition and growth may forewarn of longer-term impacts on individual survival and population viability, but understanding sublethal effects of coral depletion may also help to elucidate how and why reef fishes associate with coral-dominated habitats. For example, *Chaetodon auriga* declines in abundance following localised coral loss (Bouchon-Navaro et al. 1985; Pratchett et al. 2015b) despite feeding very little, if at all, on scleractinian corals throughout much of its

Table 11.1 Sublethal effects of mass coral bleaching and coral depletion on coral reef fishes, highlighting (A) behavioural shifts associated with declines in the local abundance, cover or diversity of corals and (B) consequences for individual fitness, such as declines in condition and growth

(A) Behavioural shifts			
Effect	Observed change	Time frame	Species and data source(s)
Feeding on bleached corals	Preferential feeding on bleached corals	Hours to days	*Labrichthys unilineatus* (McIlwain and Jones 1997; Cole et al. 2009) *Chaetodon baronessa* (Cole et al. 2009)
	Active avoidance of bleached corals	9 Days	*Chaetodon plebeius* (Pisapia et al. 2012)
Overall bite rates	Increased with increasing coral cover	Space for time comparison	*Chaetodon auriga* (Pratchett et al. 2014)
	No difference	Space for time comparison	*Chaetodon vagabundus* (Pratchett et al. 2014)
Shifts in dietary composition	Reduced intake of benthic invertebrates	1–2 Years	Juvenile *Plectropomus maculatus* (Wen et al. 2016)
	Increased intake of herbivorous fishes	3–7 Years	*Plectropomus maculatus* (Hempson et al. 2017a)
	Increased use of massive corals	2 Years	*Chaetodon lunulatus* (Pratchett et al. 2004)
	No change despite loss of preferred prey	1 Year	*Oxymonacanthus longirostris* (Brooker et al. 2014)
Territoriality and aggression	Larger territories with declining coral cover	Space for time comparison	*Labrichthys unilineatus* (McIlwain and Jones 1997)
	Larger territories and reduced aggression at low coral cover	Space for time comparison	*Chaetodon baronessa* (Berumen and Pratchett 2006)
	Increased inter- vs intraspecific aggression in degraded habitats	20 Days	*Pomacentrus moluccensis* (Kok et al. 2016)
Susceptibility and exposure to predators	Failure to respond to predator odour cues on dead corals	Immediate	*Pomacentrus amboinensis* (Lönnstedt et al. 2014)
	Failure to respond to conspecific alarm cues in degraded habitats	Immediate	*Pomacentrus moluccensis* and *Chromis viridisi* (Ferrari et al. 2017b)
	Water from dead corals impedes escape responses	Immediate	*Pomacentrus amboinensis*, *P. chrysurus*, *P. wardi*, (McCormick and Allan 2017)
	Dead coral impedes social learning and predator recognition	Immediate	*Pomacentrus amboinensis*, *P. nagasakiensis* (Chivers et al. 2016)
	Higher strike rates by predators on prey fishes against bleached corals	Immediate	*Pomacentrus moluccensis*, *Dascyllus aruanus* (Coker et al. 2009)

Table 11.1 (continued)

(B) Consequences for individual fitness			
Effect	Observed change	Time frame	Species and data source(s)
Physiological condition	Declines in condition when feeding on suboptimal prey	2 Years	*Chaetodon lunulatus* (Pratchett et al. 2004)
	No differences between bleached versus unbleached corals	Space for time comparison	*Dascyllus aruanus* (Coker et al. 2015)
	No change, despite increased use of suboptimal habitats	1 Month	*Chrysiptera parasema, Dascyllus melanurus* (Feary et al. 2009)
Spawning	Lack of spawning for fishes deprived of access to preferred prey	3 Weeks	*Oxymonacanthus longirostris* (Brooker et al. 2013)
Growth rates	Limited growth following extensive depletion of coral prey	1 Year	*Oxymonacanthus longirostris* (Kokita and Nakazono 2001)
	Growth rates directly related to tissue cover of coral hosts	1 Month	*Chrysiptera parasema, Dascyllus melanurus* (Feary et al. 2009)
	No difference when feeding on bleached versus unbleached corals	23 Days	*Chaetodon aureofasciatus, C. lunulatus* (Cole et al. 2014)

geographical range. Moreover, *C. auriga* preferentially settles to near-shore patch reef habitats with limited cover of live corals (Pratchett et al. 2008b), questioning why this species would be negatively affected by coral depletion. However, Pratchett et al. (2015b) showed that feeding rates of *C. auriga* (on non-coral substrates) increase with increasing coral cover. This suggests that corals support increased abundance of prey items (such as small crustaceans and other cryptofauna living within the algal turfs) consumed by *C. auriga*. The cryptofauna associated with algal turfs is an important contributor to the trophic dynamics of shallow reef systems (Kramer et al. 2013), and though it is unknown whether high coral cover increases overall productivity of cryptobenthic assemblages or favours only specific species consumed by *C. auriga*, this is a potentially important link in understanding the far-reaching effects of mass coral bleaching and coral depletion on coral reef fishes.

11.4.1 Behavioural Changes

Mass coral bleaching and associated changes in the structure of reef habitats have important and far-reaching effects on the availability of prey resources and not only for those fishes that feed directly on live corals (Wen et al. 2013; Pratchett et al. 2015b). Where possible, fishes would be expected to respond to changes in resource availability by altering their dietary intake and feeding behaviour (e.g. Pratchett et al.

2004). However, diets of some highly specialist species are inflexible (Berumen and Pratchett 2008; Brooker et al. 2014), making them extremely susceptible to prey depletion. Even for fishes that can modify dietary intake in accordance with changing prey availability, this may have significant consequences for individual fitness and long-term survival. Following mass coral bleaching in the central Great Barrier Reef, Australia, Pratchett et al. (2004) showed that *Chaetodon lunulatus* increased its intake of bleaching-resistant coral species. This shift in diet composition enabled adult fishes to persist following the bleaching, though it did have consequences for physiological conditions (Pratchett et al. 2004), which may, in turn, affect longer-term survival and reproductive output (discussed below). Reductions in live coral cover also increase the area over which corallivores forage (e.g. McIlwain and Jones 1997; Kokita and Nakazono 2001), potentially increasing competitive encounters and exposure to predators.

One of the foremost explanations put forward to explain high abundance and diversity of fishes in coral-rich habitats is the extent to which high levels of habitat diversity and complexity will moderate outcomes of competition and predation (Almany 2004). This hypothesis is not readily testable, because the persistence and coexistence of multiple species depend on the outcomes of numerous biological interactions over extended time scales, rather than the changes in the absolute intensity of competition and predation. It would be expected, however, that resource competition would become more intense (especially among coral-dependent fishes) following local coral depletion. Similarly, predation rates might be expected to increase with coral loss and declines in fine-scale topographic complexity of reef habitats (Almany 2004). Thus far, there has been limited evidence of increased intensity of competition among reef fishes following coral loss (Table 11.1). One of the more unexpected consequences of coral loss is that fishes appear to be much more susceptible to predation when corals bleach and die (Coker et al. 2009; Chivers et al. 2016; Ferrari et al. 2017b; Table 11.1), attributable to both changes in habitat structure and apparent changes in the behaviour of fishes in degraded reef environments. Notably, Chivers et al. (2016) showed that water that has passed over dead and degraded corals impedes social learning and predator recognition among the damselfish, *Pomacentrus amboinensis*. Lönnstedt et al. (2014) suggested that dead coral masks the odours of potential predators. Accordingly, field experiments showed that damselfish (*P. amboinensis*) associated with dead coral hosts did not exhibit characteristic sheltering within corals when exposed to the odour of a predator but did so upon seeing the predator. Interestingly, *P. amboinensis* is one of the few coral-dwelling damselfishes that is commonly found on dead coral hosts, especially after major disturbances (Pratchett et al. 2012), and these effects may be even stronger for obligate coral-dwelling species.

There has been comparatively little research on the specific behavioural responses of fishes to host coral bleaching or mortality (but see Coker et al. 2009, 2013). It is implicitly assumed, for example, that declines in the abundance of coral-dwelling fishes following extensive and widespread coral loss are due to elevated rates of individual mortality, due to compromised health of the individual fishes and increased susceptibility to predation (Sano et al. 1984, 1987; Jones et al. 2004;

Pratchett et al. 2008a), which may be compounded by declines in local settlement rates (Feary et al. 2007). However, Coker et al. (2009) showed that prey fishes associated with bleached corals are much more susceptible to predation compared to conspecifics living on unbleached corals, which was attributed to both visual and chemical camouflage provided by live coral tissues. Even if predation rates are not actually any higher for fishes on bleached corals, it is possible that increased exposure to predators may provide significant motivation for coral-dwelling fishes to rapidly vacate bleached coral hosts (Sano et al. 1987; Coker et al. 2009). This might also explain the reluctance of fishes to settle on bleached corals (e.g. Feary et al. 2007).

11.4.2   Effects of Coral Bleaching Versus Coral Loss on Individual Fitness of Fishes

Where coral bleaching and/or coral mortality leads to depletion of resources for reef fishes, species losses are likely to be preceded or accompanied by declines in individual condition or fitness (Kokita and Nakazono 2001; Pratchett et al. 2006; Brooker et al. 2013). Kokita and Nakazono (2001) documented localised extirpation of *Oxymonacanthus longirostris* over 2 years following coral bleaching in Okinawa, Japan (see also Brooker et al. 2014). However, even before these fishes disappeared, growth rates were severely compromised (Kokita and Nakazono 2001), reflecting limited access to their preferred coral prey, *Acropora*, which had succumbed to the bleaching and died. Experimental studies conducted by Brooker et al. (2013) also showed that constrained access to preferred coral prey by breeding pais of *O. longirostris* resulted in reproductive failure. It is also possible that declines in the nutritional quality of coral prey may occur even during bleaching, due to rapid depletion of lipid reserves (but see Pisapia et al. 2012). Some coral-feeding fishes will initially target bleached corals over healthy coral prey, potentially due to increased mucous production or limited tissue retraction, but preferentially target healthy corals over colonies subject to prolonged bleaching (Cole et al. 2009). It is clear that corallivorous fishes will consume bleached corals, but protracted feeding on bleached corals may constrain nutritional intake. However, Cole et al. (2014) found no apparent differences in the growth rates of juvenile butterflyfishes that were restricted to feeding on bleached versus healthy corals for 23 days. The findings suggest that bleaching per se may have limited effects on corallivorous reef fishes (see also Bonin et al. 2009; McCormick et al. 2010). Rather, it is the subsequent mortality of bleached coral colonies that impacts on food availability leading to declines in the physiological condition and ultimately the survival of corallivorous fishes.

Aside from coral-feeding fishes (e.g. butterflyfishes), coral-dwelling fishes have the most direct and explicit reliance on corals (Pratchett et al. 2012) and are extremely vulnerable to local depletion of their specific coral hosts (Munday

2004). Many coral-dwelling fishes vacate their coral hosts as soon as they bleach, let alone die (Feary et al. 2007; Coker et al. 2012). Redistribution of coral-dwelling fishes among remnant coral hosts may moderate the susceptibility of these fishes to host coral depletion, though overall densities often decline in approximate accordance with the proportional loss of preferred coral habitats (Wilson et al. 2008; Pratchett et al. 2012). The proximate causes of declines in the abundance of coral-dwelling fishes following host coral mortality remain largely unknown. Explicit comparisons of the physiological condition of several different species of coral-dwelling damselfishes (Table 11.1) constrained to living on bleached versus healthy coral hosts reveal little or no differences. This suggests that declines in the abundance of coral-dwelling fishes within habitats subject to host coral depletion are due to extrinsic processes (e.g. predation) rather than intrinsic factors. However, sublethal effects of coral depletion need to be considered across a much wider range of reef fish species.

11.5   Conclusions

Highly diverse and productive assemblages of coral reef fishes rely on the combination of high abundance (cover) and diversity of scleractinian corals, as well as high levels of topographic complexity, which in itself is often provided by high coral growth. Mass coral bleaching, which can cause extensive coral loss, will, therefore, have significant effects on the structure and function of reef fish assemblages (e.g. Wilson et al. 2006; Graham et al. 2006, 2008), with potential consequences for fisheries production and coral reef resilience. The loss of entire functional groups that comprise multiple species may appear unlikely. However, biodiversity of coral reef fishes is not equally apportioned among different functional groups (Mouillot et al. 2014). There are also entire functional groups that respond similarly to coral bleaching and coral loss, such that certain ecological functions will be severely compromised, if not lost altogether (Graham et al. 2011). It is now clear that effects of coral bleaching and associated coral loss extend well beyond those species traditionally thought to have specific reliance on corals for food and shelter (e.g. butterflyfishes, damselfishes, gobies). In extreme cases, the abundance and species richness of fishes may decline >60% following extensive coral depletion and topographic collapse of reef habitats, combined with increasing dominance of non-coral biota. The spatial extent of mass bleaching events is also far greater than other major disturbances, potentially threatening widespread species with extinction. This provides significant imperative for reducing greenhouse gas emissions, to reduce the incidence and severity of future mass coral bleaching while also addressing other more localised disturbances that contribute to coral loss and reef degradation.

References

Adam TC, Schmitt RJ, Holbrook SJ, Brooks AJ, Edmunds PJ, Carpenter RC et al (2011) Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. PLoS One 6:e23717. https://doi.org/10.1371/journal.pone.0023717

Ainsworth CH, Mumby P (2015) Coral–algal phase shifts alter fish communities and reduce fisheries production. Glob Change Biol 21:165–172. https://doi.org/10.1111/gcb.12667

Almany GR (2004) Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? Oikos 106:275–284. https://doi.org/10.1111/j.0030-1299.2004.13193.x

Alvarez-Filip L, Dulvy NK, Côté IM, Watkinson AR, Gill JA (2011) Coral identity underpins architectural complexity on Caribbean reefs. Ecol Appl 21:2223–2231. https://doi.org/10.1890/10-1563.1

Baird AH, Marshall PA (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Mar Ecol Prog Ser 237:133–141. https://doi.org/10.3354/meps237133

Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. Estuar Coast Shelf Sci 80:435–471. https://doi.org/10.1016/j.ecss.2008.09.003

Bell JB, Ganachaud A, Gehrke PC, Griffiths SP, Hobday AJ, Hoegh-Guldberg O et al (2013) Mixed responses of tropical Pacific fisheries and aquaculture to climate change. Nat Clim Change 3:591–599. https://doi.org/10.1038/nlimate1838

Bell JD, Cisneros-Montemayor A, Crowder L, Hanich Q, Johnson J, Lehodey P et al (2017) Adaptations to maintain the contributions of small-scale fisheries to food security in the Pacific Islands. Mar Policy. https://doi.org/10.1016/j.marpol.2017.05.019

Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecol Lett 6:281–285. https://doi.org/10.1046/j.1461-0248.2003.00432.x

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827–833. https://doi.org/10.1038/nature02691

Bellwood DR, Hoey AS, Ackerman JL, Depczynski M (2006) Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. Glob Change Biol 12:1587–1594. https://doi.org/10.1111/j.1365-2486.2006.01204.x

Bellwood DR, Hoey AS, Hughes TP (2012) Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. Proc R Soc B 279:1621–1629. https://doi.org/10.1098/rspb.2011.1906

Berumen ML, Pratchett MS (2006) Effects of resource availability on the competitive behaviour of butterflyfishes (Chaetodontidae). In: Proceedings of 10th international coral reef symposium, Japan, vol 1, pp 644–650

Berumen ML, Pratchett MS (2008) Trade-offs associated with dietary specialization in corallivorous butterflyfishes (Chaetodontidae: Chaetodon). Behav Ecol Sociol 62:989–994. https://doi.org/10.1007/s00265-007-0526-8

Blowes S, Pratchett MS, Connolly S (2013) Heterospecific aggression, dominance and specialization in a guild of corallivorous reef fishes. Am Nat 182:157–168. https://doi.org/10.1086/670821

Bonin MC, Munday PL, McCormick MI, Srinivasan M, Jones GP (2009) Coral-dwelling fishes resistant to bleaching but not to mortality of host corals. Mar Ecol Prog Ser 394:215–222. https://doi.org/10.3354/meps08294

Bouchon-Navaro Y, Bouchon C, Harmelin-Vivien ML (1985) Impact of coral degradation on a chaetodontid fish assemblage (Moorea, French Polynesia). In: Proceedings of 5th coral reef symposium, Tahiti, vol 5, pp 427–432

Bozec YM, O'Farrell S, Bruggemann JH, Luckhurst BE, Mumby PJ (2016) Tradeoffs between fisheries harvest and the resilience of coral reefs. Proc Natl Acad Sci USA 113:4536–4541. https://doi.org/10.1073/pnas.1601529113

Brander KM (2007) Global fish production and climate change. Proc Natl Acad Sci USA 104:19709–19714. https://doi.org/10.1073/pnas.0702059104

Brandl SJ, Emslie MJ, Ceccarelli DM, Richards ZT (2016) Habitat degradation increases functional originality in highly diverse coral reef fish assemblages. Ecosphere 7:e01557. https://doi.org/10.1002/ecs2.1557

Brooker RM, Jones GP, Munday PL (2013) Prey selectivity affects reproductive success of a corallivorous reef fish. Oecologia 172:409–416. https://doi.org/10.1007/s00442-012-2521-7

Brooker RM, Munday PL, Brandl SJ, Jones GP (2014) Local extinction of a coral reef fish explained by inflexible prey choice. Coral Reefs 33:891–896. https://doi.org/10.1007/s00338-014-1197-3

Cheal AJ, MacNeil MA, Emslie MJ, Sweatman HPA (2017) The threat to coral reefs from more intense cyclones under climate change. Glob Change Biol 23:1511–1524. https://doi.org/10.1111/gcb.13593

Cheung WW, Lam VW, Sarmiento JL, Kearney K, Watson R, Zeller D et al (2010) Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. Glob Change Biol 16:24–35. https://doi.org/10.1111/j.1365-2486.2009.01995.x

Cheung WW, Watson R, Pauly D (2013) Signature of ocean warming in global fisheries catch. Nature 497:365–368. https://doi.org/10.1038/nature12156

Chivers DP, McCormick MI, Allan BJ, Ferrari MC (2016) Risk assessment and predator learning in a changing world: understanding the impacts of coral reef degradation. Sci Rep 6:32542. https://doi.org/10.1038/srep32542

Chong-Seng KM, Graham NAJ, Pratchett MS (2014) Bottlenecks to coral recovery in Seychelles. Coral Reefs 33:449–461. https://doi.org/10.1007/s00338-014-1137-2

Cinner JE, Huchery C, Darling ES, Humphries AT, Graham NA, Hicks CC et al (2013) Evaluating social and ecological vulnerability of coral reef fisheries to climate change. PloS One 8:e74321. https://doi.org/10.1371/journal.pone.0074321

Coker DJ, Pratchett MS, Munday PL (2009) Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. Behav Ecol 20:1204–1210. https://doi.org/10.1093/beheco/arp113

Coker DJ, Graham NAJ, Pratchett MS (2012) Interactive effects of live coral and structural complexity on the recruitment of reef fishes. Coral Reefs 31:919–927. https://doi.org/10.1007/s00338-012-0920-1

Coker DJ, Walker S, Munday P, Pratchett MS (2013) Social group entry rules may limit population resilience to patchy habitat disturbance. Mar Ecol Prog Ser 493:237–242. https://doi.org/10.3354/meps10493

Coker DJ, Wilson SK, Pratchett MS (2014) Importance of live coral habitat for reef fishes. Rev Fish Biol Fish 24:89–126. https://doi.org/10.1007/s11160-013-9319-5

Coker DJ, Nowicki JP, Pratchett MS (2015) Body condition of the coral-dwelling fish Dascyllus aruanus (Linnaeus 1758) following host colony bleaching. Environ Biol Fish 98:691–695. https://doi.org/10.1007/s10641-014-0277-0

Cole AJ, Pratchett MS, Jones GP (2008) Diversity and functional importance of coral-feeding fishes on tropical coral reefs. Fish Fish 9:286–307. https://doi.org/10.1111/j.1467-2979.2008.00290.x

Cole AJ, Pratchett MS, Jones GP (2009) Effects of coral bleaching on the feeding response of two species of coral-feeding fish. J Exp Mar Biol Ecol 373:11–15. https://doi.org/10.1016/j.jembe.2009.02.016

Cole AJ, Lawton RJ, Pisapia C, Pratchett MS (2014) The effects of coral bleaching on settlement preferences and growth of juvenile butterflyfishes. Mar Environ Res 98:106–110. https://doi.org/10.1016/j.marenvres.2014.03.003

Dahlgren CP, Eggleston DB (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology 81:2227–2240. https://doi.org/10.1890/0012-9658(2000)081[2227,EPUOHS]2.0.CO;2

Dalzell P, Adams TJH, Polunin NVC (1996) Coastal fisheries in the Pacific Islands. Oceanogr Mar Biol Annu Rev 34:395–531

De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27–year decline of coral cover on the Great Barrier Reef and its causes. Proc Natl Acad Sci USA 109:17995–17999. https://doi.org/10.1073/pnas.1208909109

Diaz-Pulido G, McCook LJ (2002) The fate of bleached corals: patterns and dynamics of algal recruitment. Mar Ecol Prog Ser 232:115–128. https://doi.org/10.3354/meps232115

Dixson DL, Abrego D, Hay ME (2014) Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery. Science 345:892–897. https://doi.org/10.1126/science.1255057

Doherty PJ, Dufour V, Galzin R, Hixon MA, Meekan MG, Planes S (2004) High mortality during settlement is a population bottleneck for a tropical surgeonfish. Ecology 85:2422–2428. https://doi.org/10.1890/04-0366

Dorenbosch M, Grol MGG, Nagelkerken I, Van der Velde G (2006) Seagrass beds and mangroves as potential nurseries for the threatened Indo-Pacific humphead wrasse, Cheilinus undulatus and Caribbean rainbow parrotfish, Scarus guacamaia. Biol Conserv 129:277–282. https://doi.org/10.1016/j.biocon.2005.10.032

Elmqvist T, Folke C, Nyström M, Peterson M, Bengtsson J, Walker B et al (2003) Response diversity, ecosystem change, and resilience. Front Ecol Environ 1:488–494. https://doi.org/10.1890/1540-9295(2003)001[0488,RDECAR]2.0.CO;2

Emslie MJ, Pratchett MS, Cheal AJ (2011) Effects of different disturbance types on butterflyfish communities of Australia's Great Barrier Reef. Coral Reefs 30:461–471. https://doi.org/10.1007/s00338-011-0730-x

Emslie MJ, Cheal AJ, Johns KA (2014) Retention of habitat complexity minimizes disassembly of reef fish communities following disturbance: a large-scale natural experiment. PLoS One 9:e105384. https://doi.org/10.1371/journal.pone.0105384

Emslie MJ, Cheal AJ, Logan M (2017) The distribution and abundance of reef-associated predatory fishes on the Great Barrier Reef. Coral Reefs 36:829–846. https://doi.org/10.1007/s00338-017-1573-x

Evans RD, Wilson SK, Field SN, Moore JAY (2014) Importance of macroalgal fields as coral reef fish nursery habitat in north-west Australia. Mar Biol 161:599–607. https://doi.org/10.1007/s00227-013-2362-x

Feary DA, Almany GR, McCormick MI, Jones FP (2007) Habitat choice, recruitment and the response of coral reef fishes to coral degradation. Oecologia 153:727–737. https://doi.org/10.1007/s00442-007-0773-4

Feary DA, McCormick MI, Jones GP (2009) Growth of reef fishes in response to live coral cover. J Exp Mar Biol Ecol 373:45–49. https://doi.org/10.1016/j.jembe.2009.03.002

Ferrari R, Figueira WF, Pratchett MS, Boube T, Adam A, Kebelkowsky-Vidrio T et al (2017a) 3D photogrammetry quantifies growth and external erosion of individual coral colonies and skeletons. Sci Rep 7. https://doi.org/10.1038/s41598-017-16408-z

Ferrari MC, McCormick MI, Allan BJ, Chivers DP (2017b) Not equal in the face of habitat change: closely related fishes differ in their ability to use predation-related information in degraded coral. Proc R Soc B 284. https://doi.org/10.1098/rspb.2016.2758

Gardiner NM, Jones GP (2005) Habitat specialisation and overlap in a guild of coral reef cardinal fishes (Apogonidae). Mar Ecol Prog Ser 305:163–175. https://doi.org/10.3354/meps305163

Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. Science 301:958–960. https://doi.org/10.1126/science.1086050

Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS (2013) Recovery of an isolated coral reef system following severe disturbance. Science 340:69–71. https://doi.org/10.1126/science.1232310

Glynn PW (1997) Bioerosion and coral reef growth: a dynamic balance. In: Birkeland C (ed) Life and death of coral reefs. Chapman & Hall, New York, pp 68–95

Goreau T, McClanahan TR, Hayes R, Strong A (2000) Conservation of coral reefs after the 1998 global bleaching event. Conserv Biol 14:5–15. https://doi.org/10.1046/j.1523-1739.2000.00011.x

Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef ecosystems. Coral Reefs 32:315–326. https://doi.org/10.1007/s00338-012-0984-y

Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. Proc Nat Acad Sci USA 103:8425–8429. https://doi.org/10.1073/pnas.0600693103

Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Robinson J, Bijoux JP et al (2007) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. Conserv Biol 21:1291–1300. https://doi.org/10.1111/j.1523-1739.2007.00754.x

Graham NAJ, McClanahan TR, MacNeil MA, Wilson SK, Polunin NVC, Jennings S et al (2008) Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. PLoS One 3:e3039. https://doi.org/10.1371/journal.pone.0003039

Graham NAJ, Wilson SK, Pratchett MS, Polunin NVC, Spalding MD (2009) Coral mortality versus structural collapse as drivers of corallivorous butterflyfish decline. Biodivers Conserv 18:3325–3336. https://doi.org/10.1007/s10531-009-9633-3

Graham NAJ, Chabanet P, Evans RD, Jennings S, Letourneur Y, MacNeil AM et al (2011) Extinction vulnerability of coral reef fishes. Ecol Lett 14:341–348. https://doi.org/10.1111/j.1461-0248.2011.01592.x

Graham NA, Cinner JE, Norström AV, Nyström M (2014) Coral reefs as novel ecosystems: embracing new futures. Curr Opin Environ Sustain 7:9–14. https://doi.org/10.1016/j.cosust.2013.11.023

Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518:94–97. https://doi.org/10.1038/nature14140

Grandcourt EM, Cesar HS (2003) The bio-economic impact of mass coral mortality on the coastal reef fisheries of the Seychelles. Fish Res 60:539–550. https://doi.org/10.1016/S0165-7836(02)00173-X

Gratwicke B, Speight MR (2005) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. J Fish Biol 66:650–667. https://doi.org/10.1111/j.0022-1112.2005.00629.x

Green AL (1998) Spatio-temporal patterns of recruitment of labroid fishes (Pisces: Labridae and Scaridae) to damselfish territories. Environ Biol Fish 51:235–244. https://doi.org/10.1023/A:1007389206099

Guest JR, Baird AH, Maynard JA, Muttaqin E, Edwards AJ, Campbell SJ et al (2012) Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. PLoS One 7:e33353. https://doi.org/10.1371/journal.pone.0033353

Halford AR, Caley MJ (2009) Towards an understanding of resilience in isolated coral reefs. Glob Change Biol 15:3031–3045. https://doi.org/10.1111/j.1365-2486.2009.01972

Hamilton RJ, Almany GR, Brown CJ, Pita J, Peterson NA, Choat JH (2017) Logging degrades nursery habitat for an iconic coral reef fish. Biol Conserv 210:273–280. https://doi.org/10.1016/j.biocon.2017.04.024

Hart AM, Klumpp DW, Russ GR (1996) Response of herbivorous fishes to crown-of-thorns starfish Acanthaster planci outbreaks. II. Density and biomass of selected species of herbivorous fish and fish habitat correlations. Mar Ecol Prog Ser 132:21–30. https://doi.org/10.3354/meps132021

Hempson TN, Graham NAJ, MacNeil MA, Williamson DH, Jones GP, Almany GR (2017a) Coral reef mesopredators switch prey, shortening food chains, in response to habitat degradation. Ecol Evol 7:2626–2635. https://doi.org/10.1002/ece3.2805

Hempson TN, Graham NAJ, MacNeil MA, Bodin N, Wilson SK (2017b) Regime shifts shorten food chains for mesopredators with potential sublethal effects. Funct Ecol. https://doi.org/10.1111/1365-2435.13012

Heron SF, Maynard J, van Hooidonk R, Eakin CM (2016) Warming trends and bleaching stress of the world's coral reefs 1985–2012. Sci Rep 6:38402. https://doi.org/10.1038/srep38402

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshwater Res 50:839–866. https://doi.org/10.1071/MF99078

Hoey AS, Bellwood DR (2009) Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. Ecosystems 12:1316–1328. https://doi.org/10.1007/s10021-009-9291-z

Hoey AS, Bellwood DR (2011) Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? Ecol Lett 14:267–273. https://doi.org/10.1111/j.1461-0248.2010.01581.x

Hoey AS, Brandl SJ, Bellwood DR (2013) Diet and cross-shelf distribution of rabbitfishes (f. Siganidae) on the northern Great Barrier Reef: implications for ecosystem function. Coral Reefs 32:973–984. https://doi.org/10.1007/s00338-013-1043-z

Hoey AS, Howells E, Johansen JL, Hobbs JPA, Messmer V, McCowan DM et al (2016) Recent advances in understanding the effects of climate change on coral reefs. Diversity 8:12. https://doi.org/10.3390/d8020012

Holbrook SJ, Schmitt RJ, Brooks AJ (2008) Resistance and resilience of a coral reef fish community to changes in coral cover. Mar Ecol Prog Ser 371:263–271. https://doi.org/10.3354/meps07690

Holbrook SJ, Schmitt RJ, Messmer V, Brooks AJ, Srinivasan M, Munday PL et al (2015) Reef fishes in biodiversity hotspots are at greatest risk from loss of coral species. PLoS One 10: e0124054. https://doi.org/10.1371/journal.pone.0124054

Houlahan JE, Currie DJ, Cottenie K, Cumming GS, Ernest SKM, Findlay CS et al (2007) Compensatory dynamics are rare in natural ecological communities. Proc Natl Acad Sci USA 104:3273–3277. https://doi.org/10.1073/pnas.0603798104

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C et al (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933. https://doi.org/10.1126/science.1085046

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli DM, Hoegh-Guldberg O, McCook LJ et al (2007) Phase shifts, herbivory and the resilience of coral reefs to climate change. Curr Biol 17:360–365. https://doi.org/10.1016/j.cub.2006.12.049

Hughes TP, Graham NA, Jackson JB, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. Trends Ecol Evol 25:633-642. doi:https://doi.org/10.1016/j.tree.2010.07.011

Hughes TP, Kerry JT, Alvarez-Noriega M, Alvarez-Romero JC, Anderson KD, Baird AH et al (2017) Global warming and recurrent mass bleaching of corals. Nature 543:373–377. https://doi.org/10.1038/nature21707

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM et al (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359:80–83. https://doi.org/10.1126/science.aan8048

Jokiel PL, Coles SL (1990) Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. Coral Reefs 8:155–162. https://doi.org/10.1007/BF00265006

Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. Proc Natl Acad Sci USA 101:8251–8253. https://doi.org/10.1073/pnas.0401277101

Kerry JT, Bellwood DR (2012) The effect of coral morphology on shelter selection by coral reef fishes. Coral Reefs 31:415–424. https://doi.org/10.1007/s00338-011-0859-7

Kok JE, Graham NAJ, Hoogenboom MO (2016) Climate-driven coral reorganisation influences aggressive behaviour in juvenile coral-reef fishes. Coral Reefs 35:473–483. https://doi.org/10.1007/s00338-016-1411-6

Kokita T, Nakazono A (2001) Rapid response of an obligately corallivorous filefish *Oxymonacanthus longirostris* (Monacanthidae) to a mass coral bleaching event. Coral Reefs 20:155–158. https://doi.org/10.1007/s00338100153

Komyakova V, Munday PL, Jones GP (2013) Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. PLoS One 8:e83178. https://doi.org/10.1371/journal.pone.0083178

Kramer MJ, Bellwood O, Bellwood DR (2013) The trophic importance of algal turfs for coral reef fishes: the crustacean link. Coral Reefs 32:575–583. https://doi.org/10.1007/s00338-013-1009-1

Light PR, Jones GP (1997) Habitat preference in newly settled coral trout (*Plectropomus leopardus*, Serranidae). Coral Reefs 16:117–126. https://doi.org/10.1007/s003380050065

Linares C, Pratchett MS, Coker MS (2011) Recolonisation and growth of *Acropora hyacinthus* following climate-induced coral bleaching on the Great Barrier Reef. Mar Ecol Prog Ser 438:97–104. https://doi.org/10.3354/meps09272

Lönnstedt OM, McCormick MI, Chivers DP, Ferrari MC (2014) Habitat degradation is threatening reef replenishment by making fish fearless. J Anim Ecol 83:1178–1185. https://doi.org/10.1111/1365-2656.12209

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and losers. Ecol Lett 4:122–131. https://doi.org/10.1046/j.1461-0248.2001.00203.x

Madin JS, Connolly SR (2006) Ecological consequences of major hydrodynamic disturbances on coral reefs. Nature 444:477–480. https://doi.org/10.1038/nature05328

McClanahan TR, Maina J, Pet-Soede L (2002) Effects of the 1998 coral mortality event on Kenyan coral reefs and fisheries. Ambio 31:543–550. https://doi.org/10.1579/0044-7447-31.7.543

McClanahan TR, Baird AH, Marshall PA, Toscano MA (2004) Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. Mar Pollut Bull 48:327–335. https://doi.org/10.1016/j.marpolbul.2003.08.024

McCormick MI, Allan BJ (2017) Interspecific differences in how habitat degradation affects escape response. Sci Rep 7:426. https://doi.org/10.1038/s41598-017-00521-0

McCormick MI, Moore JAY, Munday PL (2010) Influence of habitat degradation on fish replenishment. Coral Reefs 29:537–546. https://doi.org/10.1007/s00338-010-0620-7

McCowan DM, Pratchett MS, Baird AH (2012) Variation in bleaching susceptibility and mortality attributable to growth forms. In: Proceedings of 12th international coral reef symposium, Cairns, vol 9A, pp 1–6

McIlwain JL, Jones GP (1997) Prey selection by an obligate coral-feeding wrasse and its response to small-scale disturbance. Mar Ecol Prog Ser 155:189–198. https://doi.org/10.3354/meps155189

Messmer V, Jones GP, Munday PL, Holbrook SJ, Schmitt RJ, Brooks AJ (2011) Habitat diversity as a determinant of fish community structure on coral reefs. Ecology 92:2285–2298. https://doi.org/10.1890/11-0037.1

Mouillot D, Villéger S, Parravicini V, Kulbicki M, Arias-González JE, Bender M et al (2014) Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proc Natl Acad Sci USA 111:13757–13762. https://doi.org/10.1073/pnas.1317625111

Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends Ecol Evol 23:555–563. https://doi.org/10.1016/j.tree.2008.06.011

Munday PL (2001) Fitness consequences of habitat use and competition among coral-dwelling fishes. Oecologia 128:585–593. https://doi.org/10.1007/s004420100690

Munday PL (2004) Habitat loss, resource specialization, and extinction on coral reefs. Glob Change Biol 10:1642–1647. https://doi.org/10.1111/j.1365-2486.2004.00839.x

Munday PL, Jones GP, Pratchett MS, Williams A (2008) Climate change and the future for coral reef fishes. Fish Fish 9:261–285. https://doi.org/10.1111/j.1467-2979.2008.00281

Nash KL, Graham NAJ, Jennings S, Wilson SK, Bellwood DR (2016) Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. J Appl Ecol 53:646–655. https://doi.org/10.1111/1365-2664.12430

Noonan SHC, Jones GP, Pratchett MS (2012) Coral size, health and structural complexity: effects on the ecology of a coral reef damselfish. Mar Ecol Prog Ser 456:127–137. https://doi.org/10.3354/meps09687

Pisapia C, Pratchett MS, Cole A (2012) Butterflyfishes feeding responses to bleached corals. In: Proceedings of 12th international coral reef symposium, Cairns, vol 13C, pp 1–5

Pratchett MS (2014) Feeding preferences and dietary specialization among obligate coral-feeding butterflyfishes. In: Pratchett MS, Berumen ML, Kapoor B (eds) Biology of butterflyfishes. CRC, Boca Raton, pp 140–179

Pratchett MS, Wilson SK, Berumen ML, McCormick MI (2004) Sub-lethal effects of coral bleaching on an obligate coral feeding butterflyfish. Coral Reefs 23:352–356. https://doi.org/10.1007/s00338-004-0394-x

Pratchett MS, Wilson SK, Baird AH (2006) Declines in the abundance of Chaetodon butterflyfishes (Chaetodontidae) following extensive coral depletion. J Fish Biol 69:1269–1280. https://doi.org/10.1111/j.1095-8649.2006.01161.x

Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinner JE, Bellwood DR et al (2008a) Effects of climate-induced coral bleaching on coral-reef fishes: ecological and economic consequences. Oceanogr Mar Biol 46:251–296. https://doi.org/10.1201/9781420065756.ch6

Pratchett MS, Berumen ML, Marnane MJ, Eagle JE, Pratchett DJ (2008b) Habitat associations of juvenile versus adult butterflyfishes. Coral Reefs 27:541–551. https://doi.org/10.1007/s00338-008-0357-8

Pratchett MS, Wilson SK, Graham NAJ, Munday PL, Jones GP, Polunin NVC (2009) Coral bleaching and consequences for motile reef organisms: past, present and uncertain future effects. In: van Oppen MJH, Lough JM (eds) Coral bleaching: patterns, processes, causes and consequences. Springer, Heidelberg, pp 139–158

Pratchett MS, Bay LK, Gehrke PC, Koehn J, Osborne K, Pressey RL et al (2011a) Contribution of climate change to degradation and loss of critical fish habitats in Australian aquatic environments. Mar Freshwater Res 62:1062–1081. https://doi.org/10.1071/MF10303

Pratchett MS, Hoey AS, Wilson SK, Messmer V, Graham NAJ (2011b) Changes in the biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. Diversity 3:424–452. https://doi.org/10.3390/d3030424

Pratchett MS, Munday PL, Graham NAJ, Kronen M, Pinica S, Friedman K et al (2011c) Vulnerability of coastal fisheries in the tropical Pacific to climate change. In: Bell JD, Johnson JE, Hobday AJ (eds) Vulnerability of tropical pacific fisheries and aquaculture to climate change. Secretariat for the Pacific Community, Noumea, New Caledonia, pp 493–576

Pratchett MS, Coker DJ, Jones GP, Munday PL (2012) Specialization in habitat use by coral reef damselfishes and their susceptibility to habitat loss. Ecol Evol 2:2168–2180. https://doi.org/10.1002/ece3.321

Pratchett MS, McCowan DM, Heron S, Maynard JA (2013) Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea, French Polynesia. PLoS One 8:e70443. https://doi.org/10.1371/journal.pone.0070443

Pratchett MS, Hoey AS, Wilson SK (2014) Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. Curr Opin Environ Sustain 7:37–43. https://doi.org/10.1016/j.cosust.2013.11.022

Pratchett MS, Anderson KD, Hoogenboom MO, Widman E, Baird AH, Pandolfi JM et al (2015a) Spatial, temporal and taxonomic variation in coral growth: implications for the structure and function of coral reef ecosystems. Oceanogr Mar Biol 53:215–295. https://doi.org/10.1201/b18733-7

Pratchett MS, Blowes SA, Coker D, Kubacki E, Nowicki J, Hoey AS (2015b) Indirect benefits of scleractinian corals for non-corallivorous butterflyfishes. Coral Reefs 34:665–672. https://doi.org/10.1007/s00338-014-1254-y

Pratchett MS, Cameron D, Donelson J, Evans L, Frisch AJ, Hobday AJ et al (2017) Effects of climate change on coral grouper (Plectropomus spp.) and possible adaptation options. Rev Fish Biol Fish 27:297–316. https://doi.org/10.1007/s11160-016-9455-9

Rasher DB, Hoey AS, Hay ME (2013) Consumer diversity interacts with prey defenses to drive ecosystem function. Ecology 94:1347–1358. https://doi.org/10.1890/12-0389.1

Richardson LE, Graham NA, Pratchett MS, Hoey AS (2017) Structural complexity mediates functional structure of reef fish assemblages among coral habitats. Environ Biol Fish 100:193–207. https://doi.org/10.1007/s10641-016-0571-0

Rogers A, Blanchard JL, Mumby PJ (2014) Vulnerability of coral reef fisheries to a loss of structural complexity. Curr Biol 24:1000–1005. https://doi.org/10.1016/j.cub.2014.03.026

Sano M (2001) Short term responses of fishes to macroalgal overgrowth on coral rubble on a degraded reef at Iriomote Island, Japan. Bull Mar Sci 68:543–556

Sano M, Shimizu M, Nose Y (1984) Changes in structure of coral-reef fish communities by destruction of hermatypic corals — observational and experimental views. Pac Sci 38:51–79

Sano M, Shimizu M, Nose Y (1987) Long-term effects of destruction of hermatypic corals by Acanthaster planci infestation of reef fish communities at Iriomote Island, Japan. Mar Ecol Prog Ser 37:191–199. https://doi.org/10.3354/meps037191

Sheppard CRC, Spalding S, Bradshaw C, Wilson SK (2002) Erosion vs recovery of coral reefs after 1998 El Niño: Chagos reefs, Indian Ocean. Ambio 31:40–48. https://doi.org/10.1579/0044-7447-31.1.40

Smith SV, Buddemeier RW (1992) Global change and coral reef ecosystems. Annu Rev Ecol Syst 23:89–118. https://doi.org/10.1146/annurev.es.23.110192.000513

Speers AE, Besedin EY, Palardy JE, Moore C (2016) Impacts of climate change and ocean acidification on coral reef fisheries: an integrated ecological–economic model. Ecol Econ 128:33–43. https://doi.org/10.1016/j.ecolecon.2016.04.012

Stella JS, Pratchett MS, Hutchings PA, Jones GP (2011) Coral-associated invertebrates: diversity, ecological importance and vulnerability to disturbance. Oceanogr Mar Biol 49:43–104

Syms C, Jones GP (2000) Disturbance, habitat structure, and the dynamics of a coral-reef fish community. Ecology 81:2714–2729. https://doi.org/10.1890/0012-9658(2000)081

Walther G-R, Post E, Convey P, Menzels A, Parmesan C, Beebee TJC et al (2002) Ecological responses to recent climate change. Nature 416:389–395. https://doi.org/10.1038/416389a

Wen C, Pratchett MS, Almany G, Jones GP (2013) Patterns of recruitment and microhabitat associations for three predatory coral reef fishes on the southern Great Barrier Reef, Australia. Coral Reefs 32:389–398. https://doi.org/10.1007/s00338-012-0985-x

Wen CKC, Bonin MC, Harrison HB, Williamson DH, Jones GP (2016) Dietary shift in juvenile coral trout (Plectropomus maculatus) following coral reef degradation from a flood plume disturbance. Coral Reefs 35:451–455. https://doi.org/10.1007/s00338-016-1398-x

Wilkinson CR (2000) World-wide coral reef bleaching and mortality during 1998: a global climate change warning for the new millennium? In: Sheppard CRC (ed) Seas at the millennium: an environmental evaluation. Elsevier Science, Amsterdam, pp 43–57

Williamson DH, Ceccarelli DM, Evans RD, Jones GP, Russ GR (2014) Habitat dynamics, marine reserve status, and the decline and recovery of coral reef fish communities. Ecol Evol 4:337–354. https://doi.org/10.1002/ece3.934

Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin N (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? Glob Change Biol 12:1–15. https://doi.org/10.1111/j.1365-2486.2006.01252.x

Wilson SK, Burgess SC, Cheal AJ, Emslie M, Fisher R, Miller I et al (2008) Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. J Anim Ecol 77:220–228. https://doi.org/10.1111/j.1365-2656.2007.01341.x

Wilson SK, Depczynski M, Fisher R, Holmes TH, O'Leary R, Tinkler P (2010) Habitat associations of juvenile fish at Ningaloo Reef, Western Australia: the importance of coral and algae. PLoS One 5:e15185. https://doi.org/10.1371/journal.pone.0015185

Wilson SK, Graham NAJ, Pratchett MS (2014) Susceptibility of butterflyfish to habitat disturbance: Do 'chaets' ever prosper? In: Pratchett MS, Berumen ML, Kapoor B (eds) Biology of butterflyfishes. CRC, Boca Raton, pp 226–245

Wilson SK, Depczynski M, Holmes TH, Noble MM, Radford BT, Tinkler P et al (2017) Climatic conditions and nursery habitat quality provide indicators of reef fish recruitment strength. Limnol Oceanogr. https://doi.org/10.1002/lno.10540