Effects of Coral Bleaching on Coral Reef Fish Assemblages

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Abstract

Coral reefs have emerged as one of the ecosystems most vulnerable to climate variation and change. While the contribution of climate warming to the loss of live coral cover has been well documented, the associated effects on fish have not. Such information is important as coral reef fish assemblages provide critical contributions to ecosystem function and services. This thesis assesses the medium to long term impacts of coral loss on fish assemblages in the western Indian Ocean. Feeding observations of corallivorous butterflyfish demonstrates that considerable feeding plasticity occurs among habitat types, but strong relationships exist between degree of specialisation and declines in abundance following coral loss. Furthermore, obligate corallivores are lost fairly rapidly following decline in coral cover, whereas facultative corallivores are sustained until the structure of the dead coral begins to erode. Surveys of benthic and fish assemblages in Mauritius spanning 11 years highlight small changes in both benthos and fish through time, but strong spatial trends associated with dredging and inter-specific competition. In Seychelles, although there was little change in biomass of fishery target species above size of first capture, size spectra analysis of the entire assemblage revealed a loss of smaller individuals (<30cm) and an increase in the larger individuals (>45cm). This represents a lag effect where fishery production cannot be assured for the long term. A targeted before (mid-1990s) – after (2005) sampling program of coral reef benthos and fish assemblages in 7 countries across the Indian Ocean demonstrated changes in size structure, diversity and trophic composition of the reef fish community have followed coral declines in both fished and protected areas. The thesis highlights the pivotal role that loss of reef structural complexity plays in the effects of bleaching on

fish assemblages and that coral reef management needs to radically adapt to address climate change issues.

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Chapter 1

General introduction

There exists an extensive literature on the effects of natural disturbances in structuring ecological communities. Indeed, many ecological theories, including the intermediate disturbance hypothesis (Connell 1978), have their foundations in research related to disturbance regimes. Such research and knowledge is well founded in the study of shallow coastal, marine habitats, with natural disturbances such as storms, rainfall, temperature anomalies and diseases, playing key roles in the structuring and dynamic nature of many of these habitats (Connell 1978; Dayton 1971; Sousa 1979; Thistle 1981).

Anthropogenic disturbances have also affected the structure and dynamics of shallow marine habitats for at least the past two centuries (Jackson et al. 2001; Pandolfi et al. 2003), and the intensity and frequency of such disturbances are increasing exponentially. Indeed, anthropogenic stressors are becoming the dominant drivers of community structure in many systems (Hughes et al. 2003; Nyström et al. 2000; Polunin 2008). This is leading to concerns over the long-term persistence of a variety of ecosystems, including kelp forests (Steneck et al. 2002), seagrass beds (Duarte 2002), mangrove forests (Alongi 2002) and coral reefs (McClanahan 2002). A range of anthropogenic disturbances threaten coastal ecosystems, including overfishing, nutrient input, sedimentation, land reclamation and dredging. However, climate change is rapidly emerging as the most substantial threat for many ecosystems (Walther et al. 2002; Hughes et al. 2003; Hoegh-Guldberg et al. 2007; Polunin 2008).

1.1 Climate warming and impacts on coral reef benthos

Although the climate has been warmer in the past, the current rate of increase in global temperatures is unmatched in the last 1000 years (Houghton 2005) and likely in the last 420,000 years (Hoegh-Guldberg et al. 2007). Global atmospheric concentrations of carbon dioxide, methane and nitrous oxide now far exceed pre-industrial values determined from ice cores (IPCC 2007). This has led to an average temperature increase of ocean sea surface water of 0.74°C over the last century, with projected increases in temperature of ~0.2°C per decade over the next two decades (IPCC 2007). Ecological communities respond to climate change in various ways, including range shifts, habitat modifications, invasions of new species, changes in trophic interactions, and changes in physiological performance (Perry et al. 2005; Walther et al. 2002; Munday et al. 2008; Polunin 2008). Although these changes are impacting many systems, coral reefs have emerged as one of the most vulnerable and threatened ecosystems to climate variability and change (Hoegh-Guldberg 1999; Hughes et al. 2003; Sheppard 2003; Hoegh-Guldberg et al. 2007).

Coral reefs are impacted by climate change in a variety of ways. Warming climatic conditions are leading to an increase in the frequency and severity of hurricanes (Webster et al. 2005), which can have large impacts on reefs (Halford et al. 2004). Increased concentrations of dissolved CO_2 are resulting in a more acidic ocean chemistry, which leads to slowed deposition of calcium carbonate skeletons (Kleypas et al. 1999). This is expected to slow extension rates and lead to weaker, less dense carbonate skeletons of scleractinian corals (Hoegh-Guldberg et al. 2007). However, perhaps the greatest impact of climate change on coral reefs to date, and predicted to be a main determinant of change in the future, is ‘coral bleaching’. Scleractinian corals exhibit a restricted thermal tolerance, closely adapted to local temperature conditions. If temperatures rise above the normal summer maximum (i.e. threshold) for a given region, a breakdown of the symbiosis between the single-celled algae (zooxanthellae), that provide corals with most of their energy, and their coral hosts occurs; so called ‘coral bleaching’ (Brown 1997). The bleaching response involves a loss in colour of the symbionts and results from a reduction in the number of zooxanthellae, either through in situ degradation, expulsion from the host animal cell, or through detachment of the animal cell itself (Brown 1997; Douglas 2003). If temperatures remain above a threshold for several weeks, the coral is unable to meet nutritional requirements through feeding alone, cannot retrieve or maintain sufficient densities of zooxanthellae, and mortality can occur (Brown 1997; Hoegh-Guldberg 1999, 2004).

Such thermally-induced mortality events can occur over large spatial scales, whereby vast areas of live coral are mostly lost (Hoegh-Guldberg 1999; Hughes et al. 2003; Hoegh-Guldberg et al. 2007). Regional bleaching events occurred in 1979, 1982, 1987, 1991 and 1994 (Hoegh-Guldberg 1999). However, by far the most spatially extensive and severe bleaching event to date, was caused by the 1998 El Niño event. All coral reef regions of the world were affected, resulting in the loss of 16% of the world’s coral cover (Wilkinson 2000). The severity of the event varied geographically, with the western Indian Ocean being one of the most severely impacted regions (Goreau et al. 2000), where the El Niño event interacted with the warm portion of the Indian Ocean Dipole (Saji et al. 1999). Coral cover in this region declined by an average of 46%, with some locations, such as the inner Seychelles, Maldives and Chagos archipelago losing as much as 90% of shallow water coral cover (Goreau et al. 2000; Wilkinson 2000; Linden et al. 2002; Sheppard 2003). Subsequent bleaching events have occurred in the Pacific in 2000 and 2002 (Berkelmans et al. 2004), mild events in the Indian Ocean in 2003 and 2005 (McClanahan et al. 2007a) and a severe event in the Caribbean in 2005 (Donner et al. 2007; Oxenford et al. 2008). However, the 1998 event remains the most geographically extensive and severe on record (Hoegh-Guldberg 2004).

The severity and spatial extent of bleaching events have been increasing (Hoegh-Guldberg 1999). Initial attempts to predict future coral bleaching events indicated extremely bleak outlooks for the future persistence of coral reefs. Models of change in sea temperatures predicted coral bleaching on the scale of the 1998 event would become a yearly phenomenon by 2040 (Hoegh-Guldburg 1999). Indeed, predictions of the 'extinction' of coral reefs between 2020 and 2040 have been made for the Indian Ocean (Sheppard 2003). These predictions are now thought to be a little pessimistic, due to the potential for corals and their symbionts to exhibit some degree of acclimatization and adaptation to warming (Hughes et al. 2003). Furthermore, empirical data and spatial modelling suggest predictable patterns in location specific bleaching stress (McClanahan et al. 2007b; Maina et al. 2008). However, recent models still suggest bleaching could be an annual or biannual event within 20-30 years (Donner et al. 2005), and if acclimatization of corals and symbionts does occur, this will only reduce the impact of bleaching events until the second half of this century (Donner et al. 2007). With bleaching events becoming ever more frequent and severe, the recovery interval between episodes is shrinking, further reducing the ability of reefs to rebound to coral dominated states. Coral bleaching appears increasingly to be the dominant threat to the future of coral reefs, and a major management and conservation concern. Targeted policies to manage reefs in the face of climate change will require a thorough understanding of the ecological responses and ramifications of climate induced coral mortality (Walther et al. 2002).

Although coral bleaching can be devastating to a coral reef, the vulnerability of a given reef to bleaching can depend on background temperature variation (McClanahan & Maina 2003), water flow (Nakamura et al. 2003; McClanahan et al. 2005) and water depth (Sheppard & Obura 2005). Furthermore, the bleaching response is highly species / genus specific (Baird & Marshall 1998; Marshall & Baird 2000; McClanahan 2004; McClanahan et al. 2004, 2007a). Certain species of coral are extremely thermally sensitive, and are among the first to bleach and die during a temperature anomaly. These genera include *Acropora*, *Pocillopora*, *Stylophora* and *Millepora* (Marshall & Baird 2000; McClanahan et al. 2007a). Conversely, genera such as *Galaxea*, massive *Porites* and *Psammocora* tend to be fairly resistant to bleaching (Marshall & Baird 2000; McClanahan et al. 2007a), although they will still bleach under severe conditions. Although there is some variation, these genus specific patterns generally hold across regions in the Indo-Pacific (McClanahan et al. 2004, 2007a). This means that reefs are not totally disappearing, but there is a reduction in coral cover and a change in composition from coral communities dominated by *Acropora* and other branching and physically complex genera to those dominated by *Porites*, *Galaxea* and other largely massive and encrusting coral functional forms (Hughes et al. 2003; McClanahan et al. 2007a). As the former types of corals provide most of the 3-dimentional habitat that many other organisms depend on (Bellwood et al. 2004; Jones et al. 2004), the change is one toward a less desirable state.

Following coral bleaching events, a large amount of space can become available on the coral reef benthos, which is rapidly colonised by epilithic and turfing algae (Diaz-Pulido & McCook 2002). This algae may or may not develop into erect macroalgae depending on site specific nutrient loads (Hunter & Evans 1995; Fabricius et al. 2005) and herbivory (Smith et al. 2001; Mumby et al. 2006). If the bleaching event is severe, local herbivore stocks may be swamped by the amount of free space made available for algal growth (Williams et al. 2001) and the reef may progress on a trajectory toward erect macroalgal dominance and a stable change in state (Mumby et al. 2007a). Conversely, if the spatial impacts of disturbance are smaller, herbivory is sufficient and spatial pockets of live coral remain, recovery back to a coral dominated state may be fairly rapid (Halford et al. 2004; Mumby et al. 2007a; Sheppard et al. 2008).

If a reef does not recover its coral cover, or if a large proportion of branching and plating corals died, dead reef structures may erode to coral rubble in the medium (5-10 years) or longer-term (Sheppard et al. 2002; Graham et al. 2006). The mechanisms for this collapse of reef structure can include physical erosion (Scoffin 1993) and bioerosion (Hutchings 1986) and will be partly dependent on the original composition of the coral community (Done et al. 1996). The result is much reduced structural complexity of the reef matrix. If the resultant rubble is not consolidated or removed from the reef, it can become a hindrance to coral recovery (Fox et al. 2003; Victor

2008). Conversely this process of removing fragile dead reef structures can be critical to the recovery process in some situations (Bellwood et al. 2004).

The changing composition and structure of benthic communities on reefs has now been studied at multiple spatial scales and is increasingly well understood (Gardner et al. 2003; Bruno & Selig 2007; Hughes et al. 2007a; McClanahan et al. 2007a). However, given the substantial changes occurring in coral reef benthos described above, there is a growing need to assess the secondary effects on other components of the ecosystem, which to date have received scarce attention (Walther et al. 2002; Wilson et al. 2006; Pratchett et al. 2008a, b). One of the most important groups to assess are the reef fish, because they provide crucial ecosystem functions on coral reefs (Bellwood et al. 2004; Mumby et al. 2007a), are the main focus of tourist attention (Williams & Polunin 2000), provide protein and other ecosystem services to the burgeoning human populations of many tropical countries (Russ 1991; Moberg & Folke 1999), represent over a quarter of all fish species (Spalding et al. 2001) and are the most species dense vertebrate communities on Earth (Jones et al. 2002).

At the start of this PhD there was a limited amount of information on the impacts of bleaching, or disturbance in general, on fish. The majority of studies that had been conducted were limited in both time and space. Here I provide a review of what was known about these short-term responses of fish to coral loss. The thesis Discussion (Chapter 7) will update how that knowledge has been furthered in the previous 3 years, both through the work of this thesis and the increase in studies assessing the topic in general.

1.2 Short-term impacts of bleaching on fish

One of the key reasons why fish species may be vulnerable to the short-term impacts of coral loss is if they have a component of their life history that is specialised towards dependence on live coral. This can be through feeding requirements, habitat choice or settlement site. Currently, much more is known about the first two types of specialisation. Jones et al. (2004) estimated that, from a selection of 538 species of fish in 20 families, only ~11% were obligately associated with live coral for diet or shelter. Conversely ~65% of fish species they surveyed preferentially settled into live coral from the plankton. It is, however, unclear how much live coral larval fish need to successfully settle, and the impacts of feeding and habitat specialisation are much better understood.

Obligate corallivores (those fish that will only feed on live coral polyps) have been shown to be among the first species to decline in abundance following disturbances such as crown-of-thorn starfish outbreaks (Sano et al. 1987) or hurricanes (Halford et al. 2004). This trend also holds true for the short term impacts of coral bleaching. A number of studies have reported declines in abundance of obligate coral feeding butterflyfish (Shibuno et al. 1999; Adjeroud et al. 2002; McClanahan et al. 2002; Sheppard et al. 2002; Spalding & Jarvis 2002; Sano 2004), the coral feeding filefish *Oxymonacanthus longirostris* (Shibuno et al. 1999; Kokita & Nakazono 2001; Spalding & Jarvis 2002; Sano 2004) and the coral feeding wrasse *Labrichthys unilineatus* (Sheppard et al. 2002; Sano 2004). Indeed, a meta-analysis of studies investigating the short-term impacts of coral loss on reef fish species abundance indicated consistent and significant declines in 7 of the 9 species of obligate corallivore studied (Figure 1.1).

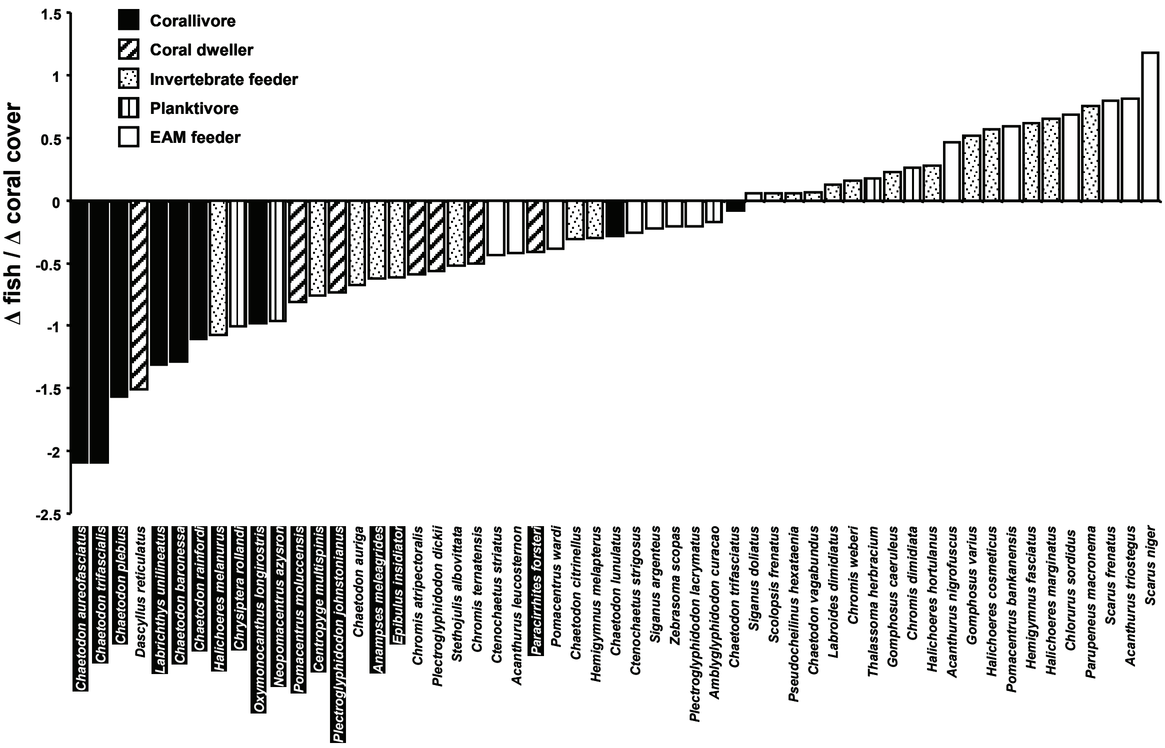

Figure 1.1. Meta-analysis of short-term (<3 years) response of 55 fish species to declines in coral cover. Y-axis metric is change in species abundance divided by change in coral cover. Data from 17 studies are included in the analysis. Species level responses represent mean values, calculated from a minimum of four studies. Only studies reporting a 10% or greater decline in coral were included in the analysis. Data on a species was only included if 5 or more individuals were surveyed in before disturbance counts. Species names are highlighted if mean value with 95% confidence interval fails to intersect zero, indicating consistency of responses among locations. Figure adapted from Wilson et al. (2006)*.

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* Figure adapted from a review article by Wilson et al. (2006), on which the author of this thesis is second author.

Assessments of the initial impacts of coral loss, or where the extent of coral loss was not large, have suggested some sub-lethal responses to coral loss can occur in obligate corallivorous fish, prior to, or in the absence of, any decline in abundance. Pratchett et al. (2004) found the abundance of *Chaetodon lunulatus* did not decline in abundance following a reduction in coral cover from 33.4% to 15%. However, in response to the loss of their preferred corals, the fish responded by a shift in the types of corals they fed upon. This led to an overall reduction in the physiological condition of the fish as measured using hepatocyte vacuolation of the liver, which gives an indication of lipid stores (Pratchett et al. 2004). The authors concluded that such reduction in condition would likely reduce growth rates, reproductive potential and possibly lead to population declines (Pratchett et al. 2004). Kokita & Nakazono (2001) monitored a population of the filefish *Oxymonacanthus longirostris* through a mass coral bleaching event in Okinawa, Japan. During the course of the study the fish demonstrated reduced growth rates, reduced reproductive outputs and ultimately reductions in abundance (Kokita & Nakazono 2001). A further possible sublethal response in corallivores, which is likely related to a reduction in availability of preferred food sources, is a break-down of previously strong feeding territories (Tricas 1989a). Such a breakdown of rigid territorial behaviour was documented on a severely bleached reef in the inner Seychelles (Samways 2005). Both butterflyfish species studied, *Chaetodon trifascialis* and *C. trifasciatus*, increased feeding excursions beyond territory boundaries, which is likely to result in increased intra- and inter-specific competition (Samways 2005).

Although the obligate corallivores are probably the best studied group of fish in terms of responses to disturbance, various key questions remain unanswered. For example, it seems likely that the degree of feeding specialisation would be related to extend of decline following coral loss. However, although comparison between species that consistently display greatest declines (Figure 1.1) and which have more specialised diets (Pratchett 2005) indicates such patterns may exist, few studies have formally quantified such trends. This is because detailed information on degree of specialisation has been lacking until recently and still is for many species and / or coral reef regions. Furthermore, why some species are more specialised than others is very poorly understood (Pratchett 2005). It is also clear that while obligate corallivores may decline following live coral mortality, the response of facultative corallivores is likely to be much more variable (Wilson et al. 2006) and may be linked to other processes and changes in the reef system.

Coral dwelling fish were the other group identified by the meta-analysis of Wilson et al. (2006) to show consistent declines in abundance following coral loss (Figure 1.1). All 7 species included in the analysis displayed declines in abundance following coral mortality, and 3 of those declines were consistent across all studies included in the analysis. Species of damselfish (Lindahl et al. 2001; Booth & Beretta 2002; Shibuno et al. 2002; Spalding & Jarvis 2002), gobies (Munday 2004) and hawkfish (Sheppard et al. 2002) are known to spend a large part of their post-settlement life in certain species or growth forms of live coral and all these species can exhibit declines in abundance following coral loss. Up to 40-50% of damselfish species are known to associate with live coral (Wilson et al. 2008a) and certain species, such as *Plectroglyphidodon dickii*, *P. johnstonianus* and *Pomacentrus moluccensis*, have particularly strong associations with certain types of coral and consistently decline following coral mortality (Figure 1.1; Wilson et al. 2006). The degree of specialisation in coral dwelling gobies has been measured in Papua New Guinea (Munday et al. 1997) and the patterns of decline and threat of extinction to these fish is tightly related to this specialisation and initial population size (Munday 2004).

The degree of settlement specialisation of reef fish is poorly understood. Jones et al. (2004) estimated that 65% of reef fish species require live coral at settlement and attributed substantial declines in fish species richness in Kimbe Bay, Papua New Guinea, to this requirement. However a study of damselfish indicated only species that dwell in live coral as adults, preferentially settle into this habitat (Öhman et al. 1998). Furthermore, a study of a damselfish assemblage through a bleaching event on the Great Barrier Reef indicated that following coral mortality, recruitment declined most for those species that associate with live coral as adults (Booth & Beretta 2002). How much coral is required, whether certain species of coral are favoured and for how long fish require live coral are all unclear. A deeper understanding of the settlement requirements of a range of coral reef fish is clearly necessary.

The planktivore trophic group included in underwater visual census counts is diverse and often includes species from the damselfish, fusilier, wrasse and bigeye families. It is also notable that several species of damselfish that dwell in live coral (Wilson et al. 2006, 2008a), for example *Chromis atripectoralis* and *Dacyllus carneus*, feed on plankton (Froese & Pauly 2008). Many studies group these fish together with other planktivores that are not coral dwellers, thus resulting in a high diversity of responses to disturbance within this group. Spalding & Jarvis (2002) found that the response of planktivores 1 year after the 1998 bleaching event in the southern and granitic islands of the Seychelles was varied. Eleven of the 14 species sampled declined in abundance, but only 1 of those species displayed a significant decline. A non-significant increase at 3 of 5 sites surveyed across the Chagos archipelago, 3 years after the 1998 bleaching event, was driven by schooling fusilier species (Sheppard et al. 2002). However, this family is not benthic associated and is known to be highly variable in underwater visual surveys (Graham et al. 2003). Other studies have also generally shown no significant changes in planktivore abundance following coral mortality, but high variability at the species level, with declines usually associated with those species that dwell in live coral (Lindahl et al. 2001).

Herbivores, or epilithic algal matrix feeders, have been promoted as a particularly important functional group on coral reefs (Bellwood et al. 2004). As corals and algae compete for space on coral reefs, herbivores are thought to be a key group that control algal growth and allow settlement and dominance of coral dominated states (Bellwood et al. 2004). Following coral mortality, the newly available space is rapidly colonised by epilithic and turfing algae, and may or may not develop into erect macroalgae depending on local nutrient loads and herbivore stocks (Diaz-Pulido & McCook 2001). As the space, and therefore the algal resource, increases following a bleaching event, the expectation is that herbivores will increase in abundance and biomass to maintain the increased algal biomass in a cropped state (Sheppard et al. 2002). Some studies of the short-term impacts of bleaching on fish assemblages have reported increases in herbivore abundance and biomass (Shibuno et al. 1999; Lindahl et al. 2001; McClanahan et al. 2002; Sheppard et al. 2002), while others have indicated no change (Riegl 2002; Sano 2004; Spalding & Jarvis 2002). When data from these studies were combined in a meta-analytical framework, there was an indication of increases in about half of the species, with declines in the other half, but a great deal of variation between studies resulting in no consistent changes for any individual species (Figure 1.1). The short time following disturbance that the majority of these studies represent may limit the extent to which demographic changes can occur, and there is a need to understand changes in herbivore populations in response to coral mortality over greater temporal scales. Studies of other disturbances, that were conducted 5-7 years after coral loss, indicated little effect of increased turf algal cover on herbivore abundance (Hart et al. 1996), but identified faster growth rates and larger sizes of certain species (Hart & Russ 1996).

Invertebrate feeding and mixed diet, or omnivorous, fish species may also be expected to respond positively to coral mortality, as a great amount of space is made available for benthic meso-invertebrates to inhabit. Although there are examples of increased dominance of this group of fish in the assemblage following disturbance (Riegl 2002), the majority of studies indicate no overall change in abundance through time (Lindahl et al. 2001; Sheppard et al. 2002; Spalding & Jarvis 2002; Sano 2004). Variation in response at the species level is high (Spalding & Jarvis 2002), with roughly half of the species displaying declines in abundance (several significantly), with other species increasing in abundance to the extent of some of the epilithic algal matrix feeders (Figure 1.1.; Wilson et al. 2006).

Most piscivores on reefs are relatively large and not dependent on live coral for refuge. The most likely impact of a bleaching event on these fish would be through indirect trophic effects, such as a reduction in abundance of their prey. Such predator-prey coupling on reefs may be weak at aggregated family levels (Jennings & Polunin 1997), but stronger at the species level (Graham et al. 2003) or size based aggregations (Dulvy et al. 2004). The short-term impacts of bleaching indicate no measurable impact on these piscivores (Riegl 2002; Sheppard et al. 2002; Spalding & Jarvis 2002), but the time-scales are likely too short to identify any trophic cascading impacts. Furthermore, medium-sized piscivores, such as rock cods, which are more dependent on habitat for ambush predation, are poorly surveyed in underwater visual census. The only piscivores to display declines in abundance following coral mortality are some species of small bodied hawkfish that dwell in live corals and feed on fish recruits and juveniles (Sheppard et al. 2002).

At the assemblage level, the majority of short-term studies indicate very little impact in overall abundance and species richness of the fish assemblage following coral mortality (Riegl 2002; Sheppard et al. 2002; Spalding et al. 2002; Downing et al. 2005; McClanahan 2006). This is probably because most changes are associated with declines of species dependent on live coral for food, shelter or settlement, which make up a relatively small proportion of the assemblage. However, there is some evidence for small decreases in both variables (Sano 2004) or increases in abundance, largely attributed to movement of herbivores in an experimental transplant experiment (Lindahl et al. 2001). A longer-term study in Papua New Guinea, of four focal families, indicated that fish species richness declined with substantial declines in coral cover, and attributed that decline to 65% of the fish assemblage requiring live coral at settlement (Jones et al. 2004). When multiple studies were examined in a meta-analysis, small declines in coral cover actually resulted in increases in fish species richness, likely due to increased habitat heterogeneity, but larger declines (>20%) led to a 20-30% reduction in species richness (Wilson et al. 2006).

Apart from the loss of larval settlement sites (Jones et al. 2004), the longer-term impacts of bleaching leads to the erosion of the reef structural framework (Sheppard et al. 2002; Graham et al. 2006). A number of the studies of the short-term impacts of bleaching speculated that such erosion of 3-dimentional structure would greatly increase the impact of the bleaching event beyond those species directly dependent on live coral for key life history stages (Shibano et al. 1999; Lindahl et al. 2001; Riegl 2002; Sheppard et al. 2002; Spalding & Jarvis 2002). The additional impacts of loss of structural complexity have been indicated from long-term studies of crown-of-thorn starfish impacted reefs (Sano et al. 1987) or through experimental manipulation of the reef benthos (Lewis 1997; Syms & Jones 2000). To better understand the additional consequences of loss of structural complexity, Wilson et al. (2006) compared the impact of disturbances that resulted in loss of live coral, but maintained structural complexity (short-term impacts of bleaching and crown-of-thorns starfish outbreaks), to the impacts of disturbances that caused both the loss of live coral and structural complexity (storms and experimental manipulations). The decline in abundance was consistently greater for five functional groups of fish following the disturbances that included loss of structural complexity (Figure 1.2). These results are likely because the structural matrix of reefs is extremely important for small bodied fish (Munday & Jones 1998) and most reef fish associate with refuge holes at some stage in their life history to avoid predation (Hixon & Beets 1993; Dulvy et al. 2004). This analysis suggests that, if a reef does not recover its coral cover, the longer-term impacts of bleaching are likely to be far more severe and affect more functional groups than the short term impacts.

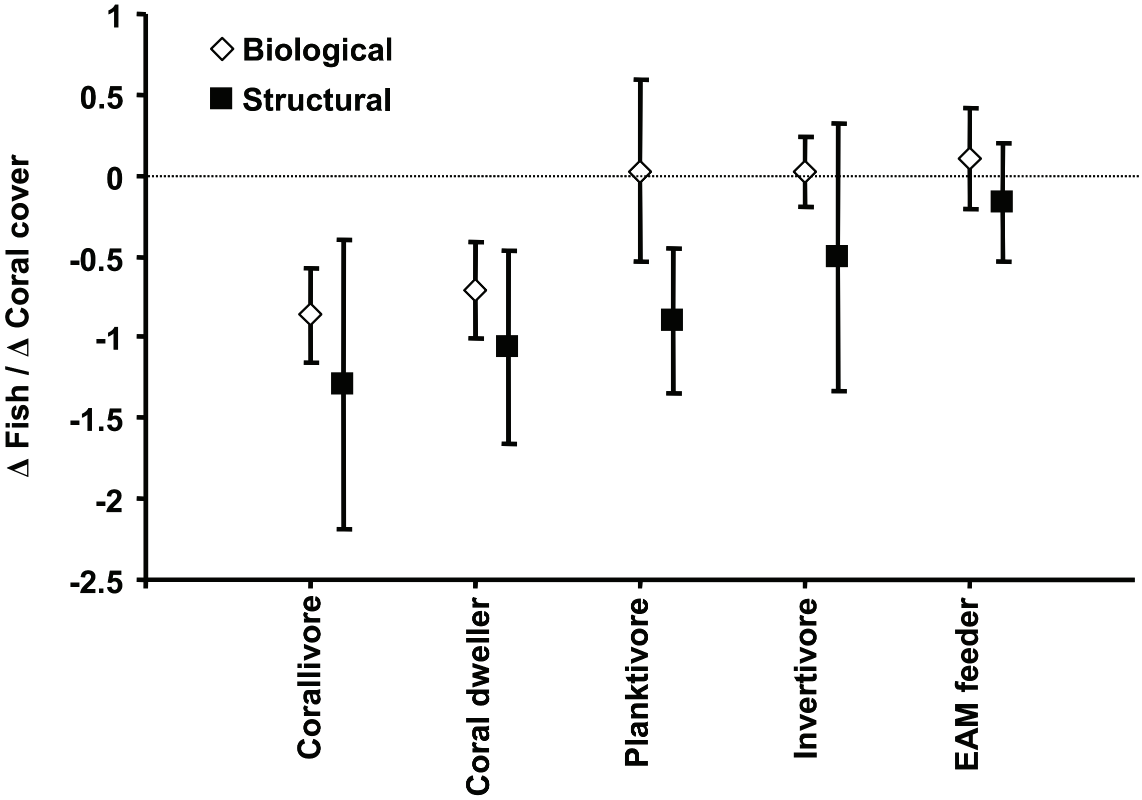

Figure 1.2. Meta-analysis of responses of fish functional groups to two types of disturbance. Y-axis metric is change in fish group abundance divided by change in coral cover. Biological disturbances represent those disturbances that reduce live coral cover, but do not impact the structural complexity of the benthos. Structural disturbances cause a reduction in both live coral cover and structural complexity. Error bars are 95% confidence intervals calculated from the data of ten or more studies. Adapted from Wilson et al. (2006)*.

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* Figure adapted from a review article by Wilson et al. (2006), on which the author of this thesis is second author.

Along with understanding the ecological ramifications of coral bleaching, it is important to understand the socio-economic impacts. Coral reefs provide a wealth of ecosystem goods and services to human societies (Moberg & Folke 1999), with one of the most tangible activities being fisheries (Pet-Soude 2000). As with the studies investigating the impacts of bleaching on fish in situ, the studies assessing impacts on fisheries have generally been conducted shortly after bleaching events have occurred (within 3 years), limiting the ability to detect long-term trends. Grandcourt and Cesar (2003) detected no negative trends in most of the principal target families of reef fish in the inner Seychelles up to 3 years following the 1998 bleaching event. There was a declining trend in Siganidae, however the decline began prior to 1998 and was not thought to be associated with the coral mortality. Kenyan fishery yields declined by 8% following the 1998 bleaching event, however this was associated with a 17% increase in effort, making it difficult to ascribe any causality to the coral mortality event (McClanahan et al. 2002). This lack of short-term detectable impact on fisheries following coral bleaching has also been highlighted from other regions (Pet-Soude 2000). Most reef-associated fisheries target larger fish in the assemblage, and so the impacts of coral mortality will likely take some time to affect these species and individuals. It is possible that a loss of structural complexity and prey fish abundance could ultimately impact fishery target species, but such understanding will require data over greater temporal scales and using various fishery dependant and independent approaches.

The studies of the short-term impacts of bleaching on fish and fisheries indicate a number of research priorities. There is a great need to understand the impacts of bleaching on fish, fisheries and associated goods and services at much greater spatial and temporal scales. The mechanisms of fish decline following coral mortality are not clear; they need to be refined within coral dependent and other groups. It seems likely that if the structural complexity of the reef collapses it will have greater impacts on the fish assemblage, but the dynamics of this are poorly understood. There is very limited knowledge of the importance of live coral as a fish settlement site. As herbivores are such an important functional group on reefs (Bellwood et al. 2004), it is important to understand how they will respond to the longer-term impacts of bleaching. Most studies to date have focussed on abundance, biomass and diversity metrics, whereas changes in the size structuring of the fish assemblage may provide important insights. As reefs are increasingly threatened by multiple disturbances (Nyström et al. 2000; Hughes et al. 2003; Wilson et al. 2006) it is important to understand the interactions among differing disturbances and coral bleaching. Perhaps one of the greatest research needs is to understand if local-scale management can protect reefs against such a global-scale problem (Knowlton & Jackson 2008). The information for this will come from a greater understanding of the impacts and mechanisms for change, but there is also a pressing need to assess the effectiveness of current management frameworks in protecting or promoting recovery from such disturbance.

This thesis aims to address several of these unanswered questions, considering impacts on fishes at the species, functional, size and community levels, over both local and regional spatial scales. Chapter 2 improves understanding of the degree of specialisation of corallivorous butterflyfish in the Indian Ocean and assesses their associated patterns of decline. The chapter also investigates why certain coral prey are targeted more frequently by these fish. Chapter 3 uses obligate and facultative corallivores to better understand the loss of live coral versus loss of structural complexity as driving mechanisms of decline in reef fish assemblages. The analysis also enhances understanding of the spatial and temporal patterns of decline and likely recovery trends of reef fish. Chapter 4 investigates the impacts of coral bleaching versus local impacts on a reef flat in Mauritius. The importance of local disturbances and the structuring processes of competition are elucidated. Chapter 5 reveals that a stable fish biomass above size at first capture in the Seychelles has resulted in no impacts on the fishery to date. However, large changes in the size structure of the fish assemblage suggest a lag effect whereby impacts on the fishery and the ecosystem as a whole are yet to be manifest. Finally, Chapter 6 analysed data from 66 sites, in 7 Indian Ocean countries over a decade. Bayesian meta-analysis is used to assess changes in benthic composition and structure and associated reef fish assemblages. The study explicitly tests the ability of local management, in the form of no take areas, to reduce impacts and enhance recovery from large scale bleaching events. It also assesses the ability of herbivore stocks to increase in abundance to control algal cover.

Chapter 2

Ecological versatility and the decline of coral feeding fishes following climate driven coral mortality[1]

2.1 Abstract

Coral reefs are under threat due to climate mediated coral mortality, which affects some reef coral genera more severely than others. The impact this has on coral reef fish is receiving increasing attention, with one focal area assessing impacts on fish that feed directly on live coral. It appears that the more specialised a species of corallivore, the more susceptible it is to coral declines. However data are sparse for the Indian Ocean, and little is known about why some corals are preferentially fed upon over others. Here I assess feeding specialisation in three species of coral feeding butterflyfish in the Chagos Archipelago, central Indian Ocean, assess the food quality of the coral genera they target and document patterns of decline in the Seychelles following a severe coral mortality event. *Cheatodon trifascialis* was the most specialised coral feeder, preferentially selecting for *Acropora* corals, however, when *Acropora* was scarce, individuals showed considerable feeding plasticity, particularly for the dominant *Pocillopora* corals. *C. trifasciatus* also preferentially fed on *Acropora* corals, but fed on a much more diverse suite of corals and also displayed some selectivity for *Porites*. *C. auriga* is a facultative corallivore and consumed

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~55% live coral, which lies within the wide range of coral dependence reported for this species. C:N ratio analysis indicated *Lobophyllia* and *Acropora* have the highest food quality, with *Pocillopora* having the lowest, which conforms with diet selection of corallivores and helps explain preferential feeding. Obligate specialist feeders displayed the greatest declines through coral mortality in the Seychelles with obligate generalists also declining substantially, but facultative feeders showing little change. Clearly a greater understanding of the species most vulnerable to disturbance, their habitat requirements and the functional roles they play will greatly assist biodiversity conservation in a changing climate.

2.2 Introduction

The decline of coral dominated reef systems and a change in coral composition from diverse and often *Acropora* dominated reefs, to less structurally complex encrusting and massive coral dominated reefs (McClanahan et al. 2007a) is being driven increasingly by coral bleaching, mediated by climate change (Hoegh-Guldberg 1999; Sheppard 2003). The impacts of coral decline on the wider ecosystem has received increasing attention, with the effects on fish being especially well investigated (reviewed by Wilson et al. 2006). While in the medium-term (5-10 years post disturbance) the diversity and abundance of a wide range of species can be affected (Jones et al. 2004; Garpe et al. 2006; Graham et al. 2006), in the short-term (< 3 years post disturbance), the impacts appear limited to species that specialise on coral for diet, recruitment or habitat purposes (Williams 1986; Kokita & Nakazono 2001; Wilson et al. 2006; Munday et al. 1997). However, even for specialised fish, the full effects can take some time to reach fruition (Pratchett et al. 2004), and seem to vary according to the degree to which the fish are specialised (Munday 2004; Pratchett et al. 2006).

Corallivorous fish can vary in their dependence on live coral and although the majority of species feed mainly on scleractinian corals (Hourigan et al. 1988), their diet may include hard corals, soft corals, gorgonians, sponges, algae, polychaetes and crustaceans (Pratchett 2005). Many feeding studies of corallivores have assessed hard coral as a single category (Reese 1975; Harmelin-Vivien & Bouchon-Navaro 1981, 1983; Bouchon-Navaro 1986; Zekeria et al. 2002), however, other studies have partitioned feeding patterns at the scale of genera or species of coral, which enables the degree of specialisation to be elucidated (Cox 1994; Irons 1989; Pratchett 2005; Berumen et al. 2005). Assessing the degree of specialisation of species enables a continuum of ecological versatility to be assessed against resource availability or through disturbance (Munday 2000, 2004), or a greater number of broad categories of feeding or functional groups to be assessed (Pratchett et al. 2006).

Although data on the extent of ecological versatility in coral feeding fish is increasing, we have little knowledge as to why some species are specialists, sometimes preferentially targeting only one species of coral, whilst other species feed on a far broader range of prey. Furthermore, although our understanding of the degree of feeding specialisation and resource partitioning among corallivores has greatly advanced in the Pacific (Pratchett 2005; Berumen et al. 2005) and this has enabled a better understanding of declines in corallivores following disturbances (Pratchett et al. 2006) or switches in assemblage composition following reorganisation of benthic resources (Berumen & Pratchett 2006), whether these patterns and trends transcend into the Indian Ocean is not clear. Indeed geographical variation in feeding preferences of corallivores has been reported for specialist feeders (Irons 1989) and faculatative coral feeders (Pratchett 2005; Harmelin-Vivien & Bouchon-Navaro 1983), indicating a need to broaden the geographical extent of such studies.

Here I assess, in the central Indian Ocean, the degree of specialisation in three species of coral feeding butterflyfishes representing specialist, generalist and facultative corallivores. I assess how this specialisation changes between habitats with differing dominance and diversity of corals available. To assess whether feeding selection is related to nutritional value, I assess the food quality of the four dominant corals selected by the fish. Finally, to assess the impact of coral loss on species with differing dependency on coral resources, patterns of temporal change in abundance of corallivores were examined through a major coral mortality event in the Seychelles.

2.3 Methods

2.3.1 Study sites

The study was conducted at two locations: diet analysis and associated work was conducted at Diego Garcia atoll in the Chagos Archipelago, central Indian Ocean, while temporal change in corallivore density was assessed in the granitic islands of the Seychelles. Although it would have been preferable to conduct the feeding study and change in abundance through disturbance at the same location, the two locations have very similar coral communities. Indeed, in an assessment of coral species diversity across the entire Indian Ocean, Sheppard (1998) showed that Chagos, the granitic Seychelles and the Maldives clustered together into a distinct group in terms of species similarity and that the Seychelles and Chagos were particularly similar.

In Diego Garcia, two sites were selected for substrate assessment, corallivore density counts, feeding selectivity and coral food quality assessments. One reef (Diego East; 7°14.359'S, 72°26.411'E) was in a sheltered bay in the north east corner of the atoll and, although hosting a fairly diverse coral assemblage, was dominated by *Pocillopora*. The second reef (Diego Central; 7°14.534'S, 72°24.636'E) was a large platform patch reef in the north central section of the atoll, which was less diverse and dominated by *Acropora*. Both reefs were between 1-3m depth and all observations were conducted on snorkel. Change in density of corallivores was assessed through a major bleaching event in the Seychelles. Data were collected in 1994 and 2005, spanning the 1998 bleaching event. For full details of study sites see Jennings et al. (1995) and Graham et al. (2006).

2.3.2 Substratum Availability

To determine whether feeding preferences were influenced by the availability of potential food resources, substratum availability was quantified. At both Diego East and Diego Central the benthos along five randomly placed 10m transect lines was quantified using the line intercept method, whereby the distance of tape occupied by each substratum category was quantified. These data were converted into percent covers of each category and means plotted with standard errors per site. Differences in cover by genera were assessed using one-way ANOVA. *Acropora* cover had to be Log_{10} transformed to meet the assumptions of the test.

2.3.3 Feeding observations

Feeding observations were conducted for three species of chaetodontid butterflyfish, one obligate specialist coral feeder, *Chaetodon trifascialis*, which is expected to consistently favour certain prey items, whether these items are common or rare, one obligate generalist coral feeder, *C. trifasciatus*, which is expected to feed on a wider variety of prey items, in closer proportions to those available in the environment and one facultative coral feeder, *C. auriga*, which is expected to feed on coral, but also injest other non-coral prey (Hourigan et al. 1988). The range and proportional consumption of various prey items targeted by each individual was recorded during 3 minute observation periods (following Pratchett 2005). The majority of individuals continued to feed during observation, however observations were discontinued if the fishes were disturbed by the observer. No intra-specific aggressive interactions were noted during feeding observations. Coral prey were identified to the genus level (16 genera were fed upon during the study), and other prey items included soft coral, sponge, epilithic algae, coralline algae and consolidated reef pavement. Reefs were surveyed in a zig zag pattern from one end to the other to try to ensure the same individual was not observed twice. All observations at both sites were made between 10am and 2pm, with no bias for time between sites. Between 20 and 30 individuals were surveyed per species per site (Table 2.1).

Table 2.1. Bite rate and dietary composition of three species of butterflyfishes on two reefs with differing benthic composition in the Chagos Archipelago.

	n	Mean No. of bites per 3 min observation	% hard coral consumed	No. of coral genera consumed
Acropora dominated				
C. trifascialis	26	13.0	100%	1
C. trifasciatus	26	16.7	97%	4
Pocillopora dominated				
C. trifascialis	30	17.8	100%	4
C. trifasciatus	27	14.4	97%	14
C. auriga	20	6.5	55%	5

As data were collected on selection of resource units by individual animals, but resource availability was assessed at the population level, resource selection functions ($\hat{W}_i$) were calculated following Manly et al. (1993) using the formula:

$$\hat{W}_i = u_{i+}/(\pi_i u_{++})$$

where u_{i+} is the number of bites taken on food type i by all individuals, π_i is the proportion of that food type in the population and u_{++} is the total number of bites taken on all substrate types by all individuals (Manly et al. 1993). Bonferroni corrected 95% confidence intervals were calculated such that any function where the mean and confidence intervals were higher than 1 indicated selection, and if lower than 1 indicated avoidance. Data are presented as percent availability of resource verses percent number of bites for each area, with selection or avoidance indicated with a + or – symbol. Data are only presented for the four most common coral genera consumed (*Acropora*, *Lobophyllia*, *Pocillopora* and *Porites*) which represented 93% of corals consumed in Diego Central and 56% in Diego East. The non-coral substratum categories were combined and selectivity of this category also presented.

2.3.4 Chaetodon density surveys

The density of each of the three target butterflyfish and any other species of butterflyfish at the same locations as the benthic and feeding observations at both Diego East and Diego Central was quantified. The density of each species was recorded along 5 randomly placed 50*4m belt transects in each of the two study sites (following Berumen et al. 2005). Overall differences in the assemblages between the two study sites was assessed by MANOVA and differences at the species level using one-way ANOVA.

2.3.5 Coral food quality

Eight samples of each of the four most commonly eaten coral genera (*Acropora*, *Lobophyllia*, *Pocillopora* and *Porites*) were taken at random from the field sites and dried on land. Every effort was made to ensure the most common species of each genera was consistently sampled. Once dried, the samples were ground with pestle and mortar and placed in plastic vials for transport. On return to the lab the corals were placed in an oven at 50°C to ensure they remained dry. Each sample was then further ground into a powder, before being decalcified using 5% HCL to remove the skeleton. This solution was then freeze dried and the resultant solid residue was ground into a powder and placed in glass vials. Carbon, hydrogen and nitrogen values were obtained by testing each sample on a Carlo Erba 1108 Elemental Analyser controlled with CE Eager 200 software, and weighed using a Mettler MT 5 Microbalance (e.g. Wilson 2000). Two runs were performed on each sample and an average taken. C:N ratios were then calculated for each sample run. C:N ratio's are a measure of food quality, a low value infers higher nitrogen to carbon, which indicates there is more protein present for growth (Purcell and Bellwood 2001; Wilson et al. 2003).

A one-way ANOVA was used to test for differences in C:N ratios among the four coral genera. The ANOVA was performed both with and without a clear outlier for the *Acropora* results, this data point displaying nearly double that of the median for the group. Normality of data was examined with histograms and normal probability plots of the residuals and homogeniety of variances were tested with Levene's test.

2.3.6 Temporal change in coral feeding fish densities

In both 1994 and 2005 the density of 134 species of diurnally active, non-cryptic reef fish were surveyed at 21 sites, spanning three different habitat types (carbonate fringing reefs, granitic rocky reefs with coral growth, and patch reef habitats on a sand, rubble or rock base), in the Seychelles, with sixteen 7m radius point counts at each site conducted at the bottom of the reef slope (for full details see Jennings et al. 1995; Graham et al. 2006). In the present study, only the density data of corallivores are considered, which includes 13 species from the families Chaetodontidae, Monocanthidae and Labridae. Benthic data was also collected at each of the study sites, quantifying percent cover of different growth forms of live coral and other non-coral benthic categories (Jennings et al. 1995; Graham et al. 2006).

Density of the three species of chaetodontid for which feeding observations were made were analysed individually and all species were also assigned to three main feeding strategies based on the literature (McIlwain & Jones 1997; Allen et al. 1998; Kokita & Nakazono 2001; Pratchett 2005; www.fishbase.org). Three species were classified as obligate specialist coral feeders (*Chaetodon trifascialis*, *Labrichthys unilineatus* and *Oxymonocanthus longirostris*), four species as obligate generalist coral feeders (*Chaetodon melannotus*, *C. meyeri*, *C. trifasciatus* and *C. zanzibarensis*) and six species as facultative coral feeders (*Chaetodon auriga*, *C. guttatissimus*, *C. kleinii*, *C. lineolatus, C. lunula* and *C. xanthocephalus*). From the current literature, the similar findings of this study as compared to those in the Pacific and the clear patterns observed in the data, these groupings appear to be robust.

Change in density of the individual species and aggregated feeding groups was assessed with a two-factor crossed ANOVA design with factors year and habitat type, however as habitat alone was not significant for any comparison, the data are presented for year only. Normality of data was examined with histograms and normal probability plots of the residuals and homogeniety of variances were tested with Levene's test. Aggregated level obligate generalists and specialist groups required $\log_{10}$ transformation to meet the assumptions of the test.

2.4 Results

2.4.1 Substratum Availability

The two sites had similar live coral cover (55% Diego East and 52% Diego Central), but the dominance and diversity of coral genera varied greatly (Figure 2.1). Diego East was dominated by *Pocillopora*, with a mean cover of 34% compared to 2.2% for Diego Central ($F_{1,9} = 21.23$, $P < 0.01$). Conversely Diego Central was dominated predominately by *Acropora* colonies, with a mean cover of 49% compared to 4.4% in Diego East ($F_{1,9} = 69.43$, $P < 0.001$). Cover of other live coral genera and non-coral substrate did not vary significantly, however the richness of coral genera was greater for Diego East (Figure 2.1).

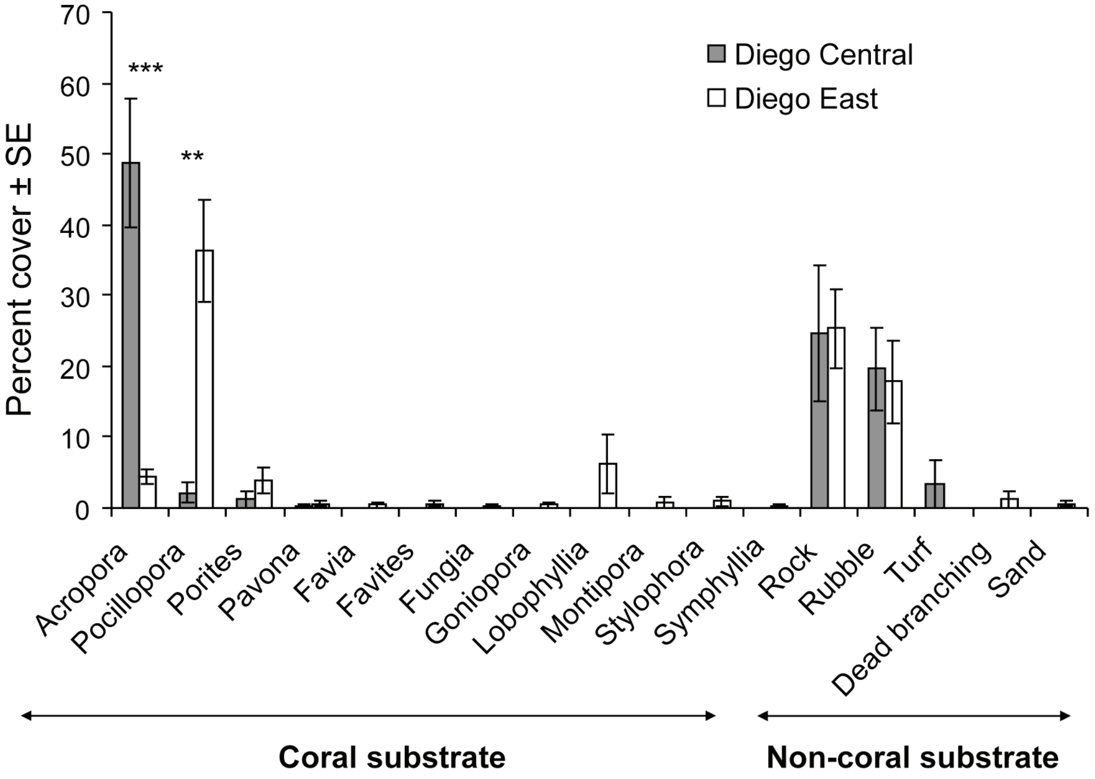

Figure 2.1. Benthic resource availability at Diego East and Diego Central, Chagos Archipelago. *** P<0.001, ** P<0.01.

2.4.2 Feeding observations

The greatest bite rates in Diego Central were recorded for *C. trifasciatus*, whereas in Diego East, *C. trifascialis* had the highest rates and *C. auriga* had considerably lower bite rates than the other two species (Table 2.1). *C. trifascialis* took 100% of bites from live coral at both sites, while *C. trifasciatus* took 97% and *C. auriga* took 55% (Table 2.1). In the lower diversity site, Diego Central, *C. trifascialis* took all its bites from *Acropora* colonies, principally *Acropora tenuis*, the dominant species at the site, but also *Acropora clathrata*. *C. trifasciatus* took bites from four different genera at Diego Central. At Diego East *C. trifascialis* consumed four genera of coral, while *C. trifasciatus* consumed 14 genera and *C. auriga* consumed 5 genera, a considerable proportion of its bites from non-coral substrata (Table 2.1).

Selectivity analysis shows that *C. trifascialis* is preferentially selecting *Acropora* and avoiding other available genera in Diego Central (Figure 2.2). *C. trifasciatus* displays a similar trend, however there is also evidence for selectivity on *Porites* spp. (Figure 2.2). In Diego East *C. trifascialis* is preferentially selecting *Acropora*, but also taking a large proportion of bites on *Pocillopora* colonies. While *C. trifasciatus* appears to have a much more general diet, it is only selecting preferentially for *Acropora*. *C. auriga* appears to have a very general diet, and does not select for any resource in greater proportion to its availability (Figure 2.2).

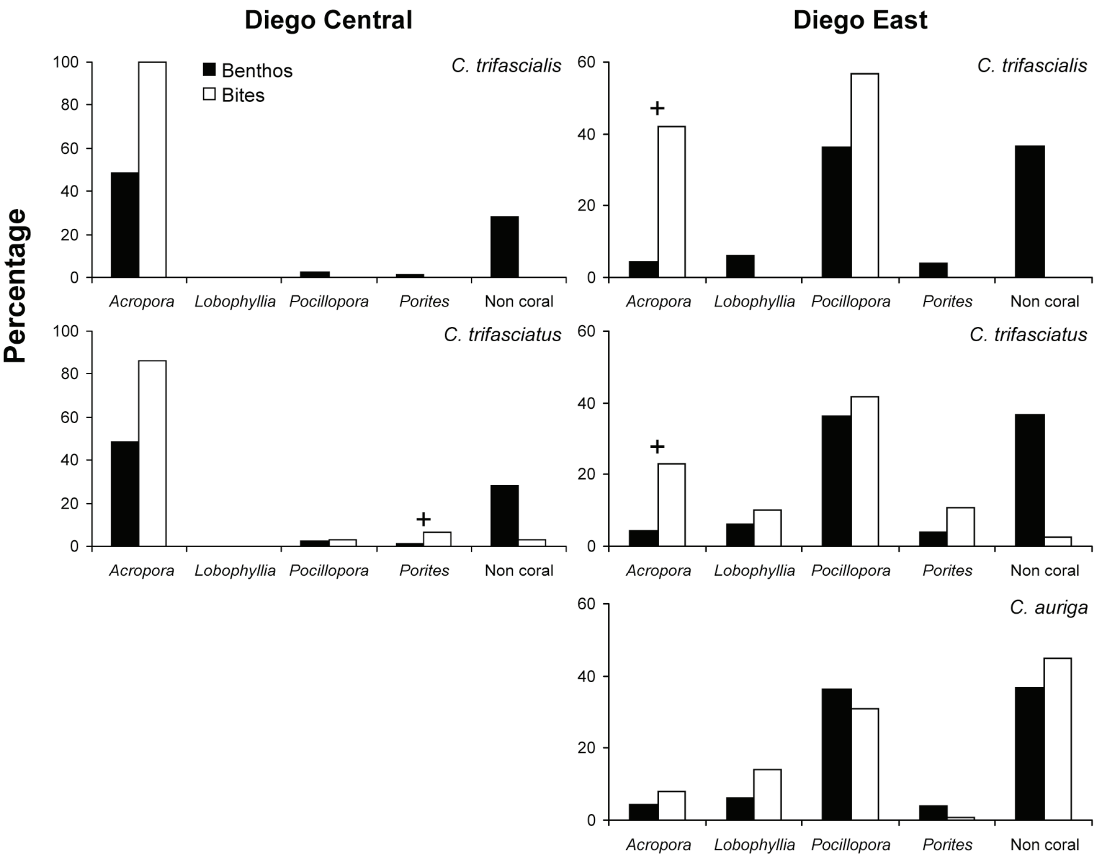

Figure 2.2. Feeding selectivity of *C. trifascialis*, *C. trifasciatus* and *C. auriga* at Diego Central and Diego East, Chagos Archipelago. Data only presented for the four coral genera most preferentially consumed. Black bars indicate percent resource availability, open bars indicate percent feeding bites on that resource. + symbol indicates positive selectivity.

2.4.3 Corallivore density surveys

The overall assemblage structure of corallivores between the two sites varied significantly in terms of density (MANOVA, Wilks = 0.017, $F_{3,6} = 28.45$, $P < 0.01$) (Figure 2.3). *C. trifascialis* had a greater density in Diego Central ($F_{1,9} = 28.77$, $P < 0.001$) while *C. trifasciatus* and *C. auriga* had higher densities in Diego East ($F_{1,9} = 22.43$, $P < 0.001$ and $F_{1,9} = 6.94$, $P < 0.05$ respectively). Although not significant, the remaining species all displayed higher densities in the more diverse Diego East site (Figure 2.3).

2.4.4 Coral food quality

The lowest C:N ratios, and therefore highest food quality, were for *Acropora* and *Lobophyllia* coral genera, while P*ocillopora* had the highest C:N ratio (Figure 2.4). ANOVA results indicate this difference is significant ($F_{3,30} = 4.25$, $P < 0.05$), with the only pairwise difference between *Lobophyllia* and *Pocillopora* ($P < 0.01$). However if the analysis is re-run with the clear outlier for *Acropora* (Figure 2.4) removed, the trend is considerably stronger ($F_{3,29} = 7.86$, $P < 0.001$), and *Acropora* is also different from *Pocillopora* in pairwise tests ($P < 0.01$).

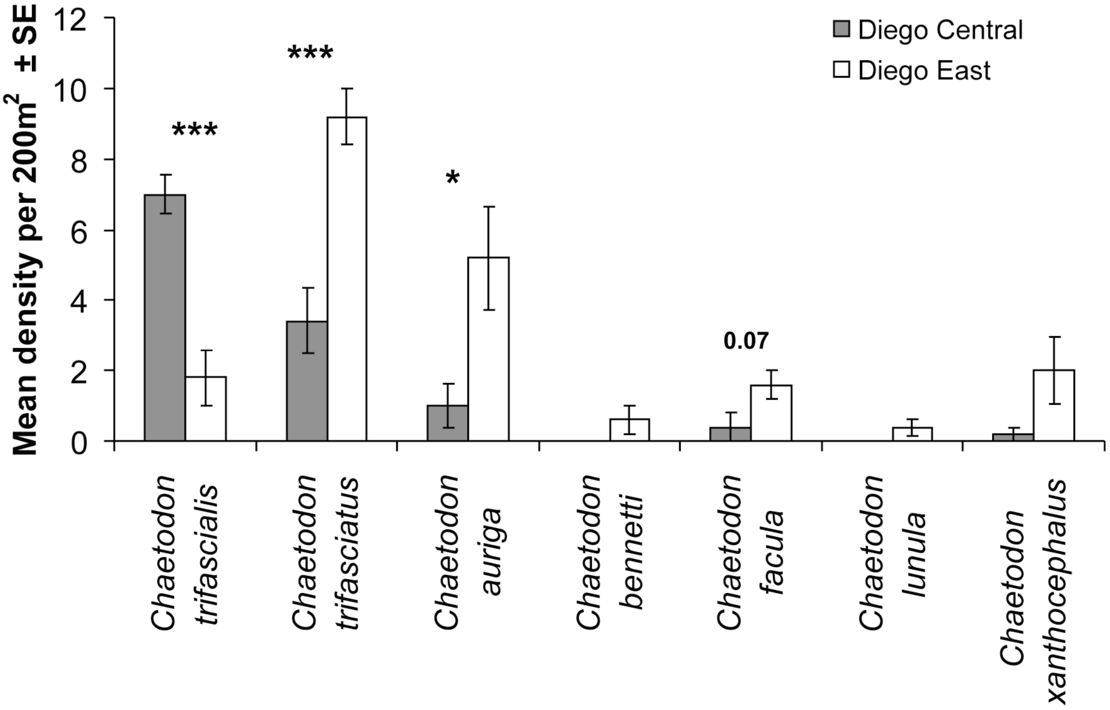

Figure 2.3. Mean density of corallivores present in Diego Central and Diego East. *** P<0.001, ** P<0.01, * P<0.05.

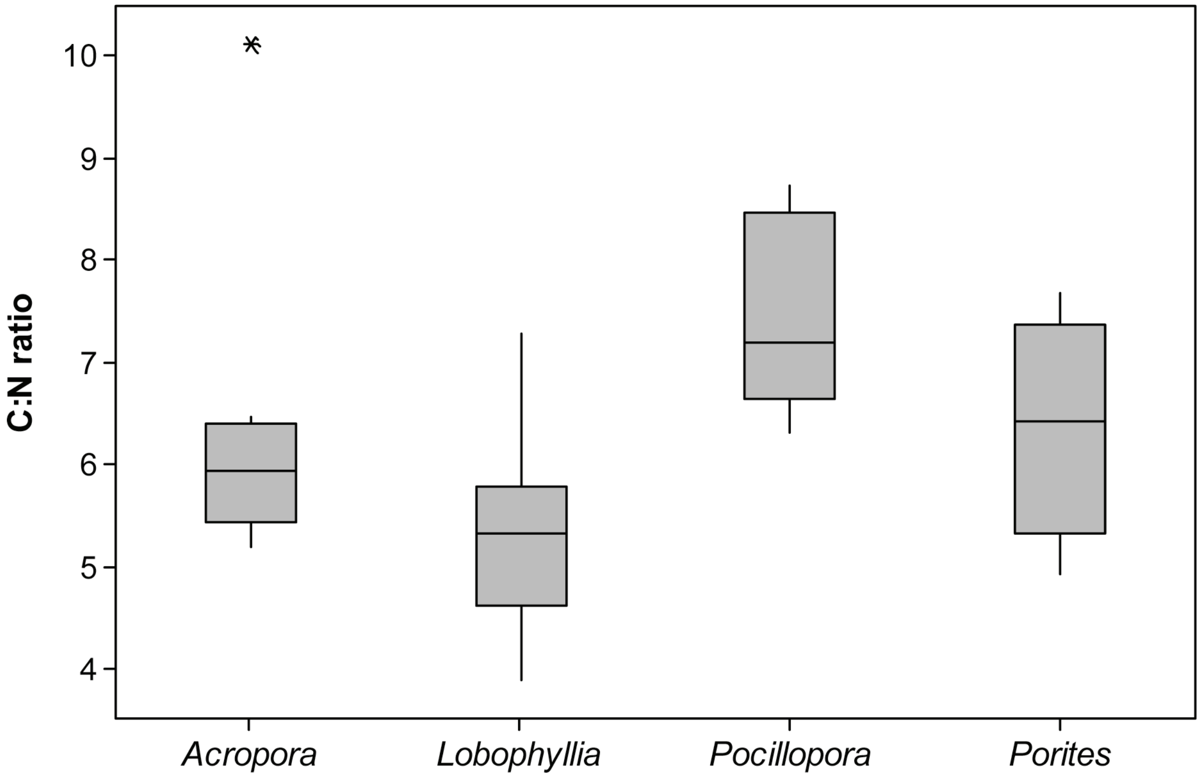

Figure 2.4. Box and whisker plots of C:N ratios for four coral genera. Box indicates median value, lower and upper quartiles. Whiskers indicate range up to 1.5 times the box. Outliers indicated with an asterix.

2.4.5 Temporal change in coral feeding fish densities

Between 1994 and 2005 total live coral cover declined by an average of 73% at the sites studied in the Seychelles, with complex branching and plating corals declining by 95% to a new base level of 1% cover across the study area (Graham et al. 2006, 2007). Change in densities of the three focal Chaetodontids through this major bleaching event indicates the most specialist species (*C. trifascialis*) declined the most ($F_{1,41} = 11.16$, $P < 0.01$), followed by the generalist obligate coral feeder (*C. trifasciatus*) ($F_{1,41} = 9.47$, $P < 0.01$), while the facultative corallivore (*C. auriga*) did not show any decline (Figure 2.5). Habitat was not a significant factor for any of the species, however *C. trifasciatus* displayed a significant year*habitat interaction term, which was due to a greater decline in carbonate and patch reef habitats than granitic reef habitats ($F_{2,41} = 3.36$, $P < 0.05$). If all the corallivores in the assemblage are assigned to the above three feeding categories, the obligate specialist feeders show a 98% decline ($F_{1,41} = 120.11$, $P < 0.001$), the obligate generalist coral feeders display a 73% decline ($F_{1,41} = 24.51$, $P < 0.001$) and the facultative coral feeders show a 32% decline ($F_{1,41} = 4.20$, $P = 0.048$)(Figure 2.5).

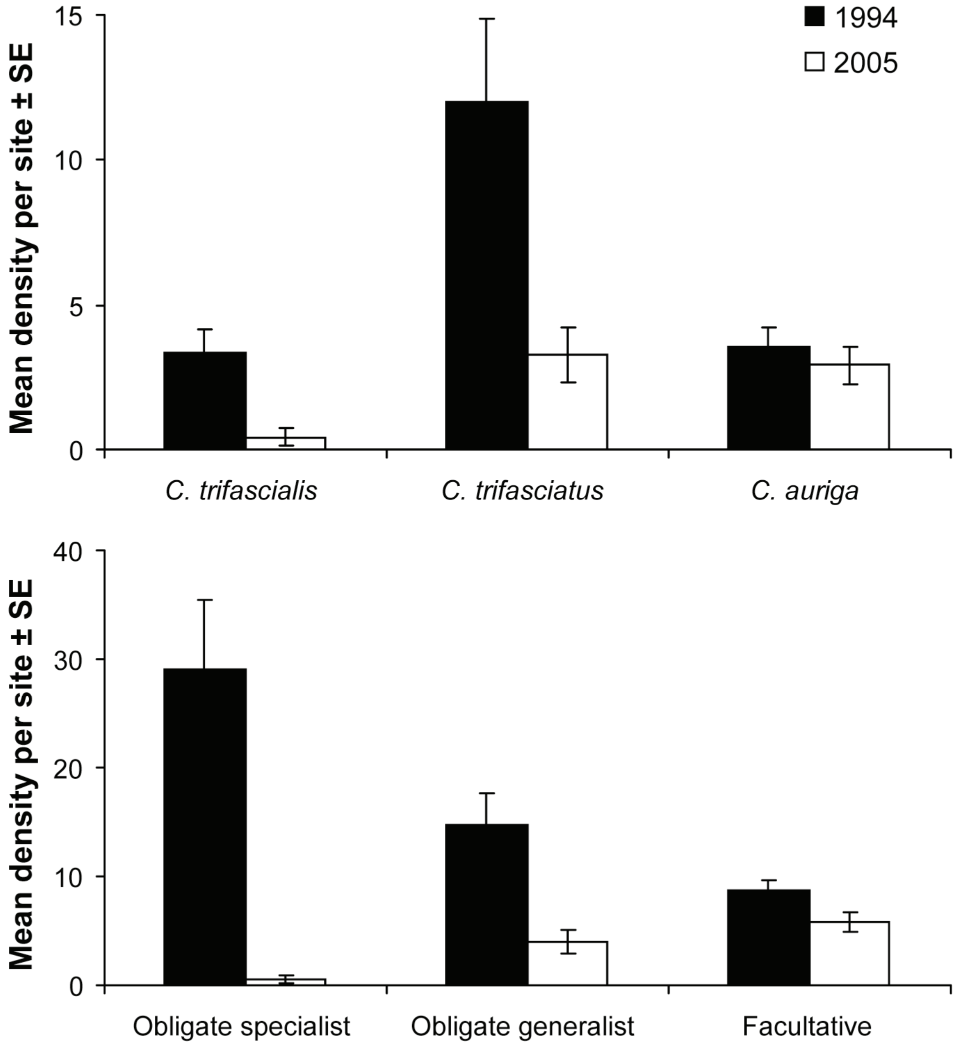

Figure 2.5. Change in density of *C. trifascialis*, *C. trifasciatus* and *C. auriga* and obligate specialists, obligate generalists and facultative feeders in Seychelles before and after the 1998 bleaching event.

2.5 Discussion

Here I have shown that although there may be greater feeding plasticity than previously documented in some species of corallivore, there are obvious differences between obligate specialist, obligate generalist and facultative feeders, which may in part be due to the quality of food. Similar to a previous study (Pratchett et al. 2006), the degree of specialisation is reflected in the extent of decline in density following mass coral bleaching. The obligate specialist feeders were severely impacted in this study, with a potential local extinction of *Labrichthys unilineatus* (Graham et al. 2006).

The number of bites taken per 3 minute observation varied among species and between the two study reef sites. Although bite rates of *C. trifasciatus* did not change markedly between reefs, *C. trifascialis* took a greater number of bites at Diego East (the *Pocillopora* dominated reef) than Diego Central (the *Acropora* dominated reef). Although the sample sizes were not large, this could reflect abundance of preferred resources, with greater feeding rates required when preferred corals are not in abundance (Bowen et al. 1995). *C. trifascialis* are known to defend their territories aggressively (Reese 1975, 1981), so it is interesting that feeding rates were higher at the site where a greater number of other species were present and thus potentially a greater number of aggressive interactions may be expected. The lack of a difference in bite rates in *C. trifasciatus* was also noted before and after coral decline at Trunk Reef, Australia for *C. lunulatus* (closely related Pacific species) (Pratchett et al. 2004, but see Irons 1989). The lowest numbers of bites per observation were recorded for *C. auriga*, which again could reflect nutritional value of food items, this species often targeting polychaete worms and other invertebrates (Bouchon-Navaro 1986).

Both *C. trifascialis* and *C. trifasciatus* preyed on a greater number of coral genera in the more diverse *Pocillopora* dominated habitat, although *C. trifasciatus* was clearly the more generalist feeder and both species preferentially selected for *Acropora* corals. *C. trifascialis* is a highly specialised coral feeder, almost always selecting *Acropora*, often *Acropora hyacinthis* (Pratchett 2005, 2007), although the preferred species can vary geographically (Reese 1981). However, some plasticity in feeding has been observed when *Acropora* cover is very low (Irons 1989; Samways 2005), as is apparent in the current study. Feeding plasticity has also previously been documented between reefs of varying coral availability for *C. baronessa* and *C. lunulatus* at Lizard Island, Great Barrier Reef (Berumen et al. 2005). When preferred corals were not in abundance, the physiological condition of the fish, as measured by hepatocyte vacuolation in the liver, declined (Berumen et al. 2005). A decline in physiological condition was also noted for *C. lunulatus* following declines in cover of *Acropora* corals, which resulted in declines in abundance, but a shift in diet away from *Acropora* (Pratchett et al. 2004). It is possible that *C. trifascialis* may have lower fitness and fecundity in Diego East due to sub-optimal diet, however analyses such as those described above would be required to ascertain this. Interestingly, *C. trifasciatus* selected for *Porites* corals in Diego Central and took a greater proportion than available in Diego East, albeit taking very few bites from them overall. *C. trifasciatus* (now *C. lunulatus*) has been shown to feed primarily on poritid corals in Hawaii at sites where poritid and montiporid corals dominate (Cox 1994), suggesting that selectivity for *Porites* may be common in this species.

In this study *C. auriga* individuals took ~55% of bites from live coral. There appears to be a great deal of biogeographic variation in the feeding patterns of this species, with studies in Australia finding live coral made up just 4% of its diet (Pratchett 2005), ~61% in French Polynesia (Harmelin-Vivien & Bouchon-Navaro 1983) and ~29% in the Red Sea (Harmelin-Vivien & Bouchon-Navaro 1981; Bouchon-Navaro 1986). The species is clearly a facultative coral feeder, but whether the variation in coral dependence is a spatial or temporal artefact is yet to be elucidated.

As can be seen with *Acropora* in the Diego Central site, selection functions do not always perform well when data are aggregated. In this study data were collected on selection of resource units by individual animals, but resource availability was assessed at the population level. Although the selection function chosen largely accounts for this (Manly et al. 1993), there is still a problem with resources in low availability, particularly when they are clumped in distribution, and/or the animals are territorial. In such situations assessment of resource availability within the specific boundaries of an individual territory may produce clearer results (however there are inherent problems in assessing butterflyfish territory size, as described by Reese (1981)). For example the low cover of *Lobophyllia* in Diego East was clumped, but when it did occur in a fishes territory, they took the majority of their bites from it. This coral has the fleshiest polyp and so potentially offers the greatest nutritional return per bite effort. Although *Lobophyllia* was recorded in the random benthic line intercept transects, because it only occurred in the territory of several fish, the selection function did not indicate positive selection.

There was an overall difference in species abundance between the two sites, with *C. trifascialis* having a significantly greater density in the *Acropora* dominated Diego Central, and all other species present being in greater density in the more diverse

Diego East. *C. trifascialis* is known to be very territorial and actively defend its territory from intruders (Reese 1975), suggesting that this species may dominate in such mono-specific *Acropora* rich areas (Pratchett 2005) inhibiting the presence of other species. Even competitively similar species can display inverse relationships in terms of abundance (Reese 1981). It has been suggested that competitively subordinate species may have a broader diet to avoid competition with more specialised aggressive species (Pratchett 2005). *C. trifascialis* lives as a solitary individual and defends a specific territory, whereas other species, such as *C. trifasciatus* and sometimes *C. auriga* occur in heterosexual pairs (Reese 1975, 1981). There is also variation in territory size, with *C. trifascialis* and *C. trifasciatus* utilising fairly small territories, whereas *C. auriga* forages over a wider area (Reese 1975). It appears *C. trifascialis* dominates over other species where *Acropora* is in abundance, as has been described in previous studies (Reese 1981; Pratchett 2005), and thus other species are in greater number on more diverse reefs, not dominated by *Acropora*, where coexistence is more likely achieved through partition of food resources (Zekeria et al. 2002).

One possible explanation for differences in feeding specialisation could be variation in food quality. C:N analysis indicated that *Lobophyllia* and *Acropora* tissue has a lower C:N ratio, thus greater food quality, than *Pocillopora* corals. If this is the case it could help explain why many corallivores preferentially feed on *Acropora* corals (Pratchett 2005), i.e. selecting for protein rich resources (Bowen et al. 1995). It could also help explain why species in habitats with low availability of preferred corals have been shown to have reduced physiological condition (Pratchett et al. 2004; Berumen et al. 2005). However the latter studies assessed lipid stores in the liver which equate to short-term energy needs more than the C:N ratios examined here, which give an indication of protein availability and energy for growth (Bowen et al. 1995). Whether the same corals found to have low C:N ratios in the present study also have high lipid content remains to be tested.

Methodological variation in C:N ratios should be minimised when techniques are standardised within a study, so one would hope the results presented here are comparable. As only one species per genera was assessed in the current study, it is not clear how much variation there is within genera of corals compared to among them. This is clearly an area for future research. However, given that in the current study area, certain species of coral dominated within a genera, and it was these that were both preyed upon by the fish and assessed for C:N ratios, the results are robust for the purpose of feeding selectivity.

It is clear from previous studies that coral tissue is a valuable food source (e.g. Bythell 1988; Rotjan & Lewis 2005), with algal and related food sources likely being of less nutritional value (Wilson 2000; Rotjan & Lewis 2005, but see Wilson et al. 2003 for variation) and invertebrates, such as polychaete worms having higher nutritional value (Rotjan & Lewis 2005). The higher nutritional value of invertebrates such as polychaetes may help explain why the feeding rates of *C. auriga* are less than obligate coral feeders. There will obviously be other reasons why species preferentially choose certain coral prey, which may involve resource partitioning (Zekeria et al. 2002; but see Pratchett 2005), functional jaw morphology (Motta 1988), morphology of corals (Tricas 1989b) and presence of nematocysts (Gochfield 2004). It is likely that all these factors contribute to the final selectivity of fish.

Declines in density of corallivores between 1994 and 2005 in the Seychelles further highlight the importance of specialisation when assessing the vulnerability of fish to disturbance (Munday 2004; Pratchett et al. 2006; Wilson et al. 2006). In this study *C. trifascialis* and the aggregated obligate specialist feeders showed the greatest declines, followed by *C. trifasciatus* and the obligate generalists and *C. auriga* and the aggregated facultative feeders showed little change. This directly corresponds to predictions based on feeding selectivity, and the fact that *Acropora*, the preferred food of many specialists, is among the most vulnerable taxa of corals to coral bleaching and other disturbances such as crown-of-thorns starfish outbreaks and storms (McClanahan et al. 2004, 2007a; Wilson et al. 2006). Pratchett et al. (2006) also found obligate coral feeding butterflyfish declined on the Great Barrier Reef following extensive coral mortality, but facultative and non-coral feeders did not. This study furthers this knowledge by highlighting the distinction between obligate specialist and obligate generalist feeders, and also includes species from the monocanthid and labrid families. Declines in density of coral feeders in the Seychelles were greater in Marine Protected Areas than fished areas (Chapter 5 & Graham et al. 2007), suggesting this management option offered no insurance against the disturbance. Clearly when disturbances are so severe and spatially extensive, specialist species have little refuge.

There is a growing literature highlighting the vulnerability of specialist fish to disturbance (reviewed by Wilson et al. 2006), suggesting that measures of feeding (Pratchett 2005) or habitat (Munday et al. 1997) specialisation will be important criterion to predict which species are vulnerable to extinction on reefs (see Munday 2004). Indeed, in the Seychelles, where the 1998 coral bleaching event devastated reefs, there is evidence of the local extinction of four specialist species (Graham et al. 2006). Local extinction of coral specialists has also been documented from Papua New Guinea following extensive coral mortality (Jones et al. 2004; Munday 2004). If we are to manage and conserve biodiversity in a changing climate, a greater understanding of the species most vulnerable to disturbance, their habitat needs and the functional roles they offer to the rest of the ecosystem will be imperative.

2.6 Acknowledgements

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Chapter 3

Coral mortality versus structural collapse as drivers of corallivorous butterflyfish decline[2]

3.1 Abstract

Climate change is a key threat to biodiversity and ecosystem function. Understanding the spatial and temporal scales at which drivers of species decline operate and the attributes of species most vulnerable to decline is a key challenge to ecologists and conservationists. Coral reefs have emerged as one of the ecosystems most threatened by climate impacts, where both reef corals and associated fish assemblages can be severely altered. Here we assess the effects of coral loss versus structural complexity collapse on obligate and facultative coral feeding butterflyfishes. The abundance of the obligate coral feeding group declined markedly in response to live coral mortality ($r^2 = 0.48$), which represents rapid declines, but showed no further loss once the physical matrix of the reef eroded. Conversely, the facultative feeding group showed no decline in response to live coral loss, reflecting their feeding versatility; however they did decline once the structure of the reef began to erode ($r^2 = 0.26$). While coral dependant fishes are highly vulnerable to coral loss caused by climate-induced coral bleaching, the structural collapse of dead coral colonies may have significant, but

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more variable, impacts across a wide range of fishes. If conservation and mitigation planning are to be effective, there is a clear need to better understand the mechanisms of reef structural collapse and the dynamics of system recovery following large-scale disturbance.

3.2 Introduction

Climate change has emerged as one of the greatest threats to the world's ecosystems (Walther et al. 2002) and the impacts this is having on biodiversity is of key concern (Thomas et al. 2004; Balmford et al. 2005). To enable suitable management and mitigation plans to be developed for species preservation, it is necessary to identify the key drivers of species decline, the temporal and spatial scales over which they operate and the attributes of individual species that render them more or less susceptible to environmental disturbance (Sala et al. 2000; Dulvy et al. 2003).

One of the ecosystems most vulnerable to climate change effects are coral reefs (Hughes et al. 2003; Hoegh-Guldberg et al. 2007), which are suffering widespread loss of live coral due to coral bleaching; a decoupling of the symbiotic relationship between the energy providing dinoflagellates and the host corals (Brown 1997). Associated with this loss in coral cover is a considerable reorganisation of the coral genera present (McClanahan et al. 2007a) and ultimately, through biological and physical processes, a reduction in the structural complexity of the reef matrix (Sheppard et al. 2002; Graham et al. 2006). Understanding the impacts of such large-scale disturbance to coral reef benthos on associated organisms is in its infancy (Pratchett et al. 2008b). It is clear that species richness and abundance of certain groups of fishes may decline following coral loss (Sano et al. 1987; Jones et al. 2004;

Garpe et al. 2006; Graham et al. 2006; Wilson et al. 2006), that specialist species are most vulnerable (Munday 2004; Pratchett et al. 2006; Wilson et al. 2008a) and that loss of recruitment habitat (Feary et al. 2007a) or structural complexity (Graham et al. 2006, Chapter 5 & Graham et al. 2007a) may lead to long-term declines. However, an unequivocal understanding of these drivers, which species they effect and the spatial and temporal scales over which they operate is clearly necessary.

Corallivorous butterflyfish are an ideal group of fish to test these ideas as they display varying degrees of specialisation or versatility in dependence on live coral for food (Irons 1989; Cox 1994; Berumen et al. 2005; Pratchett 2005; Chapter 2 & Graham 2007; Berumen & Pratchett 2008). The extent of feeding specialisation by butterflyfish has been shown to relate to vulnerability to disturbance, with more specialised obligate coral feeders declining substantially more following coral loss than versatile facultative coral feeders (Pratchett et al. 2006; Chapter 2 & Graham 2007). Butterflyfish are also small bodied, with maximum total lengths typically <20 cm, which has been highlighted as a key attribute of fish, making them vulnerable to collapse of the reef structural matrix (Graham et al. 2006; Chapter 5 & Graham et al. 2007a; Pratchett et al. 2008a). Such collapse generally occurs some time (5-10 years) after the initial live coral loss and so the associated impact on the fish assemblage is likely to be delayed compared to the impacts of live coral loss.

Here we assess the impacts of loss of live coral cover versus loss of the structural complexity of reefs on obligate and facultative coral feeding butterflyfish. This study was conducted in the inner Seychelles, which was devastated during the 1998 bleaching event, with a loss of >90% live coral cover (Sheppard 2003). By 2005 reefs in the inner Seychelles were showing very little coral recovery and variable collapse of structural complexity (Graham et al. 2006).

3.3 Methods

The study was conducted in the inner islands of the Seychelles. Benthic and fish data were collected before (1994) and after (2005) the devastating 1998 bleaching event from 21 sites, comprising 3 different habitat types; carbonate fringing reefs, granitic rocky reefs with coral growth and patch reef habitats on a sand, rubble or rock base. At each site 16 randomly selected underwater point counts of 7m radius were surveyed along the bottom of the reef slope (5-13 m depth). S. Jennings collected all 1994 data (Jennings et al. 2005) and N. Graham and S. Wilson collected 2005 data (Graham et al. 2006). Benthic cover of functional forms of hard corals, soft corals, macroalgae, sand, rock and rubble was estimated visually and checked for accuracy against the line-intercept method (Wilson et al. 2007). Structural complexity of the benthos was quantified at each site using a 6 point visual scale which captures complexity comparable to a range of other techniques (Wilson et al. 2007). All adult butterflyfishes (>5cm TL) within each 7m radius station were counted and recorded to species. All butterflyfishes were then categorised into obligate coral feeding or facultative coral feeding groups based on the literature (Harmelin-Vivien 1989a; Pratchett 2005; Chapter 2 & Graham 2007) and Fishbase (Froese & Pauly 2007)(Table 3.1). Full details of survey techniques and a study map can be found in Jennings et al. (1995).

Table 3.1. Change in total butterflyfish species abundance within each habitat type (17,248m^2) and change in species richness of facultative and obligate groups.

		Carbonate		Granitic		Patch reef	
Species	Category	1994	2005	1994	2005	1994	2005
Chaetodon melannotus	Obligate	21	1	6	0	3	0
Chaetodon meyeri	Obligate	3	0	1	2	0	0
Chaetodon trifascialis	Obligate	31	0	15	9	24	0
Chaetodon trifasciatus	Obligate	139	8	43	34	70	27
Chaetodon zanzibariensis	Obligate	8	4	6	8	9	0
Change in species richness	Obligate	-2		-1		-3	
Chaetodon auriga	Facultative	19	26	24	29	32	6
Chaetodon guttatisimus	Facultative	2	0	8	12	10	4
Chaetodon kleinii	Facultative	3	4	9	4	15	9
Chaetodon lineolatus	Facultative	1	0	0	0	2	0
Chaetodon lunula	Facultative	9	4	6	7	10	6
Chaetodon xanthocephalus	Facultative	16	0	11	6	5	6
Change in species richness	Facultative	-3		0		-1	

To account for varying initial values (Côté et al. 2005), we calculated change in coral cover, structural complexity and abundance of butterflyfish between 1994 and 2005 using the following equation:

$$\%difference\Delta = [(A_a - A_b)/A_b] \times 100 \qquad (1)$$

Where A_b and A_a were mean values at sites in 1994 and 2005 respectively. Because percent differences can have a strong right-tailed distribution, i.e. a maximum potential decline of 100%, but potentially limitless increases, we transformed data following Kaiser et al. (2006):

$$Y = \log_e(1 + [\Delta/101]) \qquad (2)$$

The transformation approximately normalises the error distribution and stabilises its variance. The data are balanced around zero and a common maximum decline and increase of -4.6 and +4.6 is imposed (Kaiser et al. 2006).

The relationship between loss of live coral cover and loss of structural complexity was assessed using correlation analysis. The influence of the change in live coral cover versus change in structural complexity on fish groups was assessed using analysis of covariance, where habitat type was a categorical predictor and change in coral cover or structural complexity a covariate. Data were tested for normality and homogeneity of variances by inspecting residual plots and Levene's test respectively, and no transformations were necessary.

3.4 Results

Declines in coral cover in the inner Seychelles as a result of the 1998 bleaching event were immediate and substantial (Sheppard 2003), whereas declines in reef structural complexity took much longer to become manifest. The reef began to erode in 2003 (Engelhardt 2004) and by 2005 the 21 sites studied were in varying degrees of collapse (Graham et al. 2006). Changes in fish abundance observed during this study may be due to either the short-term effects of coral loss or longer-term effects of structural collapse. Importantly, there was no collinearity between the loss of live coral at each site and the reduction of structural complexity ($r = 0.177$, $P = 0.443$), ensuring that the two drivers could be assessed as independent variables.

Obligate coral feeders show substantial declines at the species level, although slightly less severe in the granitic habitat (Table 3.1). Conversely, facultative feeders showed more moderate declines and considerable stability in the granitic reef habitat (Table 3.1). Species richness followed similar trends, with generally greater and more consistent declines for obligate coral feeders (Table 3.1). The obligate corallivore group displayed strong patterns of decline associated with loss of live coral cover ($r^2 = 0.48$) whereas facultative corallivores showed no relationship (Table 3.2, Figure 3.1). Conversely change in structural complexity did not explain any patterns of decline for obligate corallivores, but did explain declines in facultative corallivores ($r^2 = 0.26$) (Table 3.2, Figure 3.2). Habitat was only a significant factor for obligate corallivores in the structural complexity change model and this was due to a greater decline in abundance in carbonate reef habitats than granitic rocky reef habitats (Table 3.2).

Table 3.2. Results of univariate analysis of covariance on densities of obligate and facultative corallivores for both the coral decline and structural complexity decline models. Values given are *F* ratios (probability results given in brackets. ** *P* < 0.01; * *P* < 0.05; ns = not significant.

	Coral cover model		**Structural complexity model**	
Fish group	Habitat effect (2,17 *df*)	Coral decline covariate (1,17 *df*)	Habitat effect (2,17 *df*)	Structural loss covariate (1,17 *df*)
Obligate corallivores	3.21 (ns)	10.80 (**)	4.88 (*)	0.77 (ns)
Facultative corallivores	1.30 (ns)	0.09 (ns)	1.45 (ns)	6.28 (*)

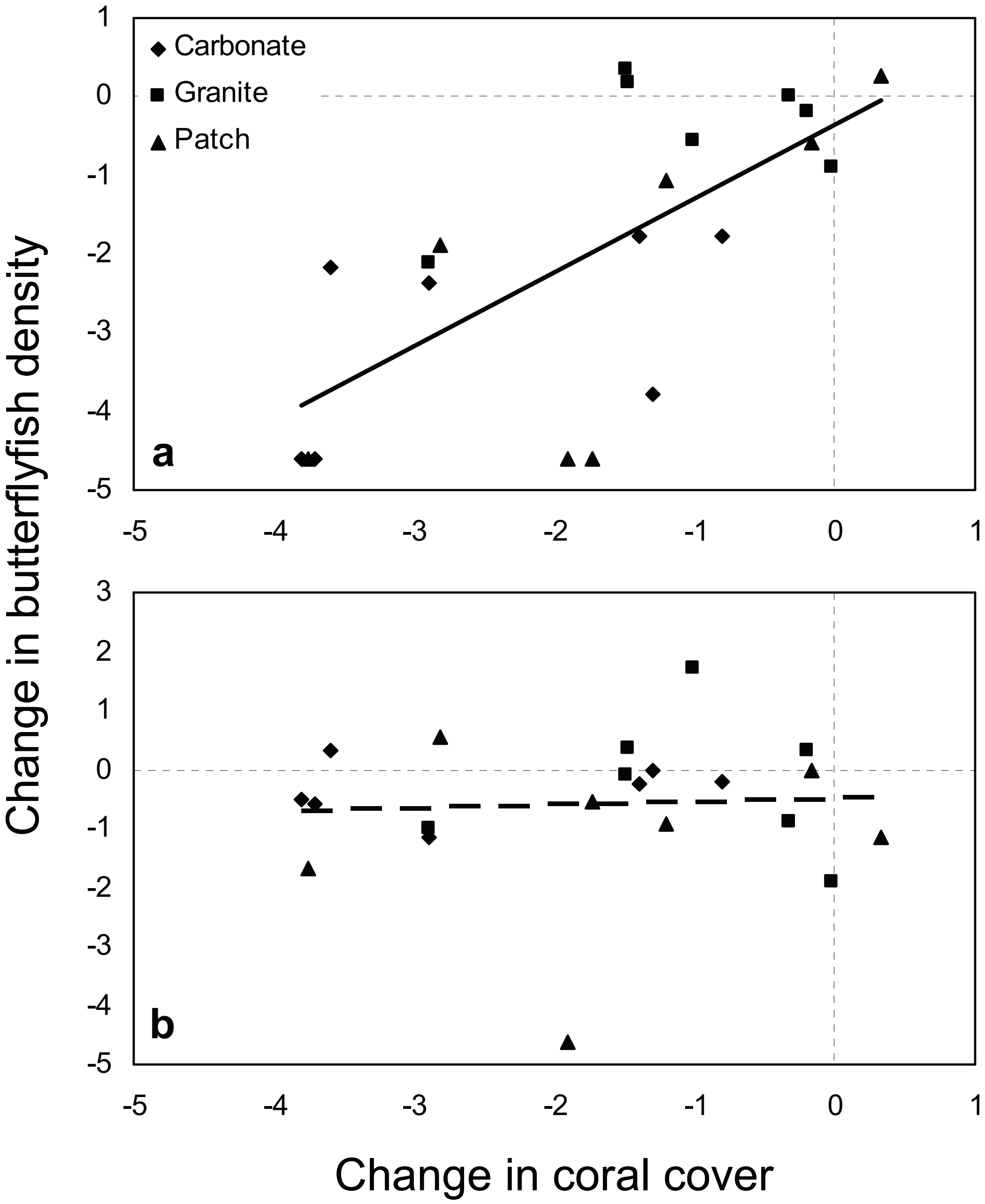

Figure 3.1. Change in abundance of **(a)** obligate corallivores and **(b)** facultative corallivores in response to loss of live coral loss. Solid line represents significant trend.

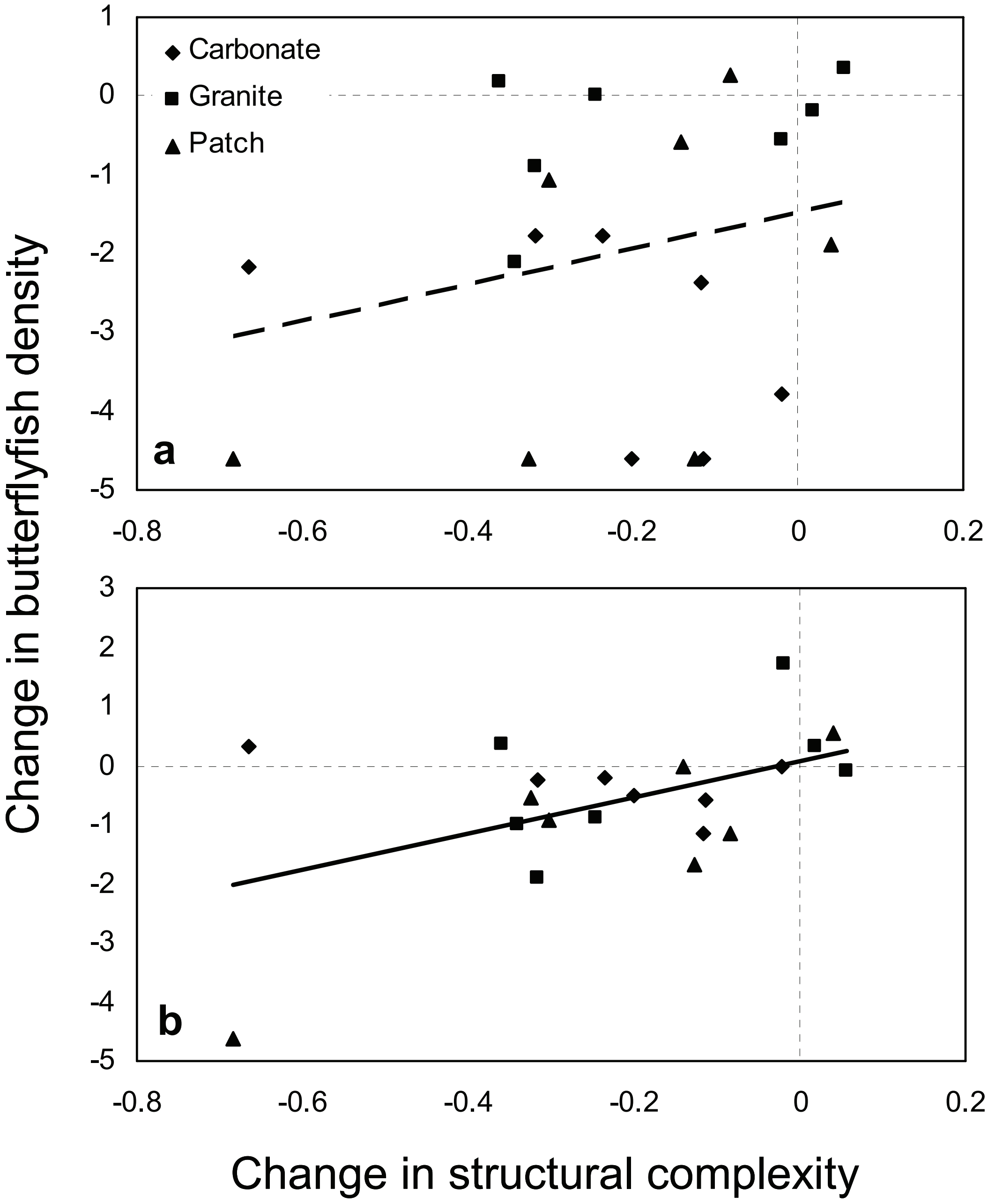

Figure 3.2. Change in abundance of **(a)** obligate corallivores and **(b)** facultative corallivores in response to reduced reef structural complexity. Solid line represents significant trend.

3.5 Discussion

We have shown that declines in obligate coral feeding butterflyfish are mainly associated with loss of live coral, whereas declines in facultative coral feeding butterflyfish are mainly associated with loss of structural complexity. This suggests that loss of obligate coral feeders are likely to be fairly rapid following extensive coral mortality, although some delays associated with feeding on sub-optimal prey may occur (Pratchett et al. 2004). In comparison, abundance change of obligate corallivores relative to loss of structure was more variable and non-significant. This is most likely because by the time reef structure starts to erode and collapse the majority of decline has already occurred.

The failure to detect any relationship between change in abundance of facultative corallivores and change in coral cover highlights the high level of feeding versatility in these species, many of which satisfy their dietary requirements by feeding on algae and motile invertebrates (Harmelin-Vivien & Bouchon-Navaro 1981; Harmelin-Vivien 1989a; Pratchett 2005). However facultative corallivores did decline in response to a reduction in structural complexity, reflecting their reliance on the shelter provided by the reef matrix. Small bodied species are known to be vulnerable to structural complexity loss (Graham et al. 2006) likely because they generally inhabit narrower niches and are more reliant on the reef matrix to avoid predators (Munday & Jones 1998). The weaker relationship and smaller decline in abundance and species richness of facultative feeders may be associated with variable collapse in structure among sites, or because the impacts of reduced structure are not as devastating as a complete loss of dietary resources (i.e. for obligate feeders). This suggests that facultative feeders, although escaping declines immediately following coral loss, may decline in a longer time frame and from a different driver (structural loss). However, their loss is likely to be less substantial than that of obligate feeders (Pratchett et al. 2006; Chapter 2 & Graham 2007).

An alternative explanation for a delayed decline in facultative corallivores is that these species recruit to live coral, and high coral mortality eventually reduces replenishment rate of adult stocks (*sensu* Jones et al 2004). For facultative coral feeding butterflyfish this explanation seems unlikely, as most species recruit preferentially to non-coral habitats (Pratchett et al. 2008c). It is feasible, however, that a loss of fine scale habitat complexity has reduced refuge space for juvenile fish, which would contribute to long term declines in adult populations (Chapter 5 & Graham et al. 2007a).

Our results suggest that obligate corallivores should be impacted more rapidly than facultative corallivores when subjected to disturbances such as coral bleaching, which result in rapid coral mortality, but delayed loss of habitat structural complexity. Furthermore, the spatial scales over which the impact is realised differ. Mass coral bleaching is generally devastating to coral cover over wide spatial scales (Hughes et al. 2003), although some depth refuge of live coral can occur (Sheppard & Obura 2005). Conversely, the collapse of habitat structure can be spatially variable (Graham et al. 2006), which likely results in more patchy reductions in abundance of species effected by structural loss. Thus, the more specialised obligate coral feeding species are more vulnerable to population declines and local extinctions due to both more substantial responses to disturbance and because the disturbance is manifested more uniformly and is spatially extensive.

Although predicting and understanding effects of bleaching on live coral loss and re-organisation has greatly increased (Sheppard 2003; Hoegh-Guldberg et al. 2007; McClanahan et al. 2007a, c), the same is not true for loss of structural complexity. The mechanisms for collapse of reef structural complexity following live coral mortality can include physical erosion (Scoffin 1993) and bioerosion (Hutchings 1986) and will be partly dependant on the original composition of the coral community (Done et al. 1996). As collapse of this matrix appears to be a major determinant of secondary impacts on fish assemblages (Garpe et al. 2006; Graham et al. 2006; Chapter 5 & Graham et al. 2007a; Wilson et al. 2006), a greater understanding of the mechanisms behind differential collapse of reef structures following coral mortality and how this can be predicted will be of great benefit to conservation planning.

The patterns of decline in obligate and facultative corallivores identified in this study beg the question as to the dynamics of any recovery in their populations following benthic recovery. One may hypothesize that the obligate feeders may recover more rapidly as live coral cover returns to a reef more rapidly than the structure it provides. However, if the declines observed for obligate feeders are great, an allee effect may operate whereby the broodstocks of adults are not sufficient to facilitate a rapid recovery. Conversely, although the structural complexity of the reef may take longer to regenerate, facultative feeders may more readily respond to any such recovery as their population decline is less severe and more variable. Previous studies have shown that recovery of fish species richness and abundance of some groups may track recovery of the benthos (Sano 2000; Halford et al. 2004), however for butterflyfish, if the composition of corals that recover is different to the pre-disturbance composition, the resultant assemblage of butterflyfish may also be radically different (Berumen & Pratchett 2006). With climate change leading to an altered and depauperate composition of corals on reefs (Hughes et al. 2003; McClanahan et al. 2007a), it is imperative to understand how fish groups will respond to such changes.

Understanding the likely composition and functional capacity of fish assemblages on reefs in a changing climate is a key conservation question. Such information is imperative to inform biodiversity preservation and to understand the likely trajectories of coral reef ecosystems through continued and multiple disturbance regimes. Coral reefs provide a variety of critical goods and services to human societies (Moberg & Folke 1999) and so further understanding of the drivers of decline, the spatial and temporal scales over which they operate, and projections of how these services are likely to change, are key research priorities.

3.6 Acknowledgements

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Chapter 4

Anthropogenic stressors, inter-specific competition and ENSO effects on a Mauritian coral reef[3]

4.1 Abstract

Much of the western Indian Ocean suffered widespread loss of live coral in 1998 and interest is now focused on the indirect effects of this coral loss on other components of the ecosystem, in particular fishes. However, it is just as important to identify changes in fish assemblages at locations that did not suffer coral mortality in order to understand local versus regional drivers. We surveyed benthic and fish communities on a reef flat in Mauritius five times between 1994 and 2005. The design allowed for comparison through time, along the coast and between inshore and offshore reef locations. The benthic community demonstrates a clear trend along the coast which is likely to be in response to a dredged water ski lane, but little change through time. Branching *Acropora* colonies dominate much of the live coral and best explain patterns in the fish assemblage ($p<0.01$). Few changes in overall fish species richness through time were identified, and observed changes were within fishery target families rather than species reliant on live coral. Departure from expected levels of taxonomic distinctness suggests degradation in the community associated with the

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dredged ski lane. Non-metric multi-dimensional scaling of the fish assemblage demonstrates a similar pattern to that seen in the benthos; greater differences along the coast (Global R = 0.34) than through time (Global R = 0.17) and no trend between reef positions. SIMPER analysis identified two species of *Stegastes* as the main drivers of trends in the MDS plot and the most dominant of these, *S. lividus*, appears to be reducing species richness of the remaining fish community. The study highlights Mauritius as a regional refugia of thermally-sensitive corals and specialised fish, suggesting a need for careful management.

4.2 Introduction

Coral reefs globally are suffering increasingly frequent events of thermally induced bleaching and associated mortality (Hoegh-Guldberg 1999, Sheppard 2003). Loss of live coral cover at this scale is expected to affect other components of the ecosystem (Walther et al. 2002), and studies of such impacts are growing in number. Much attention is focused on likely ramifications for reef-associated fish assemblages. The majority of studies to date have been on the scale of a few months to years and indicate limited community change aside from species directly dependant on live coral or algae for food or shelter (Kokita and Nakazono 2001, Lindahl et al. 2001, Booth and Berretta 2002, Chabanet 2002, McClanahan et al. 2002, Sheppard et al. 2002, Spalding & Jarvis 2002, Sano 2004), whereas the longer term effects may be much greater (Jones et al. 2004, Graham et al. 2006). This may be due to lag effect associated with changes in physiological condition of fish (Pratchett et al. 2004) and collapse of the physical structure of the reef matrix (Graham et al. 2006, Chapter 5 & Graham et el. 2007a). Understanding such effects and processes will clearly be essential for future use and management of affected reef systems.

When trying to understand the effects of bleaching on fish assemblages, it is just as important to assess change through the same time period at locations that did not suffer badly from bleaching, as it is to study sites where severe mortality occurred. This acts as a control for bleaching effects where other drivers in fish community dynamics can be identified in a region over the same time period. Ecological processes such as variable recruitment (Doherty & Williams 1988, Letourneur et al. 1998a, Doherty et al. 2004), predation (Hixon 1991, Graham et al. 2003) or competitive interactions (Robertson 1996, Letourneur 2000, McClanahan 2000a) could be driven by natural processes and influence fish assemblages. They may also be driven by changes in habitat associated with effects such as eutrophication (McCook 1999), sedimentation (Rogers 1990), or fishing (Jennings at al. 1995, McClanahan & Graham 2005), or actions that may cause physical damage to the habitat (Brown et al. 1990, Adjeroud et al. 1998). Identifying such processes and collecting baseline data at a location that has escaped much of the thermal damage characterised at other sites, will provide information for future monitoring and management, particularly when future effects of bleaching at regional scales are expected to be significant (Sheppard 2003).

The warm phase of the El Niño Southern Oscillation (ENSO) event of 1998 resulted in the greatest global bleaching event on record (Hoegh-Guldberg 1999) and was particularly devastating to the western Indian Ocean (WIO) (Goreau et al. 2000) where it interacted with the warm portion of the Indian Ocean dipole (Saji et al. 1999). However, the effects varied greatly, with some locations, such as the Maldives and the inner Seychelles suffering 75-99% mortality, whereas other locations, such as

Réunion and South Africa suffering low to negligible damage (Goreau et al. 2000, Obura 2005). Bleaching in Maurtius was also minimal with less than 10% coral cover affected in 1998 (Moothien Pillay et al. 2002, Turner & Klaus 2005), and 24% in 2004 (McClanahan et al. 2005). After these two events coral cover is still dominated by thermally sensitive genera such as *Acropora* and overall cover appears to have risen since a broad survey in 1992 (McClanahan et al. 2005).

This study assesses changes in benthic and fish communities on a narrow reef flat in north-west Mauritius that escaped much of the bleaching mortality experienced by other locations in the WIO in 1998. Temporal and spatial trends through a period 1994-2005, thus spanning the 1998, 2003 and 2004 bleaching events, are studied, aiming to identify any change in benthic and fish community structure. Alternative hypotheses are considered and, using a suite of multivariate tools, a case is built for the most plausible explanations for the observed trends.

4.3 Methods

4.3.1 Study site and sampling techniques

Mauritius is located in the southwestern Indian Ocean, 200 km east of Réunion Island, and 800 km east of Madagascar, between latitudes 19.58 and 20.31ºS, and longitudes 57.18 and 57.46ºE. The study was conducted in the northwest coast of the island (Figure 4.1), which is sheltered from the dominant southeast trade winds. The study site, Pointe aux Piments, is located 10 km north of the capital, Port-Louis, this part of the coast being developed with hotels. The fringing reef, dominated largely by branching *Acropora* corals, is approximately 250 m wide and 1-2 m deep along this section of the coast, and largely used for recreational purposes. Within the study area a dredged water ski lane has been in active use since 1995 (Figure 1). Fishing pressure around Mauritius is high (~1600 t yr^{-1} from lagoons and reefs) and is thought to exceed maximum sustainable yields (Turner & Klaus 2005).

Data were collected on benthic and fish communities at 10 stations over a 10 year period, where samples were collected in 1994, 1995, 1996, 1997 and 2005. The design allowed for comparison through time, along the coast and between inshore and offshore locations. Five transects (T1-T5) perpendicular to the shore, each had a landward (A) and seaward (B) sampling station, where a 50m transect tape was laid down parallel to the shore in a southerly orientation (Figure 1). The study site comprised approximately 1 km of shoreline, each transect being separated by 200-350 m. Land sampling stations (A) were located 50 m from the shore, whereas sea stations (B) were ~200 m from the shore.

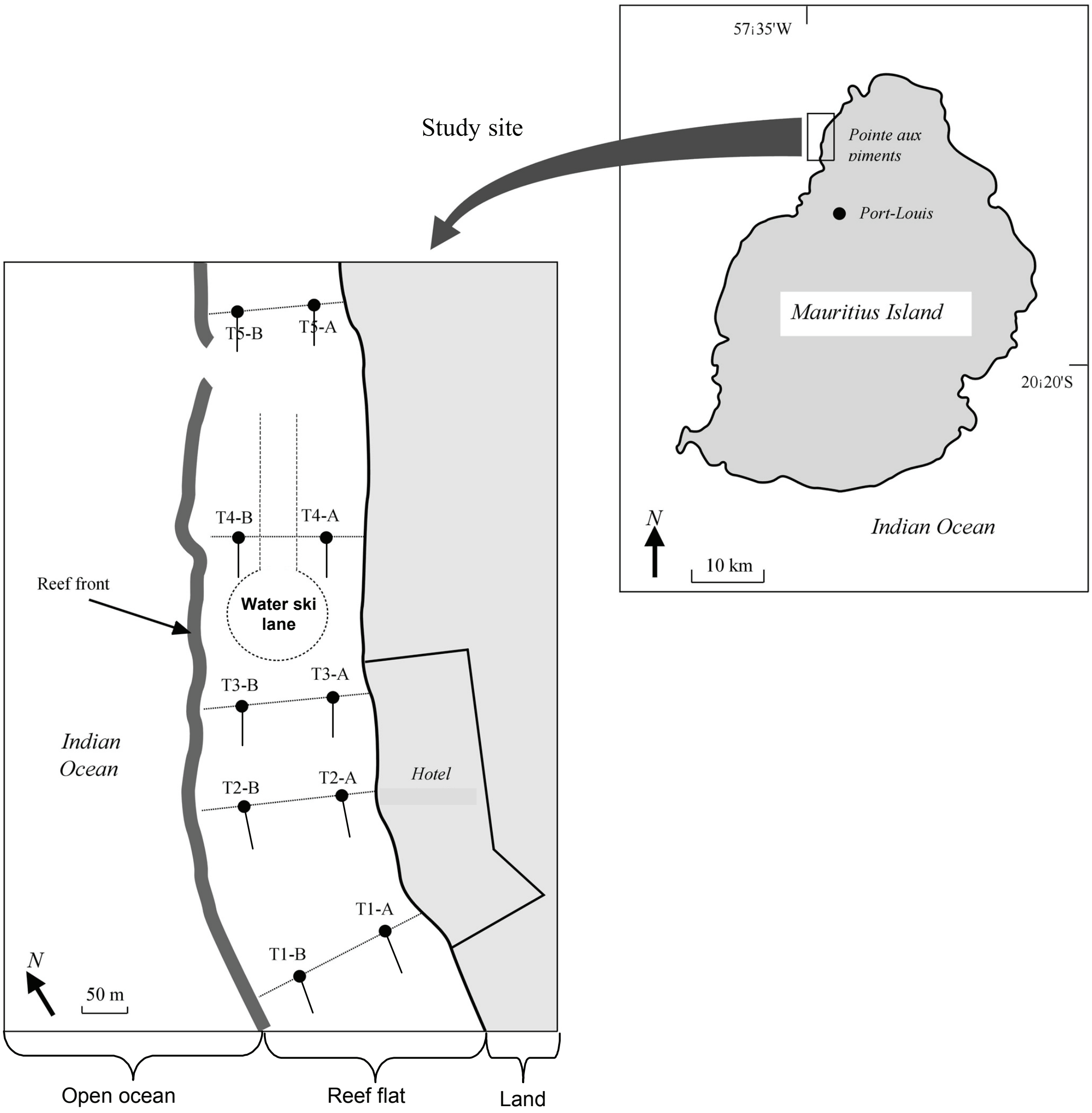

Figure 4.1. Map of the study site, indicating location in Mauritius, proximity of the ten sampling stations, direction of transects and location of dredged water ski lane. Adapted from Aderoud et al. 1998.

Full fish censuses were carried out by snorkel along 50*2m belt transects at each of the 10 sampling stations. Fish were identified to the species level (within 29 families) and abundance estimated. The discrete group sampling technique was used, whereby fish in different families and mobility groups were surveyed during different passes of the transect (4 in total) to account for varying behaviours (Harmelin-Vivien et al. 1985). This process was repeated 3 times for each station and an average abundance for each species attained. A presence/absence survey was also conducted around each station area during a 30-minute timed swim. Although fish counts were conducted by three different observers over the 5 sampling years, all observers were highly experienced and inter-observer variation is expected to be minimal (Williams et al. 2006, McClanahan et al. 2007d). After a fish census was complete the benthos along the same 50m transect line was quantified using the line intercept method (Loya 1978), whereby the distance of tape occupied by the following substratum categories was quantified: live branching coral, live plating coral, live other coral and dead substratum. These data were converted into percent covers of each category for each of the 10 stations surveyed within each year. Data were collected during peak daylight hours. Surveys in 1994, 1996 and 2005 were during the Austral winter, whereas surveys in 1995 and 1997 were during the Austral summer, however analysis of 1994-1997 data indicated little seasonal variation (Galzin, R. unpublished data).

4.3.2 Data analysis

Due to the multi-species nature of the data and the design of the survey, the most appropriate analyses were multivariate (Clarke & Warwick 2001a). To assess patterns in benthic data from all stations in all years we used correlation-based principle components analysis. Data were log(x+1) transformed to account for some right skewness detected in draftsman's plots and normalised. Eigenvectors were overlaid on the resultant plot to identify direction and contribution of the different variables to the patterns and to identify any correlation between variables. Percent total live coral was also quantified for each transect and landward and seaward sampling stations cross the 5-year period. Two-way ANOVAs were used to assess differences through time associated with both trends along and away from the shore. Normality of data was examined with histograms and normal probability plots of the residuals. Homogeniety of variances were tested with Bartlett's test. Where a significant difference was found, Tukey's test identified those samples driving the differences.

Presence / absence fish diversity data from timed swims was pooled to the year level to represent the reef as a whole. Overall species richness (S) and richness within key families was calculated for each year.

We examined the taxonomic diversity of the fish assemblage for each station and year. Average taxonomic distinctness (AvTD) was calculated by assessing the degree to which species in a sample are taxonomically related, measuring the average path length between every pair of species based on a taxonomic tree (Clarke & Warwick 1998). Variation in taxonomic distinctness (VarTD) was assessed by measuring the evenness to which the taxa were spread across the tree (Clarke & Warwick 2001b). Funnel plots were constructed for both variables with expected mean and 95% confidence limits constructed from a simulation distribution using random subsets of the master taxonomy list (constructed following Helfman et al. (1997)). Any departure from expected values could thus be identified, where low AvTD and low to normal VarTD indicates degraded locations (Clarke & Warwick 2001b). General patterns related to our study design were tested using two-way crossed ANOVAs with the factors year and transect, as these were identified as the key sources of variation by Analysis of Similarities (ANOSIM).

Fish assemblages within each station in each year were compared using non-metric multi-dimensional scaling (MDS) based on Bray-Curtis similarity measures. Species abundance data were square-root transformed to down weight abundant species. Differences between years, transects and reef position (A-B) were tested using ANOSIM, which is a non-parametric permutation procedure. After identification of which transects and years (the 2 significant factors) differed the most (ANOSIM pair-wise test output), SIMPER analysis was run on the data matrix. SIMPER decomposes Bray-Curtis dissimilarities between all pairs of samples to identify those species that contribute most to differences (Clarke & Warwick 2001a).

As SIMPER identified *Stegastes lividus* followed by *Stegastes nigricans* as the species contributing most to the significant trends in the MDS plot for both year and transects along the shore, bubble plots were used to overlay relative abundance of both of these species enabling identification of the trends they were contributing to. As these species are both highly aggressive and territorial (Randall et al. 1997, Letourneur 2000), the influence that their abundance has on species richness of the rest of the fish assemblage was tested using linear regression analysis.

In order to link the benthic and fish data, bubble plots were used to overlay relative value of benthic variables on the fish species MDS plot. This allowed identification of any trends driven by the benthic variables. The BEST BIO-ENV routine was then run using Spearman rank correlation between benthic Euclidean distance and fish species Bray-Curtis similarity matrices to identify the benthic variable or group of variables that best explained the patterns in the fish species MDS plot (Clarke & Warwick 2001a). The significance of this result was tested using a permutation test.

4.4 Results

The benthos at this location in Mauritius experienced very little change through the 10-year study period. Principal Components Analysis indicates a trend along the shore line, from Transects 1 and 2 to Transects 4 and 5, but little change with time (Figure 4.2). The main factors influencing this pattern along PC1 (~57% of variation) are higher cover of live branching and plating corals towards the southern end of the study site, or away from the ski lane, and higher cover of dead substratum towards the north (Figure 4.2). Percent cover of other live substratum (mainly massive corals) appears to be driving patterns along PC2, however this cover was often low. These trends are further highlighted by looking at overall percent live coral cover. The decline along the coast in a northerly direction is significant ($F_{4,37} = 13.9$, $p<0.001$), Tukey's test indicating that T1 differs from T4 and T5, and T2 differs from T3, T4 and T5, whereas no such trend is found through time ($p = 0.70$)(Figure 4.3a). The greater cover at near shore locations compared to seaward locations (A-B) in 1994 was not nearly as great in subsequent years, and the overall difference between sites A and B and through time is not significant ($p = 0.15$ and $p = 0.85$)(Figure 4.3b).

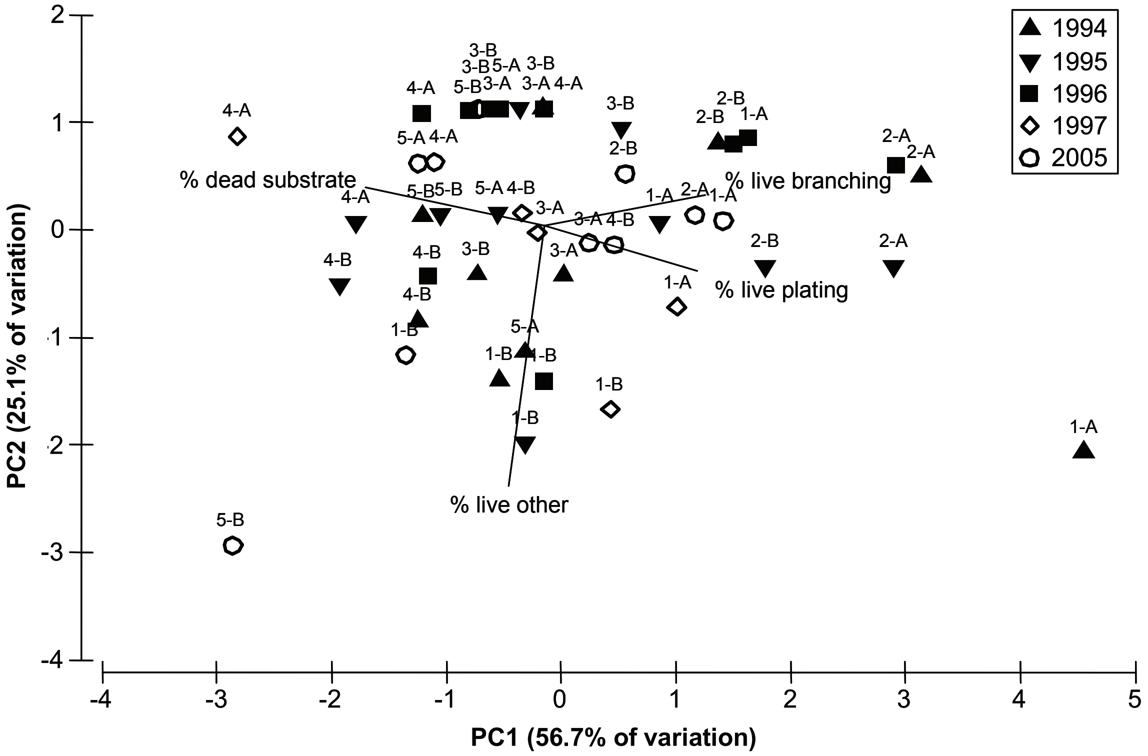

Figure 4.2. Correlation-based Principal Components Analysis of log(χ + 1) transformed and normalised environmental data.

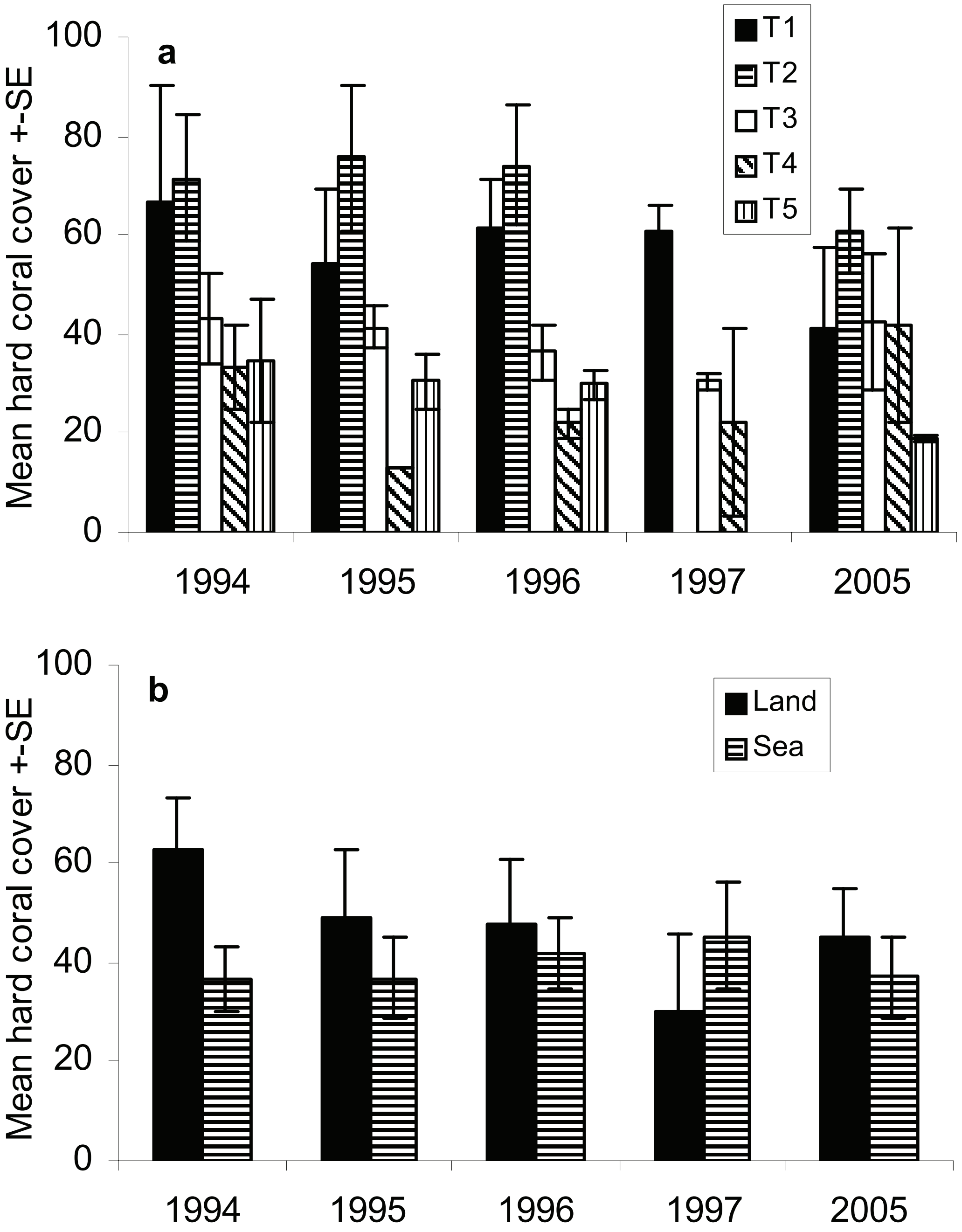

Figure 4.3. Percent cover of total live coral in (a) each year by transect and (b) each year by position from the shore.

The timed swim presence / absence surveys demonstrate remarkable stability in overall fish species richness through time (Table 4.1). Stability is consistent in nearly all the key families involved, including those dependant on live coral such as the chaetodontids. Notable declines in number of species are seen for lethrinids, lutjanids (though both were already in low number) and in particular serranids, all of which are common fishery target species (Table 4.1).

Conversely, at the level of stations, a number of samples depart negatively from the expected values of AvTD, suggesting some samples may be taxonomically depauperate (Figure 4.4a). The only significant decline in the ANOVA model was for the factor year ($F_{4,25} = 3.22$, $p = 0.03$) and Tukey's pair-wise comparisons indicates that this was influenced by lower values in 1997 versus 2005 ($p = 0.03$). Much less departure from expected values is noticed for VarTD (Figure 4.4b), however a weak significant difference is detected for the factor transect ($F_{4,25} = 2.95$, $p = 0.04$), which is driven by a difference between Transect 1 and 3 ($p = 0.04$).

The fish species MDS plot indicates a very similar pattern to that found in the benthic PCA, some difference in years, but an overall trend along the coast from T1 and T2 to T4 and T5 (Figure 4.5a). Samples from T1 and T2 are located in the bottom left side of the plot for all years, with samples from more northerly transects located to the top and right of the plot. This pattern is highlighted by the ANOSIM results, with significant differences for Year and Transect, but not Position on the reef (Table 4.2). Pair-wise testing identified 1994 departing from all other years and 2005 from 1996 and 1997. Pair-wise tests for Transect identified T1 departing from T4 and T5, and T2 from T4 (Table 4.2).

Table 4.1. Reef fish species richness from presence / absence timed swim data at level of whole assemblage (S) and within selected families.

	1994	**1995**	**1996**	**1997**	**2005**
Total species richness (S)	104	102	110	99	101
Acanthuridae	7	9	8	8	7
Balistidae	2	1	2	1	3
Chaetodontidae	8	9	8	11	10
Holocentridae	3	4	5	4	3
Labridae	19	22	21	24	20
Lethrinidae	3	3	2	2	2
Lutjanidae	1	0	2	0	0
Monacanthidae	4	5	5	3	5
Mullidae	6	5	4	5	7
Pomacentridae	13	13	12	12	14
Scaridae	7	7	9	7	6
Serranidae	7	3	4	4	1
Siganidae	1	1	1	0	1

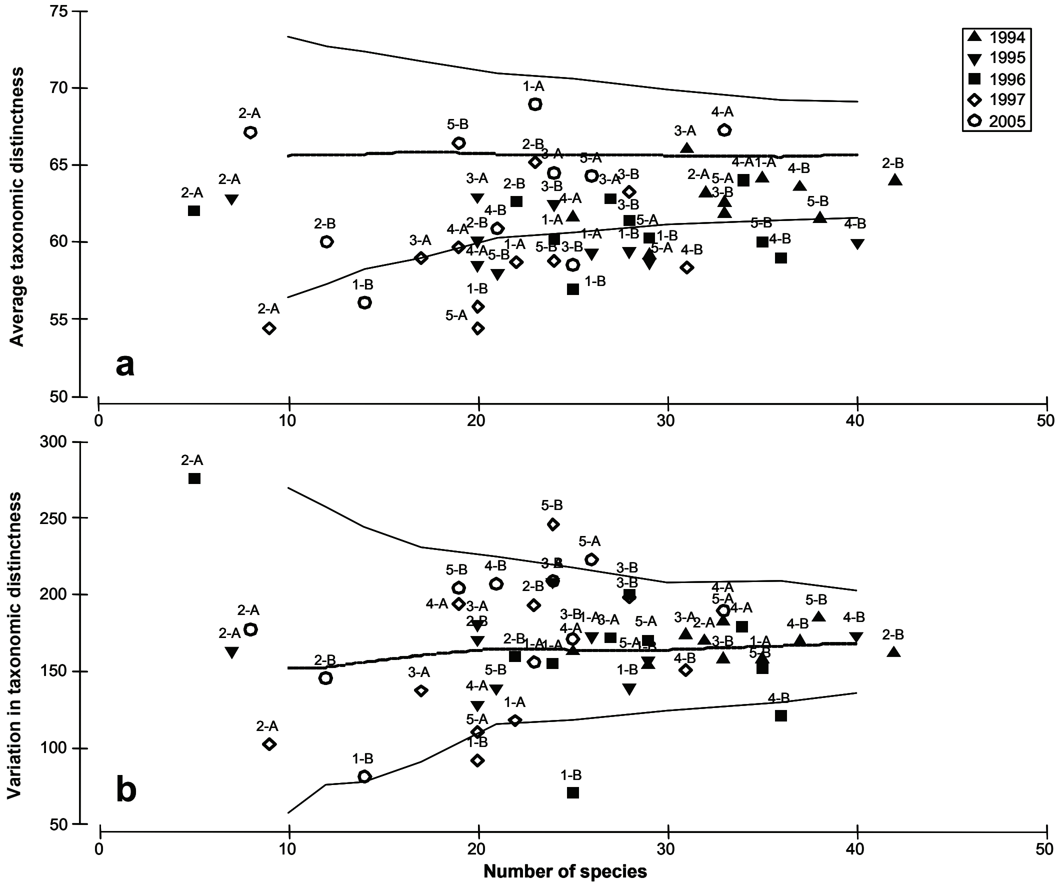

Figure 4.4. Funnel plots of (a) average taxonomic distinctness and (b) variation in taxonomic distinctness of each sampling station (belt transects) within each year with mean and 95% confidence limits from expected values using master taxonomy aggregation file.

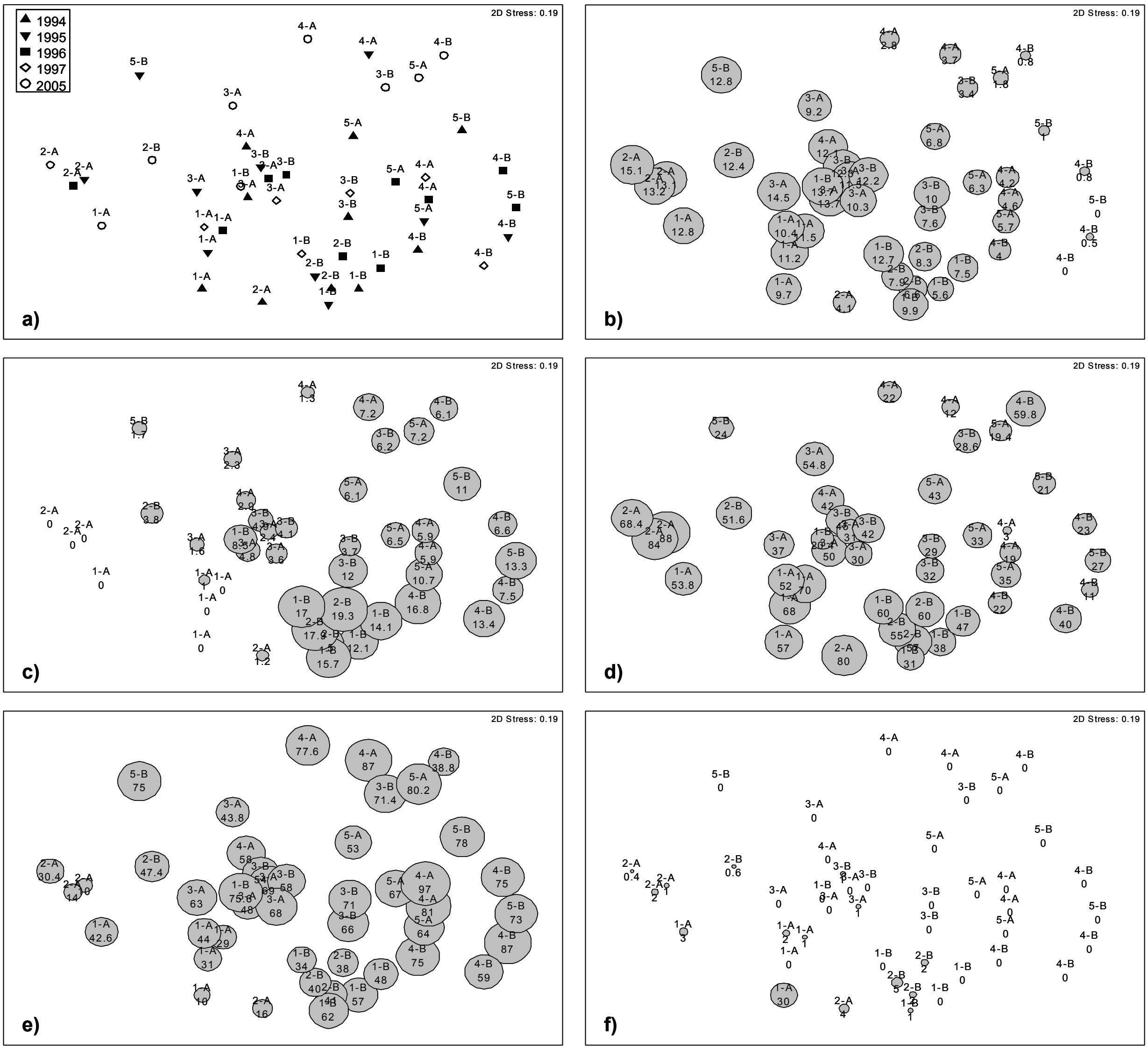

Figure 4.5. (a) Non-metric Multi-Dimensional Scaling (MDS) plot of fish assemblages at each of the ten stations (belt transects) within each of the five sample years based on Bray-Curtis similarity measures. (b) Bubble plots for *Stegastes lividus* and (c) *Stegastes nigricans* over species MDS sample points indicating patterns driven by their presence. Abundance at each sample station given below station name (scale of bubbles: 0-20). Bubble plots for cover of (d) branching coral, (e) dead substrate and (f) plating coral indication which patterns in the species MDS are driven by these benthic variables. Percent cover at each station given below station name (scale of bubbles: 0-100%).

Table 4.2. Analysis of Similarity (ANOSIM) outputs for the fish sampling stations. Global and pair-wise test results given for each of the three factors in the design.

Factor	**Global R**	**Significance**	**Pair-wise test**
Year	0.167	P<0.01	1994 diff to all, 2005 diff to 1996 & 1997
Transect	0.335	P<0.01	T1 diff to T4 & T5 T2 diff to T4
Position	0.022	ns	

SIMPER analysis, for the two years and transects that differed the greatest from one another, highlighted that *Stegastes lividus* followed by *S. nigricans* were contributing by far the greatest to the observed differences (Table 4.3). Pomacentrids and more mobile scarids, acanthurids and wrasses make up the majority of the remaining species contributing 60% of the differences (Table 4.3). The trends driven by *S. lividus* and *S. nigricans* are highlighted by the bubble plots (Figure 4.5b and c), the former being more dominant in the southerly sites that have greater live coral cover (Figure 4.3a), whereas the latter is more dominant in the northerly sites. Furthermore, and likely exacerbating the patterns, is that the abundance of *S. lividus* but not *S. nigricans* is negatively correlated with overall fish species richness, though the trend is not consistently significant among all years (Figure 4.6).

Bubble plots overlaying percent cover of benthic variables on the fish species MDS further highlight these trends; samples to the bottom left of the plot being dominated more by live branching and plating corals (Figure 4.5d and f), whereas samples to the right of the plot have a greater cover of dead substratum (Figure 4.5e). Rank correlation of benthic variables to the fish species data indicates that the best single and significant (BioEnv Rho statistic: $p<0.01$) benthic variable driving the patterns in the fish data is the percent cover of live branching coral ($r = 0.36$).

Table 4.3. SIMPER outputs for greatest pair-wise differences in year and transect identified by ANOSIM. Species that contributed 60% of the overall difference are listed in descending order of most contribution.

Year (1994 & 2005)		***Transect (T1 & T4)***	
Species	% Contribution	Species	% Contribution
Stegastes lividus	10.64	*Stegastes lividus*	12.03
Stegastes nigricans	10.07	*Stegastes nigricans*	10.84
Dascyllus aruanus	4.77	*Scarus psittacus*	6.56
Chromis viridis	4.21	*Dascyllus aruanus*	4.78
Chlorurus sordidus	4.18	*Chlorurus sordidus*	3.92
Ctenochaetus striatus	4.15	*Scarus scaber*	3.36
Halichoeres scapularis	2.78	*Ctenochaetus striatus*	3.26
Stegastes limbatus	2.65	*Chromis viridis*	3.18
Scarus scaber	2.55	*Halichoeres scapularis*	2.79
Acanthurus triostegus	2.41	*Calotomus spinidens*	2.69
Gomphosus caeruleus	2.03	*Thalassoma hardwickii*	2.36
Zebrasoma scopas	2.02	*Stegastes limbatus*	1.91
Acanthurus nigrofuscus	1.95	*Stethojulis bandanensis*	1.76
Stethojulis bandanensis	1.86	*Epinephelus merra*	1.68
Chrysiptera unimaculata	1.82		
Oxymonacanthus longirostris	1.79		
Parupeneus macronema	1.43		

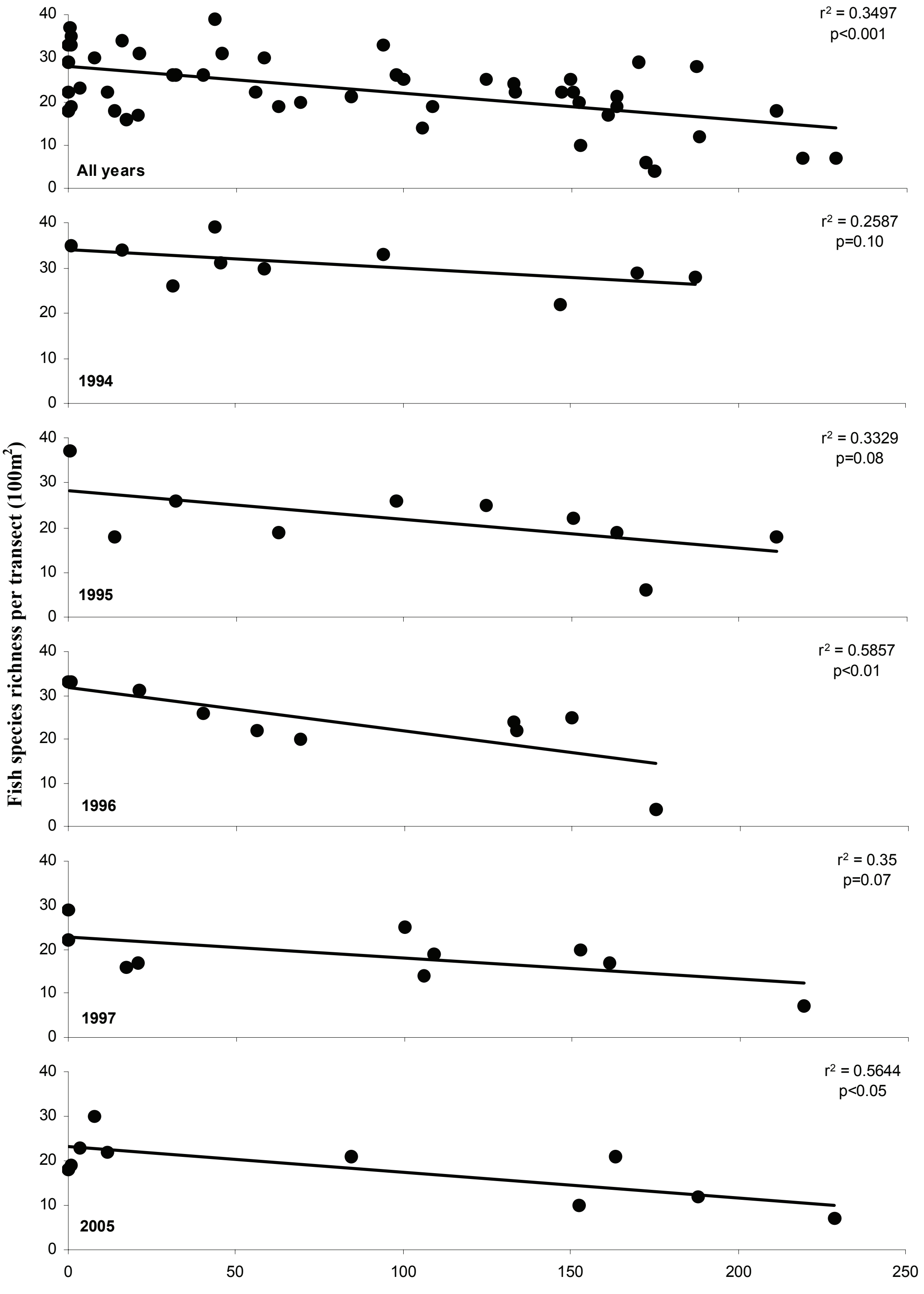

Figure 4.6. Regressions of *Stegastes lividus* density against fish species richness per station (belt transects) overall and for each year separately. R^2 and regression analysis results given on plots.

4.5 Discussion

Coral and fish communities appear to have experienced very little change over 10 years at this location in Mauritius, in contrast to other studied sites in the western Indian Ocean (Lindahl et al. 2001, McClanahan et al. 2002, Sheppard et al. 2002, Graham et al. 2006, Chapter 6 & Graham et al. 2008). Indeed the dominant trend at the study location appears to be along the coast, rather than through time. This suggests that the benthic community has changed very little through the 1998 ENSO event and the more minor 2003 and 2004 bleaching events. Unfortunately, reefs were not sampled between 1997 and 2005, which raises the question as to what happened during this sampling hiatus. The 1998 ENSO event resulted in less than 10% of coral colonies bleaching in Mauritius (Moothien Pillay et al. 2002). The 2003 bleaching event was most evident on the southwest of the island and a cyclone was implicated in the recovery of bleached corals (Turner & Klaus 2005, Ahamada et al. 2004). In 2004, 24% of corals bleached (McClanahan et al. 2005), however recovery was again high (Ahamada et al. 2004) and coral cover was higher than surveys conducted in 1992 (McClanahan et al. 2005). Although we can not discount the possibility of rapid re-colonisation and recovery of the reef with the predominant fast growing *Acropora* colonies, the above studies and the remarkably similar cover estimates through time suggest a minor influence from bleaching events. Furthermore, *Acropora* is one of the most susceptible genera to thermal stress in the region (McClanahan et al. 2001, 2004) and has experienced large declines in many other locations (Goreau et al. 2000, McClanahan 2000b, McClanahan et al. 2001, Sheppard et al. 2002). Indeed, branching and plating corals now make up less than 1% of the benthos in the inner Seychelles, a decline of over 95% (Graham et al. 2006). Study and protection of this apparent refugia of sensitive, habitat forming corals in Mauritius is important given predictions of further widespread degradation of the region in coming decades (Sheppard 2003).

The observed trend in benthic composition along the coast within the study location is most likely due to the dredged water ski lane that has fragmented the reef flat in this section, likely still results in increased sediment loads and is subject to high recreational use. The disparity between near shore and sea (A-B) stations that was quite apparent and a dominant driver of trends in 1994 (Adjeroud et al. 1998) is not as great on a temporal scale. Given the dominance of the reef flat by fast growing branching *Acropora* corals, it is possible that this may be due to some recovery following completion of the ski lane (1993-1994).

Although overall species richness of the reef fish assemblage has remained stable through this time period, the richness is fairly low compared to studies in nearby islands such as Réunion (Letourneur 1996a), Madagascar (Harmelin-Vivien 1989b) and Mayotte (Letourneur 1996b, Chabanet 2002). This is likely due to the surveys being restricted to the reef flat and because the reef is narrow along this section of the coast (Adjeroud et al. 1998), although reef flats of a similar width in Réunion had higher species richness (Letourneur 1996a). It could also be due to anthropogenic stress on the system through past dredging of the water ski lane and ongoing effects of fishing and recreational use. Indeed, many samples depart from expected values of taxonomic distinctness, and common fishery target species, in the families Lutjanidae, Lethrinidae and Serranidae, are missing. The years driving the main difference in taxonomic distinctness were 1997 and 2005, with 1997 having lower values. Although coral cover was lowest in this year, the magnitude was small and it is hard to ascribe causation to this trend. Indeed, the stability of species richness from the presence / absence survey within families that often feed on (Chaetodontidae) or dwell in (Pomacentridae) live coral indicates that these patterns are likely not driven by ENSO effects on the benthos, in contrast to other locations in the region (Spalding & Jarvis 2002, Graham et al. 2006). As samples from all years demonstrated departure from expected values, it is more likely that long-term effects are causing the trends.

The overall pattern in the fish community from MDS analysis is remarkably similar to that for the benthos, with the greatest differences identified along the coast (Global R = 0.34) as opposed to time (Global R = 0.17). This lends further support to our conclusion that the ecosystem has remained stable through the ENSO event and other factors are likely responsible for the observed changes. The heavy fishing pressure in Mauritius (Turner & Klaus 2005) and the apparent loss of diversity in key fishery target groups, of which many species are piscivores, may be driving trends related to predation pressure. Studies of predator control on reefs indicate trends both at the level of single species (Graham et al. 2003), aggregated by size class (Dulvy et al. 2004), and evidence suggesting there is a direct relationship between gape size of the predator and size of prey (Mumby et al. 2006). Recruitment has also been shown to drive variation in fish assemblages on reefs (Doherty & Williams 1988), particularly following mass-events (Letourneur et al. 1998a). Given the time between surveys and the narrow spatial scale over which the study has been conducted, variable recruitment could influence the small temporal patterns detected, but is unlikely to be driving the larger trends along the coast. Given that the availability of habitat types has not altered a great deal, competition for resources among fish species may be expected to have remained stable through this time period. However changes in certain dominant species, such as *Stegastes*, could well be causing changes in the rest of the assemblage.

The coastline adjacent to the study site has experienced rapid development for tourism in the last 10-15 years, and this is likely to be exerting stress on the reef ecosystem. Along the 1-km stretch of coast, two large hotel complexes actively use the reef for water sports activities. High use of reefs for snorkelling and diving can have detrimental effects (Hawkins et al. 1999, Zakai & Chadwick-Furman 2002). In this case, however, the greatest effect is likely to be from the dredged water ski lane through the middle of the reef flat. Increased pollution, sedimentation and changes in current regimes are all likely to be effecting both the coral and fish assemblages, and may be partly responsible for the changes through time. However, the greatest effects of the ski lane appear to be along the coast in the survey area.

Both the benthic and fish communities display the strongest patterns along the coast from Transects 1 and 2 to Transects 4 and 5, with greater live coral to the south end of the study site away from the dredged area. Branching coral is likely to be causing the observed patterns in the fish assemblages given that it was best at predicting the patterns in the fish assemblage structure and because it provides important three-dimensional structure (Bellwood et al. 2004). Furthermore, this habitat is critical at the early life history stage when fish settle from the plankton; 65% settling directly into live coral (Jones et al. 2004).

The two species of *Stegastes* were influencing the greatest difference along the coast and through time in the MDS plots. Although the preferred habitat of both species is branching coral (Randall et al. 1997), it appears that *Stegastes lividus* dominates the area of the reef where branching coral is most abundant. This may be explained by *S. lividus* growing to a larger maximum size than *S. nigricans* (Randall et al. 1997); size of individual correlating to size of territory and dominance over more favourable habitats in this genus (Robertson 1996, Letourneur 2000). If the relationship between *S. lividus* abundance and overall fish species richness is causal, this one species of small reef fish appears to account for a large portion of the variation in fish species richness; benthic variables and *Stegastes nigricans* demonstrates no measurable control. Although the competitive dominance of larger species of *Stegastes* over abundance of other *Stegastes* species in the same area has been identified (Robertson 1996), and the influence of territorial pomacentrids on behaviour and foraging of individual species of other reef fish is well documented (e.g. Jones 2005), we believe this influence on the species richness of an entire fish community has not been demonstrated before.

Dominance of space by branching coral and *Stegastes lividus* clearly contributes to the patterns in the MDS plot but not necessarily in the direction one may expect from previous positive relationships between coral cover and fish species richness (Bell & Galzin 1984). Areas of high cover of live branching coral in Mauritius are dominated by large numbers of *S. lividus* and their territorial behaviour may actually reduce species richness, such that the relationship between coral cover and fish species richness is negative. Consequently, mono-specific stands of branching coral result in an ecosystem that is more susceptible to competitive dominance by fewer species (Almany 2004). Indeed, dominance of a reef by one main taxa of coral will not necessarily promote high species diversity, rather a range of different taxa and habitat types is expected to provide more niches and a more diverse ecosystem (Almany 2004). This will be particularly true for small-bodied species of reef fish that are closely reliant on habitat for shelter and food and are often specialised (Munday & Jones 1998).

The western Indian Ocean has suffered the greatest effects from coral bleaching in the Indo-Pacific (Goreau et al. 2000) and future bleaching is predicted to result in the 'extinction' of these reefs in coming decades (Sheppard 2003). However, various locations in the southern western Indian Ocean, including Mauritius, currently seem to be a refuge from coral bleaching, demonstrating "protection" from serious thermal stress (Obura 2005) and host high coverage of thermally sensitive corals that still support specialist fish species. This study has demonstrated minimal community change through time on a coral reef in Mauritius, and identified other factors likely to be driving trends. Such data and future monitoring in these areas of bleaching refugia will be important to understand natural variation in fish communities and associated management implications.

4.6 Acknowledgements

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Chapter 5

Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems[4]

5.1 Abstract

Recent coral bleaching episodes have led to wide-scale loss of reef corals and raised concerns over the effectiveness of existing conservation and management efforts. The 1998 bleaching event was most severe in the western Indian Ocean where coral declined by up to 90% in some locations. Using fisheries-independent data, we assessed the long-term impacts of this event in the Seychelles on fishery target species, the overall size structure of the fish assemblage, and the effectiveness of two marine protected areas (MPAs) in offering resilience to fish communities. Fishery-target species above size retained in fish traps showed little change in biomass between 1994 and 2005, indicating no current effect on fishery yields. Biomass remained higher in MPAs, indicating they are still effective in protecting fish stocks. However, the size structure of the fish communities, as described with size-spectra, changed in both fished areas and MPAs, with a decline in smaller fish (<30 cm) and an increase in larger fish (>45 cm). We believe this represents a time-lag response, due to fish that were lost to natural mortality and fishing no longer being replaced by

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[4] Published as: Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Robinson J, Bijoux JP, Daw TM (2007) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. Conservation Biology 21:1291-1300. NAJ Graham collected post-disturbance data, analysed and interpreted data and wrote the paper.

juveniles following the bleaching event. This effect is expected to be greater in terms of fisheries productivity and, because congruent patterns are observed for herbivores, suggests no long-term resilience in the MPAs. Corallivores and planktivores declined strikingly in numerical abundance, particularly in MPAs, which was associated with a similar pattern of decline in their preferred corals. We suggest that climate-mediated disturbances, such as coral bleaching, be at the fore of conservation planning for coral reefs.

5.2 Introduction

Coral reefs and their associated communities are threatened by anthropogenic and natural disturbances including overharvesting, sedimentation, pollution, disease, and warming waters (Hughes et al. 2003; Bellwood et al. 2004; Wilson et al. 2006). Although multiple stressors often act in synergy, climate-driven coral bleaching has emerged as one of the greatest threats to coral reef ecosystems (Hughes et al. 2003; Sheppard 2003). The 1998 bleaching event was the most severe on record, and in the most heavily affected region, the western Indian Ocean, coral cover declined by up to 90% (Sheppard 2003). Recovery from such severe disturbances is likely to be slow and affect other reef associated organisms.

The short-term effects of bleaching on fish are mainly manifest in species that specialize on live coral for diet, shelter, or recruitment habitat (reviewed by Wilson et al. 2006). In the medium- to long-term, declines in coral feeders can continue (Pratchett et al. 2006), but the greatest impacts occur if the physical matrix of the reef collapses, reducing overall species richness (Garpe et al. 2006; Glynn 2006, Graham et al. 2006). The medium to long-term impacts of bleaching on the size structure of fish populations and assemblages are currently unknown (Wilson et al. 2006). These impacts are important because they determine the future viability of populations and assemblages and thus interact with fisheries management and conservation measures that may have been proposed or implemented prior to a bleaching event.

Assessments of the impacts of mass bleaching on fisheries and associated socioeconomic factors are currently limited to fisheries-dependant data and are considered small in relation to the direct impacts of fishing (McClanahan et al. 2002; Grandcourt & Cesar 2003). However, such assessments have all been made within 5 years of bleaching events. Because loss in structural complexity of the reef framework, which can take over 5 years (Wilson et al. 2006), is likely to affect small individuals and because these may take some time to recruit to the fishery, a lag effect may exist before the full impact of coral bleaching on reef fisheries is realised.

To conserve and manage reefs in the face of unpredictable disturbance, scientists and managers are increasingly proposing that no-take marine protected areas (MPAs) can increase resilience of the reef ecosystem (Hughes et al. 2003; Bellwood et al. 2004). Although it is clear that MPAs cannot prevent coral bleaching, the expected ecological communities in MPAs (e.g. a greater biomass, density and size of herbivorous fishes in regions where herbivores are fished) should promote coral recovery, thus providing spatial resilience in the form of populations that can reseed depleted areas (Hughes et al. 2003). There is some evidence of an initial build-up of fish biomass in MPAs even during habitat degradation (Hawkins et al. 2006), however both abundance and diversity may subsequently decline (Jones et al. 2004) and it is unclear how the size-structure of the fish assemblage may respond.

Using fisheries-independent data collected across the inner granitic islands of the Seychelles, we assessed the medium to long-term effects of mass coral bleaching on target reef fish above size retained in fish traps; overall size structure of the whole assemblage and particular feeding groups; and effectiveness of existing no-take MPAs in offering spatial resilience to the disturbance.

5.3 Methods

5.3.1 Study sites

The inner granitic islands of the Seychelles lie on the Mahé Plateau, a shallow, extensive, submarine platform that reaches mean depths of 44-65 m. The fringing reefs of the islands are typically shallow; the reef slope terminates at 6-13 m (Jennings et al. 1995). The 1998 bleaching event reduced live coral cover from 27 to 3%, an overall reduction of approximately 90%. Furthermore, coral mortality extended throughout the depth range of the coral reefs in this area. Recovery has been extremely slow, with collapse in the physical complexity of the reefs accelerating since 2003 (Engelhardt 2004) and mean coral cover attaining only 7.5% by 2005 (Graham et al. 2006). Other than climate-mediated bleaching mortality of corals, Seychelles reefs have experienced relatively little change in other stressors over the study period (Graham et al. 2006).

We conducted reef surveys in seven areas, around Mahé, Praslin and associated islands, which included most of the shallow fringing reef around the inner islands (for map see Jennings et al. 1995). Five fished areas were subject to similar levels of fishing intensity, whereas the other two areas were long-standing MPAs. Sainte Anne

Marine National Park was gazetted by the Government of Seychelles in 1973 as it is suitably located for tourist use, whereas Cousin Island Special Reserve was established by Birdlife International who bought the island in 1968 to protect an endangered species of bird (Jennings et al. 1996). Both MPAs are within the same geographic area as the other sites and have similar bathymetry and habitat types. There are significant differences in the diversity and biomass of fish between the two MPAs and the five fished areas but not within the MPAs or fished areas per se (Jennings et al. 1995). Spatial studies of MPA effects are expected to reflect the outcome of temporal studies (Russ et al. 2005); therefore, we believe that the higher levels of diversity and biomass in the MPAs reflect the effect of protection from fishing. Studies conducted within other reef systems have also highlighted the disproportionate effect of small amounts of fishing on fish communities and the more subtle impacts of further increases in fishing effort (Jennings & Polunin 1997; Hawkins & Roberts 2004). For these reasons, we assessed the interaction between bleaching impacts and management by comparing the two MPAs with the five fished areas before and after coral bleaching in 1998.

5.3.2 Assessment of fish assemblage and benthic community structure

We surveyed 21 sites, covering over 50,000 m^2 of coral reef habitat, at the same time of year in 1994 and 2005. Three sites were surveyed in each of the seven areas of coast described above, to include one site in each of three statistically different habitat types (Jennings et al. 1995); carbonate fringing reefs, granitic rocky reefs with coral growth and patch reef habitats on a sand, rubble or rock base. At each site 16 replicate 7 m radius point counts were completed using underwater visual census along the base of the reef slope. This technique maximised area coverage and replication, yet allowed for detailed searching for territorial species so that it provided a quantitative estimate of the number of fish of varying sizes and behaviour. We separated replicates by a random number of fin kicks with the proviso that each count was separated by a minimum of 15 m; thus a ~ 0.5-km stretch of reef was covered at each site.

The numerical abundance and size of 134 species of reef-associated, diurnally-active, noncryptic fish (>8 cm) was estimated within each count area. The time taken to complete a count varied depending on the number and diversity of fish present. Size estimation of fish was to the nearest centimetre, validated by estimating the lengths of a random selection of PVC pipes before the first count at each site. Length estimates were not consistently shorter or longer than actual lengths in both 1994 and 2005, with a mean error of 8 to 35 cm pipes of 3.1% and 2.2% respectively. Fish counts in 1994 were conducted by S.J. and in 2005 by N.A.J.G. Although small errors can exist among observers (Thompson & Mapstone 1997), bias among experienced divers has been shown to be the smallest component of variation in fish counts (Williams et al. 2006; McClanahan et al. 2007d). We converted data on fish counts to biomass with published length-weight relationships (Letourneur et al. 1998b; Froese & Pauly 2006). Species were assigned to feeding groups (herbivores, piscivores and mixed diet feeders; species consuming animal and plant material or fish and invertebrates) based on dietary literature and Froese and Pauly (2006).

After a fish count was complete, we assessed the benthic composition and structural complexity of the count area. Percent cover of benthic categories (live branching, plating, massive, corymbose and encrusting coral, soft coral, macroalgae, rock, rubble, sand and dead branching coral) was estimated visually and found to be accurate when assessed against the line-intercept method (no significant difference, MANOVA $F_{6,35} = 0.56$, $P = 0.76$)(Wilson et al. 2007). We assessed structural complexity of the benthos with a 6 point visual scale and tested the accuracy of this method with the linear verses contour chain method; the two methods were highly correlated (linear regression $r = 0.85$ $P < 0.001$)(Wilson et al. 2007).

5.3.3 Establishment of fishery target species and size of first capture

Fish species that are targeted by the local artisanal fishery were assigned to three groups: primary targets, important targets, and occasional targets (Grandcourt 1999). There is a strong relationship between body depth of retained fish and the maximum width of trap meshes (Munro et al. 2003). In Seychelles the minimum hexagonal mesh diameter that is legal is 4 cm, but fishers often use trap meshes larger than this and fish are able to squeeze through meshes smaller than their specific body depth (Robichaud et al. 1999). We calculated size at first capture from length frequency data of 5651 trap-caught fish between January 1992 and June 1994 (SFA, unpublished data). Ninety-five percent of fish in the sample had a body depth of over 6.0 cm. Data on target fish species from the 1994 and 2005 reef surveys were filtered to exclude individuals with a body depth of < 6 cm for species level and aggregated feeding group analyses to assess the impact of the bleaching event on the dominant inshore trap fishery.

5.3.4 Data analysis

Along with structural complexity, we categorized live corals into two groups; (1) complex; branching, plating, and corymbose functional forms, which offer the most structure for other organisms to live in (Jones et al. 2004) and are generally the favoured corals for diet and habitat specialists (Munday 2004; Pratchett 2005) and (2) simple; massive and encrusting functional forms which offer limited structure for other organisms to live in (Jones et al. 2004). We assessed differences between years, habitat types, and management status (fished versus protected) with three-way crossed fixed-effects orthogonal analysis of variances (ANOVAs). Homogeniety of variances was assessed with Levene's test, and normality of the data was assessed with histograms and normal probability plots of the residuals. Counts of complex corals were square root transformed to meet assumptions. Tukeys post-hoc test was used to identify where differences occurred among habitats.

Changes in the biomass of individual species and aggregated feeding groups of fishery targets above size at first capture were also assessed with the same ANOVA design. At the species level, we used log transformation to meet the assumption of homogeneity of variances for a number of species. Ten species that still failed to meet assumptions could not be analysed (Table 5.1).

The overall size structure of the assemblage at each site (including size below first capture) was described using the slope of the abundance-size relationships of the assemblage (Dulvy et al. 2004; Graham et al. 2005). Slopes of the size spectra were calculated from linear regressions of $\log_{10}(x + 1)$ numbers per size class (5 cm) on the rescaled $\log_{10}$ midpoint of each length class. Centring the independent variable provides values of mid-point height (community abundance) that are comparable among spectra. A steepening of the slope can be the result of a decrease in the number of large fish, an increase in the number of small fish, or both. Change in the slope and midpoint height of the size spectra were assessed with the same ANOVA design described above.

To assess what was driving the observed trends in slopes of the size spectra, changes in the numerical abundance of fishes in individual size bins of 5 cm between 1994 and 2005 were assessed for the entire assemblage and for five key feeding groups: mixed diet feeders, piscivores, herbivores, corallivores and planktivores. To partition any effects of marine protection and habitat type, we plotted data separately by management status and within this by habitat type.

5.4 Results

Structural complexity of the benthos declined between years ($F_{1,30} = 19.94$, $p < 0.001$), but did not vary with habitat or protection (Figure 5.1a). The cover of live complex corals fell by over 95% (Figure 5.1b)($F_{1,30} = 100.22$, $p < 0.001$), with the greatest reductions on carbonate habitats (significant interaction: $F_{2,30} = 3.71$, $p < 0.05$) and greater reductions on reefs in MPAs than fished areas ($F_{1,30} = 7.30$, $p < 0.05$). The greater impact in MPAs resulted from a higher initial cover of complex corals within MPAs in 1994, which declined to a similar base level (<1%) in 2005, irrespective of whether the site was in an MPA or fished. Cover of simple corals remained relatively stable between 1994 and 2005, with no significant factors in the model (Figure 5.1c).

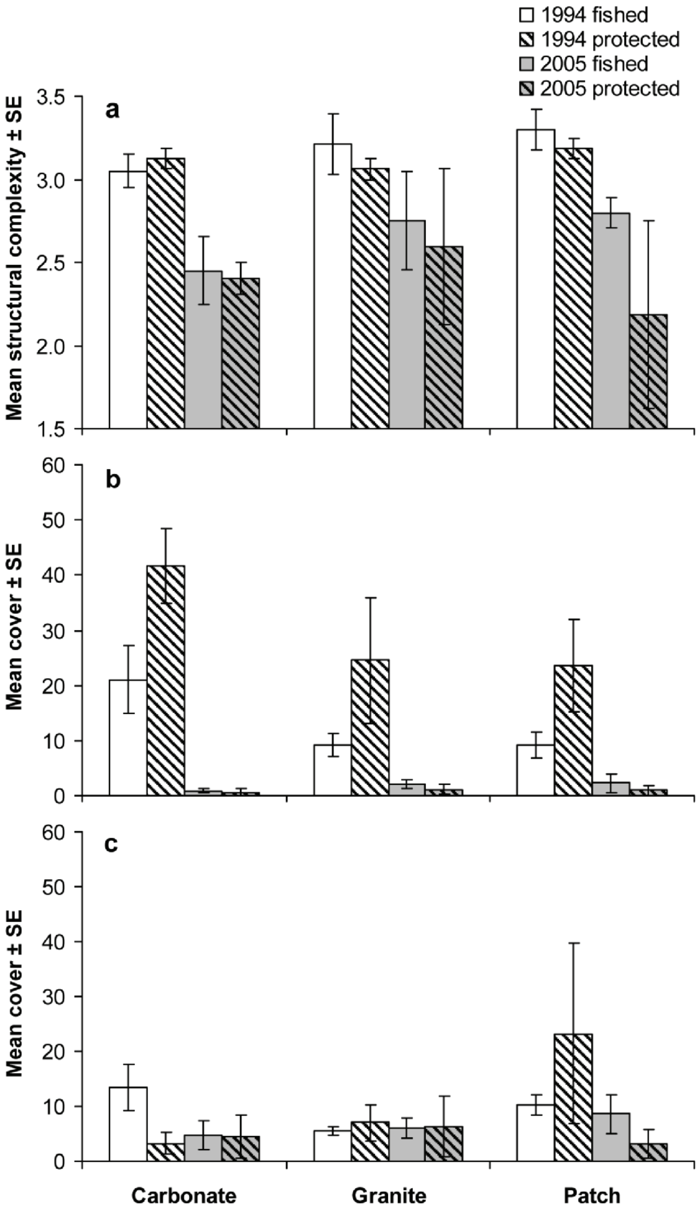

Figure 5.1. Change in (a) structural complexity, (b) complex corals (coral cover) and (c) simple corals (coral cover) between 1994 and 2005 for three habitat types (carbonate, granite, patch) and two management scenarios (fished, protected).

The biomass of individual target fish species above size at first capture showed variable trends between years; some increased, some decreased, and over 70% did not change significantly (Table 5.1). The entire target assemblage and mixed diet feeders showed greater biomass in MPAs than in fished areas ($F_{1,30} = 28.29$, $p < 0.001$ and $F_{1,30} = 14.44$, $p = 0.001$ respectively), but no trends between years or among habitat types (Figure 5.2a, b). Piscivore biomass did not differ among habitats, but differed between years ($F_{1,30} = 4.69$, $p < 0.05$) and with protection ($F_{1,30} = 16.65$, $p < 0.001$). A significant year-protection interaction term ($F_{1,30} = 5.49$, $P < 0.05$) showed that the main change between years was associated with a decreased biomass in MPAs (Figure 5.2c). Herbivore biomass was greater in 2005 ($F_{1,30} = 4.67$, $p < 0.05$) and in MPAs ($F_{1,30} = 11.65$, $p = 0.002$) and had no interaction or habitat effect (Figure 5.2d). These results indicate that although there were some small changes between years for certain groups, MPAs continued to support a higher biomass of targeted reef fish than fished areas (Figure 5.2).

Table 5.1. Change in biomass and results of univariate three-factor crossed analysis of variance for primary, important and occasional target fish species above size at first capture.[a]

Species	Size at first capture	Biomass (g) 1994	Biomass (g) 2005	Δ	Year (1,30 df)	Habitat (2,30 df)	Protection (1,30 df)
Primary Targets							
Aprion virescens	25.5cm	4141	3497	-	0.75	2.01	11.30***
Cephalopholis leopardus [b]	20.1cm	100	0	-	2.10	0.65	0.17
Chlorurus sordidus	19.2cm	7073	7369	+	0.11	0.75	0.03
Lutjanus bohar [b]	18.9cm	966	1308	+	1.63	1.74	1.83
Scarus ghobban	16.7cm	1137	2708	+	4.79*	2.73	6.93*
Scarus rubroviolaceus [b]	18.7cm	871	5079	+	4.16*	0.35	0.32
Siganus sutor [b]	15.4cm	338	0	-	2.79	1.12	0.56
Important targets							
Acanthurus tennentii [b]	15.3cm	332	2307	+	1.06	0.34	0.08
Anyperodon leucogrammicus [b]	24.2cm	287	37	-	3.64	0.27	0.09
Calotomus carolinus [b]	16.0cm	79	1211	+	3.78	0.03	2.67
Cephalopholis argus [b]	20.9cm	3063	988	-	9.44**	0.32	1.32
Cephalopholis miniata	21.4cm	75	259	+	2.50	1.39	0.03
Cetoscarus bicolour [b]	17.3cm	410	0	-	15.45***	0.20	4.14
Cheilinus fasciatus [b]	19.0cm	219	66	-	4.95*	0.13	0.05
Cheilinus trilobatus	17.7cm	1963	1281	-	1.67	0.55	2.91
Chlorurus gibbus	17.5cm	1282	1138	-	0.07	2.59	0.96
Ctenochaetus striatus	13.8cm	3703	1035	-	6.57*	0.25	5.24*
Epinephelus fasciatus	22.3cm	59	159	+	1.46	0.18	0.07
Epinephelus merra [b]	22.1cm	58	32	-	0.27	2.36	2.00
Leptoscarus vaigiensis	21.8cm	77	478	+	1.45	4.01*	0.70
Lethrinus enigmaticus	16.7cm	13	52	+	0.52	0.96	0.36
Lethrinus harak	18.4cm	2594	2659	+	0.03	0.67	2.90
Lethrinus lentjan [f]	16.7cm	27	93	+	3.03	3.36*, [c]	7.61**
Lethrinus mahsena	15.9cm	119	68	-	0.70	0.18	0.02
Lethrinus nebulosus [b]	17.2cm	139	734	+	8.43**	1.62	3.52
Lethrinus obsoletus [b]	18.3cm	1381	421	-	4.20*	0.08	12.71***
Lethrinus olivaceus [b]	20.8cm	70	254	+	0.92	0.11	1.64
Lutjanus fulviflamma [b]	20.2cm	1206	692	-	1.31	3.19	5.45*
Lutjanus gibbus [b]	16.2cm	1257	684	-	0.28	1.07	0.31
Lutjanus kasmira	18.5cm	29	9	-	0.02	1.07	0.02
Lutjanus rivulatus	16.1cm	133	51	-	0.00	0.31	0.00
Macolor niger [g]	16.6cm	478	158	-	3.93	4.02*, [c]	0.09
Monotaxis grandoculis	15.7cm	325	723	+	0.93	0.43	0.07
Mulloidichthys flavolineatus [b]	25.5cm	366	31	-	1.82	0.26	3.43
Parupeneus barberinus [b]	21.9cm	1200	529	-	0.64	1.05	1.57
Parupeneus ciliatus [b]	21.8cm	1006	797	-	0.37	0.43	0.11
Parupeneus cyclostomus [b]	22.7cm	196	50	-	1.69	1.13	0.00
Parupeneus macronemus	21.4cm	410	139	-	2.46	1.52	0.10
Parupeneus rubescens [b]	20.2cm	17	25	+	0.24	0.40	1.57
Plectorhinchus orientalis	20.8cm	823	610	-	0.70	1.21	1.44

Plectorhinchus schotaf[b]	18.7cm	397	721	+	0.14	0.06	0.14
Scarus caudofasciatus	17.2cm	117	642	+	1.92	1.07	0.19
Scarus falcipinnis [b]	17.4cm	200	291	+	0.01	0.49	0.50
Scarus frenatus [h]	19.1cm	1882	660	-	15.66***	1.17	13.57***
Scarus globiceps	18.3cm	189	667	+	0.74	0.34	0.07
Scarus niger [i, j]	17.6cm	3692	5583	+	3.67	2.45	3.16
Scarus prasiognathos	17.8cm	1080	4357	+	5.43*	2.54	0.46
Scarus psittacus	19.4cm	574	840	+	0.42	0.75	3.72
Scarus scaber [b]	19.4cm	784	192	-	4.92*	4.90**,[d]	0.02
Scarus tricolour	20.5cm	570	338	-	0.47	0.70	4.50*
Scarus viridifucatus	17.5cm	48	42	-	0.00	0.15	1.10
Siganus argenteus [b]	18.1cm	1482	3238	+	2.63ns	0.33	3.46
Siganus puelloides [b, h]	16.4cm	2114	922	-	17.93***	0.84	1.78
Siganus stellatus [k]	14.9cm	477	589	+	0.09	4.33*	9.82**
Occasional targets							
Acanthurus leucosternon	12.1cm	886	393	-	0.45	1.96	0.43
Acanthurus lineatus [b]	14.1cm	247	278	+	0.28	3.43*,[e]	1.69
Acanthurus nigrofuscus	15.1cm	511	484	-	0.06	0.43	0.02
Aethaloperca rogaa [b]	17.3cm	210	784	+	0.61	0.35	4.68*
Chlorurus atrilunula [b]	18.4cm	731	2187	+	4.01	1.37	1.40
Ctenochaetus binotatus	13.2cm	20	42	+	0.40	0.24	0.72
Ctenochaetus strigosus [b]	12.8cm	1045	382	-	7.51**	1.41	3.01
Epinephelus caeruleopunctatus	23.2cm	110	227	+	2.51	1.60	2.07
Hipposcarus harid [b]	18.9cm	3621	3160	-	2.91	0.31	2.38
Scolopsis frenatus [b, h]	20.7cm	2922	2303	-	7.70**	1.22	0.76

[a] Values given for year, habitat and protection are F ratios. Probability results: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; no asterisk, not significant. *Cephalopholis urodeta*, *Diagramma pictum*, *Epinephelus hexagonatus*, *E. spilotoceps*, *E. tukula*, *Lethrinus rubrioperculatus*, *L. argentimaculatus*, *Lutjanus monostigma*, *Oxycheilinus diagrammus* and *Paracanthurus hepatus* were not analysed as assumptions could not be met due to too many zero's in counts.

[b] Log$_{10}$ transformation necessary,

[c] Tukey's output: Co>Gr, [d] Tukey's output: (Co=Gr)>Pa, [e] Tukey's output:Gr>(Co=Pa),

[f] Significant year*habitat interaction due to higher biomass in carbonate reefs in 2005, but lower biomass in granite and patch reefs,

[g] Significant year*habitat interaction due to a greater biomass in granite reefs than carbonate and patch reefs in 1994, but similar in 2005.

[h] Significant year*protection interaction due to a greater decline in biomass in protected than fished areas between years,

[i] Significant three-way interaction due to greater changes in carbonate reefs than granite and patch reefs for both year and protection,

[j] Levene's test could only be passed at 0.036, so significance was set at 0.03 for this species.

[k] Significnat three-way interaction due to a greater biomass in granite and patch reefs than carbonate reefs in protected areas, particularly in 2005.

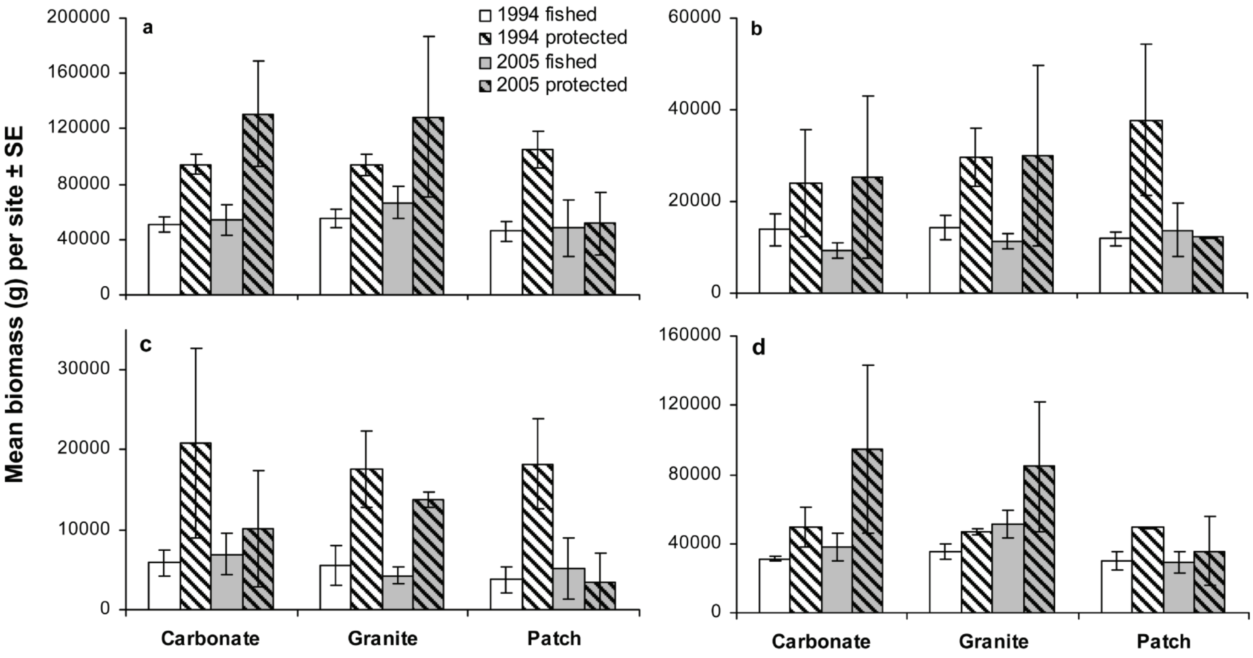

Figure 5.2. Change in biomass of fishery target species above size at first capture between 1994 and 2005 for (a) whole fishery target species assemblage, (b) mixed diet feeders, (c) piscivores, and (d) herbivores in three habitat types (carbonate, granite, patch) and under two types of management (fished, protected).

The slope of the size spectra became less steep from 1994 to 2005 in all but one fished granite site (Figure 5.3a). This trend between years ($F_{1,30} = 18.90$, $p < 0.001$) did not vary among habitats and was not affected by management status (Figure 5.3b). The height of the size spectra did not differ between years or among habitats; however, there was an effect of management status ($F_{1,30} = 17.53$, $p < 0.001$) that showed a greater abundance of fish in MPAs.

The decreasing steepness of the size spectra slope was a result of a relative decline in smaller fish (<30 cm) and increase in larger fish (>45 cm) in the assemblage. This trend was consistent for both fished areas and MPAs (Figure 5.4a). Different size classes in the mixed diet group showed various trends, and there was no common pattern apparent (Figure 5.4b). The piscivores also responded variably; however, medium size classes (20-50 cm) tended to decline, especially in MPAs (Figure 5.4c). The herbivores declined in smaller size classes (<30 cm) and increased in larger size classes (>40 cm) in both fished areas and MPAs (Figure 5.4d). Corallivores and planktivores consistently and markedly declined, which was greatest in MPAs (Figure 5.4e, f). Although there was some variation, particularly for the mixed diet feeders and piscivores, the trends were generally similar among habitat types.

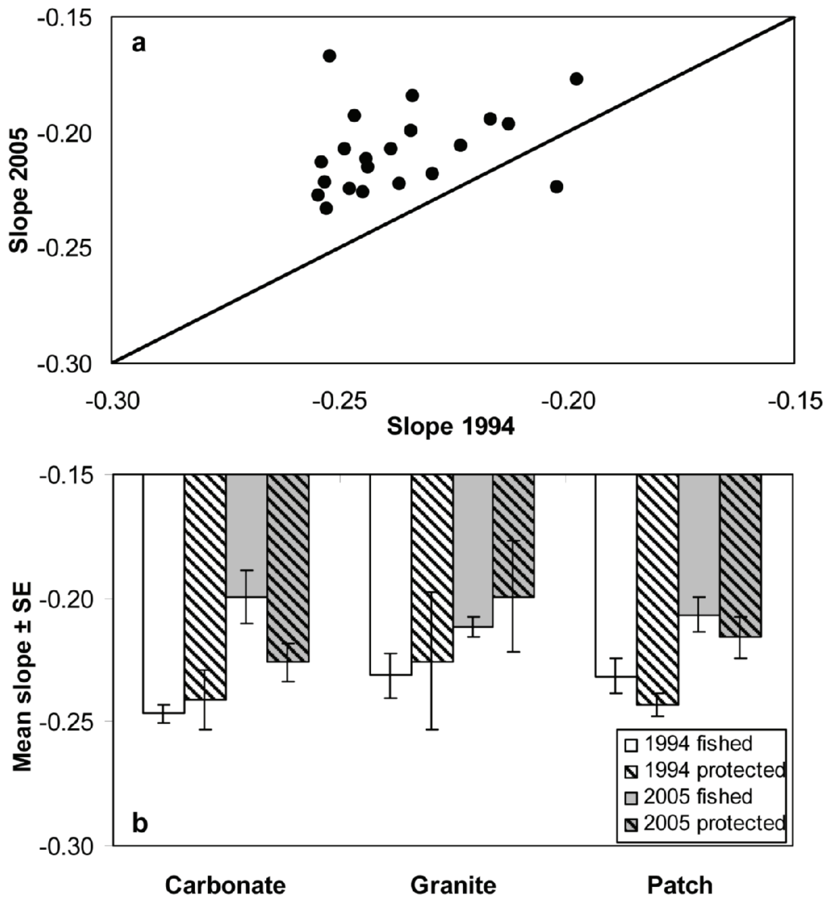

Figure 5.3. (a) Change in the slope of size spectra of the fish assemblage for individual survey sites. Sites falling above the 1:1 trend line had a lower slope value in 2005. (b) Mean change in slope of size spectra of the fish assemblage by habitat type (carbonate, granite, patch) and management status (fished, protected).

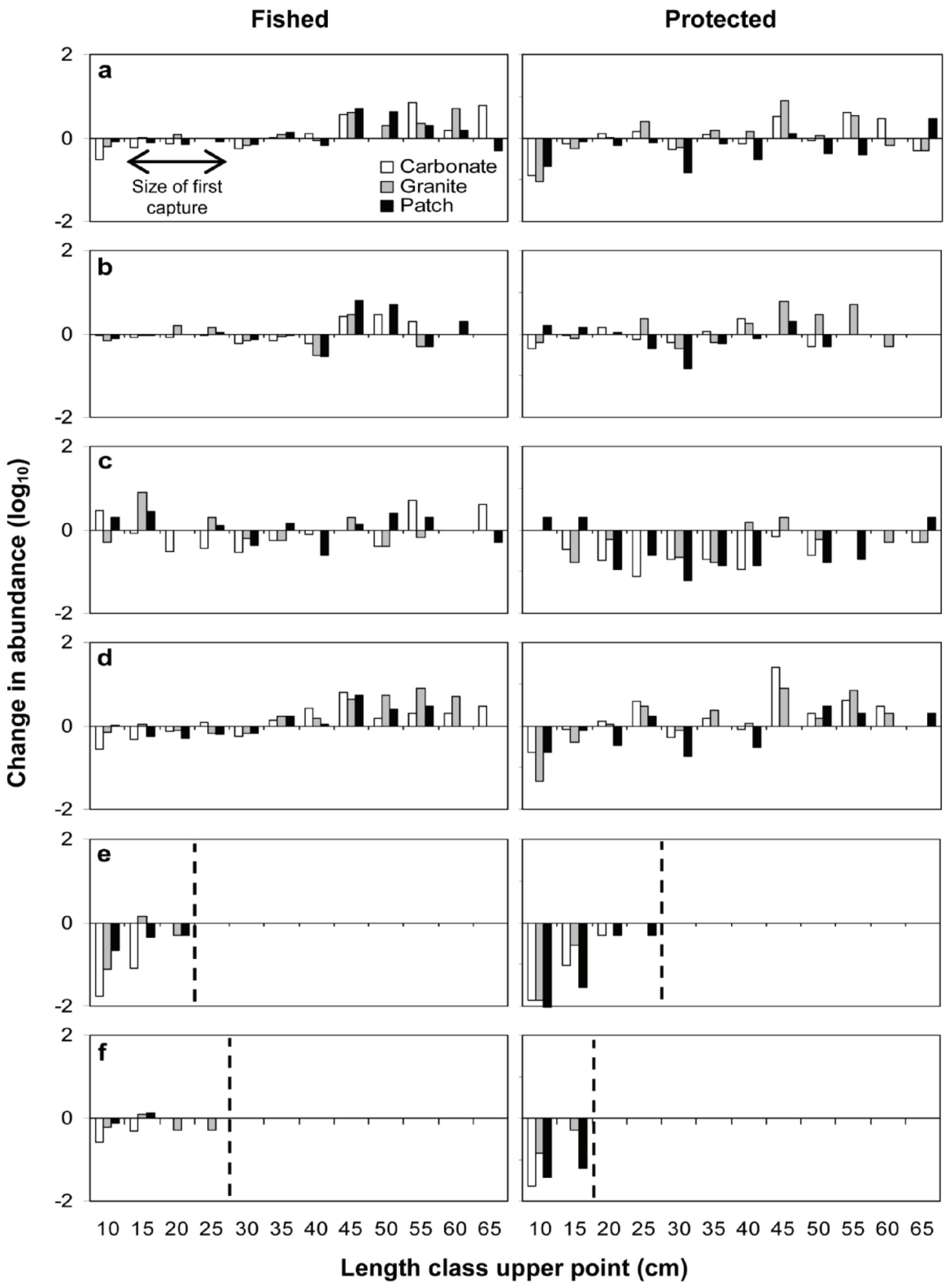

Figure 5.4. Change in log abundance of individual size classes of fish for (a) the entire assemblage, (b) mixed diet feeders, (c) piscivores, (d) herbivores, (e) corallivores, and (f) planktivores by habitat type (carbonate, granite, patch). Plots in left hand column are fished sites, plots in right hand column are protected sites. Size of first capture range indicated on plot (a) for fishery target species. Maximum size detected indicated with vertical dashed line on plots (e) and (f).

5.5 Discussion

We document an impending recruitment failure to reef-fishery size classes in the Seychelles following a major coral bleaching event. This is because the decline in juvenile abundance (<30 cm) in the assemblage will ultimately lead to declines in adult abundance, as is consistently shown in fisheries (Hilborn & Walters 1992). Although our data predict this effect will happen, the lack of time series data and knowledge of the growth trajectories of individual species prevent us from projecting the likely time-span over which this effect will impact larger size classes. Our data also highlight a potential decline in the resilience of coral communities within MPAs due to the decline in smaller size classes of herbivorous fishes in these management areas.

There were only minor changes in the biomass of target species available to the Seychelles artisanal trap fishery following the 1998 mass bleaching event. However, these small changes belie apparent system-wide failures of recruitment to fished size classes that are expected to have long-term impacts on the viability of populations, assemblages, and the fishery. Our results suggest that the current biomass and reef fishery are maintained primarily by the growth of fishes that had already recruited to the reefs at the time of the bleaching event, and/or before topographic structure was reduced, and have now grown sufficiently to reach fishable size. This corroborates other evidence for there being no short-term change in yield associated with mass bleaching (McClanahan et al. 2002; Grandcourt & Cesar 2003).

The surveyed MPAs still supported a higher biomass of target species above size of first capture than fished areas. The greater size-spectra height in the Seychelles MPAs is consistent with the expected effects of reduced fishing mortality on abundance (McClanahan & Graham 2005). However, the reduction in slope of the size spectra was consistent across all but one site and similar for both the fished areas and MPAs suggesting the same drivers are affecting the size distribution of fish in these areas and are unrelated to fishing pressure.

Plotting each individual size class bin by its change in numerical abundance highlights that the change in the slope of the size spectra was driven by both an increase in large individuals (>45 cm) and a decrease in smaller individuals (<30 cm). Because fishing pressure has not changed, the most likely drivers for the increase in larger-bodied fishes are increased growth and/or survivorship. The decline in smaller-bodied individuals could be driven by various processes. We consider consistently high mortality of small and juvenile fish in the years since the bleaching event the most likely explanation, based on the expectation that the larger fishes have retained their abundance and have good feeding conditions, and that many smaller species and individuals are most dependent on refuge availability and live coral (Munday & Jones 1998; Dulvy et al. 2004; Graham et al. 2006). Furthermore, the diversity and numerical abundance of fish 10-30cm in length was correlated with structural complexity in 2005 (Wilson et al. 2007) and showed marked decline between 1994 and 2005 following a loss in structure. While the existence of several years of high larval supply prior to the bleaching event and several years of poor larval supply post-bleaching could also account for the patterns we observed, the latter possibly as a result of reduced live coral as a settlement cue, we consider this unlikely when the effects are manifest for all species and at a large spatial scale. Based on the size-based analyses, we predict a time lag effect whereby the full effects of the bleaching on the fringing-reef fishery species and the fish assemblage as a whole are yet to be realised.

The MPAs seem to offer no long-term resilience to the populations and assemblages. Although the MPAs may meet short-term conservation objectives by reducing fishing mortality on larger fish, future replacement by small fish may be insufficient to maintain abundance over the long-term. The collapse of the physical structure of Seychelles reefs accelerated as recently as 2003 (Engelhardt 2004), so the longer-term consequences of this process are yet to manifest in larger size classes. The lag effect of reduced replenishment will likely be longer in MPAs than in fished areas because mortality rates are likely to be lower and age structures of the populations therefore extended. However, greater predator biomass inside the MPAs could result in higher rates of predation mortality on smaller individuals (Graham et al. 2003; Mumby et al. 2006), ultimately increasing the severity of the lag impact.

The effects on assemblage productivity and hence on fishery yield are expected to be even more substantial than the effects on biomass because the production to biomass (P/B) ratios of smaller individuals and species are higher. Therefore a community of a given biomass that is dominated by larger species will be relatively less productive (Kerr & Dickie 2001). The observed changes in the size-spectra therefore suggest that total production will fall faster than biomass, owing to a decline in abundance of smaller fish and smaller size classes.

The responses of mixed diet feeders and piscivores varied among size classes. Some of the families that make up these groups, for example lethrinids and lutjanids, are generalist in their juvenile habitat use and often associate with soft-bottom habitats (Dorenbosch et al. 2005). Therefore, they may not be as reliant on the reef structure for predator evasion. Within the piscivores there was a decline in the number of fishes in medium size classes (20-50 cm), which was most pronounced in the MPAs. The consistent nature of this decline among habitats suggests a deterministic driver. Piscivores on coral reefs tend to select prey according to their gape size (Mumby et al. 2006) and reef fish predator-prey dynamics are highly size structured (Dulvy et al. 2004), so it is likely that the substantial decline in smaller size classes of the assemblage, which was most evident for the MPAs, may have reduced prey availability for medium-sized Piscivores and thus caused an indirect decline in their numbers.

Of the indirect effects of bleaching that we have identified, one of the most significant for the reef ecosystem as a whole is likely to be the substantial decline in smaller size classes of herbivorous fishes in both fished and protected areas. The surveyed assemblage consisted mainly of surgeonfishes (Acanthuridae) and parrotfishes (Scaridae), but also some rabbitfishes (Siganidae) and two species of damselfishes (Pomacentridae). Separate plots of the changes in size classes over time of acanthurids, scarids, or species that span a large number of size classes showed the same patterns of reduction in small size classes. Many of these species use the reef for habitat as juveniles (Dorenbosch et al. 2005), and because the trend was consistent among habitats and management strategies, it is likely that habitat degradation, which leads to greater competition and predation (Hixon & Jones 2005), is the cause of decline in smaller sizes. Acanthurids can live over 25 years and scarids live 5-20 years (Choat & Robertson 2002), so individuals currently contributing to the increase in numerical abundance of large size classes likely recruited prior to the 1998 bleaching event or the collapse of the reef framework in 2003 (Engelhardt 2004). When disturbances are extensive and occur over large spatial scales, increased abundance of large herbivores can result from faster growth rates (Hart & Russ 1996) and potentially higher survivorship associated with greater food abundance. However, fewer fish in smaller size classes are surviving to replace adults, and a subsequent decline in overall biomass of herbivores seems likely. Herbivores are common targets of the trap fishery in the Seychelles (Grandcourt 1999), and yields have remained stable through the bleaching event (Grandcourt & Cesar 2003), despite the increase in larger fish we identified. This is consistent because the decline in small-sized fish extends up to 30 cm, resulting in no substantial increase in biomass above size at first capture.

Herbivores are important to the resilience of coral reefs because they control algae and promote coral recovery (Bellwood et al. 2004; Mumby et al. 2006). Our results suggest that mass bleaching and the loss of structural complexity may ultimately lead to a reduction in the abundance of herbivores, including larger size classes, and as such, resilience of reefs may decline over the long-term. Because the trend is also apparent in the sampled MPAs, our data suggest the MPAs offer no long-term refuge from the impacts of coral bleaching.

What are the consequences for reef fisheries? In Seychelles 50-60% of trap fishing effort occurs close to the shore and within the depth range of the data collected in this study (T.D., unpublished data), suggesting that a future decline in biomass of target species will affect the trap fisheries. However, given that a substantial portion of trap fishing grounds lie on deeper shoals and submerged reefs of the Mahé Plateau, there is potential for a degree of spatial mobility in the fishery if declines in target-species biomass are restricted to the shallow fringing reefs. If other locations suffer coral mortality and collapse on the scale of the Seychelles, target species assemblages will likely respond in the same way. In locations where the topography does not allow for a diversity of demersal fishery habitats and depths and the entire demersal fishery is restricted to the inshore reef (e.g. Fiji; Jennings & Polunin 1997), the long-term impacts of bleaching on fishers could be more substantial.

The corallivores and planktivores demonstrated very large and consistent declines between years. Corallivores are well known to suffer declines and even local extinctions as a result of mass mortality of corals (Graham et al. 2006; Wilson et al. 2006; Pratchett et al. 2006, Chapter 2 & Graham 2007). The planktivores in our study were principally coral dwelling damselfish, which suffer large declines through coral mortality (Wilson et al. 2006). Furthermore, both groups have small body size, suggesting they are more reliant on the reef matrix to avoid predation (Munday & Jones 1998). The decline in both cases was greatest in the MPAs. Corallivore numbers declined from a mean of 31.7 to 5.3/site in fished areas and from 74.5 to 2.7/site in MPAs. Similarly, planktivore numbers declined from a mean of 90.3 to 44.4/site in fished areas and from 279.8 to 11.2/site in MPAs. These declines are associated with the greater cover of the complex coral category in the MPAs prior to the bleaching event, which is the preferred habitat of many specialist fish (Munday 2004; Pratchett 2005). The result is a subsequent homogenization of the MPAs and fished areas in terms of benthic cover and composition, and the numerical abundance of small specialized fish species post-bleaching.

In recent decades conservation of marine resources on coral reefs has focused on the use of MPAs. Previous studies have highlighted that reef fish diversity and abundance can be compromised in MPAs following coral mortality (Jones et al. 2004), and here we provide evidence that the size structure of fish assemblages are subject to the same long-term effects in MPAs and fished areas. Because future bleaching events seem inevitable (Sheppard 2003), the implementation of methods to ameliorate climate-mediated disturbance should be treated as a priority in conservation and management plans for coral reefs. We recognise that some areas are less susceptible to climate-induced disturbance and some show greater recovery and therefore support the notion that MPAs should increasingly be sited in areas of resistance or resilience to bleaching to build up spatial resilience in the system (West & Salm 2003). In Seychelles the reefs north of Praslin and south of Mahé, and the granitic habitats in general are currently displaying the most recovery and the most stable fish populations (Graham et al. 2006) and would be suitable locations for future MPAs. Marine protected areas are not the only management tool available, however, and it is important to manage areas outside MPAs to minimise other stressors, such as overfishing and nutrient enrichment, to create conditions where a recovery may be possible if brood stocks are available.

5.6 Acknowledgements

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Chapter 6

Climate Warming, Marine Protected Areas and the Ocean-Scale Integrity of Coral Reef Ecosystems[5]

6.1 Abstract

Coral reefs have emerged as one of the ecosystems most vulnerable to climate variation and change. While the contribution of a warming climate to the loss of live coral cover has been well documented across large spatial and temporal scales, the associated effects on fish have not. Here, we respond to recent and repeated calls to assess the importance of local management in conserving coral reefs in the context of global climate change. Such information is important, as coral reef fish assemblages are the most species dense vertebrate communities on earth, contributing critical ecosystem functions and providing crucial ecosystem services to human societies in tropical countries. Our assessment of the impacts of the 1998 mass bleaching event on coral cover, reef structural complexity, and reef associated fishes spans 7 countries, 66 sites and 26 degrees of latitude in the Indian Ocean. Using Bayesian meta-analysis we show that changes in the size structure, diversity and trophic composition of the reef fish community have followed coral declines. Although the ocean scale integrity

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of these coral reef ecosystems has been lost, it is positive to see the effects are spatially variable at multiple scales, with impacts and vulnerability affected by geography but not management regime. Existing no-take marine protected areas still support high biomass of fish, however they had no positive affect on the ecosystem response to large-scale disturbance. This suggests a need for future conservation and management efforts to identify and protect regional refugia, which should be integrated into existing management frameworks and combined with policies to improve system-wide resilience to climate variation and change.

6.2 Introduction

Coral reefs are one of the ecosystems most threatened by climate variability and change (Walther et al. 2002; Hughes et al. 2003; Hoegh-Guldberg et al. 2007). Reef corals, the building blocks of carbonate reefs, have a restricted thermal tolerance, resulting in 'bleaching' events (loss of symbiotic algae) when sea surface temperatures rise above a given threshold (Brown 1997). This has contributed to widespread loss of live coral cover (Goreau et al. 2000; Gardner et al. 2003; Bellwood et al. 2004; Bruno & Selig 2007), the restructuring of benthic community composition (McClanahan et al. 2007a) and has resulted in dire predictions for the future persistence of coral-dominated ecosystems within decadal time scales (Hoegh-Guldberg 1999; Sheppard 2003). There is now a need to understand resultant large-scale implications for other components of the ecosystem, which, to date, have received limited attention or been the focus of local studies (Jones et al. 2004; Graham et al. 2006; Pratchett et al. 2008a). Assessing ecosystem trends and patterns at regional scales is necessary if informed management choices are to be made that will mitigate the effects of large-scale climate disturbance. Importantly, there is a need to test key paradigms, such as the ability of no-take areas (NTAs) to enhance recovery from climate change impacts (Hughes et al. 2003), and the potential for herbivorous fish to increase in abundance following coral mortality and functionally compensate for increased algal coverage (Wilson et al. 2006).

At large scales, remote pristine areas may have a greater capacity to absorb climate impacts and maintain a coral dominated and diverse ecosystem (Sandin et al. 2008). However, most coral reef NTAs are small and embedded in heavily fished and degraded environments (Bellwood et al. 2004; McClanahan et al. 2007e). Assessing the importance of local management for conserving coral reefs in the context of global change has been identified as a key research challenge for coral reef scientists (Knowlton & Jackson 2008). Although there are expectations that NTAs will promote resilience and faster recovery from climate disturbance (Worm et al. 2006), site-specific studies suggest this may not be the case (Jones et al. 2004; Chapter 5 & Graham et al. 2007a; McClanahan 2008), and the effectiveness of such management needs to be assessed across regional spatial scales.

Grazing by herbivores, by creating space for invertebrate larval settlement, is thought to be key to maintaining reefs in a coral dominated state (Hughes 1994; Bellwood et al. 2004; Mumby et al. 2006). However, it is increasingly evident that the majority of herbivorous fish in the Indo-Pacific will crop turf algae, but feed less on or avoid erect macroalgae once it has developed (Bellwood et al. 2006a; Ledlie et al. 2007). Following large-scale disturbances that open up large amounts of space on reefs, such as mass coral bleaching, herbivores may become swamped by the biomass of the new algal resource (Williams et al. 2001) and reefs can progress on a trajectory to macroalgal dominance (Mumby et al. 2007a). It is therefore important to assess whether herbivorous reef fish increase in abundance following large-scale coral loss and thus have the ability to prevent reefs from becoming dominated by erect macroalgae.

Coral mortality through climate induced bleaching was particularly severe in the Indian Ocean in 1998, with ~45% of coral cover lost across the region (Hoegh-Guldberg 2004), although the effects were spatially variable (Goreau et al. 2000; McClanahan 2007a). We assess the longer-term effects of this event in fished areas and NTAs across 7 countries, 66 sites and 26 degrees of latitude. Specifically, we conducted a targeted research program whereby the original investigators who collected comprehensive benthic and fish assemblage data from Maldives, Chagos, Seychelles, Kenya, Tanzania, Mauritius, and Réunion in the mid-1990s repeated their surveys post-bleaching, in 2005. We use continuous model Bayesian meta-analysis to quantify effects of changes in live coral cover and physical complexity of reefs on the diversity, size structure, trophic structure and abundance of reef fish. The Bayesian approach not only structures the inherent uncertainty in monitoring data from multiple sources, but also allows belief statements to be made regarding future change (Clark 2005). With ever more frequent bleaching events predicted (Sheppard 2003), quantitative predictions regarding how fish will respond to future declines in coral cover over large spatial scales are needed to guide regional conservation planning, adaptation and mitigation strategies.

6.3 Methods

We identified all field studies that had comprehensively surveyed reef fish assemblages and associated benthic composition and structure from the western Indian Ocean region from 1990 to before the 1998 coral bleaching event (majority 1994-95). This resulted in eight separate large-scale studies (across seven countries). Original investigators returned to their study locations in 2005 to repeat the surveys, using field protocols identical to those used in the original surveys. The protocols were standardised within, rather than among study locations as it is more robust to quantify effect sizes in this way and then standardise when comparing among studies. Where the original investigator could not return, an experienced surveyor from the team repeated the work. An associated field study workshop for the project, which involved many of the researchers from the region, found experienced observer bias to be a very small component of the variation in fish counts (McClanahan et al. 2007d). All reef surveys were conducted on the reef flat or shallow reef slope. The abundance of all diurnally active, non-cryptic, reef-associated fish was assessed during each survey, however methods varied among study locations from point counts of differing dimensions to belt transects of differing dimensions. Replication also varied from 3 to 16. This resulted in a survey area per site of ~200m^2 to ~2500m^2. Benthic quantification also varied in spatial scale and from visual estimates to line intercept transects, but the results are expected to be comparable (Wilson et al. 2007). Estimates of change in live coral cover were calculated and plotted on a map by country and management strategy and at a more aggregated level with 95% confidence limits. Measures of structural complexity also varied and included visual assessments of reef topography, the linear versus contour method and measures of reef height. However these measures were found to be strongly correlated (Wilson et al. 2007) and these correlation coefficients were used to standardise them to a common scale. The relationship between percent change in coral cover and percent change in structural complexity was assessed by correlation analysis. The presence of variation in field methods is routine in meta-analytical studies, and thus the choice of effect size calculation and variance weighting is integral to the comparability of study results (Côté et al. 2005).

6.3.1 Effect size

Meta-analysis frequently employs unitless effect size metrics to standardize the information present among accumulated studies. The potential to observe changes in a before and after comparison can be greatly influenced by initial values at a given location; sites with larger initial values have a greater scope to reveal change than those with low values (Côté et al. 2005). To achieve a comparable metric at all locations and to account for initial cover / values, we calculated effect sizes as the percent change between the mid 1990s and 2005 (Kaiser et al. 2006);

$$\%difference\Delta = [(A_{a,i} - A_{b,i}) / A_{b,i}] \times 100 \qquad (1)$$

where A_b and A_a were mean values at sites in the mid 1990's and 2005 respectively. We did not account for study duration (Côté et al. 2005) as we made the informed assumption that the greatest changes occurred in 1998 and our measures in the mid-1990's are an appropriate estimate of pre-bleaching conditions. Furthermore as sampling date was standardised for post-1998 surveys, any incorporation of duration could unduly bias effect sizes based on pre-disturbance study dates. Finally, we are estimating a magnitude of change, rather than a rate of change. See Côté et al. (2005)

for use of rate of change metrics. We calculated individual effect sizes for change in coral cover, structural complexity, fish species richness, and fish density in four functional groups for which data were available at the majority of sites (obligate corallivores, herbivores, planktivores, and mixed-diet fishes assigned using regional fish identification guides, published literature and http://www.fishbase.org), for four size classes of fish species (maximum attainable size <20 cm, 21-40 cm, 41-60 cm, and >60 cm) and for the same four functional groups listed above within the <20 cm maximum attainable size category. Herbivores include all those species that feed on algae and or detrital aggregates from the epilithic algal matrix. Because percent-change losses have a strongly right-tailed distribution, i.e. a maximum potential decline of 100%, but a potentially limitless increase, we transformed all of the Δ^T values to be balanced around zero following Kaiser et al. (2006):

$$\Delta^T = log_e(1+[\Delta/101]). \qquad (2)$$

This transformation prevents overestimates of increases and underestimates of declines, where a maximum potential decline has a value of -4.6 and a maximum increase +4.6. The transformation approximately normalises the error distribution and stabilises its variance (Kaiser et al. 2006). Raw data were available for many of the original studies, allowing us to estimate average effect-sizes at some locations. Because data were collected from the same sites but not the same transects, we estimated effect-size means and variances at these sites using non-parametric bootstrapping of the before and after observations (R=9999) (Efron & Tibshirani 1993) with (1) and (2), by randomly matching before-after pairs at each iteration. This generated sample means and expected variance ranges for many, but not all, of the study locations.

6.3.2 Bayesian meta-analysis

We evaluated evidence for a regional relationship between coral cover and reef fish using an area-variance weighting scheme implemented in a Bayesian meta-analysis framework. The use of area surveyed as a weighting scheme in coral reef meta-analyses has become widespread because actual variance will depend on individual measurement size and replication (Côté et al. 2005). The Bayesian approach allowed us to model the hierarchical structure of the data, estimate the magnitude of regional-scale effects, and to specify a level of uncertainty about individual study estimates. By sharing information among studies, this approach maximized the strength of inferences made across the entire range of meta-data used, allowing us to make probability statements about the likelihood of reef fish declines given potential future changes in coral conditions. Although we tested five different ecologically meaningful response trajectories (asymptotic, quadratic, logistic, linear and exponential), we found no model-based evidence for non-linear responses based on Bayesian Information Criterion (BIC) scores among candidate models. We therefore quantified the regional fish community response between the mid 1990s and 2005 using a null model (intercept-only; M_0) and exchangeable linear model (M_c) of coral effect size β_{coral},

$$\Delta^T_{f,j} \sim N(\theta_{f,j}, \sigma^2_{jf}), \tag{3}$$

$$\Delta^T_{c,j} \sim N(\theta_{c,j}, \sigma^2_{jc}), \tag{4}$$

$$\sigma_j^2 = \begin{cases} \left[\dfrac{\log(area_{\max})}{\log(area_j)}\right]\sigma_{j*}^2, & \textit{if original data unavailable} \\ \left[\dfrac{\log(area_{\max})}{\log(area_j)}\right]\sigma_{jb}^2, & \textit{if original data available} \end{cases} \tag{5}$$

$$\theta_{f,j} \sim N(\beta_0 + \beta_{coral}(\theta_{c,j}), \sigma_\theta^2), \tag{6}$$

where $\Delta_{f,j}^T$ is the study point estimate of the fish effect size $\theta_{f,j}$ from the j^{th} study; $\Delta_{c,j}^T$ is the study point estimate of coral effect size $\theta_{c,j}$ in the j^{th} study; σ_j^2 is the study fish or coral variance that is assumed known; σ_{j*}^2 is the maximum of the known (bootstrap estimated) site-level variances for fish or coral among the studies used; $area_{max}$ is the maximum reef area surveyed; σ_{jb}^2 is the bootstrap-estimated site-level variance for sites where raw data was available; and σ_θ^2 is the estimated regional variance. The area-weighted σ_j^2's were likely to be conservative because they were scaled down from the largest known study variance, expressing an equal or greater level of uncertainty than any of the known sample variances, thus weighting the variance based on the area of reef surveyed.

This continuous meta-analysis model was fully-specified by non-informative prior distributions for the estimated parameters,

$$\beta_0 \sim N(0,1000) \tag{7}$$

$$\sigma_\theta^2 \sim U(0,1000) \tag{8}$$

$$\beta_{coral} \sim N(0,1000) \tag{9}$$

In addition to the coral effects model, we included a NTA model to estimate the effects of fishery protection on changes in coral and fish metrics. This protection model (M_{cp}) included a modification of equation (6) to include a dummy variable (*status*) that allowed the slopes ($\beta_{protection}$) and intercepts (β_{prot0}) of the coral relationship to vary between NTAs and fished areas:

$$\theta_{f,j} \sim N(\beta_0 + \beta_{prot0}(status) + \beta_{coral}(\theta_{c,j}) + \beta_{coral}(\theta_{c,j}) * \beta_{protection}(status), \sigma_\theta^2). \qquad (10)$$

Priors for all slopes and intercepts were as specified by equation (9). We implemented both regional models using the PyMC Markov-Chain Monte Carlo (MCMC) toolkit for the Python programming language. Meta-analytical models were run for 20 000 iterations with a 10 000 iteration burn-in period. We evaluated model convergence using Geweke's method (Efron & Tibshirani 1993). Model goodness-of-fit (GOF) was assessed using the deviance simulation methods in PyMC, where ideal models yield GOF values near 0.5, providing evidence of equivalence between simulated and observed deviance (Gelman et al. 2004). Our Bayesian meta-analyses had GOF scores between 0.46 and 0.50 for all fish metrics, confirming good model fits for estimating effect-size relationships, and model convergence was deemed adequate in every instance (Gelman et al. 2004). Site-level posterior distributions shrunk towards the regional mean, where the extreme high- and low-value effect sizes had a reduced effect on the overall estimates. Relative evidence for each model was evaluated using the Bayesian Information Criterion (BIC) (Schwartz 1978) and the uncertainty surrounding each posterior parameter estimate.

From the area of highest posterior density in the posterior distribution of each model parameter we obtained Bayesian credible intervals (CI) that defined a 95% probability of a given parameter lying within the CI range. During each MCMC simulation we also sampled from the full conditional of the model and data to construct predictive intervals (PI) that defined a 95% probability of future observations being within the PI range. The PI interval values allowed us to make probability statements about the response of fish assemblage groups to future coral depletion.

6.4 Results

Change in hard coral cover across the region between the mid 1990s and 2005 varied geographically (Figure 6.1). The changes reported here represent the combined effects of coral loss in 1998 and any subsequent recovery to 2005. The greatest declines were apparent through the low latitude island states of Maldives, Chagos, and Seychelles. Kenyan and Tanzanian nationally protected sites experienced moderate declines, while Mauritius and Réunion sustained the smallest declines, and coral cover increased in Kenyan and Tanzanian fished sites (Figure 6.1). Assessing change in coral cover at relevant scales, that consider location, management and habitat type, indicates that 10 of our 19 study locations exhibit declines that depart significantly from zero (Figure 6.2A). The study incorporated nine no-take areas (NTAs) across four countries (two in Seychelles, four in Kenya, two in Tanzania and the long-term de-facto protection of reefs of the Chagos archipelago (Sheppard 2000)). A greater proportion of NTAs (71 %) than fished (42 %) locations showed significant declines in coral cover over the study period. Based on bootstrapped 95% confidence limits, there was no evidence to suggest the percent change in coral cover differed between NTAs and fished areas, and in some cases declines were significantly greater in NTAs

(Figure 6.2A). Importantly, the NTAs had greater starting coral covers than adjacent fished areas, which, as NTAs and fished areas declined to similar final covers (Table 6.1)(with the exception of some of the less impacted Tanzanian sites), meant the NTAs had further to fall.

It is clear that the impacts of the 1998 bleaching event were highly variable across the region, and provide a continuum against which to test secondary consequences, such as the effects of coral loss on fish assemblages. Recent developments in assessing the effects of coral disturbance on fish have highlighted the importance of eroding structural complexity in driving responses (Garpe et al. 2006; Graham et al. 2006), which, as erosion of coral structures can take 5-10 years, explains the much smaller impacts on fish shortly after coral mortality (Wilson et al. 2006). Structural complexity was quantified at 50 of our 66 sites. Importantly, there was a strong correlation between loss in coral cover and loss in structural complexity across the region (r = 0.77, $P<0.001$, Figure 6.2B). The strong collinearity in the two measures precludes independent assessment of variables, and therefore the effects of changing coral cover on fish identified in the Bayesian meta-analyses are likely to result from a combination of loss in coral cover and structural complexity.

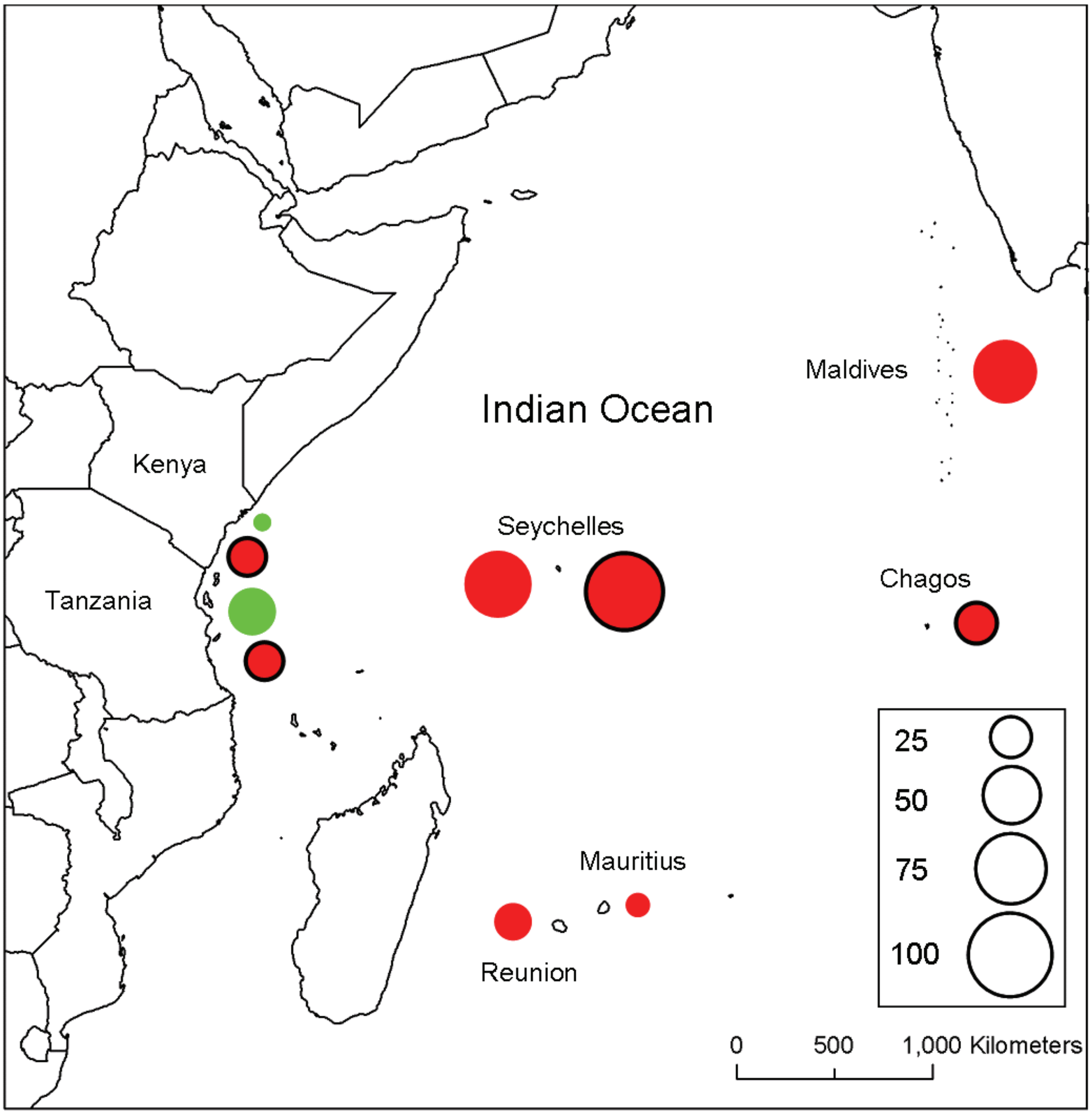

Figure 6.1. Change in coral cover at sites across the western Indian Ocean. Green and red symbols represent increases and decreases in coral cover respectively. Symbols with solid borders are sites in NTAs; Seychelles data include two NTAs, Kenya includes four, Tanzania two and the Chagos archipelago is a de-facto NTA. Data represent 66 sites across the region. Numbers in key (size of bubble) are percent changes between mid 1990s and 2005. Map produced using ESRI data and ArcGIS 9.

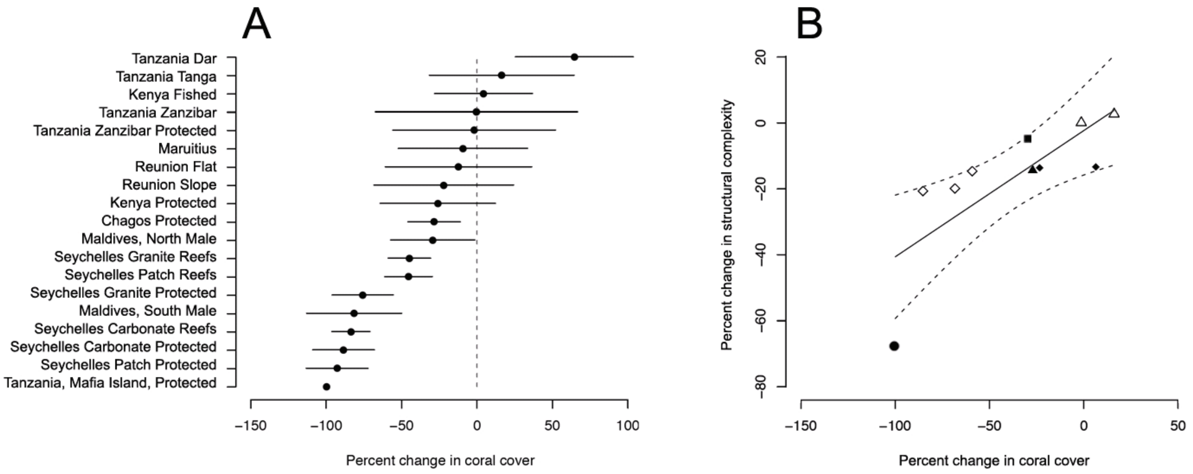

Figure 6.2. Change in coral cover and reef structural complexity. (*A*) Change in live coral cover at meaningful biogeographical aggregations and by management strategy. Three habitat types in Seychelles each replicated in the two NTAs. Kenyan protected represents four NTAs. Bootstrapped 95% confidence intervals indicate whether mean change departs significantly from zero. Locations ordered by magnitude of coral decline. (*B*) Correlation between change in live coral cover and change in structural complexity across the region. ● Mafia Island, ◊ Seychelles, ▲ Chagos, ■ Maldives, ♦ Kenya, Δ Tanzania.

Table 6.1. Mean coral cover before (mid-1990s) and after (2005) the 1998 bleaching event across the Indian Ocean. Sites aggregated at representative geographic scales that consider location, management and habitat type. Three habitat types in Seychelles each replicated in the two NTAs. Kenyan protected represents four NTAs. Number of sites per location given in brackets. Note, Tanzania, Mafia Island, received no-take status in 2000.

Location	% Coral Cover mid-1990s	± SE	% Coral Cover 2005	± SE
Maldives, North Male (3)	15.5	7.5	10.9	3.2
Maldives, South Male (2)	43.9	3.6	8.0	1.2
Chagos (9)	31.2	4.0	22.8	2.9
Seychelles Carbonate Reefs (5)	34.6	2.7	5.6	3.1
Seychelles Carbonate Protected (2)	44.9	4.8	5.1	4.5
Seychelles Granite Reefs (5)	14.8	2.0	8.2	2.3
Seychelles Granite Protected (2)	30.9	7.6	7.5	6.4
Seychelles Patch Reefs (5)	20.0	1.5	10.9	5.1
Seychelles Patch Protected (2)	46.4	7.8	3.6	3.0
Kenya Fished (4)	18.9	5.2	20.0	4.0
Kenya Protected (4)	34.8	4.5	26.8	8.1
Tanzania Dar (4)	42.6	11.9	70.0	3.2
Tanzania Tanga (4)	23.9	7.5	27.8	6.8
Tanzania Zanzibar (2)	48.5	3.8	48.3	3.3
Tanzania Zanzibar Protected (2)	62.7	11.1	61.5	2.4
Tanzania, Mafia Island, Protected (2)	33.0	N/A	0.1	N/A
Reunion Flat (2)	42.5	24.3	37.0	10.9
Reunion Slope (2)	42.0	5.0	28.4	4.5
Mauritius (5)	45.3	9.5	41.1	6.7

Coral loss predicted declines in reef-fish species richness, and abundance of obligate corallivores, planktivores and fishes < 20 cm throughout the western Indian Ocean (Table 6.2). We tested five possible trajectory descriptors in each case, but only found evidence for linear fits between coral decline and change in groupings of the fish community. Trends in species richness were significant, but weak, and largely driven by the Seychelles and Mafia Island (Figure 6.3A). There was substantial evidence for a 1:1 relationship between changes in obligate corallivore abundance and percent coral cover (Figure 6.3B). From these results we estimate, given any future 50% decline in coral cover, there is a 76% probability of equivalent declines in obligate corallivores at any given site in the western Indian Ocean. The relationship between change in diurnal planktivore abundance and coral cover was relatively strong; given a future 50% decline in coral cover, we estimate a 68% probability of observing declines in planktivore abundance (Figure 6.3E). We found no relationship between a loss of coral and change in abundance of herbivore and mixed diet feeder groups (Figure 6.3C,D).

Table 6.2. Continuous model Bayesian meta-analysis parameter estimates from the best-fitting models (see Table 3) for reef fish metrics in the western Indian Ocean. Estimates for groups with equivalent model fits are provided for both models. Values in parentheses are standard deviations; values in square brackets are 95% credible intervals.

Metric	**Model**	$\hat{\beta}_0$ **(intercept)**	$\hat{\beta}_{coral}$ **(slope)**	$\hat{\beta}_{protected}$ **(intercept)**	$\hat{\beta}_{protected}$ **(slope)**
Species richness	M_c	0.00 (0.03) [-0.07, 0.06]	0.10 (0.02) [0.06, 0.14]	-	-
Obligate corallivores	M_c	-0.26 (0.21) [-0.66, 0.16]	1.05 (0.14) [0.77, 1.30]	-	-
Herbivores	M_0	-0.28 (0.08) [-0.45, -0.12]	-	-	-
Mixed-diet feeders	M_0	-0.18 (0.06) [-0.28, 0.08]	-	-	-
Planktivores	M_{cp}	-0.42 (0.16) [-0.74, -0.10]	0.52 (0.16) [0.28, 0.77]	1.02 (0.35) [0.35, 1.69]	0.61 (0.24) [0.10, 1.07]
Planktivores	M_c	-0.15 (0.15) [-0.44, 0.14]	0.68 (0.10) [0.48, 0.87]	-	-
<20 cm	M_c	-0.17 (0.09) [-0.35, 0.00]	0.37 (0.06) [0.28, 0.49]	-	-
21-40 cm	M_0	-0.21 (0.09) [-0.40, -0.05]	-	-	-
41-60 cm	M_0	-0.59 (0.17) [-0.91, -0.26]	-	-	-
>61 cm	M_0	-0.37 (0.21) [-0.77, 0.04]	-	-	-
<20 cm obligate corallivores	M_c	-0.39 (0.19) [-0.77, -0.00]	0.94 (0.13) [0.69, 1.19]	-	-
<20 cm herbivores	M_c	-0.19 (0.16) [-0.51, 0.13]	0.50 (0.10) [0.29, 0.71]	-	-
<20 cm herbivores	M_{cp}	-0.28 (0.18) [-0.65, 0.08]	0.24 (0.14) [-0.05, 0.53]	0.37 (0.35) [-0.33, 1.06]	0.53 (0.21) [0.12, 0.95]
<20 cm mixed diet feeders	M_0	-0.46 (0.06) [-0.58, -0.34]	-	-	-
<20 cm planktivores	M_c	-0.10 (0.16) [-0.43, 0.23]	0.57 (0.110 [0.35, 0.78]	-	-

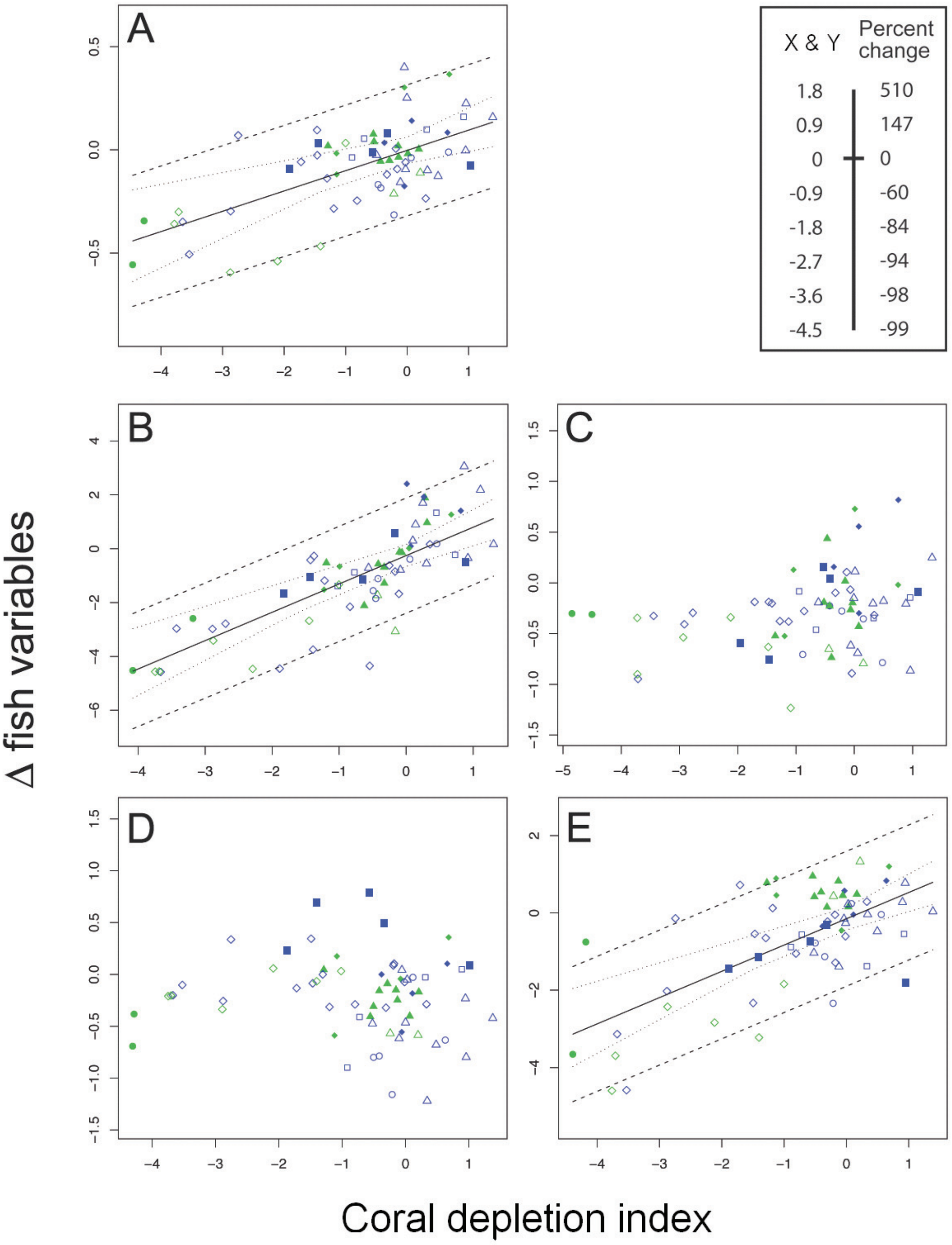

Figure 6.3. Change in fish groups in response to coral decline. Continuous model Bayesian meta-analysis of relationships between decline in coral cover and change in (*A*) species richness of fish assemblages, and (*B*) abundance of obligate corallivores, (*C*) herbivores, (*D*) mixed diet feeders, (*E*) planktivores. Scale as converted to percent change indicated in top right panel. Linear trend lines only presented where significant model fits were recorded. Green symbols indicate sites in NTAs, blue symbols indicate sites in fished areas. Inner dashed line represents 95% credible interval on the regression and outer dashed line represents the 95% prediction interval. ● Mafia Island, ◊ Seychelles, ▲ Chagos, ■ Maldives, ♦ Kenya, Δ Tanzania, □ Réunion, ○ Mauritius. Movement of points along the x-axis among panels reflects model-structured uncertainty present among studies.

When species were grouped by their maximum attainable size, a clear trend was apparent for species <20 cm total length, but no relationship was observed for 21-40 cm, 41-60 cm or >60 cm groupings (Figure 6.4A; Table 6.2). Given a future 50% decline in coral cover, we estimate a 52% probability of observing declines in the abundance of fish species with maximum body lengths <20cm. Within this size class, planktivores make up a considerable portion of the abundance (44%), and herbivores and mixed diet feeders also contribute substantially (28% and 20% respectively), but corallivores have limited input (8%) (Figure 6.4B). Separate analyses of trophic groups within the <20cm size category highlights that, along with obligate corallivores and planktivores, there was also evidence of declines in herbivores (Table 6.2).

We only found weak evidence for differences between NTAs and fished areas for change in diurnal planktivore abundance and small-bodied herbivore abundance (<20cm) (Table 6.3). In both cases the negative relationship between fish abundance and coral decline was greater for the NTAs, however there was equal support for model M_c with no differences between types of management (Table 6.3). Importantly, irrespective of body size and trophic categorization, NTAs provided no clear benefits for any of the fish groups in terms of their change in response to coral decline.

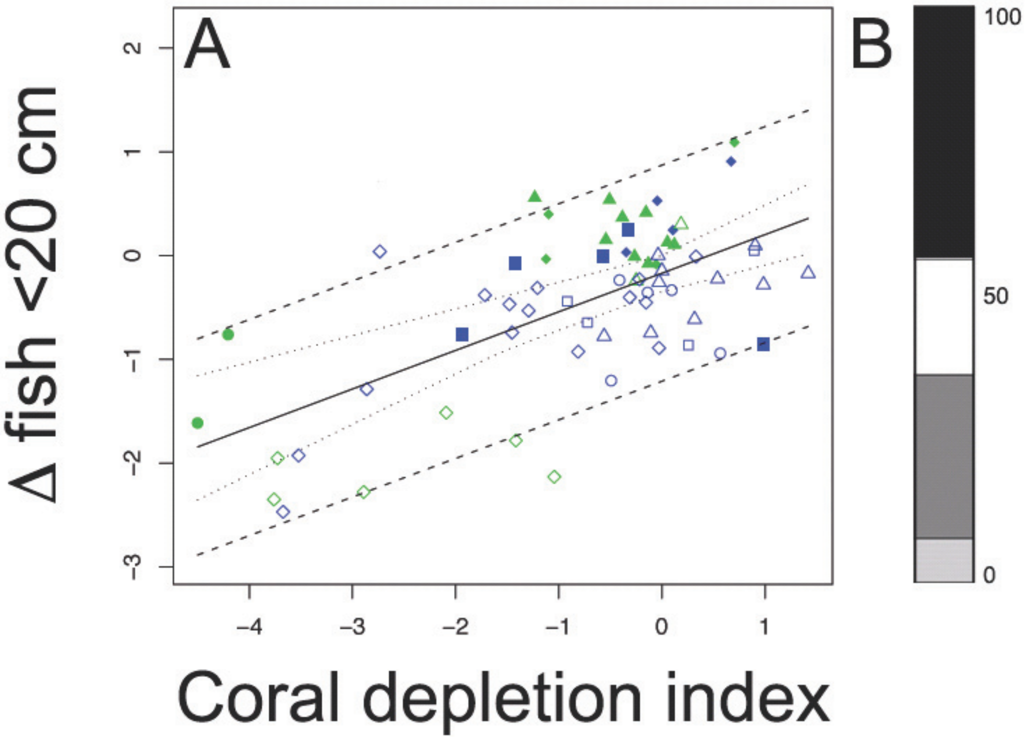

Figure 6.4. Change in small bodied fish in response to coral decline. (*A*) Continuous model Bayesian meta-analysis of relationship between decline in coral cover and change in fish <20 cm maximum attainable size. Green symbols indicate sites in NTAs, blue symbols indicate sites in fished areas. Inner dashed line represents 95% credible interval on the regression and outer dashed line represents the 95% prediction interval. ● Mafia Island, ◊ Seychelles, ▲ Chagos, ■ Maldives, ♦ Kenya, Δ Tanzania, □ Réunion, ○ Mauritius. (*B*) Percent contribution of five trophic groups to the starting (mid-1990’s) abundance of fish <20 cm maximum attainable body length across the region. Black = planktivores, dark grey = piscivores (barely present on plot; 0.05%), white = Mixed diet feeders, grey = herbivores, light grey = obligate corallivores.

Table 6.3. Model-selection results for continuous model Bayesian meta-analysis in the western Indian Ocean using the Bayesian Information Criterion (BIC). Models include a null model of no relationship (M_0), a model including a relationship between changes in coral cover and reef fish metrics (M_c), and a fish-coral model that allows for differences between protected and unprotected sites (M_{cp}). Models highlighted in bold have the greatest support, given the data; models with BIC differences of <2 are considered to have equal support.

Metric	**M_0**	**M_c**	**M_{cp}**
Species richness	17.53	**1.64**	6.35
Obligate corallivores	282.90	**248.38**	256.38
Herbivores	**145.83**	149.61	157.35
Mixed-diet feeders	**83.64**	87.40	91.90
Planktivores	237.66	**205.27**	**204.30**
<20 cm	165.25	**138.72**	140.60
21-40 cm	**146.91**	150.00	158.17
41-60 cm	**231.69**	**231.35**	235.95
>61 cm	**261.85**	266.02	272.32
<20 cm obligate corallivores	275.96	**238.91**	246.80
<20 cm herbivores	230.91	**214.86**	**216.53**
<20 cm mixed diet feeders	**94.93**	99.11	106.16
<20 cm planktivores	237.76	**218.23**	222.13

6.5 Discussion

We have identified spatially variable declines in coral cover, reef structural complexity, fish species richness and the abundance of various feeding and size groups of reef fish across the Indian Ocean following the 1998 bleaching event. These changes are substantial for some groups, and indicate little insurance offered by current small-scale NTA management across the region. The spatial patterns present in our data provide important information for future conservation planning and generic lessons for managing whole coral reef ecosystems in a changing climate.

There was little difference in the decline of coral cover between NTAs and fished areas across the Indian Ocean, with some evidence for greater declines within NTAs. This result is likely due to NTAs often being sited in areas where the cover of *Acropora* and other thermally-sensitive and branching coral species is high (Chapter 5 & Graham et al. 2007a), or may be because fishing gears reduce cover of these coral species in fished areas. Our analysis also indicated little difference between NTAs and fished areas for those fish groups that declined in response to coral loss. The only indication of a differential response was the greater decline in NTAs for planktivores and small bodied herbivores. Large, remote and pristine areas seem to be resilient to a wide range of disturbances (Sandin et al. 2008), which has led to calls to assess the effectiveness of NTAs in conserving coral reefs through climate disturbance (Knowlton & Jackson 2008). One clear difference to these remote areas is that NTAs on reefs are typically small and surrounded by much larger areas that are modified by exploitation (Bellwood et al. 2004; McClanahan et al. 2007e). As we do not have repeat temporal data since the initial coral loss in 1998, we can not explicitly infer recovery rates from our data, however the NTAs we studied show no evidence of being more resistant to declines in coral and fish groups following coral bleaching and it seems likely that, over this time scale, recovery rates are no different between NTAs and fished areas, as has been shown for some of the NTAs where temporal data were available (McClanahan 2008).

We detected declines in fish species richness across the western Indian Ocean in response to loss of live coral cover. Although only a small proportion of species are heavily coral dependent, most species are reliant on the reef matrix at some stage in their life history, and change in species richness was likely due to loss in the physical structure of the reef, rather than live coral (Garpe et al. 2006; Graham et al. 2006; Wilson et al. 2006; Pratchett et al. 2008a). The variability in loss of structural complexity may explain why the trend for species richness was not stronger, with locations such as Chagos, where recovery of coral has been rapid, potentially retaining structural complexity in the interim. Although loss of structural complexity was the most likely driver of the region-wide decline in species richness, some studies have highlighted that live coral can be an important settlement cue for larval fish (Jones et al. 2004; Feary et al. 2007a) and the nature of this relationship is an important area for future research.

Although previous studies have identified obligate corallivores as a functional group vulnerable to declines in coral cover (Wilson et al. 2006; Pratchett et al. 2008a), this is the first study to demonstrate declines over such a large spatial scale. We have also identified a 1:1 linear relationship between coral loss and obligate corallivore decline, suggesting their survival on the reef is tightly linked to coral cover and changes in obligate corallivore abundance should be easy to predict based on changes to benthic cover. The diurnal planktivores in the study were largely small-bodied species from the damselfish family (>90% contribution to group) that are often closely associated with the reef matrix (Munday & Jones 1998; Wilson et al. 2008a). Their decline is most likely due to predation vulnerability, linked to loss of coral and structural collapse (Garpe et al. 2006; Graham et al. 2006). Planktivores and corallivores showed the strongest relationships of all groups to declining coral cover and are likely to be the groups most threatened from the predicted ongoing decline in global reef health (Wilson et al. 2006; Pratchett et al. 2008a).

Although herbivores are hypothesized to increase in abundance following coral decline owing to a greater availability of algal resources, previous studies have reported high variation in this relationship and have often been conducted shortly after disturbances, limiting their ability to detect demographic changes (Wilson et al. 2006). Here we tested this hypothesis across large spatial and temporal scales where the assemblage had a moderate time to respond. Herbivores are thought to be a key functional group, responsible for the resilience of reef systems by controlling algal growth (Bellwood et al. 2004; Mumby et al. 2006; Hughes et al. 2007a) and ultimately allowing settlement of new coral recruits (Mumby et al. 2007b). However, our data show that the proliferation of algae that follows extensive coral mortality (Diaz-Pulido & McCook 2002; Jones et al. 2004; Aronson & Precht 2006; Graham et al. 2006) was unlikely to be controlled by a corresponding increase in herbivorous fish abundance. Changes to size structure and biomass of herbivore stocks cannot be ruled out and may initially encourage increased consumption and control of algae. However, studies from Seychelles suggest such changes may be indicative of future declines in herbivore abundance and biomass due to a loss of refuge from predators, leading to reduced recruitment to adult size classes (Chapter 5 & Graham et al. 2007a).

The mixed diet feeding group also showed no response to declining coral cover. This group of fish includes species from families such as Lethrinidae, Mullidae, Lutjanidae, and Labridae, many of which are habitat generalists, foraging and recruiting to non-coral reef habitats such as seagrass (Dorenbosch et al. 2005). Species in these groups also tend to forage over fairly large spatial scales, indicating a lack of reliance on specific habitat types. Due to this decoupling of reliance on reef habitat and the potential benefits they may glean from increased food resources, this may be the group that will be sustained in the long term, although a large amount of variation can be expected at the species level (Wilson et al. 2006), leading to changes in community composition.

Small-bodied fish are known to be more reliant on the reef matrix, inhabit narrower niches, and be more vulnerable to predation (Munday & Jones 1998; Wilson et al. 2008a). Our analyses highlight the vulnerability of small-bodied species to coral and structural complexity loss. Within this size category, obligate corallivore and planktivore groups showed strong declines. Interestingly, there was also a reduction in abundance of small-bodied herbivores. Although herbivore abundance may not be declining overall (Figure 6.3C), the reduction of these small-bodied species is of concern as they perform important functional roles on coral reefs (Ceccarelli et al. 2001). Small mixed diet feeders again showed no trend, demonstrating the resistance of species with generalist life history traits to coral loss.

There are some obvious limitations in our data, such as the timeframe between surveys and the influence of any change in management / fishing pressure. In most cases management and fishing pressure have not changed greatly over the ten years studied. The one main exception is Mombasa Marine National Park, Kenya, where species richness and fish density have increased owing to management action (McClanahan et al. 2007e). Although such effects may have a slight influence on the results, the relationship between reef fish and change in coral cover (and its association with loss in physical structure) is a strong signal within the regional data and is consistent with current ecological understanding of disturbance effects on coral reefs (Wilson et al. 2006; Pratchett et al. 2008a). A potential problem when conducting meta-analyses is publication bias, whereby data sets are not located or included in the analyses (Gurevitch & Hedges 1999). This is not a problem in the current study as we conducted a targeted research program where all comprehensive studies from the mid 1990's were repeated as part of the study itself. Finally, the study design does not consider the impact of disturbances after the 1998 coral bleaching event. However, the December 2004 tsunami is thought to have had negligible effects on coral reefs in the western Indian Ocean (Wilkinson et al. 2005). Furthermore, any other ensuing disturbances are just as likely to have influenced NTAs as fished areas and reflect increasing disturbance frequencies occurring on coral reefs globally (Hughes et al. 2003; Bellwood et al. 2004).

Our analyses highlight great geographic variation in the impact of coral bleaching across the region, with the Seychelles suffering the greatest in terms of coral loss and associated effects on fish, and the Mascarene Islands (Réunion and Mauritius) suffering the least. These trends could be due to several factors: 1) Prevailing currents and variation in temperatures have been identified as key determinants of coral mortality in the region, likely reducing mortality in the Mascarene Islands in particular (Sheppard 2003; McClanahan et al. 2007b). 2) Well connected reef systems are expected to contain the pockets of refugia required for landscape-scale recovery (Nyström & Folke 2001). This is evident when comparing recovery of the well connected mainland reefs of Kenya and Tanzania and the geographically extensive Chagos and Maldives to the geographically small and isolated inner Seychelles. 3) The inner Seychelles is a shallow continental shelf basin, with most fringing reefs extending to only 7-9m depth. This 'bathtub effect' likely led to extensive mortality in 1998 and precluded any depth refuge below which corals could survive. Where live coral extends to 40-50m depth, such as in the atolls of Chagos or the islands of Réunion and Mauritius, a depth refuge of broodstock may encourage faster recovery of corals at shallower depths (Sheppard & Obura 2005). 4) Finally, the atolls surveyed in Chagos are uninhabited and off limits to reef fishing. The lack of multiple anthropogenic stresses that most other reef systems endure may have helped promote recovery from the disturbance (Knowlton & Jackson 2008; Sandin et al. 2008).

The 1998 bleaching event had, and is still having, extensive effects across the western Indian Ocean. Although ocean-scale coral reef integrity has been lost, it is positive to see that effects were spatially variable and that in some locations the indirect effects on fish assemblages and likely implications for human society have been small. Geography seems to be a key determinant in the ability of reefs to absorb and recover from such large-scale disturbances and this should be considered for other regions likely to suffer similar large-scale disturbances in the future. Although there was no evidence that existing NTAs are promoting recovery of coral, these NTAs are still supporting a greater biomass of fishery stocks (Chapter 5 & Graham et al. 2007a; McClanahan et al. 2007e), indicating long-term fisheries management should not be compromised. There is, however, a need for new NTAs, incorporated into existing networks that protect source reefs resilient to large-scale disturbance, and areas likely to retain their physical structure. This will help sustain the upstream spawning stocks of corals and specialised fish species required for landscape-scale recovery. Such management is likely to be unsuccessful in isolation, and improved management of entire reef systems, reducing the stresses and pressures to areas outside NTAs will be necessary to maximise the capacity for systems to recover from large scale and ongoing disturbance.

6.6 Acknowledgements

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Chapter 7

General discussion

There has been burgeoning research interest in the impacts of coral bleaching on coral reef fish assemblages over the past 3 years with the knowledge of which species, groups and size classes decline and understanding of the mechanisms behind those declines greatly improving. Thorough reviews of these advances are scheduled for publication in 2008 (Pratchett et al. 2008a, b), including one which also considers the direct impacts of increasing water temperature and changing chemistry on crucial life history and developmental stages of coral reef fish (Munday et al. 2008). This present chapter aims to 1) discuss the current state of knowledge on the topic including the novel contributions of this thesis, 2) propose a conceptual model of the short- and long-term impacts of bleaching on fish assemblages and 3) provide directions for future management and research priorities in this field of study.

7.1 Current state of knowledge

The importance of ecological specialisation in driving declines in fish abundance is still an important research topic and has advanced considerably. One of the main advances has been an improved resolution of the degree of specialisation in various groups of coral feeding and dwelling fish. Finer resolution of the feeding preferences of a fairly comprehensive selection of Pacific butterflyfish (Pratchett 2005) has been extended to include some Indian Ocean species (Chapter 2 & Graham 2007). Potential reasons why some species are highly specialised in targeting specific species of coral have been elucidated, highlighting the high food quality of preferred coral prey (Chapter 2 & Graham 2007). This information on species-specific feeding specialisation has proved extremely powerful in predicting patterns of decline in abundance following coral mortality, with much greater and more rapid declines, and some local extinctions, occurring for those species that are highly specialised in their dietary requirements (Pratchett et al. 2006; Chapter 2 & Graham 2007; Chapter 3). Associated with these differing degrees of species specific levels of dietary specialisation or versatility and differing preferences in types of coral prey, it is apparent that if reefs recover a different assemblage of corals post-disturbance, the associated suite of corallivorous fish may also change (Berumen & Pratchett 2006). Coral cover and butterflyfish abundance returned to pre-disturbance levels on a reef in Moorea, however *Pocillopora* corals now dominated the benthic cover, rather than *Acropora*, and the butterflyfish assemblage had shifted from specialist feeders of *Acropora* to more generalist feeders that will ingest *Pocillopora* (Berumen & Pratchett 2006).

On the Great Barrier Reef 53% of juvenile damselfish dwell in live coral, preferring plating growth forms, whereas 40% of adult damselfish inhabited live coral and preferred branching corals (Wilson et al. 2008a). Coral associated juvenile damselfish had narrower niche breadths than adult conspecifics, indicating that early life history stages may be most vulnerable to coral loss. Furthermore, niche breadth, which incorporates proportional use and availability of resources, explained 74% of the variation in damselfish response to coral decline indicating that, similar to coral feeders, coral dwellers with greater specialisation are most vulnerable to declines following coral mortality (Wilson et al. 2008a). Such vulnerability of early life history stages and greater impacts on coral associated specialists was also shown in an experimental manipulation where coral colonies were degraded to varying degrees (Feary et al. 2007b). Coral dwelling specialists also appear to be more likely to remain in coral colonies as they degrade and less likely to successfully migrate to alternative live colonies following mortality of a host colony, than habitat dwelling generalists (Feary 2007). It is clear from the above studies of coral feeding and dwelling fish, and from other community composition studies (Bellwood et al. 2006b), that there is a general shift in fish communities away from coral specialists to species with more generalist life history characteristics.

The importance of live coral for coral reef fish settlement has been further investigated. In aquarium choice experiments, fish generally settled in the habitats that adult conspecifics inhabit, but several species preferentially settled into live or partially degraded coral heads, when adults do not dwell in live coral (Feary et al. 2007a). In associated field manipulations, a greater abundance and diversity of fish settled into live coral habitats, but this was driven by relatively few, abundant species that associate with live coral throughout their life history. The community composition of coral reef fish recruits changed after experimental degradation of habitat from coral associated to algal associated species (Feary et al. 2007a). A study of reef fish recruits in Mafia Island, Tanzania, after the 1998 bleaching event found that 46% of recruits used live coral habitat disproportionately compared to availability of this substrate (Garpe & Öhman 2007). Although a number of these species, particularly abundant taxa, also used live coral as adults, a proportion of them did not. A study of butterflyfish habitat use as juveniles versus adults indicated that juveniles of obligate coral feeding fish inhabited the same live coral habitats that adult conspecifics feed upon, likely due to essential dietary requirements. Conversely, juveniles of facultative coral feeders utilised distinct habitats, not always associated with either live coral or adult conspecifics (Pratchett et al. 2008c). However, the use of live coral as habitat by the juveniles was in higher proportion to the use of live coral for diet in adults, particularly for facultative feeders (Wilson et al. 2009). These studies and others (e.g. Jones et al. 2004; Wilson et al. 2008a) further suggest that the early life history stages of reef fish are likely to be the most vulnerable to coral loss.

Knowledge of the drivers of change in fish assemblages following coral bleaching has advanced. Chapter 3 highlights that loss of live coral and the loss of structural complexity can be de-coupled and that these different attributes of a degrading benthos can influence different components of the fish assemblage. The impacts of declines in coral cover are likely to be more immediate and spatially extensive, and principally affect fish that specialise on live coral. Conversely the loss of structural complexity can take longer to occur, can be more patchy in distribution and impact other small bodied species that are not so dependent on live coral, so have survived the initial impacts of bleaching (Chapter 3). Indeed, it is now becoming evident that the long-term impacts of coral loss, when the structural complexity of the reef degrades, are far greater than the initial impacts of live coral loss (Figure 7.1; Garpe et al. 2006; Graham et al. 2006). Such loss in structural complexity results in losses in species richness, taxonomic distinctness, the trophic composition and abundance of a wide range of trophic groups (Garpe et al. 2006; Graham et al. 2006; Pratchett et al. 2008a), many of which are not impacted by the short-term impacts of bleaching (Chapter 1; Wilson et al. 2006). As more structure is lost, larger bodied fish species may be lost from the system, including species that represent key functional groups on coral reefs (Graham et al. 2006). Furthermore, the size structure of the fish assemblage can change substantially with a reduction of individuals with smaller body-size (<35cm) and trophic cascading effects, indicating lag effects and potentially much greater impacts on the system as a whole in the long term (Chapter 5 & Graham et al. 2007a). Clearly the loss of structural complexity is a major mechanism driving the longer-term impacts of coral bleaching on fish assemblages.

There have been small advances in understanding the interaction among different kinds of disturbances. When bleaching impacts have been relatively limited in severity, site specific local stressors can dominate structuring of benthic and fish assemblages. This was shown in Mauritius where the 1998 bleaching event caused ~10% coral mortality and the impacts of fishing and habitat damage through dredging resulted in stronger trends in the benthic and associated fish assemblage data (Chapter 4 & Graham et al. 2007b). Conversely, in the Lau Islands of Fiji, where there have been reductions in fishing effort in recent years, the combined impacts of coral bleaching and crown-of-thorns starfish outbreaks on the benthos are causing greater changes to the fish assemblage than fishing pressure (Wilson et al. 2008b). Both fishing and habitat degradation did exert changes in the fish assemblage, however, and as these are two of the main drivers of change in fish assemblages globally, further studies of the interaction and dominant drivers of the two impacts are necessary. Indeed, although some studies have attributed coral loss to multiple impacts (e.g. Jones et al. 2004; Munday 2004; Wilson et al. 2008b), few studies have successfully partitioned the impacts of multiple disturbances or assessed how stressors interact or where synergies in impacts may occur (Wilson et al. 2006, 2008b).

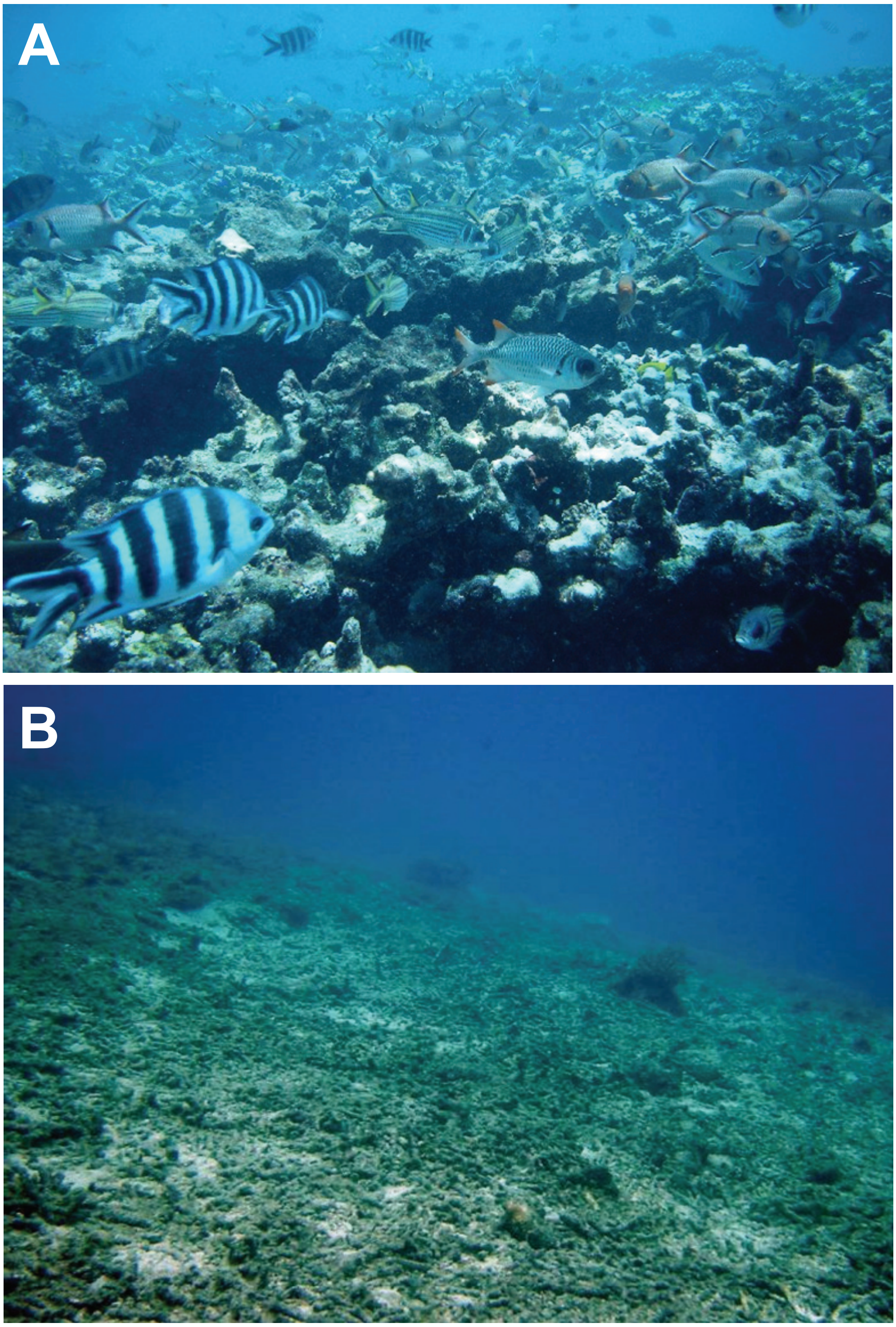

Figure 7.1. Reef plan view photographs indicating A. the short-term impacts of bleaching, where live coral is lost, but structural complexity is maintained and fish diversity can remain high, and B. a longer-term scenario of bleaching, where the structure has eroded into a rubble bank, and reef fish diversity and abundance have declined.

The scale at which many of the above trends have been assessed has recently been dramatically increased (Chapter 6 & Graham et al. 2008). Although reviews of the topic have combined information from disparate studies within meta-analytical frameworks (Wilson et al. 2006; Pratchett et al. 2008a), Chapter 6 was the first study to explicitly collect and analyse data over a spatial scale beyond individual level reef or country case studies. This assessment across such a broad spatial and temporal scale enabled predictive statements regarding future change, identified a 1:1 trend between loss of coral and declining obligate corallivore abundance and provided conclusive evidence of which trophic and size groups of fish respond to coral bleaching impacts on the benthos (Chapter 6 & Graham et al. 2008). Most groups previously identified as being vulnerable to coral loss, also displayed declines at this regional scale and the study highlighted that the invertebrate and mixed diet feeding fish may be the group that are least effected and most stable on reefs through climate change (Chapter 6 & Graham et al. 2008).

As herbivores are thought to be a key functional group (Bellwood et al. 2004), controlling algal growth and facilitating coral recruitment and recovery processes (Mumby et al. 2007b), it is important to understand how they respond to coral bleaching events. The short-term studies of coral bleaching indicated that herbivores may show increases in abundance following coral loss, but these responses were variable among studies (Wilson et al. 2006). Longer-term studies have shown that herbivore abundance and biomass do not continue to increase and control algae following large scale bleaching events (Garpe et al. 2006; Chapter 5 & Graham et al. 2007a). This lack of response of herbivore abundance has been shown at regional scales, with small bodied herbivores actually declining (Chapter 6 & Graham et al.

2008). Furthermore, changes to the size structure of the herbivore stock indicate that longer-term declines in herbivore biomass as a whole seem likely (Chapter 5 & Graham et al. 2007a). These negative impacts on herbivore stocks appear to be related to collapse of the structural matrix of the reef framework and suggest that important functional roles on reefs may decline in the long-term if coral does not recover and the reef framework erodes.

Similar to the short-term impacts of bleaching on fish ecology, the short-term impacts of coral bleaching on associated fisheries are negligible based on fisheries dependent creel surveys (Grandcourt & Cesar 2003; McClanahan et al. 2002). The lack of a change in the biomass of target species above size of first capture was confirmed using fisheries independent underwater visual census data in the inner Seychelles 7 years after the 1998 bleaching event (Chapter 5 & Graham et al. 2007a). However, large changes in the size structure of the assemblage indicate that the current stability in the fishery is bolstered by an increase in large herbivorous individuals, and that substantial reductions in smaller size classes belie a forthcoming decline in fishery yields (Chapter 5 & Graham et al. 2007a). As larger individuals are removed from the system through fisheries extraction and natural mortality, there are fewer individuals surviving to recruit into fishery size classes (Chapter 5 & Graham et al. 2007a). The most likely driver of these changes in size structure is the loss of refuge space for smaller size classes provided by reef structural complexity. An assessment of the percentage contributions of both species and individuals caught in artisanal fisheries in Kenya and Papua New Guinea indicates that although 5% or less of species caught are live coral dependent, over 60% are dependent on reef habitat complexity (Pratchett et al. 2008a). This suggests that if bleaching-associated reductions in habitat complexity (Garpe et al. 2006; Graham et al. 2006, Chapter 5 & Graham et al. 2007a; Wilson et al. 2008b) do become widespread as predicted, the long-term ramifications for coral reef associated fisheries may be substantial. The aquarium fish trade is a rapidly growing fishery on coral reefs, with a value of US$90-300 million a year (Sadovy & Vincent 2002). Most of the species in the aquarium trade are small bodied and trade statistics indicate that although only approximately 15% of these species are coral dependent, 80% associate with reef habitat structure (Pratchett et al. 2008a). However, the value per fish for coral dependent species dwarfs that of structurally associated species (Pratchett et al. 2008a) and so the impacts of coral bleaching on this industry could also be substantial.

7.2 Conceptual models

From this now fairly comprehensive body of work we can develop conceptual models of how a functioning reef ecosystem (Figure 7.2A; a simplistic model based on impacts of coral bleaching) changes in the short- and medium-term after coral bleaching. In the short-term, reduced coral cover, but stable structural complexity, lead to declines in corallivores and planktivores (as a number of species are coral dwellers). The decline in coral is associated with an increased cover of the epilithic algal matrix (EAM), which in turn leads to a small, but variable increase in EAM feeding fish (Wilson et al. 2006; Figure 7.2B). If resilience is high, coral and fish assemblages may then recover to pre-disturbance compositions (e.g. Halford et al. 2004), or may recover, but shift in both benthic and fish assemblage composition (e.g. Berumen & Pratchett 2006). However, if the system does not return to coral dominance, the impacts can become much greater (Figure 7.2C). The reduced cover of coral and increased cover of EAM can become stable due to positive feedback mechanisms maintaining the system in an unfavourable state (Bellwood et al. 2004; Mumby et al. 2007a). The structural complexity of the reef matrix can decline with a corresponding increase in rubble (Sheppard et al. 2002; Graham et al. 2006). This loss of complexity leads to a decline in most fish groups including EAM feeders (Garpe et al. 2006; Graham et al. 2006; Chapter 5 & Graham et al. 2007a). The impact of coral loss on those species that require live coral at settlement will also become manifest (Jones et al. 2004; Feary et al. 2007a; Garpe & Öhman 2007). Corallivores and planktivores further decline, due to lagged population declines partly associated with reduced physiological condition (Pratchett et al. 2004, 2006), and partly due to the loss of structural complexity (Chapter 3). Invertivores remain largely unchanged due to the interplay between the positive effects of increased dietary resources associated with rubble areas and the negative effects of structural complexity loss (Chapter 5 & Graham et al. 2007a; Chapter 6 & Graham et al. 2008; MacNeil et al. 2008; Wilson et al. 2008b). Piscivores begin to decline due to the trophic cascading effects of reduced food in the form of smaller size classes of fish (Chapter 5 & Graham et al. 2007a). Recovery potential is linked to feedback mechanisms, such as frequency and severity of disturbances (e.g. storms, bleaching, crown-of-thorns starfish outbreaks) that will further decrease coral and structural complexity (Birkeland 2004), and the impacts of physical isolation and external refugia that will largely determine the supply of larvae needed for settlement and recovery (Ayre & Hughes 2004; Graham et al. 2006). These extrinsic factors in combination with intrinsic factors such as macroalgae cover, which will potentially be mediated by herbivores (Mumby et al. 2006; Hughes et al. 2007a), although once established is less likely to be controlled (Bellwood et al. 2006a; Ledlie et al. 2006), and the extent and severity of the initial coral mortality (Mumby et al. 2007a), will determine if the system has the capacity to recover.

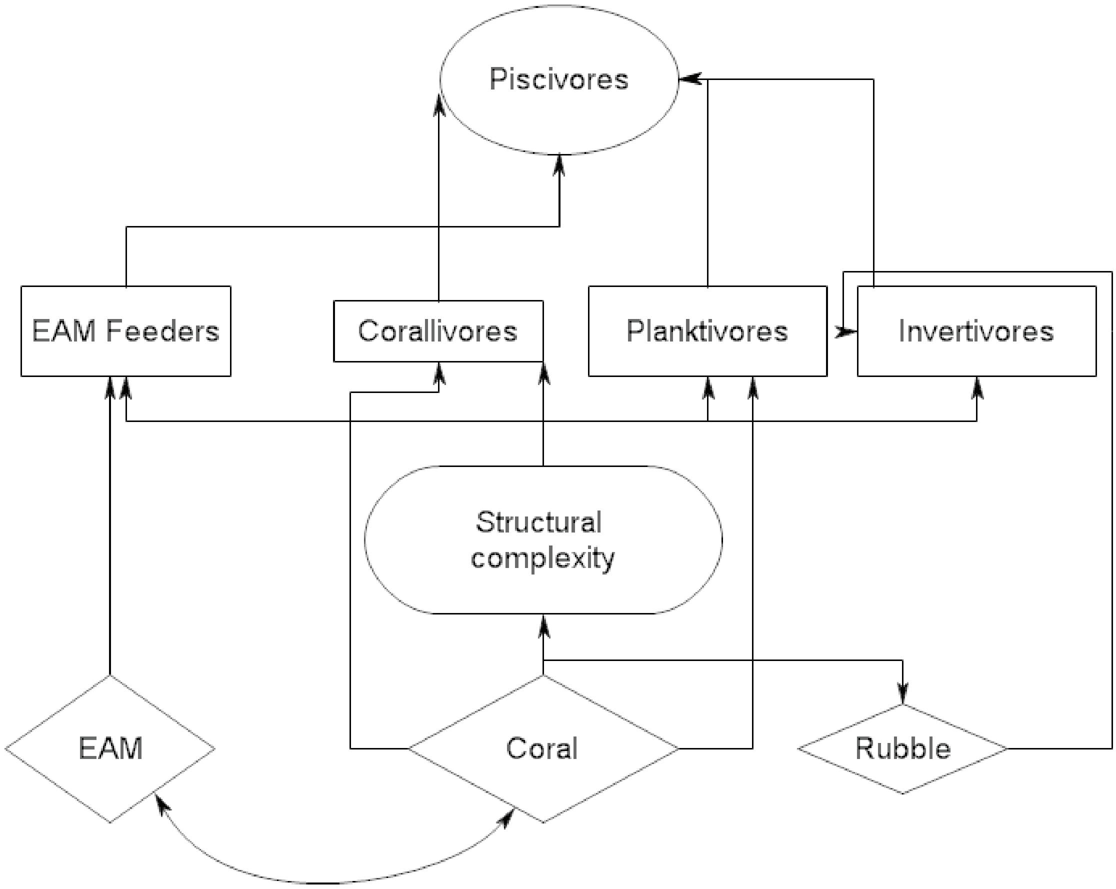

Figure 7.2A. Conceptual representation of an undisturbed functioning reef ecosystem. Arrows indicate main direction of flows in resources, contribution to habitat attributes or competition between EAM and coral. EAM = epilithic algal matrix.

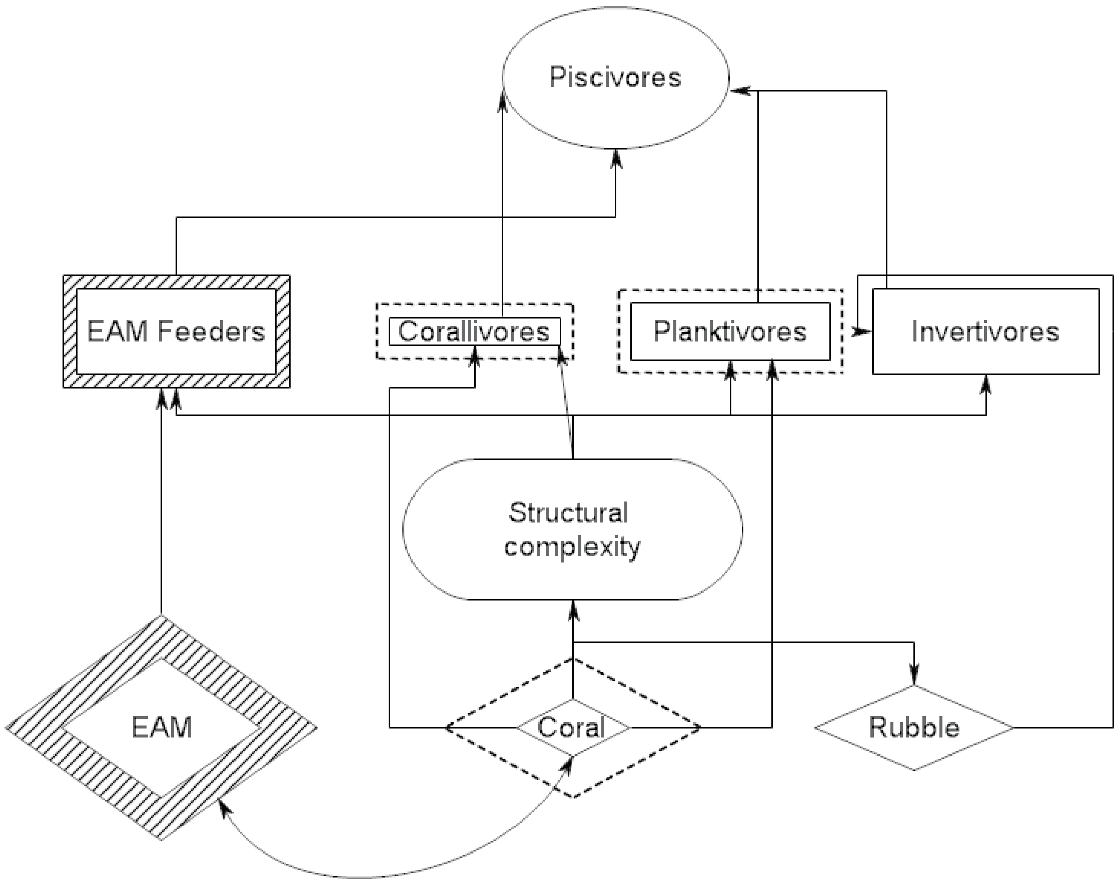

Figure 7.2B. Conceptual representation of the short-term impacts of coral bleaching to a reef ecosystem. Diagonal hatching in boxes represents increases in cover or abundance. Dashed lines represent original size of box to indicate extent of decline in cover or abundance.

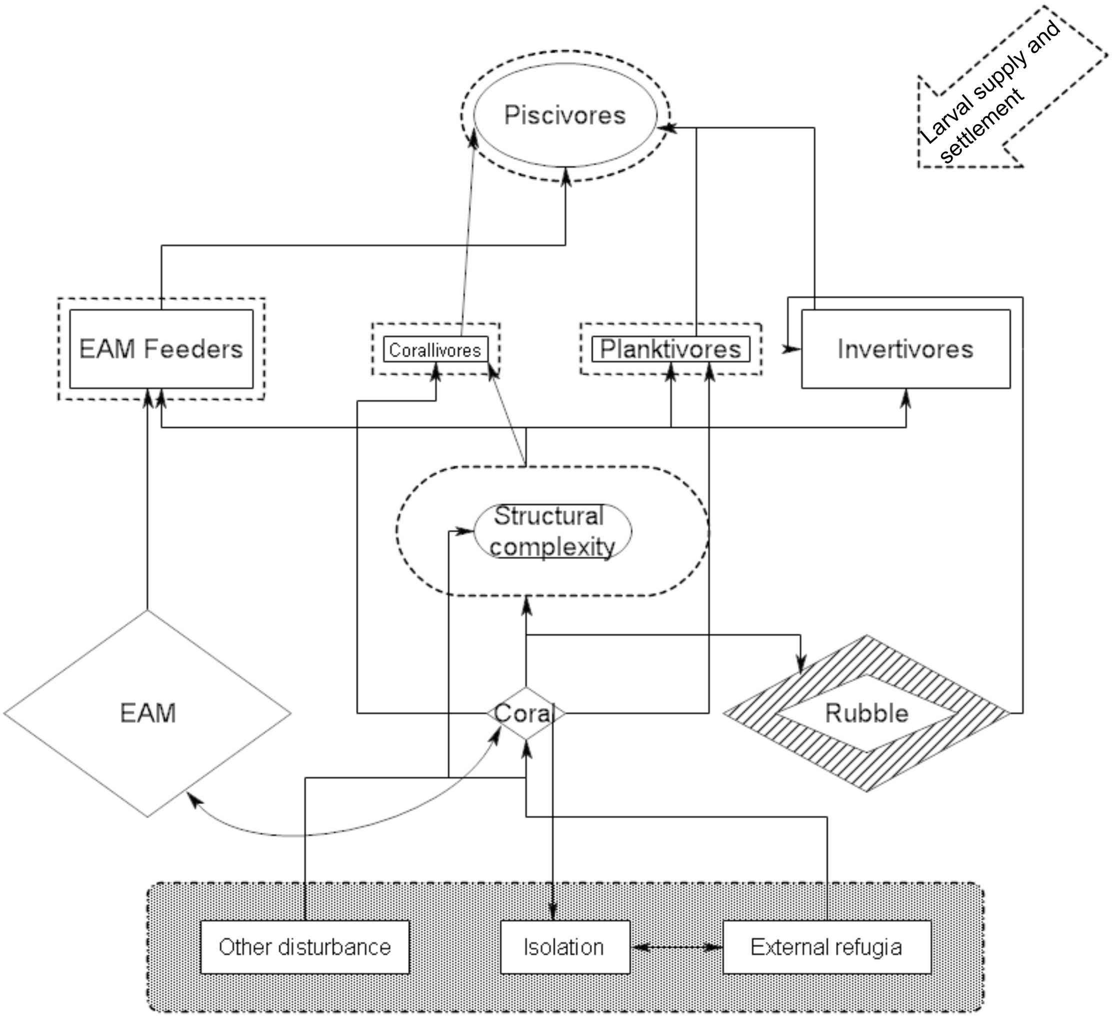

Figure 7.2C. Conceptual representation of the medium-term impacts of coral bleaching to a reef ecosystem. Diagonal hatching in boxes represents increases in cover or abundance. Dashed lines represent original size of box to indicate extent of decline in measured component or abundance. Shaded box represents extrinsic feedback mechanisms that influence recovery potential, which include larval supply and settlement.

7.3 Management and Research directions

With clear evidence growing for the longer-term impacts of coral bleaching on the ecosystem as a whole and likely consequences for coral reef fisheries, there is a clear need to assess the role of management to help reduce impacts and promote recovery (Knowlton & Jackson 2008). Review papers have presented the expectations that marine protected areas (MPAs) should protect important functional processes on coral reefs and help promote recovery of coral cover (e.g. Worm et al. 2006). However, there is growing empirical evidence that the same species and groups are impacted in MPAs as fished areas following coral bleaching events and that the impacts inside MPAs can sometimes be greater (Jones et al. 2004; Chapter 5 & Graham et al. 2007a). Indeed, across multiple locations the impacts of bleaching on the benthos and associated fish groups can be equal or greater in MPAs than fished areas, and the rates of recovery indistinguishable (Chapter 6 & Graham et al. 2008; McClanahan 2008). MPAs are often sited in areas of high coral cover, especially areas with charismatic branching and plating coral growth forms. This results in a thermally sensitive assemblage, which often declines in cover to become similar in composition and cover to fished areas after bleaching (Chapter 5 & Graham et al. 2007a; Chapter 6 & Graham et al. 2008). As small bodied fish preferentially utilise these habitats (Bellwood et al. 2004; Jones et al. 2004), the impacts on fish can also be large (Chapter 5 & Graham et al. 2007a; Chapter 6 & Graham et al. 2008). After such a loss in coral cover, fish abundance and structural complexity, it appears small MPAs are largely indistinguishable from fished areas, other than by a larger biomass of fishery target species (Chapter 5 & Graham et al. 2007a; McClanahan et al. 2007e), and do not appear to maintain the capacity to recover more rapidly (Chapter 6 & Graham et al. 2008; McClanahan 2008).

The boundaries of MPAs can not prevent the impacts of disturbances such as bleaching, nutrient loading, storms and sedimentation (Hughes et al. 2003; Bellwood et al. 2004; Nyström 2006; Mora 2008). Building a large network of MPAs that covers a much larger area of coral reef in each country may help build some of the brood stocks and connectivity necessary for recovery and resilience (Hughes et al. 2003), however, aside from examples from wealthy nations such as Australia, such targets are not possible or necessarily appropriate for many developing world situations (McClanahan et al. 2008). There is therefore a growing recognition of the need to build the resilience of the system as a whole (Nyström & Folke 2001; Bellwood et al. 2004; Nyström 2006; Hughes et al. 2007b; Chapter 6 & Graham et al. 2008). Most MPAs in coral reef environments are small and embedded in a much larger area that is exploited and often degraded. Building the resilience of the system as a whole will involve reducing the range of threats that act upon the whole system, such as nutrient and sediment inputs from land, overfishing, use of destructive fishing practices and land reclamation activities. Special attention to those areas that either escape from or recover rapidly from bleaching events, should enable future protected areas to be sited in locations likely to provide brood stocks to impacted regions (West & Salm 2003; Chapter 5 & Graham et al. 2007a; Chapter 6 & Graham et al. 2008). Managing and protecting the functional diversity of organisms on reefs and, in particular, key functional groups, such as some herbivores, will be necessary to promote continued functioning of the system and assist recovery processes (Bellwood et al. 2004; Nystrom 2006; Mumby et al. 2007a; Chapter 6 & Graham et al. 2008). At a larger scale, some areas and regions seem to escape bleaching events (McClanahan et al. 2007a, b; Maina et al. 2008; Chapter 6 & Graham et al. 2008) and the geography of some locations, such as the presence of deep water reefs that escape the impacts of warm water that typically impact shallower areas (Sheppard & Obura 2005; Chapter 6), results in much greater recovery potential. These areas should be conservation priorities, requiring a scaling up of conservation efforts to incorporate regional patterns into cross boundary policy initiatives. Ultimately, all these initiatives will fail if the local social and economic setting is not incorporated into conservation action (Hughes et al. 2005). There is a need to understand what promotes resilience in the socio-ecological systems that typify coral reef areas, and develop strategies that are most appropriate given the local social conditions and capacity to adapt and change, and the vulnerability of the environment to climate change and other threats (McClanahan et al. 2008). Such understanding and recommendations are in their infancy, but warrant a great deal of research funding and attention over coming decades.

Aside from conservation and management orientated research, many fundamental ecological questions remain unanswered. Although the understanding of the impacts of coral bleaching and climate change on reefs has greatly advanced in recent years (Hoegh-Guldberg et al. 2007; Pratchett et al. 2008a), there are still many research gaps. Some of the most apparent for fish relate to the direct impacts of a warming environment on behaviour, range, physiology, reproduction and other key life history stages (Munday et al. 2008). More studies of the interactions between and potential synergies of multiple disturbances are necessary. The impacts of changing habitat on functional composition, functional diversity, response diversity and redundancy (Elmqvist et al. 2003; Nyström 2006) of reef fish is poorly quantified. How these attributes of a fish community are impacted and more importantly how they can be maintained are fundamental unanswered research questions. Understanding the patch dynamics and temporal variation in recovery processes from disturbances is another emerging research area (Arthur et al. 2006) that warrants further attention. The use of reef restoration techniques and artificial reefs has been well studied (Edwards & Gomez 2007) and is met with scepticism by many, but with the role of structural complexity becoming so apparent and reefs on a general downward trajectory, research into direct active management techniques should also receive greater attention. As it is generally accepted that most reefs will exist in a less complex and more depauperate state, how ecological processes, such as predation, competition and herbivory will change and adapt is also a key research question. This also needs to be scaled up to understand how the ecosystem goods and services returned from coral reefs will change, and what can be expected under differing emissions scenarios. Stabilising the rate of climate warming is a major priority for coral reefs, but it is clear that major changes beyond those already identified are likely to occur in coming decades.

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Appendix A

Contributions during PhD

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Presentations

‘Coral bleaching fish and fisheries in the Seychelles’ – 4th, Western Indian Ocean Marine Science Symposium, **Mauritius**

‘Coral bleaching fish and fisheries in the Seychelles’ - Reef Conservation U K, **UK**

‘Impacts of coral loss and fishing on fish communities in the Lau Islands, Fiji’ - Public lecture, University of the South Pacific, **Fiji**

‘The long-term impacts of coral bleaching for fish and fisheries in the Seychelles’ - JCU seminar series, James Cook University, **Australia**

‘Lag effects in the impacts of the 1998 bleaching event on coral reef fisheries in the Seychelles’ - European Coral Reef Symposium, **Germany**

‘The impacts of the 1998 bleaching event on coral reef fish in the western Indian Ocean’ - Meso-scale effects of bleaching workshop, **Zanzibar**

‘Assessing the impacts of coral bleaching on fish across the Indian Ocean using continuous model meta-analysis’ - James Cook University, **Australia**

‘Ecological data: effects of coral bleaching on fish assemblages’ – 1st Social and Ecological Responses to Reef Ecosystem Change in the Western Indian Ocean workshop, Mombasa, **Kenya**

‘Assessing the impacts of coral bleaching on fish across the western Indian Ocean using continuous model meta-analysis’ - 5th Western Indian Ocean Marine Science Association, Durban, **South Africa**

‘Climate warming and the ocean-scale integrity of coral reef ecosystems’ 10th Reef Conservation UK meeting, **UK**

‘Long-term impacts of coral bleaching on fish in the inner Seychelles’ Public Lecture, Seychelles Fishing Authority, **Seychelles**

‘What are the Marine Parks of the inner Seychelles achieving in terms of fisheries and resilience to bleaching?’ – 2nd Social and Ecological Responses to Reef Ecosystem Change in the Western Indian Ocean workshop, **Mauritius**

‘Climate warming, marine protected areas and the ocean scale integrity of coral reef ecosystems’ – 11th International Coral Reef Symposium, Fort Lauderdale, Florida, **USA**

Appendix B

Reprints of published chapters

Chapter 2:

Graham NAJ (2007) Ecological versatility and the decline of coral feeding fishes following climate driven coral mortality. Marine Biology 153:119-127

Chapter 4:

Graham NAJ, McClanahan TR, Letourneur Y, Galzin R (2007) Anthropogenic stressors, inter-specific competition and ENSO effects on a Mauritian coral reef. Environmental Biology of Fishes 78:57-69

Chapter 5:

Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Robinson J, Bijoux JP, Daw TM (2007) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. Conservation Biology 21:1291-1300

Chapter 6:

Graham NAJ, McClanahan TR, MacNeil MA, Wilson SK, Polunin NVC, Jennings S, Chabanet P, Clark S, Spalding MD, Letourneur Y, Bigot L, Galzin R, Öhman MC, Garpe KC, Edwards AJ, Sheppard CRC (2008) Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. PLoS ONE 3(8): e3039. doi:10.1371/journal.pone.0003039

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RESEARCH ARTICLE

Ecological versatility and the decline of coral feeding fishes following climate driven coral mortality

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Abstract Coral reefs are under threat due to climate-mediated coral mortality, which affects some reef coral genera more severely than others. The impact this has on coral reef fish is receiving increasing attention, with one focal area assessing impacts on fish that feed directly on live coral. It appears that the more specialised a species of corallivore, the more susceptible it is to coral declines. However data are sparse for the Indian Ocean, and little is known about why some corals are preferentially fed upon over others. Here I assess feeding specialisation in three species of coral feeding butterflyfish in the Chagos Archipelago, central Indian Ocean, assess the food quality of the coral genera they target and document patterns of decline in the Seychelles following a severe coral mortality event. *Cheatodon trifascialis* was the most specialised coral feeder, preferentially selecting for *Acropora* corals, however, when *Acropora* was scarce, individuals showed considerable feeding plasticity, particularly for the dominant *Pocillopora* corals. *C. trifasciatus* also preferentially fed on *Acropora* corals, but fed on a much more diverse suite of corals and also displayed some selectivity for *Porites*. *C. auriga* is a facultative corallivore and consumed ~55% live coral, which lies within the wide range of coral dependence reported for this species. C:N ratio analysis indicated *Lobophyllia* and *Acropora* have the highest food quality, with *Pocillopora* having the lowest, which conforms with diet selection of corallivores and helps explain preferential feeding. Obligate specialist feeders displayed the greatest declines through coral mortality in the Seychelles with obligate generalists also declining substantially, but facultative feeders showing little change. Clearly a greater understanding of the species most vulnerable to disturbance, their habitat requirements and the functional roles they play will greatly assist biodiversity conservation in a changing climate.

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Introduction

The decline of coral dominated reef systems and a change in coral composition from diverse and often *Acropora* dominated reefs, to less structurally complex encrusting and massive coral dominated reefs (McClanahan et al. 2007) is being driven increasingly by coral bleaching, mediated by climate change (Hoegh-Guldberg 1999; Sheppard 2003). The impacts of coral decline on the wider ecosystem has received increasing attention, with the effects on fish being especially well investigated [reviewed by Wilson et al. (2006)]. While in the medium-term (5–10 years post disturbance) the diversity and abundance of a wide range of species can be affected (Jones et al. 2004; Garpe et al. 2006; Graham et al. 2006), in the short-term (<3 years post disturbance), the impacts appear limited to species that specialise on coral for diet, recruitment or habitat purposes (Williams 1986; Kokita and Nakazono 2001; Wilson et al. 2006; Munday et al. 1997). However, even for specialised fish, the full effects can take some time to reach fruition (Pratchett et al. 2004), and seem to vary according to the degree to which the fish are specialised (Munday 2004; Pratchett et al. 2006).

Corallivorous fish can vary in their dependence on live coral and although the majority of species feed mainly on scleractinian corals (Hourigan et al. 1988), their diet may include hard corals, soft corals, gorgonians, sponges, algae, polychaetes and crustaceans (Pratchett 2005). Many feeding studies of corallivores have assessed hard coral as a single category (Reese 1975; Harmelin-Vivien and Bouchon-Navaro 1981, 1983; Bouchon-Navaro 1986; Zekeria et al. 2002), however, other studies have partitioned feeding patterns at the scale of genera or species of coral, which enables the degree of specialisation to be elucidated (Cox 1994; Irons 1989; Pratchett 2005; Berumen et al. 2005). Assessing the degree of specialisation of species enables a continuum of ecological versatility to be assessed against resource availability or through disturbance (Munday 2000, 2004), or a greater number of broad categories of feeding or functional groups to be assessed (Pratchett et al. 2006).

Although data on the extent of ecological versatility in coral feeding fish is increasing, we have little knowledge as to why some species are specialists, sometimes preferentially targeting only one species of coral, whilst other species feed on a far broader range of prey. Furthermore, although our understanding of the degree of feeding specialisation and resource partitioning among corallivores has greatly advanced in the Pacific (Pratchett 2005; Berumen et al. 2005) and this has enabled a better understanding of declines in corallivores following disturbances (Pratchett et al. 2006) or switches in assemblage composition following reorganisation of benthic resources (Berumen and Pratchett 2006), whether these patterns and trends transcend into the Indian Ocean is not clear. Indeed geographical variation in feeding preferences of corallivores has been reported for specialist feeders (Irons 1989) and facultative coral feeders (Pratchett 2005; Harmelin-Vivien and Bouchon-Navaro 1983), indicating a need to broaden the geographical extent of such studies.

Here I assess, in the central Indian Ocean, the degree of specialisation in three species of coral feeding butterflyfishes representing specialist, generalist and facultative corallivores. I assess how this specialisation changes between habitats with differing dominance and diversity of corals available. To assess whether feeding selection is related to nutritional value, I assess the food quality of the four dominant corals selected by the fish. Finally, to assess the impact of coral loss on species with differing dependency on coral resources, patterns of temporal change in abundance of corallivores were examined through a major coral mortality event in the Seychelles.

Materials and methods

Study sites

The study was conducted at two locations: diet analysis and associated work was conducted at Diego Garcia atoll in the Chagos Archipelago, central Indian Ocean, while temporal change in corallivore density was assessed in the granitic islands of the Seychelles. Although it would have been preferable to conduct the feeding study and change in abundance through disturbance at the same location, the two locations have very similar coral communities. Indeed, in an assessment of coral species diversity across the entire Indian Ocean, Sheppard (1998) showed that Chagos, the granitic Seychelles and the Maldives clustered together into a distinct group in terms of species similarity and that the Seychelles and Chagos were particularly similar.

In Diego Garcia, two sites were selected for substrate assessment, corallivore density counts, feeding selectivity and coral food quality assessments. One reef (Diego east; 7°14.359′S, 72°26.411′E) was in a sheltered bay in the northeast corner of the atoll and, although hosting a fairly diverse coral assemblage, was dominated by *Pocillopora*. The second reef (Diego central; 7°14.534′S, 72°24.636′E) was a large platform patch reef in the north central section of the atoll, which was less diverse and dominated by *Acropora*. Both reefs were between 1 and 3 m depth and all observations were conducted on snorkel. Change in density of corallivores was assessed through a major bleaching event in the Seychelles. Data were collected in 1994 and 2005, spanning the 1998-bleaching event. For full details of study sites see Jennings et al. (1995) and Graham et al. (2006).

Substratum availability

To determine whether feeding preferences were influenced by the availability of potential food resources, substratum availability was quantified. At both Diego east and Diego central the benthos along five randomly placed 10 m transect lines was quantified using the line intercept method, whereby the distance of tape occupied by each substrate category was quantified. These data were converted into percent covers of each category and means plotted with standard errors per site. Differences in cover by genera were assessed using one-way ANOVA. *Acropora* cover had to be Log_{10} transformed to meet the assumptions of the test.

Feeding observations

Feeding observations were conducted for three species of chaetodontid butterflyfish, one obligate specialist coral feeder, *Chaetodon trifascialis*, which is expected to consistently favour certain prey items, whether these items are common or rare, one obligate generalist coral feeder, *C. trifasciatus*, which is expected to feed on a wider variety of prey items, in closer proportions to those available in the environment and one facultative coral feeder, *C. auriga*, which is expected to feed on coral, but also ingest other non-coral prey (Hourigan et al. 1988). The range and proportional consumption of various prey items targeted by each individual was recorded during 3 min observation periods (following Pratchett 2005). The majority of individuals continued to feed during observation, however observations were discontinued if the observer disturbed the fishes. No intra-specific aggressive interactions were noted during feeding observations. Coral preys were identified to the genus level (16 genera were fed upon during the study), and other prey items included soft coral, sponge, epilithic algae, coralline algae and consolidated reef pavement. Reefs were surveyed in a zigzag pattern from one end to the other to try to ensure the same individual was not observed twice. All observations at both sites were made between 10 am and 2 pm, with no bias for time between sites. Between 20 and 30 individuals were surveyed per species per site (Table 1).

As data were collected on selection of resource units by individual animals, but resource availability was assessed at the population level, resource selection functions ($\hat{W}_{\mathrm{i}}$) were calculated following Manly et al. (1993) using the formula:

$$\hat{W}_{\mathrm{i}} = u_{\mathrm{i}+}/(\pi_{\mathrm{i}} u_{++})$$

where $u_{\mathrm{i}+}$ is the number of bites taken on food type i by all individuals, π_{i} is the proportion of that food type in the population and u_{++} is the total number of bites taken on all substrate types by all individuals (Manly et al. 1993). Bonferroni corrected 95% confidence intervals were calculated such that any function where the mean and confidence intervals were higher than one indicated selection, and if lower than one indicated avoidance. Data are presented as percent availability of resource verses percent number of bites for each area, with selection or avoidance indicated with a + or – symbol. Data are only presented for the four most common coral genera consumed (*Acropora*, *Lobophyllia*, *Pocillopora* and *Porites*) which represented 93% of corals consumed in Diego central and 56% in Diego east. The non-coral substratum categories were combined and selectivity of this category also presented.

Table 1 Bite rate and dietary composition of three species of butterflyfishes on two reefs with differing benthic composition in the Chagos Archipelago

	n	Mean no. of bites per 3 min observation	Hard coral consumed (%)	No. of coral genera consumed
Diego central				
C. trifascialis	26	13.0	100	1
C. trifasciatus	26	16.7	97	4
Diego east				
C. trifascialis	30	17.8	100	4
C. trifasciatus	27	14.4	97	14
C. auriga	20	6.5	55	5

Chaetodon density surveys

The density of each of the three target butterflyfish and any other species of butterflyfish at the same locations as the benthic and feeding observations at both Diego east and Diego central was quantified. The density of each species was recorded along five randomly placed 50 × 4 m belt transects in each of the two study sites (following Berumen et al. 2005). Overall differences in the assemblages between the two study sites was assessed by MANOVA and differences at the species level using one-way ANOVA.

Coral food quality

Eight samples of each of the four most commonly eaten coral genera (*Acropora*, *Lobophyllia*, *Pocillopora* and *Porites*) were taken at random from the field sites and dried on land. Every effort was made to ensure the most common species of each genera was consistently sampled. Once dried the samples were ground with pestle and mortar and placed in plastic vials for transport. On return to the lab the corals were placed in an oven at 50°C to ensure they remained dry. Each sample was then further ground into a powder, before being decalcified to remove the skeleton using 5% HCL. This solution was then freeze-dried and the resultant substance was ground into a powder and placed in glass vials. Carbon, hydrogen and nitrogen values were obtained by testing each sample on a Carlo Erba 1108 elemental analyser controlled with CE Eager 200 software, and weighed using a Mettler MT 5 Microbalance (Wilson 2000). Two runs were performed on each sample and an average taken. C:N ratios were then calculated for each sample run. C:N ratio's are a measure of food quality, a low value infers higher nitrogen to carbon, which indicates there is more protein present for growth (Purcell and Bellwood 2001; Wilson et al. 2003).

A one-way ANOVA was used to test for differences in C:N ratios among the four coral genera. The ANOVA was performed both with and without a clear outlier for the *Acropora* results, this data point displaying nearly double that of the median for the group. Normality of data was examined with histograms and normal probability plots of the residuals and homogeneity of variances were tested with Levene's test.

Temporal change in coral feeding fish densities

In both 1994 and 2005 the density of 134 species of diurnally active, non-cryptic reef fish were surveyed at 21 sites, spanning three different habitat types (carbonate fringing reefs, granitic rocky reefs with coral growth, and patch reef habitats on a sand, rubble or rock base), in the Seychelles, with sixteen 7 m radius point counts at each site conducted at the bottom of the reef slope [for full details see Jennings et al. (1995); Graham et al. (2006)]. In the present study, only the density data of corallivores are considered, which includes 13 species from the families Chaetodontidae, Monocanthidae and Labridae. Benthic data was also collected at each of the study sites, quantifying percent cover of different growth forms of live coral and other non-coral benthic categories (Jennings et al. 1995; Graham et al. 2006).

Density of the three species of chaetodontid for which feeding observations were made were analysed individually and all species were also assigned to three main feeding strategies based on the literature (McIlwain and Jones 1997; Allen et al. 1998; Kokita and Nakazono 2001; Pratchett 2005; http://www.fishbase.org). Three species were classified as obligate specialist coral feeders (*Chaetodon trifascialis*, *Labrichthys unilineatus* and *Oxymonocanthus longirostris*), four species as obligate generalist coral feeders (*Chaetodon melannotus*, *C. meyeri*, *C. trifasciatus* and *C. zanzibarensis*) and six species as facultative coral feeders (*Chaetodon auriga*, *C. guttatissimus*, *C. kleinii*, *C. lineolatus, C. lunula* and *C. xanthocephalus*). From the current literature, the similar feeding observations of this study as compared to those in the Pacific and the clear patterns observed in the data, these groupings appear to be robust.

Change in density of the individual species and aggregated feeding groups were assessed with a two-factor crossed ANOVA design with factors year and habitat type, however as habitat alone was not significant for any comparison, the data are presented for year only. Normality of data was examined with histograms and normal probability plots of the residuals and homogeneity of variances were tested with Levene's test. Aggregated level obligate generalists and specialist groups required $\log_{10}$ transformation to meet the assumptions of the test.

Results

Substratum availability

The two sites had similar live coral cover (55% Diego east and 52% Diego central), but the dominance and diversity of coral genera varied greatly (Fig. 1). Diego east was dominated by *Pocillopora*, with a mean cover of 34% compared to 2.2% for Diego central ($F_{1,9} = 21.23$, $P < 0.01$). Conversely Diego central was dominated predominately by *Acropora* colonies, with a mean cover of 49% compared to 4.4% in Diego east ($F_{1,9} = 69.43$, $P < 0.001$). Cover of other live coral genera and non-coral substrate did not vary significantly, however the richness of coral genera was greater for Diego east (Fig. 1).

Feeding observations

The greatest bite rates in Diego central were recorded for *C. trifasciatus*, whereas in Diego east, *C. trifascialis* had the highest rates and *C. auriga* had considerably lower bite rates than the other two species (Table 1). *C. trifascialis* took 100% of bites from live coral at both sites, while *C. trifasciatus* took 97% and *C. auriga* took 55% (Table 1). In the lower diversity site, Diego central, *C. trifascialis* took all its bites from *Acropora* colonies, principally *Acropora tenuis*, the dominant species at the site, but also *Acropora clathrata*. *C. trifasciatus* took bites from four different genera at Diego central. At Diego east *C. trifascialis* consumed four genera of coral, while *C. trifasciatus* consumed 14 genera and *C. auriga* consumed five genera, a considerable portion of its bites from non-coral substrata (Table 1).

Selectivity analysis shows that *C. trifascialis* is preferentially selecting *Acropora* and avoiding other available genera in Diego central (Fig. 2). *C. trifasciatus* displays a similar trend, however there is also evidence for selectivity on *Porites* spp. (Fig. 2). In Diego east *C. trifascialis* is preferentially selecting *Acropora*, but also taking a large proportion of bites on *Pocillopora* colonies. While *C. trifasciatus* appears to have a much more general diet, it is only selecting preferentially for *Acropora*. *C. auriga* appears to have a very general diet, and does not select for

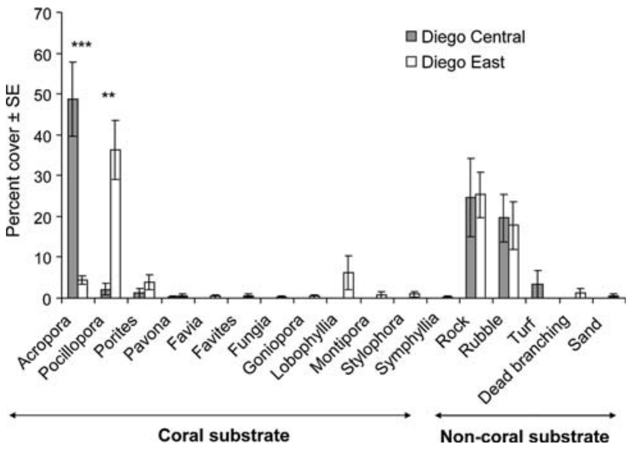

Fig. 1 Benthic resource availability at Diego east and Diego central, Chagos Archipelago. *** $P < 0.001$, ** $P < 0.01$

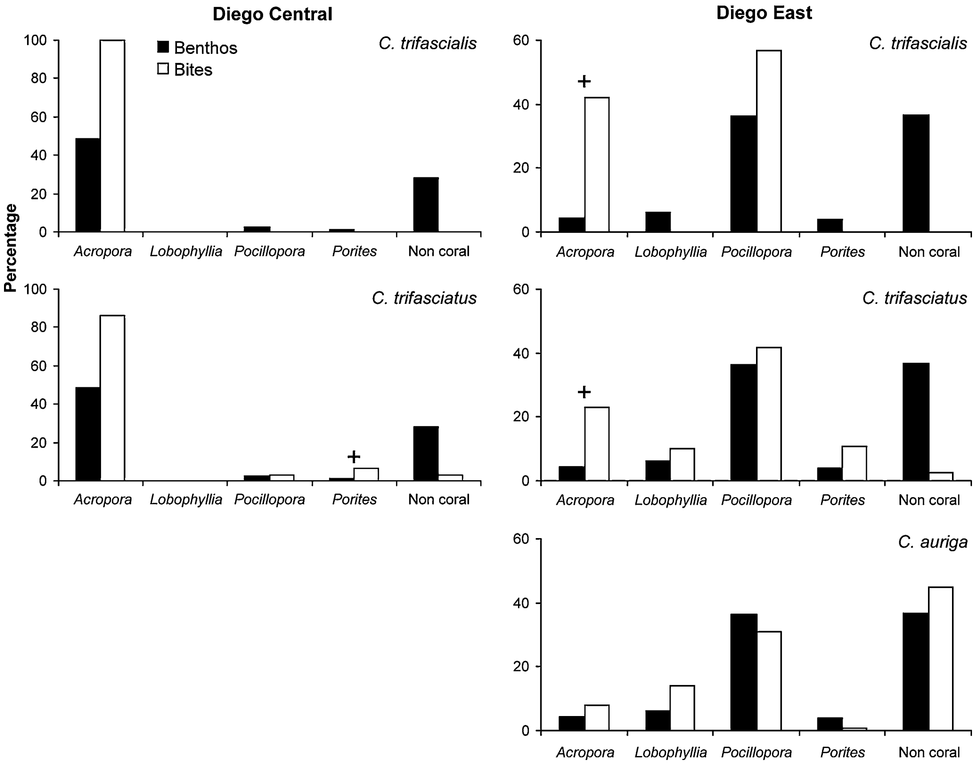

Fig. 2 Feeding selectivity of *C. trifascialis*, *C. trifasciatus* and *C. auriga* at Diego central and Diego east, Chagos Archipelago. Data only presented for the four coral genera most preferentially consumed. *Black bars* indicate percent resource availability, *open bars* indicate percent feeding bites on that resource. *Plus* symbol indicates positive selectivity

any resource in greater proportion to its availability (Fig. 2).

Corallivore density surveys

The overall assemblage structure of corallivores between the two sites varied significantly in terms of density (MANOVA, Wilks = 0.017, $F_{3,6} = 28.45$, $P < 0.01$) (Fig. 3). *C. trifascialis* had a greater density in Diego central ($F_{1,9} = 28.77$, $P < 0.001$) while *C. trifasciatus* and *C. auriga* had higher densities in Diego east ($F_{1,9} = 22.43$, $P < 0.001$ and $F_{1,9} = 6.94$, $P < 0.05$, respectively). Although not significant, the remaining species all displayed higher densities in the more diverse Diego east site (Fig. 3).

Coral food quality

The lowest C:N ratios, and therefore highest food quality, were for *Acropora* and *Lobophyllia* coral genera, while P*ocillopora* had the highest C:N ratio (Fig. 4). ANOVA results indicate this difference is significant ($F_{3,30} = 4.25$, $P < 0.05$), with the only pairwise difference between *Lobophyllia* and *Pocillopora* ($P < 0.01$). However if the analysis is re-run with the clear outlier for *Acropora* (Fig. 4) removed, the trend is considerably stronger ($F_{3,29} = 7.86$, $P < 0.001$), and *Acropora* is also different from *Pocillopora* in pairwise tests ($P < 0.01$).

Temporal change in coral feeding fish densities

Between 1994 and 2005 total live coral cover declined by an average of 73% at the sites studied in the Seychelles, with complex branching and plating corals declining by 95% to a new base level of 1% cover across the study area (Graham et al. 2006, 2007). Change in densities of the three focal Chaetodontids through this major bleaching event indicates the most specialist species (*C. trifascialis*) declined the most ($F_{1,41} = 11.16$, $P < 0.01$), followed by the generalist obligate coral feeder (*C. trifasciatus*) ($F_{1,41} = 9.47$, $P < 0.01$), while the facultative corallivore (*C. auriga*) did not show any decline (Fig. 5). Habitat was not a significant factor for any of the species, however *C. trifasciatus* displayed a significant year × habitat interaction term, which was due to a greater decline in carbonate and patch reef habitats than granitic reef habitats ($F_{2,41} = 3.36$, $P < 0.05$). If all the corallivores in the assemblage are assigned to the above three feeding categories, the obligate specialist feeders show a 98% decline ($F_{1,41} = 120.11$, $P < 0.001$), the obligate generalist coral feeders display a 73% decline ($F_{1,41} = 24.51$, $P < 0.001$) and the facultative coral feeders show a 32% decline ($F_{1,41} = 4.20$, $P = 0.048$) (Fig. 5).

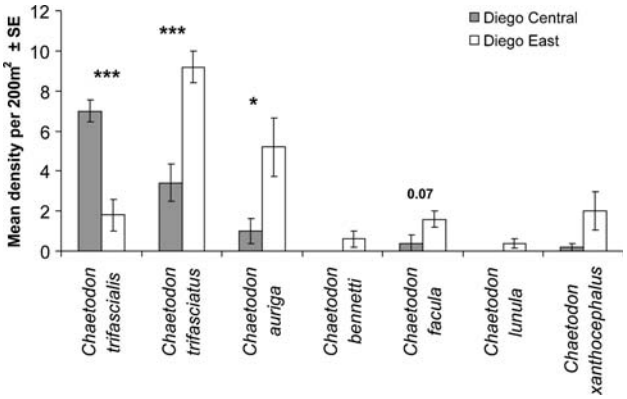

Fig. 3 Mean density of corallivores present in Diego central and Diego east. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

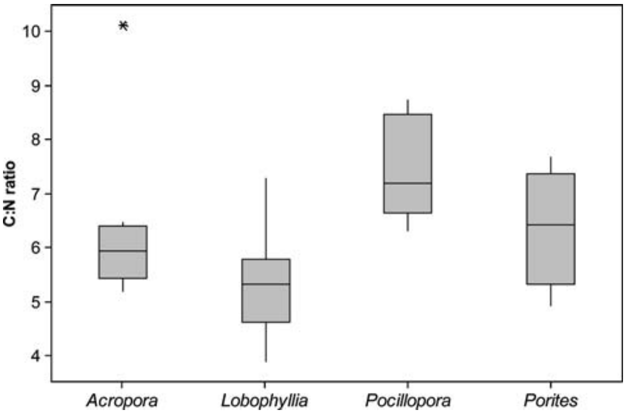

Fig. 4 Box and whisker plots of C:N ratios for four coral genera. *Box* indicates median value, lower and upper quartiles. *Whiskers* indicate range up to 1.5 times the box. *Outliers* indicated with an *asterisk*

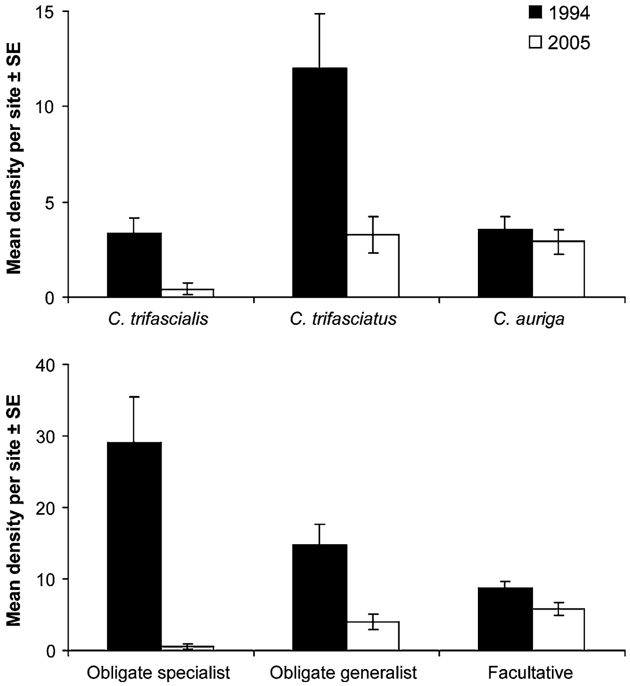

Fig. 5 Change in density of *C. trifascialis*, *C. trifasciatus* and *C. auriga* and obligate specialists, obligate generalists and facultative feeders in Seychelles before and after the 1998 bleaching event

Discussion and conclusions

Here I have shown that although there may be greater feeding plasticity than previously documented in some species of corallivore, there are obvious differences between obligate specialist, obligate generalist and facultative feeders, which may in part be due to the quality of food. Similar to a previous study (Pratchett et al. 2006), the degree of specialisation is reflected in the extent of decline in density following mass coral bleaching. The obligate specialist feeders were severely impacted in this study, with a potential local extinction of *Labrichthys unilineatus* (Graham et al. 2006).

The number of bites taken per 3 min observation varied among species and between the two study reef sites. Although bite rates of *C. trifasciatus* did not change markedly between reefs, *C. trifascialis* took a greater number of bites at Diego east (the *Pocillopora* dominated reef) than Diego central (the *Acropora* dominated reef). Although the sample sizes were not large, this could reflect abundance of preferred resources, with greater feeding rates required when preferred corals are not in abundance (Bowen et al. 1995). *C. trifascialis* are known to defend their territories aggressively (Reese 1975, 1981), so it is interesting that feeding rates were higher at the site where a greater number of other species were present and thus potentially a greater number of aggressive interactions may be expected. The lack of a difference in bite rates in *C. trifasciatus* was also noted before and after coral decline at trunk reef, Australia for *C. lunulatus* (closely related Pacific species) (Pratchett et al. 2004, but see Irons 1989). The lowest numbers of bites per observation were recorded for *C. auriga*, which again could reflect nutritional value of food items, this species often targeting polychaete worms and other invertebrates (Bouchon-Navaro 1986).

Both *C. trifascialis* and *C. trifasciatus* preyed on a greater number of coral genera in the more diverse *Pocillopora* dominated habitat, although *C. trifasciatus* was clearly the more generalist feeder and both species preferentially selected for *Acropora* corals. *C. trifascialis* is a highly specialised coral feeder, almost always selecting *Acropora*, often *Acropora hyacinthis* (Pratchett 2005, 2007), though the preferred species can vary geographically (Reese 1981). However, some plasticity in feeding has been observed when *Acropora* cover is very low (Irons 1989; Samways 2005), as is apparent in the current study. Feeding plasticity has also previously been documented between reefs of varying coral availability for *C. baronessa* and *C. lunulatus* at Lizard Island, Great Barrier Reef (Berumen et al. 2005). When preferred corals were not in abundance, the physiological condition of the fish, as measured by hepatocyte vacuolation in the liver, declined (Berumen et al. 2005). A decline in physiological condition was also noted for *C. lunulatus* following declines in cover of *Acropora* corals, which resulted in declines in abundance, but a shift in diet away from *Acropora* (Pratchett et al. 2004). It is possible that *C. trifascialis* may have lower fitness and fecundity in Diego east due to sub-optimal diet, however analyses such as those described above would be required to ascertain this. Interestingly, *C. trifasciatus* selected for *Porites* corals in Diego central and took a greater proportion than available in Diego east, albeit taking very few bites from them overall. *C. trifasciatus* (now *C. lunulatus*) has been shown to feed primarily on poritid corals in Hawaii at sites where poritid and montiporid corals dominate (Cox 1994), suggesting that selectivity for *Porites* may be common in this species.

In this study *C. auriga* individuals took ~55% of bites from live coral. There appears to be a great deal of biogeographic variation in the feeding patterns of this species, with studies in Australia finding live coral made up just 4% of its diet (Pratchett 2005), ~61% in French Polynesia (Harmelin-Vivien and Bouchon-Navaro 1983) and ~29% in the Red Sea (Harmelin-Vivien and Bouchon-Navaro 1981; Bouchon-Navaro 1986). The species is clearly a facultative coral feeder, but whether the variation in coral dependence is a spatial or temporal artefact is yet to be elucidated.

As can be seen with *Acropora* in the Diego central site, selection functions do not always perform well when data are aggregated. In this study data were collected on selection of resource units by individual animals, but resource availability was assessed at the population level. Although the selection function chosen largely accounts for this (Manly et al. 1993), there is still a problem with resources in low availability, particularly when they are clumped in distribution, and/or the animals are territorial. In such situations assessment of resource availability within the specific boundaries of an individual territory may produce clearer results (however there are inherent problems in assessing butterflyfish territory size, as described by Reese (1981)). For example the low cover of *Lobophyllia* in Diego east was clumped, but when it did occur in a fishes territory, they took the majority of their bites from it. This coral has the fleshiest polyp and so potentially offers the greatest nutritional return per bite effort. Although *Lobophyllia* was recorded in the random benthic line intercept transects, because it only occurred in the territory of several fish, the selection function did not indicate positive selection.

There was an overall difference in species abundance between the two sites, with *C. trifascialis* having a significantly greater density in the *Acropora* dominated Diego central, and all other species present being in greater density in the more diverse Diego east. *C. trifascialis* is known to be very territorial and actively defend its territory from intruders (Reese 1975), suggesting that this species may dominate in such mono-specific *Acropora* rich areas (Pratchett 2005) inhibiting the presence of other species. Even competitively similar species can display inverse relationships in terms of abundance (Reese 1981). It has been suggested that competitively subordinate species may have a broader diet to avoid competition with more specialised aggressive species (Pratchett 2005). *C. trifascialis* lives as a solitary individual and defends a specific territory, whereas other species, such as *C. trifasciatus* and sometimes *C. auriga* occur in heterosexual pairs (Reese 1975, 1981). There is also variation in territory size, with *C. trifascialis* and *C. trifasciatus* utilising fairly small territories, whereas *C. auriga* forages over a wider area (Reese 1975). It appears *C. trifascialis* dominates over other species where *Acropora* is in abundance, as has been described in previous studies (Reese 1981; Pratchett 2005), and thus other species are in greater number on more diverse reefs, not dominated by *Acropora*, where coexistence is more likely achieved through partition of food resources (Zekeria et al. 2002).

One possible explanation for differences in feeding specialisation could be variation in food quality. C:N analysis indicated that *Lobophyllia* and *Acropora* tissue has a lower C:N ratio, thus greater food quality, than *Pocillopora* corals. If this is the case it could help explain why many corallivores preferentially feed on *Acropora* corals (Pratchett 2005), i.e. selecting for protein rich resources (Bowen et al. 1995). It could also help explain why species in habitats with low availability of preferred corals have been shown to have reduced physiological condition (Pratchett et al. 2004; Berumen et al. 2005). However the latter studies assessed lipid stores in the liver which equate to short-term energy needs more than the C:N ratios examined here, which give an indication of protein availability and energy for growth (Bowen et al. 1995). Whether the same corals found to have low C:N ratios in the present study also have high lipid content remains to be tested.

Methodological variation in C:N ratios should be minimised when techniques are standardised within a study, so one would hope the results presented here are comparable. As only one species per genera was assessed in the current study, it is not clear how much variation there is within genera of corals compared to among them. This is clearly an area for future research. However, given that in the current study area, certain species of coral dominated within a genera, and it was these that were both preyed upon by the fish and assessed for C:N ratios, the results are robust for the purpose of feeding selectivity.

It is clear from previous studies that coral tissue is a valuable food source (Bythell 1988; Rotjan and Lewis 2005), with algal and related food sources likely being of less nutritional value (Wilson 2000; Rotjan and Lewis 2005, but see Wilson et al. 2003 for variation) and invertebrates, such as polychaete worms having higher nutritional value (Rotjan and Lewis 2005). The higher nutritional value of invertebrates such as polychaetes may help explain why the feeding rates of *C. auriga* are less than obligate coral feeders. There will obviously be other reasons why species preferentially choose certain coral prey, which may involve resource partitioning (Zekeria et al. 2002; but see Pratchett 2005), functional jaw morphology (Motta 1988), morphology of corals (Tricas 1989) and presence of nematocysts (Gochfield 2004). It is likely that all these factors contribute to the final selectivity of fish.

Declines in density of corallivores between 1994 and 2005 in the Seychelles further highlight the importance of specialisation when assessing the vulnerability of fish to disturbance (Munday 2004; Pratchett et al. 2006; Wilson et al. 2006). In this study *C. trifascialis* and the aggregated obligate specialist feeders showed the greatest declines, followed by *C. trifasciatus* and the obligate generalists and *C. auriga* and the aggregated facultative feeders showed little change. This directly corresponds to predictions based on feeding selectivity, and the fact that *Acropora*, the preferred food of many specialists, is among the most vulnerable taxa of corals to coral bleaching and other disturbances such as crown-of-thorns starfish outbreaks and storms (McClanahan et al. 2004, 2007; Wilson et al. 2006). Pratchett et al. (2006) also found obligate coral feeding butterflyfish declined on the Great Barrier Reef following extensive coral mortality, but facultative and non-coral feeders did not. This study furthers this knowledge by highlighting the distinction between obligate specialist and obligate generalist feeders, and also includes species from the monocanthid and labrid families. Declines in density of coral feeders in the Seychelles were greater in marine protected areas than fished areas (Graham et al. 2007), suggesting this management option offered no insurance against the disturbance. Clearly when disturbances are so severe and spatially extensive, specialist species have little refuge.

There is a growing literature highlighting the vulnerability of specialist fish to disturbance (reviewed by Wilson et al. 2006), suggesting that measures of feeding (Pratchett 2005) or habitat (Munday et al. 1997) specialisation will be important criterion to predict which species are vulnerable to extinction on reefs (Munday 2004). Indeed, in the Seychelles, where the 1998 coral bleaching event devastated reefs, there is evidence of the local extinction of four specialist species (Graham et al. 2006). Local extinction of coral specialists has also been documented from Papua New Guinea following extensive coral mortality (Jones et al. 2004; Munday 2004). If we are to manage and conserve biodiversity in a changing climate, a greater understanding of the species most vulnerable to disturbance, their habitat needs and the functional roles they offer to the rest of the ecosystem will be imperative.

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ORIGINAL PAPER

Anthropogenic stressors, inter-specific competition and ENSO effects on a Mauritian coral reef

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Abstract Much of the western Indian Ocean suffered widespread loss of live coral in 1998 and interest is now focussed on the indirect effects of this coral loss on other components of the ecosystem, in particular fishes. However, it is just as important to identify changes in fish assemblages at locations that did not suffer coral mortality to understand local versus regional drivers. We surveyed benthic and fish communities on a reef flat in Mauritius five times between 1994 and 2005. The design allowed for comparison through time, along the coast and between inshore and offshore reef locations. The benthic community demonstrates a clear trend along the coast, likely in response to a dredged water ski lane, but little change through time. Branching *Acropora* colonies dominate much of the live coral and best explain patterns in the fish assemblage ($P < 0.01$). Few changes in overall fish species richness through time were identified, and observed changes were within fishery target families rather than species reliant on live coral. Departure from expected levels of taxonomic distinctness suggests degradation in the community associated with the dredged ski lane. Non-metric multi-dimensional scaling of the fish assemblage demonstrates a similar pattern to that seen in the benthos; greater differences along the coast (Global $R = 0.34$) than through time (Global $R = 0.17$) and no trend between reef positions. SIMPER analysis identified two species of *Stegastes* as the main drivers of trends in the MDS plot and the most dominant of these, *S. lividus*, appears to be reducing species richness of the remaining fish community. The study highlights Mauritius as a regional refugia of thermally-sensitive corals and specialised fish, suggesting a need for careful management.

Keywords Climate change · Community structure · Reef fishes · Coral bleaching · Mascarene Islands · Tourism · *Stegastes* · Western Indian Ocean

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Introduction

Coral reefs globally are suffering increasingly frequent events of thermally induced bleaching and associated mortality (Hoegh-Guldberg 1999; Sheppard 2003). Loss of live coral cover at this scale is expected to affect other components of the ecosystem (Walther et al. 2002), and studies of such impacts are growing in number. Much attention is focussed on likely ramifications for reef-associated fish assemblages. The majority of studies to date have been on the scale of a few months to years and indicate limited community change aside from species directly dependant on live coral or algae for food or shelter (Kokita and Nakazono 2001; Lindahl et al. 2001; Booth and Berretta 2002; Chabanet 2002, McClanahan et al. 2002; Sheppard et al. 2002; Spalding and Jarvis 2002; Sano 2004), whereas the longer term effects may be much greater (Jones et al. 2004; Garpe et al. in press; Graham et al. 2006). This may be due to lag effects associated with changes in physiological condition of fish (Pratchett et al. 2004) and collapse of the physical structure of the reef matrix (Garpe et al. in press; Graham et al. 2006). Understanding such effects and processes will clearly be essential for future use and management of affected reef systems.

When trying to understand the effects of bleaching on fish assemblages, it is just as important to assess change through the same time period at locations that did not suffer badly from bleaching, as it is to study sites where severe mortality occurred. This acts as a control for bleaching effects where other drivers in fish community dynamics can be identified in a region over the same time period. Ecological processes such as variable recruitment (Doherty and Williams 1988; Letourneur et al. 1998; Doherty et al. 2004), predation (Hixon 1991; Graham et al. 2003) or competitive interactions (Robertson 1996; Letourneur 2000; McClanahan 2000a) could be driven by natural processes and influence fish assemblages. They may also be driven by changes in habitat associated with effects such as eutrophication (McCook 1999), sedimentation (Rogers 1990), or fishing (Jennings et al. 1995; McClanahan and Graham 2005), or actions that may cause physical damage to the habitat (Brown et al. 1990; Adjeroud et al. 1998). Identifying such processes and collecting baseline data at a location that has escaped much of the thermal damage characterised at other sites will provide information for future monitoring and management, particularly when future effects of bleaching at regional scales are expected to be significant (Sheppard 2003).

The warm phase of the El Niño Southern Oscillation (ENSO) event of 1998 resulted in the greatest global bleaching event on record (Hoegh-Guldberg 1999) and was particularly devastating to the western Indian Ocean (WIO) (Goreau et al. 2000) where it interacted with the warm portion of the Indian Ocean dipole (Saji et al. 1999). However, the effects varied greatly, with some locations, such as the Maldives and the inner Seychelles suffering 75–99% mortality, whereas other locations, such as Réunion and South Africa suffering low to negligible damage (Goreau et al. 2000; Obura 2005). Bleaching in Maurtius was also minimal with less than 10% coral cover effected in 1998 (Moothien Pillay et al. 2002; Turner and Klaus 2005), and 24% in 2004 (McClanahan et al. 2005). Post these two events coral cover is still dominated by thermally sensitive genus' such as *Acropora* and overall cover appears to have risen since a broad survey in 1992 (McClanahan et al. 2005).

This study assesses changes in benthic and fish communities on a narrow reef flat in north-west Mauritius that escaped much of the bleaching mortality experienced by other locations in the WIO in 1998. Temporal and spatial trends through a period 1994–2005, thus spanning the 1998, 2003 and 2004 bleaching events, are studied, aiming to identify any change in benthic and fish community structure. Alternative hypotheses are considered and, using a suite of multivariate tools, a case is built for the most plausible explanations for the observed trends.

Materials and methods

Study site and sampling techniques

Mauritius is located in the southwestern Indian Ocean, 200 km east of Réunion Island, and 800 km east of Madagascar, between latitudes

19.58 and 20.31°S, and longitudes 57.18 and 57.46°E. The study was conducted in the northwest coast of the island (Fig. 1), which is sheltered from the dominant southeast trade winds. The study site, Pointe aux Piments, is located 10 km north of the capital, Port-Louis, this part of the coast developed with hotels. The fringing reef, dominated largely by branching *Acropora* corals, is approximately 250 m wide and 1–2 m deep along this section of the coast, and largely used for recreational purposes by hotel guests. Within the study area a dredged water ski lane has been in active use since 1995 (Fig. 1). Fishing pressure around Mauritius is high (~1600 t yr^{-1} from lagoons and reefs) and is thought to exceed maximum sustainable yields (Turner and Klaus 2005).

Data were collected on benthic and fish communities at ten stations over a 10 year period, where samples were collected in 1994, 1995, 1996, 1997 and 2005. The design allowed for comparison through time, along the coast and between inshore and offshore reef locations. Five transects (T1–T5) perpendicular to the shore, each had a landward (A) and seaward (B) sampling station, where a 50 m transect tape was laid down parallel to the shore in a southerly orientation (Fig. 1). The study site comprised approximately 1 km of shoreline, each transect being separated by 200–350 m. Land sampling stations (A) were located 50 m from the shore, whereas sea stations (B) were ~200 m from the shore.

Full fish censuses were carried out by snorkel along 50*2 m belt transects at each of the ten sampling stations. Fish were identified to the species level (within 29 families) and abundance estimated. The discrete group sampling technique was used, whereby fish in different families and mobility groups were surveyed during different passes of the transect (four in total) to account for varying behaviours (Harmelin-Vivien et al. 1985). This process was repeated 3 times for each station and an average abundance for each species attained. A presence/absence survey was also conducted around each station area during a

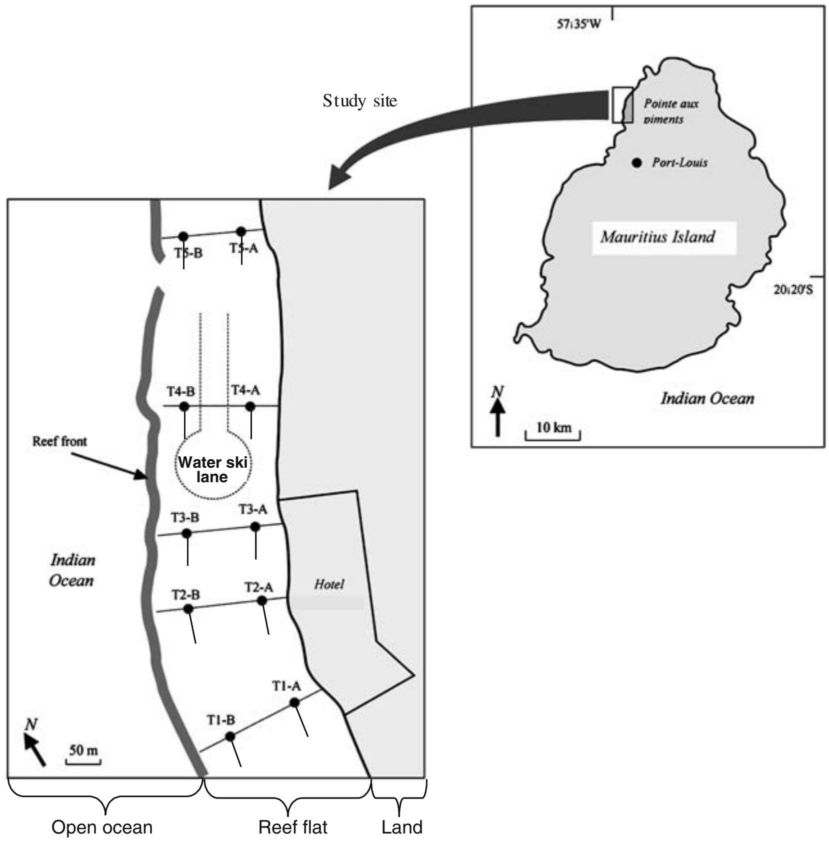

Fig. 1 Map of the study site, indicating location in Mauritius, proximity of the ten sampling stations, direction of transects and location of dredged water ski lane. Adapted from Adjeroud et al. 1998

30-min timed swim. Although fish counts were conducted by three different observers over the five sampling years, all observers were highly experienced and observer variation is expected to be minimal (Williams et al. 2006; McClanahan et al. in review). After a fish census was complete the benthos along the same 50 m transect line was quantified using the line intercept method (Loya 1978), whereby the distance of tape occupied by the following substratum categories was quantified: live branching coral, live plating coral, live other coral and dead substratum. These data were converted into percent covers of each category for each of the ten stations surveyed within each year. Data were collected during peak daylight hours. Surveys in 1994, 1996 and 2005 were during the Austral winter, whereas surveys in 1995 and 1997 were during the Austral summer, however analysis of 1994–1997 data indicated little seasonal variation (R. Galzin unpublished data).

Data analysis

Due to the multi-species nature of the data and the design of the survey, the most appropriate analyses were multivariate (Clarke and Warwick 2001a). To assess patterns in benthic data from all stations in all years we used correlation-based principle components analysis. Data were $\log(x + 1)$ transformed to account for some right skewness detected in draftsman's plots and normalised. Eigenvectors were overlaid on the resultant plot to identify direction and contribution of the different variables to the patterns and to identify any correlation between variables. Percent total live coral was also quantified for each transect and landward and seaward sampling stations across the 5-year period. Two-way ANOVA's were used to assess differences through time associated with both trends along and away from the shore. Normality of data was examined with histograms and normal probability plots of the residuals. Homogeniety of variances were tested with Bartlett's test. Where a significant difference was found, Tukey's test identified those samples driving the differences.

Presence/absence fish diversity data from timed swims was pooled to the year level to represent the reef as a whole. Overall species richness (S) and richness within key families was calculated for each year.

We examined the taxonomic diversity of the fish assemblage for each station and year. Average taxonomic distinctness (AvTD) was calculated by assessing the degree to which species in a sample are taxonomically related, measuring the average path length between every pair of species based on a taxonomic tree (Clarke and Warwick 1998). Variation in taxonomic distinctness (VarTD) was assessed by measuring the evenness to which the taxa were spread across the tree (Clarke and Warwick 2001b). Funnel plots were constructed for both variables with expected mean and 95% confidence limits constructed from a simulation distribution using random subsets of the master taxonomy list (constructed following Helfman et al. (1997)). Any departure from expected values could thus be identified, where low AvTD and low to normal VarTD indicates degraded locations (Clarke and Warwick 2001b). General patterns related to our study design were tested using two-way crossed ANOVAs with the factors year and transect, as these were identified as the key sources of variation by Analysis of Similarities (ANOSIM).

Fish assemblages within each station in each year were compared using non-metric multidimensional scaling (MDS) based on Bray–Curtis similarity measures. Species abundance data were square-root transformed to down weight abundant species. Differences between years, transects and reef position (A–B) were tested using ANOSIM, which is a non-parametric permutation procedure. After identification of which transects and years (the 2 significant factors) differed the most (ANOSIM pairwise test output), SIMPER analysis was run on the data matrix. SIMPER decomposes Bray–Curtis dissimilarities between all pairs of samples to identify those species that contribute most to differences (Clarke and Warwick 2001a).

As SIMPER identified *Stegastes lividus* followed by *Stegastes nigricans* as the species contributing most to the significant trends in the MDS plot for both year and transects along the shore, bubble plots were used to overlay relative abundance of both of these species enabling identification of the trends they were contributing to. As these species are both highly aggressive and territorial (Randall et al. 1997; Letourneur 2000), the influence that their abundance has on species richness of the rest of the fish assemblage was tested using linear regression analysis.

To link the benthic and fish data, bubble plots were used to overlay relative value of benthic variables on the fish species MDS plot. This allowed identification of any trends driven by the benthic variables. The BEST BIO-ENV routine was then run using Spearman rank correlation between benthic Euclidean distance and fish species Bray–Curtis similarity matrices to identify the benthic variable or group of variables that best explained the patterns in the fish species MDS plot (Clarke and Warwick 2001a). The significance of this result was tested using a permutation test.

Results

The benthos at this location in Mauritius experienced very little change through the 10-year study period. Principal Components Analysis indicates a trend along the shore line, from Transects 1 and 2 to Transects 4 and 5, but little change with time (Fig. 2). The main factors influencing this pattern along PC1 (~57% of variation) are higher cover of live branching and plating corals towards the southern end of the study site, or away from the ski lane, and higher cover of dead substratum towards the north (Fig. 2). Percent cover of other live substratum (mainly massive corals) appears to be driving patterns along PC2, however this cover was often low. These trends are further highlighted by looking at overall percent live coral cover. The decline along the coast in a northerly direction is significant ($F_{4,37} = 13.9$, $P < 0.001$), Tukey's test indicating that T1 differs from T4 and T5, and T2 differs from T3, T4 and T5, whereas no such trend is found through time ($P = 0.70$) (Fig. 3a). The greater cover at near shore locations compared to seaward locations (A–B) in 1994 was not nearly as great in subsequent years, and the overall difference between sites A and B and through time is not significant ($P = 0.15$ and $P = 0.85$) (Fig. 3b).

The timed swim presence/absence surveys demonstrate remarkable stability in overall fish species richness through time (Table 1). Stability is consistent in nearly all the key families involved, including those dependant on live coral such as the chaetodontids. Notable declines in number of species are seen for lethrinids, lutjanids (though both were already in low number) and in particular serranids, all of which are common fishery target species (Table 1).

Conversely, at the level of stations, a number of samples depart negatively from the expected

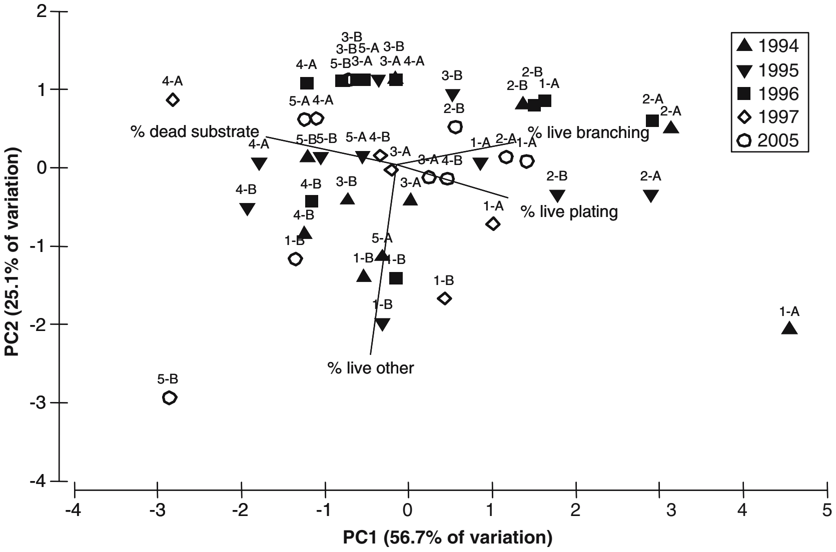

Fig. 2 Correlation-based Principle Components Analysis of log(x + 1) transformed and normalised environmental data

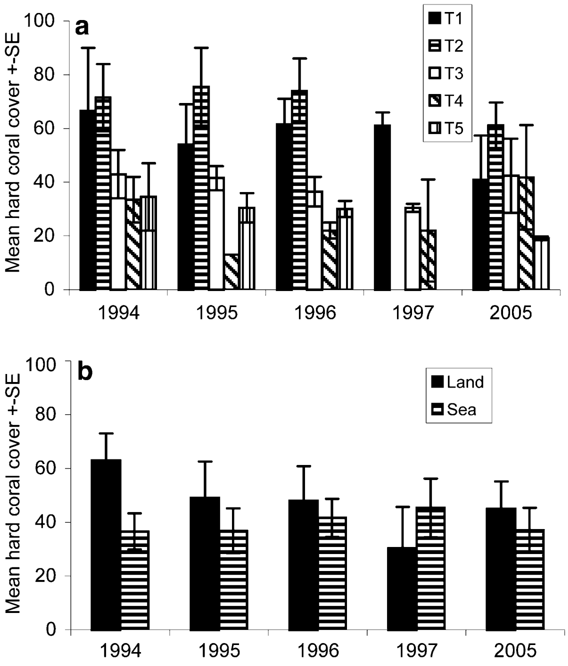

Fig. 3 Percent cover of total live coral in (**a**) each year by transect and (**b**) each year by position from the shore

values of AvTD, suggesting some samples may be taxonomically depauperate (Fig. 4a). The only significant decline in the ANOVA model was for the factor year ($F_{4,25} = 3.22$, $P = 0.03$) and Tukey's pairwise comparisons indicate that this was influenced by lower values in 1997 versus 2005 ($P = 0.03$). Much less departure from expected values is noticed for VarTD (Fig. 4b), however a weak significant difference is detected for the factor transect ($F_{4,25} = 2.95$, $P = 0.04$), which is driven by a difference between Transect 1 and 3 ($P = 0.04$).

Table 1 Reef fish species richness from presence/absence timed swim data at level of whole assemblage (S) and within selected families

	1994	1995	1996	1997	2005
Total species richness (S)	104	102	110	99	101
Acanthuridae	7	9	8	8	7
Balistidae	2	1	2	1	3
Chaetodontidae	8	9	8	11	10
Holocentridae	3	4	5	4	3
Labridae	19	22	21	24	20
Lethrinidae	3	3	2	2	2
Lutjanidae	1	0	2	0	0
Monacanthidae	4	5	5	3	5
Mullidae	6	5	4	5	7
Pomacentridae	13	13	12	12	14
Scaridae	7	7	9	7	6
Serranidae	7	3	4	4	1
Siganidae	1	1	1	0	1

The fish species MDS plot indicates a very similar pattern to that found in the benthic PCA, some difference in years, but an overall trend along the coast from T1 and T2 to T4 and T5 (Fig. 5a). Samples from T1 and T2 are located in the bottom left side of the plot for all years, with samples from more northerly transects located to the top and right of the plot. This pattern is highlighted by the ANOSIM results, with significant differences for Year and Transect, but not Position on the reef (Table 2). Pairwise testing identified 1994 departing from all other years and 2005 from 1996 and 1997. Pairwise tests for Transect identified T1 departing from T4 and T5, and T2 from T4 (Table 2).

SIMPER analysis, for the 2 years and transects that differed the greatest from one another, highlighted that *Stegastes lividus* followed by *S. nigricans* were contributing by far the greatest to the observed differences (Table 3). Pomacentrids and more mobile scarids, acanthurids and wrasses make up the majority of the remaining species contributing 60% of the differences (Table 3). The trends driven by *S. lividus* and *S. nigricans* are highlighted by the bubble plots (Fig. 5b, c), the former being more dominant in the southerly sites that have greater live coral cover (Fig. 3a), whereas the latter is more dominant in the northerly sites. Furthermore, and likely exacerbating the patterns, is that the abundance of *S. lividus* but not *S. nigricans* is negatively correlated with overall fish species richness, though the trend is not consistently significant between years (Fig. 6).

Bubble plots overlaying percent cover of benthic variables on the fish species MDS further highlight these trends; samples to the bottom left of the plot being dominated more by live branching and plating corals (Fig. 5d, f), whereas samples to the right of the plot have a greater cover of dead substratum (Fig. 5e). Rank correlation of benthic variables to the fish species data indicates that the best single and significant (BioEnv Rho statistic: $P < 0.01$) benthic variable

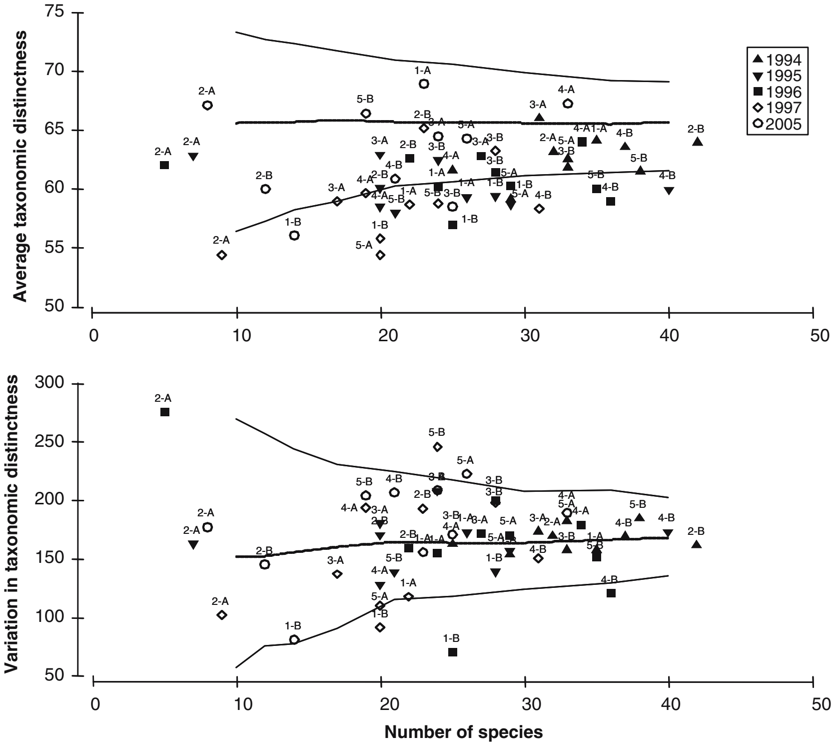

Fig. 4 Funnel plots of average taxonomic distinctness (**a**) and variation in taxonomic distinctness (**b**) of each sampling station (belt transects) within each year with mean and 95% confidence limits from expected values using master taxonomy aggregation file

driving the patterns in the fish data is the percent cover of live branching coral ($r = 0.36$).

Discussion

Coral and fish communities appear to have experienced very little change over 10 years at this location in Mauritius, in contrast to other studied sites in the western Indian Ocean (Lindahl et al. 2001; McClanahan et al. 2002, Sheppard et al. 2002; Graham et al. 2006). Indeed the dominant trend at the study location appears to be along the coast, rather than through time. This suggests that the benthic community has changed very little through the 1998 ENSO event and the more minor 2003 and 2004 bleaching events. Unfortunately, reefs were not sampled between 1997 and 2005, which raises the question as to what happened during this sampling hiatus. The 1998 ENSO event resulted in less than 10% of coral colonies bleaching in Mauritius (Moothien Pillay et al. 2002). The 2003 bleaching event was most evident on the southwest of the island and a cyclone was implicated in the recovery of bleached corals (Ahamada et al. 2004; Turner and Klaus 2005). In 2004, 24% of corals bleached (McClanahan et al. 2005), however recovery was again high (Ahamada et al. 2004) and coral cover was higher than surveys conducted in 1992 (McClanahan et al. 2005). Although we can not discount the possibility of rapid re-colonisation and recovery of the reef with the predominant fast growing *Acropora* colonies, the above studies and the remarkably similar cover estimates through time suggest a minor influence from bleaching events. Furthermore, *Acropora* is one of the most susceptible genera to thermal stress in the region (McClanahan et al. 2001, 2004) and has experienced large declines in many other locations (Goreau et al. 2000; McClanahan 2000b; McClanahan et al. 2001; Sheppard et al. 2002). Indeed, branching and plating corals now make up less than 1% of the benthos in the inner Seychelles, a decline of over 95% (Graham et al. 2006). Study and protection of this apparent refugia of sensitive, habitat forming corals in Mauritius is important given predictions of further widespread degradation of the region in coming decades (Sheppard 2003).

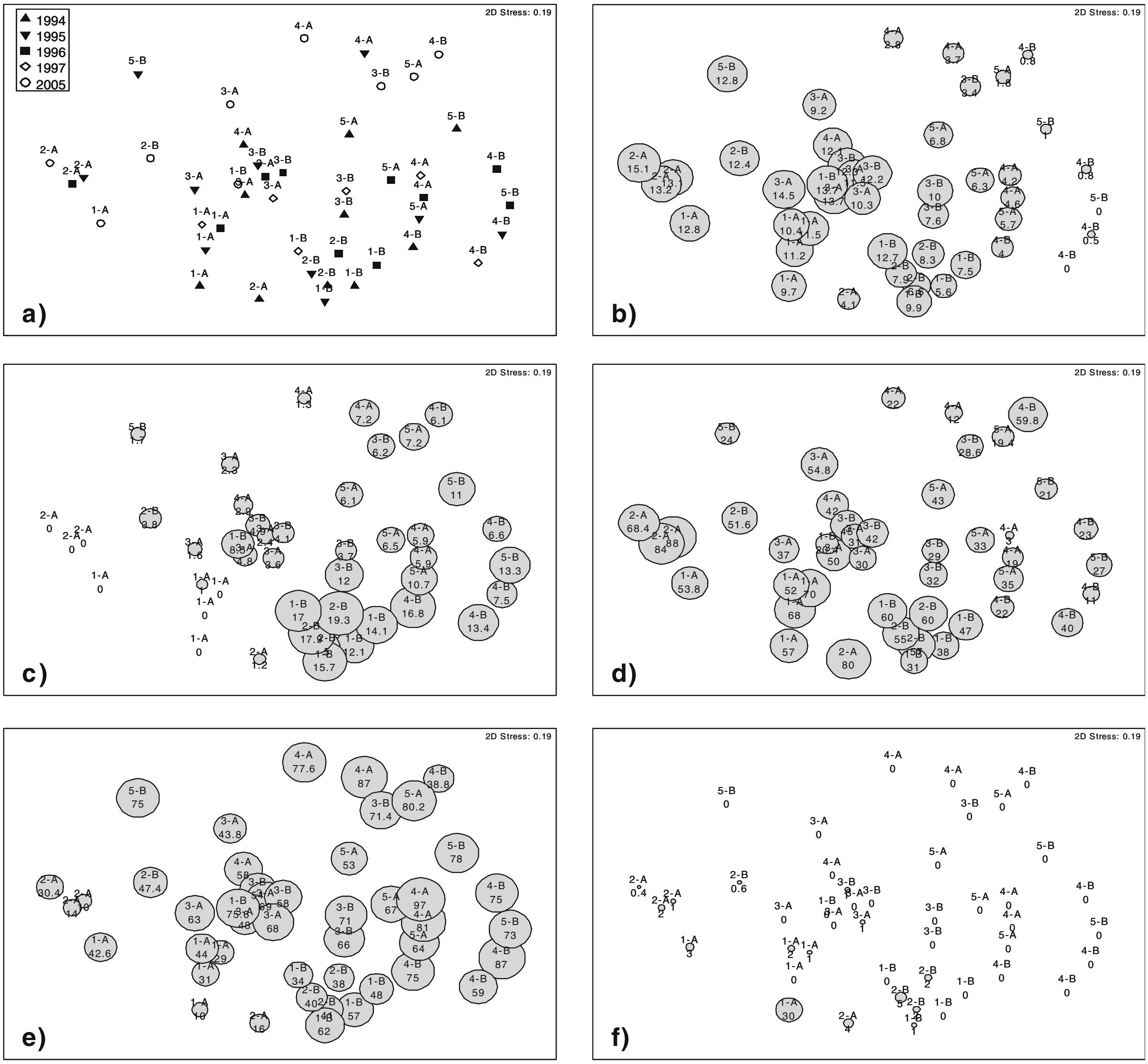

Fig. 5 Non-metric Multi-Dimensional Scaling (MDS) plot of fish assemblages at each of the ten stations (belt transects) within each of the five sample years based on Bray-Curtis similarity measures (**a**). Bubble plots for *Stegastes lividus* (**b**) and *Stegastes nigricans* (**c**) over species MDS sample points indicating patterns driven by their presence. Abundance at each sample given below station name (scale of bubbles: 0–20). Bubble plots for cover of branching coral (**d**), dead substrate (**e**) and plating coral (**f**) indicating which patterns in the species MDS are driven by these benthic variables. Percent cover at each station given below station name (scale of bubbles: 0–100%)

The observed trend in benthic composition along the coast within the study location is most likely due to the dredged water ski lane that has fragmented the reef flat in this section, likely still results in increased sediment loads and is subject to high recreational use. The disparity between near shore and sea (A–B) stations that was quite apparent and a dominant driver of trends in 1994 (Adjeroud et al. 1998) is not as great on a temporal scale. Given the dominance of the reef flat by fast growing branching *Acropora* corals, it is possible that this may be due to some recovery following completion of the ski lane (1993–1994).

Although overall species richness of the reef fish assemblage has remained stable through this time period, the richness is fairly low compared to studies in nearby islands such as Réunion (Letourneur 1996a), Madagascar (Harmelin-Vivien

Table 2 Analysis of Similarity (ANOSIM) outputs for the fish sampling stations

Factor	Global *R*	Significance	Pairwise test
Year	0.17	$P < 0.01$	1994 diff to all, 2005 diff to 1996 and 1997
Transect	0.34	$P < 0.01$	T1 diff to T4 and T5 T2 diff to T4
Position	0.02	ns	

Global and pairwise test results given for each of the three factors in the design

1989) and Mayotte (Letourneur 1996b; Chabanet 2002). This is likely due to the surveys being restricted to the reef flat and because the reef is narrow along this section of the coast (Adjeroud et al. 1998), although reef flats of a similar width in Réunion had higher species richness (Letourneur 1996a). It could also be due to anthropogenic stress on the system through past dredging of the water ski lane and ongoing effects of fishing and recreational use. Indeed, many samples depart from expected values of taxonomic distinctness, and common fishery target species, in the families Lutjanidae, Lethrinidae and Serranidae, are missing. The years driving the main difference in taxonomic distinctness were 1997 and 2005, with 1997 having lower values. Although coral cover was lowest in this year, the magnitude was small and it is hard to ascribe causation to this trend. Indeed, the stability of species richness from the presence/absence survey within families that often feed on (Chaetodontidae) or dwell in (Pomacentridae) live coral indicates that these patterns are likely not driven by ENSO effects on the benthos, in contrast to other locations in the region (Spalding and Jarvis 2002; Graham et al. 2006). As samples from all years demonstrated departure from expected values, it is more likely that long-term effects are causing the trends.

The overall pattern in the fish community from MDS analysis is remarkably similar to that for the benthos, with the greatest differences identified along the coast (Global *R* = 0.34) as apposed to time (Global *R* = 0.17). This lends further support to our conclusion that the ecosystem has remained stable through the ENSO event and other factors are likely responsible for the observed changes. The heavy fishing pressure in Mauritius (Turner and Klaus 2005) and the apparent loss of diversity in key fishery target groups, of which many species are piscivores, may be driving trends related to predation pressure. Studies of predator control on reefs indicate

Table 3 SIMPER outputs for greatest pairwise differences in year and transect identified by ANOSIM

Year (1994 and 2005)		Transect (T1 and T4)	
Species	% Contribution	Species	% Contribution
Stegastes lividus	10.64	Stegastes lividus	12.03
Stegastes nigricans	10.07	*Stegastes nigricans*	10.84
Dascyllus aruanus	4.77	*Scarus psittacus*	6.56
Chromis viridis	4.21	*Dascyllus aruanus*	4.78
Chlorurus sordidus	4.18	*Chlorurus sordidus*	3.92
Ctenochaetus striatus	4.15	*Scarus scaber*	3.36
Halichoeres scapularis	2.78	*Ctenochaetus striatus*	3.26
Stegastes limbatus	2.65	*Chromis viridis*	3.18
Scarus scaber	2.55	*Halichoeres scapularis*	2.79
Acanthurus triostegus	2.41	*Calotomus spinidens*	2.69
Gomphosus caeruleus	2.03	*Thalassoma hardwickii*	2.36
Zebrasoma scopas	2.02	*Stegastes limbatus*	1.91
Acanthurus nigrofuscus	1.95	*Stethojulis bandanensis*	1.76
Stethojulis bandanensis	1.86	*Epinephelus merra*	1.68
Chrysiptera unimaculata	1.82		
Oxymonacanthus longirostris	1.79		
Parupeneus macronema	1.43		

Species that contributed 60% of the overall difference are listed in descending order of most contribution

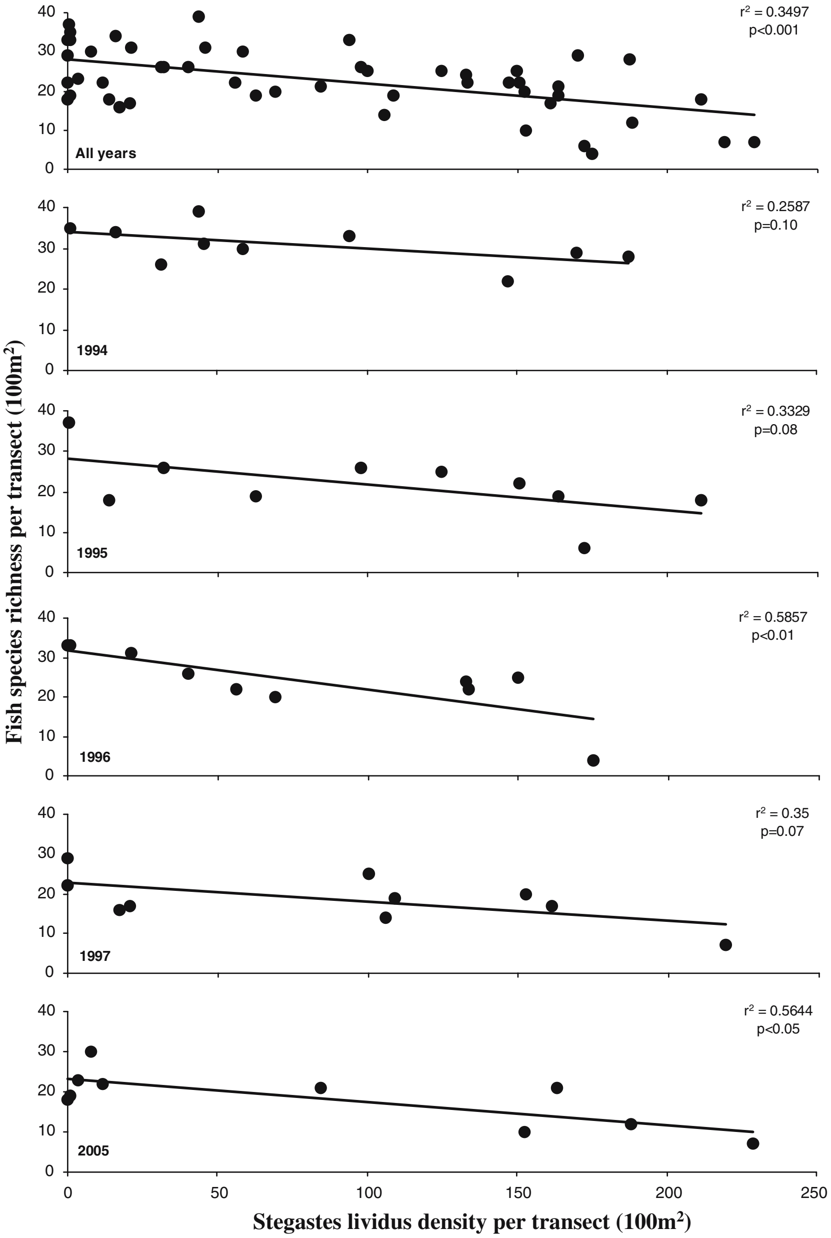

Fig. 6 Regressions of *Stegastes lividus* density against fish species richness per station (belt transects) overall and for each year separately. R^2 and regression analysis results given on plots

trends both at the level of single species (Graham et al. 2003), aggregated by size class (Dulvy et al. 2004), and evidence suggesting there is a direct relationship between gape size of the predator and size of prey (Mumby et al. 2006). Recruitment has also been shown to drive variation in fish assemblages on reefs (Doherty and Williams 1988), particularly following mass-events (Letourneur et al. 1998). Given the time between surveys and the narrow spatial scale over which the study has been conducted, variable recruitment could influence the small temporal patterns detected, but is unlikely to be driving the larger trends along the coast. Given that the availability of habitat types has not altered a great deal, competition for resources among fish species may be expected to have remained stable through this time period. However changes in certain dominant species, such as *Stegastes*, could well be causing changes in the rest of the assemblage.

The coastline adjacent to the study site has experienced rapid development for tourism in the last 10–15 years, and this is likely exerting stress on the reef ecosystem. Along the 1-km stretch of coast, two large hotel complexes actively use the reef for water sports activities. High use of reefs for snorkelling and diving can have detrimental effects (Hawkins et al. 1999; Zakai and Chadwick-Furman 2002). In this case, however, the greatest effect is likely to be from the dredged water ski lane through the middle of the reef flat. Increased pollution, sedimentation and changes in current regimes are all likely to be effecting both the coral and fish assemblages, and may be partly responsible for the changes through time. However, the greatest effects of the ski lane appear to be along the coast in the survey area.

Both the benthic and fish communities display the strongest patterns along the coast from Transects 1 and 2 to Transects 4 and 5, with greater live coral to the south end of the study site away from the dredged area. Branching coral is likely to be causing the observed patterns in the fish assemblages given that it was best at predicting the patterns in the fish assemblage structure and because it provides important three-dimensional structure (Bellwood et al. 2004). Furthermore, this habitat is critical at the early life history stage when fish settle from the plankton; 65% settling directly into live coral (Jones et al. 2004).

The two species of *Stegastes* were influencing the greatest difference along the coast and through time in the MDS plots. Although the preferred habitat of both species' is branching coral (Randall et al. 1997), it appears that *Stegastes lividus* is dominating the area of the reef where branching coral is most abundant. This may be explained by *S. lividus* growing to a larger maximum size than *S. nigricans* (Randall et al. 1997); size of individual correlating to size of territory and dominance over more favourable habitats in this genera (Robertson 1996; Letourneur 2000). If the relationship between *S. lividus* abundance and overall fish species richness is causal, this one species of small reef fish appears to be accounting for a large portion of the variation in fish species richness; benthic variables and *Stegastes nigricans* demonstrating no measurable control. Although the competitive dominance of larger species of *Stegastes* over abundance of other *Stegastes* species in the same area has been identified (Robertson 1996), and the influence of territorial pomacentrids on behaviour and foraging of individual species of other reef fish is well documented (e.g. Jones 2005), we believe this influence on the species richness of an entire fish community has not been demonstrated before.

Dominance of space by branching coral and *Stegastes lividus* is clearly contributing to the patterns in the MDS plot, but not necessarily in the direction one may expect from previous positive relationships between coral cover and fish species richness (e.g. Bell and Galzin 1984). Areas of high cover of live branching coral in Mauritius are dominated by large numbers of *S. lividus* and their territorial behaviour may actually reduce species richness, such that the relationship between coral cover and fish species richness is negative. Consequently, mono-specific stands of branching coral are resulting in an ecosystem more susceptible to competitive dominance by fewer species (Almany 2004). Indeed, dominance of a reef by one main taxa of coral will not necessarily promote high species diversity, rather a range of different taxa and habitat types is expected to provide more niches and a more diverse ecosystem (Almany 2004). This will be particularly true for small-bodied species of reef fish that are closely reliant on habitat for shelter and food and are often specialised (Munday and Jones 1998).

The western Indian Ocean has suffered the greatest effects from coral bleaching in the Indo-Pacific (Goreau et al. 2000) and future bleaching is predicted to result in the 'extinction' of these reefs in coming decades (Sheppard 2003). However, various locations in the southern western Indian Ocean, including Mauritius, currently seem to be a refuge from coral bleaching, demonstrating "protection" from serious thermal stress (Obura 2005) and host high coverage of thermally sensitive corals that still support specialist fish species. This study has demonstrated minimal community change through time on a coral reef in Mauritius, and identified other factors likely to be driving trends. Such data and future monitoring in these areas of bleaching refugia will be important to understand natural variation in fish communities and associated management implications.

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Lag Effects in the Impacts of Mass Coral Bleaching on Coral Reef Fish, Fisheries, and Ecosystems

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Abstract: *Recent episodes of coral bleaching have led to wide-scale loss of reef corals and raised concerns over the effectiveness of existing conservation and management efforts. The 1998 bleaching event was most severe in the western Indian Ocean, where coral declined by up to 90% in some locations. Using fisheries-independent data, we assessed the long-term impacts of this event on fishery target species in the Seychelles, the overall size structure of the fish assemblage, and the effectiveness of two marine protected areas (MPAs) in protecting fish communities. The biomass of fished species above the size retained in fish traps changed little between 1994 and 2005, indicating no current effect on fishery yields. Biomass remained higher in MPAs, indicating they were effective in protecting fish stocks. Nevertheless, the size structure of the fish communities, as described with size-spectra analysis, changed in both fished areas and MPAs, with a decline in smaller fish (<30 cm) and an increase in larger fish (>45 cm). We believe this represents a time-lag response to a reduction in reef structural complexity brought about because fishes are being lost through natural mortality and fishing, and are not being replaced by juveniles. This effect is expected to be greater in terms of fisheries productivity and, because congruent patterns are observed for herbivores, suggests that MPAs do not offer coral reefs long-term resilience to bleaching events. Corallivores and planktivores declined strikingly in abundance, particularly in MPAs, and this decline was associated with a similar pattern of decline in their preferred corals. We suggest that climate-mediated disturbances, such as coral bleaching, be at the fore of conservation planning for coral reefs.*

Keywords: climate change, coral bleaching, coral reef ecosystems, coral reef fishes, coral reef resilience, marine protected areas, size spectra analysis

Efectos a Largo Plazo de los Impactos del Blanqueado Masivo de Corales sobre Peces de Arrecifes Coralinos, Pesquerías y Ecosistemas

Resumen: *Episodios recientes de blanqueado de corales han llevado a la pérdida extensiva de arrecifes de coral y han incrementado la preocupación sobre la efectividad de los esfuerzos actuales de conservación y manejo. El evento de blanqueado de 1998 fue más severo en el occidente del Océano Índico, donde el coral declinó hasta en 90% en algunas localidades. Utilizando datos independientes de pesquerías, evaluamos los impactos a largo plazo de este evento sobre especies importantes para las pesquerías en las Seychelles, sobre la estructura de tallas en el ensamble de peces y sobre la efectividad de dos áreas marinas protegidas (AMPs) en la protección de las comunidades de peces. La biomasa de peces capturados por arriba de la talla retenida en las trampas de peces cambió poco entre 1994 y 2005, lo que indica que no hay efectos actuales sobre la producción de las pesquerías. La biomasa fue mayor en las AMPs, lo que indica que fueron eficientes en la protección de*

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los peces. Sin embargo, la estructura de tallas de las comunidades de peces, descritas con el análisis del espectro de tallas, cambió tanto en las áreas con pesca como en las AMPs, con una declinación en peces pequeños (<30 cm) y un incremento en peces más grandes (>45 cm). Pensamos que esto representa una respuesta a largo plazo porque se están perdiendo peces debido a la mortalidad natural y no están siendo reemplazados por juveniles. Se espera que este efecto sea mayor en términos de la productividad de las pesquerías y, debido a que se observan patrones congruentes para herbívoros, sugiere que las AMPs no ofrecen resiliencia a largo plazo contra los eventos de blanqueado de arrecifes de coral. La abundancia de coralívoros y planktívoros declinó marcadamente, particularmente en AMPs, y esta declinación se asoció con un patrón de declinación similar en sus arrecifes preferidos. Sugerimos que las perturbaciones debido al clima, como el blanqueado de corales, estén en primer plano en la planificación de la conservación de arrecifes de coral.

Palabras Clave: análisis de espectro de tallas, áreas marinas protegidas, blanqueado de corales, cambio climático, ecosistemas coralinos, peces de arrecifes coralinos, resiliencia de arrecifes coralinos

Introduction

Coral reefs and their associated communities are threatened by anthropogenic and natural disturbances, including overharvesting, sedimentation, pollution, disease, and warming waters (Hughes et al. 2003; Bellwood et al. 2004; Wilson et al. 2006). Although multiple stressors often act in synergy, climate-driven coral bleaching has emerged as one of the greatest threats to coral reef ecosystems (Hughes et al. 2003; Sheppard 2003). The 1998 bleaching event was the largest on record, and in the most heavily affected region, the western Indian Ocean, coral cover declined by up to 90% (Sheppard 2003). Recovery from such severe disturbances is likely to be slow and affect other reef-associated organisms.

The short-term effects of bleaching on fish are mainly manifest in species that specialize on live coral for diet, shelter, or recruitment habitat (reviewed by Wilson et al. 2006). In the medium to long term declines in coral feeders can continue (Pratchett et al. 2006), but the greatest impacts occur if the physical matrix of the reef collapses, reducing overall species richness (Garpe et al. 2006; Glynn 2006; Graham et al. 2006). The medium to long-term impacts of bleaching on the size structure of fish populations and assemblages are currently unknown (Wilson et al. 2006). These impacts are important because they determine the future viability of populations and assemblages and thus interact with fisheries management and conservation measures that may have been proposed or implemented prior to a bleaching event.

Assessments of the impacts of mass bleaching on fisheries and associated socioeconomic factors are currently limited to fisheries-dependant data and are considered small in relation to the direct impacts of fishing (McClanahan et al. 2002; Grandcourt & Cesar 2003). Nevertheless, such assessments have all been made within 5 years of bleaching events. Because loss in structural complexity of the reef framework, which can take over 5 years (Wilson et al. 2006), is likely to affect small individuals and because these may take some time to recruit to the fishery, a lag effect may exist before the full impact of coral bleaching on reef fisheries is realized.

To conserve and manage reefs in the face of unpredictable disturbance, scientists and managers are increasingly proposing that no-take marine protected areas (MPAs) can increase resilience of the reef ecosystem (Hughes et al. 2003; Bellwood et al. 2004). Although it is clear that MPAs cannot prevent coral bleaching, the expected ecological communities in MPAs (e.g., a greater biomass, density, and size of herbivorous fishes in regions where herbivores are fished) should promote coral recovery, thus providing spatial resilience in the form of populations that can reseed depleted areas (Hughes et al. 2003). There is some evidence of an initial build up of fish biomass in MPAs even during habitat degradation (Hawkins et al. 2006); however, both abundance and diversity may subsequently decline (Jones et al. 2004), and it is unclear how the size-structure of the fish assemblage may respond.

Using fisheries-independent data collected across the inner granitic islands of the Seychelles, we assessed the medium to long-term effects of mass coral bleaching on target reef fish above the size retained in fish traps, overall size structure of the whole assemblage and particular feeding groups, and effectiveness of existing no-take MPAs in offering spatial resilience to the disturbance.

Methods

Study Sites

The inner granitic islands of the Seychelles lie on the Mahé Plateau, a shallow, extensive, submarine platform that reaches mean depths of 44–65 m. The fringing reefs of the islands are typically shallow; the reef slope terminates at 6–13 m (Jennings et al. 1995). The 1998 bleaching event reduced live coral cover from 27% to 3%, an overall reduction of approximately 90%. Furthermore, coral mortality extended throughout the depth range of the coral reefs in this area. Recovery has been extremely slow, with collapse in the physical complexity of the reefs accelerating since 2003 (Engelhardt 2004), and mean coral cover attaining only 7.5% by 2005 (Graham et al. 2006). Other than climate-mediated bleaching mortality of corals, Seychelles reefs experienced relatively little change in other stressors over the study period (Graham et al. 2006).

We conducted reef surveys in seven areas, around Mahé, Praslin, and associated islands, that included most of the shallow fringing reef around the inner islands (for map see Jennings et al. 1995). Five fished areas were subject to similar levels of fishing intensity, whereas the other two areas were long-standing MPAs. Sainte Anne Marine National Park was gazetted by the Government of Seychelles in 1973 because it is suitably located for tourist use. Cousin Island Special Reserve was established by Birdlife International, who bought the island in 1968 to protect an endangered bird (Jennings et al. 1996). Both MPAs are within the same geographic area as the other sites and have similar bathymetry and habitat types. There are significant differences in the diversity and biomass of fish between the two MPAs and the five fished areas but not within the MPAs or fished areas per se (Jennings et al. 1995). Spatial studies of MPA effects are expected to reflect the outcome of temporal studies (Russ et al. 2005); therefore, we believe that the higher levels of diversity and biomass in the MPAs reflect the effect of protection from fishing. Studies conducted within other reef systems highlight the disproportionate effect of small amounts of fishing on fish communities and the more subtle impacts of further increases in fishing effort (Jennings & Polunin 1997; Hawkins & Roberts 2004). For these reasons we assessed the interaction between bleaching impacts and management by comparing the two MPAs with the five fished areas before and after coral bleaching in 1998.

Assessment of Fish Assemblage and Benthic Community Structure

We surveyed 21 sites, covering over 50,000 m^2 of coral reef habitat, at the same time of year in 1994 and 2005. Three sites were surveyed in each of the seven areas so that one site in each of three different habitat types (Jennings et al. 1995) would be included: carbonate fringing reefs; granitic rocky reefs with coral growth; and patch reef habitats on sand, rubble, or rock base. At each site 16 replicate 7-m radius point counts were completed with underwater visual censuses along the base of the reef slope. This technique maximized area coverage and replication, yet allowed for detailed searching for territorial species so that it provided a quantitative estimate of the number of fish of varying sizes and behavior. We separated replicates by a random number of fin kicks with the proviso that each count was separated by a minimum of 15 m; thus, an approximately 0.5-km stretch of reef was covered at each site.

The number and size of 134 species of reef-associated, diurnally active, noncryptic fish (>8 cm) were estimated within each count area. The time taken to complete a count varied depending on the number and diversity of fish present. Size estimation of fish was to the nearest centimeter, validated by estimating the lengths of a random selection of PVC pipes before the first count at each site. Length estimates were not consistently shorter or longer than actual lengths in both 1994 and 2005, with a mean error of 8- to 35-cm pipes of 3.1% and 2.2%, respectively. Fish counts in 1994 were conducted by S.J. and in 2005 by N.A.J.G. Although small errors can exist among observers (Thompson & Mapstone 1997), bias among experienced divers is the smallest component of variation in fish counts (Williams et al. 2006; McClanahan et al. 2007). We converted data on fish counts to biomass with published length-weight relationships (Letourneur et al. 1998; Froese & Pauly 2006). Species were assigned to feeding groups (herbivores, piscivores, corallivores, planktivores, and mixed-diet feeders [i.e., species consuming animal and plant material or fish and invertebrates]) based on dietary literature and Froese and Pauly (2006).

After a fish count was complete, we assessed the benthic composition and structural complexity of the count area. Percent cover of benthic categories (live branching, plating, massive, corymbose and encrusting coral, soft coral, macroalgae, rock, rubble, sand, and dead branching coral) was estimated visually and was accurate when assessed against the line-intercept method (no significant difference, multivariate analysis of variance (MANOVA) $F_{6,35} = 0.56$, $p = 0.76$; Wilson et al. 2007). We assessed structural complexity of the benthos with a six-point visual scale and tested the accuracy of this method with the linear versus contour chain method. The two methods were highly correlated (linear regression $r = 0.85$, $p < 0.001$; Wilson et al. 2007).

Establishment of Fishery Target Species and Size of First Capture

Fish species that are targeted by the local artisanal fishery were assigned to three groups: primary targets, important targets, and occasional targets following Grandcourt (1999). There is a strong relationship between body depth of retained fish and the maximum width of trap meshes (Munro et al. 2003). In Seychelles the minimum legal hexagonal mesh diameter is 4 cm, but fishers often use trap meshes larger than this, and fish are able to squeeze through meshes smaller than their specific body depth (Robichaud et al. 1999). We calculated size at first capture from length frequency data of 5651 trap-caught fish between January 1992 and June 1994 (S.F.A., unpublished data). Ninety-five percent of fish in the sample had a body depth of over 6.0 cm. Data on target fish species from the 1994 and 2005 reef surveys were filtered to exclude individuals with a body depth of <6 cm for species level and aggregated feeding group analyses to assess the impact of the bleaching event on the dominant inshore trap fishery.

Data Analysis

Along with structural complexity, we categorized live corals into two groups: (1) complex corals that have branching, plating, or corymbose functional forms, which offer the most structure for other organisms to live in (Jones et al. 2004) and are generally the favored corals for diet and habitat specialists (Munday 2004; Pratchett 2005) and (2) simple corals that have massive and encrusting functional forms, which offer limited structure for other organisms to live within (Jones et al. 2004). We assessed differences between years, habitat types, and management status (fished vs. protected) with three-way, crossed fixed-effects orthogonal analysis of variances (ANOVAs). We assessed homogeneity of variances with Levene's test and normality of the data with histograms and normal probability plots of the residuals. Counts of complex corals were square-root transformed to meet assumptions. We used Tukey's post hoc test to identify where differences occurred among habitats.

Changes in the biomass of individual species and aggregated feeding groups of fishery targets above size at first capture were also assessed with the same ANOVA design. At the species level we used log transformation to meet the assumption of homogeneity of variances for a number of species. Ten species that failed to meet assumptions were not analyzed (see Supplementary Material).

The overall size structure of the assemblage at each site (including size below first capture) was described with the slope of the abundance-size relationships of the assemblage (Dulvy et al. 2004; Graham et al. 2005). Slopes of the size spectra were calculated from linear regressions of $\log_{10}$ ($x + 1$) numbers per size class (5 cm) on the rescaled $\log_{10}$ midpoint of each length class. Centering the independent variable provides values of midpoint height (community abundance) that are comparable among spectra. A steepening of the slope can be the result of a decrease in the number of large fish, an increase in the number of small fish, or both. Change in the slope and midpoint height of the size spectra were assessed with the same ANOVA design described above.

To assess what was driving the observed trends in slopes of the size spectra, changes in the numerical abundance of fishes in individual size bins of 5 cm between 1994 and 2005 were assessed for the entire assemblage and for five key feeding groups: mixed-diet feeders, piscivores, herbivores, corallivores, and planktivores. To partition any effects of marine protection and habitat type, we plotted data separately by management status and within this by habitat type.

Results

Structural complexity of the benthos declined between years ($F_{1,30} = 19.94, p < 0.001$), but did not vary with habitat or protection (Fig. 1a). The cover of live complex corals fell by over 95% (Fig. 1b; $F_{1,30} = 100.22, p < 0.001$), with the greatest reductions on carbonate habitats (significant interaction: $F_{2,30} = 3.71, p < 0.05$) and greater reductions on reefs in MPAs than in fished areas ($F_{1,30} = 7.30, p < 0.05$). The greater impact in MPAs resulted from a higher initial cover of complex corals within MPAs in 1994, which declined to a similar base level (<1%) in 2005, irrespective of whether the site was in an MPA or fished. Cover of simple corals remained relatively stable

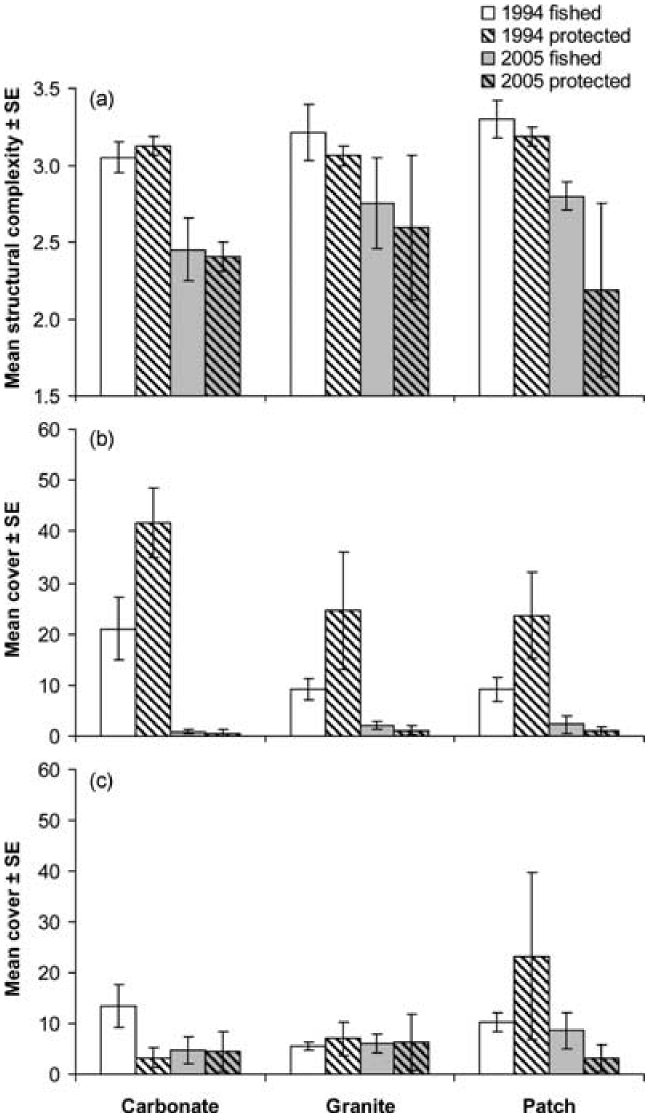

Figure 1. Change in (a) structural complexity, (b) complex corals (coral cover), and (c) simple corals (coral cover) between 1994 and 2005 for three habitat types (carbonate, granite, patch) and two management scenarios (fished, protected).

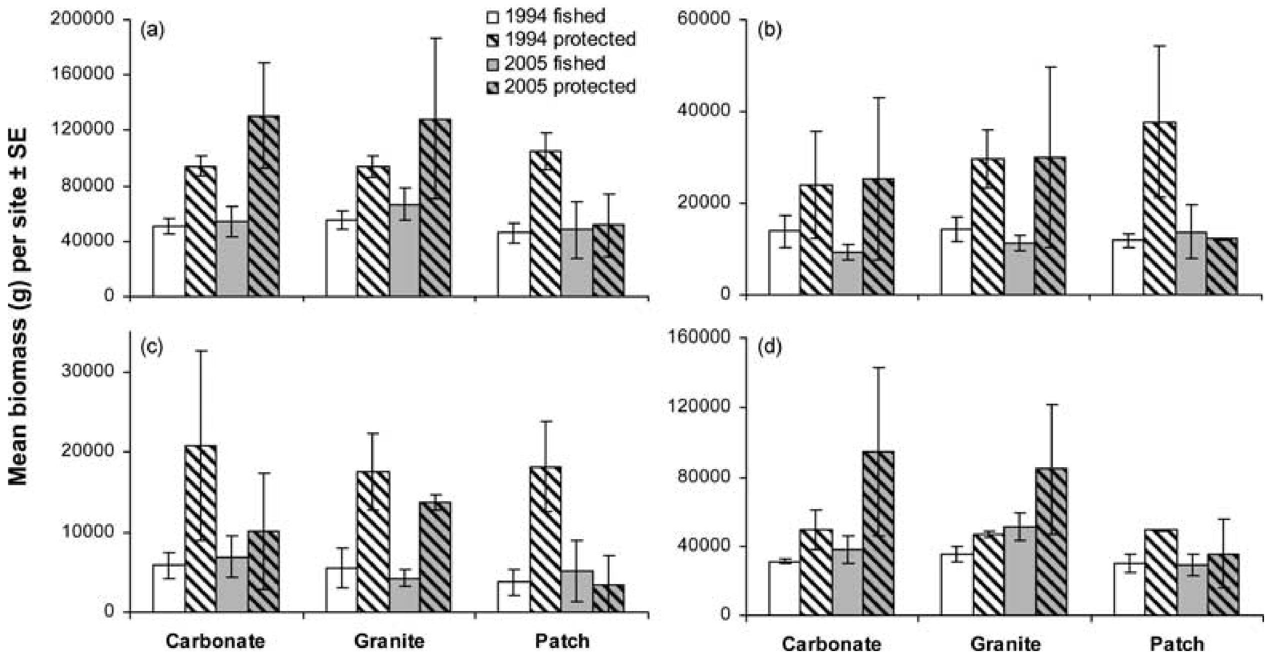

Figure 2. Change in biomass of fishery target species above size at first capture between 1994 and 2005 for (a) entire assemblage of fishery target species, (b) mixed-diet feeders, (c) piscivores, and (d) herbivores in three habitat types (carbonate, granite, patch) and under two types of management (fished, protected).

between 1994 and 2005, with no significant factors in the model (Fig. 1c).

The biomass of individual target fish species above size at first capture varied between years; some increased, some decreased, and over 70% did not change significantly (see Supplementary Material). The entire target assemblage and mixed-diet feeders showed greater biomass in MPAs than in fished areas ($F_{1,30} = 28.29, p < 0.001$ and $F_{1,30} = 14.44, p = 0.001$, respectively), but no trends between years or among habitat types (Fig. 2a-b). Piscivore biomass did not differ among habitats, but differed between years ($F_{1,30} = 4.69, p < 0.05$) and with protection ($F_{1,30} = 16.65$, $p < 0.001$). A significant year-protection interaction term ($F_{1,30} = 5.49$, $P < 0.05$) showed that the main change between years was associated with a decreased biomass in MPAs (Fig. 2c). Herbivore biomass was greater in 2005 ($F_{1,30} = 4.67, p < 0.05$) and in MPAs ($F_{1,30} = 11.65, p = 0.002$), and had no interaction or habitat effect (Fig. 2d). These results indicate that although there were some small changes between years for certain groups, MPAs continued to support a higher biomass of targeted reef fish than fished areas (Fig. 2).

The slope of the size spectra became less steep from 1994 to 2005 in all but one fished granite site (Fig. 3a). This trend between years ($F_{1,30} = 18.90, p < 0.001$) did not vary among habitats and was not affected by management status (Fig. 3b). The height of the size spectra did not differ between years or among habitats; however, there was an effect of management status ($F_{1,30} = 17.53$, $p < 0.001$) that showed a greater abundance of fish in MPAs.

The decreasing steepness of the size spectra slope was a result of a relative decline in smaller fish (<30 cm) and increase in larger fish (>45 cm) in the assemblage. This trend was consistent for both fished areas and MPAs

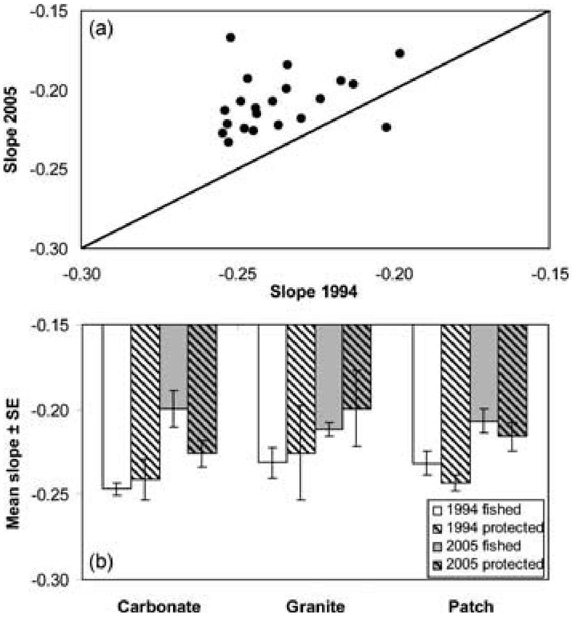

Figure 3. (a) Change in the slope of size spectra of the fish assemblage for individual survey sites. Sites falling above the 1:1 trend line had a lower slope value in 2005. (b) Mean change in slope of size spectra of the fish assemblage by habitat type (carbonate, granite, patch) and management status (fished, protected).

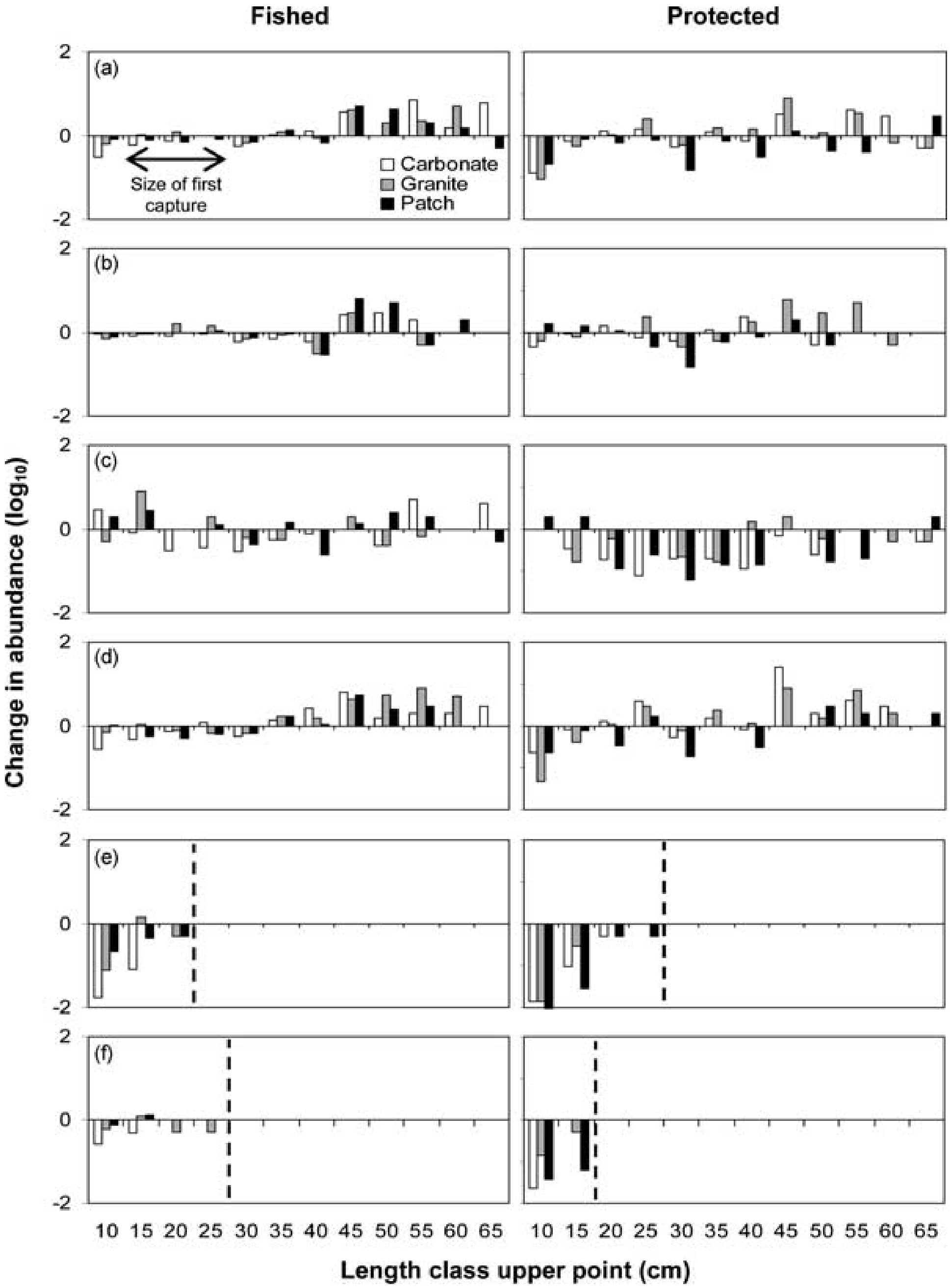

Figure 4. Change in log abundance of individual size classes of fish for (a) the entire assemblage, (b) mixed-diet feeders, (c) piscivores, (d) herbivores, (e) corallivores, and (f) planktivores by habitat type (carbonate, granite, patch). Plots in the left-hand column are fished sites, and plots in right-hand column are protected sites. Size of first capture range indicated on plot (a) for fishery target species. Maximum size detected indicated with vertical dashed line on plots (e) and (f).

(Fig. 4a). Different size classes in the mixed-diet group showed various trends, and there was no common pattern apparent (Fig. 4b). The piscivores also responded variably; however, medium size classes (20–50 cm) tended to decline, especially in MPAs (Fig. 4c). The herbivores declined in smaller size classes (<30 cm) and increased in larger size classes (>40 cm) in both fished areas and MPAs (Fig. 4d). Corallivores and planktivores consistently and markedly declined, with the greatest decline in the MPAs (Fig. 4e-f). Although there was some variation, particularly for the mixed-diet feeders and piscivores, the trends were generally similar among habitat types.

Discussion

Based on our results an impending recruitment failure to reef-fishery size classes is likely in the Seychelles following a major coral bleaching event. Our results show a decline in juvenile abundance (<30 cm) in the reef-fishery assemblage that will ultimately lead to declines in adult abundance, as has been shown consistently in fisheries (Hilborn & Walters 1992). Although our data predict this effect will happen, the lack of time-series data and knowledge of the growth trajectories of individual species prevent us from projecting the likely time span over which larger size classes will be affected. Our data also highlight a potential decline in the resilience of MPAs due to the decline in smaller size classes of herbivorous fishes in these management areas.

There were only minor changes in the biomass of target species available to the Seychelles artisanal trap fishery following the 1998 mass bleaching event. Nevertheless, these small changes belie apparent system-wide failures of recruitment to fished size classes that are expected to have long-term impacts on the viability of populations, assemblages, and the fishery. Our results suggest that the current biomass and reef fishery are maintained primarily by the growth of fishes that had already recruited to the reefs at the time of the bleaching event, and/or before topographic structure was reduced, and have now grown sufficiently to reach fishable size. This corroborates other evidence that shows there is no short-term change in yield associated with mass bleaching (McClanahan et al. 2002; Grandcourt & Cesar 2003).

The surveyed MPAs supported a higher biomass of target species above size of first capture than fished areas. The greater size-spectra height in the Seychelles MPAs is consistent with the expected effects of reduced fishing mortality on abundance (McClanahan & Graham 2005). Nevertheless, the reduction in slope of the size spectra was consistent across all but one site and similar for both the fished areas and MPAs, which suggests that the same drivers are affecting the size distribution of fish in these areas and that they are unrelated to fishing pressure.

Plotting each individual size class bin by its change in numerical abundance highlights that the change in the slope of the size spectra was driven by both an increase in large individuals (>45 cm) and a decrease in smaller individuals (<30 cm). Because fishing pressure has not changed, the most likely drivers for the increase in larger-bodied fishes are increased growth and/or survivorship. The decline in smaller-bodied individuals could be driven by various processes. We consider consistently high mortality of small and juvenile fish following the years because the bleaching event the most likely explanation, based on the expectation that the larger fishes have retained their abundance and have good feeding conditions, and that many smaller species and individuals are most dependent on refuge availability and live coral (Munday & Jones 1998; Dulvy et al. 2004; Graham et al. 2006). Furthermore, the diversity and numerical abundance of fish 10–30 cm in length was correlated with structural complexity in 2005 (Wilson et al. 2007) and showed marked decline between 1994 and 2005 following a loss in structure. Although the existence of several years of high larval supply prior to the bleaching event and several years of poor larval supply after bleaching could also account for the patterns we observed, the latter possibly as a result of reduced live coral as a settlement cue, we consider this unlikely when the effects are manifest for all species and at a large spatial scale. Based on the size-based analyses, we predict a time lag effect, whereby the full effects of the bleaching event on the fringing-reef fishery species and the fish assemblage as a whole are yet to be realized.

The MPAs seem to offer no long-term resilience to the populations and assemblages. Although the MPAs may meet short-term conservation objectives by reducing fishing mortality on larger fish, future replacement by small fish may be insufficient to maintain abundance over the long term. The collapse of the physical structure of Seychelles reefs accelerated as recently as 2003 (Engelhardt 2004), so the longer-term consequences of this process are yet to manifest in larger size classes. The lag effect of reduced replenishment will likely be longer in MPAs than in fished areas because mortality rates are likely to be lower and therefore age structures of the populations will be extended. Nevertheless, greater predator biomass inside the MPAs could result in higher rates of predation on smaller individuals (Graham et al. 2003; Mumby et al. 2006), ultimately increasing the severity of the lag effect.

The effects on assemblage productivity and hence on fishery yield are expected to be even more substantial than the effects on biomass because the production to biomass ratios of smaller individuals and species are higher. Therefore a community of a given biomass that is dominated by larger species will be relatively less productive (Kerr & Dickie 2001). The observed changes in the size-spectra therefore suggest that total production will fall faster than biomass, owing to a decline in abundance of smaller fish and smaller size classes.

The responses of mixed-diet feeders and piscivores varied among size classes. Some of the families that make up these groups, for example, lethrinids and lutjanids, are generalist in their juvenile habitat use and often associate with soft-bottom habitats (Dorenbosch et al. 2005). Therefore, they may not be as reliant on the reef structure for predator evasion. Within the piscivores there was a decline in the number of fishes in medium size classes (20–50 cm), which was most pronounced in the MPAs. The consistent nature of this decline among habitats suggests a deterministic driver. Piscivores on coral reefs tend to select prey according to their gape size (Mumby et al. 2006), and reef fish predator–prey dynamics are highly size structured (Dulvy et al. 2004). Thus, it is likely that the substantial decline in smaller size classes of the assemblage, which was most evident in the MPAs, may have reduced prey availability for medium-sized piscivores and thus caused an indirect decline in their numbers.

Of the indirect effects of bleaching that we have identified, one of the most significant for the reef ecosystem as a whole is likely to be the substantial decline in smaller size classes of herbivorous fishes in both fished and protected areas. The surveyed assemblage consisted mainly of surgeonfishes (Acanthuridae) and parrotfishes (Scaridae), but also contained some rabbitfishes (Siganidae) and two species of damselfishes (Pomacentridae). Separate plots of the changes in size classes over time of acanthurids, scarids, or species that span a large number of size classes showed the same patterns of reduction in small size classes. Many of these species use the reef for habitat as juveniles (Dorenbosch et al. 2005), and because the trend was consistent among habitats and management strategies, it is likely that habitat degradation, which leads to greater competition and predation (Hixon & Jones 2005), is the cause of decline in smaller sizes.

Acanthurids can live over 25 years and scarids live 5–20 years (Choat & Robertson 2002), so individuals currently contributing to the increase in numerical abundance of large size classes likely recruited prior to the 1998 bleaching event or the collapse of the reef framework in 2003 (Engelhardt 2004). When disturbances are extensive and occur over large spatial scales, increased abundance of large herbivores can result from faster growth rates (Hart & Russ 1996) and potentially higher survivorship associated with greater food abundance. Nevertheless, fewer fish in smaller size classes are surviving to replace adults, and a subsequent decline in overall biomass of herbivores seems likely. Herbivores are common targets of the trap fishery in the Seychelles (Grandcourt 1999), and yields have remained stable throughout the bleaching event (Grandcourt & Cesar 2003), despite the increase in larger fish we identified. Yields were stable despite increases in larger fish because the decline in small-sized fish extended up to 30 cm, resulting in no substantial increase in biomass above size at first capture.

Herbivores are important to the resilience of coral reefs because they control algae and promote coral recovery (Bellwood et al. 2004; Mumby et al. 2006). Our results suggest that mass bleaching and the loss of structural complexity may ultimately lead to a reduction in the abundance of herbivores, including larger size classes and thus, resilience of reefs may decline over the long term. Because the trend is also apparent in the sampled MPAs, our data suggest the MPAs offer no long-term refuge from the impacts of coral bleaching.

What are the consequences for reef fisheries? In Seychelles 50–60% of trap fishing effort occurs close to the shore and within the depth range of the data collected in this study (T.D., unpublished data), which suggests that a future decline in biomass of target species will affect the trap fisheries. Nevertheless, given that a substantial portion of trap fishing grounds lie on deeper shoals and submerged reefs of the Mahé Plateau, there is potential for a degree of spatial mobility in the fishery if declines in target-species biomass are restricted to the shallow fringing reefs. If other locations suffer coral mortality and collapse on the scale of the Seychelles, target-species assemblages will likely respond in the same way. In locations where the topography does not allow for a diversity of demersal fishery habitats and depths and the entire demersal fishery is restricted to the inshore reef (e.g., Fiji; Jennings & Polunin 1997), the long-term impacts of bleaching on fishers could be more substantial.

The corallivores and planktivores demonstrated very large and consistent declines between years. Declines in corallivores, and even local extinctions, as a result of mass mortality of corals have been documented previously (Graham et al. 2006; Pratchett et al. 2006; Wilson et al. 2006). The planktivores in our study were principally coral-dwelling damselfish, which suffer large declines through coral mortality (Wilson et al. 2006). Furthermore, both groups have small body size, suggesting they are more reliant on the reef matrix to avoid predation (Munday & Jones 1998). The decline in both cases was greatest in the MPAs. Corallivore numbers declined from a mean of 31.7 to 5.3/site in fished areas and from 74.5 to 2.7/site in MPAs. Similarly, planktivore numbers declined from a mean of 90.3 to 44.4/site in fished areas and from 279.8 to 11.2/site in MPAs. These declines are associated with the greater cover of the complex coral category in the MPAs prior to the bleaching event, which is the preferred habitat of many specialist fish (Munday 2004; Pratchett 2005). The result is a subsequent homogenization of the MPAs and fished areas in terms of benthic cover and composition and the numerical abundance of small specialized fish species after bleaching.

In recent decades conservation of marine resources on coral reefs has focused on the use of MPAs. Results of previous studies show that reef fish diversity and abundance can be compromised in MPAs following coral mortality (Jones et al. 2004). Here we provide evidence that the size structure of fish assemblages is subject to the same long-term effects in MPAs and fished areas. Because future bleaching events seem inevitable (Sheppard 2003), the implementation of methods to ameliorate climate-mediated disturbance should be treated as a priority in conservation and management plans for coral reefs. We recognize that some areas are less susceptible to climate-induced disturbance and some show greater recovery and therefore support the notion that MPAs should increasingly be sited in areas of resistance or resilience to bleaching to build up spatial resilience in the system (West & Salm 2003). In Seychelles the reefs north of Praslin and south of Mahé, and the granitic habitats in general are currently displaying the most recovery and the most stable fish populations (Engelhardt 2004; Graham et al. 2006), and would be suitable locations for future MPAs. Marine protected areas are not the only management tool available, however, and it is important to manage areas outside MPAs to minimize other stressors, such as overfishing and nutrient enrichment, to create conditions where a recovery may be possible if brood stocks are available.

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Supplementary Material

Change in biomass and results of univariate, three-factor crossed analysis of variance for primary, important, and occasional target fish species above size at first capture (Appendix S1) are available as part of the on-line article from http://www.blackwell-synergy.com/. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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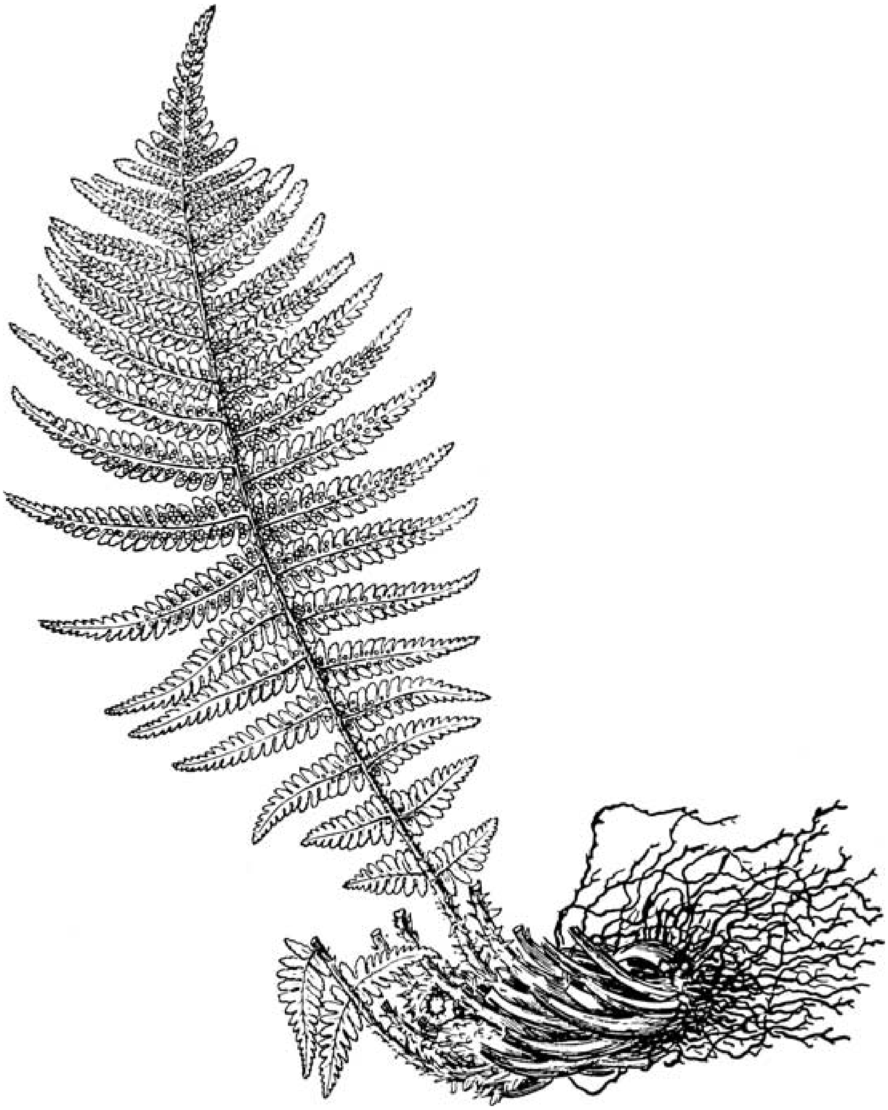

Supplementary Material

Table S1. Change in biomass and results of univariate three-factor crossed analysis of variance for primary, important, and occasional target fish species above size at first capture.[a]

Species	Size at first capture	Biomass (g) 1994	Biomass (g) 2005	Δ	Year (1,30 df)	Habitat (2,30 df)	Protection (1,30 df)
Primary Targets							
Aprion virescens	25.5cm	4141	3497	-	0.75	2.01	11.30***
Cephalopholis leopardus [b]	20.1cm	100	0	-	2.10	0.65	0.17
Chlorurus sordidus	19.2cm	7073	7369	+	0.11	0.75	0.03
Lutjanus bohar [b]	18.9cm	966	1308	+	1.63	1.74	1.83
Scarus ghobban	16.7cm	1137	2708	+	4.79*	2.73	6.93*
Scarus rubroviolaceus [b]	18.7cm	871	5079	+	4.16*	0.35	0.32
Siganus sutor [b]	15.4cm	338	0	-	2.79	1.12	0.56
Important targets							
Acanthurus tennentii [b]	15.3cm	332	2307	+	1.06	0.34	0.08
Anyperodon leucogrammicus [b]	24.2cm	287	37	-	3.64	0.27	0.09
Calotomus carolinus [b]	16.0cm	79	1211	+	3.78	0.03	2.67
Cephalopholis argus [b]	20.9cm	3063	988	-	9.44**	0.32	1.32
Cephalopholis miniata	21.4cm	75	259	+	2.50	1.39	0.03
Cetoscarus bicolour [b]	17.3cm	410	0	-	15.45***	0.20	4.14
Cheilinus fasciatus [b]	19.0cm	219	66	-	4.95*	0.13	0.05
Cheilinus trilobatus	17.7cm	1963	1281	-	1.67	0.55	2.91
Chlorurus gibbus	17.5cm	1282	1138	-	0.07	2.59	0.96
Ctenochaetus striatus	13.8cm	3703	1035	-	6.57*	0.25	5.24*
Epinephelus fasciatus	22.3cm	59	159	+	1.46	0.18	0.07
Epinephelus merra [b]	22.1cm	58	32	-	0.27	2.36	2.00
Leptoscarus vaigiensis	21.8cm	77	478	+	1.45	4.01*	0.70
Lethrinus enigmaticus	16.7cm	13	52	+	0.52	0.96	0.36
Lethrinus harak	18.4cm	2594	2659	+	0.03	0.67	2.90
Lethrinus lentjan [f]	16.7cm	27	93	+	3.03	3.36*, [c]	7.61**
Lethrinus mahsena	15.9cm	119	68	-	0.70	0.18	0.02
Lethrinus nebulosus [b]	17.2cm	139	734	+	8.43**	1.62	3.52
Lethrinus obsoletus [b]	18.3cm	1381	421	-	4.20*	0.08	12.71***
Lethrinus olivaceus [b]	20.8cm	70	254	+	0.92	0.11	1.64
Lutjanus fulviflamma [b]	20.2cm	1206	692	-	1.31	3.19	5.45*
Lutjanus gibbus [b]	16.2cm	1257	684	-	0.28	1.07	0.31
Lutjanus kasmira	18.5cm	29	9	-	0.02	1.07	0.02
Lutjanus rivulatus	16.1cm	133	51	-	0.00	0.31	0.00
Macolor niger [g]	16.6cm	478	158	-	3.93	4.02*, [c]	0.09
Monotaxis grandoculis	15.7cm	325	723	+	0.93	0.43	0.07
Mulloidichthys flavolineatus [b]	25.5cm	366	31	-	1.82	0.26	3.43
Parupeneus barberinus [b]	21.9cm	1200	529	-	0.64	1.05	1.57
Parupeneus ciliatus [b]	21.8cm	1006	797	-	0.37	0.43	0.11
Parupeneus cyclostomus [b]	22.7cm	196	50	-	1.69	1.13	0.00
Parupeneus macronemus	21.4cm	410	139	-	2.46	1.52	0.10
Parupeneus rubescens [b]	20.2cm	17	25	+	0.24	0.40	1.57
Plectorhinchus orientalis	20.8cm	823	610	-	0.70	1.21	1.44
Plectorhinchus schotaf [b]	18.7cm	397	721	+	0.14	0.06	0.14

Scarus caudofasciatus	17.2cm	117	642	+	1.92	1.07	0.19
Scarus falcipinnis [b]	17.4cm	200	291	+	0.01	0.49	0.50
Scarus frenatus [h]	19.1cm	1882	660	-	15.66***	1.17	13.57***
Scarus globiceps	18.3cm	189	667	+	0.74	0.34	0.07
Scarus niger [i, j]	17.6cm	3692	5583	+	3.67	2.45	3.16
Scarus prasiognathos	17.8cm	1080	4357	+	5.43*	2.54	0.46
Scarus psittacus	19.4cm	574	840	+	0.42	0.75	3.72
Scarus scaber [b]	19.4cm	784	192	-	4.92*	4.90**[d]	0.02
Scarus tricolour	20.5cm	570	338	-	0.47	0.70	4.50*
Scarus viridifucatus	17.5cm	48	42	-	0.00	0.15	1.10
Siganus argenteus [b]	18.1cm	1482	3238	+	2.63ns	0.33	3.46
Siganus puelloides [b, h]	16.4cm	2114	922	-	17.93***	0.84	1.78
Siganus stellatus [k]	14.9cm	477	589	+	0.09	4.33*	9.82**
Occasional targets							
Acanthurus leucosternon	12.1cm	886	393	-	0.45	1.96	0.43
Acanthurus lineatus [b]	14.1cm	247	278	+	0.28	3.43*[e]	1.69
Acanthurus nigrofuscus	15.1cm	511	484	-	0.06	0.43	0.02
Aethaloperca rogaa [b]	17.3cm	210	784	+	0.61	0.35	4.68*
Chlorurus atrilunula [b]	18.4cm	731	2187	+	4.01	1.37	1.40
Ctenochaetus binotatus	13.2cm	20	42	+	0.40	0.24	0.72
Ctenochaetus strigosus [b]	12.8cm	1045	382	-	7.51**	1.41	3.01
Epinephelus caeruleopunctatus	23.2cm	110	227	+	2.51	1.60	2.07
Hipposcarus harid [b]	18.9cm	3621	3160	-	2.91	0.31	2.38
Scolopsis frenatus [b, h]	20.7cm	2922	2303	-	7.70**	1.22	0.76

[a] Values given for year, habitat and protection are *F* ratios. Probability results: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; no asterisk, not significant. *Cephalopholis urodeta, Diagramma pictum, Epinephelus hexagonatus, E. spilotoceps, E. tukula, Lethrinus rubrioperculatus, L. argentimaculatus, Lutjanus monostigma, Oxycheilinus diagrammus* and *Paracanthurus hepatus* were not analysed as assumptions could not be met due to too many zero's in counts.

[b] Log$_{10}$ transformation necessary,

[c] Tukey's output: Co>Gr, [d] Tukey's output: (Co=Gr)>Pa, [e] Tukey's output:Gr>(Co=Pa),

[f] Significant year*habitat interaction due to higher biomass in carbonate reefs in 2005, but lower biomass in granite and patch reefs,

[g] Significant year*habitat interaction due to a greater biomass in granite reefs than carbonate and patch reefs in 1994, but similar in 2005.

[h] Significant year*protection interaction due to a greater decline in biomass in protected than fished areas between years,

[i] Significant three-way interaction due to greater changes in carbonate reefs than granite and patch reefs for both year and protection,

[j] Levene's test could only be passed at 0.036, so significance was set at 0.03 for this species.

[k] Significicnat three-way interaction due to a greater biomass in granite and patch reefs than carbonate reefs in protected areas, particularly in 2005.

Climate Warming, Marine Protected Areas and the Ocean-Scale Integrity of Coral Reef Ecosystems

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Abstract

Coral reefs have emerged as one of the ecosystems most vulnerable to climate variation and change. While the contribution of a warming climate to the loss of live coral cover has been well documented across large spatial and temporal scales, the associated effects on fish have not. Here, we respond to recent and repeated calls to assess the importance of local management in conserving coral reefs in the context of global climate change. Such information is important, as coral reef fish assemblages are the most species dense vertebrate communities on earth, contributing critical ecosystem functions and providing crucial ecosystem services to human societies in tropical countries. Our assessment of the impacts of the 1998 mass bleaching event on coral cover, reef structural complexity, and reef associated fishes spans 7 countries, 66 sites and 26 degrees of latitude in the Indian Ocean. Using Bayesian meta-analysis we show that changes in the size structure, diversity and trophic composition of the reef fish community have followed coral declines. Although the ocean scale integrity of these coral reef ecosystems has been lost, it is positive to see the effects are spatially variable at multiple scales, with impacts and vulnerability affected by geography but not management regime. Existing no-take marine protected areas still support high biomass of fish, however they had no positive affect on the ecosystem response to large-scale disturbance. This suggests a need for future conservation and management efforts to identify and protect regional refugia, which should be integrated into existing management frameworks and combined with policies to improve system-wide resilience to climate variation and change.

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Introduction

Coral reefs are one of the ecosystems most threatened by climate variability and change [1–3]. Reef corals, the building blocks of carbonate reefs, have a restricted thermal tolerance, resulting in 'bleaching' events (loss of symbiotic algae) when sea surface temperatures rise above a given threshold [4]. This has contributed to widespread loss of live coral cover [5–8], the restructuring of benthic community composition [9] and has resulted in dire predictions for the future persistence of coral-dominated ecosystems within decadal time scales [10,11]. There is now a need to understand resultant large-scale implications for other components of the ecosystem, which, to date, have received limited attention or been the focus of local studies [12–14]. Assessing ecosystem trends and patterns at regional scales is necessary if informed management choices are to be made that will mitigate the effects of large-scale climate disturbance. Importantly, there is a need to test key paradigms, such as the ability of no-take areas (NTAs) to enhance recovery from climate change impacts [2], and the potential for herbivorous fish to increase in abundance following coral mortality and functionally compensate for increased algal coverage [15].

At large scales, remote pristine areas may have a greater capacity to absorb climate impacts and maintain a coral dominated and diverse ecosystem [16]. However, most coral reef NTAs are small and embedded in heavily fished and degraded environments [8,17]. Assessing the importance of local management for conserving coral reefs in the context of global change has been identified as a key research challenge for coral reef scientists [18]. Although there are expectations that NTAs will promote resilience and faster recovery from climate disturbance [19], site-specific studies suggest this may not be the case [12,20,21], and the effectiveness of such management needs to be assessed across regional spatial scales.

Grazing by herbivores, by creating space for invertebrate larval settlement, is thought to be key to maintaining reefs in a coral dominated state [22,8,23]. However, it is increasingly evident that the majority of herbivorous fish in the Indo-Pacific will crop turf algae, but feed less on or avoid erect macroalgae once it has developed [24,25]. Following large-scale disturbances that open up large amounts of space on reefs, such as mass coral bleaching, herbivores may become swamped by the biomass of the new algal resource [26] and reefs can progress on a trajectory to macroalgal dominance [27]. It is therefore important to assess whether herbivorous reef fish increase in abundance following large-scale coral loss and thus have the ability to prevent reefs from becoming dominated by erect macroalgae.

Coral mortality through climate induced bleaching was particularly severe in the Indian Ocean in 1998, with ~45% of coral cover lost across the region [28], although the effects were spatially variable [7,9]. We assess the longer-term effects of this event in fished areas and NTAs across 7 countries, 66 sites and 26 degrees of latitude. Specifically, we conducted a targeted research program whereby the original investigators who collected comprehensive benthic and fish assemblage data from Maldives, Chagos, Seychelles, Kenya, Tanzania, Mauritius, and Réunion in the mid-1990s repeated their surveys post-bleaching, in 2005. We use continuous model Bayesian meta-analysis to quantify effects of changes in live coral cover and physical complexity of reefs on the diversity, size structure, trophic structure and abundance of reef fish. The Bayesian approach not only structures the inherent uncertainty in monitoring data from multiple sources, but also allows belief statements to be made regarding future change [29]. With ever more frequent bleaching events predicted [11], quantitative predictions regarding how fish will respond to future declines in coral cover over large spatial scales are needed to guide regional conservation planning, adaptation and mitigation strategies.

Results

Change in hard coral cover across the region between the mid 1990s and 2005 varied geographically (Figure 1). The changes reported here represent the combined effects of coral loss in 1998 and any subsequent recovery to 2005. The greatest declines were apparent through the low latitude island states of Maldives, Chagos, and Seychelles. Kenyan and Tanzanian nationally protected sites experienced moderate declines, while Mauritius and Réunion sustained the smallest declines, and coral cover increased in Kenyan and Tanzanian fished sites (Figure 1). Assessing change in coral cover at relevant scales, that consider location, management and habitat type, indicates that 10 of our 19 study locations exhibit declines that depart significantly from zero (Figure 2A). The study incorporated nine no-take areas (NTAs) across four countries (two in Seychelles, four in Kenya, two in Tanzania and the long-term de-facto protection of reefs of the Chagos archipelago [30]). A greater proportion of NTAs (71%) than fished (42%) locations showed significant declines in coral cover over the study period. Based on bootstrapped 95% confidence limits, there was no evidence to suggest the percent change in coral cover differed between NTAs and fished areas, and in some cases declines were significantly greater in NTAs (Figure 2A). Importantly, the NTAs had greater starting coral covers than adjacent fished areas, which, as NTAs and fished areas declined to similar final covers (Table 1)(with the exception of some of the less impacted Tanzanian sites), meant the NTAs had further to fall.

It is clear that the impacts of the 1998 bleaching event were highly variable across the region, and provide a continuum against which to test secondary consequences, such as the effects of coral loss on fish assemblages. Recent developments in assessing the effects of coral disturbance on fish have highlighted the importance of eroding structural complexity in driving responses [13,31], which, as erosion of coral structures can take 5–10 years, explains the much smaller impacts on fish shortly after coral mortality [15]. Structural complexity was quantified at 50 of our 66 sites. Importantly, there was a strong correlation between loss in coral cover and loss in structural complexity across the region ($r = 0.77$, $P<0.001$, Figure 2B). The strong collinearity in the two measures precludes independent assessment of variables, and therefore the effects of changing coral cover on fish identified in the Bayesian meta-analyses are likely to result from a combination of loss in coral cover and structural complexity.

Coral loss predicted declines in reef-fish species richness, and abundance of obligate corallivores, planktivores and fishes <20 cm throughout the western Indian Ocean (Table 2). We tested five possible trajectory descriptors in each case, but only found evidence for linear fits between coral decline and change in groupings of the fish community. Trends in species richness were significant, but weak, and largely driven by the Seychelles and Mafia Island (Figure 3A). There was substantial evidence for a 1:1 relationship between changes in obligate corallivore abundance and percent coral cover (Figure 3B). From these results we estimate, given any future 50% decline in coral cover, there is a 76% probability of equivalent declines in obligate corallivores at any given site in the western Indian Ocean. The relationship between change in diurnal planktivore abundance and coral cover was relatively strong; given a future 50% decline in coral cover, we estimate a 68% probability of observing declines in planktivore abundance (Figure 3E). We found no relationship between a loss of coral and change in abundance of herbivore and mixed diet feeder groups (Figure 3C,D).

When species were grouped by their maximum attainable size, a clear trend was apparent for species <20 cm total length, but no relationship was observed for 21–40 cm, 41–60 cm or >60 cm groupings (Figure 4A; Table 2). Given a future 50% decline in coral cover, we estimate a 52% probability of observing declines in the abundance of fish species with maximum body lengths <20 cm. Within this size class, planktivores make up a considerable portion of the abundance (44%), and herbivores and mixed diet feeders also contribute substantially (28% and 20% respectively), but corallivores have limited input (8%) (Figure 4B). Separate analyses of trophic groups within the <20 cm size category highlights that, along with obligate corallivores and planktivores, there was also evidence of declines in herbivores (Table 2).

We only found weak evidence for differences between NTAs and fished areas for change in diurnal planktivore abundance and small-bodied herbivore abundance (<20 cm) (Table 3). In both cases the negative relationship between fish abundance and coral decline was greater for the NTAs, however there was equal support for model M_c with no differences between types of management (Table 3). Importantly, irrespective of body size and trophic categorization, NTAs provided no clear benefits for any of the fish groups in terms of their change in response to coral decline.

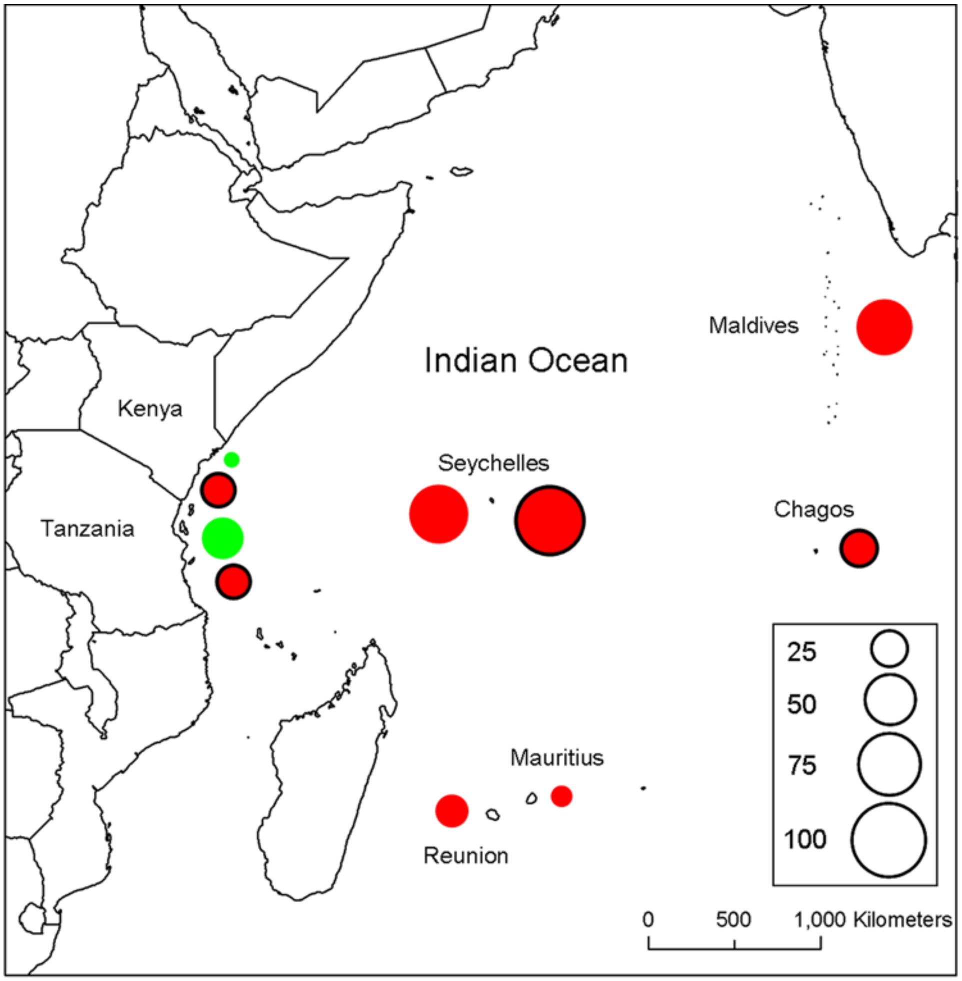

Figure 1. Change in coral cover at sites across the western Indian Ocean. Green and red symbols represent increases and decreases in coral cover respectively. Symbols with solid borders are sites in NTAs; Seychelles data include two NTAs, Kenya includes four, Tanzania two and the Chagos archipelago is a de-facto NTA. Data represent 66 sites across the region. Numbers in key (size of bubble) are percent changes between mid 1990s and 2005. Map produced using ESRI data and ArcGIS 9.
doi:10.1371/journal.pone.0003039.g001

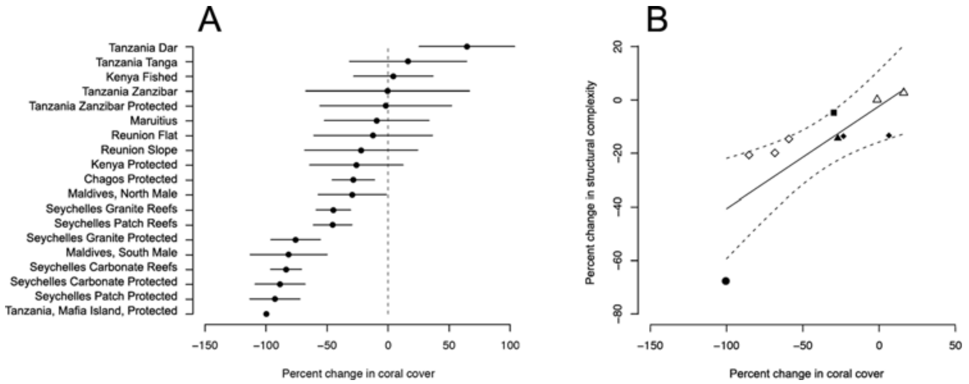

Figure 2. Change in coral cover and reef structural complexity. (*A*) Change in live coral cover at meaningful biogeographical aggregations and by management strategy. Three habitat types in Seychelles each replicated in the two NTAs. Kenyan protected represents four NTAs. Bootstrapped 95% confidence intervals indicate whether mean change departs significantly from zero. Locations ordered by magnitude of coral decline. (*B*) Correlation between change in live coral cover and change in structural complexity across the region. • Mafia Island, ◇ Seychelles, ▲ Chagos, ■ Maldives, ♦ Kenya, △ Tanzania.
doi:10.1371/journal.pone.0003039.g002

Table 1. Mean coral cover before (mid-1990s) and after (2005) the 1998 bleaching event across the Indian Ocean.

Location	% Coral Cover mid-1990s	±SE	% Coral Cover 2005	±SE
Maldives, North Male (3)	15.5	7.5	10.9	3.2
Maldives, South Male (2)	43.9	3.6	8.0	1.2
Chagos Protected (9)	31.2	4.0	22.8	2.9
Seychelles Carbonate Reefs (5)	34.6	2.7	5.6	3.1
Seychelles Carbonate Protected (2)	44.9	4.8	5.1	4.5
Seychelles Granite Reefs (5)	14.8	2.0	8.2	2.3
Seychelles Granite Protected (2)	30.9	7.6	7.5	6.4
Seychelles Patch Reefs (5)	20.0	1.5	10.9	5.1
Seychelles Patch Protected (2)	46.4	7.8	3.6	3.0
Kenya Fished (4)	18.9	5.2	20.0	4.0
Kenya Protected (4)	34.8	4.5	26.8	8.1
Tanzania Dar (4)	42.6	11.9	70.0	3.2
Tanzania Tanga (4)	23.9	7.5	27.8	6.8
Tanzania Zanzibar (2)	48.5	3.8	48.3	3.3
Tanzania Zanzibar Protected (2)	62.7	11.1	61.5	2.4
Tanzania, Mafia Island, Protected (2)	33.0	N/A	0.1	N/A
Reunion Flat (2)	42.5	24.3	37.0	10.9
Reunion Slope (2)	42.0	5.0	28.4	4.5
Mauritius (5)	45.3	9.5	41.1	6.7

Sites aggregated at representative geographic scales that consider location, management and habitat type. Three habitat types in Seychelles each replicated in the two NTAs. Kenyan protected represents four NTAs. Number of sites per location given in brackets. Note, Tanzania, Mafia Island, received no-take status in 2000.
doi:10.1371/journal.pone.0003039.t001

Discussion

We have identified spatially variable declines in coral cover, reef structural complexity, fish species richness and the abundance of various feeding and size groups of reef fish across the Indian Ocean following the 1998 bleaching event. These changes are substantial for some groups, and indicate little insurance offered by current small-scale NTA management across the region. The spatial patterns present in our data provide important information for future conservation planning and generic lessons for managing whole coral reef ecosystems in a changing climate.

There was little difference in the decline of coral cover between NTAs and fished areas across the Indian Ocean, with some evidence for greater declines within NTAs. This result is likely due to NTAs often being sited in areas where the cover of *Acropora* and other thermally-sensitive and branching coral species is high [20], or may be because fishing gears reduce cover of these coral species in fished areas. Our analysis also indicated little difference between NTAs and fished areas for those fish groups that declined in response to coral loss. The only indication of a differential response was the greater decline in NTAs for planktivores and small bodied herbivores. Large, remote and pristine areas seem to be resilient to a wide range of disturbances [16], which has led to calls to assess the effectiveness of NTAs in conserving coral reefs through climate disturbance [18]. One clear difference to these remote areas is that NTAs on reefs are typically small and surrounded by much larger areas that are modified by exploitation [8,17]. As we do not have repeat temporal data since the initial coral loss in 1998, we can not explicitly infer recovery rates from our data, however the NTAs we studied show no evidence of being more resistant to declines in coral and fish groups following coral bleaching and it seems likely that, over this time scale, recovery rates are no different between NTAs and fished areas, as has been shown for some of the NTAs where temporal data were available [21].

We detected declines in fish species richness across the western Indian Ocean in response to loss of live coral cover. Although only

Table 2. Continuous model Bayesian meta-analysis parameter estimates from the best-fitting models (see Table 3) for reef fish metrics in the western Indian Ocean.

Metric	Model	$\hat{\beta}_0$ (intercept)	$\hat{\beta}_{coral}$ (slope)	$\hat{\beta}_{protected}$ (intercept)	$\hat{\beta}_{protected}$ (slope)
Species richness	M_c	0.00 (0.03) [−0.07, 0.06]	0.10 (0.02) [0.06, 0.14]	-	-
Obligate corallivores	M_c	−0.26 (0.21) [−0.66, 0.16]	1.05 (0.14) [0.77, 1.30]	-	-
Herbivores	M_0	−0.28 (0.08) [−0.45, −0.12]	-	-	-
Mixed-diet feeders	M_0	−0.18 (0.06) [−0.28, 0.08]	-	-	-
Planktivores	M_{cp}	−0.42 (0.16) [−0.74, −0.10]	0.52 (0.16) [0.28, 0.77]	1.02 (0.35) [0.35, 1.69]	0.61 (0.24) [0.10, 1.07]
Planktivores	M_c	−0.15 (0.15) [−0.44, 0.14]	0.68 (0.10) [0.48, 0.87]	-	-
<20 cm	M_c	−0.17 (0.09) [−0.35, 0.00]	0.37 (0.06) [0.28, 0.49]	-	-
21–40 cm	M_0	−0.21 (0.09) [−0.40, −0.05]	-	-	-
41–60 cm	M_0	−0.59 (0.17) [−0.91, −0.26]	-	-	-
>61 cm	M_0	−0.37 (0.21) [−0.77, 0.04]	-	-	-
<20 cm obligate corallivores	M_c	−0.39 (0.19) [−0.77, −0.00]	0.94 (0.13) [0.69, 1.19]	-	-
<20 cm herbivores	M_c	−0.19 (0.16) [−0.51, 0.13]	0.50 (0.10) [0.29, 0.71]	-	-
<20 cm herbivores	M_{cp}	−0.28 (0.18) [−0.65, 0.08]	0.24 (0.14) [−0.05, 0.53]	0.37 (0.35) [−0.33, 1.06]	0.53 (0.21) [0.12, 0.95]
<20 cm mixed diet feeders	M_0	−0.46 (0.06) [−0.58, −0.34]	-	-	-
<20 cm planktivores	M_c	−0.10 (0.16) [−0.43, 0.23]	0.57 (0.110 [0.35, 0.78]	-	-

Estimates for groups with equivalent model fits are provided for both models. Values in parentheses are standard deviations; values in square brackets are 95% credible intervals.
doi:10.1371/journal.pone.0003039.t002

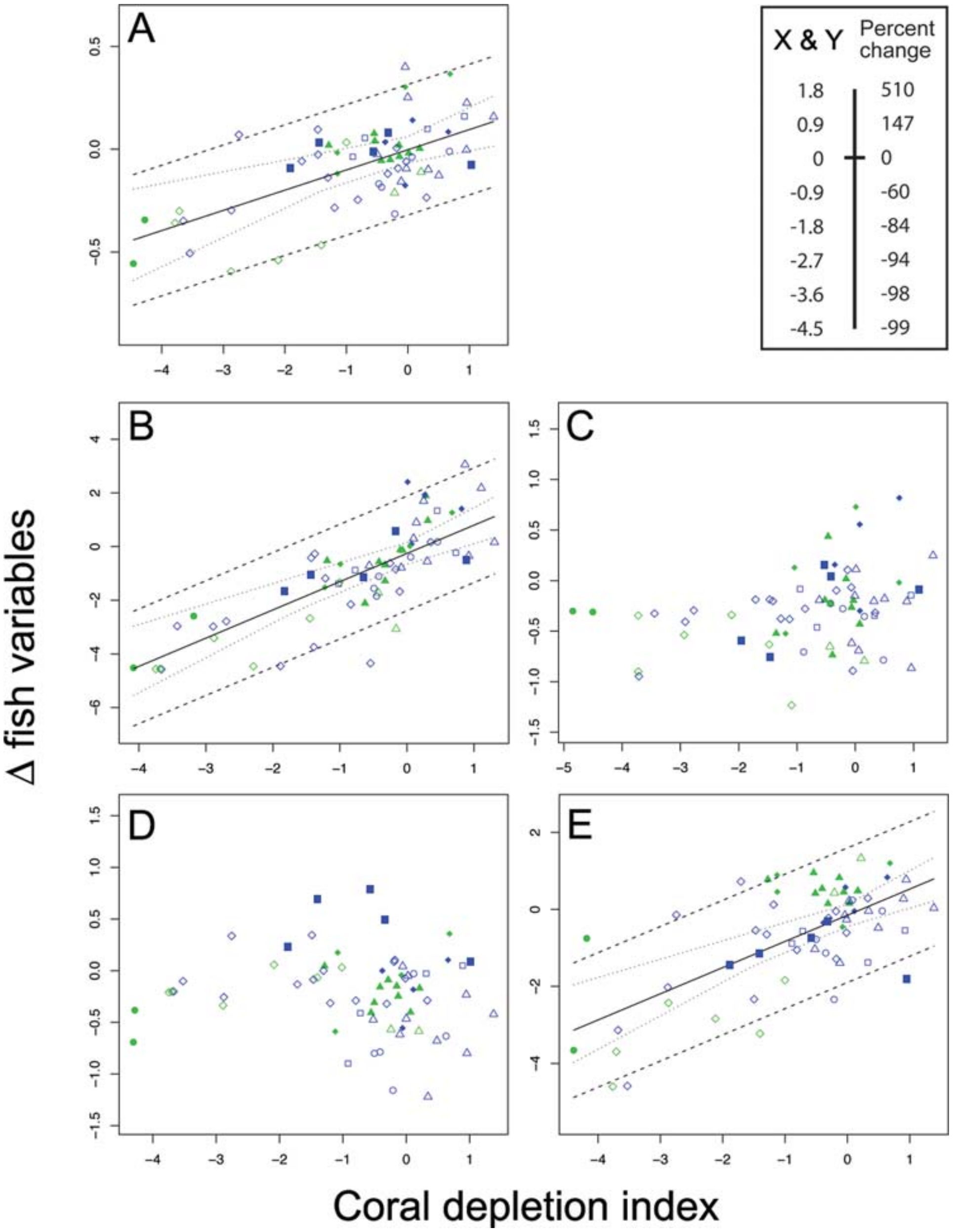

Figure 3. Change in fish groups in response to coral decline. Continuous model Bayesian meta-analysis of relationships between decline in coral cover and change in (*A*) species richness of fish assemblages, and (*B*) abundance of obligate corallivores, (*C*) herbivores, (*D*) mixed diet feeders, (*E*) planktivores. Scale as converted to percent change indicated in top right panel. Linear trend lines only presented where significant model fits were recorded. Green symbols indicate sites in NTAs, blue symbols indicate sites in fished areas. Inner dashed line represents 95% credible interval on the regression and outer dashed line represents the 95% prediction interval. • Mafia Island, ◇ Seychelles, ▲ Chagos, ■ Maldives, ♦ Kenya, △ Tanzania, □ Réunion, ○ Mauritius. Movement of points along the x-axis among panels reflects model-structured uncertainty present among studies.
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a small proportion of species are heavily coral dependent, most species are reliant on the reef matrix at some stage in their life history, and change in species richness was likely due to loss in the physical structure of the reef, rather than live coral [13–15,31]. The variability in loss of structural complexity may explain why the trend for species richness was not stronger, with locations such as Chagos, where recovery of coral has been rapid, potentially retaining structural complexity in the interim. Although loss of structural complexity was the most likely driver of the region-wide decline in species richness, some studies have highlighted that live coral can be an important settlement cue for larval fish [12,32] and the nature of this relationship is an important area for future research.

Although previous studies have identified obligate corallivores as a functional group vulnerable to declines in coral cover [14,15], this is the first study to demonstrate declines over such a large spatial scale. We have also identified a 1:1 linear relationship between coral loss and obligate corallivore decline, suggesting their survival on the reef is tightly linked to coral cover and changes in obligate corallivore abundance should be easy to predict based on changes to benthic cover. The diurnal planktivores in the study were largely small-bodied species from the damselfish family

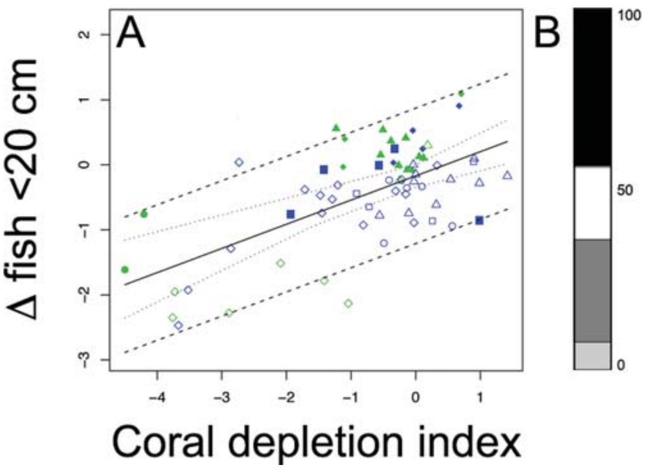

Figure 4. Change in small bodied fish in response to coral decline. (*A*) Continuous model Bayesian meta-analysis of relationship between decline in coral cover and change in fish <20 cm maximum attainable size. Green symbols indicate sites in NTAs, blue symbols indicate sites in fished areas. Inner dashed line represents 95% credible interval on the regression and outer dashed line represents the 95% prediction interval. • Mafia Island, ◇ Seychelles, ▲ Chagos, ■ Maldives, ♦ Kenya, △ Tanzania, □ Réunion, ○ Mauritius. (*B*) Percent contribution of five trophic groups to the starting (mid-1990's) abundance of fish <20 cm maximum attainable body length across the region. Black = planktivores, dark grey = piscivores (barely present on plot; 0.05%), white = Mixed diet feeders, grey = herbivores, light grey = obligate corallivores.

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Table 3. Model-selection results for continuous model Bayesian meta-analysis in the western Indian Ocean using the Bayesian Information Criterion (BIC).

Metric	**M_0**	**M_c**	**M_{cp}**
Species richness	17.53	**1.64**	6.35
Obligate corallivores	282.90	**248.38**	256.38
Herbivores	**145.83**	149.61	157.35
Mixed-diet feeders	**83.64**	87.40	91.90
Planktivores	237.66	**205.27**	**204.30**
<20 cm	165.25	**138.72**	140.60
21–40 cm	**146.91**	150.00	158.17
41–60 cm	**231.69**	**231.35**	235.95
>61 cm	**261.85**	266.02	272.32
<20 cm obligate corallivores	275.96	**238.91**	246.80
<20 cm herbivores	230.91	**214.86**	**216.53**
<20 cm mixed diet feeders	**94.93**	99.11	106.16
<20 cm planktivores	237.76	**218.23**	222.13

Models include a null model of no relationship (M_0), a model including a relationship between changes in coral cover and reef fish metrics (M_c), and a fish-coral model that allows for differences between protected and unprotected sites (M_{cp}). Models highlighted in bold have the greatest support, given the data; models with BIC differences of <2 are considered to have equal support.

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(>90% contribution to group) that are often closely associated with the reef matrix [33,34]. Their decline is most likely due to predation vulnerability, linked to loss of coral and structural collapse [13,31]. Planktivores and corallivores showed the strongest relationships of all groups to declining coral cover and are likely to be the groups most threatened from the predicted ongoing decline in global reef health [14,15].

Although herbivores are hypothesized to increase in abundance following coral decline due to a greater availability of algal resources, previous studies have reported high variation in this relationship and have often been conducted shortly after disturbances, limiting their ability to detect demographic changes [15]. Here we tested this hypothesis across large spatial and temporal scales where the assemblage had a moderate time to respond. Herbivores are thought to be a key functional group, responsible for the resilience of reef systems by controlling algal growth [8,23,35] and ultimately allowing settlement of new coral recruits [36]. However, our data show that the proliferation of algae that follows extensive coral mortality [12,13,37,38] was unlikely to be controlled by a corresponding increase in herbivorous fish abundance. Changes to size structure and biomass of herbivore stocks cannot be ruled out and may initially encourage increased consumption and control of algae. However, studies from Seychelles suggest such changes may be indicative of future declines in herbivore abundance and biomass due to a loss of refuge from predators, leading to reduced recruitment to adult size classes [20].

The mixed diet feeding group also showed no response to declining coral cover. This group of fish includes species from families such as Lethrinidae, Mullidae, Lutjanidae, and Labridae, many of which are habitat generalists, foraging and recruiting to non-coral reef habitats such as seagrass [39]. Species in these groups also tend to forage over fairly large spatial scales, indicating a lack of reliance on specific habitat types. Due to this decoupling of reliance on reef habitat and the potential benefits they may glean from increased food resources, this may be the group that will be sustained in the long term, although a large amount of variation can be expected at the species level [15], leading to changes in community composition.

Small-bodied fish are known to be more reliant on the reef matrix, inhabit narrower niches, and be more vulnerable to predation [33,34]. Our analyses highlight the vulnerability of small-bodied species to coral and structural complexity loss. Within this size category, obligate corallivore and planktivore groups showed strong declines. Interestingly, there was also a reduction in abundance of small-bodied herbivores. Although herbivore abundance may not be declining overall (Figure 3C), the reduction of these small-bodied species is of concern as they perform important functional roles on coral reefs [40]. Small mixed diet feeders again showed no trend, demonstrating the resistance of species with generalist life history traits to coral loss.

There are some obvious limitations in our data, such as the timeframe between surveys and the influence of any change in management / fishing pressure. In most cases management and fishing pressure have not changed greatly over the ten years studied. The one main exception is Mombasa Marine National Park, Kenya, where species richness and fish density have increased owing to management action [17]. Although such effects may have a slight influence on the results, the relationship between reef fish and change in coral cover (and its association with loss in physical structure) is a strong signal within the regional data and is consistent with current ecological understanding of disturbance effects on coral reefs [14,15]. A potential problem when conducting meta-analyses is publication bias, whereby data sets are not located or included in the analyses [41]. This is not a problem in the current study as we conducted a targeted research program where all comprehensive studies from the mid 1990's were repeated as part of the study itself. Finally, the study design does not consider the impact of disturbances after the 1998 coral bleaching event. However, the December 2004 tsunami is thought to have had negligible effects on coral reefs in the western Indian Ocean [42]. Furthermore, any other ensuing disturbances are just as likely to have influenced NTAs as fished areas and reflect increasing disturbance frequencies occurring on coral reefs globally [2,8].

Our analyses highlight great geographic variation in the impact of coral bleaching across the region, with the Seychelles suffering the greatest in terms of coral loss and associated effects on fish, and the Mascarene Islands (Réunion and Mauritius) suffering the least. These trends could be due to several factors: 1) Prevailing currents and variation in temperatures have been identified as key determinants of coral mortality in the region, likely reducing mortality in the Mascarene Islands in particular [11,43]. 2) Well connected reef systems are expected to contain the pockets of refugia required for landscape-scale recovery [44]. This is evident when comparing recovery of the well connected mainland reefs of Kenya and Tanzania and the geographically extensive Chagos and Maldives to the geographically small and isolated inner Seychelles. 3) The inner Seychelles is a shallow continental shelf basin, with most fringing reefs extending to only 7–9 m depth. This 'bathtub effect' likely led to extensive mortality in 1998 and precluded any depth refuge below which corals could survive. Where live coral extends to 40–50 m depth, such as in the atolls of Chagos or the islands of Réunion and Mauritius, a depth refuge of broodstock may encourage faster recovery of corals at shallower depths [45]. 4) Finally, the atolls surveyed in Chagos are uninhabited and off limits to reef fishing. The lack of multiple anthropogenic stresses that most other reef systems endure may have helped promote recovery from the disturbance [16,18].

The 1998 bleaching event had, and is still having, extensive effects across the western Indian Ocean. Although ocean-scale coral reef integrity has been lost, it is positive to see that effects were spatially variable and that in some locations the indirect effects on fish assemblages and likely implications for human society have been small. Geography seems to be a key determinant in the ability of reefs to absorb and recover from such large-scale disturbances and this should be considered for other regions likely to suffer similar large-scale disturbances in the future. Although there was no evidence that existing NTAs are promoting recovery of coral, these NTAs are still supporting a greater biomass of fishery stocks [17,20], indicating long-term fisheries management should not be compromised. There is, however, a need for new NTAs, incorporated into existing networks that protect source reefs resilient to large-scale disturbance, and areas likely to retain their physical structure. This will help sustain the upstream spawning stocks of corals and specialised fish species required for landscape-scale recovery. Such management is likely to be unsuccessful in isolation, and improved management of entire reef systems, reducing the stresses and pressures to areas outside NTAs will be necessary to maximise the capacity for systems to recover from large scale and ongoing disturbance.

Materials and Methods

We identified all field studies that had comprehensively surveyed reef fish assemblages and associated benthic composition and structure from the western Indian Ocean region from 1990 to before the 1998 coral bleaching event (majority 1994–95). This resulted in eight separate large-scale studies (across seven countries). Original investigators returned to their study locations in 2005 to repeat the surveys, using field protocols identical to those used in the original surveys. The protocols were standardised within, rather than among study locations as it is more robust to quantify effect sizes in this way and then standardise when comparing among studies. Where the original investigator could not return, an experienced surveyor from the team repeated the work. An associated field study workshop for the project, which involved many of the researchers from the region, found experienced observer bias to be a very small component of the variation in fish counts [46]. All reef surveys were conducted on the reef flat or shallow reef slope. The abundance of all diurnally active, non-cryptic, reef-associated fish was assessed during each survey, however methods varied among study locations from point counts of differing dimensions to belt transects of differing dimensions. Replication also varied from 3 to 16. This resulted in a survey area per site of $\sim 200\ \text{m}^2$ to $\sim 2500\ \text{m}^2$. Benthic quantification also varied in spatial scale and from visual estimates to line intercept transects, but the results are expected to be comparable [47]. Estimates of change in live coral cover were calculated and plotted on a map by country and management strategy and at a more aggregated level with 95% confidence limits. Measures of structural complexity also varied and included visual assessments of reef topography, the linear versus contour method and measures of reef height. However these measures were found to be strongly correlated [47] and these correlation coefficients were used to standardise them to a common scale. The relationship between percent change in coral cover and percent change in structural complexity was assessed by correlation analysis. The presence of variation in field methods is routine in meta-analytical studies, and thus the choice of effect size calculation and variance weighting is integral to the comparability of study results [48].

Effect size

Meta-analysis frequently employs unitless effect size metrics to standardize the information present among accumulated studies. The potential to observe changes in a before and after comparison can be greatly influenced by initial values at a given location; sites with larger initial values have a greater scope to reveal change than those with low values [48]. To achieve a comparable metric at all locations and to account for initial cover / values, we calculated effect sizes as the percent change between the mid 1990s and 2005 [49];

$$\%\mathit{difference}\Delta = [(A_{a,i} - A_{b,i})/A_{b,i}] \times 100 \qquad (1)$$

where A_b and A_a were mean values at sites in the mid 1990's and 2005 respectively. We did not account for study duration [48] as we made the informed assumption that the greatest changes occurred in 1998 and our measures in the mid-1990's are an appropriate estimate of pre-bleaching conditions. Furthermore as sampling date was standardised for post-1998 surveys, any incorporation of duration could unduly bias effect sizes based on pre-disturbance study dates. Finally, we are estimating a magnitude of change, rather than a rate of change, which would require a different effect size metric [48]. We calculated individual effect sizes for change in coral cover, structural complexity, fish species richness, and fish density in four functional groups for which data were available at the majority of sites (obligate corallivores, herbivores, planktivores, and mixed-diet fishes assigned using regional fish identification guides, published literature and http://www.fishbase.org), for four size classes of fish species (maximum attainable size <20 cm, 21–40 cm, 41–60 cm, and >60 cm) and for the same four functional groups listed above within the <20 cm maximum attainable size category. Herbivores include all those species that feed on algae and or detrital aggregates from the epilithic algal matrix. Because percent-change losses have a strongly right-tailed distribution, i.e. a maximum potential decline of 100%, but a potentially limitless increase, we transformed all of the Δ^T values to be balanced around zero following Kaiser et al. [49]:

$$\Delta^T = log_e(1+[\Delta/101]). \tag{2}$$

This transformation prevents overestimates of increases and underestimates of declines, where a maximum potential decline has a value of −4.6 and a maximum increase +4.6. The transformation approximately normalises the error distribution and stabilises its variance [49]. Raw data were available for many of the original studies, allowing us to estimate average effect-sizes at some locations. Because data were collected from the same sites but not the same transects, we estimated effect-size means and variances at these sites using non-parametric bootstrapping of the before and after observations (R = 9999) [50] with (1) and (2), by randomly matching before-after pairs at each iteration. This generated sample means and expected variance ranges for many, but not all, of the study locations.

Bayesian meta-analysis

We evaluated evidence for a regional relationship between reef fish and coral cover using an area-variance weighting scheme implemented in a Bayesian meta-analysis framework. The use of area surveyed as a weighting scheme in coral reef meta-analyses has become widespread because actual variance will depend on individual measurement size and replication [48]. The Bayesian approach allowed us to model the hierarchical structure of the data, estimate the magnitude of regional-scale effects, and to specify a level of uncertainty about individual study estimates. By sharing information among studies, this approach maximized the strength of inferences made across the entire range of meta-data used, allowing us to make probability statements about the likelihood of reef fish declines given potential future changes in coral conditions. Although we tested five different ecologically meaningful response trajectories (asymptotic, quadratic, logistic, linear and exponential), we found no model-based evidence for non-linear responses based on Bayesian Information Criterion (BIC) scores among candidate models. We therefore quantified the regional fish community response between the mid 1990s and 2005 using a null model (intercept-only; M_0) and exchangeable linear model (M_c) of coral effect size β_{coral},

$$\Delta^T_{f,j} \sim N\left(\theta_{f,j}, \sigma^2_{jf}\right), \tag{3}$$

$$\Delta^T_{c,j} \sim N\left(\theta_{c,j}, \sigma^2_{jc}\right), \tag{4}$$

$$\sigma_j^2 = \left\{ \begin{array}{l} \left[\frac{\log(area_{\max})}{\log(area_j)}\right] \sigma^2_{j*}, \quad \textit{if original data unavailable} \\ \left[\frac{\log(area_{\max})}{\log(area_j)}\right] \sigma^2_{jb}, \quad \textit{if original data available} \end{array} \right\} \tag{5}$$

$$\theta_{f,j} \sim N\left(\beta_0 + \beta_{coral}\left(\theta_{c,j}\right), \sigma^2_\theta\right), \tag{6}$$

where $\Delta^T_{f,j}$ is the study point estimate of the fish effect size $\theta_{f,j}$ from the j^{th} study; $\Delta^T_{c,j}$ is the study point estimate of coral effect size $\theta_{c,j}$ in the j^{th} study; σ^2_j is the study fish or coral variance that is assumed known; σ^2_{j*} is the maximum of the known (bootstrap estimated) site-level variances for fish or coral among the studies used; $area_{max}$ is the maximum reef area surveyed; σ^2_{jb} is the bootstrap-estimated site-level variance for sites where raw data was available; and σ^2_θ is the estimated regional variance. The area-weighted σ^2_j's were likely to be conservative because they were scaled down from the largest known study variance, expressing an equal or greater level of uncertainty than any of the known sample variances, thus weighting the variance based on the area of reef surveyed.

This continuous meta-analysis model was fully-specified by non-informative prior distributions for the estimated parameters,

$$\beta_0 \sim N(0{,}1000) \tag{7}$$

$$\sigma^2_\theta \sim U(0{,}1000) \tag{8}$$

$$\beta_{coral} \sim N(0{,}1000) \tag{9}$$

In addition to the coral effects model, we included a NTA model to estimate the effects of fishery protection on changes in coral and fish metrics. This protection model (M_{cp}) included a modification of equation (6) to include a dummy variable (*status*) that allowed the slopes ($\beta_{protection}$) and intercepts ($\beta_{prot\ 0}$) of the coral relationship to vary between NTAs and fished areas:

$$\begin{aligned} \theta_{f,j} \sim N\big(&\beta_0 + \beta_{prot\,0}(status) + \beta_{coral}\left(\theta_{c,j}\right) \\ &+ \beta_{coral}\left(\theta_{c,j}\right) * \beta_{protection}(status), \sigma^2_\theta\big). \end{aligned} \tag{10}$$

Priors for all slopes and intercepts were as specified by equation (9). We implemented both regional models using the PyMC Markov-Chain Monte Carlo (MCMC) toolkit for the Python programming language. Meta-analytical models were run for 20 000 iterations with a 10 000 iteration burn-in period. We evaluated model convergence using Geweke's method [50]. Model goodness-of-fit (GOF) was assessed using the deviance simulation methods in PyMC, where ideal models yield GOF values near 0.5, providing evidence of equivalence between simulated and observed deviance [51]. Our Bayesian meta-analyses had GOF scores between 0.46 and 0.50 for all fish metrics, confirming good model fits for estimating effect-size relationships, and model convergence was deemed adequate in every instance [51]. Site-level posterior distributions shrunk towards the regional mean, where the extreme high- and low-value effect sizes had a reduced effect on the overall estimates. Relative evidence for each model was evaluated using the Bayesian Information Criterion (BIC) [52] and the uncertainty surrounding each posterior parameter estimate.

From the area of highest posterior density in the posterior distribution of each model parameter we obtained Bayesian credible intervals (CI) that defined a 95% probability of a given parameter lying within the CI range. During each MCMC simulation we also sampled from the full conditional of the model and data to construct predictive intervals (PI) that defined a 95% probability of future observations being within the PI range. The PI interval values allowed us to make probability statements about the response of fish assemblage groups to future coral depletion.

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Conceived and designed the experiments: NAJG TM NP. Performed the experiments: NAJG TM SKW SJ PC SC MDS YL LB RG MCO KCG AJE CRCS. Analyzed the data: NAJG MAM. Wrote the paper: NAJG TM MAM SKW NP SJ PC SC MDS YL LB RG MCO KCG AJE CRCS.

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