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**Effects of habitat versus fisheries management on spatio-temporal
variation in fish assemblages on the Great Barrier Reef.**

PhD thesis submitted by

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Alistair Cheal, Hugh Sweatman, Murray Logan, Kerryn Johns, Kate Osborne, Ian Miller, Michelle Jonker, Aaron MacNeil, Steve Delean, Morgan Pratchett, Dani Ceccarelli, Andrew Hoey, David Williamson, Anthony Ayling, Richard Evans, Shaun Wilson, and Garry Russ.

Contributions to the seven manuscripts

The seven data chapters presented in this thesis include previously published manuscripts representing my research from 2008 to 2015. The contributions of myself and co-authors to each manuscript is as follows:

Chapter 2. Spatial patterns in butterflyfishes.

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My contribution – conception of manuscript (95%), fish data collection (25%)*, statistical analyses (95%), figure production (100%), primary writing of the manuscript (100%), incorporating input from co-authors (100%), co-ordinating final manuscript (100%), addressing reviewers comments (100%).

Co-author contributions -Alistair Cheal was involved in fish data collection (32%) and contributed to the manuscript concept (2.5%) and edited and commented on drafts. Kate Osborne was involved in benthic data collection (20%), contributed to some statistical analyses (5%) and edited and commented on drafts. Morgan Pratchett contributed to the manuscript concept (2.5%) and edited and commented on drafts.

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Chapter 6 – The importance of habitat complexity to reef fishes.

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Chapter 8 – The utility of no-take marine reserves on the GBR.

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Signature

Date 23/12/16

Abstract

Reef fishes are an important component of coral reef ecosystems, providing pathways of energy transfer from primary producers through to higher trophic levels. Reef fishes also exert substantial influence on the structure and functioning of reef ecosystems, and are in turn influenced by the biotic and physical structure of reef habitats. While there has been extensive research into habitat associations of coral reef fishes, much of the knowledge of their distribution and abundance has been accumulated from numerous small-scale studies. Broad-scale assessments of taxonomic differences in the distribution of reef fishes across large reef systems have been largely prevented by logistical constraints. On Australia's Great Barrier Reef (GBR), for example, cross-shelf variation in the structure of reef fish assemblages has been studied in just two distinct latitudinal bands, while large scale patterns in the abundance and distribution of reef fishes have rarely been considered. Similarly, there is a paucity of information regarding temporal dynamics in the structure of reef fish assemblages, particularly in response to large-scale disturbances.

Coral reefs are inherently dynamic systems and disturbances (e.g., coral bleaching, outbreaks of the corallivorous starfish (*Acanthaster planci*) coral disease and storms) have frequently impacted reefs on the GBR over the last few decades. While many studies have reported impacts to reef fish assemblages by natural disturbances, they are generally opportunistic and restricted to one type of disturbance at one location. Thus, there is a lack of knowledge about how different disturbances impact reef fish assemblages and whether impacts vary across large spatial scales. There is increasing recognition that cumulative impacts have degraded coral reefs in many parts of the world and many advocate the use of no-take marine reserves to protect reef biodiversity and increase resilience. However, whether no-take marine reserves can indeed impart resilience to coral reefs and buffer the effects of disturbances remains the subject of much debate. This thesis aims to fill a number of substantial knowledge gaps by documenting the distribution and abundance of reef fishes across much of the GBR, how they respond to multiple types of disturbances and whether no-take marine reserves can offer any insurance against the increasing frequency and severity of disturbances.

Comprehensive and extensive surveys of coral reef fishes undertaken at 47 reefs across the GBR revealed marked spatial differences in species composition across several distinct groups of fishes, including butterflyfishes, damselfishes, and parrotfishes. Variation in the structure of fish assemblages was most apparent when comparing along cross-shelf gradients from inshore to offshore reefs. Cross-shelf variation in fish assemblages was conspicuous across all taxa, latitudes and years, suggesting the existence of pervasive underlying drivers of reef fish assemblage structure across the continental shelf, most likely related to environmental gradients in water quality and exposure and their differential effects on settlement preferences and survival of larval fish. While there was substantial temporal variation, reef fish assemblages of the GBR are defined by their subregional setting. This is a novel finding. Despite some level of temporal variation in reef fish assemblages usually brought about by disturbance impacts, it was never strong enough to disrupt the spatial structure such that a given community in a sub-region changed to resemble another. This thesis also highlighted that the impacts of disturbances to reef fishes were variable depending on the type of disturbance and the closeness of association of fishes to live coral and habitat complexity. Importantly, the combined effects of loss of both live coral cover and habitat complexity affected a greater variety of fishes than impacts to live coral alone. Indeed, the impact of disturbances on reef fishes and their subsequent recovery was largely determined by the level of habitat complexity, afforded by both the underlying rugosity of the substrate and the fine scale complexity offered by the skeletons of scleractinian corals. An exciting result to emerge from this thesis was that not only do no-take marine reserves boost populations of exploited fishes inside their boundaries, but they can also retain benefits for exploited fish stocks in the face of strong tropical cyclones that are predicted to occur with greater frequency in the coming decades.

This body of work has greatly improved our knowledge of the distribution and abundance of coral reef fishes across much of the GBR. It demonstrates that there is strong spatial structure to reef fish assemblages, and despite a long disturbance history, reef fish assemblages appear largely resilient to the effects of disturbances. The level of impact is closely linked to the closeness of association with live coral cover, but importantly is strongly determined by the level of alteration in habitat complexity. While reef fishes are impacted by disturbances, exemplified by changes to their abundance, diversity and assemblage structure, they have shown the ability to recover

to pre-disturbance levels. Somewhat surprisingly, no-take marine reserves also contributed to reef fish resilience, ensuring the maintenance of important ecological functions essential to recovery following disturbances.

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Chapter 1. General Introduction.

Coral reefs are unique, diverse and iconic ecosystems (e.g., Hughes et al. 2007a), largely owing to the biological and physical structure provided by scleractinian (*reef-building* or *hard*) corals. Scleractinian corals provide three fundamental functions on coral reefs. Firstly, corals are the primary *structural engineers* of reef ecosystems; the accretion of the carbonate skeletons over countless generations provides the very foundation upon which the living veneer of the contemporary reef community grows (Hopley et al. 2007). Secondly, corals are one of the principal *foundation species* (along with highly productive turf algae) of reef ecosystems. Corals are both heterotrophs and autotrophs (Goreau et al. 1971) and as such play an important role in energy production and transfer (Porter 1976). Carbon production from scleractinian corals is made available to higher trophic levels by specialist reef organisms (e.g., butterflyfishes – family Chaetodontidae) that feed directly on coral tissues (Cole et al. 2008) and through extensive energy contained within coral propagules and mucous (Wild et al. 2004). Thirdly, corals are unequivocally the main *habitat-forming* species on coral reefs; the complex carbonate skeletons formed by corals provide habitat and shelter for a vast array of creatures, including crustaceans, polychaetes and fishes (Stella et al. 2011; Coker et al. 2014).

Coral reef fishes are one of the foremost groups of reef organisms that benefit from the essential habitat and resources provided by coral rich habitats (Cole et al. 2008). Accordingly, there has been extensive research showing how reef fish assemblages are structured by the abundance (Wilson et al. 2006; Pratchett et al. 2008, 2014), diversity (Messmer et al. 2011), and topographic complexity provided by scleractinian corals (Graham et al. 2006; Alvarez-Filip et al. 2009). The fishes themselves are also an important component of reef ecosystems and exert considerable influence on the structure and functioning of coral habitats (Bellwood et al. 2004; Cheal et al. 2010). Herbivorous fishes, for example, regulate the abundance of fleshy macroalgae, which can otherwise impede growth, settlement and even survivorship of reef-building corals (Hughes et al. 2007b). Reef fishes perform a diversity of important ecological roles (Mouillot et al. 2014), ranging from the transfer of energy through reef food webs to facilitation of the settlement of coral larvae. However, current research attention is

unequivocally focused on the role of herbivorous fishes in preventing phase-shifts and thereby contributing to the resilience of coral reefs (e.g., Bellwood et al. 2004; Mumby et al. 2006; Nystrom 2006; Nash et al. 2016) as discussed later.

1.1 Natural versus anthropogenic disturbances

Coral reef ecosystems exist in an inherently stochastic and highly dynamic environmental setting and are frequently impacted by a wide variety of disturbances (Connell 1978; Nystrom et al. 2000). However, intensifying frequency and severity of disturbances is increasingly leading to extensive and widespread coral loss and degradation of coral reef ecosystems (Jackson et al. 2001; Pandolfi et al. 2003). Importantly, natural disturbances (including outbreaks of the corallivorous starfish *Acanthaster planci*, coral bleaching, coral diseases, tropical revolving storms such as cyclones, typhoons and hurricanes [hereafter ‘cyclones’] and sub-cyclonic storms) all contribute to coral loss and are being increasingly exacerbated or compounded by anthropogenic disturbances. For example, rising ocean temperatures due to global warming are expected to increase the frequency and intensity of severe tropical storms (Goldenberg et al. 2001; Webster et al. 2005). Correlative evidence suggests that outbreaks of *A. planci* may be linked to enhanced larval survival brought about by increased nutrient loads in runoff (Moran & Bradbury 1989), and/or overfishing of key predators (Dulvy et al. 2004; Sweatman et al. 2008; McCook et al. 2010). Moreover, sustained increases in ocean temperatures caused by global climate change (Pachauri et al. 2014) have caused increased frequency and severity of coral bleaching as evidenced by the 1998, 2002 and 2016 global bleaching events, which suppressed growth and caused elevated rates of mortality in scleractinian corals throughout the Indo-Pacific (Hoegh-Guldberg 1999; Goreau et al. 2000; McClanahan 2000; Edwards et al. 2001; Graham et al. 2006, 2007; Berkelmens et al. 2004; Garpe et al. 2006; De’ath et al. 2009; Hughes et al. 2017).

Anthropogenic disturbances, which directly impact coral reefs, include extractive activities, coastal development, catchment modification, freshwater runoff, pollution, and eutrophication, particularly in areas close to urban centres (Loya 1990; Jackson et al. 2001; Pandolfi et al. 2003). Activities such as dredging, smothering from land reclamation or explosions or poisons used in destructive fishing can cause direct coral mortality, but also indirectly affect coral health and mortality by altering the

coral's environment/habitat by increasing sediment and nutrient loads, which elevates water turbidity and reduces light levels (Dodge & Vaisnys 1977; Bak 1978; Rogers 1983, 1990; Pastorok & Bilyard 1985; Fabricius 2005; Erftemeijer et al. 2012; Brodie et al. 2013). Settling sediment can smother corals, while increased nutrients may facilitate the proliferation of macro-algae (Lapointe 1997; Smith et al. 2001; Lapointe et al. 2004; Littler et al. 2006a, b) as well as potentially contributing to outbreaks of the starfish *A. planici* (Fabricius et al. 2010). Additionally, the burgeoning requirements of growing human populations place increasing pressure on marine environments in many ways. Of all of the stressors applied by mankind, our contribution to climate change ensures the planet's oceans and atmosphere will warm in coming decades (Karl & Trenberth 2003; Hansen et al. 2006) causing alterations to contemporary climate, sea levels and disturbance regimes with unknown but potentially severe consequences for coral reef ecosystems. While climate change may increase the severity and frequency of natural disturbance regimes, ocean acidification is directly attributable to greenhouse gas accumulation (Caldeira & Wickett 2003; Feely et al. 2004; Doney et al. 2009) and is likely to alter the basic chemistry of the ocean to such an extent that corals have difficulty performing basic physiological functions such as calcium deposition (Kleypas et al. 1999, 2005; Joikel et al. 2008) and fishes may exhibit abnormal behaviours detrimental to their survival (Munday et al. 2009, 2010; Dixon et al. 2010).

Due to the increasing anthropogenic pressures and the natural disturbance history of the last few decades the global trajectory of coral cover has been downward, and with the looming threat of climate change and ocean acidification, it seems likely that world-wide coral cover will continue its downward trajectory in the near future. Persistent degradation of coral reefs has resulted in sustained declines in coral cover at many reef locations. In the Caribbean, degradation of reef ecosystems has occurred since the 1980s (Gardner et al. 2003), due largely to losses in hard corals attributable to cyclones and disease, coinciding with a reduction in herbivory resulting in the proliferation of macroalgae (Hughes 1994; Shulman & Robertson 1996). Aside from large-scale widespread disturbances, coral reefs globally are also plagued by frequent local or regional scale disturbances. Recent estimates suggested the GBR has lost half of its coral cover since the mid-1980s (De'ath et al. 2012), but this was due to a spatio-temporal mosaic of perturbations, particularly *A. planici* infestations, storms and cyclones (Osborne et al. 2011) rather than a regional or global phenomenon, and is

indicative of the underlying natural disturbance regime faced by many reefs across the globe. Despite the global degradation of coral reef ecosystems, evidence is also emerging that coral reefs can and do recover from disturbance impacts, given enough time between consecutive events (Halford et al. 2004; Emslie et al. 2008). However, the worry is that the frequency of disturbance events will increase to the point where recovery is not possible and a ‘ratcheting down’ of coral reef health will occur (Birkeland 2004).

1.2 Consequences of coral loss and habitat degradation for reef fishes

On coral reefs, the broader ecosystem consequences of habitat perturbations depend on the level of coral mortality as well as the magnitude of declines in structural complexity (Wilson et al. 2006; Graham et al. 2007; Alvarez et al. 2009; Pratchett 2014). Changes to structural complexity following disturbance generally occur because topographic complexity has been reduced, either by the immediate removal of live coral skeletons due to mechanical breakage by physical disturbances (Woodley et al. 1981; Halford et al. 2004; Emslie et al. 2014), or by longer term skeletal erosion and decomposition of dead corals following biological disturbances (e.g., Graham et al. 2007). Abundance and diversity of reef fishes is positively correlated with both coral cover (Bell & Galzin 1984; Sano et al. 1984; Findley & Findley 1985; Sano 2000; Jones et al. 2004) and structural complexity (Gratwick & Speight 2005; Graham et al. 2006; Wilson et al. 2006; Emslie et al. 2014), and greatest impacts on reef fishes occur when extensive coral mortality is combined with extensive loss of structural complexity provided by living and intact corals (Wilson et al. 2006; Pratchett et al. 2008). For the most part, broad scale rugosity of the reef matrix, including any vertical relief, overhangs, holes, caves (collectively referred to as *substrate rugosity*) is resistant to most disturbances. However, changes to substrate rugosity may occur when severe tropical storms or cyclones redistribute large volumes of carbonate material or directly modify reef structure (Connell 1997). Fine-scale complexity (*topographic complexity*) provided by contemporary coral growth, meanwhile, invariably declines following extensive coral mortality. Localised declines in structural complexity in the aftermath of major disturbances are, therefore, dependent on the relative contributions of substrate rugosity versus topographic complexity to habitat structure in different reef habitats (Pratchett et al. 2008).

Specific effects of habitat degradation on different groups of fishes depend on their reliance on corals for food, shelter or recruitment (Jones et al. 2004). Many reef fishes have a close association with scleractinian corals and will likely be hardest impacted by coral mortality. Corallivorous fishes such as butterflyfishes which target coral polyps for food, will likely be heavily impacted by disturbances which only cause coral mortality (e.g., Sano et al. 1984). There have been numerous examples of immediate reductions in their abundance and diversity following acute disturbances that cause localised coral depletion (Sano et al. 1984; Bouchon-Navaro et al. 1985; Pratchett et al. 2006, 2008; Wilson et al. 2006; Emslie et al. 2011). However, the consequences for fishes with looser associations with live corals can be highly variable, both in the short and long term. Numerous species utilise the fine scale habitat complexity afforded by coral skeletons as settlement sites and shelter from predators and these will likely also be deleteriously affected by disturbances, both in the short term by the removal of skeletons through wave action, and in the longer term as dead coral skeletons erode through time. A greater array of fishes will, therefore, be impacted by disturbances which reduce both live coral tissue and habitat complexity (Graham et al. 2007; Emslie et al. 2014). In these instances, even fishes with no obvious close association with live corals can exhibit declines in abundance. For example, there have been increases and decreases in herbivorous fish numbers immediately following bleaching and this appears tied to changes in algal resources or the loss of shelter sites where complexity has been reduced (Graham et al. 2006; Wilson et al. 2006; Adam et al. 2014; Emslie & Pratchett In Press; Emslie et al. 2014). However, longer term changes in the abundance of herbivorous and other fishes have also been documented and this lagged response appears to be related to loss of settlement habitat and gradual declines in habitat complexity (Graham et al. 2006; Garpe et al. 2006).

In recent decades there has been a high frequency of large scale and severe disturbances. The 1998 and 2002, near-global mass coral bleaching events provided multiple opportunities to examine how the degradation of coral reefs has impacted associated fish assemblages. For example, reductions of coral cover in the Seychelles led to local extirpations of reef fishes, substantial reduction of the number of species, diminished taxonomic distinctness and loss of functional redundancy among groups of fishes performing important ecological functions (Graham et al. 2006). The same bleaching event also saw ocean scale alterations to the size structure of fish populations,

as well as changes in diversity and trophic composition following coral loss (Lindahl et al. 2001; Garpe et al. 2006; Graham et al. 2007). Similarly, a long temporal dataset from Moorea in French Polynesia, has provided valuable insights into how reef fishes respond to disturbance. Multiple disturbances (e.g., cyclones and *A. planci* outbreaks) have differentially impacted various reef habitats (e.g., lagoonal reefs, back reefs and fore reefs) at Moorea. Comparative analyses across habitats suggest that there is a critical threshold of hard coral cover (10%) above which reef fish diversity and abundance are generally resistant to changes in coral cover (Holbrook et al. 2008). If, however, coral cover declines below 10%, abundance and diversity of reef fishes decline dramatically (see also Wilson et al. 2006). Another study at Moorea described the responses of butterflyfish assemblages to extensive coral loss caused by outbreaks of *Acanthaster* spp. in the early 1980s (Berumen & Pratchett 2006). Despite the apparent recovery of the overall abundance of butterflyfishes, the relative abundance of different species was fundamentally altered in response to recurrent disturbances and changes in the composition of coral assemblages. Notably, many important coral species (e.g., *Acropora*) did not recover and butterflyfish species reliant on these corals for food were largely absent in the aftermath of the disturbance (Berumen & Pratchett 2006). While our knowledge of how fishes respond to disturbances has increased markedly in recent years, this knowledge has been gained piecemeal and incrementally through opportunistic disparate studies of individual disturbances. This thesis will address the impacts of multiple types of disturbances to reef fish assemblages spread over a vast swathe of the GBR using data collected via a standard methodology.

1.3 Importance of reef fishes

Fishes are a diverse and important component of coral reef ecosystems, performing many essential ecological functions such as providing pathways of energy transfer among coral reef food webs, their grazing activities remove algae and sediment detrimental to coral health and recovery following disturbances, and they also have nutritional, economic and social benefits for human populations (Moberg & Folke 1999). Reef fishes transfer energy through different trophic levels and from pelagic to reef based habitats (McMahon et al. 2015). Some fishes have been shown to feed directly on coral polyps (reviewed in Cole et al. 2008) but also to feed on energy rich mucus containing wax esters (Benson & Muscatine 1974), a major product of coral

metabolism. Both modes of feeding transfer the energy obtained in part through primary productivity from symbiotic zooxanthellae within coral tissues, through coral reef food webs. The activities of planktivorous fishes also transfer energy from the surrounding oligotrophic waters into reef based food webs (Emery, 1968; Davis & Birdsong, 1973; McMahon et al. 2015), through the prodigious amount of fecal droppings they produce which rain down on the reef and are fed upon by other fishes (Robertson 1982), but to a lesser extent through predation as some planktivores are consumed by predators (Choat 1968; Hartline et al. 1972).

Many fishes, nominally defined as herbivores or detritivores, feed from the epilithic algal matrix (EAM – *sensu* Wilson et al. 2003). Their capacity to crop/scrape/excavate or graze the EAM provides bare surfaces to facilitate coral settlement (Steneck 1988), but also prevents the establishment of algal turfs which can cause post settlement mortality in corals (Birkeland 1977; Birrell et al. 2005). Their grazing activities also indirectly remove immature macro-algae thalli thereby preventing the proliferation of large beds of mature fleshy macro-algae, which can outcompete corals through over shading and chemical deterrence (Tanner 1995; McCook et al. 2001) or reduce growth rates (Box & Mumby 2007). Fishes may also play a role in the proliferation of coral disease (Aeby & Santavy 2006), as some corallivorous fishes were hypothesised to be vectors for the transmission on coral disease (Raymundo et al. 2009), although other studies refute this (e.g., Cole et al. 2009). Reef-associated predatory fishes (families Labridae, Lethrinidae, Lutjanidae and Serranidae), transfer energy among different trophic levels. Predatory fishes no doubt impact the abundance of their prey (e.g., Graham et al. 2003; Boaden & Kingsford 2015), but whether the magnitude of these impacts represents top down regulation strong enough to result in trophic cascades affecting numerous parts of the food web on high diversity coral reefs remains equivocal.

Reef fishes are also important from a socio-economic perspective, forming the basis of recreational, commercial and artisanal fisheries across the Indo-Pacific. Losses of predatory fishes due to extractive fishing and in response to natural disturbances have clear socio-economic consequences; the ramifications for ecosystem function remain unclear. Notwithstanding the important trophic and ecological functions they perform, reef-associated predatory fishes also form the basis of many fisheries world-

wide, and add aesthetic value for tourism. In many developing countries, particularly small island nations, fish acquired through artisanal or subsistence fisheries is the primary source of dietary protein (Zann & Veikila 2000; Bene & Heck 2005). In developed countries, fisheries also provide substantial income and livelihood to many communities.

1.4 Consequences for reef recovery and resilience

Resilience is defined as the ability of a system to undergo disturbances, but still maintain critical functions and structure (Holling 1973). However, measuring resilience is difficult for two reasons; firstly, resilience can only be inferred retrospectively, by establishing the extent to which the composition of natural assemblages is maintained or retained and continues to perform key ecological functions in the aftermath of major disturbances, and secondly, loss of resilience is manifest as a fundamental shift to an alternate stable state of species composition and function, but establishing the permanency of such shifts (as distinct from temporary transitions to early successional stages of recovery) requires long-term monitoring of both state variables and feedback mechanisms (Bellwood et al. 2004). One cornerstone of the theory of resilience is the idea of functional redundancy. Within an ecosystem, individual species all perform functions which drive important ecosystem processes. A greater the range of functions (functional diversity) equates to a greater diversity of processes supporting ecosystem health (Walker, et al. 1999). As discussed above, many ecosystems like coral reefs are inherently dynamic systems that are impacted by various perturbations. Recovery from disturbances requires the full range of ecosystem functions to be preserved. However, the extent and direction of change in ecological function is determined largely by the response diversity (the spread of change in numerical abundance of individual species within a functional group) and functional redundancy (the number of species performing a given ecological function) (Elmqvist et al. 2003). Functional redundancy is fundamental to an understanding of how losses of species affect ecosystem function. Functional redundancy is theorised to occur where many species perform similar ecological roles, and species may be substituted following disturbances with minimal loss of function (Lawton & Brown 1993). While the use of functional redundancy may be helpful in identifying species for conservation, at its heart it is based on the flawed assumption that all species perform equivalent ecological functions. By definition,

species must perform slightly different roles, although the extent will likely vary along different functional axes. However, it seems reasonable to assume that there are greater similarities among some species than others (Rosenfield 2002) and so functional redundancy likely exists, especially among groups of species that respond differently to disturbance (high response diversity).

The continuing degradation of coral reefs will likely result in a reduced ability of coral reef fishes to provide ecosystem services essential to reef recovery and resilience. Many studies have documented the impacts of various disturbances on coral reefs (e.g., Allen 1985; Glynn 1990; Harmelin-Vivien 1994; Hughes 1994; Marshall & Baird 2000; Hoegh-Guldberg et al. 2007; Osborne et al. 2010; De'ath et al. 2012), however fewer data exist with a temporal series long enough to report on the recovery dynamics of coral reef communities following disturbances (but see Halford et al. 2004; Berumen & Pratchett 2006; Emslie et al. 2008; Adjeroud et al. 2009; Gilmour et al. 2013). The recovery of hard corals is largely dependent upon connectivity to sufficient brood stock from undisturbed or less disturbed communities and enough suitable cues and substrate for larvae to settle upon arrival. There is now also recognition that the ecological functions performed by reef fishes described earlier can play a role in the recovery dynamics of reef communities by influencing the success of coral recruitment and survivorship. The grazing activities of large roving herbivorous reef fishes may facilitate larval coral settlement by at least three mechanisms. Firstly, grazing provides bare substrate and helps encourage coralline algae growth whilst limiting macro-algae, resulting in more space for the settlement of coral planulae (Steneck 1988). Secondly, grazing prevents thick algal turf establishment, which can trap detritus and lead to elevated mortality of coral recruits (Birkeland 1977; Birrell et al. 2005). Finally, the removal of immature thalli by herbivorous fish grazing results in less competitive interactions for young corals with competitively superior macro-algae (Hay 1981; Carpenter 1986; Lewis 1986; Williams & Polunin 2001; Williams et al. 2001; Mumby et al. 2006; Burkepile & Hay 2008). Thus the grazing behaviour of herbivorous fishes should be beneficial to corals and aid in their recovery following disturbances. However, the same feeding activities may also inadvertently consume newly settled corals, although the extent to which this occurs is at present largely unknown. In addition to the feeding activities of large roving herbivores, recent evidence has emerged that small territorial 'farming' damselfish have the potential to influence coral

settlement and survivorship (Gochfeld 2010; Casey et al. 2015). They aggressively defend specific algal assemblages within cultivated turfs inside their territories and may have a potent effect on benthic community composition (Ceccarelli et al. 2001, 2006; Hata & Kato 2004; Ceccarelli 2007), particularly in areas of high abundance where their territories cover upward of 90% of available substrate.

In addition to their role aiding coral recovery, herbivorous fishes can also influence levels of macro-algae and the two functions are strongly inter-connected. Empirical studies have also demonstrated that the removal of herbivorous fishes results in increased macro algal cover and the loss of corals (Hughes et al. 2007b; Mumby 2006). Herbivorous parrotfishes (tribe Scarini, family Labridae) scrape and excavate the substrate as they feed (Bellwood & Choat 1990) and may indirectly consume immature macro-algae thalli during their feeding, thereby preventing the replenishment and proliferation of mature macro algal stands, which directly outcompete corals for light and space (Tanner 1995; McCook et al. 2001). Other grazing herbivorous fishes such as rabbitfishes (family Siganidae) and some surgeonfishes (family Acanthuridae) can consume mature macro-algae directly, but studies to date have shown that consumption rates tend to be low, especially where macro algal biomass is high (Hoey & Bellwood 2010). As different groups of herbivores appear to have variable contributions to preventing macro-algae spread, changes in the abundance and diversity of different groups of herbivorous fishes following coral mortality may have serious repercussions for reef recovery. High numbers of scraping or excavating herbivorous fishes may help restrict levels of macro-algae and facilitate coral settlement and recovery (Mumby et al. 2006), but if these fish are removed or naturally occur in low numbers, macro-algae may flourish to such an extent that it retards coral recovery. This may result in undesirable shifts to alternate stable states (regime shifts), where corals are replaced by macro-algae as the dominant component of the benthic community. (Hughes 1994; Hughes et al. 2003; Cheal et al. 2010). The loss of macro-algal browser herbivorous fishes may not be as critical, as it is doubtful that their browsing capacity would be able to reverse the abundance of macro-algae once it has become well established and widespread. While the ramifications of decreases in the abundance and diversity of herbivorous fishes seem clear, the consequences of losing fishes performing other ecological roles appear less clear.

Corallivorous fishes likely affect the health of coral colonies (Lasker 1985; Cole et al. 2009). Removal of coral tissue requires the corals to reallocate resources to repair or regenerate tissue (reviewed by Henry & Hart 2005), and can result in the suppression of new coral growth for up to a month following the cessation of regeneration (Meesters et al. 1994). The feeding activities of corallivorous fishes can also impact coral reproduction. Corals have limited energy, and reproduction, which is energetically expensive, can be decreased in lieu of tissue regeneration of fish feeding scars leading to suppressed reproductive output (Szmant-Froelich 1985; Rinkevich & Loya 1989; Harrison & Wallace 1990; Van Veghel & Bak 1994). Aside from direct removal of coral tissue, feeding by corallivorous fishes may also have indirect impacts on coral growth and fitness. For example, they can act as vectors for the transfer of coral diseases such as black-band disease (Aeby & Santavy 2006), although the extent to which this occurs is still mostly undetermined (Cole et al. 2009). Overall, it appears that corallivores have detrimental impacts on the fitness of individual colonies, however their contribution to changes in coral assemblage abundance and diversity and their impacts on the ability of corals to recover from disturbances remains largely unknown and a potential avenue for future research.

1.5 No-Take Marine Reserves

Globally, coral reefs face multiple stressors and in many regions, have been severely degraded by the cumulative impacts of anthropogenic and natural disturbances. There has been considerable discourse about how best to conserve coral reefs and the diversity they contain (e.g., Bohnsack 1993; Halpern & Walters 2002; Roberts et al. 2002; Pandolfi et al. 2003; Bellwood et al. 2004). One of the most widely promoted tools for achieving the conservation and management of marine systems is the implementation of networks of fully protected, no-take marine reserves (NTMRs). While historically a fisheries management tool to protect exploited stocks, their use has broadened in recent years to include the protection of biodiversity and ecosystem processes, thereby imparting resistance and resilience into the system (Mumby et al. 2006; Micheli et al. 2013; Mellin et al. 2016). While there is now abundant evidence that fully protected NTMRs boost populations of exploited species (e.g., Babcock et al. 2010; Williamson et al. 2004; Mumby et al. 2007; Russ et al. 2008; Emslie et al. 2015), evidence for broader ecological effects such as increased resilience or protection of biodiversity

remains equivocal. That notwithstanding, our expectations of NTMR performance must be placed in a clear regional context. For example, NTMRs placed in a developing nation with limited resources and high fishing pressure on a wide range of species using destructive fishing techniques, should be expected to not only protect exploited species and boost their populations, but also have wider ranging benefits in terms of the protection of biodiversity. In contrast, the GBR is one of the largest and best-managed networks of NTMRs in the world. It has relatively light fishing pressure targeting a narrow range of reef associated predatory fishes, and for the coral reef line fishery at least, no use of destructive fishing techniques. This means the benefits of NTMR protection on the GBR should realistically be limited to protection of exploited species. Unless invoking predatory fish mediated top down control of trophic cascades, it is likely that NTMRs on the GBR should produce few benefits to the wider reef ecosystem, particularly coral communities and non-exploited fishes. This means that unless GBR NTMRs can boost or preserve numbers of herbivorous fishes following disturbances NTMRs on the GBR are unlikely to play a major role in facilitating the recovery of reefs as herbivorous fishes are not exploited on the GBR.

In 2004, the GBR reserve network underwent a substantial alteration to its zoning, resulting in an increase of reefs protected inside NTMRs from about 5% to roughly a third of the Marine Park. With a key aim of preserving biodiversity, the Representative Areas Program (RAP) was the foundation for rezoning and was based on the advice of an expert panel which designated 80 bioregions within the Great Barrier Reef Marine Park (GBRMP) (Day et al. 2002; Fernandez et al. 2005). The RAP process was a bold political move and underwent considerable public consultation, generating substantial controversy among a variety of reef stakeholders. In this environment it is essential any benefits due to the expansion of NTMRs on the GBR be rigorously demonstrated and effectively communicated and this thesis will add substantially to our knowledge of the performance of NTMR networks on the GBR.

1.6 Australia's Great Barrier Reef

The GBR is an extensive and iconic reef system that is recognised internationally for its outstanding biodiversity. It extends across 14 degrees of latitude, stretching two and a half thousand kilometres along the north-east coast of Australia. The almost 4000 individual reefs and islands provide myriad habitats for a vast array of creatures,

including ~1625 species of fishes and ~450 species of hard corals. The GBR is situated within the GBRMP, which is a network of multi-use zones including NTMRs and areas where extractive activities such as fishing and collecting are permitted. The GBRMP is globally considered the gold standard for coral reef management. Numerous management strategies are employed, including legislation, zoning plans and permits, as well as research, partnerships, education and compliance measures. Despite the seemingly effective management, the GBR still faces numerous natural and anthropogenic stressors and has undergone large reductions in habitat quality in recent decades. Natural disturbances such as cyclones, coral bleaching and *A. planci* outbreaks have all contributed to sustained and substantial declines in cover of scleractinian corals (Osborne et al. 2011; De'ath et al. 2012). Additionally, man-made stressors have been implicated in habitat degradation of many inshore GBR reefs (McCook 1996, 1999; van Woesik et al, 1999; Thompson et al. 2014). Coastal development and farming practices in water catchments adjacent to the GBR can elevate nutrient and sediment loads in freshwater runoff entering coastal waters (Mitchell et al. 1997, 2001; Bramley & Roth 2002; Brodie et al. 2003; Furnas 2003; Fabricius et al. 2005), increasing turbidity and smothering corals (Rogers 1990; Fabricius 2005). The GBR also has several well developed fisheries, including the commercial line fishery which targets reef-associated predatory fishes, and was worth about \$30 million in 2014 (Leigh et al. 2014). Despite all of these pressures and the inherent multi-faceted value of the GBR, we still have limited basic information on ecological patterns for many species residing within the GBR, including reef fishes. Such information is necessary for the effective management and preservation of the GBR's reef fishes and to provide a baseline against which to gauge impacts from contemporary and future stressors.

The diversity and abundance of coral reef fishes are fundamental in supporting tourism and fisheries industries on the GBR. However, there is still limited knowledge of even the most basic ecological parameters such as the distribution and abundance of many reef fishes across most of the GBR. Prior to the commencement of the Long Term Monitoring Program (LTMP) at the Australian Institute of Marine Science (AIMS) in 1992, such information was limited to comparisons across the continental shelf in two latitudinal bands of the GBR near 14°S and 19°S, with little information extending beyond these limits except for some important fishery species, like the coral trout (*Plectropomus* spp., *Variola* spp, family Serranidae.). To date, most of these studies

have described strong changes in the community structure of reef fishes across the continental shelf (Williams & Hatcher 1982; Williams 1982; Russ 1984; Gust et al. 2001; Hoey & Bellwood 2008) and similar patterns exist for other coral reef organisms including corals (Done 1982), soft corals (Dinesen 1983), algae (Drew 1983) phytoplankton (Sammarco & Crenshaw 1984). This suggests the existence of persistent fundamental drivers of reef fish community structure across the continental shelf, such as the effect of exposure regimes and water quality on larval fish choice of settlement habitats (Williams 1982). Thus there is a need to assess whether strong cross shelf patterns in community structure evident in early studies persist across much of the GBR for a broad range of fishes. Data presented in this thesis will significantly increase the spatial extent of our understanding of the distribution and abundance of reef fishes on the GBR. Such information can aid in the effective management of reef fishes highlighting species most vulnerable to habitat degradation, as well as providing a yardstick from which to measure change related to natural and anthropogenic stressors, particularly in light of the expected changes to disturbance regimes in the coming decades (Pachauri et al. 2014).

1.7 Aims

Here using an extensive spatio-temporal data set collected as part of the LTMP, I explore the broad-scale distribution and abundance of several groups of reef fishes on the GBR, whether disturbances altered spatial patterns of community organisation or reduced ecological functioning, and finally, what role NTMRs can play in the preservation of coral reef biodiversity. The LTMP has collected monitoring data on 215 species of reef fishes spread across 92 reefs since 1992, enabling an evaluation of the distribution and abundance of reef fishes over much of the GBR. This will greatly expand our knowledge of reef fishes across much of the GBR, and given the looming threat of climate change and its attendant ramifications for coral reefs, such basic ecological data on reef fishes is needed to provide a baseline from which to gauge the impact of any future disturbances on their populations, identify vulnerable species and to provide effective information to aid management. Additionally the temporal scope of the data also allows an examination of the impacts of natural disturbances on reef fishes, with approximately fifty disturbances documented since monitoring began. While disturbance effects on reef fishes have been well documented, most of our

knowledge stems from isolated studies of single disturbance events. Two real strengths of the LTMP dataset is its spatial and temporal scope, and that it was collected in a consistent way. This allows a robust examination of the effects of multiple disturbance types on reef fish communities over a large geographic scale.

Since effective broad-scale monitoring of the GBR began in the early 1990s, the GBR has been subject to a range of disturbances resulting in wide-spread declines in hard coral cover. The vast majority of reefs have been impacted by at least one disturbance, and many have been impacted by several (Osborne et al. 2011). Loss of hard coral cover has varied depending of the frequency, duration and intensity of the disturbance, but there were few instances where habitat complexity (the underlying substrate rugosity plus fine scale complexity contributed by coral skeletons) was significantly reduced. Until recently, the response of GBR reef fishes to these disturbances was largely unknown and constrained to a handful of studies of restricted spatial scope. Such small scale studies have yielded conflicting results. On one hand, the bleaching event in 1998 resulted in extensive coral loss and while there was no detectable effect on the abundance, diversity or richness of the crypto-benthic fish community, the authors noted an extensive shift in reef fish assemblage structure, with little evidence of recovery after many generations of these short-lived species (Bellwood et al. 2006). Conversely, dramatic loss of coral on the southern GBR resulted in substantial reductions in the abundance and diversity of reef fishes; however most fishes recovered their pre-disturbance abundance within a decade (Halford et al. 2004). Such contrasting results from studies of limited spatial extent mean that generalities about the effects of disturbances on reef fishes are hard to elucidate. Thus this thesis will fill the need for a comprehensive study examining baseline levels of reef fish distribution and abundance and how these are altered by various natural disturbances.

1.8 Thesis Plan

The overarching objectives of the research presented in this thesis were three-fold.

Objective 1. Document the distribution and abundance of GBR reef fishes.

Chapter 2 – The distribution and abundance of butterflyfishes.

Emslie, M. J., Pratchett, M. S., Cheal, A. J., & Osborne, K. (2010). Great Barrier Reef butterflyfish community structure: the role of shelf position and benthic community type. *Coral Reefs*, 29(3), 705-715.

Quantifying the distribution and abundance of the butterflyfishes across the length and breadth of the GBR is addressed in this first data chapter. Butterflyfishes are intimately associated with hard coral cover and although there are numerous studies which have investigated their association with living hard coral (e.g., Harmelin-Vivien & Bouchon-Navaro 1983; Bouchon-Navaro et al. 1989; Berumen & Pratchett 2006; Pratchett et al. 2006; Pratchett & Berumen 2008; Cole et al. 2008), these studies have generally been at small spatial scales limited to a single reef. In addition, two previous studies investigated the distribution and abundance of GBR butterflyfishes across the continental shelf in one latitudinal band at around 19°S, however the distribution and abundance of butterflyfishes across much of the GBR remains unresolved. Thus this chapter represents a novel examination of the differences in the structure of butterflyfish assemblages across 11 degrees of latitude and, importantly, among reefs with marked differences in habitat structure.

Chapter 3- Spatio-temporal patterns in territorial farming damselfishes.

Emslie, M. J., Logan, M., Ceccarelli, D. M., Cheal, A. J., Hoey, A. S., Miller, I., & Sweatman, H. P. A. (2012). Regional-scale variation in the distribution and abundance of farming damselfishes on Australia's Great Barrier Reef. *Marine Biology*, 159(6), 1293-1304.

This represents a first examination of the distribution and abundance of farming damselfishes across much of the GBR. These fishes are ubiquitous but largely overlooked group and much of the previous study of this group has centred on their reproduction, recruitment, behaviour (e.g., Feary et al. 2007; Medeiros et al. 2010;

White & O'Donnell 2010; Johnson & Hixon 2011), how they manipulate algal assemblages within their territories (Hata & Kato 2004; Ceccarelli et al. 2005a, b; Jones et al. 2006) and to what extent they influence patterns of coral recruitment and survivorship (Wellington 1982; Gleason 1996; Gochfeld 2010; Casey et al. 2015). These studies have generally been conducted over restricted spatial scales and information on their broad scale distribution and abundance, and an understanding of how they help to structure benthic communities at such a scale is very limited.

Chapter 4 – The distribution and abundance of herbivorous fishes.

Cheal, A., Emslie, M., Miller, I., & Sweatman, H. (2012). The distribution of herbivorous fishes on the Great Barrier Reef. *Marine Biology*, 159(5), 1143-1154.

This chapter examines the spatial structure of the functionally important groups of herbivorous fishes, the parrotfishes (family Labridae), the surgeonfishes and the rabbitfishes. For the first time we examine the distribution and abundance of herbivorous fishes across the length and breadth of the GBR, greatly extending our understanding of their spatial distribution which was previously restricted to two latitudinal bands in the central GBR (Williams 1982; Russ 1984; Gust et al. 2001; Hoey & Bellwood 2008).

Objective 2. Quantify disturbance impacts on reef fishes

Chapter 5 – Response of butterflyfishes to disturbance.

Emslie, M. J., Pratchett, M. S., & Cheal, A.J. (2011). Effects of different disturbance types on butterflyfish communities of Australia's Great Barrier Reef. *Coral Reefs*, 30(2), 461-471.

Temporal dynamics, and how four types of disturbance (bleaching, *A. planci* infestations, storms and coral disease) alter the community structure of GBR butterflyfishes is addressed in this chapter. Previous studies have typically examined the impact of a single disturbance on butterflyfishes at a single location (e.g., Bouchon-Navaro et al. 1985; Berumen & Pratchett 2006). This chapter is original in that it examines the impacts of numerous disturbances on butterflyfishes across the length and breadth of the GBR. These results are supplemented with additional co-authored

manuscripts provided in Appendix 2 which look more broadly at the effects of disturbances on reef fish diversity and abundance (Cheal et al. 2008; Wilson et al. 2009), but also focus on the role of herbivorous fishes in contributing to reef resilience and preventing coral-macro-algal phase shifts (Cheal et al. 2010).

Chapter 6 – The importance of habitat complexity to reef fishes.

Emslie, M. J., Cheal, A. J., & Johns, K. A. (2014). Retention of habitat complexity minimizes disassembly of reef fish communities following disturbance: a large-scale natural experiment. *PLoS One*, 9(8), e105384.

Using an innovative approach, this chapter addresses the question of the importance of habitat complexity in structuring reef fish assemblages. While previous studies have highlighted the importance of habitat complexity to reef fishes (e.g., Lewis 1997; Gratwick & Speight 2005; Graham et al 2007; Coker et al. 2012), they generally used gradient or meta-analyses which lacked an experimental design over broad spatial scales to separate the influences of live coral cover from habitat complexity. This study used a natural experiment based on long-term monitoring data covering much of the GBR to reveal the fundamental importance of habitat complexity in structuring reef fish assemblages.

Chapter 7 – Recovery of coral reef communities.

Emslie, M., Cheal, A., Sweatman, H., & Delean, S. (2008). Recovery from disturbance of coral and reef fish communities on the Great Barrier Reef, Australia. *Marine Ecology Progress Series*, 371, 177–190.

Chapter 7 is a logical extension of the previous two chapters and asks what role habitat complexity plays in the recovery of reef fishes following disturbances. Its novelty lies in the examination of two groups of reefs spread over 1000 kilometres apart, that had similar benthic communities but differences in the complexity of the underlying substrate, which influence the structure of fish communities. It highlights that coral and fish communities of the GBR can recover and are resilient following disturbances and furthermore, that the interaction of coral recovery and the complexity of the underlying reef framework determine the functional structure of associated fish communities.

Objective 3. Examine the role of NTMRs in protecting reef fishes against extractive activities and natural disturbances

Chapter 8 – The utility of no-take marine reserves on the GBR.

Emslie, M. J., Logan, M., Williamson, D. H., Ayling, A. M., MacNeil, M. A., Ceccarelli, D., ... & Miller, I. R. (2015). Expectations and outcomes of reserve network performance following re-zoning of the Great Barrier Reef Marine Park. *Current Biology*, 25(8), 983-992.

This chapter centres on the role that networks of NTMRs can play in altering reef fish assemblage structure and whether they can confer any resilience in the face of large environmental disturbances like tropical cyclones. For the first time, this chapter demonstrated that while no-take marine reserves cannot directly protect coral reefs from regional scale disturbance, they can confer a degree of resilience to populations of exploited fishes. Furthermore it highlighted that the GBRMP was performing as would be expected in terms of protection of exploited fish stocks and biodiversity in a developed nation where fishing is not excessive and targets a narrow range of predatory fish species.

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Objective 1. Document the distribution and abundance of GBR reef fishes.

This objective serves to lay the foundations for the following sections, by describing the basic patterns of distribution and abundance of GBR reef fishes across ten degrees of latitude, and a gradient of environmental conditions from turbid coastal waters to clear, oceanic waters at the edge of the continental shelf. While the structure of GBR reef fish assemblages is known to vary among habitats within reefs, little is known about their distribution and abundance over larger scales, from tens to hundreds of kilometres. This section builds on the pioneering efforts of workers over the last four decades who discovered strong spatial structure in reef fish assemblages across the continental shelf in two latitudinal bands of the GBR. It will examine whether these patterns hold true across much of the GBR, and whether there appears to be underlying mechanisms that determine the distribution of fishes, both closely (butterflyfishes), and loosely (roving and farming herbivores) associated with hard coral. These chapters provide the spatial context necessary for determining how reef fish populations change through time, and in particular, how they are impacted by disturbances.

Chapter 2 – The distribution and abundance of butterflyfishes.

Emslie, M. J., Pratchett, M. S., Cheal, A. J., & Osborne, K. (2010). Great Barrier Reef butterflyfish community structure: the role of shelf position and benthic community type. *Coral Reefs*, 29(3), 705-715.

Great Barrier Reef butterflyfish community structure: the role of shelf position and benthic community type

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Chapter 3- Spatio-temporal patterns in territorial farming damselfishes.

Emslie, M. J., Logan, M., Ceccarelli, D. M., Cheal, A. J., Hoey, A. S., Miller, I. & Sweatman, H. P. A. (2012). Regional-scale variation in the distribution and abundance of farming damselfishes on Australia's Great Barrier Reef. *Marine Biology*, 159(6), 1293-1304.

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Regional-scale variation in the distribution and abundance of farming damselfishes on Australia’s Great Barrier Reef

**M. J. Emslie · M. Logan · D. M. Ceccarelli ·
A. J. Cheal · A. S. Hoey · I. Miller ·
H. P. A. Sweatman**

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Chapter 4 – The distribution and abundance of herbivorous fishes.

Cheal, A., Emslie, M., Miller, I., & Sweatman, H. (2012). The distribution of herbivorous fishes on the Great Barrier Reef. *Marine Biology*, 159(5), 1143-1154.

The distribution of herbivorous fishes on the Great Barrier Reef

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Objective 2. Quantify disturbance impacts on reef fishes.

Coral reefs exist in a highly dynamic, stochastic environment and are frequently impacted by disturbances. The frequency and severity of disturbances are projected to intensify in coming decades, furthering the widespread habitat degradation and loss of coral evident around the globe today. Fishes are a diverse and important component of coral reefs, fulfilling critical biological and ecological functions as well as providing socio-economic benefits to humans. To date our knowledge of reef fish responses to disturbances, while substantial, mostly stem from studies of one-off single events at restricted spatial scales. How reef fishes respond to different types of disturbances in varying parts of the GBR remains largely unknown. Here I document the response of reef fish assemblages to more than 50 individual disturbance events, and examine the role that habitat complexity play in modifying fish responses. Finally, I examine the recovery dynamics of reefs in the northern and southern GBR, separated by hundreds of kilometres.

Chapter 5 – Response of butterflyfishes to disturbance.

Emslie, M. J., Pratchett, M. S., & Cheal, A.J. (2011). Effects of different disturbance types on butterflyfish communities of Australia's Great Barrier Reef. *Coral Reefs*, 30(2), 461-471.

Effects of different disturbance types on butterflyfish communities of Australia's Great Barrier Reef

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Chapter 6 – The importance of habitat complexity to reef fishes.

Emslie, M. J., Cheal, A. J., Johns, & K. A. (2014). Retention of habitat complexity minimizes disassembly of reef fish communities following disturbance: a large-scale natural experiment. *PLoS One*, 9(8), e105384.



Retention of Habitat Complexity Minimizes Disassembly of Reef Fish Communities following Disturbance: A Large-Scale Natural Experiment

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Abstract

High biodiversity ecosystems are commonly associated with complex habitats. Coral reefs are highly diverse ecosystems, but are under increasing pressure from numerous stressors, many of which reduce live coral cover and habitat complexity with concomitant effects on other organisms such as reef fishes. While previous studies have highlighted the importance of habitat complexity in structuring reef fish communities, they employed gradient or meta-analyses which lacked a controlled experimental design over broad spatial scales to explicitly separate the influence of live coral cover from overall habitat complexity. Here a natural experiment using a long term (20 year), spatially extensive (~115,000 kms²) dataset from the Great Barrier Reef revealed the fundamental importance of overall habitat complexity for reef fishes. Reductions of both live coral cover and habitat complexity had substantial impacts on fish communities compared to relatively minor impacts after major reductions in coral cover but not habitat complexity. Where habitat complexity was substantially reduced, species abundances broadly declined and a far greater number of fish species were locally extirpated, including economically important fishes. This resulted in decreased species richness and a loss of diversity within functional groups. Our results suggest that the retention of habitat complexity following disturbances can ameliorate the impacts of coral declines on reef fishes, so preserving their capacity to perform important functional roles essential to reef resilience. These results add to a growing body of evidence about the importance of habitat complexity for reef fishes, and represent the first large-scale examination of this question on the Great Barrier Reef.

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Data Availability: The authors confirm that all data underlying the findings are fully available without restriction. Data are freely available from the AIMS Data Centre for all researchers upon request. Data are from the Long Term Monitoring Project whose authors may be contacted at m.emslie@aims.gov.au.

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Introduction

Habitat complexity is fundamentally important for the maintenance of high biodiversity across a range of ecosystems [1–5]. Coral reef ecosystems are among the most diverse on the planet with reefs with higher habitat complexity often housing more species than less complex reefs due to the greater variety of niches and shelter [6–8]. Habitat complexity on coral reefs has two major components; the underlying substrate rugosity and the skeletal structure provided by live and dead hard corals. Coral reefs are subject to many types of disturbance that can have negligible to severe impacts on coral cover and habitat complexity. For example, disturbances such as *Acanthaster planci* (crown-of-thorns starfish) outbreaks and coral bleaching cause coral mortality but leave skeletons intact [9–11], so habitat complexity remains largely unchanged in the short term. Subsequently, coral skeletons may erode due to natural processes causing longer term declines in habitat complexity. Conversely, waves from storms can obliterate entire coral colonies removing the habitat complexity previously afforded by their skeletons [11,12]. However, loss of coral structures due to storms or skeletal erosion will not necessarily

lead to low habitat complexity if substrate rugosity is high. Indeed, reefs with high substrate rugosity should maintain a greater diversity of organisms than reefs with low substrate rugosity once hard corals are removed, with the exception of those organisms fundamentally dependent on intact coral skeletons or living coral tissue for survival.

Disturbances on coral reefs can dramatically impact the diversity, abundance and community structure of reef fishes, because many fish species are closely associated with live corals and their structures [6–8,13–15]. To date, many studies have attributed changes in fish communities to loss of hard coral cover [9,13,16–20]. Numerous reef fishes rely on hard corals for food and/or shelter and many of these species decline in abundance following hard coral decline [9,16–22]. However, numerous fish species with seemingly limited reliance on hard corals *per se* (e.g. non-coralivorous butterflyfishes, large predators, some herbivorous fishes) have also declined in abundance following disturbances, and in these cases the role of habitat complexity has been implicated [8,9,11,13,20,23]. Declines in abundance and diversity of reef fishes following disturbances can be detrimental to ecosystem functioning and reef resilience due to a reduction in

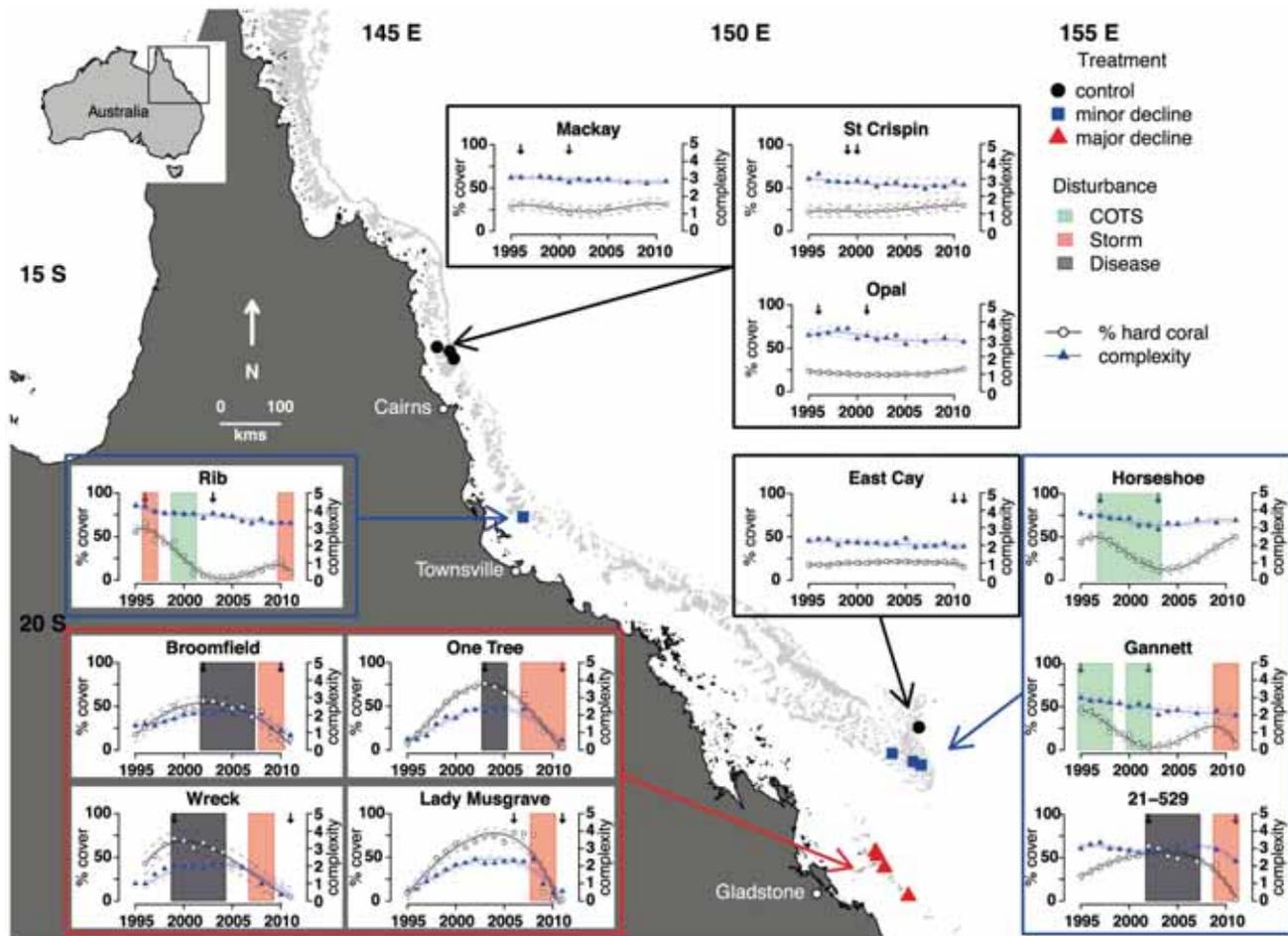


Figure 1. Location of the study reefs in each of the three treatments (Major Decline, Minor Decline and Control). Small panels display trends in hard coral cover and habitat complexity, along with shaded periods of time when disturbances (COTS=*Acanthaster planci* outbreaks, storms & coral disease) occurred. Points are raw data means, while solid lines indicate modelled average trends and dotted lines show 2 x standard errors from a linear mixed effects model fitted separately to hard coral cover and habitat complexity. Arrows mark the years of greatest and least hard coral cover.
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the capacity of reef fishes to perform trophic functions. For example, a reduction in the number and diversity of herbivorous fishes decreases their capacity to prevent proliferation of macroalgae that may limit recovery of corals following disturbances [24–32]. Clearly, declines in both live corals and habitat complexity must be important to reef fishes, and disentangling the relative influence of each will provide clues to the relative threat to reef fishes of disturbances which do and do not alter habitat complexity.

It has previously been demonstrated through experimentation [7,33,34] and longer term datasets [12–14,16–22] that reductions in habitat complexity and live coral cover adversely affect reef fish communities. Manipulative experiments have generally been conducted at restricted spatio-temporal scales, typically small (~10 s of m²) patch reefs surveyed over several months [7,33,34], and results are difficult to scale up to ecosystem levels. Projects conducted over larger spatio-temporal scales have generally employed gradient/regression type analyses (e.g. [13]) or meta-analyses (e.g. [11]), which are useful approaches for highlighting relationships among variables, changes in variables along a gradient and for integrating many disparate datasets, but lack rigorous experimental designs with which to definitively attribute

causation. Here we use data collected from reefs spread over 115,000 km² of the Great Barrier Reef (GBR), gathered over 20 years and employ a natural experiment to formally test how the loss of live coral versus loss of habitat complexity influences reef fish community structure, the diversity of reef fish families and functional groups, and the abundance of individual species.

Methods

Sampling

Data were gathered as part of the Long Term Monitoring Program at the Australian Institute of Marine Science (GBRMPA permit number G13/36390.1); in which fish and benthic communities have been surveyed on 47 reefs of the GBR since 1995. Large-scale disturbances, such as storms and *A. planci* outbreaks that have occurred over the last two decades on the GBR [22,35–36], facilitate opportunities to test macro-ecological hypotheses that due to their scope, require manipulations of a scale (100 s kilometres) that are logistically impossible for researchers to attempt using traditional experimental frameworks [37]. We were able to perform a natural experiment to investigate the effects of reductions in live coral cover versus habitat complexity on reef fish

communities, by retrospectively assigning replicate reefs into three treatments based on the effects of disturbances. Eight reefs were chosen based on comparable levels of live coral cover (>50%) and subsequent similar and very large relative declines in cover (~90%) due to disturbances. These reefs were separated into two equal treatments based on relative reductions in habitat complexity: 1. a major decline in habitat complexity from high/moderate to very low levels (hereafter “Major Decline”), and 2. a minor decline in habitat complexity from high to moderate levels (hereafter “Minor Decline”). A further four reefs had minimal declines in hard coral cover and no change in habitat complexity (hereafter “Control”; Fig. 1). Even though reefs in each treatment were unevenly distributed geographically (Fig. 1), 77% of fish species were common to all reefs in the study thus enabling valid comparisons of changes to fish communities. Furthermore, our analysis determined the magnitude of change in individual species abundance and community structure, plus the proportion of the community affected (irrespective of identity) before and after disturbances. Thus species identity *per se* was not important but rather the magnitude of changes and the proportion of the community affected.

Three sites of five permanently marked 50 m transects were situated in comparable reef slope habitats (n = 15 transects per reef) and were surveyed on SCUBA annually from 1995 until 2006 and then biennially thereafter. From 1995 until 2005, the benthic community was described using a 30-cm video swathe along the transects. Forty frames from each video transect were sampled and the benthic organisms beneath five points projected on to each frame in a quincunx pattern were identified to the finest taxonomic resolution possible, yielding 200 samples per transect. After 2006, a digital still image was taken every metre along each transect, and forty images were selected and analysed as before [38]. These data were then converted to percent cover of total hard coral for use in univariate analyses. For multivariate analyses, data were converted to percent cover of finer taxonomic groupings that included different growth forms of the most abundant coral family Acroporidae and other hard corals (including all other non-Acroporidae hard coral families), fire coral (genus *Millepora*), soft corals, coralline, turf and macro-algae, rubble, dead coral, sand, abiotic, sponges and other (rare benthic organisms of very low abundance e.g., ascidians, anemones). Fish communities were surveyed concurrently on the same transects using underwater visual census. The abundance and number of species of fishes recorded during surveys were taken from a list of 215 mobile, diurnally active species (including the families Acanthuridae, Chaetodontidae, Labridae, Lethrinidae, Lutjanidae, Pomacentridae, Scaridae, Siganidae, Zanclidae and the commercially important *Plectropomus* spp., hereafter “coral trout”). While parrotfishes are now considered as a tribe Scarinae within the family Labridae, we use the term “Scaridae” to distinguish this group of fishes from other Labridae. We define “species richness” as the number of species recorded and use this term hereafter. Cryptic species such as gobies and blennies were not included. Two transect widths were used: 50×1 m belts for the Pomacentridae and 50×5 m belts for the remaining families [39]. Habitat complexity was independently estimated retrospectively by two observers using a scale of zero (least complex - minimal vertical relief, few holes, crevices and overhangs) to five (most complex - high vertical relief, many holes, crevices and overhangs) from 360° video panoramas taken at the start of each transect. This 0 to 5 scale correlates strongly with a range of other rugosity metrics and has been found to be a good predictor of reef fish diversity and abundance [40].

Analyses

To provide the clearest picture of absolute changes in fish communities under varying degrees of change in habitat complexity, we compared metrics of reef fish communities at times of greatest (hereafter “Before”) and least (hereafter “After”) percent coral cover (indicated by arrows in Fig 1). All analyses were conducted in R [41]. To visualise the changes in fish and benthic communities before and after disturbances, we performed a non-metric Multi-Dimensional Scaling (nMDS) based on the Bray-Curtis similarity co-efficient using the iso-MDS package. To reduce the influence of highly abundant taxa, benthic cover data were row centred and square-root transformed. Similarly, to visualise changes to the whole community rather than a few highly abundant species, fish abundances were row centred and fourth root transformed prior to analysis. To examine the magnitude of change in fish and benthic communities before and after disturbances, we conducted a permutational multivariate analysis of variance using distance matrices and assessed the sums of squares for each Treatment and used the ADONIS function from the VEGAN package in R [41]. As the Treatment by Time interaction was significant, we re-ran the analysis separately for each Treatment (Major Decline, Minor Decline, Control).

Changes in fish and benthic communities were further investigated using Bayesian hierarchical models [42], fitted separately for hard coral cover, habitat complexity, total fish species richness and the species richness of eight reef fish families surveyed (Acanthuridae, Chaetodontidae, Labridae, Lethrinidae, Lutjanidae, Pomacentridae, Scaridae, Siganidae), plus the commercially important coral trout (*Plectropomus* spp.). In order to assess the effects of loss of habitat complexity and live coral on functional roles performed by reef fishes, we examined changes to the species richness of broad functional groups including corallivorous and generalist butterflyfishes, herbivores, planktivores and predators. Models had the fixed factors of Time (Before or After) and Treatment (Major Decline, Minor Decline, Control), and random factors of reef, site and transect. Most variables were modelled against a gaussian distribution in the MCMCglmm package [43]; however some were modelled against negative binomial distributions (log link) to account for zero-inflation and over-dispersion inherent in ecological count data [44] (Table S1). Negative-binomial models were fitted through Just Another Gibbs Sampler (JAGS) via the R2JAGS package in R and used non-informative, flat gaussian priors and the posterior distributions were derived from three Markov chain Monte Carlo (MCMC) (see Table S1 for further model details including number of iterations, burn in and thinning). Model convergence and mixing of Markov chains was assessed visually from trace plots and autocorrelation of the chains was always less than 0.2. Inferences about temporal changes were based on 95% Bayesian Higher Posterior Density (HPD) intervals of cell means predicted from posterior distributions of model parameters. Specific post-hoc contrasts were examined including differences in Time (before and after disturbance) among Treatments and differences among Treatments.

We assessed changes in the abundance of individual reef fish species by plotting a comparable metric to account for differences in initial coral cover [45], calculated as the percent change in abundance from before to after disturbance;

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

Where A_b and A_a were mean values at before and after disturbance respectively. Fish species were only included in these analyses if their summed abundance was ≥ 10 per reef (= 15

transects) in one of the two years. Changes in individual species abundance were then averaged across the four reefs within each Treatment.

Results

Benthic and fish community structure changed from times of greatest to least coral cover, but the magnitude of change varied among habitat complexity treatments (Fig 2). On reefs with a major decline in complexity, there were substantial shifts in the structure of both fish communities (ADONIS Time: $F = 19.134$, d. f. = 1, $\text{Pr}(>F) = 0.001$) and benthic communities (ADONIS Time: $F = 85.902$, d. f. = 1, $\text{Pr}(>F) = 0.001$) (Fig 2). Similarly, a large shift occurred in the benthic communities on reefs with minor declines in habitat complexity, (ADONIS Time: $F = 32.429$, d. f. = 1, $\text{Pr}(>F) = 0.001$), but a much smaller shift was evident for the fish communities (ADONIS Time: $F = 2.1751$, d. f. = 1, $\text{Pr}(>F) = 0.059$) on these reefs compared to those in the Major Decline treatment (Fig 2). Very little change occurred in either the fish communities (ADONIS Time: $F = 0.3885$, d. f. = 1, $\text{Pr}(>F) = 0.909$) or benthic communities (ADONIS Time: $F = 1.0507$, d. f. = 1, $\text{Pr}(>F) = 0.304$) on Control reefs (Fig 2).

Hard coral cover declined in all treatments but the decline was negligible on Control reefs. Habitat complexity only declined substantially on Major Decline reefs; reductions were minimal on reefs in the Minor Decline treatment and were similar to changes at Control reefs (Fig 3). Reductions in fish total species richness and the species richness of the Chaetodontidae and Labridae occurred on reefs in both complexity decline treatments, though the loss was greatest on in the Major Decline reefs (Fig 3). Also, species richness of Acanthuridae, Lutjanidae, Pomacentridae, Scaridae and coral trout declined on reefs in the Major Decline treatment, but not on those in the Minor Decline or Control treatments (Fig 3). There were large declines of species richness of all functional groups of fishes on Major Decline reefs (Fig 3). However, the species richness of only two functional groups, corallivorous butterflyfishes and predators, declined on Minor Decline reefs and these reductions were substantially smaller than those on reefs in the Major Decline treatment. There was no substantial decline in species richness of any functional group on Control reefs (Fig. 3).

Changes in the abundance of individual species varied substantially among the three habitat complexity treatments (Fig 4), with major declines in habitat complexity impacting a greater number of species than minor declines. On Major Decline reefs, 75% of species declined in abundance, 56% of species lost half their abundance and 18% were locally extirpated (declined to zero) (Fig 4). In comparison, the abundance of less than half (48%) of the fish species declined on reefs in the Minor Decline treatment, 24% declined in abundance by half and only 3% of species were locally extirpated (Fig 4). Fish species on Control reefs were far less affected; 22% of species declined in abundance, with only 3% declining by half and no species being locally extirpated (Fig 4).

The major loss of habitat complexity also greatly reduced the capacity of reef fishes to perform their functional roles. Among the functionally important herbivorous fishes, fourteen species declined in abundance by 50% or more on reefs that underwent major declines in habitat complexity, compared to four species on reefs with a minor decline and only one species on Control reefs. Additionally, abundances of some commercially important fishery species such as coral trout, were reduced to zero on Major Decline reefs, but declined by less than 5% on Minor Decline reefs. In addition, obligate corallivores accounted for a large proportion of

the species that declined in abundance in the Minor Decline treatment, but accounted for a much smaller proportion of the substantially greater number of species that declined on reefs with major declines in complexity.

Discussion

Using long-term data at ecologically meaningful scales on the GBR, this study has demonstrated the fundamental importance of habitat complexity for the maintenance of diverse fish communities, which is critical for maintaining healthy ecosystem function. Among reefs which underwent large declines in live coral cover, it was only on those reefs where habitat complexity also declined markedly that reef fish communities underwent wholesale reductions in diversity, species abundances and functional capacity. Previously small scale manipulative experiments [7,33,34], gradient/regression type analyses [13,20], or meta-analyses [11] had proposed the importance of habitat complexity for reef fishes, but whether these results reflected a broad-scale truth had not been rigorously tested. Our large-scale, natural experiment was able to demonstrate the generality of habitat complexity as a fundamental driver of reef fish community structure on the GBR, supporting findings in other regions [11,13,20,46,47]. We showed that major loss of habitat complexity affected a broad array of reef fishes from all trophic/functional groups. Additionally, although major loss of hard coral but not habitat complexity caused declines in some fish species, mostly those intimately associated with hard corals, the role of corals was not as important if overall habitat complexity remained moderate to high. Such results suggest that reefs which undergo major reductions in overall habitat complexity following disturbances will support depauperate reef fish communities, with a reduced ability to perform critical functional roles that contribute to the resilience of coral reefs.

While decreases in abundance of coral dependent species following loss of live coral were expected irrespective of changes in habitat complexity [20,22], the sweeping reductions in abundance of most reef fish species following major reduction in habitat complexity was more surprising (but see [11,13]). Large predatory fishes, planktivorous damselfishes and various herbivores were included in these decreases despite most having no obvious dependence on corals, implying that these fishes are dependent on habitat complexity for their survival, most likely through the provision of shelter and food sources. Clearly, habitat complexity affords shelter not only through live corals, but also through dead coral skeletons and by caves, cracks and fissures in the substrate. Where fish abundance declined due to lack of shelter, it was uncertain whether this resulted from migration to more suitable habitat, either around the reef or into deeper water, or from increased mortality resulting from the lack of refugia from predation. Whatever the mechanism of these declines, such dramatic shifts in reef fish community structure have implications for the ecological functioning of coral reef communities.

The extirpation of numerous species of fishes following major declines in habitat complexity contributed to a major reduction in fish diversity, with species from a range of trophic affiliations lost. High fish diversity usually equates to increased functional diversity (the number of functional groups at a site) and functional redundancy (the number of species within a functional group), both key components of reef resilience [48–53]. Higher functional diversity should enhance the capacity of a reef to deal with disturbances while functional redundancy provides a form of ecological insurance for the maintenance of a functional role despite losses of some species due to disturbances. Thus it seems

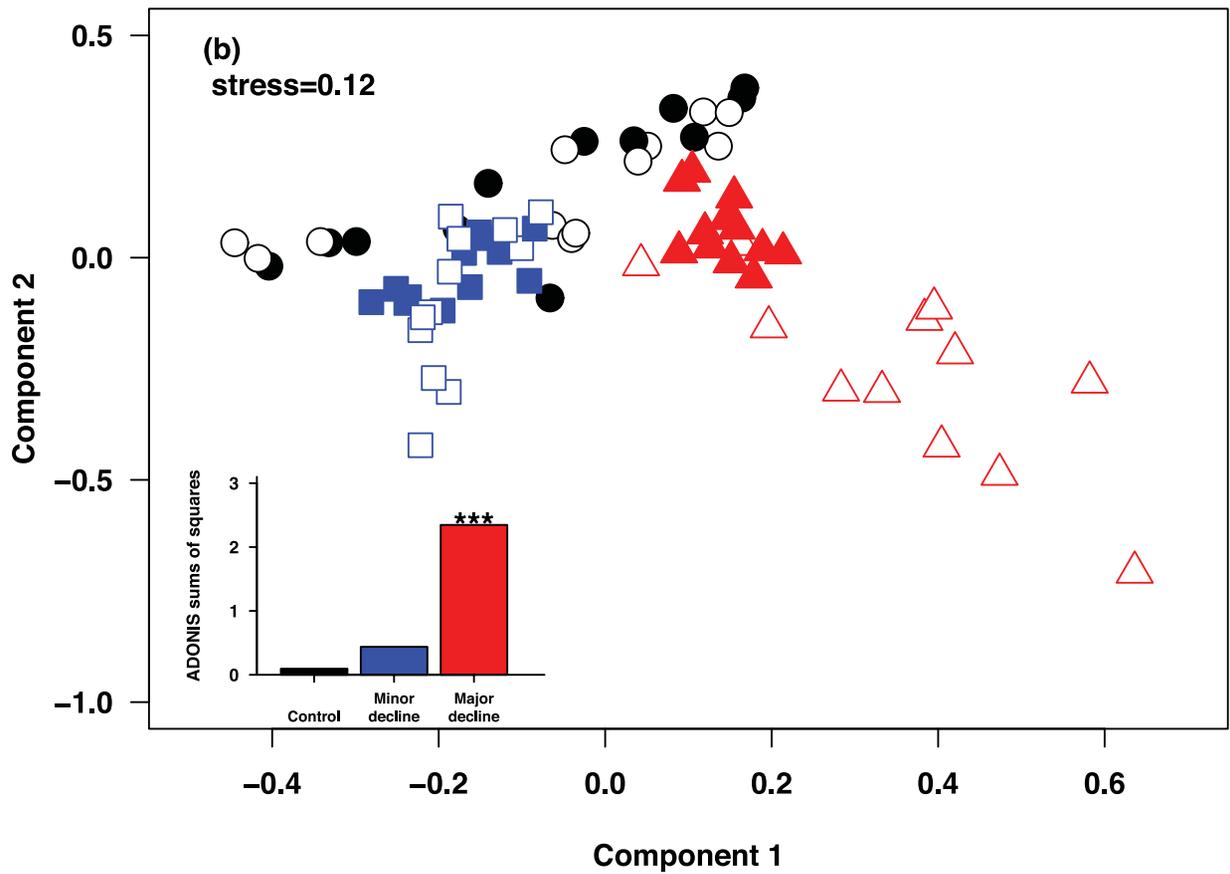
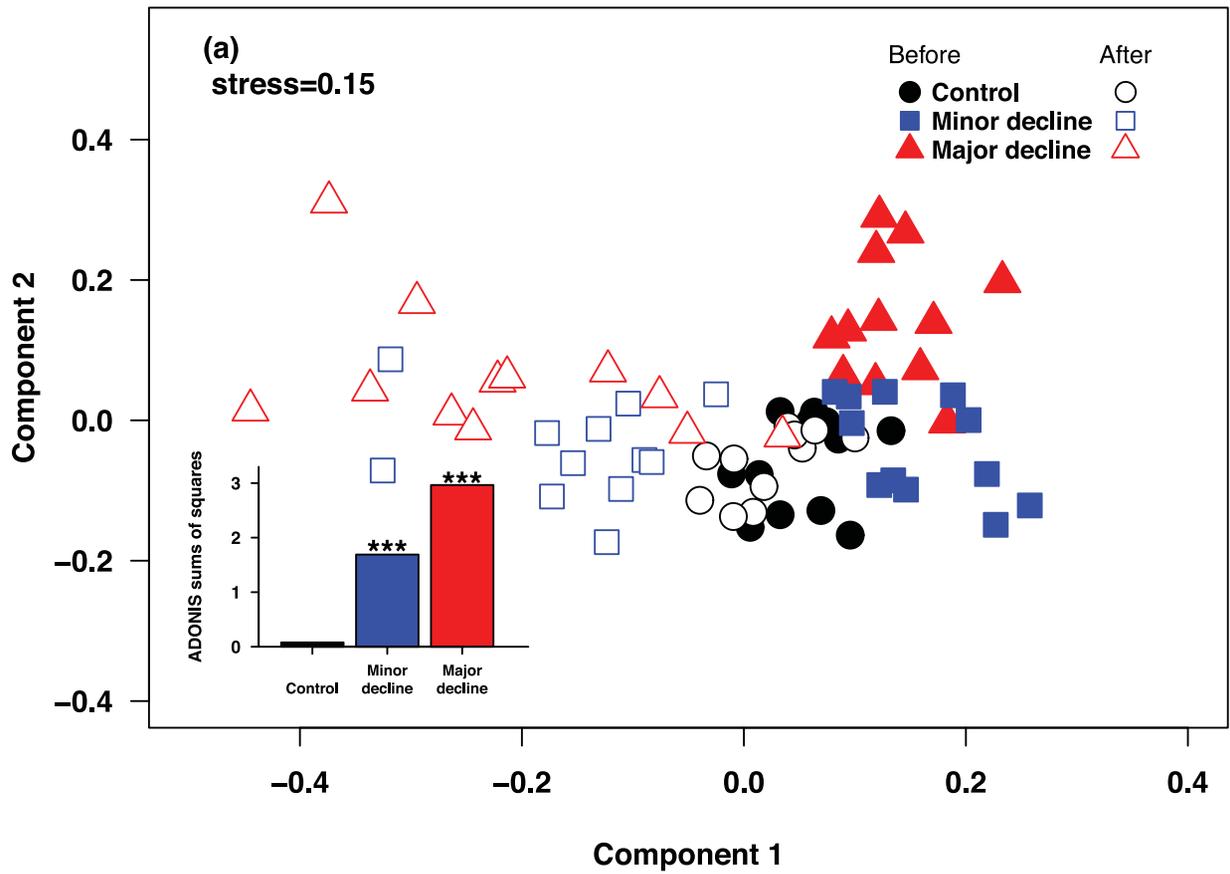


Figure 2. Multi-dimensional plot based on Bray-Curtis similarity coefficients of (a) square-root transformed percent benthic cover and (b) fourth-root transformed fish species abundances. Each panel presents changes to communities following disturbances for the three treatments (Major Decline, Minor Decline and Control). A full model ADONIS analysis revealed a significant interaction for both benthic communities (ADONIS Treatment*Time: $F = 14.293$, d. f. = 2, $Pr(>F) = 0.001$) and fish communities (ADONIS Treatment*Time: $F = 4.9225$, d. f. = 2, $Pr(>F) = 0.001$). Changes from times of greatest to least coral cover were further examined by separate ADONIS for each individual Treatment (Major Decline, Minor Decline and Control), and the small inset bar graphs display the effect sizes (Sums of Squares) from these individual analyses. ***: $Pr(>F) < 0.001$ doi:10.1371/journal.pone.0105384.g002

highly likely that resilience will be diminished following major losses of habitat complexity. For example, the functional contribution of herbivorous fishes to reef resilience has been well established. Many species of herbivorous reef fishes have the capacity to prevent algal overgrowth and aid coral recovery

through their grazing activities, thereby preventing undesirable shifts to a macro-algal dominated state [24,32,54]. In this study, the disappearance of fourteen species of herbivorous fishes on reefs where there were major declines of habitat complexity is likely to result in increased vulnerability to such phase shifts (but see [55]).

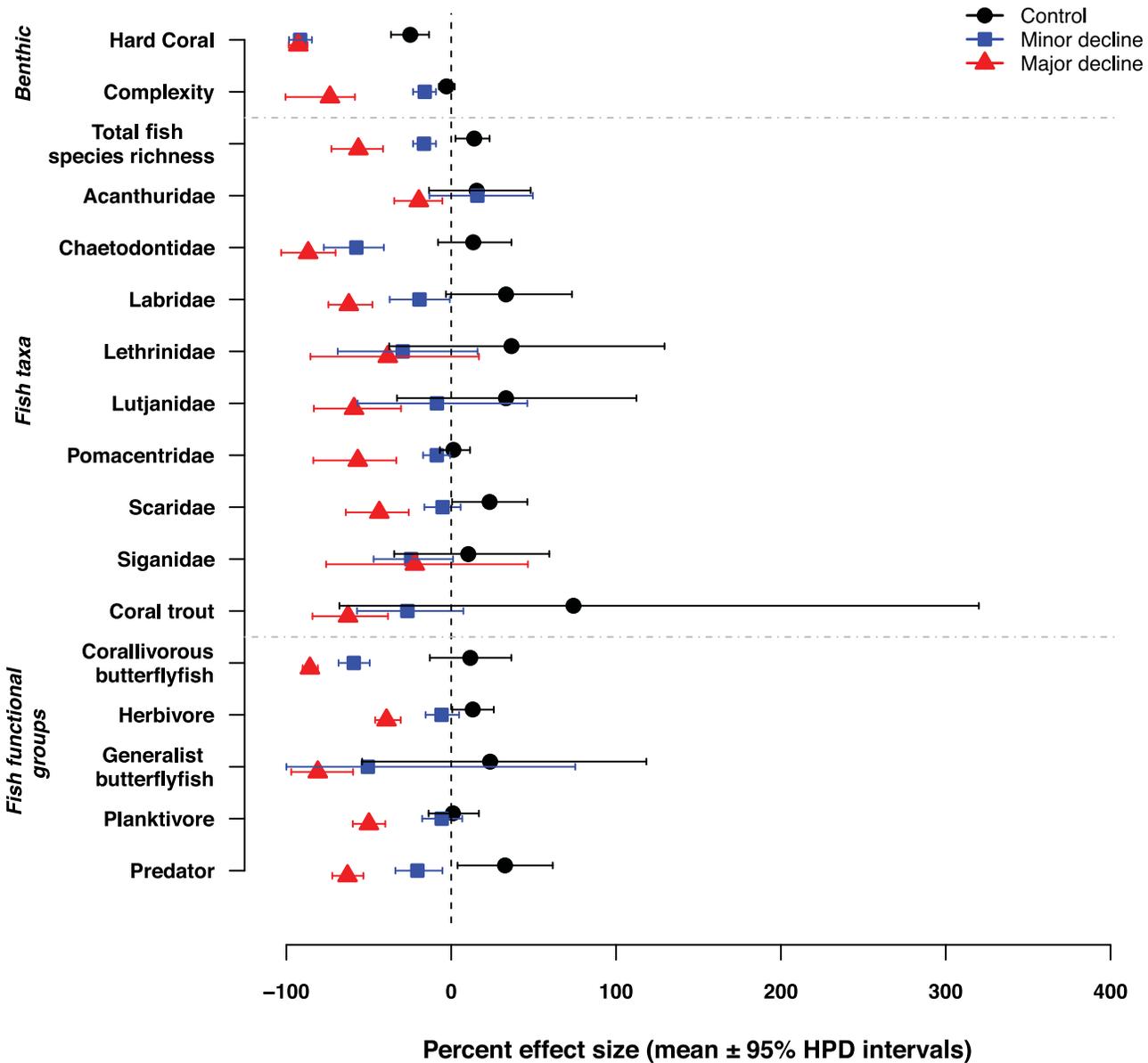


Figure 3. Differences in hard coral cover, habitat complexity, total species richness of fishes and species richness of eight fish families and five broad functional groups for each of the three treatments (Major Decline, Minor Decline and Control). Data are average effect sizes from generalized linear mixed effects model expressed as a per cent change from the time of greatest to least coral cover. Inferences about temporal changes were based on 95% Bayesian Highest Posterior Density (HPD) intervals of cell means predicted from posterior distributions of model parameters derived via Markov-chain Monte Carlo (MCMC) sampling. Effects are considered significant if the HPD intervals do not intersect zero. doi:10.1371/journal.pone.0105384.g003

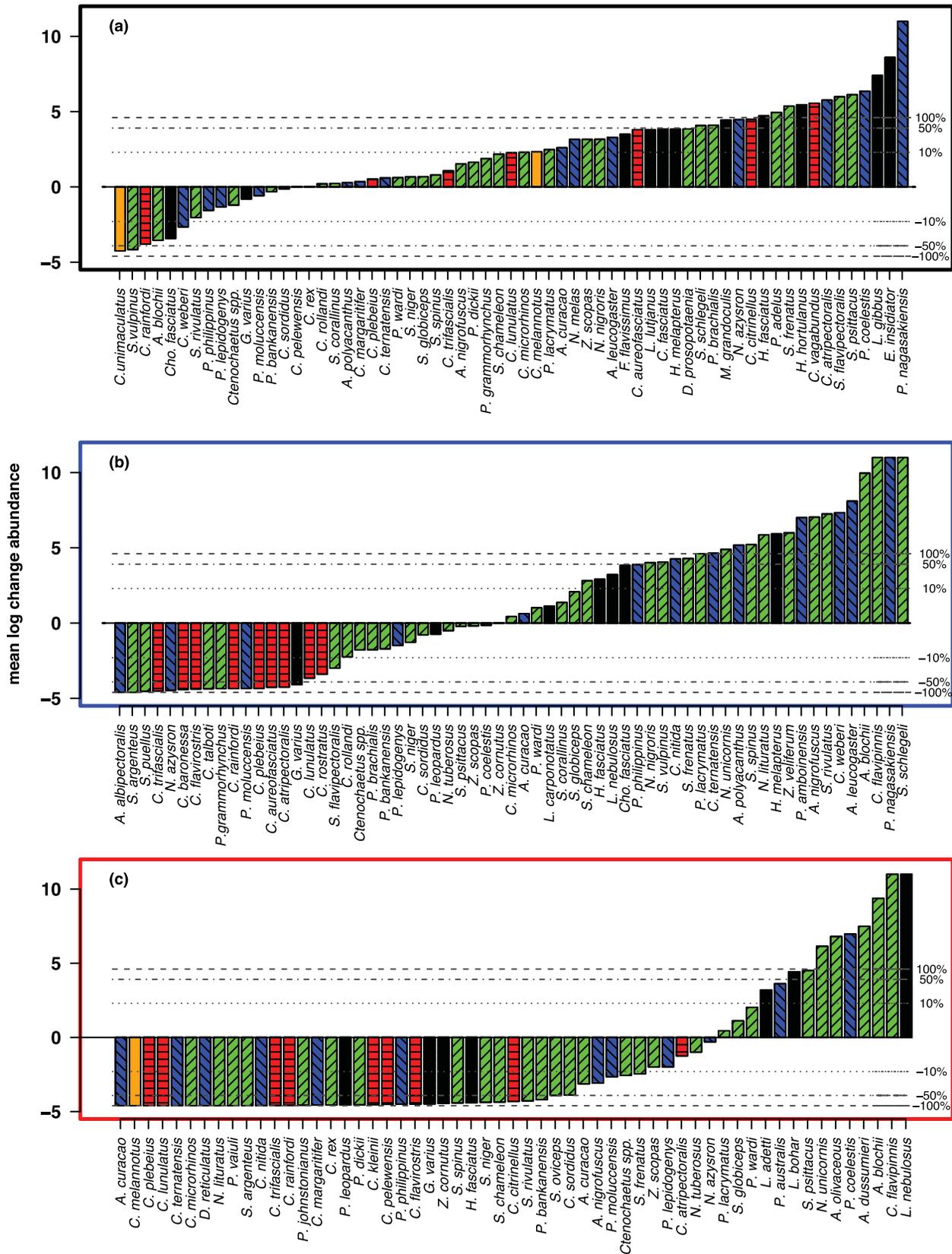


Figure 4. Average percentage change in abundance of individual fish species between times of greatest and least hard coral cover for (a) control reefs (b) reefs that underwent minor declines in complexity (c) reefs that underwent major decline in complexity. Fish species were only included in analyses if their reef wide abundance was ≥ 10 in one of the two years. Changes in individual species abundance at each reef were then averaged across the four reefs in each Treatment (Major Decline, Minor Decline and Control). Note that the y axis scale is in

natural log units and dotted horizontal lines represent 10, 50 and 100% changes in abundance and that error bars were not included to improve clarity. Coloured bars represent trophic affiliations: green with right diagonal hatching = herbivores, blue with left diagonal hatching = planktivores, red with horizontal hatching = corallivorous butterflyfishes, orange solid bars = generalist (non-coral feeding) butterflyfish, black solid bars = predators. A list of species abbreviations on the x-axis and their corresponding species names are found in Table S2. doi:10.1371/journal.pone.0105384.g004

While the role of herbivorous fishes in reef resilience has been well established, the contributions of many other reef fishes to reef resilience and healthy ecosystem functioning is less clear. However, what is certain is that the loss of a range of coral reef species performing many functional roles will likely have unknown consequences for ecosystem functioning. For example, reductions in the diversity and abundance of corallivorous fishes (e.g. butterflyfishes) will lower coral mortality [56], because corallivorous butterflyfishes can consume between 9 and 13% of the available tissue biomass of coral, representing 50 to 80% of the total annual productivity [57]. The loss of corallivorous fishes following disturbances will therefore remove substantial predation pressures from newly recruited corals and may ultimately aid recovery. Conversely, the loss of corallivorous fishes may deleteriously affect recovery as high diversity and abundance of corallivorous butterflyfishes has been demonstrated to slow or halt the transmission of coral disease [58]. Future research focused on the role played by corallivorous butterflyfishes in coral dynamics shortly following disturbances could aid our understanding of what impact, if any, the loss of corallivorous fishes plays in reef resilience and ecosystem functioning.

It appears that the short term loss following disturbances of adult fishes not directly dependent on live coral relates more closely to the lack of available shelter rather than to loss of living corals *per se*. Similarly, findings of diverse coral reef fish assemblages on artificial structures largely devoid of corals supports the idea that shelter provided by habitat complexity is fundamentally important to coral reef fish communities [59–61]. However, many reef fishes use live coral as a cue for settlement, including taxa that do not utilise live coral as adults [18]. Although fish communities may be relatively unaffected by coral mortality when habitat complexity is retained, shifts in community structure may lag behind disturbances if fish recruitment is suppressed by limited availability of living coral, while natural mortality of surviving fishes continues. Furthermore, the erosion of coral skeletons after some disturbances such as *A. planci* outbreaks, coral bleaching and coral disease slowly decreases habitat complexity, and may also produce lagged declines in fishes [20,62]. However, in this study adult fish populations were not depleted while habitat complexity remained, providing a buffer to fish population declines while coral is recovering in those cases. Thus in normal circumstances, lagged effects are likely to be balanced by coral recovery and new fish recruitment as long as complexity remains following disturbance. Nevertheless, lagged effects in reef fishes may potentially become more important in future decades, especially if predictions of increased coral bleaching and ocean acidification are correct [63]. In summary, while the retention of habitat complexity reduces the short term impact of disturbances on fish communities, the regeneration of live coral is essential for the maintenance of complex habitats and therefore, to the recovery and long term persistence of diverse reef fish communities.

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While previous studies have identified the link between habitat complexity and reef fishes, many of these studies have focused on subsets of the fish community (e.g. [20,21,64], but see [46]). We were able to tease apart the roles of reductions in coral cover versus habitat complexity on a large proportion of diurnally active and conspicuous reef fish communities over ecologically meaningful scales. To our knowledge, this is the first large-scale natural experiment conducted on the GBR to investigate the fundamental contribution of habitat complexity in driving reef fish community change. These results illustrated that reef fish communities are more adversely affected by disturbances which degrade both live coral cover and habitat complexity (i.e. storms), than those which reduce cover of live corals only (i.e. coral bleaching and outbreaks of *A. planci*). Such results should be of interest to reef managers, particularly given our finding that the major fishery target species, the coral trout (*Plectropomus* spp.) disappeared from sites of major complexity decline, with socio-economic ramifications for fishers utilising this resource. In addition, the impact of storms on reef fish communities at sites where coral skeletons account for most of the habitat complexity will be equally devastating irrespective of any zoning to protect target species from fishing. In effect, the benefits afforded by reserve zoning can be reversed almost instantaneously. Conversely, protection of fish communities at sites where complexity of the underlying substrate is high would better preserve important functional processes performed by reef fishes, encouraging rapid recovery in the event that coral cover is removed. Given the prospect of increases in storm intensity with climate change [65] which may lead to the architectural collapse of coral reefs [66], protecting sites with high underlying substrate complexity should be considered to alleviate vulnerability to disassembly of reef fish communities, reductions in the functional roles they perform and much diminished reef resilience.

Supporting Information

Table S1 Model specification for hard coral cover, complexity, total species richness and the species richness of eight families of reef fishes.

(DOCX)

Table S2 Full names for species codes and trophic affiliations used in Figure 4.

(DOCX)

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Author Contributions

Conceived and designed the experiments: MJE AJC KAJ. Performed the experiments: MJE AJC KAJ. Analyzed the data: MJE KAJ. Contributed to the writing of the manuscript: MJE AJC KAJ.

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Chapter 7 – Recovery of coral reef communities.

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Recovery from disturbance of coral and reef fish communities on the Great Barrier Reef, Australia

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ABSTRACT: Coral reefs are consistently and increasingly subject to acute disturbance events that often lead to a reduction in live coral cover with concomitant effects on the diversity and abundance of coral reef fishes. Here we examine changes in both hard coral and reef-fish assemblages over 15 yr following major losses of coral from exposed reefs in 2 widely separated sectors of the Great Barrier Reef (GBR), Australia. While the rate and extent of increase in coral cover (from <15 to >60%) was similar in the 2 sectors, differences in the rugosity of the underlying reef framework influenced the structure of fish communities. Soon after disturbance, when coral cover was very low and the limestone reef framework constituted most of the surface relief, the relatively featureless substrate on reefs of the southern sector supported fewer fish species than reefs of the northern sector, which had a more rugose substrate. At first, northern reefs also had a higher proportion of herbivorous fish species, presumably because the more complex reef surface provided shelter and allowed them to exploit the abundant algal turf. With increasing coral cover, coral colonies came to provide most of the surface relief in both sectors, and species richness and the trophic structure of the fish communities converged. Variation in the cover of branching corals explained significant variation in the fish communities in both sectors over time, reflecting the importance of this growth form to small coral-associated fishes. These results show that the recovery of the coral community and the complexity of underlying reef framework interact to determine the functional structure of associated fish communities despite differences in regional settings.

KEY WORDS: Coral disturbance · Coral recovery · Fish communities · Trophic · Great Barrier Reef · Storm damage

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INTRODUCTION

Disturbance plays a major role in structuring many ecological communities including grasslands (Collins et al. 1995) and forests (Connell 1978, Hiura 1995), and particularly in marine systems that are primarily limited by space, such as rocky shores (Sousa 1979, Underwood 1999) and coral reefs (Connell 1978, Hughes & Jackson 1985, Hughes 1989, Done 1992, Bythell et al. 2000). The short-term effects of disturbance can be wholesale destruction of major habitat components (Woodley et al. 1981, Halford et al. 2004, Gardner et al. 2005), resulting in reversion to earlier successional states (e.g. Colgan 1981). Re-colonization and growth may lead to recovery of the pre-disturbance community (resilience) or result in a phase shift to an alternate

and persistent community (Knowlton 1992). However, these phase shifts may not persist indefinitely, and there is evidence for phase shift reversals on some Caribbean reefs (Edmunds & Carpenter 2001, Idjadi et al. 2006, Mumby et al. 2007).

Disturbances on coral reefs range from local physical disturbances such as storm waves, which have differential effects on sections of the same reef and usually last a few days (Cheal et al. 2002, Halford et al. 2004, Adjeroud et al. 2005) to larger scale and longer term phenomena such as outbreaks of the crown-of-thorns starfish *Acanthaster planci* and coral bleaching, which affect numerous reefs within a sector and persist for weeks to years (Moran 1986, Sano et al. 1987, Berkelmans & Oliver 1999, Marshall & Baird 2000, Sano 2000, Wilkinson 2004, Graham et al. 2006). The major impact

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of large storms is to reduce cover of live hard corals through physical breakage of the coral skeletons. Depending on the severity of the storm, the resulting coral rubble may be washed away from the site, leaving a bare substrate (Halford et al. 2004). This contrasts with disturbances such as coral bleaching and outbreaks of *A. planci* that can also lead to high coral mortality but leave the dead coral skeletons intact until storms and bioerosion eventually reduce them to rubble (Sano et al. 1987, Sano 2000). In these cases coral skeletons may still provide shelter and refuges for reef fishes for some time after the disturbance. While the magnitude and spatial scale of damage vary with the type and duration of disturbance, a decrease in live coral cover is the usual result. The capacity of a reef to recover depends on the historical coral cover, the type and history of disturbances (multiple stressors can have additive effects), the extent of damage and demographic processes such as recruitment and growth (Colgan 1981, Hughes & Connell 1999).

Whilst disturbances may radically alter the benthic community, effects on associated reef-fish communities may not always be obvious. Natural disturbance events rarely cause mortality of coral reef fishes directly (Harmelin-Vivien 1994), but the associated habitat degradation may affect fish communities indirectly. Experimental reductions of living coral cover have been shown to lead to changes in fish community structure, although these were largely due to changes in abundance of a handful of coral-associated species, and most species were unaffected (Lewis 1997, 1998, Jones & Syms 1998, Syms 1998, Syms & Jones 2000). Changes in abundances of many species resulted from the reduction of structural complexity and loss of microhabitats and shelter as dead coral skeletons collapsed, rather than from the loss of living coral per se (Lewis 1997, 1998). Changes in the structure of fish communities following natural disturbances have been variable; short-term effects have ranged from minimal impact to wholesale changes in the community (Sano et al. 1987, Munday et al. 1997, Sano 2000, Adjeroud et al. 2002, Booth & Beretta 2002, Cheal et al. 2002, Halford et al. 2004, Bozec et al. 2005).

There have been many studies of short-term responses of fish communities to disturbance and a few longer term studies showing that reef-fish diversity and abundance decline with declining coral cover (Jones et al. 2004, Garpe et al. 2006, Graham et al. 2006, Wilson et al. 2006). However, very few studies have been sustained for long enough to record changes in reef fish assemblages as the coral recovered, and results to date are variable. In one case where reef fish communities were studied following habitat degradation and recovery, the fish community recovery closely tracked the recovery of the coral community on reefs of the south-

ern GBR (Halford et al. 2004). Seven years after the disturbance, the fish community closely resembled the pre-disturbance community in 2 metrics: species richness and abundance, suggesting that the community was resilient. These results contrast with a study in Moorea where hard coral cover and butterflyfish abundance recovered to pre-disturbance levels, but the pre- and post-disturbance assemblages of butterflyfishes included quite different species (Berumen & Pratchett 2006). This highlights the need to give careful consideration to the metrics used in attributing resilience or recovery of reef communities.

There is evidence to suggest that live coral cover is important for many fish species, such as obligate coral-livores (Sano et al. 1987, Sano 2000, Pratchett 2007) or those intimately associated in their early life history (Jones et al. 2004). However, there is also evidence that topographic complexity is important for the provision of shelter (see Sano 2000). Topographic complexity is defined here as the sum of complexity afforded by living and dead coral (structural complexity) and complexity of the underlying reef matrix (substrate complexity). It is often unclear whether structural or substrate complexity is more important in determining fish communities, and we avoid this confusion by simply referring to topographic complexity, which encompasses both.

The present study tracked annual changes in species richness and trophic structure of reef fish communities on reefs in 2 widely separated sectors of the GBR (>1200 km apart) after separate storms decimated the coral communities. The fronts of reefs in both sectors were dominated by tabulate *Acropora* spp. (Ninio & Meekan 2002). Trajectories of coral cover recovery and resultant benthic communities were very similar in the 2 sectors. This presented an opportunity to assess whether the trophic structure of fish communities, separated by >1000 km in different regional settings, that were unlikely to be linked by larval dispersal (James et al. 2002, Cowen et al. 2006) responded similarly to comparable patterns of coral recovery. Specifically, we wanted to determine: (1) the recovery trajectories of coral communities in each sector; (2) how the trophic structure of fish communities tracked changes in live coral cover in each sector and (3) the role of habitat complexity in the recovery of fish communities.

MATERIALS AND METHODS

Seven reefs were surveyed annually between 1993 and 2005 by the Long Term Monitoring Program (LTMP) at the Australian Institute of Marine Science (AIMS). Three reefs, 'Carter', 'No Name' and 'Yonge', were located in the northern GBR (~14° S) on the edge

of the continental shelf in the Cooktown/Lizard Island sector (hereafter CL) (Fig. 1). The other 4 reefs, 'Broomfield', 'Lady Musgrave', 'One Tree' and 'Wreck', were located in the southern GBR (~23° S) on the outer shelf of the Capricorn/Bunker sector (hereafter CB) (Fig. 1). CL reefs slope steeply (40 to 70°) from the crest to a narrow shelf at depths of ca. 30 m. The substrate of the slope contains many holes, gullies, overhangs and caves, which enhance topographic relief. The 4 CB reefs have shallow slopes (0 to 20°). Here the substrate consists of a hard, flat, featureless reef pavement with low relief. Occasional rubble-filled gullies run down the reef slope into deeper water. Halford et al. (2004) investigated resilience of reef fish communities on CB reefs by comparing pre- and post-disturbance communities using the first 6 yr of data from the LTMP. We build on that work by including an additional 6 yr of post-disturbance data for CB reefs and by comparing long-term patterns of recovery on CB reefs to those of another set of disturbed reefs (CL) 1200 km to the north. Furthermore, the present study focuses entirely on the response of fish communities to coral recovery.

The same methods were used to survey sites in a standard habitat, the reef slope on the northeast flanks, on each of the 7 reefs. Three sites were sampled on each reef, with 5 permanently marked 50 m transects running parallel to the reef crest at 6 to 9 m depth in each site. The benthic community was described from digital video recordings of a 30 cm swathe along each transect. Forty evenly-spaced frames from each of these video transects were projected, and the ben-

thic organisms beneath 5 points on each frame were identified to the highest possible taxonomic resolution yielding 200 points transect⁻¹. Since it was not always possible to identify benthic organisms to the species level, organisms were grouped by growth form for analysis. Initial analyses revealed that tabulate and branching *Acropora* spp. were the only groups to increase substantially during the present study; cover of all other hard coral life form groups varied little through time. Branching and tabulate *Acropora* spp. were also the most dominant, habitat-forming hard corals on all reefs. Thus subsequent analyses were focused on the percent cover of 5 broad benthic groups: (1) total hard coral, (2) tabulate *Acropora* spp., (3) branching *Acropora* spp., (4) coralline algae and (5) turf algae. Data were summed to the reef level and then averaged for each sector.

Topographic complexity was estimated retrospectively for all transects at each reef in each of 4 survey years (1993, 1997, 2000 and 2005) using 360° video panoramas of the reef slope recorded at the start of each transect. Topographic complexity was estimated using a scale between 0 (least complex) and 5 (most complex) (Polunin & Roberts 1993, Wilson et al. 2007) and then averaged over all transects on each reef in each year. This method can be done retrospectively and has been shown to correlate with other measures of complexity (Wilson et al. 2007). A single observer made all the estimates within a period of 1 wk.

Reef fishes from a list of 210 species (including species from Acanthuridae; Chaetodontidae; Labridae; Lethrinidae; Lutjanidae; Pomacentridae; Scaridae; Serranidae; Siganidae and Zanclidae that occur on the GBR) were counted on the fixed transects using underwater visual census. Two transect widths were used: 50 × 1 m belts for the Pomacentridae and 50 × 5 m belts for the remaining families. Because the surveys spanned the recruitment season, only fishes in the 1+ year class or older were recorded. For each species, 0+ fishes were identified by their size and by any distinctive juvenile coloration. Despite observers being very experienced, some subjective judgment was used in underwater estimations of cutoff lengths for 0+ fishes. Therefore cross-calibration among observers was performed regularly to ensure consistency.

Comparisons of fish community changes between the CB and CL

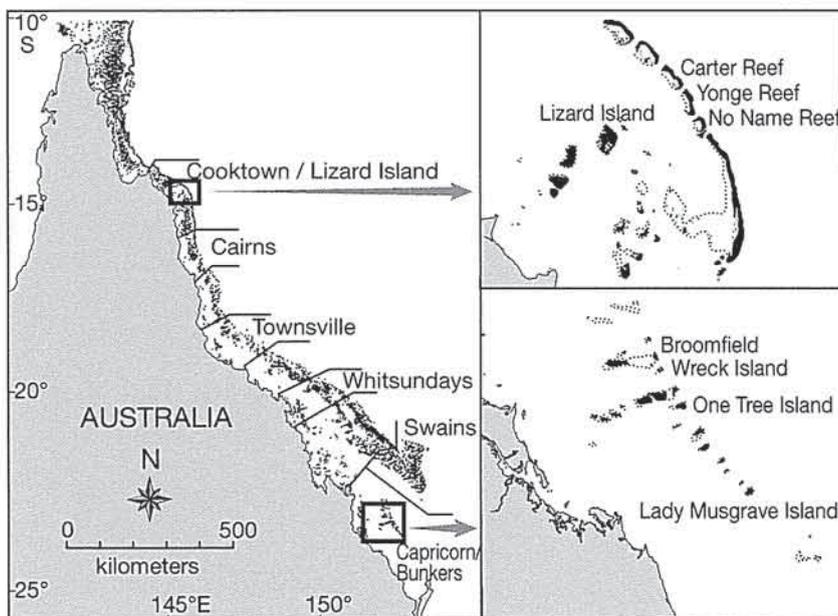


Fig. 1. Great Barrier Reef, Queensland, Australia, showing the locations of the reefs in the Cooktown/Lizard Island and Capricorn/Bunker sectors. Black: reefs; dotted lines: shoals

reefs were potentially difficult because the species pool for CL reefs was ~30% larger than for CB reefs (AIMS LTMP unpubl. data). To allow valid spatial comparisons, species were classified into 6 broad trophic groups based on published information (Sano et al. 1984, Bellwood & Choat 1990, Froese & Pauly 2006) and field observations. The trophic groups were: herbivores (included the detritus suckers e.g. *Ctenochaetus* spp., which also ingest algae, blue-green algae and diatoms), sessile benthic feeders (species that feed on sessile benthic invertebrates other than hard coral), corallivores (obligate hard coral feeders), benthic planktivores (fishes intimately associated with the benthos that supplement their benthic diet with plankton), planktivores (species that forage in the water column for plankton) and predators (piscivores and mobile nekton feeders) (Appendix 1). The numbers of individuals in these trophic groups were summed for each reef in each year, then converted to relative abundance (% of total community) and averaged over the reefs to estimate sector means. Ninety-five percent confidence intervals were also calculated.

Linear mixed effects models (Pinheiro & Bates 2000) were used to investigate spatial and temporal differences in reef fish abundances, trophic group abundance, species richness and benthic cover. Response variables were overall relative abundance and species richness of reef fishes (constrained by the species list). Topographic complexity of the reef slope and percent cover of the 5 benthic groups were included in the model. Mixed effects models accounted for dependencies associated with the repeated observations of measured variables on reefs over time. Fitted models included fixed effects for differences in cover between sectors, between years and the interaction between sector and year. Variation between reefs within sectors was fitted as a random effect. Where there were significant differences among years or between sectors, pair-wise multiple comparisons (Bonferroni-adjusted) were used to test specific *a posteriori* hypotheses about the temporal changes in the response. The models were fitted using the MIXED command in the SPSS (Norusis 2006).

Multivariate Regression Trees (MRT; De'ath 2002) were used to assess relationships between the multivariate fish assemblages (based on both species abundances and abundances of trophic groups) and measures of benthic cover over time. Estimates of percent cover of the following benthic life forms were included in this analysis: branching, tabulate, digitate, encrusting, submassive and bottlebrush *Acropora* spp. and branching, encrusting, foliose, massive and submassive corals belonging to other families, Fungiid corals, coralline, turf and macro algae, soft corals and sponges. Dissimilarity measures of the fish community

were partitioned according to changes in the percent cover of benthic groups. This approach highlights significant changes in the fish communities through time that were associated with changes in the benthic community. The groupings of years identified by MRT as having similar fish communities based on benthic cover were overlaid onto a principal components analysis (PCA) biplot using convex hulls. These biplots represented changes in fish community structure across reefs and years, and the hulls highlighted the importance of changes in benthic cover to temporal patterns. The data were transformed and standardized using the Hellinger metric (Rao 1995, Legendre & Gallagher 2001) prior to analysis. The Hellinger metric standardizes the data to a measure of relative abundance (i.e. row standardized), reducing the influence of very abundant species. The percent variation in fish community composition that was explained independently by variation in components of benthic cover was calculated using Euclidean-based Redundancy Analysis (van den Wollenberg 1977, Legendre & Gallagher 2001).

RESULTS

Trends in coral cover and reef slope complexity

In 1993, mean coral cover on the reefs in the CL sector was 14% (Fig. 2), having decreased from ~30% in 1985 to 1986 (LTMP unpubl. data). Despite the removal of most live hard coral and dead coral rubble by heavy wave action, overall topographic complexity on the slopes of these reefs was moderate at the start of surveys because of the rugosity of the underlying substrate (Fig. 3). Complexity increased as re-growth of coral colonies provided extra relief (Figs. 3 & 4). Mean

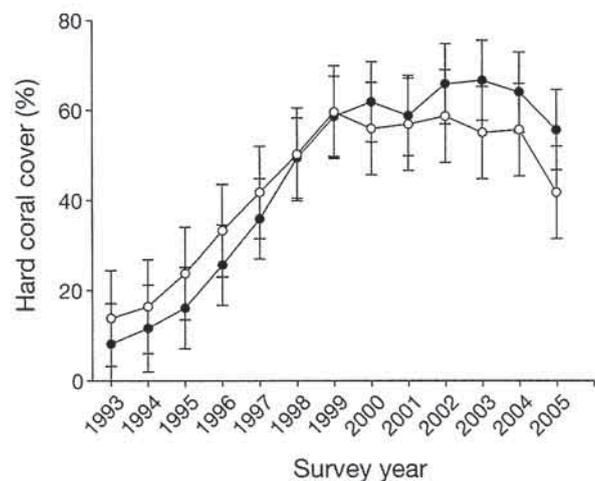


Fig. 2. Mean total hard coral cover 1993 to 2005 in the Cooktown/Lizard Island (○) and the Capricorn/Bunker (●) sectors. Error bars are 95% CIs

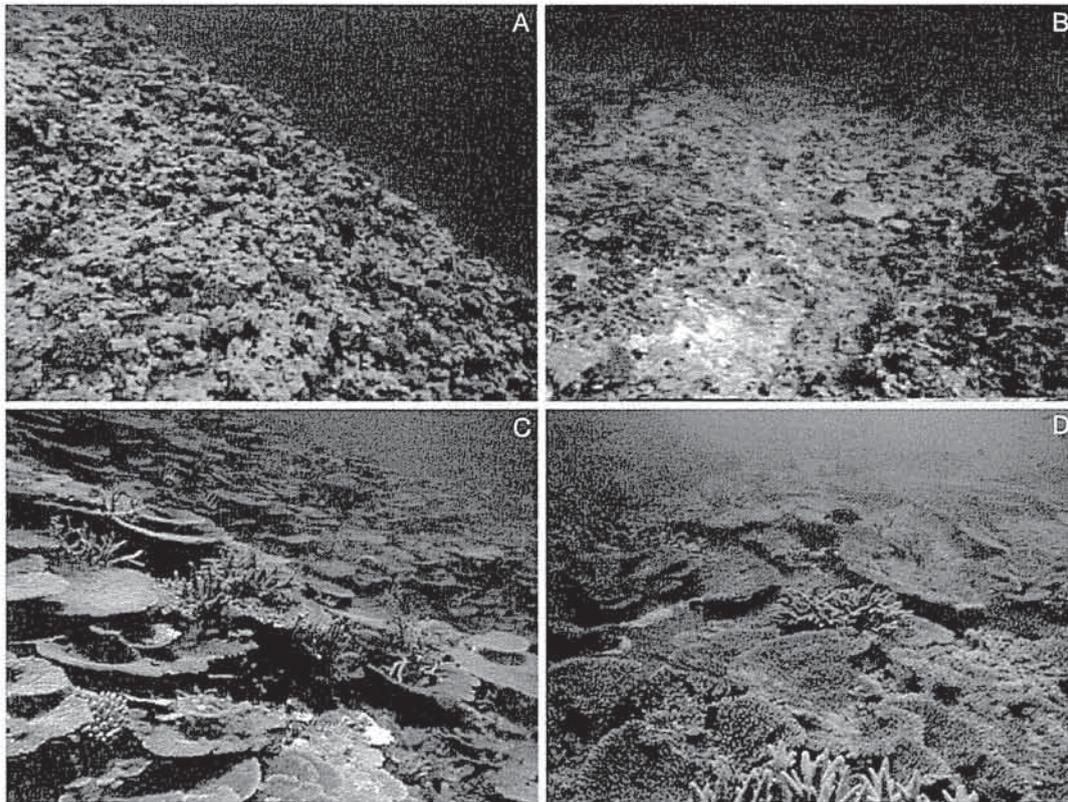


Fig. 3. Pre- and post-recovery photographs of reefs in each sector highlighting the difference in topographic complexity of the reef slope. (A,C) Cooktown/Lizard sector reef slope in (A) 1993 (topographic complexity score = 2) and (C) 2003 (topographic complexity score = 4). (B,D) Capricorn/Bunker sector reef slope in (B) 1993 (topographic complexity score = 1) and (D) 2003 (topographic complexity score = 4). For all panels, the photographer was roughly the same distance above the substrate (~1 to 2 m)

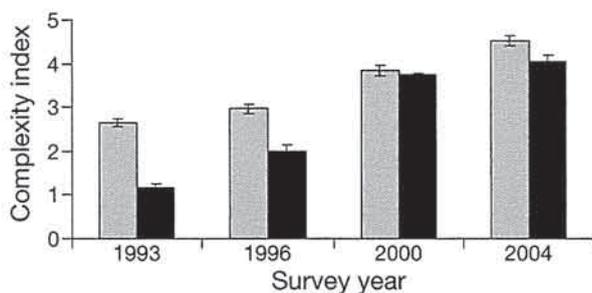


Fig. 4. Mean index of topographical complexity in the Cooktown/Lizard Island (grey) and the Capricorn/Bunkers (black) sectors. Error bars are 95% CIs

coral cover in the CB sector in 1993 was 8% (Fig. 2) after a dramatic decline from ~80% in the late 1980s (Halford et al. 2004). Heavy wave action removed the coral colonies from these reefs leaving flat, featureless terraces, devoid of rubble and with occasional shallow gullies (Fig. 3). Because of this, topographic complexity on reef slopes in the CB sector was very low in the initial surveys (Fig. 4), but was high by the end of the surveys (Fig. 4) because of the increase in relief provided

by re-growth of coral colonies. Importantly, topographic complexity in 1993 was significantly higher in the CL sector than CB (Fig. 4; $F_{1,20} = 78.050$, $p < 0.001$), though coral cover was similarly low in both sectors. By 2000, complexity in the CB sector had increased to levels similar to CL (Fig. 4; $F_{1,20} = 0.313$, $p = 0.582$). Although complexity was again higher in the CL sector by 2004 ($F_{1,20} = 7.921$, $p = 0.011$), the difference was small and unlikely to be ecologically significant (Fig. 4).

Recovery of the benthic communities

Hard coral cover recovered at a similar rate in both sectors (Table 1, Fig. 2), mainly due to the recruitment and growth of tabulate corals such as *Acropora hyacinthus* and *A. cytherea*, but the coral cover reached different levels in the 2 sectors. In 2003 and 2004, mean cover of tabulate *Acropora* spp. was 50 to 55% in the CB sector but only 25 to 30% in the CL (Fig. 5A). Cover of tabulate *Acropora* spp. (and total hard coral cover) was relatively stable 1999 to 2004.

Table 1. Fixed effects from linear mixed model analysis for each benthic variable. **Bold:** significant ($\alpha = 0.05$)

Variable	Source	df	F	p
Total hard coral	Sector	1, 6.5	0.2	0.656
	Visit	12, 31.7	25.3	<0.001
	Sector × visit	12, 31.7	2.6	0.016
Tabulate <i>Acropora</i> spp.	Sector	1, 6.1	6.7	0.041
	Visit	12, 35.4	18.9	<0.001
	Sector × visit	12, 35.3	2.3	0.027
Branching <i>Acropora</i> spp.	Sector	1, 5.3	0.1	0.725
	Visit	12, 38.0	38.1	<0.001
	Sector × visit	12, 38.9	3.7	0.001
Coralline algae	Sector	1, 9.0	23.1	0.001
	Visit	12, 30.1	19.3	<0.001
	Sector × visit	12, 29.8	5.6	<0.001
Turf algae	Sector	1, 6.9	11.2	0.013
	Visit	12, 48.9	22.9	<0.001
	Sector × visit	12, 48.2	4.0	<0.001

Cover of branching *Acropora* spp. increased in both sectors in a similar linear fashion (Fig. 5B) 1999 to 2004, but declined by ~2% in the CL sector in 2005 (Bonferroni multiple pair-wise comparison: mean difference = -11.5, $p < 0.001$, $df = 52.75$; Fig. 5B), resulting in a significant sector by visit interaction (Table 1). All other hard coral life form categories occurred in low abundance and varied little through time (Fig. 5C–F). For this reason they were excluded from further analysis.

Changes in cover of coralline and turf algae differed between the sectors (Table 1): cover of coralline algae in the CB sector showed some inter-annual variability but no overall trend, while the cover on reefs in the CL sector declined from 1993 to 1999 (Fig. 5G). Turf algae declined in both sectors from high levels in 1993 to lows in 1999 (Fig. 5H), but initial cover of turf algae was higher in the CB sector, and the decline was greater. Turf algal cover stabilized in both sectors after 1999 (Fig. 5H).

Percent cover of branching and of tabulate *Acropora* spp. were the best predictors of change in fish community structure, and cover of coralline and turf algae also explained some variation (Table 2). Fifteen other benthic cover variables were assessed but did not explain significant variation in fish community composition and are not presented here.

Response of the fish communities

The MTR analysis identified 4 types of fish communities associated with successive stages of coral recovery in the CB sector: (1) 1993 to 1995 coral cover was low (cover of branching *Acropora* spp. <2.60%, tabulate *Acropora* spp. <4.19%); (2) 1995 to 1998, (branch-

Table 2. Percent variation in fish community composition explained by benthic variables in the Cooktown-Lizard Island (CL) and Capricorn-Bunkers (CB) sectors estimated using redundancy analyses. (Total HC = total hard coral cover, ACB = branching *Acropora* spp., ACT = tabulate *Acropora* spp., CA = coralline algae, TA = turf algae)

	Variable	CL	CB
Species abundance	Total HC	14.5	22.2
	ACB	18.7	26.4
	ACT	10.1	18.1
	ACB + ACT	17.3	33.7
	CA	6.1	8.3
	TA	6.1	13.1
Trophic abundance	Total HC	38.8	52.6
	ACB	50.9	45.9
	ACT	24.9	43.3
	ACB + ACT	53.6	60.9
	CA	12.9	11.1
	TA	15.7	33.8

ing *Acropora* spp. <2.60% and tabulate *Acropora* spp. >4.19%); (3) 1998 to 2001, (branching *Acropora* spp. 2.60 to 5.13%) and (4) 2001 to 2005 (branching *Acropora* spp. >5.13%) (Fig. 6). When coral cover was very low, a single damselfish species *Pomacentrus coelestis* made up 95% of recorded individuals. The number of species began to increase between 1995 and 1998 as coral-associated species such as the butterflyfishes *Chaetodon plebius* and *Chaetodon trifascialis* and herbivores such as *Scarus globiceps* and *Chlorurus sordidus* appeared on the reefs (Fig. 6). By 2001 to 2005 these and other species characterized the community, while numbers of *P. coelestis* had declined. The number of species continued to increase, and species that live in close association with living corals such as the damselfishes *Plectroglyphidodon dickii* and *Pomacentrus moluccensis* increased in abundance (Fig. 6). From 2001 until 2005 species such as *Chromis atripectoralis* and *Dascyllus reticulatus* appeared on the reefs, 2 planktivores that mainly use live branching *Acropora* spp. for shelter. Changes in cover of tabulate and of branching *Acropora* spp. together accounted for 60% of the variation in fish trophic groups, while 53% of that variation was associated with change in total hard coral cover (Table 2).

In the CL sector, the MTR analysis identified a shift from one distinct fish community to another as the benthic community recovered: the first occurred from 1993 to 1997 when coral cover was low (<3.3% branching *Acropora* spp.) and the second from 1998 to 2005 when coral cover was higher (>3.3% branching *Acropora* spp.; Fig. 7). Initially the fish community included many species in low abundance, most notably the damselfishes *Pomacentrus coelestis* and *Stegastes fasciolatus*. The herbivores *Ctenochaetus* spp. and *Acan-*

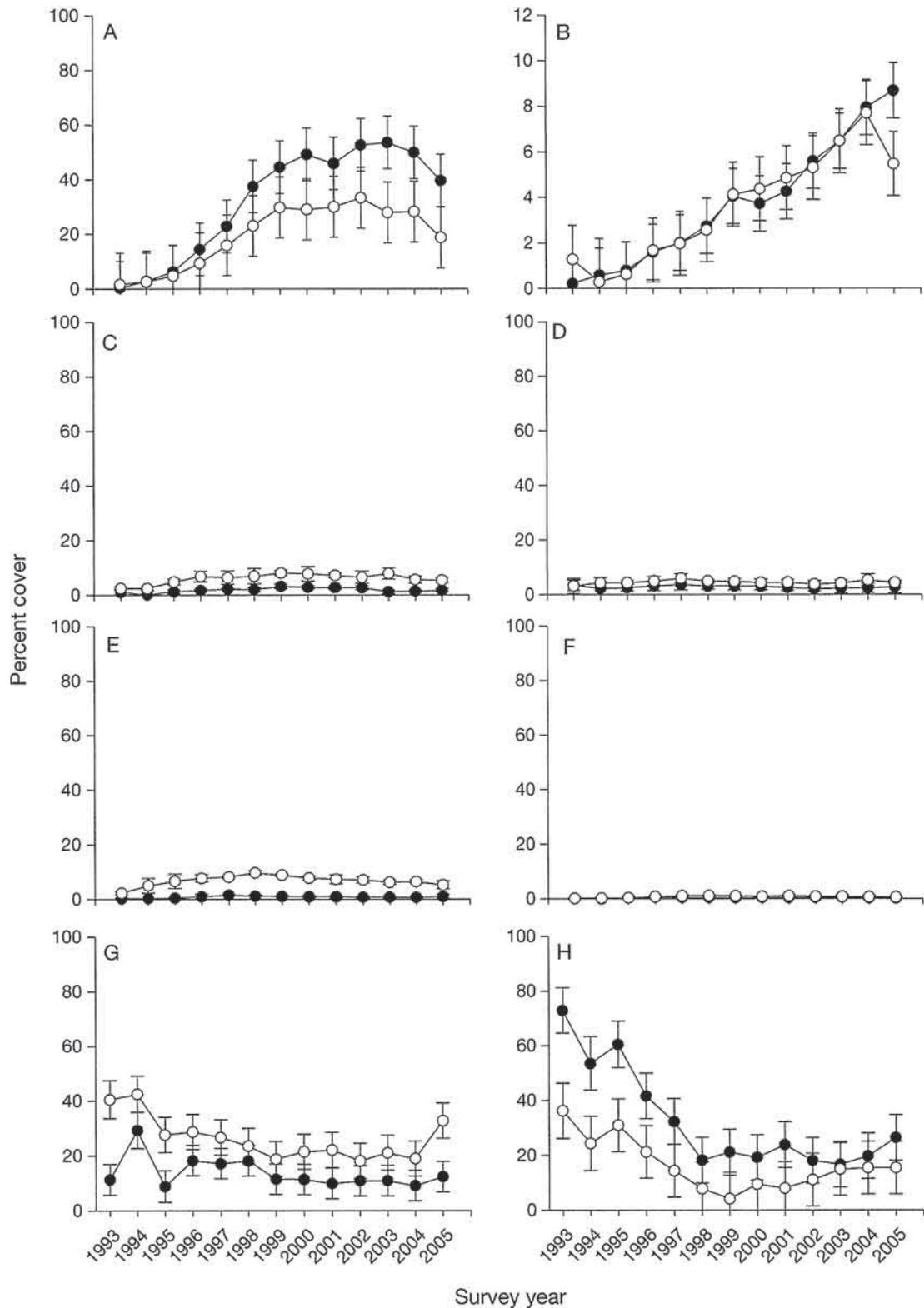


Fig. 5. Mean percent cover of benthic organisms on reefs in the Cooktown/Lizard Island (O) and Capricorn/Bunker (●) sectors 1993 to 2005. (A) tabulate *Acropora* spp.; (B) branching *Acropora* spp.; (C) other *Acropora* spp. (including bottlebrush, digitate, encrusting and submassive life forms); (D) encrusting non-*Acropora* spp.; (E) submassive non-*Acropora* spp.; (F) other non-*Acropora* spp. (including branching, foliose, massive lifeforms and fungi); (G) coralline algae and (H) turf algae. Error bars are 95% CIs

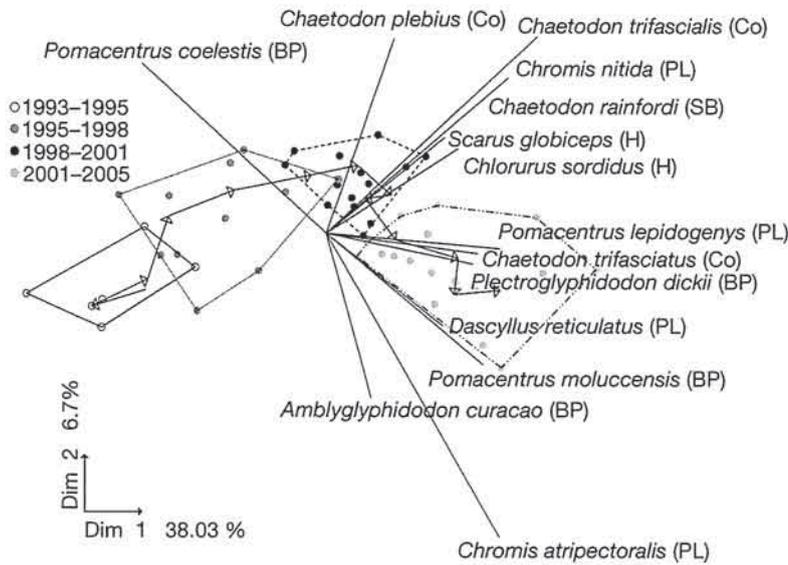


Fig. 6. Principal components biplot based on the relative abundance of fishes in the Capricorn/Bunkers sector over time showing the change in community composition as the coral recovered. Encircled points: 4 classes of fish communities on reefs at different stages of recovery of the benthic community as identified by a regression tree analysis. Each point represents a single reef in a single year. Vectors give the direction and relative magnitude of variability in abundance of the top 10% of species contributing to the variation in the multivariate assemblage. Letters in parentheses after species names: trophic group to which they belong: H = herbivores, Bp = benthic planktivores, Co = corallivores, PL = planktivores and SB = sessile benthic feeders. Arrows indicate the trajectory of the annual centroid 1993 to 2005, such that the first arrow represents the change from 1992 to 1993, the second arrow represents the change from 1993 to 1994, through to the final arrow representing change in the final year (2004 to 2005)

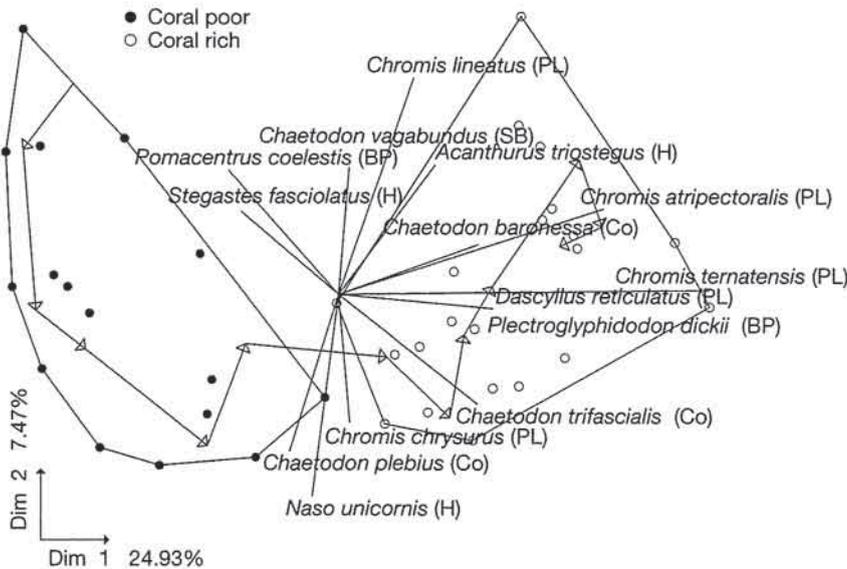


Fig. 7. Principal components biplot of the relative abundance of fishes on Cooktown/Lizard Island reefs over time showing shifts in community composition associated with the coral community succession (same organization and species abbreviations as in Fig. 6)

thurus nigrofuscus were also abundant during this period. As coral cover increased, many of these species declined in abundance, whilst the abundances of coral-associated species such as various *Chaetodon* spp. increased. By the time coral cover was high, there were numerous abundant damselfishes, most notably the planktivorous *Chromis* species such as *C. ternatensis* and *C. atripectoralis* and the coral-dwelling damselfish *Plectroglyphidodon dickii*. Changes in cover of branching *Acropora* spp. explained 51% of the variation in fish trophic groups (Table 2). Inclusion of the cover of tabulate *Acropora* spp. only explained a further 3% of the variation (Table 2).

The fish communities in each sector were quite different immediately following the initial disturbances, but their trophic structure became similar as hard coral recovered. At certain times there was significant variation between the sectors in both species richness (Visit × Sector interaction $F_{1,12} = 3.744$, $p = 0.001$) and total abundance (Visit × Sector interaction $F_{1,12} = 6.824$, $p < 0.001$). Most notably, species richness remained stable in the CL sector but increased markedly in the CB sector but increased markedly in the CB sector (Fig. 8). When coral cover was low, the fish communities in the CB sector were dominated by one abundant species, *Pomacentrus coelestis*, and total species richness was about half that of the CL (Fig. 8). By 2005, species richness in the CB sector had reached levels similar to those in the CL. Total abundance was more variable than species richness in both sectors. The temporal profiles of total fish abundance were remarkably similar in both sectors, and the significant interaction term was due mainly to disparities in a few years at the start and end of the study period (Fig. 8).

The trophic structure of fish communities in the 2 sectors differed initially after the disturbances, but was similar by the end of the study (Fig. 9). Four of the 6 trophic groups differed in both relative abundance and species richness at the start of the study, whilst only 2 of the trophic groups differed in these

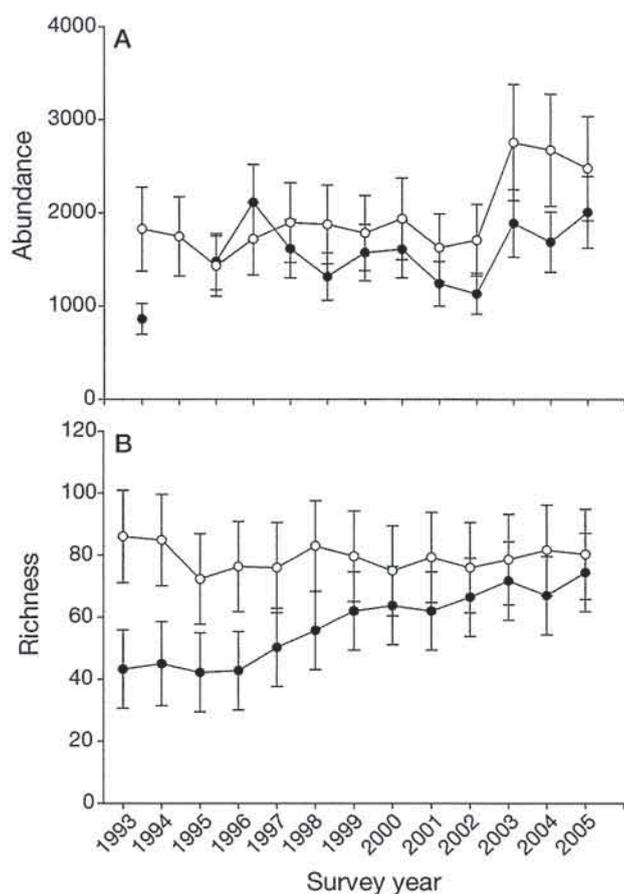


Fig. 8. Fish communities in the Cooktown/Lizard Island (○) and the Capricorn/Bunkers (●) sectors 1993 to 2005. (A) total abundance of fishes (up to 210 spp.), (B) constrained species richness (up to 210 spp.). Error bars are 95% CIs

metrics by the end of the study. There was a significant Sector \times Visit interaction term for all trophic groups except planktivores in relative abundances and all groups but planktivores and sessile benthic feeders in species richness (Table 3). The relative abundances of 4 of the 6 trophic groups differed between sectors in the first year of the study (benthic planktivores $p < 0.001$, herbivores $p < 0.001$, planktivores $p = 0.003$ and predators $p = 0.027$; Fig. 9). However, by the final year of the study the relative abundances of 3 of the 4 groups were similar in the 2 sectors (benthic planktivores $p = 0.344$, herbivores $p = 0.255$ and predators $p = 0.979$; Fig. 9). The relative abundance of planktivores remained significantly different throughout the study period (Table 3). The relative abundance of corallivores was initially similar ($p = 0.223$; Fig. 9), but diverged in 1998 ($p = 0.012$) and remained different for the duration of the study. In the first year of the study, species richness of corallivores ($p < 0.001$), herbivores ($p = 0.002$) and predators ($p = 0.001$) differed between the sectors, but attained similar richness by 2005

(corallivores, $p = 0.787$; herbivores, $p = 0.394$; predators, $p = 0.308$; Fig. 9). Benthic planktivores only substantially differed between the sectors in 2005 ($p < 0.001$; Fig. 9). Planktivores retained differences in species richness between sectors throughout the study (Table 3), and sessile benthic feeder richness did not differ between the sectors (Table 3).

DISCUSSION

Severe storm damage in 2 distant regions had quite different initial effects on the structure of fish communities on reefs where slopes had been dominated by tabulate *Acropora* spp. Shortly after the disturbance, species richness was much lower in the CB sector than the CL, and some trophic groups were underrepresented. Storms are unlikely to have caused declines in numbers of fishes and in species richness through direct mortality (Harmelin-Vivien 1994) or by a lack of potential recruits in the years following disturbance (Halford et al. 2004). Wave action removed most of the living coral colonies in both sectors, but a salient difference between reefs in the 2 locations was the rugosity of the underlying calcareous reef substrate (substrate complexity), which was flat on southern reefs but more complex and rugose in the northern sector. We suspect that the particularly low topographic complexity in the CB sector provided inadequate shelter for many species, leading to lower abundance and diversity (Almany 2004, Dominici-Arosemena & Wolff 2005, Garpe et al. 2006). Without cover and refuges, the risk of predation would have increased, and competition for available shelter would have intensified. The fate of these fishes is unknown: they may have died or have moved to other parts of the same reef or into deeper water where suitable shelter and habitat could still be found (e.g. Kaufman 1983, Walsh 1983). This did not apply in the CL sector because the higher substrate complexity of these reefs meant that they were able to provide shelter and habitat, despite the loss of living coral.

The fish communities became similar in the 2 sectors as the coral recovered, because the new coral colonies increased the topographic complexity in the CB sector and provided habitat for species that depend on living coral on reefs in both sectors. This increasing similarity of relative abundance of fishes in the 2 sectors as coral communities recovered was reflected in 4 of the 6 trophic groups (benthic planktivores, herbivores, predators and sessile benthic feeders). Species richness and relative abundance of planktivores remained much higher in the CL sector over time. This may reflect latitudinal and biogeographical differences in the species pools brought about by differences in the reef slope angle and oceanographic characteristics. The reefs in

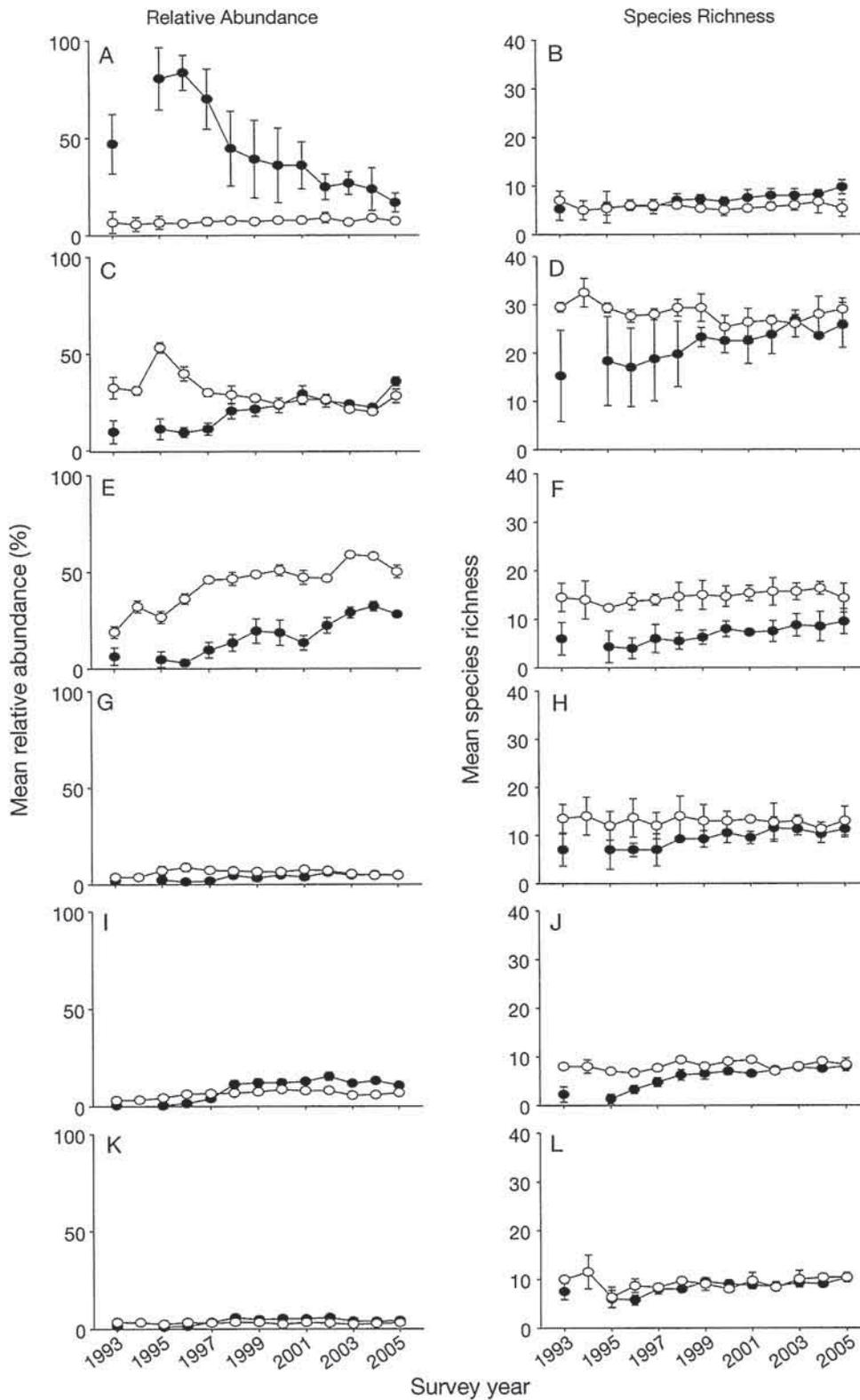


Fig. 9. Trophic structure of fish communities in the Cooktown/Lizard Island (○) and the Capricorn/Bunkers (●) sectors 1993 to 2005. Relative abundance (left column) and constrained species richness (right column) of 6 trophic groups of fishes. (A,B) benthic planktivores; (C,D) herbivores; (E,F) planktivores; (G,H) predators; (I,J) corallivores; and (K,L) sessile benthic feeders. Error bars are 95% CIs

Table 3. Fixed effects from linear mixed model analysis for each reef fish trophic group. **Bold:** significant ($\alpha = 0.05$)

Variable	Source	— Abundance —			— Species richness —		
		df	F	p	df	F	p
Benthic planktivores	Sector	1, 6	29.0	0.002	1, 5	3.6	0.114
	Visit	12, 48	6.1	<0.001	12, 27	1.9	0.084
	Sector × visit	12, 47	5.0	<0.001	12, 27	2.5	0.025
Corallivores	Sector	1, 6	16.0	0.009	1, 5	9.9	0.024
	Visit	12, 28	7.8	<0.001	12, 28	4.2	0.001
	Sector × visit	12, 28	4.4	0.001	12, 28	2.5	0.027
Herbivores	Sector	1, 5	6.6	0.051	1, 5	5.1	0.072
	Visit	12, 27	6.94	<0.001	12, 30	2.5	0.022
	Sector × visit	12, 28	8.6	<0.001	12, 31	2.3	0.034
Planktivores	Sector	1, 5	62.2	<0.001	1, 6	47.4	0.001
	Visit	12, 27	10.3	<0.001	12, 31	1.9	0.070
	Sector × visit	12, 28	1.6	0.165	12, 31	1.7	0.135
Predators	Sector	1, 5	8.9	0.031	1, 5	9.1	0.030
	Visit	12, 29	2.2	0.038	12, 23	2.7	0.022
	Sector × visit	12, 30	4.2	0.001	12, 22	2.7	0.021
Sessile benthic feeders	Sector	1, 10	8.8	0.014	1, 5	1.0	0.358
	Visit	12, 43	3.5	0.001	12, 26	2.6	0.019
	Sector × visit	12, 43	2.8	0.007	12, 27	2.1	0.056

the CL sector have very steep slopes and are prone to upwellings of nutrient-rich waters (Revelante et al. 1982, Furnas & Mitchell 1986). These conditions are ideal for the maintenance of a diverse and speciose planktivorous community, and indeed more planktivorous species occur on outer reefs in the northern GBR than in the south (AIMS LTMP unpubl. data). The divergence in relative abundance of corallivores between sectors was largely driven by a large increase in abundance of a single species, *Chaetodon trifascialis*, in the CB sector. This species is one of the most specialized feeders of all fishes, preying only on a few species of tabulate *Acropora* (Pratchett 2007). These corals occurred in greater abundance in the CB sector, which would account for the higher numbers of this species in particular and corallivores in general that were found in that sector.

The differing response of herbivorous fishes in the 2 sectors suggests a potential mechanism for the increasing similarity of the fish communities. The abundance and species richness of herbivorous fishes was low in the CB sector prior to 1996 despite the abundant turf algae, but coral cover and reef surface complexity were low, so the lack of shelter probably limited exploitation of this food resource. In contrast, numbers of herbivorous fishes were relatively high in the CL sector in the early years of the study when living coral cover was at its lowest, then declined as the algal cover declined. This suggests that the substrate complexity on the reef slopes in the CL sector provided sufficient shelter for fishes to access the abundant algae, a distinction that decreased in extent as the coral recovered.

Our analyses identified distinct fish communities associated with specific stages in the development of the coral community. The relative proportions of branching and tabulate *Acropora* spp. were identified as useful predictors of fish community structure. Other recent studies have also highlighted the importance of these coral groups to fish communities (Sano et al. 1987, Jones et al. 2004). These corals add a complex 3-dimensional structure in which fishes can shelter. Changes in cover of tabulate *Acropora* spp. explained more variation in the fish communities on reefs in the CB sector than in the CL. Tabulate *Acropora* spp. are fast-growing corals and contributed much of the early increase in topographic complexity in the CB sector. Since the reefs in the CL sector always retained some substrate complexity, this effect was less obvious. In contrast changes in

cover of branching *Acropora* spp. explained much of the variation in abundance of fishes by fish trophic group in both CB and CL sectors over the period of recovery. This is likely because a number of coral-associated species depend particularly on branching *Acropora* spp. for food or shelter (Jones et al. 2004).

The recent literature concerning the state of coral reefs is mostly based on short or intermittent time scales, limited by the time scale for academic funding (Hoegh-Guldberg 1999, Goreau et al. 2000, Bellwood et al. 2004, Jones et al. 2004, Garpe et al. 2006, Graham et al. 2006). Coral reefs are dynamic systems that are frequently affected by various forms of disturbance (Connell 1978, Hughes & Jackson 1985, Hughes 1989, Done 1992, Bythell et al. 2000, Kleypas & Eakin 2007), but corals grow slowly relative to the duration of research grants: even fast-growing corals such as tabulate *Acropora* spp. may take a decade or longer to recover. As such, many time series are not long enough to document if and how reefs recover. The benefit of the present study is its long time span, which shows these coral reefs as dynamic systems, undergoing both disturbance and recovery. However, both sectors in the present study are well offshore and remote from centres of population and coastal influences. Coral reefs in many parts of the tropics suffer a wider range of anthropogenic insults. Australia's Great Barrier Reef may represent an unusually favourable case in terms of reef recovery and resilience. The present study has shown that reefs that recover from disturbance to similar benthic communities maintain functionally similar fish communities, despite some variation due to their regional settings.

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Appendix 1. Long-term Monitoring Program species list and trophic group assignments

Trophic group	Species
Herbivores	<i>Acanthurus auranticavus</i> , <i>A. bariene</i> , <i>A. blochii</i> , <i>A. dussumieri</i> , <i>A. grammoptilus</i> , <i>A. nigroris</i> , <i>A. olivaceus</i> , <i>A. xanthopterus</i> , <i>A. lineatus</i> , <i>A. maculiceps</i> , <i>A. nigricans</i> , <i>A. nigrofuscus</i> , <i>A. nigri-cauda</i> , <i>A. pyroferus</i> , <i>A. triostegus</i> , <i>Calotomus carolinus</i> , <i>Cetoscarus bicolor</i> , <i>Chlorurus bleekeri</i> , <i>C. japonensis</i> , <i>C. microrhinos</i> , <i>C. sordidus</i> , <i>Ctenochaetus binotatus</i> , <i>C. striatus</i> , <i>Dischistodus melonotus</i> , <i>D. perspicillatus</i> , <i>D. prosopotaenia</i> , <i>D. pseudochrysopoecilus</i> , <i>Hemiglyphidodon plagiometapon</i> , <i>Hipposcarus longiceps</i> , <i>Naso lituratus</i> , <i>N. tuberosus</i> , <i>N. unicornis</i> , <i>Plectroglyphidodon lacrymatus</i> , <i>Pomacentrus adelus</i> , <i>P. chrysurus</i> , <i>P. grammorhynchus</i> , <i>P. tripunctatus</i> , <i>P. wardi</i> , <i>Siganus argenteus</i> , <i>S. corallinus</i> , <i>S. doliatus</i> , <i>S. fuscescens</i> , <i>S. javus</i> , <i>S. lineatus</i> , <i>S. punctatus</i> , <i>S. punctatissimus</i> , <i>S. spinus</i> , <i>S. vulpinus</i> , <i>Scarus altipinnis</i> , <i>S. chameleon</i> , <i>S. dimidiatus</i> , <i>S. flavipectoralis</i> , <i>S. forsteni</i> , <i>S. frenatus</i> , <i>S. ghobban</i> , <i>S. globiceps</i> , <i>S. longipinnis</i> , <i>S. niger</i> , <i>S. oviceps</i> , <i>S. psittacus</i> , <i>S. rivulatus</i> , <i>S. rubroviolaceus</i> , <i>S. schlegeli</i> , <i>S. spinus</i> , <i>Stegastes apicalis</i> , <i>S. fasciolatus</i> , <i>S. gascoynei</i> , <i>S. nigricans</i> , <i>Zebrasoma scopas</i> , <i>Z. veliferum</i>
Benthic planktivores	<i>Acanthochromis polyacanthus</i> , <i>Amblyglyphidodon curacao</i> , <i>A. leucogaster</i> , <i>Amphiprion akin-dynos</i> , <i>A. clarkii</i> , <i>A. melanopus</i> , <i>A. percula</i> , <i>A. perideraion</i> , <i>Chrysiptera rex</i> , <i>Neoglyphidodon nigroris</i> , <i>Plectroglyphidodon dickii</i> , <i>Pomacentrus amboinensis</i> , <i>P. australis</i> , <i>P. bankanensis</i> , <i>P. brachialis</i> , <i>P. coelestis</i> , <i>P. moluccensis</i> , <i>P. nagasakiensis</i> , <i>P. vaiuli</i> , <i>Premnas biaculeatus</i>
Planktivores	<i>Acanthurus albipectoralis</i> , <i>A. thompsoni</i> , <i>A. mata</i> , <i>Hemitaurichthys polylepis</i> , <i>Paracanthurus hepatus</i> , <i>Amblyglyphidodon aureus</i> , <i>Chromis acares</i> , <i>C. agilis</i> , <i>C. amboinensis</i> , <i>C. atripectoralis</i> , <i>C. atripes</i> , <i>C. chrysurus</i> , <i>C. flavomaculata</i> , <i>C. iomelas</i> , <i>C. lepidolepis</i> , <i>C. lineata</i> , <i>C. margaritifera</i> , <i>C. nitida</i> , <i>C. retrofasciata</i> , <i>C. ternatensis</i> , <i>C. vanderbilti</i> , <i>C. viridis</i> , <i>C. weberi</i> , <i>C. xanthura</i> , <i>Chrysiptera flavipinnis</i> , <i>C. rollandi</i> , <i>C. talboti</i> , <i>Dascyllus aruanus</i> , <i>D. reticulatus</i> , <i>D. trimaculatus</i> , <i>Neoglyphidodon polyacanthus</i> , <i>Neopomacentrus azyron</i> , <i>N. bankieri</i> , <i>N. cyanomos</i> , <i>Pomachromis richardsoni</i> , <i>Pomacentrus imitator</i> , <i>P. lepidogenys</i> , <i>P. philippinus</i>
Sessile benthic feeders	<i>Bolbometapon muricatum</i> , <i>Chaetodon auriga</i> , <i>C. citrinellus</i> , <i>C. ephippium</i> , <i>C. flavirostris</i> , <i>C. kleinii</i> , <i>C. lineolatus</i> , <i>C. lunula</i> , <i>C. melannotus</i> , <i>C. mertensii</i> , <i>C. rafflesii</i> , <i>C. speculum</i> , <i>C. ulietensis</i> , <i>C. unimaculatus</i> , <i>C. vagabundus</i> , <i>Chelmon rostratus</i> , <i>Forcipiger flavissimus</i> , <i>F. longirostris</i> , <i>Neoglyphidodon melas</i> , <i>Siganus puellus</i> , <i>Zanclus cornutus</i>
Corallivores	<i>Chaetodon aureofasciatus</i> , <i>C. baronessa</i> , <i>C. bennetti</i> , <i>C. meyeri</i> , <i>C. ornatissimus</i> , <i>C. pelewensis</i> , <i>C. plebius</i> , <i>C. puntatofasciatus</i> , <i>C. rainfordi</i> , <i>C. reticulatus</i> , <i>C. trifascialis</i> , <i>C. trifasciatus</i> , <i>Cheilop-rion labiatus</i> , <i>Plectroglyphidodon johnstonianus</i>
Predators	<i>Cheilinus fasciatus</i> , <i>C. undulatus</i> , <i>Choerodon fasciatus</i> , <i>Coris gaimard</i> , <i>Epibulus insidiator</i> , <i>Gomphosus varius</i> , <i>Halichoeres hortulanus</i> , <i>Hemigymnus fasciatus</i> , <i>H. melapterus</i> , <i>Lethrinus harak</i> , <i>L. atkinsoni</i> , <i>L. erythracanthus</i> , <i>L. laticaudis</i> , <i>L. lentjan</i> , <i>L. miniatus</i> , <i>L. nebulosus</i> , <i>L. obsoletus</i> , <i>L. olivaceus</i> , <i>L. ornatus</i> , <i>L. rubrioperculatus</i> , <i>L. semicinctus</i> , <i>L. xanthochilus</i> , <i>Lutjanus adetti</i> , <i>L. argentimaculatus</i> , <i>L. biguttatus</i> , <i>L. bohar</i> , <i>L. bouton</i> , <i>L. carponotatus</i> , <i>L. fulviflamma</i> , <i>L. fulvus</i> , <i>L. gibbus</i> , <i>L. kasmira</i> , <i>L. lemniscatus</i> , <i>L. lutjanus</i> , <i>L. monostigma</i> , <i>L. quinquelineatus</i> , <i>L. rivulatus</i> , <i>L. russelli</i> , <i>L. sebae</i> , <i>L. semicinctus</i> , <i>L. vitta</i> , <i>Macolor niger</i> , <i>Monotaxis grandoculis</i> , <i>Plectropomus areolatus</i> , <i>P. laevis</i> , <i>P. leopardus</i> , <i>P. maculatus</i> , <i>Variola louti</i>

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Objective 3. Examine the role of NTMRs in protecting reef fishes against extractive activities and natural disturbances.

There has been considerable discourse about the best way to conserve coral reefs and the implementation of networks of fully protected NTMRs is one of the most widely promoted tools. While there is plentiful evidence that NTMRs protect exploited stocks, evidence for broader ecological effects such as increased resilience and biodiversity protection remain equivocal. Evidence that NTMRs on the GBR are successfully achieving their goals became essential following the controversial re-zoning of the GBRMP in 2004, which increased the area of NTMRs within the GBRMP to ~33%.

Chapter 8 – The utility of no-take marine reserves on the GBR.

Emslie, M. J., Logan, M., Williamson, D. H., Ayling, A. M., MacNeil, M. A., Ceccarelli, D., ... & Miller, I. R. (2015). Expectations and outcomes of reserve network performance following re-zoning of the Great Barrier Reef Marine Park. *Current Biology*, 25(8), 983-992.

Current Biology

Expectations and Outcomes of Reserve Network Performance following Re-zoning of the Great Barrier Reef Marine Park

Highlights

- Expansion of a GBR reserve network led to substantial increases in coral trout stocks
- A large tropical cyclone impacted the reserve network, causing widespread damage
- Impacts on coral trout biomass were smaller inside NTMRs compared to fished reefs
- NTMRs may provide greater potential for replenishment after disturbances

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In Brief

No-take marine reserves (NTMRs) are widely advocated for conserving exploited fish stocks and biodiversity. Emslie et al. show that expanding NTMR networks had clear benefits for fishery target, but not non-target, species. A cyclone caused widespread degradation, but target species biomass was retained within NTMRs, with greater recovery potential.



Expectations and Outcomes of Reserve Network Performance following Re-zoning of the Great Barrier Reef Marine Park

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Chapter 9. General Discussion.

9.1 *Inherent variation in the spatial structure of reef fish assemblages*

While the local abundance of coral reef fishes is clearly subject to the vagaries of stochastic recruitment (Talbot et al. 1978; Sale et al. 1984; Doherty 1982), reef fish assemblages exhibit strong spatial structure at a range of spatial scales (Bouchon-Navaro & Harmelin-Vivien 1981; Russ 1984; Floeter et al. 2005; Emslie et al. 2010, 2012; Cheal et al. 2012). Most apparent, are marked and consistent differences in the relative abundance of species (both within and among families) among reefs with increasing distance from shore, commonly referred to as *cross-shelf* gradients (Anderson et al. 1981; Williams and Hatcher 1983; Russ 1984; Gust 2001; Munday 2000; Nemeth & Appeldoorn 2009). On Australia's GBR, cross-shelf variation in the abundance and composition of reef fishes was first established by Williams & Hatcher (1983) and Russ (1984) who compared fish assemblages among reefs at increasing distance from shore at approximately 19°S. The importance of cross-shelf gradients was then further demonstrated by extensive research comparing the composition and life-histories of herbivorous fishes at near-shore, mid-shelf and offshore reefs in the vicinity of Lizard Island (Gust 2001; Hoey & Bellwood 2008; Wismer et al. 2009). The body of work presented in this thesis has now greatly expanded our knowledge of the distribution and abundance of reef fishes on the GBR, explicitly showing that cross-shelf gradients are apparent and highly consistent along much of the length of the GBR, and seemingly consistent across a range of distinct taxa. Conspicuous cross-shelf variation in the abundance, diversity and composition of coral reef fish assemblages has now been documented for each of nine major families of fishes from 14°S to 24°S, including butterflyfishes (Chaetodontidae, Anderson et al. 1981; Emslie et al. 2010 - Chapter 2), algal farming damselfishes (Pomacentridae, Emslie et al. 2012 – Chapter 3), roving herbivores (Labridae, Acanthuridae, Siganidae, Cheal et al. 2012 – Chapter 4) and reef-associated predatory fishes (Labridae, Lethrinidae, Lutjanidae, Serranidae, Emslie et al. 2015 - Chapter 8; Emslie et al. In Review). In all cases, there was strong spatial structure evident in reef fish communities, both across the continental shelf but also with latitude. Importantly, spatial patterns in the abundance and composition of reef fishes were always apparent despite underlying temporal variability.

Cross-shelf patterns in the structure of reef fish assemblages have been variously attributed to pervasive gradients in habitat structure (Emslie et al. 2010 – Chapter 2; Emslie et al. 2012 – Chapter 3; Cheal et al. 2012 – Chapter 4), proximity to nursery habitats (e.g., coastal wetlands and mangroves), larval supply (Williams & Hatcher 1982; Russ 1984) or wave exposure (e.g., Fulton et al. 2005). By comparing among several distinct functional groups, the research presented here suggests that the mechanistic basis for cross-shelf patterns may vary with taxa. For butterflyfishes (Emslie et al. 2010 - Chapter 2) cross-shelf variation in abundance and composition appeared to be largely deterministic, dependent on the availability of appropriate habitat. This chapter described for the first time that four broad benthic habitat types representing differing levels of hard and soft coral composition supported distinct assemblages of butterflyfishes across much of the GBR (Emslie et al. 2010 – Chapter 2). Previous work has also highlighted that butterflyfish assemblages are determined by benthic composition, especially the abundance of important hard coral taxa, however these studies were restricted to single locations and a single time (Sano et al. 1984; Findley & Findley 1985; Pratchett et al. 2006; Pratchett & Berumen 2008; Cole et al. 2008). Chapter 2 also showed that despite differences in benthic community structure, obligate coral-feeding species always dominated butterflyfish assemblages, although the most abundant species changed among four broad habitat types (Emslie et al. 2010 – Chapter 2). For example, where table and branching coral dominated the benthic assemblage, *Chaetodon trifascialis* was numerically dominant and may reflect not only its highly specialised feeding preferences for a few species of *Acropora* corals (Pratchett 2007; Berumen & Pratchett 2008), but also its high aggressive behaviour towards and competitive dominance over other butterflyfish (Berumen & Pratchett 2006a; Blowes et al. 2013). In mixed and soft coral communities where table and branching *Acropora* were less abundant, more generalist species of butterflyfish tended to dominate the assemblage, no doubt reflecting their ability to feed on a wide variety of prey items. Perhaps the most interesting result to emerge from this study was that soft coral dominated benthic communities supported the greatest diversity of butterflyfishes. Not only that, but the dominant species in these soft coral habitats were also obligate corallivores, suggesting that the moderate levels of hard coral were enough to fulfil the dietary requirements of all GBR butterflyfishes. These novel findings are only made possible using datasets with such a broad spatio-temporal scope and for the first time

have enabled insights into broad-scale determinants structuring butterflyfish assemblages.

While the structure of butterflyfish assemblages is closely tied to the composition of hard and soft coral assemblages, other reef fishes, like farming damselfishes and roving herbivores, were much more dependent on non-coral benthic biota (Emslie et al. 2012 - Chapter 3; Cheal et al. 2012 - Chapter 4). Chapter 3 represented the first investigation of broad scale patterns of the distribution and abundance of farming damselfishes on the GBR, and there are few comparable studies globally. There were distinct assemblages of farming damselfishes across the continental shelf. Moreover, the abundance of three farmer trophic guilds differed with latitude and the combination of these cross-shelf and latitudinal differences resulted in strong spatial structure of farming damselfish assemblages among sub-regions. Inner-shelf assemblages were characterised by indeterminate farmers in the north while extensive farmers predominated on southern inshore reefs. In contrast, all three farmer guilds characterised outer-shelf reefs. These differences in farmer assemblage structure will likely contribute to differences in benthic algal composition, as farming damselfishes are known to alter the composition of ‘algal farms’ (Ceccarelli et al. 2001, 2005a, b). Additionally, their farming activities can influence coral recruit survivorship (Gochfeld 2010; Caesy et al. 2015), thus they likely represent an important group of fishes in the context of recovery from disturbance. Future research examining the extent to which farming damselfishes are beneficial or detrimental to coral recruits would be useful. In combination with the knowledge of the fundamental distribution and abundance of these fishes presented in this thesis, it may be possible to assess the influence of farming damselfishes on future coral recruitment and recovery in different areas of the GBR.

Chapter 4 revealed significant spatial structure in roving herbivore assemblages. The majority of parrotfishes had broad distributions occurring on more than three-quarters of the survey reefs, suggesting these fishes are habitat generalists that tolerate a wide variety of environmental conditions from turbid inshore to clear oceanic waters at the edge of the continental shelf. This is an important result as it suggests that they may be able to withstand future environmental degradation and still maintain the important ecological functions they perform. For example, their grazing activities have the

potential to play a central role in the prevention of shifts to macro-algal dominance following loss of hard coral cover (Mumby 2006; Hughes et al. 2007). Although parrotfishes are generally widespread, they tended to have lower abundance and diversity on inshore reefs. This has significant ramifications because these reefs are under the greatest threat of habitat degradation resulting from a combination of anthropogenic pressure and natural disturbances (McCook 1996, 1999; van Woesik et al. 1999; Thompson et al. 2014). If numbers of herbivorous fishes are insufficient following disturbances to ensure their capacity to remove algae matches algal propagation, then inshore coral reefs may undergo transitions to an ecosystem state dominated by less desirable algae (Hughes et al. 2007; Cheal et al. 2010). Evidence for such limited resilience was presented in an ancillary study of an inshore reef surveyed as part of the LTMP, where low numbers of herbivorous fishes appear to have contributed to the proliferation of extensive macro-algal beds in the wake of multiple disturbances (Cheal et al. 2010). There were also shifts in the relative abundance of herbivorous fishes moving across the continental shelf, resulting in the replacement of dominant species on inshore, mid-shelf and outer-shelf reefs. The mechanisms driving such changes are unclear, but certainly some species appear better able to flourish in differing environmental conditions (e.g., turbid inshore water) than others. Alternatively, species that thrive in inshore conditions have been competitively excluded from other mid- and outer-shelf habitats. While strong spatial structure existed across the continental shelf, there were few differences in parrotfishes across ten degrees of latitude. Similar results were gained by Floeter et al. (2005) and suggest that relative uniformity of tropical environments provides few drivers of assemblage change related to temperature. Taken together with the results from Chapter 2, this intimates that composition of any given reef fish assemblage is determined by distinctive aspects of the niche space and, importantly, the dimensions of the niche space are variable through space and time.

9.2 Effects of acute disturbances of reef-fish assemblages

The GBR, like coral reefs globally, is regularly and increasingly subject to major acute disturbance events, such as cyclones, outbreaks of the corallivorous starfish *A. planci*, coral bleaching and coral diseases (Osborne et al. 2011; De'ath et al. 2012). A recent analysis indicated that the GBR has lost half of its coral cover since the early 1980s

(De'ath et al. 2012), though such broad-scale analyses tend to smooth over the sub-regional mosaic of temporal fluctuations evident in coral communities (Sweatman et al. 2011; Osborne et al. 2011). The disturbance regime of the GBR is complex and varies at small spatial scales (e.g., among adjacent reefs or around the perimeters of individual reefs). Reefs within different sub-regions are in various stages of decline and recovery in response to the unique stochastic patchwork of perturbations found in each area. Since the LTMP intensive surveys commenced in the early 1990s, upwards of 50 acute disturbance events have impacted the 47 specific study reefs; many reefs had multiple concurrent impacts or a sequence of perturbations, but only a handful have escaped unscathed (Osborne et al. 2011). Among these disturbances were three widespread coral bleaching events in 1998, 2002 and 2016, plus two outbreaks of *A. planci* beginning in 1993 and 2008-09. Additionally, numerous tropical cyclones of various intensities and size have directly affected the GBR throughout the study, and since the mid-2000s, a series of severe tropical cyclones has greatly impacted the southern two-thirds of the GBR significantly reducing coral cover (Emslie et al. 2015 - Chapter 8; Cheal et al. In Press). Additionally, there are numerous examples of low levels of coral disease throughout the study. In light of this history and the predicted changes to future disturbance regimes, insights into how reef fishes are affected by disturbances are extremely valuable. This is particularly important for fishes that are ecologically or economically important, such as fishes (e.g., herbivores) that contribute to reef resilience and fisheries.

Most studies reporting the effects of disturbance on the GBR have only addressed the impacts of a single or experimental disturbance, and at generally very small spatial scales (usually at a reef or within-reef scale – e.g., Lewis 1997; Jones & Syms 1998; Syms & Jones 2000; Pratchett et al. 2004, 2006). In contrast, Emslie et al. (2011 - Chapter 5) explored spatial and temporal variation in coral loss at 47 reefs across the GBR, encompassing more than 50 different disturbances. Storms frequently had the greatest impact, although there was also considerable variation in the magnitude of impacts for individual events of a given disturbance type. Disturbances were broadly differentiated into those where coral mortality occurred but left the skeletons intact (“biological disturbances”, Emslie et al. 2011 - Chapter 5) versus those that simultaneously affected both the biological and physical habitat structure (“physical disturbance”, Emslie et al. 2011 - Chapter 5). Physical disturbances had a greater

propensity for a corresponding reduction of habitat complexity, although reductions in habitat complexity could also occur following biological disturbances, albeit after a lag of several years as dead coral skeletons gradually eroded. Notably, there was a marked distinction between the direct effects of disturbances that affected fishes with intimate ties to live coral cover, like corallivorous butterflyfishes, and the indirect impacts affecting fishes with looser affiliations to live coral cover. In the latter case, it is most likely that indirect losses arise from a loss of habitat and a reduction in complexity, which reduces the amount of settlement cues and shelter available for refuges from predation (see also Wilson et al. 2006; Pratchett et al. 2008).

The impacts of disturbances on coral reef fishes are complex and context dependent. The combination of type and severity of disturbance (usually measured as change in percent live coral cover), the disturbance history, sub-regional setting (e.g., northern inshore reef), and the composition of the benthic and fish communities, are all important factors. For example, large storm events, including severe tropical cyclone Hamish in 2008, impacted the *Acropora* dominated benthic assemblages of the southern offshore reefs in the Capricorn-Bunkers, completely removing live coral cover and the habitat complexity afforded by their skeletons, leaving only flat bare substrate in their wake (Emslie et al. 2014 - Chapter 6). These storms had a much greater impact on fish and coral assemblages than similar cyclonic events to a *Porites* dominated coral community residing on northern inshore reefs (Cheal et al. 2002) and highlight how the composition of the benthic assemblage can influence the outcome of disturbances such as cyclones and coral bleaching. Assemblages dominated by fragile growth forms are far more susceptible to storm damage and mortality from coral bleaching, than assemblages composed mainly of large robust *Porites* colonies (e.g., Marshall & Baird 2000; Madin 2006). Coral assemblages composed of fragile growth forms are also far more likely to undergo reductions in habitat complexity with concomitant reductions in the abundance and diversity of fish assemblages.

The use of monitoring data such as presented in Chapters 5 and 6 can explain the variable response of reef fishes that is often reported from disparate studies that report on the impacts of a one-off single disturbance at a single locality (e.g., Lewis 1997; Syms & Jones 1998). The use of standardised methodology across a vast area of the GBR has demonstrated that disturbance impacts on fish and benthic communities

are variable and not simply the result of differing methodologies or locations. Additionally, the variability reported in disturbance impacts on fish assemblages can be related to whether the study explored species-specific differences in responses to disturbance as opposed to summary metrics of the overall assemblage. For example, coarse summary metrics (e.g., total abundance, fish diversity or fish species richness) are often used, and in many cases reveal, little change following disturbance (Bellwood et al. 2006; Cheal et al. 2008; Wilson et al. 2009; Emslie et al. 2011; Ceccarelli et al. 2016). However, this can mask substantial turnover at finer taxonomic scale, as individual species exhibit differential responses to each disturbance event depending on their size, vulnerability and the scale and magnitude of the impact (Jones et al. 2004; Bellwood et al. 2006; Graham et al. 2006, 2007; Emslie et al. 2011, 2014; Ceccarelli et al. 2016). This causes in major shifts in community composition that are undetected by summary metrics of the overall assemblage, and may result in serious erosion of the capability of reef fishes to perform important ecological functions.

A major determinant of the susceptibility of reef fishes to disturbances is the closeness of their association with scleractinian corals (Pratchett et al. 2008). Many fishes are reliant on live hard corals for food, shelter and/or settlement (Jones et al. 2006; Coker et al. 2012, 2014). Butterflyfishes are well known for their close feeding associations with live hard coral and Emslie et al. (2011 – Chapter 5) highlighted their variable responses to six types of disturbance. Coarse summary measures such as total abundance and species richness were unchanged except for impacts of the greatest magnitude (storms and cyclones), which also diminished habitat complexity on those reefs. However, despite individual trophic groups and species having varying susceptibility to different impacts, obligate corallivores incurred the greatest impacts in all cases (Emslie et al. 2011 – Chapter 5). While such results are unsurprising given the level of feeding specialisation shown by obligate corallivores (Cole et al. 2008), it was interesting to note that butterflyfishes with looser reliance on hard coral for food (e.g., facultative corallivores) could also be impacted by habitat degradation. This implies that disturbance impacts on reef fishes go beyond simply a direct reduction of food resources and could potentially impact fishes with a range of affiliations with hard coral. For example, some facultative corallivores target motile benthic invertebrates for a large proportion of their diets (Pratchett & Berumen 2008), which have been found to be more abundant in coral rich areas (Wen et al. 2012), and loss of live coral may

indirectly reduce the amount of this prey type (Pratchett et al. 2015). Another indirect effect of loss of live corals is the reduction in important recruitment habitat for butterflyfishes. For example, *Chaetodon auriga* and *Chaetodon vagabundus* are both facultative corallivores that recruit into coral rich habitats and loss of these critical habitats decreases recruitment success (Pratchett et al. 2005). These impacts notwithstanding, there were also many instances where butterflyfishes appeared unaffected, and such responses likely also occur in other groups of fishes less closely tied to live coral and appeared particularly true of low impact biological disturbances.

While major declines in the abundance of fishes that are highly reliant on live corals are to be expected following extensive and widespread coral loss, it is important to understand how fishes with no apparent reliance on hard corals fare in the face of disturbances. Herbivorous fishes play an important part in the recovery dynamics of coral reefs post disturbance (Mumby 2006; Mumby et al. 2007; Hughes et al. 2007). Their grazing activities may have positive or negative effects on coral settlement and survivorship (Sammarco & Carleton 1981; Bellwood et al. 2004; Mumby et al. 2006), but, importantly, they limit the proliferation of competitively superior macro-algae (Hughes et al. 2007; Mumby et al. 2006). Small scale experiments have shown that algal farming damselfishes can influence coral recruitment (Casey 2015; Gochfeld 2010) and as their farms can occupy up to 99% of the benthos, they can have a major impact on coral recovery via the facilitation or suppression of coral recruitment. However, large-scale patterns in the distribution and abundance of algal farming damselfishes have rarely been considered. Emslie et al. (2012 - Chapter 3) revealed marked differences in the composition and function of algal farming damselfishes, mostly in relation to cross-shelf gradients. Moreover, declines in hard coral cover affected the abundance of farming species in ways that varied both spatially (among reefs and subregions) and with the type of disturbance (Emslie et al. 2012 – Chapter 3). For larger, roving herbivores (e.g., parrotfishes and rabbitfishes), there were intrinsic differences in abundance, diversity and composition (Cheal et al. 2010), which were largely unaffected by disturbances. In reviewing the responses of parrotfishes to various disturbances, Emslie & Pratchett (In Press) showed that most species are generally resilient to coral loss. Parrotfishes are, however, adversely affected when coral cover declines to very low levels (e.g., <10% Holbrook et al. 2008), especially where coral loss is compounded by declines in habitat complexity.

There is a growing appreciation of the importance of habitat complexity in structuring reef fish assemblages (Gratwick & Speight 2005; Graham et al. 2006, 2007; Wilson et al. 2006; Graham & Nash 2013). Importantly, the effects of extensive coral depletion may be greatly moderated if habitat complexity is retained, as suggested by Wilson et al. (2008) and explicitly demonstrated by Emslie et al. (2014 – Chapter 6). The abundance and diversity of reef fishes correlates positively with habitat complexity for several different reasons. First and foremost, increasing habitat complexity diversifies the niche space, allowing for a greater number species to co-exist in close association (Bruno & Bertness 2001; Willis et al. 2005; Graham & Nash 2013). Secondly, high habitat complexity mediates the effects of predation, not only through the provision of shelter for prey, but also by enhancing the effectiveness of ambush predators (Beukers & Jones 1998). Finally, highly complex habitats increase the number of spaces available for fishes to shelter at night. Changes to habitat complexity on reefs are generally driven by the loss of coral skeletons (topographic complexity) as alterations to substrate complexity are rare, except when phenomenal storm swells impact reefs (Fabricius et al. 2008). The co-linearity between loss of live coral and habitat complexity makes it difficult to tease apart the relative contribution each makes to changes in reef fish assemblages (Pratchett et al. 2008). The unique natural experiment presented in Emslie et al. (2014 - Chapter 6) went some way to disentangling these roles and positively identifying habitat complexity as fundamental to the maintenance of diverse reef fish assemblages. The results definitively show that on reefs that underwent high coral mortality, it was those with reduced habitat complexity where greatest changes in the structure reef fish assemblages were recorded, compared to reefs where only live coral was lost but habitat complexity remained largely unaffected. Where habitat complexity was substantially reduced, species richness declined and there was a loss of diversity within ecologically important functional groups of fishes, like herbivores. This implies that the ability of herbivores to crop algae will be diminished in such cases, and may lead to a proliferation of highly competitive macro-algae and a reduced chance of recovery. These results suggest that management efforts may be best served by targeting reefs of high substrate complexity as a priority for protection, as these reefs have the best chance of preserving important functional roles played by fishes, and also contributing to the replenishment of nearby degraded reefs through larval exchange.

Most studies (including Emslie et al. 2011- Chapter 5 & Emslie et al. 2014- Chapter 6) document the effects of disturbances on reef fishes by comparing the local abundance of individual species, families or functional groups before and after the specific disturbance (see also Lewis 1997; Munday 2004; Berumen & Pratchett 2006b; Graham et al. 2006; Wilson et al. 2009). While such studies do provide information on the immediate changes in reef fish abundance and diversity, they cannot provide information on the specific timing of declines, which is important to establishing the processes involved. For example, there may be long time lags in the effects of disturbances, either due to inherent lags in biological responses such as a reduction in suitable settlement habitats resulting in a decline in replenishment that does not equate to mortality rates (Jones et al. 2004; Pratchett et al. 2004; Graham et al. 2007) and/or highly protracted changes in habitat structure that serve to reduce the availability of shelter to adults (Graham et al. 2007). Lagged responses from fishes can be expected in circumstances where biological disturbances have caused coral mortality but left dead skeletons intact, which then erode through time. The 1998 bleaching event caused such a situation in the Seychelles (Graham et al. 2007). Lagged reductions in fish numbers were predicted because, although the abundance of adults remained stable or increased, numbers of juvenile fish, which declined in the years following the bleaching, were not replacing adults that were lost through natural mortality and fishing (Graham et al. 2007). Coral bleaching led to a gradual decay of structural complexity as skeletons eroded, and it is likely that juvenile fish numbers were not replenished due to the lack of suitable settlement cues and refuges afforded by live coral, which are required by many reef fishes (Coker et al. 2012). Furthermore, there was a correlation between juvenile fish diversity and abundance and structural complexity prior to the bleaching (Graham et al. 2007), but their numbers declined in the years following as complexity was eroded. A recent study supplemental to this thesis described lagged responses of reef fish communities to coral bleaching, coral disease, outbreaks of *A. planci* and storms (Mellin et al. 2016). This highlights that although results presented in Chapters 5 & 6 indicated that some fishes exhibited no measureable short term response to disturbances, impacts from these perturbations may become manifest only after several years. The use of long term data sets such as the LTMP is therefore, invaluable for detecting lagged response of reef fishes, but also for elucidating the probable consequences for ecosystem functioning and its implications for reef recovery from disturbance.

9.3 Recovery of reef fish assemblages

While there has been significant research showing that major disturbances that cause extensive coral depletion can have far-reaching effects on the abundance of coral reef fishes (reviewed by Pratchett et al. 2008, 2011, 2014), there has been relatively little research on the responses of fish assemblages in the aftermath of such disturbances. Importantly, there may be important feedbacks in recovery of fish assemblages and benthic habitats, whereby increases in herbivorous fishes may prevent the proliferation of macro-algae and provide suitable bare substrate that facilitates coral recruitment (e.g., Mumby 2006; Hughes et al. 2007; Cheal et al. 2010). The few previous studies that have documented responses of fishes in the aftermath of major disturbances (e.g., Halford et al. 2004; Berumen & Pratchett 2006b), have focused on mainly on strongly site-attached and coral-dependent fishes which may have limited influence on benthic recovery *per se*, but are fundamentally dependent on increases in coral cover. Similarly, Emslie et al. (2008 – Chapter 7) shows that recovery of coral-dependent butterflyfishes is fundamentally reliant upon and closely follows the recovery of live corals. For other less coral dependent species, retention of habitat complexity appears to be the key to minimising losses following disturbances and in instances where complexity is reduced, the recovery of complex coral life forms such as branching corals appears crucial to ensuring the recovery of reef fishes (Emslie et al. 2008 – Chapter 7).

9.4 Maximising resilience of coral reef environments and fishes

This thesis has demonstrated the fundamental role of disturbances in structuring coral reef assemblages. Data from the LTMP shows that disturbance regime of the last 30 years has led to marked declines in mean coral cover on GBR since the early 1980s (De'ath et al. 2012). In light of this finding, along with increasing reports of sustained coral loss at many other locations throughout the world (Gardner et al. 2003; Bruno & Selig 2007), significant attention is being focused on management practices that will reduce or reverse sustained coral loss. The foremost management tool used on coral reefs, and marine ecosystems generally, is the implementation of networks of NTMRs (Day et al. 2002; Roberts et al. 2002; Pandolfi et al. 2003; Sale 2005; Fernandes et al. 2005). However, sustained declines in coral cover on the GBR (De'ath et al. 2012) have occurred despite an established and ostensibly well-managed network of NTMRs, which begs the question as to how effective NTMRs can be, given they generally

restrict extractive activities like fishing and can do little to moderate the effects of large-scale natural disturbances. Furthermore, the controversial expansion of the area protected inside NTMRs of the GBR under the Representative Areas Program in 2004 necessitated a thorough examination of what we can realistically expect NTMRs to deliver, in terms of exploited fishery stocks, but also to reef conservation, protection of biodiversity and reef resilience. Emslie et al. (2015 - Chapter 8) detailed the most spatially extensive assessment of NTMR performance on the GBR to date, and there were numerous encouraging results. Exploited stocks were almost double inside NTMRs compared to adjacent reefs open to fishing, an expected result that is repeated around the globe (e.g., Russ & Alcala 1996; Mosquera et al. 2000; Halpern 2003; Williamson et al. 2004; McClannahan et al. 2007; Lester et al. 2009; Babcock et al. 2010). Furthermore, it is evident that placing between 5% and 33% of the Marine Park inside of NTMRs is sufficient to protect stock of fishes targeted by the line fishery given historical and contemporary fishing pressures, and that the expansion of the area of NTMRs to around a third of the GBRMP has resulted in huge increases in coral trout populations (Russ et al. 2008; Emslie et al. 2015). Importantly, the expansion of the area of NTMRs in 2004 also benefited coral trout populations on reefs open to fishing, with no evidence of a 'squeeze effect' (*sensu* Halpern et al. 2004) depleting coral trout populations. It is encouraging to know that coral trout populations appear to be currently fished at sustainable levels on the GBR and that protecting stocks inside of NTMRs can produce large rapid increases to trout numbers, and should eventually provide larval subsidies to surrounding fished areas. Evidence for such subsidies has emerged in recent years on the southern GBR (Harrison et al. 2012). While such results are expected given that NTMRs prevent fishing, the utility of NTMRs for the protection of biodiversity and for generating reef resilience remain equivocal.

While NTMRs are indisputably important and effective in conserving targeted fisheries species, controversy surrounds whether they may or may not protect other species that are not targeted by extractive activities (Graham et al. 2011). On the GBR at least, Emslie et al. (2015 – Chapter 8) show that NTMRs do have benefits that extend beyond fisheries target species. While there were few clear differences in numbers of non-exploited fishes or the percent cover of corals or algae, there were more fish species inside NTMRs than outside (Emslie et al. 2015 – Chapter 8). Furthermore, there were few differences in the assemblage structure of reef fishes or the benthos, however,

the fact that NTMRs retained higher diversity and numbers of fishes following a severe tropical cyclone suggest that they are protecting biodiversity. That there were not many clear cut differences in the variables analysed may seem disappointing at first, but this result is entirely what is expected from a well-managed reef, located in a developed nation with relatively light fishing pressure that targets a narrow range of predatory fishes and does not use destructive fishing techniques. Additionally, an unexpected but important finding presented in Emslie et al. (2015 – Chapter 8) was that the biomass of coral trout inside NTMRs did not decrease following the passage of a severe tropical cyclone, which reduced population of coral trout on adjacent reefs open to fishing. This suggests that NTMRs can offer some resistance to large scale natural disturbances and it is likely that the larger trout inside NTMRs before the storms' passage were better able to cope with its impacts, than the smaller individuals on adjacent fished reefs. Further evidence is emerging that NTMRs can impart some resilience into reef communities. A recent study, supplementary to this thesis, revealed that following natural disturbances such as *A. planci* outbreaks, coral bleaching, coral diseases and storms, fish and coral assemblage composition within NTMRs was 21-38% more stable, disturbance magnitude was 30% lower and recovery rates were faster by up to 20% than adjacent unprotected reefs (Mellin et al. 2016). Taken together, these results provide some support for the hypothesis that NTMRs can increase the resilience of coral reefs, although the mechanism by which this occurs remains at present unclear, and worthy of future research.

Information on the recovery of coral reefs following disturbance is critical, especially given the world-wide degradation of coral reef ecosystems (Hughes 1994; Gardener et al. 2003; Hughes et al. 2003; Bellwood et al. 2004; De'ath et al. 2012). However, gaining such information requires extensive long-term datasets with the temporal scope to encompass the cycle of disturbance and recovery that characterise disturbance regimes on coral reefs. The LTMP is one such dataset. Its multi-decadal scope and spatial extent allows the recovery dynamics of coral reefs from multiple sub-regions of the GBR to be examined following disturbance. The comparison of the recovery dynamics of reefs from the southern and northern ends of the GBR presented in Emslie et al. (2008 - Chapter 7) revealed first and foremost, that coral reefs of the GBR can, and do, recover from disturbances. Moreover, it demonstrated the importance of habitat complexity to reef fishes and that recovery of scleractinian corals can interact

with substrate complexity to determine the functional structure of associated fish assemblages. Corals with complex skeletons (e.g., branching *Acropora* spp.), were particularly important for recovery in fish assemblages following disturbance, and there was evidence of a progression of fish communities which followed each successional stage in the recovery of the coral community. The revelation that fish assemblage structure is tied to the successional stage of the benthic community means that, in situations of coral recovery without re-assembly (e.g., Johns et al. 2014), fish assemblage structure may be fundamentally altered (Berumen & Pratchett 2006b), with the capacity to perform vital ecological functions drastically reduced or removed.

9.5 Summary

The body of work contained in this thesis has greatly expanded our knowledge of reef fish assemblages of the GBR; how they are spatially-structured, how they have responded to recent disturbances, changes in the structure and function of reef fish assemblages in the aftermath of disturbances, and the role of spatial management (NTMRs) in moderating these effects. GBR reef fishes exhibited sub-regional spatial structure, predominantly derived from physical and biological gradients across the continental shelf. The variation in the sub-regional structure of reef fish assemblages explained by the position on the continental shelf and by latitudinal sector was always significantly higher than any variation attributed to changes through time. In essence reef fish assemblages of the GBR are defined by their sub-regional setting, and although community composition at any given reef showed some levels of temporal variation, these were never strong enough to disrupt the spatial signal such that a given community changed to resemble another. Inshore fish assemblages were less diverse and abundant than their counterparts on mid- and outer-shelf reefs and tended to have lower functional diversity and redundancy of important herbivorous fishes. Inshore reefs are also under the greatest anthropogenic stress, which may compound the impact of naturally occurring disturbances, meaning that inshore reefs are likely the most vulnerable on the GBR, and that the low diversity fish communities may be unable to assist in reef recovery. Furthermore, important fishery target species use inshore reefs as nursery grounds and undergo ontogenetic shifts in habitat use across the continental shelf. Habitat degradation on inshore reefs may therefore influence the replenishment of their populations in the offshore line fishery. Many GBR species were widely

distributed, which should buffer them against the impacts of all but the largest scale perturbations. However, being widely dispersed does not insure a species against the local-scale direct impacts of disturbances, but it should ensure that population replenishment can occur through larval exchange from un-affected populations, provided sufficient connectivity exists. The recent disturbance history of the GBR has revealed that many reef fishes are also vulnerable to the impacts of natural disturbances, especially those that simultaneously reduce levels of live coral cover and habitat complexity. However, assessing the impacts of disturbance on reef fish communities requires an examination of more than simple coarse summary measures like total abundance or species richness. While these measures can remain stable despite disturbances, examination of finer taxonomic resolution is necessary to tease apart subtle shifts in community composition that may fundamentally alter the capacity of reef fishes to perform important ecological tasks, impacting reef ecosystem function and its capacity to recover from repeated disturbances. A much vaunted tool for the preservation of coral reefs, NTMRs were shown to be beneficial for exploited fishery targets, but they also appear to increase the resilience of marine communities.

9.6 References

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Appendix 1. Published journal papers

1. Cheal, A. J., MacNeil, M. A., Emslie, M. J., & Sweatman, H. P. A. (2017). The threat to coral reefs from more intense cyclones under climate change. *Global Change Biology* 23(4), 1511-1524.
2. Brandl, S. J., Emslie, M. J., & Ceccarelli, D. M. (2016). Habitat degradation increases functional originality in highly diverse coral reef fish assemblages. *Ecosphere*, 7(11).
3. Ceccarelli, D. M., Emslie, M. J., & Richards, Z. T. (2016). Post-Disturbance Stability of Fish Assemblages Measured at Coarse Taxonomic Resolution Masks Change at Finer Scales. *PloS One*, 11(6), e0156232.
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5. Emslie, M. J., Logan, M., Williamson, D. H., Ayling, A. M., MacNeil, M. A., Ceccarelli, D., ... & Miller, I. R. (2015). Expectations and outcomes of reserve network performance following re-zoning of the Great Barrier Reef Marine Park. *Current Biology*, 25(8), 983-992.
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8. Hobbs J-P. A., Berger, M., De Brauwer, M., & Emslie, M. J. (2014). North-eastern range extension of the anemone *Stichodactyla haddoni* to the Marshall Islands represents a new record of host use by the endemic anemonefish *Amphiprion tricinctus*. *Marine Biodiversity Records*, 7, e106. doi:10.1017/S1755267214001055

9. Feary, D. A., Pratchett, M. S., Emslie, M., Fowler, A. M., Figueira, W. F., Luiz, O. J., ... & Booth, D. J. (2014). Latitudinal shifts in coral reef fishes: why some species do and others do not shift. *Fish and Fisheries*, *15*(4), 593-615.
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12. Emslie, M. J., Logan, M., Ceccarelli, D. M., Cheal, A. J., Hoey, A. S., Miller, I., & Sweatman, H. P. A. (2012). Regional-scale variation in the distribution and abundance of farming damselfishes on Australia's Great Barrier Reef. *Marine Biology*, *159*(6), 1293-1304.
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15. Cheal, A., Emslie, M., Miller, I., & Sweatman, H. (2012). The distribution of herbivorous fishes on the Great Barrier Reef. *Marine Biology*, *159*(5), 1143-1154.
16. Emslie, M. J., Pratchett, M. S., & Cheal, A. J. (2011). Effects of different disturbance types on butterflyfish communities of Australia's Great Barrier Reef. *Coral Reefs*, *30*(2), 461-471.
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Appendix 2 – A selection of technical reports and book chapters

1. Emslie, M. J., & Pratchett, M. S. (In Press). Different vulnerabilities of parrotfishes to habitat degradation. In Hoey, A. S., & Bonaldo, R. (eds) *The Biology and Ecology of Parrotfishes*. CRC Press.
2. Sweatman, H., Emslie, M., & Logan, M. (2016). Monitoring the effects of rezoning on the Great Barrier Reef: Milestone Report November 2016. Report prepared for the Great Barrier Reef Marine Park Authority. Australian Institute of Marine Science, Townsville
3. Evans-Illidge, E., Tonin, H., Lawrey, E., Miller, I., Steinberg, C., Johns, K., Emslie, M., & Brinkman, R. (2016). Preliminary baseline knowledge to support a first-stage marine-environmental assessment of proposed in-sea desalination pipeline infrastructure at Great Palm Island (Bwgcolman), Queensland. Supplementary Report – the Northern Site. Report prepared for Palm Island Aboriginal Shire Council and the Queensland Department of Infrastructure, Local Government and Planning. Australian Institute of Marine Science, Townsville. (72 pp)
4. Evans-Illidge, L., Lawrey, E., Tonin, H., Luter, H., Miller, I., Emslie, M. J., ... & Brinkman R (2015). Preliminary baseline knowledge to support a first-stage marine-environmental assessment of proposed in-sea desalination pipeline infrastructure at Great Palm Island (Bwgcolman), Queensland. Report prepared for Palm Island Aboriginal Shire Council and the Queensland Department of Infrastructure, Local Government and Planning. Australian Institute of Marine Science, Townsville. (72 pp)
5. Cappel, M., Stowar, M., Lawrey, E., MacNeil, M. A., & Emslie, M. J. (2011). The influence of zoning (closure to fishing) on fish communities of the shoals and reef bases of the Great Barrier Reef Marine Park. Complementary analysis of observations from divers and baited video surveys to quantify the influence of region, habitat and zoning with extension of results to regional groups. Marine and Tropical Sciences Research Facility (MTSRF) Transition Project Final Report. Reef and Rainforest Research Centre Limited, Cairns (50pp).

6. Beger, M., Richards, Z. T., Jacobson, D., Emslie, M., & Hess, D. (2011). Majuro Atoll temporal monitoring report, 2010. Report to NOAA. In. College of the Marshall Islands, Australian Museum, The University of Queensland Majuro, Republic of the Marshall Islands, p. 25.
7. Sweatman, H. P. A., Cheal, A. J., Coleman, G. J., Emslie, M. J., Johns, K., Jonker, M., ... & Osborne, K. (2008). Long-term Monitoring of the Great Barrier reef, Status Report. 8. Australian Institute of Marine Science. 369 p.
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9. Evans, R. D., Williamson, D. H., Sweatman, H., Russ, G. R., Emslie, M., Cheal, A., & Miller, I. (2006). "Surveys of the effects of re-zoning of then GBR Marine Park on some fish species – preliminary findings. Unpublished report to the Australian Government Department of Environment and Heritage. 18pp.
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14. Emslie, M. J., & Williamson, D. H. (2003). Visual assessment of the marine habitats adjacent to the freshwater pipeline between Cape Pallerenda & Magnetic Island. Unpublished report prepared by Scientific Marine for Maunsell Australia Pty Ltd.

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