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Ecological structure and processes on disturbed coral reefs

Thesis submitted by

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Abstract

Disturbances affecting ecosystems are becoming more diverse, frequent and intense, resulting in many examples of degraded ecosystems worldwide. Degradation involves fundamental changes to the system's community structure and function, and can have negative implications environmentally, socially and economically. Conditions, processes and management strategies that prompt recovery are therefore desirable, but details remain equivocal. Coral reefs are one such complex, diverse and threatened ecosystem. A primary consequence of coral reef degradation has been the development of alternative benthic conditions, however our understanding of their implications for other aspects of reef assemblages is limited. This thesis aims to understand the role of reef condition in shaping ecological communities and influencing key ecological processes on disturbed coral reefs.

To investigate processes operating in a particular system, it is first important to characterise the extent of its spatial variability. Reefs of the inner Seychelles islands were chosen because they were severely disturbed by the 1998 bleaching event, and now exist in a range of benthic conditions that might be representative of reef conditions elsewhere in the future. In **chapter 2**, I quantitatively characterised 21 reefs within a 3600 km^2 area of the inner Seychelles by considering their underlying substrata, benthos, and associated fish assemblages. High variability in benthic composition was found among the reefs, with a gradient from high coral cover (up to 58 %) and high structural complexity to high macroalgae cover (up to 95 %) and low structural complexity at the extremes. This gradient was associated with declining species richness of fishes, reduced diversity of fish functional groups, and lower abundance of corallivorous fishes. Reefs grouping at the extremes of complex coral habitats or low-complexity macroalgal habitats displayed markedly different fish

communities, with only two species of benthic invertebrate feeding fishes in greater abundance in the macroalgal habitat. Moreover, much of the variability seems to be independent of fishing pressure, indicating that there are deeper processes involved. These results have negative implications for the continuation of many coral reef ecosystem processes and services if more reefs shift to extremely degraded conditions dominated by macroalgae.

In systems that have suffered local population-extinctions of key organisms (e.g. branching *Acropora* corals), recruitment to replenish depauperate populations is essential. However, isolated reefs such as the Seychelles may only receive a limited supply. Other potential bottlenecks to re-establishing a thriving coral population include low settlement rates, and high mortality of new recruits or juvenile corals. In **chapter 3** I investigated spatial variation in local abundance of scleractinian corals at three distinct life history stages (recruits, juveniles, and adults) on reefs with differing benthic conditions. On rubble-dominated reefs, which were characterised by low cover of macrobenthic organisms and unconsolidated substrata, cover of adult corals was very low compared to coral-dominated reefs despite similar densities of juvenile corals and incoming coral recruits. A bottleneck caused by low juvenile colony survivorship on unconsolidated rubble-dominated reefs is possible. Macroalgal-dominated reefs received the same number of recruits as coral-dominated reefs (i.e. larval supply was not compromised), but these recruits were either unable to settle successfully on the natural substrate, or survive through to their juvenile life stage. The presence of abundant macroalgae on reefs appears to be having detrimental effects on coral replenishment following disturbances. Bottlenecks to recovery of coral assemblages were present on reefs that had shifted to more degraded conditions.

Shifts between alternative ecosystem states often involve alterations to vegetation type and quantity. Herbivory intensity, and the identity of herbivores, is therefore expected to influence the likelihood of such shifts. On coral reefs, assessments of macroalgal herbivory using bioassay experiments are primarily from systems with relatively high coral cover. In **chapter 4**, I investigated whether the species that remove macroalgae on coral-dominated reefs will still be present and performing significant algal removal on macroalgal-dominated reefs. That is, whether continued functionality can be ensured in degraded systems. Using filmed *Sargassum* bioassays, I found significantly higher *Sargassum* biomass loss on coral-dominated reefs. However, once standardised for the availability of macroalgae, the rates of removal were similar between the two reef conditions. *Sargassum*-assay consumer assemblages differed between reef conditions; nominally grazing herbivores, *Siganus puelloides* and *Chlorurus sordidus*, and the browser, *Siganus sutor*, dominated feeding on coral-dominated reefs, whereas browsing herbivores, *Naso elegans*, *N. unicornis*, and *Leptoscarus vaigiensis* prevailed on macroalgal-dominated reefs. It appeared that macroalgal density in the surrounding habitat had a strong influence on the species driving the process of macroalgal removal. This suggests that although the function of macroalgal removal may continue, the species responsible may change with context, differing between systems that are regenerating versus degrading.

Predictions of future ecosystem communities aid management and conservation initiatives yet are currently difficult to provide, especially at local scales. Using patterns in coral reef fish assemblages that are associated with reefs along a continuum of habitat quality, **chapter 5** investigated 1) whether observed relationships hold over time, and 2) whether there are particular aspects of benthic change that the fish respond to. Significant and relatively consistent spatial relationships between the two years were

identified for three aspects of the fish assemblage – species richness and the abundances of both corallivores and browsing herbivores. However, there was no consistent relationship for the remaining 10 fish assemblage variables. Nevertheless, a reef's trajectory along three different axes of benthic change (coral:macroalgae, cca:sand, other macroalgae:turf) was associated with reciprocal changes in nine (of 13) aspects of the reef fish assemblage. This suggests that while there are spatial patterns in some groups that may be used for predictions, caution should be exercised with many other ecosystem components, as unpredictable behaviour is likely.

My research emphasises the long-term detrimental effects of reef degradation, especially phase shifts to macroalgal-dominance, on important ecological processes. Moreover, the more degraded examples of Seychelles coral reefs (rubble- and macroalgal-dominated) appear to be reinforcing their current condition, developing feedbacks that may be hard to break. The work also highlights areas or time periods where management strategies may be most effective.

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CHAPTER 1

General Introduction

1.1 Ecosystem complexity and dynamism

One of the fundamental concepts of ecology has been that in the absence of disturbances, ecosystems (in particular their community of species) would exist in an equilibrium, or climax state (DeAngelis and Waterhouse 1987; Wu and Loucks 1995). Empirical evidence suggests that no real system is ever likely to exist in equilibrium because exogenous factors such as disturbances play a larger role than predicted by equilibrium theory, and heterogeneity is rife both spatially and temporally (Wu and Loucks 1995). However, although classical equilibrium theory may be unrealistic, equilibria can still be a useful concept for framing reality. This requires shifting the equilibrium concept away from the attainment of a specific self-organising community and incorporating the idea that potential equilibria are idealisations that are constantly being altered because change occurs so often and from varied sources (Holling 1973; Wu and Loucks 1995; O'Neill 1999).

An ecosystem consists of many processes and organisms that influence its formation, structure and functioning, resulting in a complex network of interactions (Holling 1973; Angert et al. 2013; Martorell et al. 2014). All aspects of the system are interconnected, and changes to one part will eventually feed through the system as a result of both direct and indirect interactions or impacts (O'Neill 1999; Carpenter 2002; Hughes et al. 2005; Nyström et al. 2012). Ecosystems are constantly subjected to disturbances (defining disturbance as any event that interferes with the structure of an ecosystem, changing resource availability or the physical environment; Pickett and

White 1985), therefore change is a common occurrence and ecosystems are considered to be dynamic (Holling 1973; Connell 1978; O‘Neill 1999; Platt and Connell 2003; Pandolfi and Kiessling 2014). Disturbances alter ecosystems because they can interfere with functional processes and have differential impacts on individuals and species that make up the community (Connell et al. 1997; Hughes and Connell 1999; Elmqvist et al. 2003; Pratchett et al. 2011a). Some species will benefit from the changes, whereas others deteriorate, causing alterations to the community composition that can further influence functioning of key ecosystem processes (Turner 2010; Cardinale et al. 2012).

The frequency and magnitude of disturbances affecting ecosystems means that at any one point in time, a system’s communities will likely be moving along trajectories towards recovery or degradation (Palumbi et al. 2008; Lotze et al. 2011), where recovery and degradation may be theoretical equilibria (or basins of attraction; Holling 1973). Recovery occurs when affected organisms re-establish themselves and the community returns to approximate pre-disturbance organisation with little change in function (e.g. Gilmour et al. 2013, Vaudrey et al. 2010, reviewed by Lotze et al. 2011). Alternatively, key organisms may not re-establish (e.g. habitat builders/providers). Systems may therefore become desertified and/or barren (Kassas 1995, Steneck et al. 2002), or other organisms may establish, filling or interfering with the niche of the displaced organisms. These replacement species can change the system fundamentally, affecting environmental conditions and habitat structure (e.g. phase shifts; Hughes 1994, Scheffer et al. 1993, reviewed by Scheffer et al. 2001).

Ecosystem processes can be modified both directly by the disturbance, and as a result of adjustments to the community structure. For example, organism dispersal is a key process that allows individuals to flow among populations, thereby influencing community composition (e.g. Platt and Connell 2003, Allison 2004) and enabling re-population following local-extinction (e.g. Hughes and Tanner 2000, Dulvy et al. 2003). Depending on dispersal strategies and the level of connectivity between populations, disturbances can interrupt organism recruitment (e.g. loss of source populations; Hughes and Tanner 2000) or enhance recruitment of unwanted organisms (invasive species; Elmhirst et al. 2009). Herbivory is another fundamental ecosystem process in many systems, mediating interactions between plants and their consumers. Variability in herbivory intensity within a system over time, often as a result of disturbances (e.g. overexploitation), has been instrumental in allowing shifts to alternative ecosystem states (e.g. woodlands versus savannah; Dublin et al. 1990, coral versus macroalgal-dominated reefs; Hughes 1994, kelp versus urchin barrens; Steneck et al. 2002).

There are patterns in the frequency, intensity and spatial extent of disturbances affecting ecosystems: the disturbance regime. However, disturbance regimes are changing (reviewed by Turner 2010) with more intense acute disturbances occurring more frequently (e.g. cyclones; Kossin et al. 2013, heat waves; Song et al. 2014) and a wider range of chronic disturbances now affecting ecosystems (e.g. overexploitation; Jackson et al. 2001, pollutants; Moe et al. 2013). This has meant that systems have shorter periods of time within which to recover, in between pulse events, yet are also experiencing slower recovery rates as organisms survive in environments with continued chronic stressors (De'ath et al. 2012). Currently, there are an increasing number of ecosystems existing in a degraded condition and many have been in altered conditions for quite some time (Jackson et al. 2001, Steneck et al. 2002, Folke et al. 2004, Lotze et al. 2006, Baldi et al. 2013).

Ecosystem degradation is thought to have negative implications environmentally (Cardinale et al. 2012), socially (McClanahan et al. 2008) and economically (Moberg and Folke 1999). Conditions, processes and management strategies that prompt recovery are therefore desirable (Hughes et al. 2010, Lotze et al. 2011). If a system is resilient (defining resilience as the capacity of ecosystem processes, and the organisms that perform them, to buffer the effects of disturbances; Holling 1973), then just the passing (e.g. cyclones; Connell et al. 1997) or removal (e.g. anthropogenic stressors such as pollutants; Hunter and Evans 1995, Vaudrey et al. 2010) of the disturbance can be enough for recovery (but see Scheffer et al. 2001 for the concept of hysteresis). It may be obvious why some systems recover whereas others do not, such as clear differences in levels of chronic stressors (e.g. fished versus unfished reefs; Rasher et al. 2013). However the reason for variability in recovery trajectories is not always obvious, especially at more local scales where effects of chronic disturbances are likely to be equivalent (e.g. Wilson et al. 2012, Russell and Connell 2012).

The most common way of quantifying ecosystem characteristics are surveys, which result in a snapshot of the system that appears to exist in a distinct state (Fig. 1.1). Unless systems are followed through time, it is easy to forget that the system is actually progressing along possible trajectories from one condition to another (Hughes et al. 2013, cf. Bruno et al. 2009). Moreover, it can be difficult to determine which direction the system is moving along its post-disturbance trajectory, and towards what outcome. Yet, the ability to predict ecosystem dynamics across time is in demand as management and conservation initiatives plan investments of time and resources (Pressey et al. 2007; Pressey and Bottrill 2009). Predictions require elucidation of system interactions that can take years to amass, and vast amounts of data, due to ecosystem complexity (e.g. Carpenter 2002; Grime and Pierce 2012). Furthermore, quantitative historical datasets are lacking for many areas worldwide. Interest is therefore growing in the potential for early warning signs of outcomes from major degradation (e.g. Carpenter et al. 2011, Mouillot et al. 2013, review by Rombouts et al.

2013). Another approach has been to make inferences and predictions using the assumption that contemporary relationships or patterns hold over time (e.g. Stockwell et al. 2009). Such an assumption seems necessary given the paucity of historical data, but requires testing (e.g. Kharouba et al. 2009; Blois et al. 2013), in particular because reality is a lot more stochastic and unorderly than classic succession theory suggested (Pickett 1989; Suding and Leger 2012).

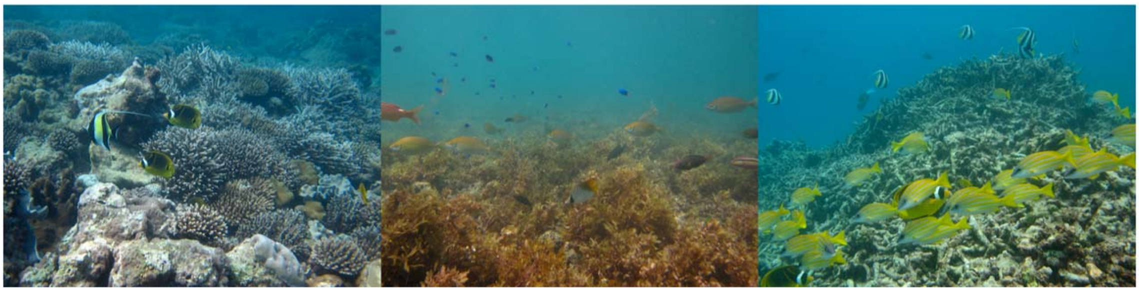

Fig. 1.1 Snapshots of three coral reefs from one point in time. They could represent (a) coral-dominated reefs, (b) macroalgal-dominated reefs and (c) barren rubbly reefs, however, unless the ecosystem has been monitored through time, it is very difficult to establish whether they are on a recovery or degradation trajectory, or the stability of the current assemblage.

1.2 Coral Reefs

Coral reefs are among the world’s most complex, diverse and threatened ecosystems, with many reefs severely degraded (Gardner et al. 2003, Bruno and Selig 2007, Ateweberhan et al. 2011). Key pulse disturbances experienced by coral reefs include cyclones (e.g. Connell et al. 1997, Connell et al. 2004), predatory starfish outbreaks (e.g. Sano et al. 1987, Moran et al. 1988), and thermal warming events – the most dramatic and far-reaching was during the 1998 El Niño year (Wilkinson et al. 1999, Goreau et al. 2000). Scleractinian corals are the foundational biota of coral reefs, but numerous other benthic organisms (e.g. soft corals, sponges, algae, burrowing invertebrates) also colonise the substratum. Consequently, coral loss has major repercussions for reefs (e.g. Wilson et al. 2006, Pratchett et al. 2008), including phase shifts where corals give way to some of the other benthic organisms. Documented shifts include changes to corallimorphs, sponges, or most often, macroalgae (Hughes 1994, Ledlie et al. 2007, reviewed by Norström et al. 2009). However, we currently have only limited knowledge on what these shifts mean for the rest of the coral reef community (e.g. reef fish).

A coral reef's physical substratum is predominantly a result of net biological accretion over thousands of years, and influences its basic underlying complexity and form. Through time, the substratum has been broken up, consolidated and rebuilt through various biological and physical processes (e.g. Braithwaite et al. 2000), resulting in differential stability between systems. Instability of a reef's post-disturbance physical structure may inhibit key functional processes such as coral recruitment (Fox et al. 2003). Sessile benthic biota overgrows, erodes and stabilises the substrate, increasing the reef's complexity and contributing to the diversity of lifeforms present – both as habitat and as organisms in their own right. Mobile organisms, such as the fish community add further diversity, playing a vital role in some of the ecological services provided by the ecosystem (Moberg and Folke 1999, Worm et al. 2006).

Strong relationships exist between coral reef fishes and their habitat. For example, coral loss, and especially the loss of the structural complexity provided by corals, is detrimental to many reef fishes (Graham et al. 2006, Wilson et al. 2006, Wilson et al. 2010a, Pratchett et al. 2008), and herbivorous reef fishes avoid foraging in high macroalgal densities (Hoey and Bellwood 2011). Patterns in these relationships have also been identified by comparing reefs that have been protected from human exploitation for different numbers of years; for example, showing more fish in areas protected for longer (McClanahan and Graham 2005; Stockwell et al. 2009). These patterns can be used to infer trajectories through time (McClanahan and Graham 2005) or changes in ecosystem processes (Stockwell et al. 2009) as a result of protection. Likewise, effects of degradation may become predictable in space by comparing a number of sites in a range of conditions. On coral reefs, our current ability to predict futures is improving (e.g. Pratchett et al. 2011b; Mumby et al. 2013; reviewed by Arias-González et al. 2011) but can be refined with further empirical data, especially at local scales where stochastic variability is high.

Coral recruitment and herbivory have both been suggested to be important ecological processes in determining whether reefs tend to recover or degrade following disturbances to the benthos (Connell et al. 1997, Hughes et al. 2010, Graham et al. 2011). Reassembly of a depauperate coral population requires recruitment of new individuals, followed by their survivorship (Connell et al. 1997, Hughes et al. 2010, Graham et al. 2011). Scleractinian corals have free-swimming dispersive larvae, which can travel for extended periods of time (Graham et al. 2008a), allowing substantial dispersal potential (Connolly and Baird 2010). Recruits can therefore originate from their natal reef, or externally (Caley et al. 1996). External recruitment is thought to be vital on reefs that have suffered extensive coral loss (Nyström et al. 2008; Done et al. 2010; Hughes et al. 2010); however some reefs may be quite isolated, which may limit external larval supply and therefore reduce recovery potential (Hughes and Tanner 2000; Gilmour et al. 2009; Wood et al. 2013). If larval supply is available, then a recruit’s post-settlement survival will depend on suitability of available settlement habitats. For example, high macro-benthic cover (macroalgae or scleractinian corals) can pre-empt settlement (space limitation; e.g. Connell et al. 1997), or a mobile substrate (e.g. unconsolidated rubble) may increase mortality rates via periodic abrasion and/or smothering of small colonies (e.g. Fox et al. 2003). Negligible coral recovery is often attributed to either limited local coral larval supply (e.g. Williams et al. 2008) or availability of suitable larval settlement habitat (e.g. Hughes et al. 2007).

The herbivore population mediates competition between corals and coral reef algae, typically maintaining the algae in a cropped state (Bellwood et al. 2004, Fong and Paul 2011). The cropped algae, which include macroalgal propagules, along with sediment, detritus and invertebrates, constitute the epilithic algal matrix (EAM; Wilson et al. 2003). The EAM is a rich food source, exploited by specific herbivorous functional groups such as grazers and scrapers (i.e. species that could prevent phase shifts; Bellwood et al. 2004). Indeed, following coral loss the densities of these particular herbivore groups may increase, preventing reefs from becoming overgrown by macroalgae (e.g. Adam et al. 2011; Gilmour et al. 2013). If reefs do shift to macroalgae, browsing herbivorous species that consume mature macroalgae may be able to reverse the shift (e.g. Bellwood et al. 2006a). However, of the nominal herbivores present in an assemblage, only a relatively small proportion is likely to be made up of browsers (Johansson et al. 2013) because macroalgae is typically an uncommon food resource on coral reefs (Bellwood et al. 2004, Fong and Paul 2011). Investigations into the process of macroalgal herbivory on coral reefs have found that the functionally important species were rarely numerically dominant; i.e. they performed a disproportionate role compared to their abundance (e.g. *Naso unicornis*; Hoey and Bellwood 2009). Moreover, most of these studies are from areas with minimal fleshy macroalgal cover, and it remains equivocal whether the fish that remove macroalgae on a coral-dominated reef will be capable of significant algal removal on a macroalgal-dominated reef.

1.3 Aims and thesis outline

Given the extensive variability in recovery potential of many coral reefs in the absence of obvious local environmental or human causes (e.g. river discharge or protective status), comparative studies may enable particular characteristics of recovering versus degrading reefs to be identified. Therefore, the overall aim of this thesis was to understand the role of reef condition in shaping ecological communities and influencing key ecological processes on disturbed coral reefs. Reef condition is defined as the current benthic community structure that has developed post-disturbance. Four specific questions were addressed.

1. What are the relationships between a reef's benthic condition, its underlying substrata, and associated fish assemblages?
2. Are there bottlenecks in coral replenishment processes associated with different benthic conditions?
3. How is macroalgal herbivory influenced by differing reef benthic condition?
4. Are reef benthic-fish relationships predictable through time?

The different components of this study are addressed in a series of four data chapters, which correspond directly to the publications derived from this thesis. **Chapter 2** characterises relationships between three components of a reef system, the underlying foundational substratum, the benthic biota and resident fish. This chapter investigates whether a reef's benthic condition can be explained by its physical underlying structure, and whether differential benthic condition has implications for resident fish assemblages. In doing so, the extent of variability in reef condition at the study site is quantified, creating a solid foundation for the rest of the thesis. **Chapter 3** investigates a key ecological process, coral recruitment. Specifically, coral replenishment is measured on (1) reefs that have recovered coral cover following disturbance, (2) reefs with low cover of living macro-benthic organisms and mobile rubble substrates, and (3) reefs that have become dominated by macroalgae. The possible development of demographic bottlenecks during a coral's life history following major disturbance events is investigated. **Chapter 4** assesses another key ecological process, macroalgal herbivory, on reefs that have recovered coral cover following disturbance, and on reefs that have become dominated by macroalgae. The consistency of this key ecological function and the identities and activities of the species involved, are investigated on reefs with highly disparate benthic conditions. **Chapter 5** returns to the complete range of reefs from chapter 2, re-evaluating the relationships between a reef's benthic biota and resident fish assemblage, in the light of progression over time. The possibility that observed relationships can be used to predict future communities, is investigated, along with an enquiry about which specific attributes of their habitat, reef fish functional groups respond to. **Chapter 6** is a general discussion that assesses the outcomes of the four data chapters, evaluating the overall hypothesis that if comparisons are made of reefs characterised by differential benthic conditions, particular characteristics may be revealed that promote recovery, rather than continued degradation, following a major disturbance.

1.4 Study site

This thesis was based on reefs surrounding the Seychelles islands, a group of granitic and coralline islands and atolls, located in the western Indian Ocean with an extensive reef system. They cover a large area, and I concentrated on the geographically isolated inner granitic islands (4°30'S, 55°30'E). The reefs around Mahé were first described in the 1960s, and were coral-dominated with lots of structure and complexity (Lewis 1968; Taylor 1968). Similar findings came from Jennings et al. (1995) who surveyed reefs surrounding Mahé, Praslin and associated islands in 1994, and Spalding and Jarvis (2002) who surveyed Cousine Island in 1997. Both studies found mean coral cover to be around 30 % with no other significant cover of macro-benthic organisms (e.g. macroalgae or soft corals). Therefore, for the purpose of this thesis I assumed that most reefs around the inner Seychelles islands are likely to have been coral-dominated (i.e. were the dominant macro-benthic organism present) with high structural complexity.

However, these reefs were amongst the most severely affected by the extensive mass bleaching event in 1998, losing up to 90 % coral cover (Goreau et al. 2000, Ateweberhan et al. 2011). Post-disturbance, the reefs have been showing variable recovery, despite no obvious environmental or human influences (Wilson et al. 2012). There are examples of reefs (both fished areas, and well-enforced marine protected areas) where coral cover has returned equal or higher than pre-disturbance levels, and reefs with minimal return of coral cover (Wilson et al. 2012). There have also been documented phase shifts to macroalgae (Ledlie et al. 2007). Fishing activity has relatively low variability among the shallow fringing reefs among the islands, with most fishing occurring in deeper water (Daw et al. 2011). Therefore, the inner Seychelles have extensive variability in reef condition following a major disturbance, there are no obvious external causes of these differences, which means that the reefs are an ideal system for a spatial comparison of reefs in varying benthic conditions.

CHAPTER 2

The influence of coral reef benthic condition on associated fish assemblages[1]

2.1 Abstract

Accumulative disturbances can erode a coral reef's resilience, often leading to replacement of scleractinian corals by macroalgae or other non-coral organisms. These degraded reef systems have been mostly described based on changes in the composition of the reef benthos, and there is little understanding of how such changes are influenced by, and in turn influence, other components of the reef ecosystem. This study investigated the spatial variation in benthic communities on fringing reefs around the inner Seychelles islands. Specifically, relationships between benthic composition and the underlying substrata, as well as the associated fish assemblages were assessed. High variability in benthic composition was found among reefs, with a gradient from high coral cover (up to 58 %) and high structural complexity to high macroalgae cover (up to 95 %) and low structural complexity at the extremes. This gradient was associated with declining species richness of fishes, reduced diversity of fish functional groups, and lower abundance of corallivorous fishes. There were no reciprocal increases in herbivorous fish abundances, and relationships with other fish functional groups and total fish abundance were weak. Reefs grouping at the extremes of complex coral habitats or low-complexity macroalgal habitats displayed markedly different fish communities, with only two species of benthic invertebrate feeding fishes in greater abundance in the macroalgal habitat. These results have negative implications for the

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continuation of many coral reef ecosystem processes and services if more reefs shift to extreme degraded conditions dominated by macroalgae.

2.2 Introduction

An ecosystem's ability to recover from degradation is eroded by increases in frequency, intensity and array of disturbances (O'Neill 1999; Nyström and Folke 2001; Hughes et al. 2003; Parmesan 2006). On coral reefs, increasing anthropogenic pressures (e.g. fisheries exploitation) and climate change, are compounding upon pre-existing disturbances (e.g. cyclones) and causing declines in coral cover and structural complexity (Bruno and Selig 2007; Graham et al. 2008b), associated changes in coral and fish community composition (Marshall and Baird 2000; Halford et al. 2004; Pratchett et al. 2008), and shifts in the dominant benthic biota (Done 1992; Hughes 1994; Norström et al. 2009). Documented shifts on coral reefs include changes to corallimorphs, sponges, or most often, macroalgae domination of the benthos (Done 1992; Hughes 1994; Norström et al. 2009). Although these other benthic lifeforms are typical components of most reefs, scleractinian coral domination is considered preferable; corals function as the main provider of the complex structural habitat that is largely responsible for the high diversity of reef associated organisms, and the provision of a range of ecosystem services, such as vital food resources (Costanza et al. 1997; Littler and Littler 2007; Knowlton and Jackson 2008).

All major coral reef regions of the world have undergone declines in coral cover (Gardner et al. 2003; Bruno and Selig 2007; Ateweberhan et al. 2011). In conjunction with these reductions in coral cover, is an increasing documentation of shifts in the dominant benthic biota (reviewed by Norström et al. 2009) that focus primarily on causes of the shifts, and subsequent changes in the benthic community composition. For example, although the causes attributed to the shift from coral to macroalgae on

Jamaican coral reefs included overfishing of herbivorous fish, hurricane Allen and disease mediated collapse of urchin populations, the description was based solely on benthic composition (Hughes 1994). How these changing benthic communities interact with underlying substrata, or influence the rest of the coral reef ecosystem, for example reef fish assemblages, is poorly understood.

Complex interconnections among organisms and with their physical environment, imply that changes to one aspect of the ecosystem may lead to a subsequent series of, often unanticipated, changes to the ecosystem's community assemblage (Wootton 2002; Doak et al. 2008; Connell et al. 2011). Strong relationships exist between coral reef fishes and their habitat (McCormick 1994; Garpe and Ohman 2003), although there is variability in the specific responses of different fishes, and of different ontogenetic stages, to changes in coral cover (Wilson et al. 2006; Pratchett et al. 2008; Lecchini et al. 2012). Live coral loss can trigger shifts in the entire fish assemblage (Bellwood et al. 2006b; Bellwood et al. 2012a), and prompt declines in abundance and diversity of fishes (Jones et al. 2004; Graham et al. 2006). The potential for other benthic organisms to provide the necessary habitat for reef fishes has not been widely investigated, although Syms and Jones (2001) showed that soft coral was not a favourable habitat replacement for hard corals. From non-marine ecosystems it appears possible that some organisms may provide habitat for an equally, or more diverse community, or alternatively, that changes in the habitat-providing organisms can be detrimental to diversity. As an example of the former, Brazilian forests contained 26 lizard species whereas the grassland alternative contained 30 species (Nogueira et al. 2009). In contrast, lakes lose their high submerged macrophyte and animal diversity following shifts to turbid eutrophic waters (Scheffer et al. 1993), while shifts from rangelands to desert lead to much reduced diversity (Walker 1993).

The interactions between the foundational structure upon which the live reef is built, the underlying substratum, and changes in the benthic community, may hinder essential ecosystem processes required for recovery, and perpetuate an alternative community. For example, coral recruit survivorship is considered an essential process for recovery (Hughes et al. 2010; Graham et al. 2011) and can be inhibited by burial and damage of new recruits by highly mobile rubble substrata during storms (Fox 2004; Victor 2008; Duckworth and Wolff 2011). The relationships between a reef's underlying substratum and dominant benthos are generally unknown, but knowledge of such relationships would further our understanding of the development and endurance of degraded conditions on coral reefs.

Coral reefs of the Seychelles archipelago offer a unique opportunity to assess differing benthic communities. The inner Seychelles islands are geographically isolated, were severely impacted by the 1998 mass bleaching event, and there is a good record of post-disturbance degradation (Goreau 1998; Ahamada et al. 2008; Graham et al. 2008b; Ateweberhan et al. 2011). Ten years after this major bleaching event, coral cover in the inner Seychelles ranged from <5% coral cover to >20% coral cover, which is amongst the lowest in the region (Ledlie et al. 2007; Graham et al. 2008b). Individual reefs have shown highly varied responses to disturbance, and there have been reports of benthic community shifts on some reefs (Graham et al. 2006; Ledlie et al. 2007). However, detailed characterisation of the benthic condition of these reefs is lacking, along with the implications of benthic condition for other aspects of the reef community. We therefore quantitatively characterised the benthos, underlying substratum, and fishes of inner Seychelles reefs to investigate: 1) if there was a link between underlying substrata and benthic condition; and 2) the relationship between benthic condition and the taxonomic and functional composition of associated fish assemblages.

2.3 Methods

2.3.1 ***Study site and sampling design***

Twenty-one carbonate fringing reefs within a 3600 km^2 area around the inner Seychelles islands (4 30’S, 55 30’E) were surveyed in October 2010. Fishing practices in the inner Seychelles use non-destructive techniques (handlines, traps and octopus harpooning are the most widely used; Grandcourt and Cesar 2003), and there is relatively low variability in fishing pressure along the shallow fringing reefs among the islands, with most fishing occurring in deeper water (Daw et al. 2011a, b). At each reef, four 50 m transects were laid at approximately 4 m depth, perpendicular to the reef slope. The following data were collected along each transect; 1) live benthic cover directly beneath the tape recorded at 0.5 m intervals, 2) underlying substratum quantified at 0.5 m intervals, 3) density and identity of all fish greater than 8cm were recorded along a 5 m wide belt (to minimise disturbance, large, mobile species were counted as the transect was laid; Halford and Thompson 1994), and 4) structural complexity was recorded using both a 6-point scale (ranging from 0: no vertical relief, to 5: exceptionally complex with numerous caves and overhangs) and by estimating the number of small refuge holes, <10 cm diameter, along two 10 x 1 m sub-transects (following Wilson et al. 2007). Scleractinian corals and macroalgae were identified to genus and/or morphological group, while other algae were identified to functional group. Other benthic organisms recorded included corallimorphs, sponges and zoanthids. For analyses, branching acroporids, massive *Porites*, and favids were differentiated from the rest of the coral genera (grouped as ‘other hard corals’) due to their high coverage. The underlying substratum, defined as the substratum below recorded benthic cover or the top 10 mm of sand/sediment, was categorised into loose dead coral rubble, consolidated rubble (rubble pieces that were showing visual and tactile signs of amalgamation), solid carbonate pavement, or bommie (isolated coral outcrops). Fish species were assigned to eight functional groups based on the literature and FishBase: obligate corallivores, browsing herbivores, other herbivores (including scrapers, grazers, excavators, detritivores), planktivores, piscivores, non-coral invertivores (hereafter invertivores), omnivores (consume animal and plant material) and generalist carnivores (fish and invertebrate feeders). Additionally, the level of exploitation sustained by different fish species was assigned at four levels: primary targets, important by-catch, occasional by-catch and non-fished species (Grandcourt 1999).

2.3.2 ***Analyses***

The data were organized into four matrices; i) benthic habitat (11 variables; including the two complexity measures) that was natural log transformed to improve the spread of the data, and standardized because variables were measured on different scales, ii) underlying substrata cover (four variables), iii) fish functional group abundances (eight variables) that were square-root transformed to downweigh abundant groups (Clarke and Warwick 2001), and iv) fish species abundances (152 species) that were also square-root transformed to downplay the influence of highly abundant species. The complexity measures were included with the benthic cover variables because these measures are thought, at least in part, to reflect the complexity provided by live benthic organisms (e.g. Chabanet et al. 1997; Graham et al. 2008b; Wilson et al. 2008). Within- and among-reef variation was assessed using ordination methods on dissimilarity matrices in the statistical software PRIMER; correlation-based principal components analysis (PCA) on Euclidean distances for the underlying substratum and benthic cover matrices (as the data is continuous and needed to be normalised; Clarke and Warwick 2001), and non-metric multidimensional scaling (nMDS) on Bray-Curtis dissimilarities to account for high zero counts (Clarke and Warwick 2001), for the fish matrices. Pairwise relationships between all variables within a matrix showed no collinearity ($r < 0.7$; Zuur et al. 2007). Groupings in the benthic cover PCA were assessed by overlaying slices from a hierarchical cluster analysis using group averaging of the same Euclidian distance matrix.

2.3.3 ***Relationship between data matrices***

Variability in benthic composition among reefs was related to underlying substratum, and also the composition of fish assemblages, in two ways. First, data points (= transects) on the underlying substratum and fish assemblage ordinations were colour-coded according to groups identified from the benthic cover hierarchical cluster analysis to visualize relationships. Second, the BEST BIO-ENV routine was carried out using a Spearman rank correlation between the different similarity resemblance matrices to identify the variable or group of variables that best explained similarities among the data matrices (Clarke and Warwick 2001). The overall significance of the BEST routine was assessed using a permutation test under the null hypothesis of no linkage of variables between matrices (maximum permutations = 999; Clarke et al. 2008).

2.3.4 ***Comparing variables along a gradient of contrasting benthic states***

A combination of cluster analysis and ordination showed the presence of contrasting benthic assemblages along a gradient from coral to macroalgae. To investigate whether there were any fish species that typified either assemblage, we ran a similarity of percentages (SIMPER) analysis using a subset of the fish species matrix that reflected the two extreme clusters of transects identified by the slice through the benthic cluster diagram. This represented transects dominated by macroalgae versus transects with high coral cover and structural complexity. An index of the fish functional group diversity was calculated using the Shannon-Weiner diversity index, *H'*, which takes into account both abundance and the number of functional groups (maximum n = 8). The relationships between the benthic gradient (the benthic PCA's first principal component) and fish functional group diversity (*H'*), fish species richness, total fish abundance, and individual functional group abundances were examined using General Additive Models (GAM). GAMs incorporate the possibility of non-linear relationships between the response and predictive variables (Zuur et al. 2007). Reef was included as a random effect variable using restricted maximum likelihood estimation (REML) using the gam and gamm functions of the mgcv package in R.

2.4 Results

2.4.1 ***Benthic reef assemblages***

Benthic cover of reef organisms was highly variable among the 21 reefs in the inner Seychelles. Live coral cover ranged from 0 to 47 % (± 5.1 SE) and macroalgae cover from 0 to 76 % (± 6.7 SE) per reef (Appendix A Fig. S1). The first principal components axis (PC1) of the benthic PCA differentiated transects along a gradient from high coral cover (up to 58 % per transect) and structural complexity (rugosity score up to 4, and up to 1150 10 cm holes) at negative PC1 scores, to high macroalgae cover (up to 95 %) and low structural complexity (rugosity score down to 0.5, and as few as 30 10 cm holes) at positive PC1 scores (Fig. 2.1). A separation from sand and sediment-laden turf to crustose coralline algae was represented by PC2. A slice through a cluster analysis at a Euclidean distance of 4 represented six groupings in the data, including two groups at extreme ends of PC1, and four intermediate groups (Fig. 2.1).

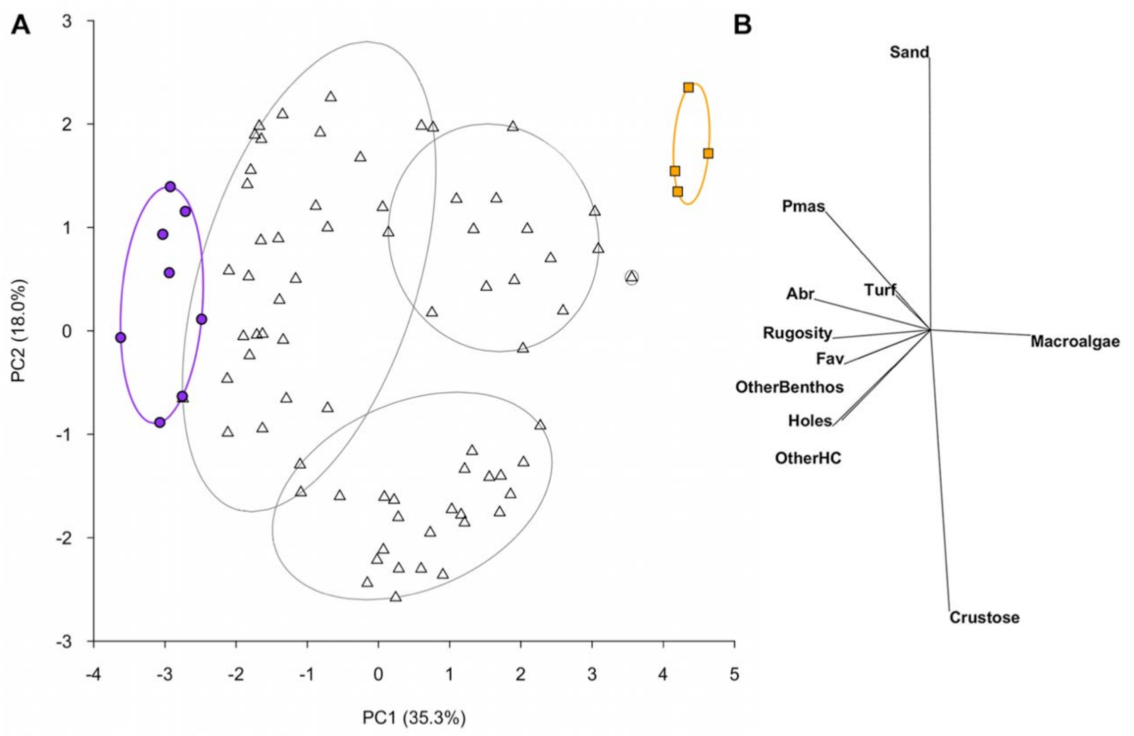

Fig. 2.1 Principal components analysis of benthic habitat variables. (A) Spatial variation in benthic habitat on reefs at the transect level, shown for the first two components from a principal components analysis on natural log(x+1) transformed and normalised data. Ellipses show groupings calculated from a slice taken through a hierarchical cluster analysis at a Euclidean distance value of 4. Data symbols represent transects within reefs; filled circles and squares highlight transects within the extreme clusters for visualisation purposes. Purple circles and ellipse shows high complexity coral cluster consisting of 8 transects from 2 reefs; orange squares and ellipse shows low-complexity, high macroalgae cluster consisting of 4 transects from 1 reef; triangles are transects that fall within intermediate clusters. (B) The relative contribution of the 11 benthic habitat categories to the observed variation in reef benthic condition. Pmas – massive *Porites*; Abr – branching *Acropora*; Fav – favids; OtherBenthos – non-coral or algae benthic organisms; OtherHC – all other scleractinian corals; CCA – crustose coralline algae.

2.4.2 ***Underlying substrata***

The underlying substrata of the reefs varied from loose rubble to consolidated carbonate pavement. When highlighted on the underlying substrate PCA plot, transect groupings from the benthic cluster analysis were not apparent, however reefs found at both extreme ends of the benthic PC1 were associated with more stable substrata. It is to be noted that the stress level of the MDS was fairly high, so although general patterns are robust, details need to be interpreted with some caution (Clarke and Warwick 2001). A BEST analysis ($r_s = 0.16$, $p < 0.05$) corroborated this pattern, finding a weak but significant correlation between the benthic and underlying substrata distance matrices, specifying the presence of pavement rather than rubble as the principal cause of similarity.

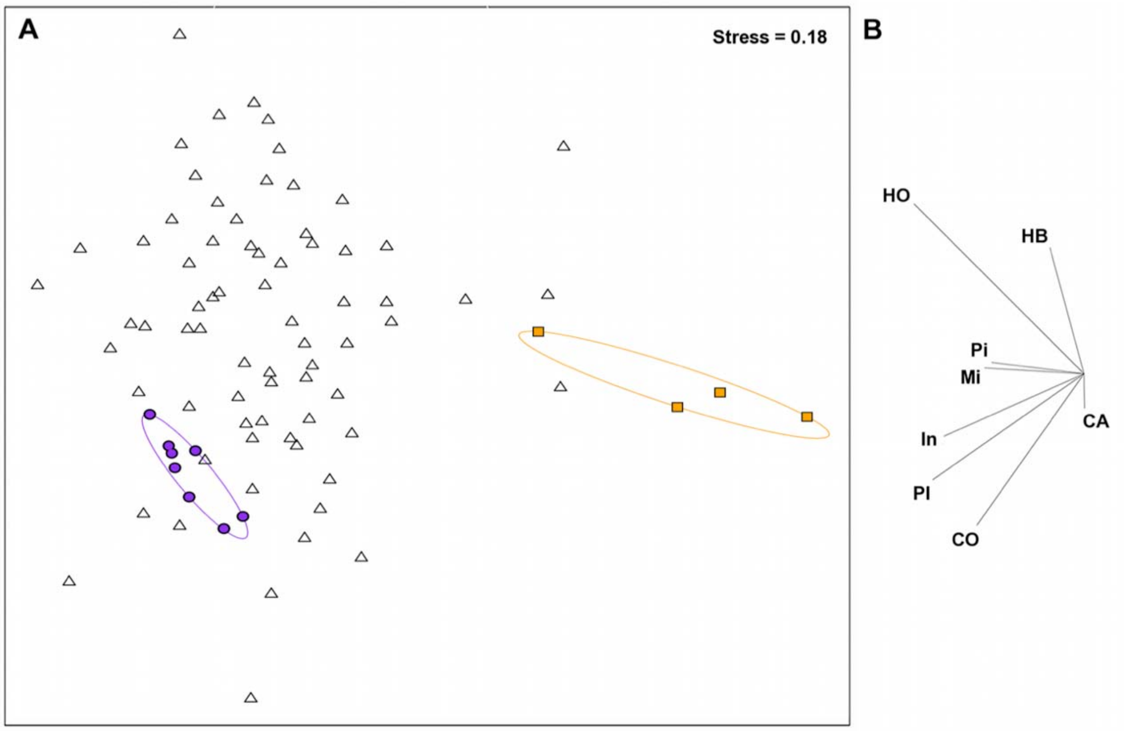

Fig. 2.2 Non-metric multidimensional scaling analysis of fish functional groups. (A) Spatial variation in the reef fish functional group abundances on reefs at the transect level, assessed using a non-metric multidimensional scaling plot on square-root transformed data. Data symbols represent transects within reefs. For visualisation purposes, filled circles and squares, and ellipses highlight the transects within the extreme clusters calculated from a slice taken through the Benthic data's hierarchical cluster analysis at a Euclidean distance value of 4. Purple circles and ellipse shows high complexity coral cluster, orange squares and ellipse shows low-complexity, high macroalgae cluster. (B) The relative contribution of the 8 fish functional groups to the observed variation on reefs. HB – browsing herbivores; HO – non-browsing herbivores; Pi – piscivores; Om – omnivores; In – non-coral invertivores; Pl – planktivores; Co – obligate corallivores; Ca – generalist carnivores.

2.4.3 ***Fish Assemblages***

A total of 152 fish species were recorded from the study site, with 3 to 38 species observed per transect. All of the eight fish functional groups were more strongly associated with transects plotted on the left hand side of the MDS plot (Fig. 2.2). Highlighting transects that clustered in terms of their benthos, on the fish functional group MDS plot, indicated similar clustering of the reefs. The more fish-depauperate transects corresponded to transects with the highest levels of macroalgae (BEST r_s =

0.48, $p < 0.001$). Fourteen fish species, including planktivores, invertivores, an obligate corallivore and non-browsing herbivores (a bioeroder, a scraper and two detritivores) contributed to 70% of the similarity within the cluster of transects at the high coral cover, high complexity end (herein referred to as complex coral habitats) of the benthic PC1 (Table 2.1). These 14 species included a primary fishery target species, *Chlorurus sordidus*, and three important- and three occasional fishery by-catch species (Table 2.1). In comparison, only three species – *Thalassoma herbraicum* (an invertivore), *Cheilio inermis* and *Lethrinus harak* (both generalist carnivores, and the latter is an important fishery by-catch species), contributed to 70 % of the similarity within the cluster of transects at the high macroalgae cover, low-complexity end (herein referred to as low-complexity macroalgae habitats) of the benthic PC1 (Table 2.1). One species, *T. herbraicum* was common to both groups. Sixteen species explained 49.3 % of the dissimilarity between the complex coral and low-complexity macroalgae habitats and represent five of the eight defined functional groups (Table 2.1).

The transition along the benthic gradient from complex coral to low-complexity macroalgae associated with PC1 (Fig. 2.1), corresponded with a decline in fish functional group diversity ($r^2 = 0.375$, $p < 0.001$; Fig. 2.3a), overall fish species richness ($r^2 = 0.434$, $p < 0.001$; Fig. 2.3b) but not total fish abundance ($r^2 = 0.081$, $p > 0.05$, Fig. 2.3c)(Table 2.2). For the abundance of fish within functional groups, PC1 of the benthic PCA corresponded with a strong decline in obligate corallivore abundance ($r^2 = 0.754$, $p < 0.001$, Fig. 2.4a), a weak decline in invertivore abundance ($r^2 = 0.139$, $p < 0.05$, Fig. 2.4b), and a very weak increase in browsing herbivore abundance ($r^2 = 0.066$, $p < 0.05$, Fig. 2.4c)(Table 2.2). No relationships were found between the benthic habitat gradient and the abundances of the other five fish functional groups (Table 2.2; non-browsing herbivorous species also Fig. 2.4d).

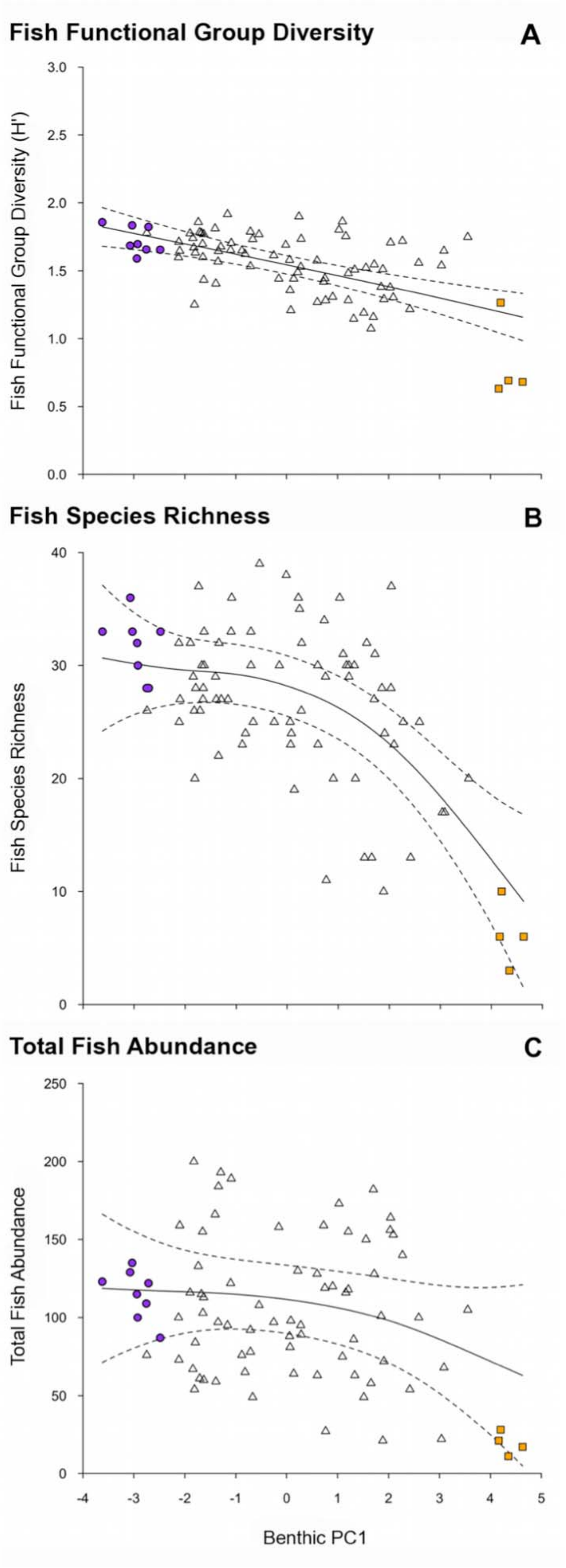

Fig. 2.3 Relationships between the gradient in benthic habitat condition and fish assemblage metrics. Benthic habitat condition (PC1 axis): negative values – complex coral habitats; high values – low-complexity macroalgae habitats. Fish assemblage metrics: (a) fish functional group diversity (an index calculated using the Shannon-Weiner diversity index (H') at the functional group level), (b) fish species richness, (c) total fish abundance. Plotted are fitted parameter estimates ± 95% confidence intervals based on GAM with Reef as a random variable. Note that (c) represents a statistically non-significant relationship. Two extreme outliers were excluded from (C) to aid visual representation, but were included in the analysis. Symbols as in previous Figures. Note different scales along y-axis.

Table 2.1 Fish taxa contributing to the similarity within, and dissimilarity between, the extreme groups of low-complexity macroalgae and complex coral.

			Similarity		Dissimilarity
Species	FG	FP	Macroalgae (49.5%)	Coral (46.8%)	(88.7%)
Lethrinus harak	Ca	I	35.69		2.67
Cheilio inermis	Ca	N	30.91		3.21
Thalassoma herbraicum	In	N	14.68	6.02	2.11
Chromis atripectoralis	Pl	N		9.75	5.45
Chlorurus sordidus	HO	P		8.95	4.12
Chaetodon trifasciatus	Co	N		8.19	4.42
Plectroglyphidodon lacrymatus	HO	N		5.43	3.87
Pomacentrus sulfureus	Pl	N		5.29	3.92
Gomphosus caeruleus	In	O		5.09	3.11
Ambyglyphidodon leucogaster	Pl	N		4.08	3.33
Cheilinus trilobatus	In	I		4.03	1.63
Labroides dimidiatus	In	N		3.69	2.30
Scarus niger	HO	I		3.26	2.68
Halichoeres marginatus	In	O		2.73	2.23
Ctenochaetus striatus	HO	I		2.70	2.21
Halichoeres hortulanus	In	O		2.70	2.05
Pomacentrus trilineatus	Pl	N			2.24
Carangidae	Pi	P			2.00
Hemigymnus fasciatus	In	O			1.76
Halichoeres nebulosus	In	O			1.69
Zanclus cornutus	In	O			1.55
Stethojulis albovittata	In	O			1.53
Labrichthys unilineatus	Co	O			1.44
Macropharyngodon bipartitus	In	O			1.40
Oxymonacanthus longirostris	Co	N			1.32
Centropyge multispinis	In	O			1.30
Scolopsis frenatus	In	O			1.27
Lethrinus obsoletus	Ca	I			1.24
Chromis ternatensis	Pl	N			1.18
Zebrasoma scopas	HO	N			1.11
TOTAL % contribution			81.28	71.91	70.33

SIMPER analysis performed on square-root transformed abundance data. Cutoff for low contributions: 70%. Average similarity or dissimilarity reported in parentheses. Functional group (FG) acronyms defined in Fig. 2 legend. Fishing pressure (FP) exerted on the species. P – primary target; I – important by-catch; O – occasional by-catch; N – not targeted.

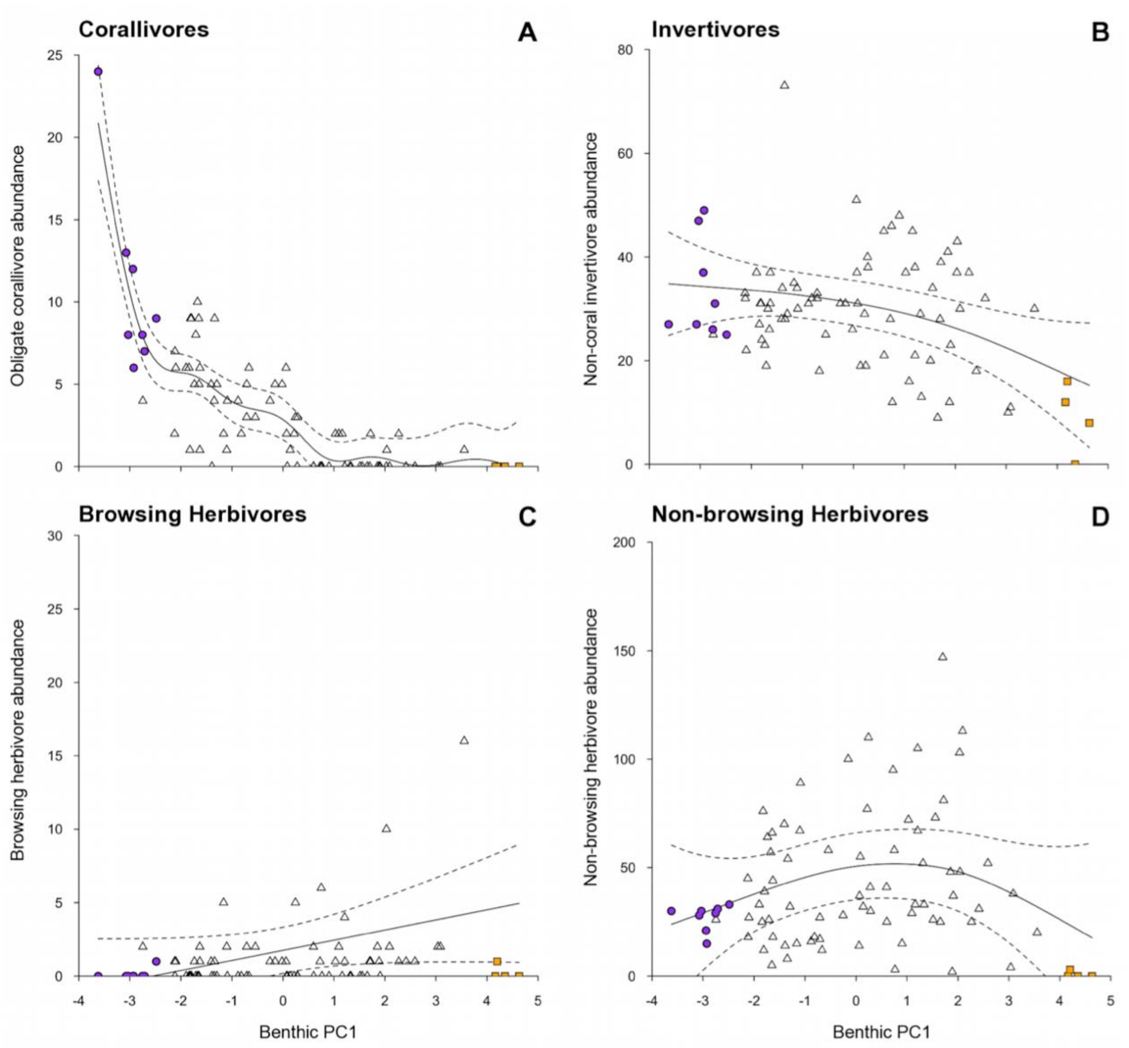

Fig. 2.4 Relationships between the gradient in benthic habitat condition and abundances of fish functional groups. Benthic habitat condition (PC1 axis): low values – complex coral habitats; high values – low-complexity macroalgae habitats. Abundances of fish functional groups: (a) obligate corallivores, (b) non-coral invertivores, (c) browsing herbivores, and (d) non-browsing herbivores. Plotted are fitted parameter estimates ± 95% confidence intervals based on GAM with Reef as a random variable. Note that (d) represents a statistically non-significant relationship. An extreme outlier was excluded to aid visual representation from (B), (C), and (D), but was included in the analyses. Symbols as in previous Fig.s. Note different scales along y-axis.

The transition along the benthic gradient from complex coral to low-complexity macroalgae associated with PC1 (Fig. 2.1), corresponded with a decline in fish functional group diversity ($r^2 = 0.375$, $p < 0.001$; Fig. 2.3a), overall fish species richness ($r^2 = 0.434$, $p < 0.001$; Fig. 2.3b) but not total fish abundance ($r^2 = 0.081$, $p > 0.05$, Fig. 2.3c)(Table 2.2). For the abundance of fish within functional groups, PC1 of the benthic PCA corresponded with a strong decline in obligate corallivore abundance ($r^2 = 0.754$, p

< 0.001, Fig. 2.4a), a weak decline in invertivore abundance ($r^2 = 0.139$, $p < 0.05$, Fig. 2.4b), and a very weak increase in browsing herbivore abundance ($r^2 = 0.066$, $p < 0.05$, Fig. 2.4c)(Table 2.2). No relationships were found between the benthic habitat gradient and the abundances of the other five fish functional groups (Table 2.2; non-browsing herbivorous species also Fig. 2.4d).

Table 2.2 Results of generalized additive mixed models (GAMM) used to model response variables with respect to the gradient in benthic habitat (Benthic PC1), with Reef as a random variable.

Response variable	*Df*	*F*	*p*	r^2
Fish functional group diversity	1.15	26.024	**	0.375
Fish species richness	2.687	27.135	**	0.434
Total fish abundance	1.642	3.133	NS	0.081
Obligate corallivores	7.546	26.938	**	0.749
Browsing herbivores	1	2.789	*	0.066
Non-browsing herbivores	2.226	1.756	NS	0.094
Non-coral invertivores	1.775	4.963	*	0.139
Generalist carnivores	1	0.002	NS	-0.012
Omnivores	2.336	3.593	NS	0.104
Piscivores	1	3.523	NS	0.05
Planktivores	1	2.127	NS	0.08

df: estimated degrees of freedom for smooth term (Benthic PC1; 1 = linear).
p: ** p <0.001, * p <0.05, NS p > 0.05
r^2: proportion of variation explained by the benthic habitat gradient (negative value = model is a worse representation than the Null model).

2.5 Discussion

This study found markedly different fish composition along a multivariate gradient of reef benthic conditions ranging from complex coral habitats to low-complexity macroalgae habitats. Very different fish assemblages were linked with the two habitat extremes, not only in terms of species present, but also richness and diversity at both species and functional group level. The strongest relationships with the habitat gradient were found at the overall fish assemblage scale, rather than at the individual functional group scales. Obligate corallivorous fishes were the exception, and are known for their dependence upon live corals (Pratchett 2005). The dependence of reef fish assemblages on the coral reef benthos has been demonstrated through numerous before-after studies of fish and benthic changes through disturbance events (reviewed by: Wilson et al. 2006; Pratchett et al. 2008). In contrast, this study assesses links between a broad array of benthic conditions following disturbance and their resident reef fish assemblages, providing useful insights into potential future compositions of reef communities.

At the extreme ends of the benthic gradient, complex coral habitats support a higher number of fish species and functional groups than low-complexity habitats dominated by macroalgae. A major consequence for many ecosystems facing degradation is ecological homogenisation, whereby multiple specialist species or groups are replaced by fewer, more generalist species or groups leading to much simpler ecosystems (McKinney and Lockwood 1999; Devictor et al. 2008). Our results appear to support this theory with the low-complexity macroalgae habitats lacking many of the more specialised coral reef fish functional groups (e.g. obligate corallivores and coral-associated planktivores; Munday 2004; Wilson et al. 2007) and also the essential groups for the provision of key ecological processes (e.g. herbivores; Bellwood et al. 2004; Arthur et al. 2006; Bellwood et al. 2006a). While macroalgae provide 3-dimensional structure, in comparison to the often intricate and unyielding skeletal structures of scleractinian corals, it is a more homogeneous and flexible habitat that appears to be less favourable to reef fishes (Hoey and Bellwood 2011).

Macroalgal-dominated reefs have long been regarded as degraded reef states (Hughes 1994). This study provides some empirical evidence that macroalgal-dominated reefs are unfavourable for the wider ecosystem’s ecological communities and economic potential. Nevertheless, habitats with abundant macroalgae can be naturally occurring and provide important refuges for juvenile reef-associated fishes

(Wilson et al. 2010b). Juvenile *Cheilio inermis* for example, are present only in *Sargassum* stands in Western Australia (Wilson et al. 2010b). Also, *Sargassum* and *Turbinaria* algal stands have been present on Seychelles coral reefs for some time (Taylor 1968; Stoddart 1984), although the influence of human settlement on macroalgal presence is not known. Importantly, macroalgal cover has shown substantial expansion following the 1998 bleaching event (Graham et al. 2006) and is continuing to increase in cover (Wilson et al. 2012). Given the high cover of macroalgae documented in our study, and the habitats surveyed, it is likely that some of the sites represented recently degraded reef states. Our study suggests that expansion of macroalgae on reefs may have substantial negative repercussions for associated fish diversity.

Herbivores are considered the most important functional group of fish on coral reefs through their role in mediating the competition for space between corals and algae (Bellwood et al. 2004; Hughes et al. 2007; Pratchett et al. 2011a). Indeed, negative relationships exist between herbivore biomass and macroalgae cover (Fox and Bellwood 2007; Friedlander et al. 2007; Mumby et al. 2007a; Wismer et al. 2009), although a distinction has been found between herbivorous species that maintain low algal biomass, and browsing species that will consume mature macroalgae thalli (Bellwood et al. 2006a; Hoey and Bellwood 2009). Surprisingly therefore, there was no substantial increase in either of the two herbivorous functional groups along the benthic gradient found in this study. Similarly, a study of benthic changes across seven countries in the Indian Ocean spanning the 1998 coral bleaching event found no increase in herbivore abundance in response to the increase in benthic space available for algal growth (Graham et al. 2008b), while browsing species in Australia show no correlation with increasing macroalgal cover on the GBR (Wismer et al. 2009) or Ningaloo reef (Johansson et al. 2010). Although browsing herbivores have been able to reverse phase shifts in small-scale experimental settings surrounded by intact reef (Bellwood et al. 2006a), reefs with high fleshy macroalgal cover tend to have low functional redundancy amongst browsing herbivores (Hoey and Bellwood 2009), and dense macroalgal stands can inhibit herbivory (Hoey and Bellwood 2011). Indeed, the ability of browsing herbivores to perform their vital function on macroalgae-dominated reef systems is very poorly understood.

The identified differences in the fish community with changing benthic condition are likely to have implications for ecosystem service provision (Done 1992; Elmqvist et al. 2003; Payet and Agricole 2006; Thrush et al. 2009). Major ecosystem services associated with reef fishes include the provision of fisheries and tourism (Costanza et al. 1997; Moberg and Folke 1999; Worm et al. 2006). Therefore, as fish species richness and functional group diversity decreases across the benthic condition gradient, the multi-species fishery and substantial dive tourism industry of the Seychelles are likely to be negatively affected by shifts away from complex coral-dominated reefs (Grandcourt and Cesar 2003; Payet and Agricole 2006; Graham et al. 2007). Specifically, there was a 5-fold difference in fish abundances at the benthic extremes of our study: reefs with high macroalgal cover had an average of 19.3 (± 3.6 SE) fish per 250 m^2 compared to 105.3 (± 5.4 SE) fish per 250 m^2 at the reef with the highest overall coral cover and complexity. Moreover, two of the five primary fishing target species, and 19 important by-catch species (Grandcourt 1999) were present on reefs with highest overall coral cover and complexity compared to no primary target species, and only one important by-catch species on low complexity and macroalgae-dominated reefs. This 5-fold difference in total fish abundance and the reduction in target species, is likely to reflect a decline in fishery potential. This contrasts with results from the Caribbean where macroalgae-dominated reefs appeared to sustain high fish species richness (Mumby et al. 2008). Similarly, studies of tourist preferences show that fish abundance and diversity play a major role in attracting and satisfying dive tourists (e.g. Shafer and Inglis 2000; Williams and Polunin 2000; Uyarra et al. 2005).

Although we predicted that the stability of the underlying substratum would interact with the condition of the benthos, with stable substrata having higher coral cover than mobile rubble reefs, we found only weak relationships. Studies in rubble-dominant locations, such as former dynamite fishing areas, have found substantially lower coral cover on rubble versus stable rocky sites (Fox 2004). Furthermore, other macro-benthic organisms such as reef sponges have been found to have decreased growth rates on mobile rubble substrata compared to stable rock substrata (Duckworth and Wolff 2011). Our results showed that many of the rubble dominated transects did have low coral cover (where rubble was > 80%, mean coral cover was 4.9% (± 1.9 SE)). However, many other transects that had little rubble also had low coral cover (22 of 46 transects with < 5% rubble had < 10% coral cover), indicating that substratum stability was not the only variable influencing coral cover. Interestingly however, both the coral-dominated and macroalgal-dominated extremes were associated with more stable substrata, suggesting that substratum stability is important in enabling these macrobenthic organisms to survive to maturity.

The multivariate gradient of benthic conditions found in this study indicates a continuum of reef states. However, in the absence of long-term time series data and/or experimental manipulations it is not possible to establish the stability of our extreme benthic state categories (Petraitis et al. 2009). Similarly, the reefs in the middle of the continuum may be fairly stable in their own right, or in transition (i.e. degrading or recovering) between different characteristic equilibrium states because of various natural disturbances or perturbations (Walker 1993; Brown 1997; Halford et al. 2004;

Hughes et al. 2010). Regardless, it is clear that more degraded reefs, in terms of coral cover, diversity and structural complexity, host more depauperate reef fish assemblages.

As coral reefs continue to degrade due to a range of anthropogenic drivers, and alterations in community compositions occur, it is imperative that we understand how changes in one aspect of an ecosystem affect the rest of the ecosystem. From a management perspective, the fact that many reefs do not exist in discrete states means that few generalisations are possible, and reef specific data may be required to implement necessary management plans (Westoby et al. 1989; Walker 1993). While many previous studies have linked loss of fish diversity with loss of coral cover, the lack of reciprocal increases in herbivorous fishes to counter increases in algal cover is alarming, with negative implications for the continuation of many coral reef ecosystem processes and services if more reefs shift to macroalgal-dominated states. Clearly, prevention of further reef degradation through a reduction in anthropogenic pressures, is of critical importance because the repercussions of declining habitat condition may be far reaching.

CHAPTER 3

Bottlenecks to coral recovery in the Seychelles[2]

3.1 Abstract

Processes that affect recovery of coral assemblages require investigation because coral reefs are experiencing a diverse array of more frequent disturbances. Potential bottlenecks to coral recovery include limited larval supply, low rates of settlement, and high mortality of new recruits or juvenile corals. We investigated spatial variation in local abundance of scleractinian corals in the Seychelles at three distinct life history stages (recruits, juveniles, and adults) on reefs with differing benthic conditions. Following widespread coral loss due to the 1998 bleaching event, some reefs are recovering (i.e. relatively high scleractinian coral cover: ‘coral-dominated’), some reefs have low cover of living macro-benthos and unconsolidated rubble substrates (‘rubble-dominated’), and some reefs have high cover of macroalgae (‘macroalgal-dominated’). Rates of coral recruitment to artificial settlement tiles were similar across all reef conditions, suggesting that larval supply does not explain differential coral recovery across the three reef types. However, acroporid recruits were absent on macroalgal-dominated reefs (0.0 ± 0.0 recruits tile^{-1}) in comparison to coral-dominated reefs (5.2 ± 1.6 recruits tile^{-1}). Juvenile coral colony density was significantly lower on macroalgal-dominated reefs (2.4 ± 1.1 colonies m^{-2}), compared to coral-dominated reefs (16.8 ± 2.4 m^{-2}) and rubble-dominated reefs (33.1 ± 7.3 m^{-2}), suggesting that macroalgal-dominated reefs have either a bottleneck to successful settlement on the natural substrates, or a high post-settlement mortality bottleneck. Rubble-dominated reefs had very low cover of adult corals (10.0 ± 1.7%) compared to coral-dominated reefs (33.4 ± 3.6%) despite

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no statistical difference in their juvenile coral densities. A bottleneck caused by low juvenile colony survivorship on unconsolidated rubble-dominated reefs is possible, or alternatively, recruitment to rubble-dominated reefs has only recently begun. This study identified bottlenecks to recovery of coral assemblages that varied depending on post-disturbance habitat condition.

3.2 Introduction

Recovery of coral reefs in the aftermath of major disturbances involves reassembly of the scleractinian coral community, in particular habitat-forming corals (Connell 1997; Jones et al. 2004). Scleractinian corals are characterised by open populations (Roughgarden et al. 1988; Caley et al. 1996), with complex life histories that are typically categorised into two phases: a dispersive pelagic larval phase and a sessile benthic phase during which the organism develops from recruit (< 1 cm diameter) to juvenile (< 5 cm diameter) to adult (Ritson-Williams et al. 2009; Penin et al. 2010). Reef recovery is stimulated by coral recruitment (Connell et al. 1997; Hughes et al. 2010; Graham et al. 2011), the addition to and/or resupply of local populations (i.e. a spatially distinct aggregation of individuals) via the inflow of new individuals. The endurance of the recovery process will be influenced by the recruits' post-settlement survivorship. Even on relatively undisturbed reefs, processes such as mortality and differential growth rates strongly influence the community structure of juvenile and adult assemblages (e.g. Edmunds 2000; Penin et al. 2010; Trapon et al. 2013).

Demographic bottlenecks can hinder the growth of a population to its full potential at each developmental stage of a coral population's life cycle. Demographic bottlenecks refer to low survival of individuals at key stages in their life history as a result of strong regulatory processes, thereby restricting population growth and recovery (e.g. Beck 1995). For scleractinian corals, demographic bottlenecks may first occur because of limited larval supply (Hughes and Tanner 2000; Elmhirst et al. 2009). Due to the dispersive larval phase, coral recruits can originate both locally (i.e. parent colonies are located in the same population that the recruit has settled into) or externally (i.e. parent colonies are located in a different population from which the recruit has settled into; Roughgarden et al. 1988; Caley et al. 1996). Local recruitment (also known as self-recruitment; reviewed by Swearer et al. 2002) is common among corals with a brooding life history strategy (e.g. *Pocillopora damicornis*; Harriott and Fisk 1988) and is thought to be important on isolated reefs, but requires sufficient local broodstock (Smith et al. 2008). If disturbances have severely denuded local adult coral populations, preventing recovery via regrowth of surviving colonies (e.g. Gilmour et al. 2013), external recruitment is thought to be a vital process for a reef's recovery (Nyström et al. 2008; Done et al. 2010; Hughes et al. 2010). Therefore, isolated reefs may be disproportionately affected by disturbances that cause extensive coral loss due to a demographic bottleneck in coral larval supply (e.g. many Western Indian Ocean reefs after the 1998 mass bleaching event; Goreau et al. 2000; Graham et al. 2006).

Aside from larval supply, bottlenecks to recovery may occur in subsequent life history processes, such as successful settlement to the substrate, survival of coral larvae to juvenile corals, and survival of juvenile colonies to adults. Successful settlement may be pre-empted if a reef's benthic community offers few suitable habitats. For example, high macro-benthic cover (macroalgae or scleractinian corals) can pre-empt settlement (space limitation; e.g. Connell et al. 1997), as can dense, minimally grazed algal turfs (Arnold et al. 2010). Coral larvae respond to settlement cues (reviewed by Birrell et al. 2008b), but cues may be received from inadvisable settlement substrates (e.g. the ephemeral algae *Halimeda opuntia*; Nugues and Szmant 2006). A further bottleneck may occur if settled coral larvae do not survive to the juvenile stage. For example, high macro-benthic cover may lead to intense competition for space (Chadwick and Morrow 2011), reducing growth or survivorship (Hughes et al. 2007). Even if corals survive to become juveniles, physical characteristics such as mobile substrata (e.g. unconsolidated rubble) may increase mortality rates via periodic abrasion and/or smothering of small colonies (e.g. Fox et al. 2003). Therefore, local habitat conditions may result in survivorship bottlenecks at settlement and post-settlement stages.

Here we explore demographic bottlenecks for scleractinian corals in an attempt to understand key processes that determine differential recovery and condition of reefs in the inner Seychelles Islands, following extensive coral bleaching and coral loss in 1998 (Goreau et al. 2000). Specifically, we quantify the density and identity of incoming coral recruits, juvenile corals and adult coral cover on reefs in three prominent benthic conditions (defined by their dominant macro-benthic organisms; > 5 cm tall); 1) recovering coral-dominated reefs, 2) reefs now dominated by fleshy brown macroalgae, and 3) reefs with unconsolidated rubble banks. These latter reefs tended to have low cover of living macro-benthic organisms. We use this design to ask 1) whether demographic bottlenecks to coral recovery occur following a major disturbance event, and 2) whether different bottlenecks occur on reefs of differing condition.

3.3 Methods

The Seychelles comprises a mix of granitic and carbonate islands in the western Indian Ocean. The inner islands (4°30’S, 55°30’E) rise from the Mahé Plateau (20-70 m depth) and are predominantly granitic with well-developed carbonate fringing reefs (Braithwaite 1971). Live coral cover on these reefs was decimated by a major bleaching event in 1998 (~90% loss; Goreau et al. 2000), and there have since been additional thermal anomalies in 2003 and 2010 (NOAA 2013). In October 2010, surveys of the reefs around the inner islands revealed a variety of reef benthic conditions, with reefs primarily differentiated by the amount of scleractinian coral versus macroalgal cover present (Chong-Seng et al. 2012: Chapter 2). Also, high cover of macro-benthic organisms (e.g. corals and/or macroalgae) was associated with more stable underlying substrates, whereas unconsolidated rubble substrates had much lower cover of larger benthic organisms (Chong-Seng et al. 2012). The current study was carried out at approximately 4 m depth, on a subset of nine of these surveyed carbonate fringing reefs (Fig. 3.1). Three reefs (C1-3) had stable substrates with low macroalgal cover, but high coral cover, hereafter “coral-dominated”. Three reefs (M1-3) had relatively stable substrates with high macroalgal cover (a mix of *Sargassum* spp., *Turbinaria* spp., *Lobophora* spp., *Chlorodesmis* spp., *Halimeda* spp., and *Asparagopsis taxiformis*), but low scleractinian coral cover, hereafter “macroalgal-dominated”. Three reefs (R1-3) had mobile, unstable substrates with low macroalgal and coral cover, but a mixture of turf and crusotose coralline algae growing on rubble pieces, hereafter “rubble-dominated” (Fig. 3.2, Table 3.1). All of these reefs had high coral cover pre-disturbance (Jennings et al. 1995; Spalding and Jarvis 2002). Prevailing winds around the inner Seychelles come from the southeast between May and October, and the northwest between December and March, with the former bringing the strongest winds (monthly means 10 versus 6 knots respectively; M Belmont and V Amelie, Seychelles Meteorological Services). The study reefs are placed fairly indiscriminately around the two larger, populated islands (Mahé and Praslin), with no obvious physical reasons for the disparate recovery trajectories post-disturbance, although the rubble-dominated reefs as a group may be more exposed to the prevailing southeasterly winds (Fig. 3.1).

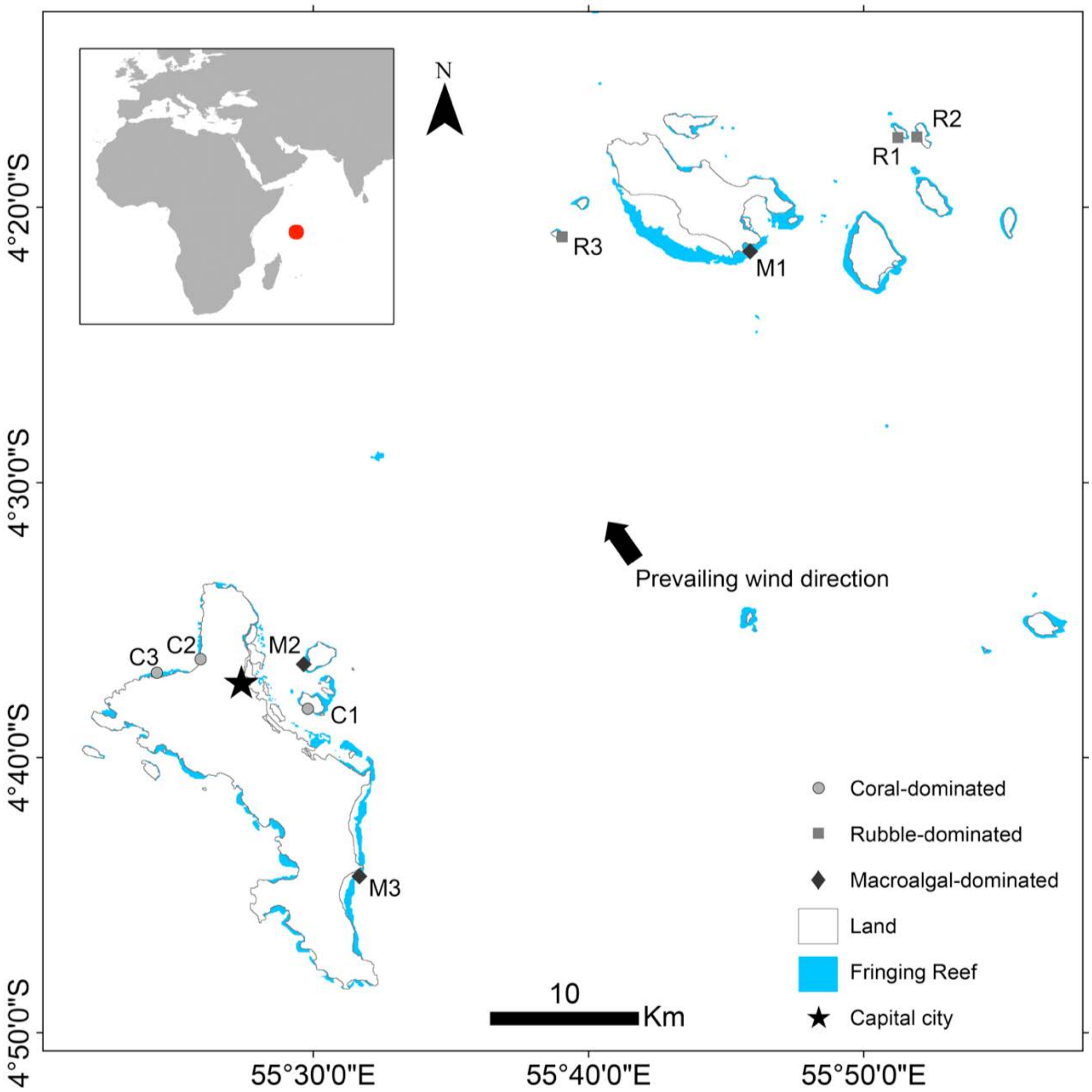


Fig. 3.1 Map of the study sites, with the location of the Seychelles Islands within the Western Indian Ocean inset. Predominant prevailing wind direction is shown (see text). The three larger, populated islands are labelled in italics. Base map from Andréfouët et al. (2006).

3.3.1 ***Recruitment patterns***

To assess spatial variation in settlement among reefs in different conditions, 10 clay tiles (11 x 11 x 1 cm), unglazed on the base, were attached to half concrete construction blocks using stainless steel bolts and spacers. Concrete blocks were used, rather than the more common method of base plates for direct attachment (Mundy 2000), due to difficulty attaching tiles directly to a rubble substrate (e.g. Fox 2004). In

January 2012, tiles were haphazardly placed onto each reef within an area of approximately 125 m^2, with adjacent tiles separated by a minimum of 1 m. After three months, all tiles were collected, bleached, sun-dried, and the underside examined for coral recruits using a dissecting microscope. Only three families of newly settled corals were distinguished (Acroporidae, Pocilloporidae, Poritidae), following Babcock et al. (Babcock et al. 2003). All other families were pooled into a category, ‘other’, while recruits that were damaged, or had insufficient development to be excluded from the known families were listed as ‘unknown’.

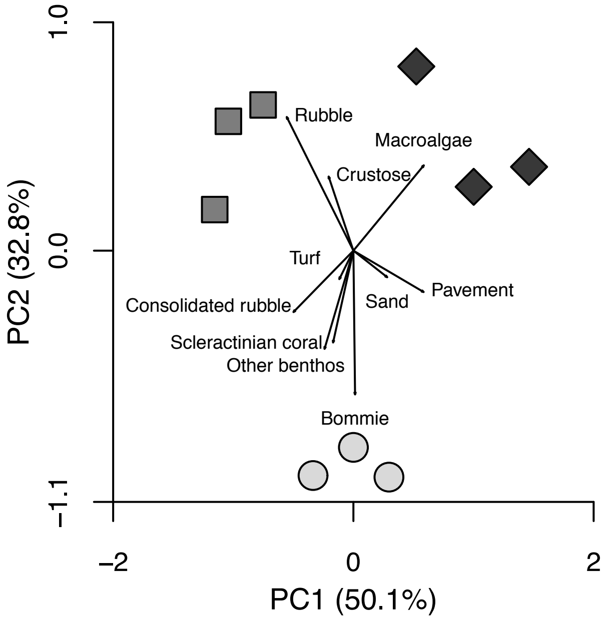


Fig. 3.2 Correlation-based Principal Components Analysis of the nine study reefs, depicting the cover of biotic benthos and underlying substrate. Data units were percentage cover based on simultaneous collection of cover of biotic benthos (macroalgae, scleractinian coral, turf algae, crustose coralline algae, sand) and underlying physical substrate (Rubble – loose dead coral rubble; Consolidated rubble – rubble pieces that were showing visual and tactile signs of amalgamation; Bommie – isolated coral outcrops; Pavement – solid carbonate reef structure) from four 50 m point-intercept transects. Data was natural log transformed to improve spread of the data. Pale gray circles – coral-dominated reefs; medium gray squares – rubble-dominated reefs; dark gray diamonds – macroalgal-dominated reefs.

3.3.2 ***Juvenile abundance patterns***

The size and genus of all juvenile scleractinian corals (< 5 cm in diameter) with their centre point enclosed in 10 haphazardly placed 0.11 m^2 (33 x 33 cm) quadrats were recorded at each of the nine reefs in the area surrounding the recruitment tiles in January 2012. Small quadrat sizes were chosen since 1 m^2 quadrats can greatly under-sample true juvenile coral abundance (Miller et al. 2000). Colonies obviously resulting from fission, shrinkage, or fragmentation of older colonies were excluded (Hughes and Jackson 1985).

3.3.3 ***Adult cover patterns***

Adult coral density was approximated using percentage cover. Coral cover estimates were collected in October 2010 using four haphazardly placed 50 m point-intercept transects, perpendicular to the reef slope, recording the live benthos under the tape to genera and/or functional group every 0.5 m (Chong-Seng et al. 2012). Although this represents coral cover 15 to 18 months prior to the collection of the juvenile and recruit data, there were no significant physical disturbances in the interim and coral cover patterns are therefore unlikely to have changed substantially over that time period.

3.3.4 ***Statistical Analyses***

Variation in settlement rates, juvenile coral density, and adult cover were each examined using Poisson distributed, generalised linear mixed effects models (GLMM) fit by the Laplace Approximation using the lme4 package in R (Bates et al. 2011; R Development Core Team 2011), with Reef nested within Condition (coral-, rubble-, macroalgal-dominated). The analyses were performed for each of the three dominant families separately (Acroporidae, Pocilloporidae, Poritidae), and for all individuals pooled. Where overdispersion was present, an observation-level random effect was included in the model (Elston et al. 2001).

To determine whether there were differences in the family-level community compositions of settling recruits, juvenile corals and adult coral cover, on reefs in different conditions, we performed three two-factor permutational multivariate analyses of variance (PERMANOVA) with Condition (fixed factor, three levels: coral-, rubble- and macroalgal-dominated) and Reef (random factor). PERMANOVAs used zero-adjusted Bray-Curtis dissimilarities among samples (Clarke et al. 2006) calculated from untransformed data. Where significant variation was found amongst groups (e.g. at the Condition or Reef level), analyses of similarity (ANOSIM), with pairwise comparisons, were performed to identify which conditions or reefs were driving the differences (Clarke 1993). Additionally, similarity of percentages analyses (SIMPER) were used to determine which coral families contributed most to observed differences (Clarke 1993). These analyses were performed in PRIMER v6 with the PERMANOVA+ add on package (n = 9999 permutations; Clarke and Gorley 2006, Anderson et al. 2008). Additionally, we checked whether adult cover influenced recruitment rates (i.e. supply-side relationships) at the reef level using a linear regression for each of the Acroporidae, Poritidae, Pocilloporidae, and all families combined. This analysis did not take reef condition into account, but rather investigated the contribution of local adult corals to the recruitment rate. Due to the small sample sizes (n = 9 reefs), bootstrapping was used to estimate confidence intervals around the regression coefficients (n = 9999 randomisations; Logan 2010).

3.4 Results

3.4.1 ***Recruits***

Reef condition had no significant influence on total recruitment rates (likelihood ratio test between models with and without Condition as a fixed effect; $\chi^2 = 1.43$, df = 2, p = 0.490), or recruitment rates of two of the three dominant families (Pocilloporidae: $\chi^2 = 2.21$, df = 2, p = 0.331 and Poritidae: $\chi^2 = 2.78$, df = 2, p = 0.249; Fig. 3.3a-d, Tables 3.1, 3.2). Significantly fewer Acroporidae recruits were found on macroalgal-dominated reefs compared to coral-dominated reefs (GLMM, z=-2.3, p=0.02), although rubble-dominated reefs did not differ significantly in acroporid recruitment rates from either coral- or macroalgal-dominated reefs (Fig. 3.3b, Table 3.2).

There was no significant difference among reef conditions for the coral recruit community (PERMANOVA, $F_P = 0.8$, df = 2, p = 0.57) although there was large variation among reefs (PERMANOVA, $F_P = 6.9$, df = 6, p < 0.001; Appendix B Fig. S1). ANOSIM and SIMPER contrasts revealed that among reef variation was driven primarily by reef C2 (average ANOSIM R_{C2} contrasts = 0.82) having significantly higher acroporid recruits than all the other reefs in pairwise comparisons (Fig. 3.3b). There was also a significant difference between C1 and M1 reefs (ANOSIM $R_{\mathrm{C1\text{-}M1}} = 0.56$, p = 0.02), driven by pocilloporid recruits (Fig. 3.3d).

3.4.2 ***Juveniles***

Total coral juvenile density was significantly lower on macroalgal-dominated reefs, compared to both coral- and rubble-dominated reefs (coral; GLMM, z = -2.6, p = 0.009; rubble: GLMM, z = -2.7, p = 0.007; Tables 3.1, 3.2). Comparing juvenile densities of the three dominant families individually found no significant influence of reef condition for Pocilloporidae (likelihood ratio test between models with and without

Condition as a fixed effect; $\chi^2 = 3.3$, df = 2, p = 0.192) and Poritidae ($\chi^2 = 3.7$, df = 2, p = 0.154; Table 3.2). A significant effect of reef condition was indicated for acroporid juveniles ($\chi^2 = 11.0$, df = 2, p < 0.01), likely driven by macroalgal-dominated reefs because coral- and rubble-dominated reefs did not differ significantly, however there was high uncertainty around the estimates for macroalgal-dominated reefs (Table 3.2).

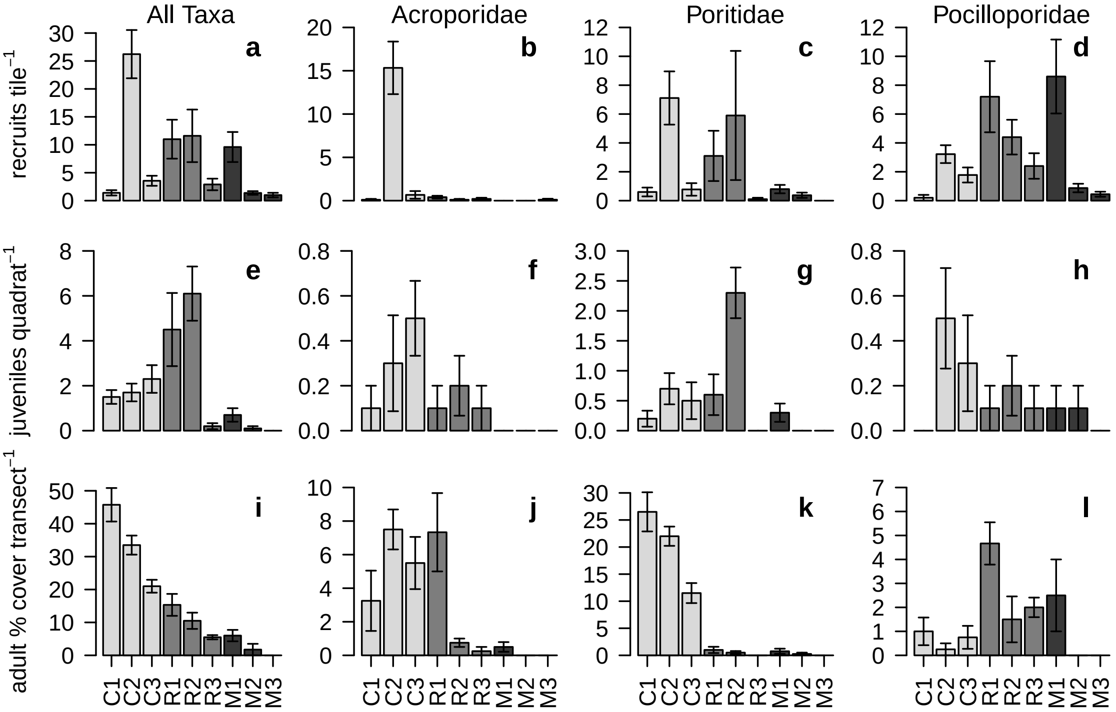


Fig. 3.3 Mean (± SE) coral colony densities on each of the nine reefs in the three benthic conditions. Pale gray bars – coral-dominated reefs; medium gray bars – rubble-dominated reefs; dark gray bars – macroalgal-dominated reefs. **(a-d)** number of coral recruits per tile **(e-h)** number of juvenile coral colonies (≤5 cm) per quadrat **(i-l)** percent coral cover per transect. Data are presented for all individuals combined and for Acroporidae, Poritidae and Pocilloporidae separately.

There was no significant difference among reef conditions for the juvenile coral community (PERMANOVA, $F_P = 2.0$, df = 2, p = 0.11) although there was large variation among reefs (PERMANOVA, $F_P = 5.9$, df = 6, p < 0.001) (Fig. 3.3e-h, Appendix B Fig. S2). ANOSIM and SIMPER contrasts revealed that this variation between reefs was driven by reef R2 (average ANOSIM R_{R2} contrasts = 0.64), with higher poritid and fungiid juvenile densities than other reefs (excluding C2 and R1; Fig. 3.3e-h).

Table 3.1 For each benthic condition, reef-level averages (% mean ± SE) of key benthic fauna (scleractinian corals and macroalgae) and mobile underlying substrate (see Chong-Seng et al. 2012 for methods distinguishing between the live macrobenthos and the underlying substrate). Also, reef-level averages (mean ± SE) of coral juvenile densities and recruitment rates. Recruitment rates are expressed as both no. recruits tile^{-1} and no. recruits m^{-2}. The latter represent standardised units, enabling comparisons with other studies.

Benthos (units)		Coral-dominated	Rubble-dominated	Macroalgae-dominated
Macroalgae	(% cover)	1.8 ± 0.6	0.5 ± 0.5	58.3 ± 6.9
Rubble	(% cover)	1.4 ± 1.0	71.6 ± 7.8	18.1 ± 10.6
Coral adults	(% cover)	33.4 ± 3.6	10 ± 1.7	2.6 ± 1.1
Coral recruits	(recruits tile^{-1})	10.1 ± 2.5	8.5 ± 2.0	4.3 ± 1.3
Coral recruits	(recruits m^{-2})	832 ± 210	703 ± 169	355 ± 104
Coral juveniles	(colonies m^{-2})	16.8 ± 2.4	33.1 ± 7.3	2.4 ± 1.1

3.4.3 ***Adults***

Adult coral cover differed significantly depending on reef condition. Of the three reef conditions, coral-dominated reefs had the highest total coral cover (GLMM, $z = 9.5$, $p < 0.001$), particularly poritid corals (GLMM, $z = 14.4$, $p < 0.001$; Fig. 3.3k, Tables 3.1, 3.2). Macroalgal-dominated reefs had the lowest total coral cover (GLMM, $z = -5.2$, $p < 0.001$), particularly acroporid corals (GLMM, $z = -3.5$, $p < 0.001$; Fig. 3.3j, Tables 3.1, 3.2). Rubble-dominated reefs had significantly higher total coral cover (GLMM, $z = 3.0$, $p = 0.003$) and pocilloporid cover (GLMM, $z = 1.9$, $p = 0.042$; Fig. 3.3l) than macroalgal-dominated reefs (Tables 3.1, 3.2).

Adult coral communities also differed significantly depending on reef condition (PERMANOVA, $F_P = 7.8$, df = 2, $p < 0.001$; Fig. 3.3i, Appendix B Fig. S3). ANOSIM (Global $R = 0.82$, $p = 0.01$) and SIMPER contrasts revealed that coral communities on coral-dominated reefs were characterised by poritids and acroporids (66.6 % similarity), on rubble-dominated reefs by free-living fungiids and pocilloporids (44.1 % similarity), and on macroalgal-dominated reefs by occasional faviid and pocilloporid colonies (6.1 % similarity; Fig. 3.3i-l). There was also large variation among individual reefs within each condition (PERMANOVA, $F_P = 4.4$, df = 6, $p < 0.001$).

3.4.4 ***Supply-side relationship***

The only statistically significant supply-side relationship between adult cover and recruitment rates was a positive relationship for the (primarily) brooding family Pocilloporidae ($R^2_{adj}=0.55$, F=10.6, df=1,7, p=0.014; Fig. 3.4). No other relationships were found for other coral families, or all the data combined (Acroporidae: F=3.5, df=1,7, p=0.102; Poritidae: F=0.5, df=1,7, p=0.507; combined: F=0.8, df=1,7, p=0.407).

3.4.5 ***Bottlenecks***

Taken together, these results suggest key bottlenecks are present on the rubble- and macroalgal-dominated reefs (summarised in Fig. 3.5). Although macroalgal-dominated reefs received significantly fewer acroporid recruits than coral-dominated reefs, larval supply did not appear to be limiting on study reefs. However, there were significantly fewer juvenile coral colonies on macroalgal-dominated reefs than the other two conditions indicating a potential bottleneck caused by high post-settlement recruit mortality, or unsuccessful settlement. Rubble-dominated reefs had similar juvenile coral communities to coral-dominated reefs, but differed significantly in terms of total adult coral cover, driven particularly by poritid cover. A bottleneck on rubble-dominated reefs caused by high juvenile colony mortality, resulting in poor survivorship to adult colony size classes, is therefore possible. On coral-dominated reefs, all three coral life history stages investigated were present in moderate to high numbers relative to the other two reef conditions in this study.

Table 3.2 Results of Poisson distributed linear multi-level regressions, estimating the influence of reef condition on coral recruitment, juvenile coral density, and adult coral cover of the three most common families (Acr – Acroporidae; Poc – Pocilloporidae; Por – Poritidae), and all colonies combined (Tot – total). Estimates are on a log scale with the coral-dominated condition as the reference level. Reef was a random factor. * – an observation-level random effect was included in the model to account for overdispersion.

		Fixed Effect	Estimate ± Std.Error	z value	Pr(>|z|)
Recruits	Acr*	(Intercept)	0.01 ± 0.87	0	0.993
		Condition:Rubble	-1.9 ± 1.28	-1.5	0.137
		Condition:Macroalgae	-4.17 ± 1.78	-2.3	**0.020**
	Poc*	(Intercept)	-0.09 ± 0.58	-0.1	0.882
		Condition:Rubble	1.19 ± 0.81	1.5	0.139
		Condition:Macroalgae	0.28 ± 0.82	0.3	0.737
	Por*	(Intercept)	-0.11 ± 0.7	-0.2	0.872
		Condition:Rubble	-0.41 ± 1	-0.4	0.681
		Condition:Macroalgae	-1.81 ± 1.07	-1.7	0.090
	Tot*	(Intercept)	1.42 ± 0.58	2.4	**0.015**
		Condition:Rubble	0.13 ± 0.82	0.2	0.870
		Condition:Macroalgae	-0.82 ± 0.83	-1.0	0.326
Juveniles	Acr	(Intercept)	-1.2 ± 0.33	-3.6	**0.000**
		Condition:Rubble	-0.81 ± 0.6	-1.4	0.177
		Condition:Macroalgae	-19.1 ± 4678.32	0.0	0.997
	Poc	(Intercept)	-1.32 ± 0.35	-3.7	**0.000**
		Condition:Rubble	-0.69 ± 0.61	-1.1	0.258
		Condition:Macroalgae	-1.39 ± 0.79	-1.8	0.080
	Por	(Intercept)	-0.93 ± 0.66	-1.4	0.155
		Condition:Rubble	0.26 ± 0.93	0.3	0.777
		Condition:Macroalgae	-1.89 ± 1.13	-1.7	0.094
	Tot*	(Intercept)	0.4 ± 0.57	0.7	0.490
		Condition:Rubble	0.11 ± 0.82	0.1	0.895
		Condition:Macroalgae	-2.43 ± 0.93	-2.6	**0.009**
Adults	Acr	(Intercept)	1.62 ± 0.53	3.1	**0.002**
		Condition:Rubble	-1.29 ± 0.79	-1.6	0.102
		Condition:Macroalgae	-3.77 ± 1.08	-3.5	**0.000**
	Poc	(Intercept)	-0.57 ± 0.59	-1.0	0.332
		Condition:Rubble	1.42 ± 0.77	1.9	0.064
		Condition:Macroalgae	-0.2 ± 0.86	-0.2	0.813
	Por	(Intercept)	2.94 ± 0.2	14.4	**0.000**
		Condition:Rubble	-3.77 ± 0.54	-7.0	**0.000**
		Condition:Macroalgae	-4.1 ± 0.58	-7.0	**0.000**
	Tot*	(Intercept)	3.45 ± 0.36	9.5	**0.000**
		Condition:Rubble	-1.2 ± 0.52	-2.3	**0.020**
		Condition:Macroalgae	-2.9 ± 0.56	-5.2	**0.000**

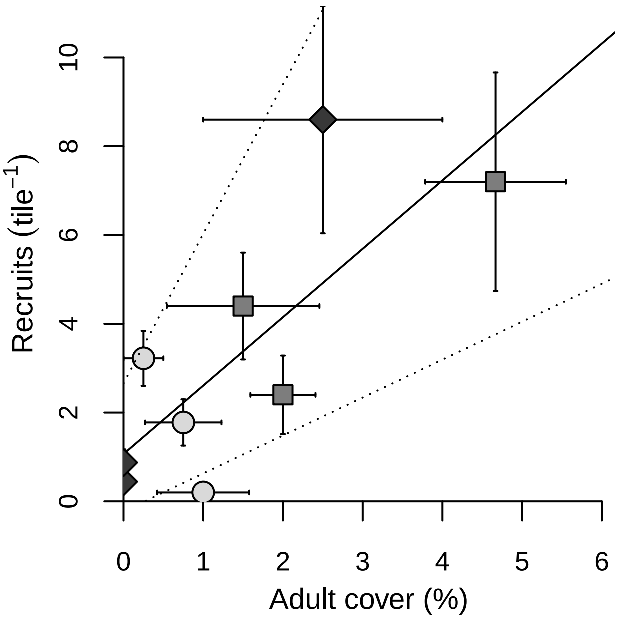
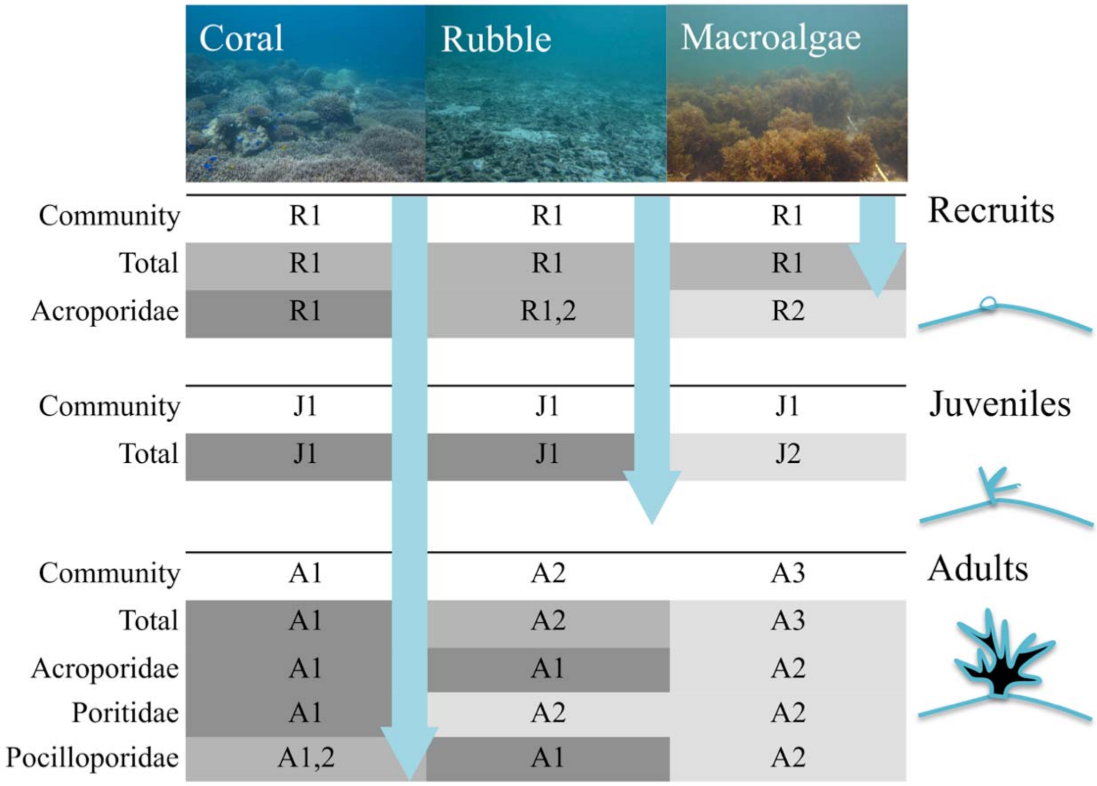


Fig. 3.4 The relationship between cover of adult colonies and density of recruits at each reef for the Pocilloporidae. Error bars represent standard error. Dotted lines represent 95% confidence intervals from bootstrapped regression parameters. Pale gray circles – coral-dominated reefs; medium gray squares – rubble-dominated reefs; dark gray diamonds – macroalgal-dominated reefs.

3.5 Discussion

Differential recovery of coral assemblages in the aftermath of major disturbances is often attributed to local supply of coral larvae (e.g. Williams et al. 2008; Gilmour et al. 2013) or availability of suitable settlement substrate (e.g. Connell et al. 1997; Hughes et al. 2007). Our research in the Seychelles suggests that there are a number of distinct demographic bottlenecks to coral recovery, which vary among habitat types. Approximately equivalent numbers of coral recruits were recorded on settlement tiles across coral-, rubble- and macroalgal-dominated reefs. This indicates that spatial variation in coral recovery and condition in the inner Seychelles are not explained by differences in larval supply (Connell et al. 1997; Hughes et al. 2010; Graham et al. 2011). For reefs dominated by macroalgae, coral recovery appears to be constrained by unsuccessful settlement or poor post-settlement survivorship. On rubble-dominated reefs, a bottleneck was evident between juvenile and adult life history stages.

High densities of juvenile corals failed to translate into high cover of adult corals. Recurrent high water flow events may be causing high juvenile coral mortality on these unstable substrates (e.g. Loch et al. 2004).



	Coral	Rubble	Macroalgae
Community	R1	R1	R1
Total	R1	R1	R1
Acroporidae	R1	R1,2	R2
Community	J1	J1	J1
Total	J1	J1	J2
Community	A1	A2	A3
Total	A1	A2	A3
Acroporidae	A1	A1	A2
Poritidae	A1	A2	A2
Pocilloporidae	A1,2	A1	A2

Fig. 3.5 Schematic summary of comparisons between reef conditions (along the top of the figure) for each life history stage (down the right of the figure), with regards to their Community composition, Total density, and densities of each of three main coral families (down the left of the figure). Reading along the rows, shared numbers indicate no statistical differences between reef conditions (letters preceding the numbers indicate coral life history stage). Densities are highest for darker shadings and lowest for lighter shadings. For clarity, family-level comparisons were only shown if there were significant differences between reef conditions. Arrows represent survivorship through the demographic stages, halting at the possible bottleneck, on each of the three reef conditions.

Rates of settlement onto artificial tiles in the inner Seychelles (average 355-832 recruits m^{-2} depending on reef condition) were low compared to tropical Australian reefs (over 2000 recruits m^{-2} across the GBR: Hughes et al. 1999; and over 1900 acroporid recruits m^{-2} at Scott Reef, Western Australia: Gilmour et al. 2013), but are comparable to other Indo-Pacific locations (Kenya - 620 recruits m^{-2}: Mangubhai et al.

2007a; Spermonde Archipelago, Indonesia - 527 recruits m^{-2}: Sawall et al. 2013; Palau - 479 recruits m^{-2}: Victor 2008; and French Polynesia - 569 recruits m^{-2}: Penin and Adjeroud 2013). All of these locations represent a mix of reef conditions – from areas where coral cover (if not community structure) has effectively recovered in the aftermath of major disturbances (e.g. Palau: Golbuu et al. 2007; French Polynesia: Berumen and Pratchett 2006) to areas experiencing chronic human impacts (e.g. Indonesia - blast fishing and land run-off: Sawall et al. 2013). Clearly, there are instances where local larval supply limits settlement and coral recovery (e.g. Caribbean: Hughes and Tanner 2000; Williams et al. 2008), and these instances may become more prevalent with increases in the incidence and extent of major disturbances. On the whole, recovery of Indo-Pacific reefs is not clearly and consistently limited by larval supply; chronic human influences are likely playing a major role in preventing recovery (cf. Gilmour et al. 2013). Although recruitment rates in the inner Seychelles varied at the site level (reef C2 received 2167 recruits m^{-2} whereas reef M3 received 82 recruits m^{-2}, which is comparable to rates immediately post-bleaching in other locations; Arthur et al. 2006; Gilmour et al. 2013), based on the three broad habitat types, the availability of coral larvae should not limit reef recovery in the inner Seychelles.

One of the greatest threats to the persistence of coral-dominated reef ecosystems are phase-shifts, in particular where disturbances result in permanent or semi-permanent shifts to macroalgal dominance (Hughes et al. 2010). Hughes et al. (2007) showed that experimentally induced phase shifts resulted in 60-70% reductions in rates of coral settlement on Australia’s GBR, compared to nearby control plots. Similarly, the macroalgal-dominated reefs in our study had 80-90% fewer juvenile corals compared to coral- and rubble-dominated reefs. Furthermore, on the macroalgal-dominated reefs, substrate uncovered by macroalgae was typically overlaid in a mixture of sand and sediment-laden turf algae, which is considered unsuitable settlement substrate for corals (Arnold et al. 2010). Consequently, coral settlement may be inhibited or physically prevented by high cover and biomass of macroalgae and other benthos not conducive to coral settlement, including via alteration of bacterial communities that can provide important settlement cues (Smith et al. 2006; Birrell et al. 2008a; Vermeij et al. 2009). Even if larvae were able to settle successfully, large fleshy macroalgae can also restrict light, smother, or directly injure small corals through mechanisms such as allelopathy and abrasion (reviewed by McCook et al. 2001; Birrell et al. 2008b; Ritson-Williams et al. 2009). Accordingly, coral-algae interactions may help explain why juvenile coral colonies were significantly lacking on macroalgal-dominated reefs when compared with both coral- and rubble-dominated reefs, despite receiving comparable densities of larvae on artificial settlement plates.

A demographic bottleneck, caused by detrimental coral recruit-macroalgae interactions and resulting in a decline in coral settlement and growth, may be considered part of a feedback loop that enhances the cover of macroalgae (e.g. Nyström et al. 2012). In our study, acroporid recruits were significantly under-represented on macroalgal-dominated reefs compared to densities on coral-dominated reefs. Acroporidae are relatively fast growing (Morgan and Kench 2012), and are generally thought to be influential in driving reef recovery in the Indo-Pacific (Arthur et al. 2006; Sheppard et al. 2008; Ceccarelli et al. 2011), contributing to rapid increases in coral cover in the aftermath of disturbances (Done et al. 1991; Halford et al. 2004; Sheppard et al. 2008; Linares et al. 2011). However, pocilloporids may be an intermediate recovery community in the Indo-Pacific (Wakeford et al. 2008; Pratchett et al. 2011c), and were once a major component of the coral community in the Seychelles (Taylor 1968; Braithwaite 1971; Rosen 1971). One of the study reefs, M1, although covered in a mix of *Asparagopsis taxiformis* and *Sargassum* spp., has the second highest pocilloporid cover of the nine study reefs (2.5%, the highest is reef R1 with 4.7%), and received 30% of all pocilloporid recruits in the study (probably through self-recruitment, given the positive supply-side relationship). *Pocillopora damicornis* colonies can be sexually mature as small as 25 cm^2 (Combosch and Vollmer 2013), which takes approximately 3 years (Aliño et al. 1985). If pocilloporid colonies and recruits begin to thrive on macroalgal-dominated reefs, this may be a window of opportunity to break feedbacks favouring macroalgae (Nyström et al. 2012; Graham et al. 2013). Management interventions that improve corals as competitors could promote recovery, for example, active removal of macroalgae following storm damage or periods of seasonal senescence.

Given the strong influence of macroalgae on coral settlement, survivorship and recovery, a key question is why some reefs in the inner Seychelles have become overgrown with macroalgae in the aftermath of the 1998-bleaching event, whereas others have not. It is possible that terrestrial runoff and sedimentation resulting from land reclamation and coastal development may be influential (Spalding and Jarvis 2002; Erftemeijer et al. 2012; Wilson et al. 2012). However, coral- versus macroalgal-dominated sites in this study were randomly positioned and did not seem to be associated solely with areas of coastal development. In other geographic locations, local variation in the growth and standing crop of macroalgae is linked to local densities of herbivorous fishes and or invertebrates (Hughes 1994; Hughes et al. 2007). Herbivorous fishes had highly variable biomass among all reefs in the study, with no apparent relationship with macroalgal cover (Chong-Seng, unpublished data). Further study will be necessary to try to understand why macroalgae is proliferating only on certain reefs in the Seychelles.

Rubble-dominated reefs are characterised by unconsolidated substrate composed of dead fragments of erect branching corals that once dominated these habitats. Unconsolidated coral rubble substrates result from the physical breakdown of extensive stands of branching corals (e.g. during cyclones: Harmelin-Vivien 1994; ship groundings: GBRMPA 2011; blast fishing: Fox and Caldwell 2006), or the decomposition and erosion of corals that invariably follows high levels of coral mortality (e.g. bleaching episodes: Loch et al. 2004; Graham et al. 2006). Although consolidation of rubble beds (via overgrowth of crustose coralline algae, which binds rubble pieces) can occur relatively quickly (e.g. three years; Victor 2008), reefs can remain unconsolidated for decades (e.g. Fox et al. 2003). Recurrent periods of high wave energy or water movement continually disrupt consolidation (Obura and Abdulla 2008). The inner Seychelles' rubble-dominated reefs were created after the 1998 bleaching event (presumably because many reefs were originally staghorn acroporid fields; cf. Rosen 1971). Their rubble condition was exacerbated after a tsunami in 2004 (Obura and Abdulla 2008) where bottom velocities reached 3.6 to 4.4 m s^{-1} (Jackson et al. 2005). Mean monthly wind speeds around the islands are 7.9 knots, with maximum speeds between 14 to 27 knots (M Belmont and V Amelie, Seychelles Meteorological Services). Over the last 40 years strong winds have only blown for a total of 259 hours (i.e. 0.08% of the time; wind speeds exceeded 21 knots only in 1973, 1989, and 2009-2011; M Belmont and V Amelie, Seychelles Meteorological Services). This means that there are extended calm periods on these reefs during which recruits can grow. In fact, recruit survival appears relatively high based on the numbers of juvenile colonies found on the reefs. However, adult coral cover was significantly lower on these rubble-dominated reefs when compared to coral-dominated reefs, despite having similar juvenile densities. This is likely a result of high juvenile colony mortality during the occasional periods when wind or water velocities intensify. Alternatively, these habitats may have only recently become sufficiently consolidated to enable increased survivorship of vulnerable newly settled corals, such that ongoing settlement and strong post-settlement growth and survivorship could lead to rapid recovery of coral assemblages within these habitats. Consolidation of the reef substrate is obviously of key importance, and restorative efforts to stabilise the substrate will be valuable (e.g. Edwards 2010), again offering a potential opportunity to break unwanted ecological feedbacks (Nyström et al. 2012; Graham et al. 2013).

Although larval supply does not seem to be limited 14 years post-disturbance, the source of these larvae is uncertain. A year after the 1998 bleaching event in the Seychelles, Turner et al. (2000) estimated 0.2 to 4.3 coral juveniles m^{-2} (defined as colonies 1-15 cm diameter). Ten years post-bleaching, Harris (2010) estimated 8.6 juveniles m^{-2} (defined as colonies $\leq$10 cm diameter). Here we are documenting 17.4 ± 2.9 juveniles m^{-2} in 2012 (defined as colonies $\leq$5 cm diameter). Despite differences in definitions of the size of juvenile corals, these gradual increases in juvenile densities suggest that coral recruitment and population recoveries may be due to localised reproductive output (Wilson et al. 2012). However, a significant supply-side correlation was found only for the family Pocilloporidae (primarily composed of brooding species; Baird et al. 2009), indicating that local abundance (at least at the scale of individual sites surveyed) of adult colonies from families with more broadcast spawning species (e.g. Acroporidae and Poritidae) is not driving local patterns in larval supply. Alternatively, given that reefs in many surrounding countries have been recovering well from the 1998 bleaching event (e.g. Maldives, Chagos, Kenya, Tanzania, and the atolls of the outer Seychelles; Wilkinson 2004, 2008; Ateweberhan et al. 2011), perhaps the inner Seychelles have higher connectivity to surrounding reefs than previously thought

(Graham et al. 2006; Wood et al. 2013). Indeed, larval corals are now known to be able to survive and settle after 100 d (Graham et al. 2008a), allowing substantial dispersal potential (Connolly and Baird 2010). Temporal studies are required to fully elucidate incoming recruitment patterns in the Seychelles.

Coral settlement is known to be variable in both space and time (Connell et al. 1997; Hughes et al. 1999). Most notably, settlement tends to be concentrated in 1-2 months each year, though the timing to peak settlement varies among locations (Baird et al. 2009). There has been limited research on temporal patterns of coral reproduction and larval settlement in the Seychelles. Therefore, for this study, we assumed that the spawning period would be similar to Kenyan reefs (i.e. November to March; Mangubhai et al. 2007a; Mangubhai and Harrison 2008), which are 1000 km to the west, and reefs of Chagos (spawning documented in February; Mangubhai et al. 2007b), 1000 km to the east, which both have similar climate and latitude to the inner Seychelles. If so, peak recruitment would be expected to occur in January-April. In a previous study where tiles were deployed from April to June (Chong-Seng, unpublished data), negligible levels of settlement were recorded, supporting the likelihood of peak settlement between January and April.

Our study indicates that there are demographic bottlenecks affecting the recovery of the inner Seychelles' coral assemblages. The bottlenecks appear to vary among reefs depending on their post-disturbance habitat condition. While high cover of macroalgae may prevent the recruitment of, or inhibit subsequent growth and survival of newly settled corals, there appears to be strong settlement and survival to juvenile stages in areas of unconsolidated reef rubble. However, corals settling on rubble-dominated reefs do not appear to be surviving to become adults. Periodic hydrodynamic disturbances and turnover of accumulated rubble may be the reason. Alternatively, substrates may have only recently become sufficiently consolidated to enable increased survivorship of new recruits, and recovery may now be on-going. Uncovering differential processes that inhibit recovery of coral assemblages following major and widespread disturbances is a critical step in understanding and managing coral reef ecosystems, especially given sustained and ongoing increases in the frequency, severity, and diversity of disturbances that are affecting these valuable marine ecosystems. Importantly, limitations to coral recovery and required management actions vary depending on habitat condition.

CHAPTER 4

Macroalgal herbivory on recovering versus degrading coral reefs[3]

4.1 Abstract

Macroalgal-feeding fishes are considered to be a key functional group on coral reefs due to their role in preventing phase shifts from coral to macroalgal dominance, and potentially reversing the shift should it occur. However, assessments of macroalgal herbivory using bioassay experiments are primarily from systems with relatively high coral cover. This raises the question of whether continued functionality can be ensured in degraded systems. It is clearly important to determine whether the species that remove macroalgae on coral-dominated reefs will still be present and performing significant algal removal on macroalgal-dominated reefs. We compared the identity and effectiveness of macroalgal-feeding fishes on reefs in two conditions post-disturbance – those regenerating with high live coral cover (20-46 %) and those degrading with high macroalgal cover (57-82 %). Using filmed *Sargassum* bioassays, we found significantly different *Sargassum* biomass loss between the two conditions; mean assay weight loss due to herbivory was 27.9 ± 4.9 % on coral-dominated reefs, and 2.2 ± 1.1 % on reefs with high macroalgal cover. However, once standardised for the availability of macroalgae on the reefs, the rates of removal were similar between the two reef conditions (4.8 ± 4.1 g m^{-2} h^{-1} on coral-dominated and 5.3 ± 2.1 g m^{-2} h^{-1} on macroalgal-dominated reefs). Interestingly, the *Sargassum*-assay consumer assemblages differed between reef conditions; nominally grazing herbivores, *Siganus puelloides* and *Chlorurus sordidus*, and the browser, *Siganus sutor*, dominated feeding on high coral

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cover reefs, whereas browsing herbivores, *Naso elegans, N. unicornis,* and *Leptoscarus vaigiensis*, prevailed on macroalgal-dominated reefs. It appeared that macroalgal density in the surrounding habitat had a strong influence on the species driving the process of macroalgal removal. This suggests that although the function of macroalgal removal may continue, the species responsible may change with context, differing between systems that are regenerating versus degrading.

4.2 Introduction

Phase shifts in ecosystems can be defined as a change in the dominant species assemblage and are often undesirable, both ecologically and sociologically, as they affect functional processes and ecosystem services (Scheffer et al. 2001; Folke et al. 2004; Nyström et al. 2008; Hughes et al. 2010). On coral reefs, scleractinian corals are the dominant habitat builder and algal cover is usually minimal, existing primarily as micro-vegetation in the form of <10-mm tall algal turfs (e.g. Hatcher 1988; Goatley and Bellwood 2011). During phase shifts, scleractinian corals may give way to larger plants such as leathery brown macroalgae (e.g. Done 1992; Hughes 1994), which alters the ecosystem's habitat structure. Herbivory, the interaction between plants and their consumers is consequently considered to be a key ecosystem process, mediating both the prevalence of phase shifts and the likelihood that they will be reversed (Walker et al. 1999; Folke et al. 2004; Mumby et al. 2007b; Mumby 2009; Hughes et al. 2010).

The process of herbivory is diverse and performed by a wide range of species with different specific functions (e.g. Bellwood et al. 2004). Each function is thought to be more sustainable if it has high redundancy (i.e. multiple species are performing the function; Walker 1992; Rosenfeld 2002; Nyström 2006), and high response diversity (i.e. the different species performing a function do not all respond to perturbation in the same way; Walker et al. 1999; Elmqvist et al. 2003; Pratchett et al. 2011a). As such, identifying which species contribute to a specific function can be informative in assessing system resilience (Walker 1992; Walker et al. 1999; Johnson 2000). Further, with many ecosystems now existing in a degraded or altered condition (Folke et al. 2004), it is essential to investigate how functions, and the species contributing to them, differ in systems of differing condition (Walker 1992; Nyström 2006).

Research into the process of macroalgal removal on coral reefs has increased our understanding of one of the most common coral reef benthic shifts: live coral being replaced by fleshy macroalgae (e.g. Done 1992; Hughes 1994). Over the last 5-10 yr, studies of *Sargassum* herbivory on coral-rich reefs have expanded geographically from the Great Barrier Reef (GBR), Australia (e.g. Fox and Bellwood 2008), to include Ningaloo Reef on the western coast of Australia (Vergés et al. 2012; Michael et al. 2013), and the reefs of Fiji (Rasher et al. 2013). All of these studies have transplanted *Sargassum* to coral-dominated reefs to assess which fish species target the algae. On reefs that are coral-dominated, the majority of naturally occurring algae exist in the epilithic algal matrix (EAM), a conglomeration of small algal turfs, sediment, detritus, and invertebrates (Wilson et al. 2003). The EAM is where macroalgal propagules begin life, and this rich food source is exploited by specific functional groups, such as grazing and scraping herbivores (i.e. species that could prevent phase shifts; Bellwood et al. 2004). If herbivory on the EAM is sufficient, active removal of fully developed macroalgae should not be necessary. In such cases, macroalgal herbivory performed by browsing herbivores (i.e. species that consume mature macroalgae, and thus have potential to reverse a phase shift; Bellwood et al. 2006a) is likely to be undertaken by a relatively small proportion of the nominal herbivores present in an assemblage (Johansson et al. 2013). However, if a reef has undergone a phase shift to a high fleshy macroalgal cover, the need for macroalgal browsers becomes much greater. Accordingly, it is important to also assess macroalgal feeding on reefs that are already dominated by fleshy algae (e.g. Vergés et al. 2011).

Frequently, a single species dominates ecosystem function in any one location. For example, *Siganus canaliculatus* in the central inshore GBR (Fox and Bellwood 2008), *Kyphosus vaigiensis* in southern Ningaloo (Michael et al. 2013), and *Naso lituratus* in Viti Levu, Fiji (Rasher et al. 2013) have all been identified as the primary macroalgal consumer in bioassay studies in which known quantities of algae are made available for consumption. The total number of species recorded feeding on macroalgae in one location ranges between 6 and 38 species (Rasher et al. 2013; Hoey and Bellwood 2009 respectively), which may indicate functional redundancy through a combination of dominant and minor species (as defined by Walker et al. 1999). However, the functionally dominant species were rarely numerically dominant; i.e. they performed a disproportionate role compared to their abundance (e.g. *Naso unicornis*; Hoey and Bellwood 2009). Whether the fish that remove macroalgae on a coral-dominated reef will still be present and performing significant algal removal on a macroalgal-dominated reef, is currently unknown.

The majority of previous studies have been in well-managed reef systems (GBR and Ningaloo Reef), where herbivores are not important fishery species, and on study sites with minimal (<5 %) fleshy macroalgae cover. This study expands the knowledge of herbivorous fishes that consume macroalgae in the Western Indian Ocean (WIO), an area that was devastated by the 1998 mass bleaching event (Goreau et al. 2000;Graham et al. 2008b), with many reefs now covered in macroalgae (e.g. McClanahan et al. 1999; Ledlie et al. 2007; Chong-Seng et al. 2012: Chapter 2), and where herbivorous fish make up an important part of fisheries catches (e.g. Grandcourt 1999; Hicks and

McClanahan 2012). We compare the potential macroalgal-removing fish assemblages on reefs that have high live coral cover and on those that have recently shifted to high macroalgal cover. In particular, we wanted to answer the following questions: (1) Is there a difference in *Sargassum* removal rates on coral- versus macroalgal-dominated reefs? (2) Do different fish assemblages consume *Sargassum* on coral- versus macroalgal-dominated reefs, and if so, are there specific species that drive the loss of macroalgal assay biomass?

4.3 Methods

4.3.1 ***Study sites***

This study was conducted between May and June 2011 among the inner Seychelles Islands (4°30’S, 55°30’E) in the WIO. Six reefs were chosen based on their benthic biota (defined by their dominant macro-benthic organisms, > 5 cm tall); Chong-Seng et al. 2012: Chapter 2). Three reefs (C1-3) had high scleractinian coral cover, but minimal visible macroalgal cover; and three reefs (M1-3) had high macroalgal cover, but minimal scleractinian coral cover (hereafter referred to as ‘coral-dominated’ and ‘macroalgal-dominated’ reefs respectively). To quantify benthic cover on the reefs, we surveyed two to six 50 m point-intercept transects, recording the live benthos to genus and/or functional group every 0.5 m. Fish were surveyed on five of the six reefs (excluding reef C1) using two to three 5 x 50 m belt transects, recording the number and identity (species) of all fish greater than 8 cm. These six reefs are in areas known to have had high coral cover, but low macroalgal cover prior to the 1998 mass bleaching event (Jennings et al. 1995; Spalding and Jarvis 2002; Graham et al. 2006; Wilson et al. 2012). Fishing practices in the inner Seychelles use non-destructive techniques (handlines, traps, and octopus harpooning are the most widely used; Grandcourt and

Cesar 2003), and there is relatively low variability in fishing pressure along the shallow fringing reefs among the islands, with most fishing occurring in deeper water (Daw et al. 2011a, b). Two of the six sites are protected from fishing, however exhibit very different benthic conditions: one was categorised as coral-dominated and the other macroalgal-dominated.

4.3.2 ***Macroalgal assays***

To quantify variation in the removal of macroalgae by fishes among reefs, and between coral- and macroalgal-dominated reefs, four *Sargassum* bioassays were transplanted on two non-consecutive days on each of the six reefs (eight assays per reef). *Sargassum* was selected, as it is the dominant macroalgae identified in phase shifts in the WIO, GBR, and Fiji (Ledlie et al. 2007; Hughes et al. 2007; Rasher et al. 2013). On each day, *Sargassum* was collected from one of two source reefs, spun in a salad spinner to remove excess water, and then weighed (249 ± 13 g: mean ± SE). Assays were attached to the reef using elastic bands and were left for 4.5 h, then collected, spun, and re-weighed (following Hoey and Bellwood 2009). One additional assay was caged daily (two assays per reef) to prevent fish herbivory, thus acting as a control for the influence of handling. The percentage of handling loss recorded from caged assays was 1.1 ± 0.3 % and 2.9 ± 1.5 % on coral and macroalgal-dominated reefs respectively. The losses in algal biomass due to herbivory were estimated using the equation (following Bennett and Bellwood 2011):

$$\mathrm{A}r = 1 - \mathrm{A}a / (\mathrm{A}i * (1 - hl))$$

where $\mathrm{A}r$ is the proportion of algae removed, $\mathrm{A}a$ is the algal mass (g) after 4.5 h, $\mathrm{A}i$ is the initial algal mass (g) and hl is the mean proportion of algal mass lost due to handling.

Uncaged assays were filmed using stationary underwater video cameras (Sony DCR-HC1000E). Recording began immediately after assay attachment to the reef substrate, with a tape measure held up against the assay at the beginning of filming to enable a rough calibration of fish sizes on the video footage. All videos, and the full 4.5 h, were examined. We recorded the species of fish feeding on the assays, the number of bites taken per fish, and the estimated total length of each individual fish. *Acanthurus nigrofuscus* and *Ctenochaetus striatus,* and *A. nigroris* and *C. binotatus* differ primarily because of mouth orientation and tooth structure (Purcell and Bellwood 1993) and can be hard to distinguish (e.g. Bouchon-Navaro and Harmelin-Vivien 1981), especially when using video footage (e.g. Holmes et al. 2013). Therefore, these species, along with *C. truncatus*, were grouped into '*Acanthurus*/*Ctenochaetus* spp'. All other *Acanthurus* species were pooled into '*Acanthurus* spp'. Brown, initial phase parrotfishes were grouped into '*Scarus* spp'. Fish species were assigned to functional groups based on the literature and FishBase (Green and Bellwood 2009; Froese and Pauly 2011).

4.3.3 ***Statistical analysis***

A linear mixed-effects model was used to determine whether there was a difference in *Sargassum* removal rates on coral- versus macroalgal-dominated reefs, comparing logit transformed proportional assay loss against Condition (two levels: coral versus macroalgal, fixed) and Reef (three levels, random, nested in Condition). The factor Day (two levels, random, nested in Reef and Condition), which accounted for any temporal variability in herbivory patterns on a reef, was deemed to add minimal information (likelihood ratio test between models with and without Day as a random factor, $\chi^2 = 0.56$, df = 1, $p = 0.46$), and was therefore excluded from the final model (Zuur et al. 2009). Due to the proportional, though non-binomial nature of the data, the logit transformation was used to account for linear modelling assumptions (Warton and Hui 2011). Analyses were performed using the lme4 R package (Bates et al. 2011; R Development Core Team 2011). *p* values for the model were calculated using Markov chain Monte Carlo (MCMC) sampling (9999 iterations) in the languageR package (Baayen 2011).

In light of the underlying differences in the addition of an assay to a coral- versus macroalgal-dominated reef, and to understand the implications of the rates of bioassay removal in the context of the natural levels of macroalgae, we performed some broad calculations of feeding rate (bites) in relation to macroalgal availability. To convert our measurements of natural macroalgal availability in percentage cover to g m^{-2}, we first estimated the circular areal cover of an average assay with mean diameter 20 cm (based on 41 measurements of bioassays used) and calculated how many assays would fit into 1 m^2 area of the reef (31.8 assays). Second, we converted the number of assays m^{-2} to g m^{-2} by taking the average assay weight of 250 g from the pre-feeding weights (see 'Macroalgal assays' section). Finally, estimates of proportional bioassay loss could be predicted at the reef level from the mixed-effects model, and multiplied with these estimates of natural macroalgal availability to get an indication of macroalgal removal on each reef (in g removed m^{-2} h^{-1}).

A fish species' number of bites on an assay was used as a proxy for its role in the *Sargassum*-consuming fish community. *Sargassum*-consuming fish assemblages for each assay were described by zero-adjusted Bray-Curtis dissimilarities among samples (Clarke et al. 2006). Zero adjustment involves the addition of a dummy variable of 1s to the data set; allowing two empty assemblages (i.e. assays received no bites) with an otherwise undefined relationship, to be described as 100% similar, while having no effect on assemblages with high values (Clarke et al. 2006). Pairwise dissimilarities between each assay's fish assemblage were calculated from untransformed data and visualised using non-metric multidimensional scaling. A comparison of the *Sargassum*-consuming fish assemblages on reefs covered with coral versus macroalgae was performed using a three-way permutational multivariate analysis of variance (PERMANOVA) with the following factors: Condition (two levels, fixed), Reef (three levels, random, nested in Condition), and Day (two levels, random, nested in Reef and Condition, accounting for temporal variability). The analysis was performed in PRIMER v6 with the PERMANOVA+ add on package (n = 9999 permutations; Clarke and Gorley 2006; Anderson et al. 2008).

To identify the fish species that drove the loss of assay biomass on reefs in different conditions, species that contributed > 5% of bites in each condition were selected for further analysis. Multiple regressions were used to compare assay biomass loss (coral-dominated reefs), or logit transformed assay biomass loss (macroalgal-dominated reefs), with the number of bites taken by the dominant species and the rest of the species pooled. Where heteroscedasticity was present in the data, alpha values were lowered to 0.01. Analyses comparing fish assemblages and the influence of individual fish species were repeated using mass standardised bites (body mass (kg) x number of bites, with body mass estimated from published length-weight relationships; Letourneur 1998; Kulbicki et al. 2005; Green and Bellwood 2009) to account for variation in the impact of individual bites due to body size (cf. Hoey and Bellwood 2009). The mass standardised bites analyses showed very similar patterns to analyses performed on the actual number of bites (Appendix C Figs. S1, S2, Appendix C Tables S1, S2).

Differences in identities of the dominant *Sargassum*-feeding fish species on coral- versus macroalgal-dominated reefs may be related to differences in their abundance on the reefs, or to changes in their behaviour in response to differences in ambient resource availability. Therefore, for each of the relatively dominant species (taking >5 % of all bites on assays) we calculated a measure of effect size based on differences in fish abundances (from visual surveys) between the two reef conditions, with 95 % confidence intervals (Hedges et al. 1999) using

$$\text{Effect Size} = ln(\bar{X}_{\text{Coral}}) - ln(\bar{X}_{\text{Macroalgae}})$$

where $\bar{X}_{\text{Coral}}$ is the mean fish species abundance on coral-dominated reefs, and $\bar{X}_{\text{Macroalgae}}$ is the mean fish species abundance on macroalgal-dominated reefs. We compared these findings with the reef condition where the species was functionally important, highlighting whether fish were more, equally, or less abundant on reefs where they provided important *Sargassum* removal.

4.4 Results

Benthic condition varied among the six reefs. Scleractinian coral cover was 29.5 ± 3.1 % (mean ± SE) and macroalgal cover was 1.5 ± 0.8 % on the coral-dominated reefs, whereas 0.9 ± 0.4 % scleractinian coral cover and 59.7 ± 3.8 % macroalgal cover (primarily *Sargassum* spp., and some *Lobophora* spp.) were recorded on the macroalgal-dominated reefs (Appendix C Fig. S3). *Sargassum* biomass lost due to fish herbivory averaged 27.9 ± 4.9 % of initial assay weight on coral-dominated reefs whereas assays on macroalgal-dominated reefs lost 2.2 ± 1.1 % (Fig. 4.1). After accounting for reef-level variation, the linear mixed effects model (LMM) predicted that on inner Seychelles reefs with high coral cover, *Sargassum* assays may be expected to lose approximately 18.9 % of their weight due to fish herbivory over the sample period (LMM, $t = -2.2$, df = 4,42, $p_{\text{mcmc}} < 0.05$), compared to only 0.5 % on reefs dominated by macroalgae (LMM, $t = -3.4$, df=4,42, $p_{\text{mcmc}} < 0.01$). Therefore, a broad estimate of *Sargassum* assay removal is 10 g h^{-1} on coral-dominated reefs (based on 18 % removal of ~250 g in 4.5 h) and 0.28 g h^{-1} on macroalgal-dominated reefs. Using reef-level estimates of proportional bioassay loss, and accounting for the influence of ambient resource availability, gave standardised macroalgal herbivory rates of 4.8 ± 4.1 g m^{-2} h^{-1} on coral-dominated reefs and 5.3 ± 2.1 g m^{-2} h^{-1} on macroalgal-dominated reefs (Table 4.1).

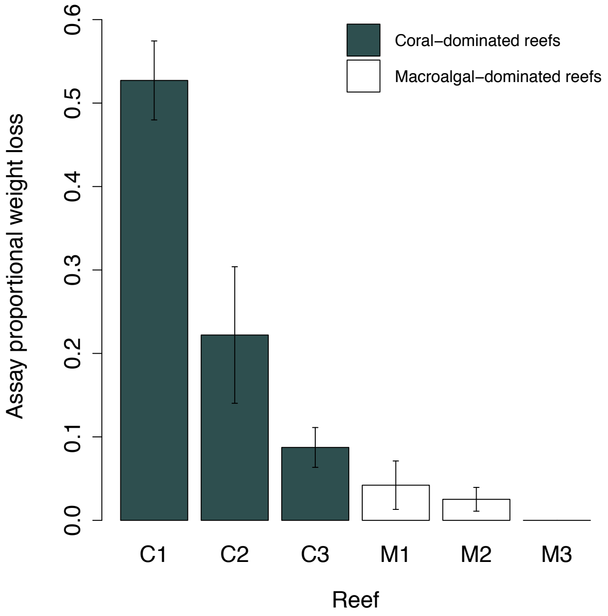

Fig. 4.1 Variation in *Sargassum* bioassay weight loss due to fish herbivory for each reef (mean ± SE) over 4.5 h. C1 - C3 represent the three coral-dominated reefs. M1 - M3 represent the three macroalgal-dominated reefs.

The assemblage of fishes feeding on the assays showed distinctive patterns in multidimensional space (Fig. 4.2) and varied significantly between reef conditions (PERMANOVA, $F_P = 4.8$, df = 1, $p < 0.001$). There was also some daily variation in fish assemblages (PERMANOVA, $F_P = 1.7$, df = 6, $p < 0.01$), although minimal variation between reefs in each state (PERMANOVA, $F_P = 1.8$, df = 4, $p > 0.05$). Twenty-three fish species were observed to take 19,832 bites on the *Sargassum* assays during the study (91.6 % of the bites were on assays in coral-dominated reefs, and four assays on macroalgal-dominated reefs received no bites). Of the 23 species, eight species were recorded to only feed in coral-dominated reefs and one species fed only in macroalgal-dominated reefs (Fig. 4.3).

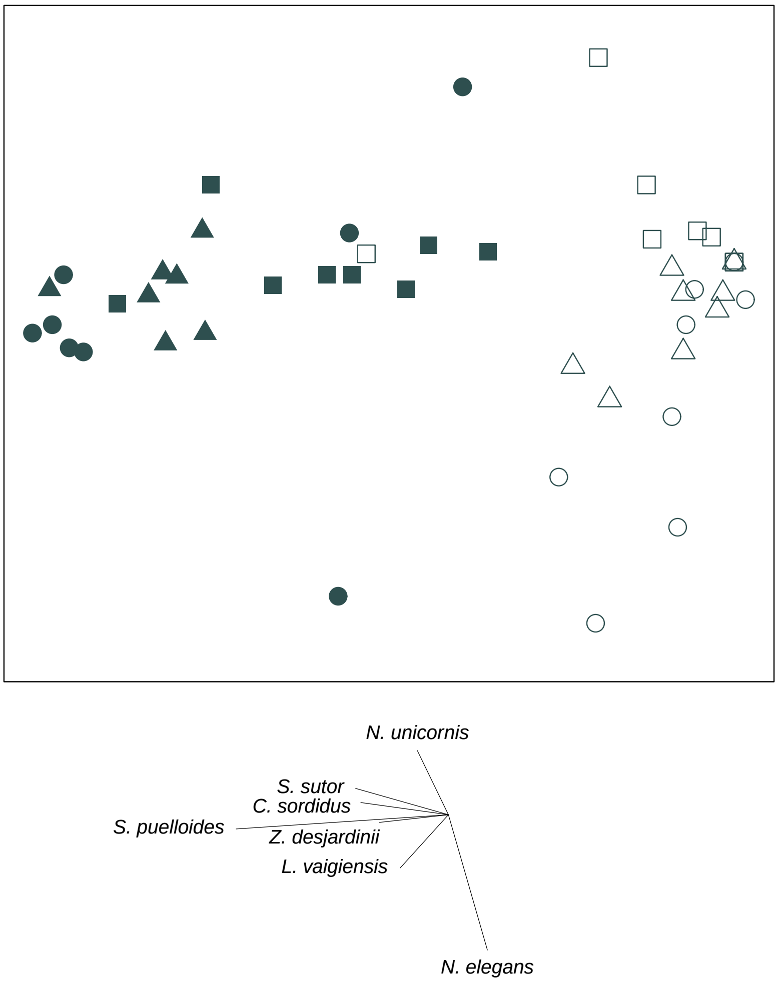

Fig. 4.2 Multi-dimensional scaling plot of the composition of fish assemblages feeding on *Sargassum* bioassays on coral- and macroalgal-dominated reefs. Filled symbols represent assays on coral-dominated reefs; circles – C1, squares – C2, triangles – C3. Open symbols represent assays on macroalgal-dominated reefs; circles – M1, squares – M2, triangles – M3. Vectors visualise the directional associations of the seven fish species that took > 5 % of the bites in each reef state based on spearman rank correlations. Stress = 0.15.

One grazing herbivorous species, *Siganus puelloides*, accounted for >60 % of bites taken on coral-dominated reefs, whereas *Naso elegans*, a browsing herbivore, accounted for nearly 50% of bites taken on assays on macroalgal-dominated reefs (Table 4.2, Fig. 4.3). Based on mass standardised bites, this was 82 % and 94 % respectively (Appendix C Fig. S3). *S. puelloides* was the most ubiquitous species, feeding on 21 out of 23 assays on high coral cover reefs, but only on one assay on high macroalgal cover reefs. *Leptoscarus vaigiensis* was also a regular feeder, feeding on 13 assays, 10 of which were on macroalgal-dominated reefs (Table 4.2). Only four species took more bites on macroalgal versus coral-dominated reefs: *N. elegans* (383 versus 0 bites, respectively), *Acanthurus* spp. (37 versus 16) *Calotomus carolinus* (11 versus 6) and *Zanclus cornutus* (6 versus 2).

Table 4.1 Calculation of relative herbivory rates on the six study reefs.

Reef	Bioassay loss (%)	Macroalgal cover (%)	Macroalgal density (g m^{-2})	Herbivory (g m^{-2} h^{-1})
C1	79.15	0.10	7.96	1.4
C2	10.26	7.10	565.00	12.88
C3	8.30	0.10	7.96	0.15
M1	0.82	62.90	5005.42	9.12
M2	0.79	34.77	2766.64	4.85
M3	0.22	53.35	4245.46	2.04

'C1-3' – coral-dominated reefs; 'M1-3' macroalgal-dominated reefs.
Estimates of bioassay loss (% removed in 4.5 h) from the linear mixed effects model
Availability of leathery macroalgae expressed as % cover per reef, and converted to g m^{-2} using the conversion that one assay would cover ~ 0.03 m^2 and weighed ~ 250 g.
Reef level herbivory (bioassay loss * macroalgal density) expressed as grams removed per m^2 in 1 h.

On coral-dominated reefs, *S. puelloides*, *Zebrasoma desjardinii*, *Chlorurus sordidus,* and *Siganus sutor* were each responsible for >5 % of total bites on the assays (Table 4.2). Together with the pooled bites from the other species, the bites taken by these four species explained 72.3 % of the variation in *Sargassum* biomass loss (R^2_{adj} = 0.73, F = 12.7, df = 5,17, p < 0.001; Table 4.3), with *S. sutor* being individually responsible for most biomass reduction. On macroalgal-dominated reefs, *L. vaigiensis, N. elegans*, and *Naso unicornis* were each responsible for >5 % of total bites on the assays (Table 4.2). Together with the pooled bites from the other species, the bites taken by these three species explained 34.1 % of the variation in logit transformed *Sargassum* biomass loss, but was non-significant due to adjustment of the alpha value ($R^2_{adj} = 0.34$, F = 4.0, df= 4,19, p = 0.017).

The eight species identified as important for *Sargassum* removal on the two reef conditions showed disparate ambient abundances on coral- versus macroalgal-dominated reefs (Fig. 4.4, Appendix C Table S4). *C. sordidus, S. puelloides* and *N. unicornis* were present in approximately equal abundances on both coral- and macroalgal-dominated reefs, yet the two former species were only important macroalgal feeders on coral-dominated reefs, and the latter species only on macroalgal-dominated reefs. *L. vaigiensis* and *Z. desjardinii* were present in higher abundances on reefs where they were functionally more important (macroalgal- and coral-dominated reefs, respectively), whereas *S. sutor* was more abundant on macroalgal-dominated reefs yet fed on macroalgae predominantly on coral-dominated reefs. *N. elegans* was not recorded on any of the surveys.

Table 4.2 Functional group, importance to local fishery, and macroalgal-feeding metrics of the dominant fishes contributing to Sargassum assay removal (> 5% of bites). Functional groups (FG): HO – non-browsing herbivore; HB – browsing herbivore. Fishing pressure (FP) represents the level of exploitation (fishing) sustained by different fish species in the Seychelles (Grandcourt 1999): P – primary target; I – important by-catch; N – not targeted. For reefs in each condition: "% bites" represents the contribution of that species' bites to the total number taken on all assays. "Total bites" represents the total number of bites observed for that species. "No. assays" represents the number of assays where that species was observed to take bites. "Bites assay-1" represents the mean (± SE) number of bites taken on an assay by that species when present and feeding.

Condition	Fish	FG	FP	%	Total	No.	Bites assay^{-1}
Coral	*Siganus puelloides*	HO	I	66.5	12072	21	574.9 ±
	Zebrasoma	HO	N	7.2	1312	5	262.4 ±
	Chlorurus sordidus	HO	P	6.9	1251	11	113.7 ± 76.0
	Siganus sutor	HB	P	5.2	943	5	118.6 ± 48.1
Macroalgae	*Naso elegans*	HB	N	49.6	383	4	95.8 ± 61.5
	Leptoscarus	HB	I	17.5	135	10	13.5 ± 8.8
	Naso unicornis	HB	N	10.0	77	1	77

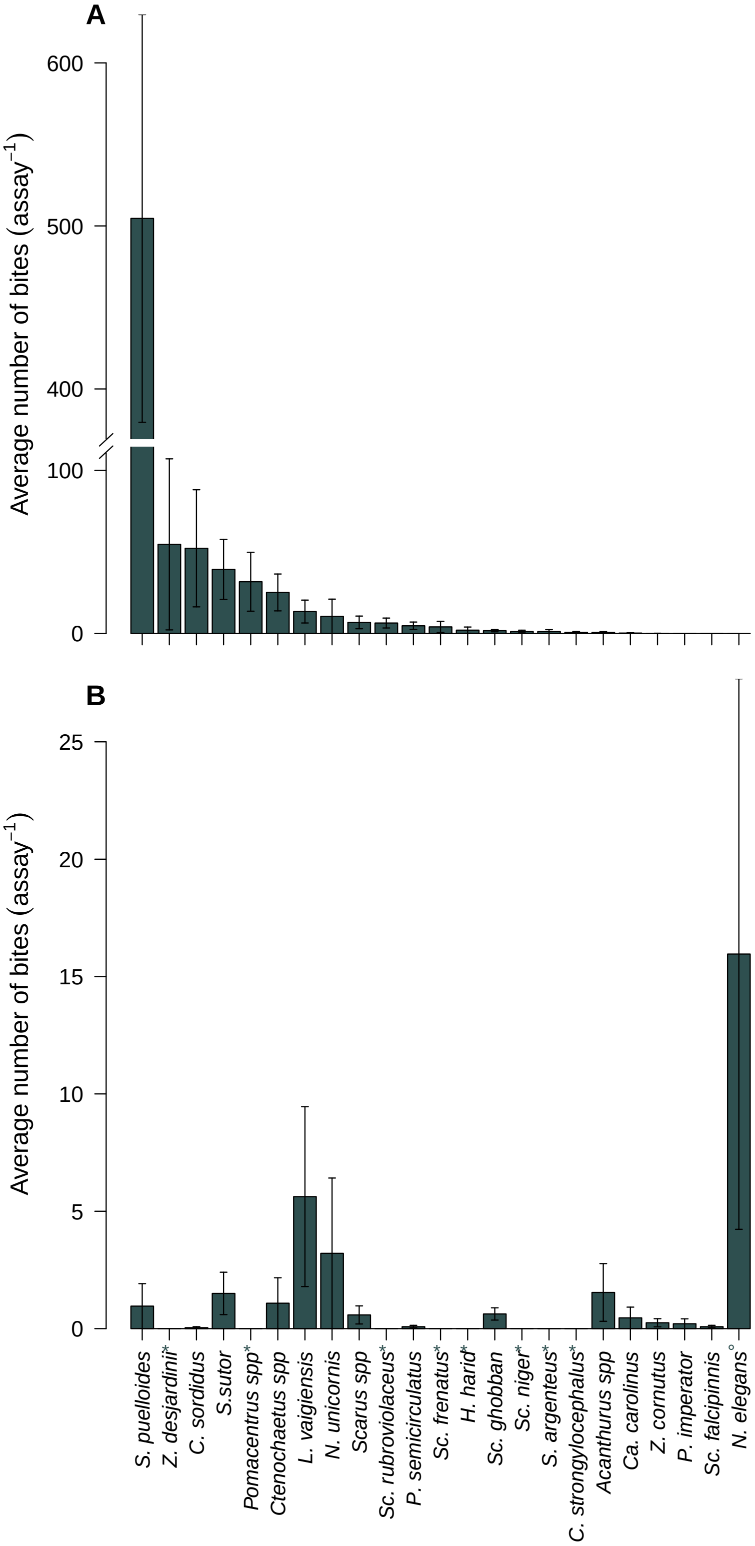

Fig. 4.3 Average bites (± SE) per assay taken by the 23 species recorded to feed on *Sargassum* assays placed in (A) coral- versus (B) macroalgal-dominated reefs. '*' – Species that fed only on assays in coral-dominated reefs. '°' – Species that fed on assays only in macroalgal-dominated reefs. Genera: Ca – *Calotomus*; C – *Chlorurus*; H – *Hipposcarus*; L – *Leptoscarus*; N – *Naso*; P – *Pomacanthus*; S – *Siganus*; Sc – *Scarus*; Z – *Zebrasoma.*

Table 4.3 Relative influence of dominant macroalgal-feeding fishes on *Sargassum* loss in coral-dominated reefs.

Source	Estimate	SE	t	p
C. sordidus	0.0005	0.0002	3.19	**0.005**
S. puelloides	0.0002	0.0001	3.47	**0.003**
S. sutor	0.0017	0.0003	5.64	**0.000**
Z. desjardinii	-0.0002	0.0001	-1.71	0.11
Sum of all other species	0.0005	0.0002	2.19	**0.04**

Significant probabilities are indicated in bold

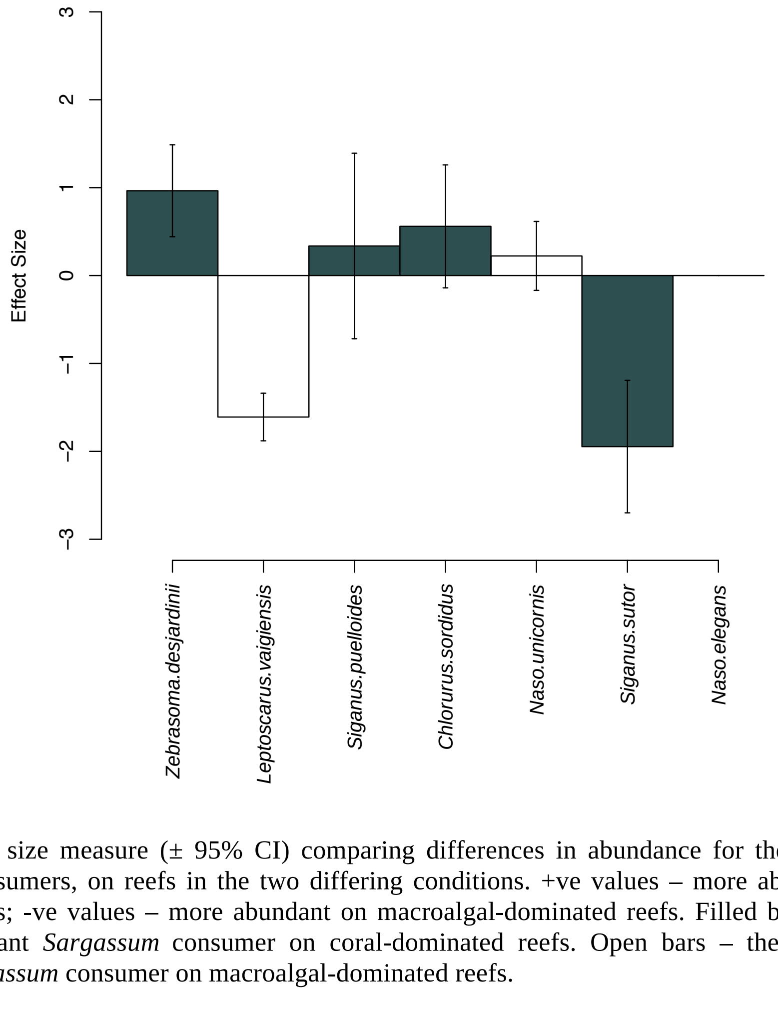

Fig. 4.4 Effect size measure (± 95% CI) comparing differences in abundance for the eight dominant *Sargassum* consumers, on reefs in the two differing conditions. +ve values – more abundant on coral-dominated reefs; -ve values – more abundant on macroalgal-dominated reefs. Filled bars – the species was an important *Sargassum* consumer on coral-dominated reefs. Open bars – the species was an important *Sargassum* consumer on macroalgal-dominated reefs.

4.5 Discussion

Reefs where coral cover had recovered to high levels following a major disturbance were found to have markedly different species assemblages performing a valuable ecosystem function, macroalgal removal, when compared to reefs that had become dominated by macroalgae. Interestingly, two species that played relatively minor roles on the coral-dominated reefs were more dominant among the species driving algal removal on macroalgal-dominated reefs. Moreover, the species having the largest impact in the macroalgal-dominated condition, *Naso elegans*, was not observed in the coral-dominated condition. Thus, although having high redundancy of this functional role on reefs prior to disturbance is likely to be important, it may not be a strong indicator of response to disturbance, because a different suite of species may come to dominate functional roles once macroalgae are established.

Macroalgal herbivores in the WIO appear very similar to species reported from the GBR, Ningaloo, and Fiji. Some of the functionally important species recorded are closely related to species reported from the other regions; *S. sutor* is closely related to *S. canaliculatus* (Borsa et al. 2007), an important macroalgal herbivore on inshore reefs of the GBR (Fox and Bellwood 2008; Cvitanovic and Bellwood 2009; Bennett and Bellwood 2011). *Z. desjardinii* is similar to *Z. veliferum*, which has been recorded feeding on macroalgae in both the GBR (Hoey and Bellwood 2009) and Ningaloo (Vergés et al. 2012). *N. elegans* is a sister species of *N. lituratus* (Klanten et al. 2004) which appears to be important in Fiji (Rasher et al. 2013), and has been recorded to feed on *Sargassum* on reefs in Ningaloo (Vergés et al. 2012; Michael et al. 2013). Other species are widespread across the Indo-Pacific; *C. sordidus* and *N. unicornis* have been observed feeding on *Sargassum* assays in all regions of study (e.g. GBR: Bennett and Bellwood 2011; Ningaloo: Vergés et al. 2012; Fiji: Rasher et al. 2013). *N. unicornis* is also one of the few known ‘true’ herbivores (in terms of assimilation; Choat et al. 2004). The importance of two other species in macroalgal removal was previously unrecorded from bioassay studies elsewhere; *S. puelloides* is endemic to the WIO and is known to consume algae (Woodland and Randall 1979). *L. vaigiensis* is primarily known as an important seagrass feeder (Unsworth et al. 2007), although it has been reported to consume algae (Almeida et al. 1999; Nakamura et al. 2003).

Based on video footage, *S. sutor* was the most effective species at removing *Sargassum* biomass, yet it did not take the most bites, was not always present, and sometimes did not feed when it was present (i.e. observed in videos but no bites were taken). We found a discrepancy between the number of bites taken, and the amount of biomass lost (i.e. large numbers of bites did not necessarily correspond to high biomass loss, and conversely, high biomass loss was not always coincident with large numbers of bites). Furthermore, this disparity was not resolved by accounting for individual fish size (cf. Fox and Bellwood 2008; Hoey and Bellwood 2009). The primary cause appeared to be fish tearing off more of the assay than they actually consumed. This was also observed by Bellwood et al. (2006a) when the batfish, *Platax pinnatus*, almost singlehandedly reversed an experimentally manipulated phase shift using a combination of *Sargassum* feeding and dislodgement. Unconsumed and undigested material is likely to have died and entered the detrital food chain, because *Sargassum* is unlikely to regenerate from non-holdfast pieces (Li et al. 2010) or to be propagated faecally (Vermeij et al. 2013).

Siganus sutor was found to be the most effective species at removing *Sargassum* in areas with low surrounding macroalgal biomass, occurring in relatively low abundances, which indicated high per capita macroalgal removal efficiency at these sites. However, on macroalgal-dominated reefs, very low per capita macroalgal removal efficiency was observed, despite the importance of macroalgal beds to various life stages of *S. sutor* (Wilson et al. 2010b). Historically, macroalgal removal could be considered a ‘backup’ function in case of disturbances, as other herbivory functions should pre-empt macroalgal development in the first place (e.g. Arthur et al. 2006; Nash et al. 2013). Relatively few species have been identified that preferentially consume mature macroalgae (e.g. Bellwood et al. 2006a; Hoey and Bellwood 2009), and even fewer are thought to be true macroscopic algae herbivores (in terms of assimilation; Choat et al. 2004). Therefore, there are few species that perform this function to the exclusion of all other functions, with the majority of the coral reef herbivore guild made up of grazers (i.e. species that could prevent a phase shift) rather than browsers (i.e. species with potential to reverse a phase shift; Bellwood et al. 2006a). Indeed, on coral-dominated reefs, the functionally important macroalgal removers were species typically defined as grazers (*S. puelloides*, *Z. desjardinii*) and excavators (*C. sordidus*; Green and Bellwood 2009). Only one of the functionally important species was a browsing species (*S. sutor*). This raises questions about potential plasticity of functional roles among coral reef herbivores.

The relationships between individual species' ambient abundance on reefs of differing condition and their importance in macroalgal feeding were highly variable. Two species were recorded feeding on macroalgae where their abundances were greatest (*Z. desjardinii* and *L. vaigiensis*). Three species were equally abundant on reefs in both conditions, yet functionally important in only one reef condition (*S. puelloides, C. sordidus, N. unicornis*). One species fed most on macroalgae in the reef condition where it was least abundant based on visual surveys (*S. sutor*). These results suggest that some species of macroalgal browsers may change their feeding habits in response to reef condition, independent of their abundance. Such changes have been shown to occur for EAM feeding parrotfishes (Nash et al. 2012), but this is the first evidence we know of for macroalgal browsers. Variation in the relationships between abundance and feeding highlights the difficulty in estimating functional redundancy in a system. It will be easy to overestimate or underestimate redundancy if species known to be functionally important in one system are not functionally important when the resource availability changes. Indeed, a species' functional importance appears to be context dependent.

Recent attempts to investigate the impact of high macroalgal cover on herbivory have shown that high macroalgal density negatively affects macroalgal feeding (Hoey and Bellwood 2011), a finding corroborated for some of the macroalgal-feeding fishes in the current study. Although much useful information can be garnered regarding identities and proportional importance of individual species, the macroalgal assay methods widely used in coral-dominated habitats may not fully capture ecosystem function in macroalgal-dominated habitats. There may be a lower probability of any one fish taking a bite from an assay, due to high resource abundance (Hoey and Bellwood 2010; Vergés et al. 2011). Increasing the scale of the bioassays to account for high resource abundance (e.g. 1-m^2 bioassay plots rather than a single thallus; cf. Klaassen et al. 2006) may enable further quantitative assessment of patterns found in this study. Conversely, it may be that the addition of 250 g of *Sargassum* to a reef with no other *Sargassum* will stand out substantially, attracting individuals from beyond their regular foraging range. We estimated the effect of differential resource abundance on herbivory rates and found equal macroalgal removal rates (assay biomass loss; g m^{-2} h^{-1}) between the two reef conditions, indicating that the rates of removal may not change whether a reef is dominated by macroalgae or has very little. In the inner Seychelles, where several reefs have shifted to macroalgal dominance (Graham et al. 2006; Ledlie et al. 2007; Chong-Seng et al. 2012: Chapter 2), the macroalgal-feeding fish species appear to be having little effect on the prevalence of fleshy algae. This may be because the feeding capacity of macroalgal-feeding fishes is swamped by the amount of algae available (Williams et al. 2001), that other processes, such as nutrient enrichment (Burkepile and Hay 2006), are driving macroalgal abundance, or that fishing pressure is decreasing the abundance of important macroalgal-feeding species (Hicks and McClanahan 2012).

Assay biomass loss due to herbivorous fishes in the Seychelles appears to be fairly low compared to most studies on the GBR or Ningaloo (the Fiji study was not comparable). Our data indicated that *Sargassum* removal (not standardising for available cover) on a coral-dominated reef would be approximately 10 g h^{-1}, and 0.28 g h^{-1} on macroalgal-dominated reefs (based on 18 % and 0.5 % removal of ~250 g in 4.5 h respectively). While comparisons among studies are complicated because of slight differences in methods and data reporting, a broad estimate of assay biomass loss due to herbivorous fishes using the same approximation as for our data, gives a range of 2 to 100 g h^{-1} for the GBR (Hoey and Bellwood 2010; Lefèvre and Bellwood 2011). Michael et al. (2013) report the range of assay biomass loss due to herbivorous fishes in Ningaloo as 42-53 g h^{-1}. These rates provide an interesting insight into the large variation that exists in macroalgal feeding by fishes, among reefs, latitudes, environments, and oceans. While a multitude of factors are likely driving this variation (Cheal et al. 2013), the potential of browsing fishes to regulate macroalgal biomass on heavily disturbed reefs appears to be relatively low unless management policies to increase herbivore populations are put in place (Stockwell et al. 2009; Rasher et al. 2013).

Aside from environmental and physical factors, the WIO region differs from the well-protected GBR and Ningaloo systems in that herbivorous fishes are important in local fisheries (Grandcourt 1999; Hicks and McClanahan 2012). Of the 23 species identified that feed on *Sargassum* in this study, four are primary targets (*S. sutor*, *C.*

sordidus, Scarus ghobban, Sc. rubroviolaceus) and ten are important targets of the Seychelles artisanal fishery (Grandcourt 1999). Four of the species are also amongst the top 15 most commonly caught species in the nearby Kenyan reef fisheries (*S. sutor, L. vaigiensis, C. carolinus, A. nigrofuscus*; Hicks and McClanahan 2012). Although some of these species can be long lived, they typically have rapid growth to maturity (Choat and Robertson 2002), and appear to withstand fairly heavy harvesting (McClanahan and Hicks 2011; Bellwood et al. 2012b). It is possible that such fisheries, if well managed, may not necessarily be a threat to ecosystem function (Robinson et al. 2011). Nevertheless, there is a history of overfishing in many parts of this region (Grandcourt and Cesar 2003; Hicks and McClanahan 2012), indicating the need for careful management to ensure sufficient reef fish herbivores are available to deliver important ecosystem functions. Indeed, the ability of well-managed protected areas to increase herbivore biomass on otherwise fished reefs, and in turn reduce macroalgae cover, has been demonstrated in both the Philippines and Fiji (Stockwell et al. 2009; Rasher et al. 2013). In Fiji, for example, three protected areas had high herbivore biomass and diversity, including the presence of key browsers, resulting in low macroalgal cover and high coral cover, whereas macroalgae dominated benthic cover on adjacent fished reefs (Rasher et al. 2013).

Our study provides new empirical information highlighting differences in the functional characterisation of reefs that have recovered coral cover following disturbance compared to those which have become dominated by macroalgae. We found evidence that species dominating macroalgal removal on the reefs with high coral cover performed only limited function in areas with high surrounding macroalgal biomass. Our study emphasises the need to improve our understanding of the ecology of degraded reef systems and how such degradation may be reversed (Graham et al.

2013). To date, most work on macroalgal feeding by fishes on coral reefs has focused on reefs dominated by corals, whereas our study highlights the need for caution in extrapolating findings from ‘healthy’ or regenerating habitats to degraded systems.

CHAPTER 5

Do relationships between reef condition and reef fish assemblages hold over time?[4]

5.1 Abstract

Ecosystems are dynamic, which makes it hard to predict their future compositions, especially in the face of climate change. Yet predictions are necessary for management and conservation initiatives, especially at local scales. In an earlier study patterns were found where coral reef fish assemblages were associated with reefs of differing habitat quality, placed along a continuum of benthic condition from complex coral-dominated to low complexity and high macroalgal cover. This study investigated whether observed local scale relationships held over time, and whether there were particular aspects of benthic change that the fish responded to. I found significant and relatively consistent spatial relationships over a two-year period, for three aspects of the fish assemblage – species richness and the abundances of both corallivores and browsing herbivores. However, there was no consistent relationship for the remaining 10 fish assemblage variables. This suggests that there are spatial patterns in some groups, such as corallivores, browsing herbivores and species richness, which may be used for predictions. However caution should be exercised with many other ecosystem components, as unpredictable behaviour is likely. In terms of site by site change, a reef's trajectory along three different axes of benthic change (coral:macroalgae, crustose algae:sand, other macroalgae:turf) was associated with reciprocal changes in nine (of 13) aspects of the reef fish assemblage. High variation despite approximately zero benthic change was apparent in some cases, which may represent baselines of local variability. It remains to be seen how ubiquitous these relationships are in other parts of

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[4] A manuscript of this chapter is in revision following submission to the journal *Ecosystems*

the world. However the study identifies ecosystem elements that may be predictable through time, which is becoming more pertinent as management attempts to cope with an increasingly changing world.

5.2 Introduction

Disturbances are part of the dynamic nature of ecosystems (Holling 1973; O‘Neill 1999; Pandolfi and Kiessling 2014). Patterns in their frequency, intensity and spatial extent – an ecosystem’s disturbance regime – influence community composition and habitat structure. However, disturbance regimes are changing (reviewed by Turner 2010) with more intense acute disturbances occurring more frequently (e.g. cyclones; Kossin et al. 2013, heat waves; Song et al. 2014) and a wider range of chronic disturbances now affecting ecosystems (e.g. overexploitation; Jackson et al. 2001, pollutants; Moe et al. 2013). This has meant that there are an increasing number of ecosystems currently existing in a degraded condition, and many have been in altered conditions for quite some time (Jackson et al. 2001; Steneck et al. 2002; Lotze et al. 2006; Bruno and Selig 2007; Baldi et al. 2013).

Disturbances alter an ecosystem’s community because individuals and species respond differently to them, some positively and some negatively (Connell et al. 1997; Hughes and Connell 1999; Elmqvist et al. 2003; Pratchett et al. 2011a). On coral reefs for example, cyclones can result in major coral loss, subsequent increases in turf algae and herbivore abundances, but declines in corallivores (Adam et al. 2011). Following such acute disturbances, the community can either begin to recover or further degrade. Chronic disturbances exert continuous pressures, which can weaken the resilience of a system and affect its response to acute disturbances (Nyström and Folke 2001; Scheffer et al. 2001). Recovery occurs when affected organisms re-establish themselves and the community returns to approximate pre-disturbance organisation with no change in function (e.g. Gilmour et al. 2013; Vaudrey et al. 2010). Alternatively, key organisms may not re-establish (e.g. habitat builders/providers). Systems may therefore become degraded; for example, desertified and/or barren (Kassas 1995; Steneck et al. 2002), or other organisms may establish, filling or interfering with the niche of the displaced organisms (Hughes 1994; Scheffer et al. 1993). Effects of degradation can be predictable in space by comparing a number of sites in a range of conditions (Connell et al. 1997; Driscoll et al. 2001; Stockwell et al. 2009; Chong-Seng et al. 2012).

As the influence of disturbances increases and ecosystems become more degraded, and as management and conservation initiatives plan investments of time and resources, the ability to predict ecosystem dynamics across time is in demand (Pressey et al. 2007; Pressey and Bottrill 2009). Predictions require elucidation of system interactions that can take years to amass, and vast amounts of data, due to the complexity of ecosystems (e.g. Carpenter 2002; Grime and Pierce 2012; Martorell et al. 2014). However quantitative historical datasets are lacking for many areas worldwide. Inferences and predictions have been made using the assumption that contemporary relationships or patterns hold over time (e.g. Stockwell et al. 2009). Such an assumption seems necessary given the paucity of historical data available for many areas, but requires testing (e.g. Kharouba et al. 2009; Blois et al. 2013), in particular because reality is a lot more stochastic and unorderly than classic succession theory suggested (Pickett 1989; Suding and Leger 2012).

On coral reefs, our current ability to predict futures is improving (e.g. Pratchett et al. 2011b; Mumby et al. 2013; reviewed by Arias-González et al. 2011) but can be refined with further empirical data, especially at local scales where stochastic variability is high. Our study investigates whether spatial patterns in communities at a local scale hold across time given the dynamic nature of reefs. In particular, we focus on the strong relationships that exist between reef fish and their habitat, the sessile benthos. The coral reef ecosystem is interconnected, so alterations to either the fish (e.g. Hughes 1994) or the benthos (e.g. Spalding and Jarvis 2002) cause a variety of reciprocal changes in the other (Berumen and Pratchett 2006; Graham et al. 2006; Pratchett et al. 2008, 2011a; Bellwood et al. 2012b; Lecchini et al. 2012). The current study specifically investigates 1) whether fish assemblages can be predicted from a reef's benthic assemblage, based on previously observed fish~habitat relationships and 2) whether there are specific aspects of the benthic assemblage that different fish assemblage metrics respond to.

5.3 Methods

*5.3.1 **Study site***

I build on an earlier study from one point in time (Chong-Seng et al. 2012: Chapter 2) that measured differences in reef fish assemblages along a continuum of reef degradation, in the inner Seychelles 13 years post extensive devastation caused by the mass bleaching event in 1998 (Goreau et al. 2000). The Seychelles suffered further thermal warming events in 2003 and 2010 (NOAA 2013) and its reef waters are also subject to chronic stress. Chronic stressors include terrestrial runoff and sedimentation from land reclamation efforts and coastal development, and while there are established and functioning marine reserves (e.g. Wilson et al. 2012), the remaining area is moderately fished (Grandcourt and Cesar 2003; Daw et al. 2011a).

Twenty carbonate fringing reefs within a 3600 km^2 area around the inner Seychelles islands (4°30'S, 55°30'E) were surveyed in October 2010 (Chong-Seng et al. 2012) and December 2012. At each reef in each year, four 50 m transects were haphazardly laid at approximately 4 m depth, perpendicular to the reef slope. The following data were collected along each transect by the same observers in both years; 1) live benthic cover recorded at 0.5 m intervals, 2) structural complexity recorded using both a 6-point scale (Wilson et al. 2007) and by estimating the number of small refuge holes, < 10 cm diameter, along two 10 x 1 m sub-transects, and 3) number and identity of all fish greater than 8 cm along a 5 m wide belt, counting large, mobile species first as the transect was laid. Scleractinian corals and macroalgae were identified to genus and/or morphological group, while other algae were identified to functional group. For further sampling details, see Chapter 2.

5.3.2 ***Benthic composition***

For analyses, branching *Acropora* and massive *Porites* were differentiated from the rest of the coral genera (grouped as ‘other hard corals’) due to their high cover. Similarly, corallimorphs had high cover and were distinguished from ‘other benthic organisms’, which included soft corals, *Millepora*, sponges and zoanthids. Algae were grouped into five functional groups (based on Steneck 1988): turfs (incl. cyanobacteria), crustose coralline algae (CCA), leathery macroalgae (*Sargassum* and *Turbinaria* sp.), foliose macroalgae (e.g. *Lobophora* and *Padina* sp.) and ‘other macroalgae’ (incl. *Dictyota*, *Caulerpa*, *Halimeda* sp.). The complexity measures were combined with the benthic cover data to provide a more comprehensive overview of the reef benthos as a habitat (e.g. Chabanet et al. 1997; Graham et al. 2008b; Wilson et al. 2008).

To examine among-reef variation in benthic composition, data were log-transformed and ordinated using three correlation-based principal component analyses (PCA); 1) 2010 data only, 2) 2012 data only, and 3) combining both years. For each PCA, I plotted the first two principal components (PC1 and PC2), which explained the majority of the variation in reef benthic condition. PC1 distinguished between reefs that had high coral cover and complexity (coral-dominated) versus reefs with low complexity and high leathery macroalgal cover (macroalgal-dominated). Both the 2010 PC1 (benthic condition continuum in 2010) and 2010/2012 PC1 (benthic condition continuum across both years) were used for further analyses.

5.3.3 ***Fish assemblages***

Fish species were assigned to 11 functional groups based on the literature and FishBase: obligate corallivores, herbivores (distinguishing browsers, excavators, grazers, and scrapers), detritivores, planktivores, piscivores, non-coral invertivores (hereafter invertivores), omnivores (consume animal and plant material) and generalist carnivores (fish and invertebrate feeders). Additionally, I calculated species richness (total no. species).

5.3.4 ***Relationships between fish and benthos between years***

To investigate whether there was consistency between years in the fish~benthos relationships first investigated in Chong-Seng et al. (2012), general additive models (GAMs) were estimated for each of the various fish metrics described above (11 functional groups, species richness, and total fish abundance; 13 response variables). GAMs incorporate the possibility of non-linear relationships between the response and explanatory variables (Zuur et al. 2007). The models were testing for a relationship between the fish metric and the benthic gradient (2010/2012 PC1; continuous variable), first using the 2010 data only (i.e. 2010 scores from the 2010/2012 PC1), and then using the 2012 data only (i.e. 2012 scores from the 2010/2012 PC1). For each fish metric, if a significant relationship with the benthic gradient was found in both years (i.e. 2010 and 2012 GAMs were significant), we then combined both years of data and tested whether the relationship between fish metrics and the benthic gradient varied between years. There was deemed to be no interactive effect of year if removal of the terms (interactive and main) improved the Akaike information criterion corrected for small data sets (AICc; Burnham and Anderson 2002). We also determined Akaike weights, which represent the ‘normalised relative likelihoods’ that sum up to 1, giving the probability that the chosen model is the best among the set of alternatives considered (Burnham and Anderson 2002). From the best-fit model, I calculated residuals of the observed fish metrics in 2012 based on predicted fits from the 2010 relationship or if there was no significant effect of year, the overall relationship between the fish metric and PC1.

For the fish metrics with a significant relationship with PC1 in both years, I investigated whether it was possible to use the observed changes in the benthic condition to predict the changes in the fish community that occurred in 2012 based on the relationship between the benthic condition and fish response metric in 2010. First I estimated the relationship between fish metrics and the 2010 PC1 using GAMs. Second, I predicted the values of the relevant fish metrics in 2012 from the benthic condition in 2012 (2012 scores along the 2010/2012 PC1). I assessed the predictive fit by regressing observed versus predicted values (Piñeiro et al. 2008). A positive correlation (and with slope $\neq 0$) would indicate an informative fit (Mesplé et al. 1996). The deviation from the perfect 1:1 fit was assessed by testing the significance of slope = 1 and intercept = 0 (Mesplé et al. 1996; Piñeiro et al. 2008).

Analyses were conducted using reef-level averages of each variable because more complex, nested designs that accounted for within-reef variation (i.e. transect-level data) did not change the results (Bolker et al. 2013). I used R for all analyses (R Development Core Team 2013). GAMs were set up with the R function *gam* (mgcv package; Wood 2006), using cubic regression smoothing splines (bs = ’cr’) with a maximum four degrees of freedom (k = 4) to model the explanatory variable (PC1). All models had a Gaussian error distribution and assumptions were checked visually with plots of residuals.

5.3.5 ***Partitioning benthic drivers of change at the site level***

The PCA combining both years of data visualised the similarity in the reefs' benthic condition between the two survey periods. Principal components that explained over 10 % of the variance were chosen for further analysis. For each of the first three principal components, the principal component score of a reef in 2010 was subtracted from the principal component score of the reef in 2012, estimating the change in benthic condition during the two-year period between surveys. The change in the various fish metrics was calculated similarly (e.g. 2012 abundances minus 2010 abundances). To investigate which aspect(s) of benthic change (∆pc1, ∆pc2 or ∆pc3) the changes in fish (∆fish) were related to, a series of increasingly complex GAMs were estimated. First, ∆fish was related to each benthic change using maximum likelihood estimation and the best model was selected based on AICc. The model with the strongest effect of benthic change (e.g. ∆pc1) was then expanded to include one other aspect of benthic change (i.e. + s(∆pc2) or s(∆pc3)). Akaike weights were determined for all models, giving the probability that model *i* is the best among the set of alternatives considered (Burnham and Anderson 2002). The final model was the one with the lowest AICc value, and largest Akaike weight, refit using restricted maximum likelihood estimation (REML).

5.4 Results

Net change in total coral cover from 2010 to 2012 averaged across all reefs studied was 2.81 % (± 1.49 SE) and in leathery macroalgae was -0.47 % (± 2.40), but this belies high variation at the reef level (Fig. 5.1a). The first PC explained 37.7 % and 42.8 % of the variation in reef benthic condition in 2010 and 2012 respectively. When combining both years of data, 11 reefs (n = 20) shifted along PC1 (39.2 %) towards low complexity, high macroalgal cover and nine reefs shifted towards high complexity, high coral cover (Fig. 5.1b). The net shift along PC1 in the two-year period was from corals and high complexity towards macroalgae and low complexity (Fig. 5.1a), from high CCA cover to high sand cover along PC2 (19.8 %; Fig. 5.1b) and from high turf algal cover to high cover of ‘other macroalgae’ along PC3 (11.9 %). Branching *Acropora* experienced a 3.50 % (± 1.16) net increase. Turf algae showed the largest net decrease, -5.85 % (± 3.09).

The relationship between corallivore abundance and the gradient in coral reef benthic condition (from coral- to macroalgal-domination) was the strongest found and the only that differed between the two years (Fig. 5.2a; Table 5.1, 5.2). The curve was steeper in 2012 than in 2010. Corallivore abundance tended to increase towards coral-domination, decreasing towards macroalgal-domination. Residuals were predominantly positive (mean 2.28) and largest at the coral-dominated end of PC1 indicating that the fish tended to be found in higher abundances than predicted by the 2010 relationship (Fig. 5.2d). Species richness was also highest when benthic condition was coral-dominated and lowest on macroalal-dominated reefs, however the response curve showed no difference across the two years (Fig. 5.2b; Table 5.1, 5.2). Residuals were highly variable but slightly negative overall (mean -0.11; Fig. 5.2e). In comparison, highest browsing herbivore abundances were found closer to the macroalgal-dominated end of the benthic gradient, with lower abundances at the coral-dominated end. The relationship was consistent between the two years (Fig. 5.2c; Table 5.1, 5.2). Residuals were predominantly negative, indicating that the fish tended to be found in lower abundances than predicted by the 2010 relationship, particularly at the macroalgal-dominated end of PC1 (Fig. 5.2f). However two reefs did not conform to this general trend with relatively large positive residuals at the macroalgal-dominated end of PC1, which resulted in an overall positive mean deviance (0.01; Fig. 5.2f). No relationship was found for any of the other 10 fish metrics.

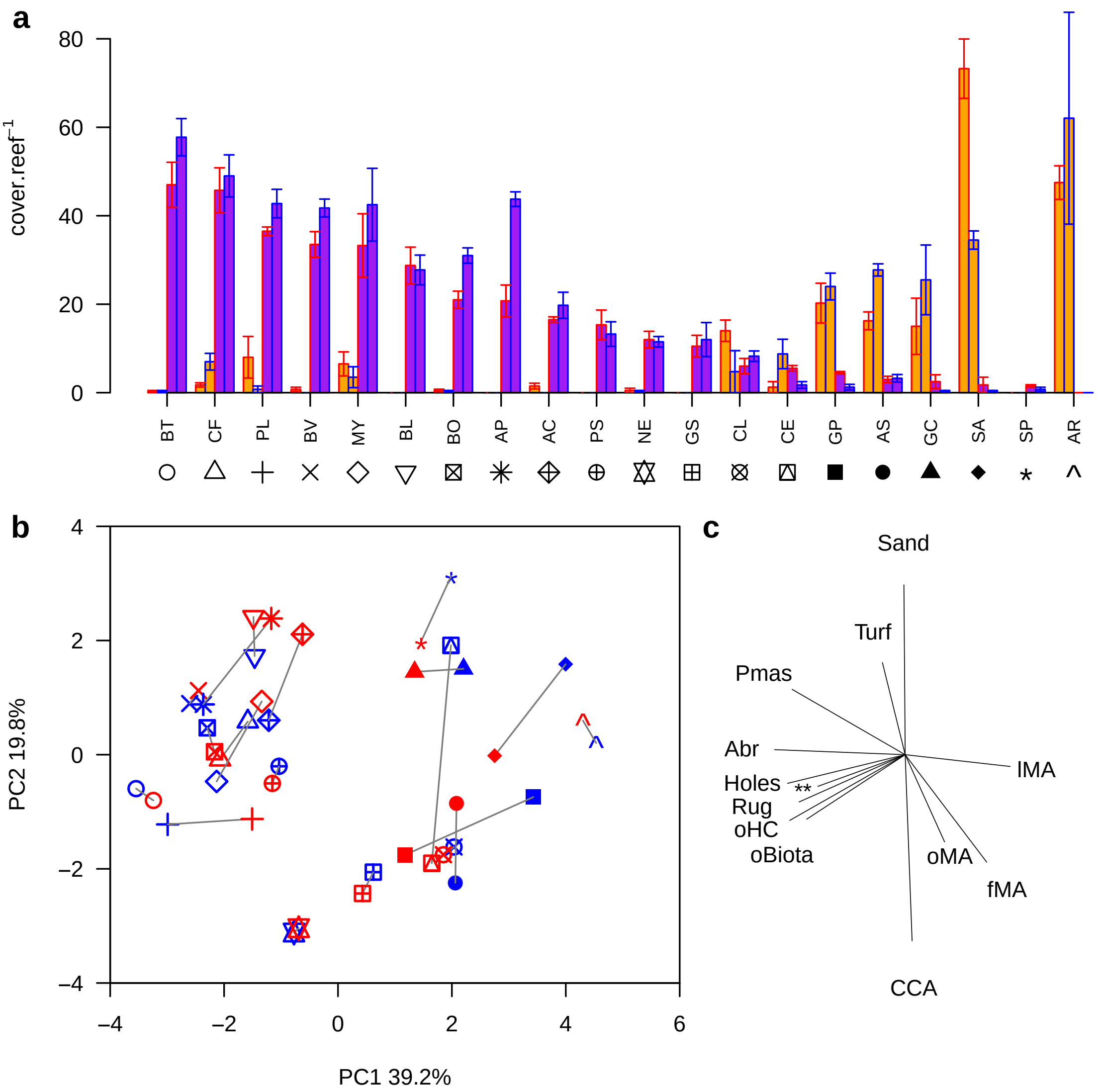
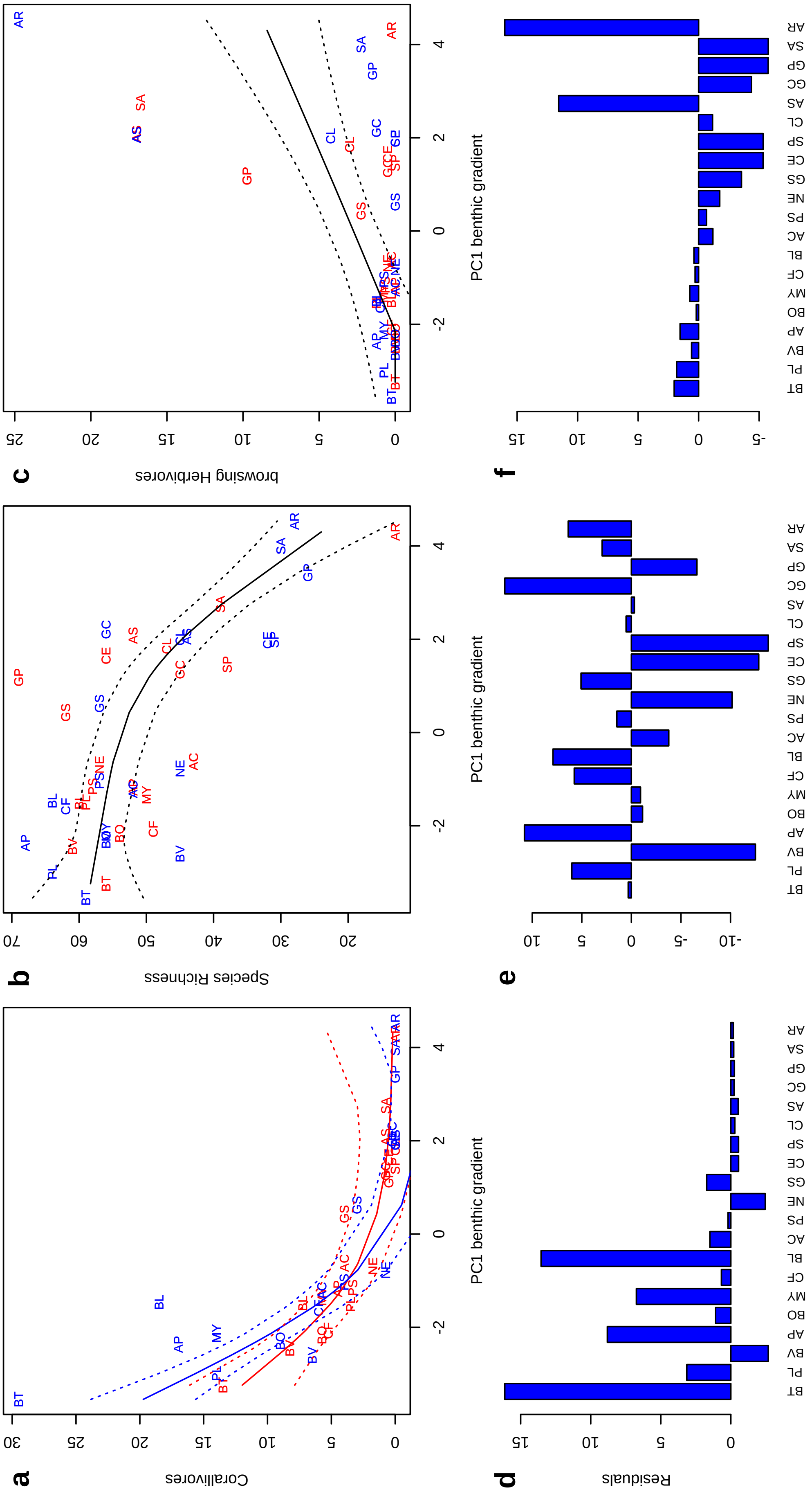


Fig. 5.1 (a) Cover of scleractinian corals (purple bars) and leathery macroalgae (orange bars) in 2010 (red outline) and 2012 (blue outline) for all study reefs. (b) PCA of study reefs in 2010 and 2012 (symbols match (a)) with (c) vectors showing influence of benthic variables. Abr: branching *Acropora*, Pmas: massive *Porites*, **: corallimorphs, Rug: rugosity, oHC: other hard corals, oBiota: other benthic organisms, CCA: crustose coralline algae, lMA: leathery macroalgae, fMA: foliose macroalgae, oMA: other macroalgae; see Methods.


a
Corallivores
b
Species Richness
c
browsing Herbivores
d
Residuals
e
f
PC1 benthic gradient
BT
PL
BV
AP
BO
MY
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PS
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GS
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Fig. 5.2 GAM of significant fish responses to the gradient in benthic condition from high coral cover and complexity to low complexity and high macroalgal cover in 2010 (red) and 2012 (blue). (a-c) Solid lines: GAM smoother, Dotted lines: approximate 95% CI and points represent the raw data. For species richness and browsing herbivores, the inclusion of Year in the model was insignificant, so the model only incorporates PC1 (see Table 5.2). (d-f) GAM residuals for 2012, based on predicted fits from the 2010 relationship (corallivores) or overall relationship (species richness and browsing herbivores) between the fish metric and PC1. (a,d) Corallivore abundance, (b,e) fish species richness and (c,f) browsing herbivore abundance.

Further supporting the findings above, positive relationships indicating an informative fit, were found between observed and predicted fish species richness, and the abundances of both browsing herbivores and corallivores in 2012 (Appendix D Fig. S1, Table S1). However, the predictive fits deviated from the perfect fit (Appendix D Fig. S1). For corallivores, 95 % confidence intervals around the slope showed it to be significantly different from the 1:1 line of perfect fit (Appendix D Fig. S1, Table S1). Nevertheless, the intercept was not significantly different from zero indicating that the deviation in predictions was proportional to the observed values (Mesplé et al. 1996), and over 75 % of the variation in observed values was explained by the predicted values. For species richness and browsing herbivores, although 95 % confidence intervals around the slope and intercept estimates indicated a relationship that was not significantly different from the perfect fit, the variation in observed values explained by the predicted values was only 57.7 % and 26.8 % respectively (Appendix D Fig. S1; Table S1).

Nine of the 13 fish metrics responded significantly to at least one of the site-specific changes in benthic community (Fig. 5.3; Table 5.3; Appendix D Fig. S2). Species richness, corallivores, detritivores, invertivores, omnivores, browsing and scraping herbivores responded to changes in benthic community along PC1, from high coral cover and complexity (-ve scores) to low complexity and high leathery macroalgal cover (+ve scores)(Fig. 5.3a,b,c; Appendix D Fig. S2). Invertivores and species richness had a bimodal response to change in PC1, appearing to be highly variable with small changes in PC1, but tending to decrease with large increases in PC1 (Fig. 5.3b; Appendix D Fig. S2). Additionally, species richness, detritivores and invertivores also responded to changes in PC2, decreasing as the benthic community shifted from high CCA cover (-ve scores) to high sand cover (+ve scores)(Fig. 5.3d; Appendix D Fig. S2). Browsing herbivores also responded to changes in PC3, increasing as the benthic condition shifted from one with more ‘other macroalgae’ (-ve scores) to one with higher turf cover (+ve scores; Fig. 5.3e). Total fish abundance and planktivores only responded to changes in the benthic community along PC2, unsurprisingly decreasing with increases in sand cover (Appendix D Fig. S2).

Table 5.1 P-values for initial GAMs that estimate the relationship between the 13 fish metrics and the gradient in benthic condition along PC1, in two years (2010 versus 2012)

Fish metrics	2010	2012
Species Richness	**0.000**	**0.000**
Total fish abundance	0.221	**0.007**
Carnivores	0.943	0.253
Corallivores	**0.000**	**0.000**
Detritivores	0.141	**0.009**
Herbivore (browsers)	**0.034**	**0.029**
Herbivore (excavators)	0.265	0.332
Herbivore (grazers)	0.192	0.837
Herbivore (scrapers)	0.755	**0.032**
Non-coral invertivores	**0.049**	0.410
Omnivores	0.220	**0.003**
Piscivores	0.180	**0.007**
Planktivores	0.131	0.230

Table 5.2 Parameters of the best fitting GAM which estimates the relationship between three fish metrics and the gradient in benthic condition along PC1, in two years (2010 versus 2012). D_{Null}: null deviance, D_{Expl}: proportion of explained deviance, Estimates of the parametric terms: model intercept (± SE)[#], Smooth terms edf: estimated degrees of freedom of PC1 smooth function[#] with significant p-values, $AICc_{weights}$: probability that model is the best of the set of alternatives considered.

Fish metrics	D_{Null}	D_{Expl} (%)	Parametric estimates (± SE)	Smooth terms edf		$AICc_{weights}$ (%)
Corallivores[#]	1603	75.8	3.6 ± 0.8	pc1	2.4 **	87.8
			2.6 ± 1.1	pc1:2010	0.0	
				pc1:2012	2.0 *	
Species Richness	6141	62.3	50.0 ± 1.3	pc1	2.4 ***	60.6
Herbivore (browsers)	1309	23.6	2.8 ± 0.8	pc1	1 **	72.7

[#] Corallivores were best estimated with y ~ yr + *f*(pc1) + yr**f*(pc1); i.e. including the interaction between *f*(pc1) and Year. Therefore there are parametric estimates for the intercept (reference level is 2010) and the second year (2012), and smooth terms for the overall relationship with PC1, and the curves along PC1 in 2010 and in 2012. Otherwise, metrics were best estimated with y ~ *f*(pc1); where *f*(pc1) represents the smooth function (i.e. no effect of Year).

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 5.3 Parameters of the best fitting GAM which estimates the relationship between the change in 13 fish metrics and the change in three aspects of the benthic community, between two years (2010 versus 2012). D_{Null}: null deviance, D_{Expl}: proportion of explained deviance, Estimates of the parametric terms: model intercept (± SE), Smooth terms edf: estimated degrees of freedom of smooth function(s) with significant p-values, ΔPC1: change in coral cover and complexity versus macroalgae cover, ΔPC2: change in CCA versus sand cover, ΔPC3: change in 'other macroalgae' versus turf cover, $AICc_{weights}$: probability that chosen model is the best of the set of alternatives considered.

Fish metrics	D_{Null}	D_{Expl} (%)	Parametric estimates (± SE)	Smooth terms edf			$AIC_{weights}$ (%)
				ΔPC1	ΔPC2	ΔPC3	
Species Richness	3899	71.9	-2.2 ± 1.9	2.8 **	1.0 **		51.1
Total fish abundance	57510	21.7	-16.3 ±11.2		1.0 *		33.1
Carnivores	2265	6.5	-1.3 ± 2.4			1.0	37.7
Corallivores	568	43.8	2.9 ± 1.0	1.8 **			72.1
Detritivores	660	62.8	0.1 ± 0.9	2.6 *	1.7 *		56.8
Herbivore (browsers)	889	84.6	0.2 ± 0.7	2.0 *		2.9 ***	76.8
Herbivore (excavators)	807	6.5	-1.7 ± 1.4			1.0	29.4
Herbivore (grazers)	13257	6.9	-11.7 ± 5.9			1.0	36.1
Herbivore (scrapers)	1938	50.5	-1.2 ± 1.7	2.4 **			50.1
Non-coral invertivores	2535	56.3	-9.0 ± 1.9	2.8 *	1.0 **		71.3
Omnivores	1514	46.1	2.6 ± 1.5	1.0 ***			52.2
Piscivores	113	8.2	-0.7 ± 0.5		1.0		40.8
Planktivores	3327	27.9	3.5 ± 2.6		1.0 *		58.6

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

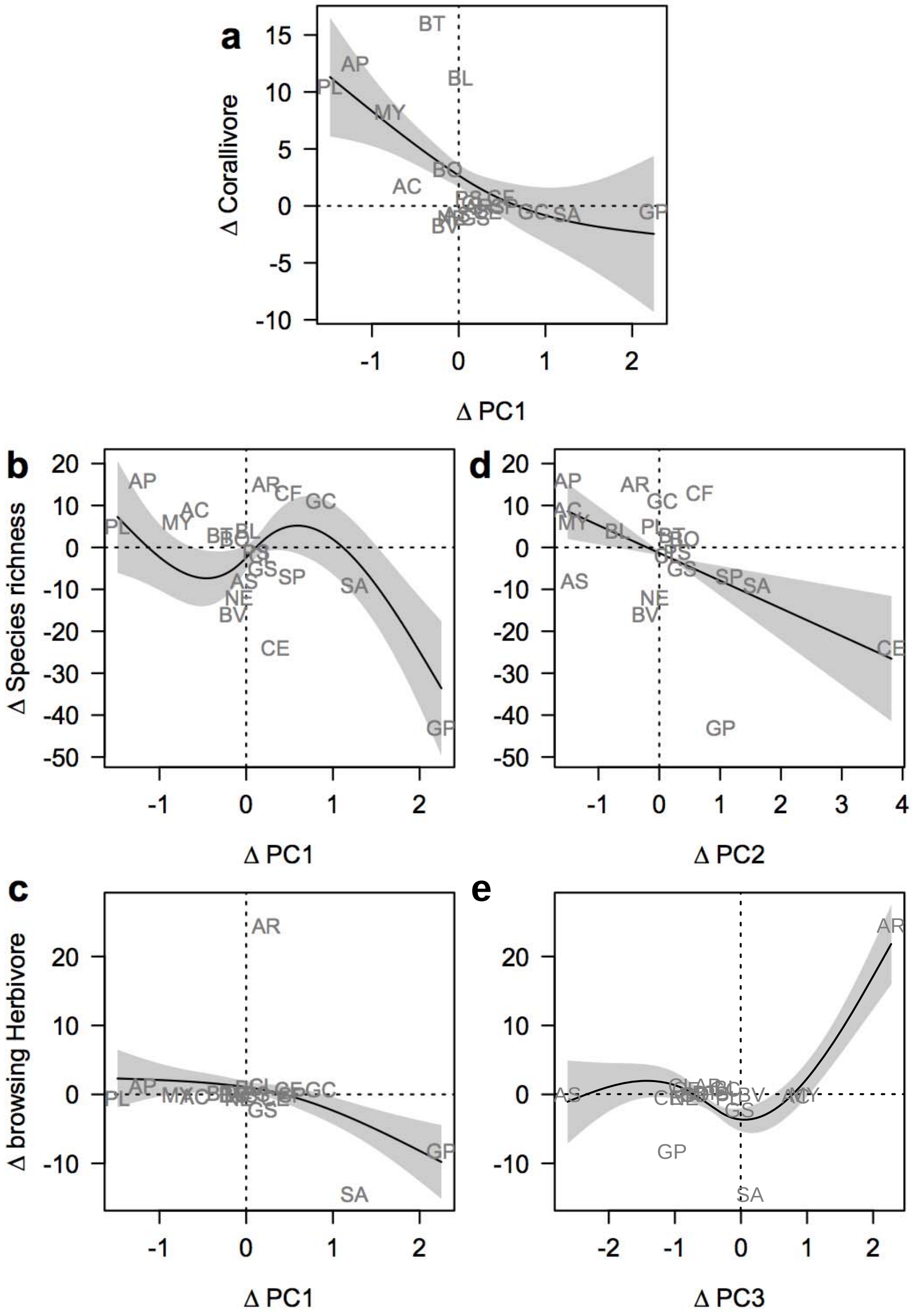

Fig. 5.3 Magnitude and direction of changes in benthic assemblages, with reciprocal changes in fish species richness (b, d), and abundances of corallivores (a) and browsing herbivores (c, e). Dotted lines: zero change, Letters: reefs (see Fig. 5.1), Solid lines: GAM smoother, shaded region: 95% confidence intervals. Δ PC1: high coral cover and complexity (-) to low complexity and high leathery macroalgal cover (+), Δ PC2: high CCA cover (-) to high sand cover (+), Δ PC3: high 'other macroalgae' (-) to high turf cover (+).

5.5 Discussion

On coral reefs, interactions between fish and their habitat are well studied (e.g. corals; Pratchett et al. 2008, corals and habitat complexity; Graham et al. 2007, habitat complexity and macroalgae; Hoey and Bellwood 2011) with increasingly complex studies facilitating better predictions of coral reef futures (Pratchett et al. 2011b; Pandolfi et al. 2011; Mumby et al. 2013; Riegl et al. 2013). The current study investigates relationships across time at a local scale and attempts to move beyond spatial snapshot surveys. I found that a continuum of benthic condition from coral- to macroalgal-dominance was associated with similar patterns for three aspects of the fish assemblage in both survey years, despite dynamism within individual reefs. This implies that a reef's benthic habitat can provide predictable information about fish species richness and abundances of corallivores and browsing herbivores: coral-dominated reefs have higher species richness and more corallivores; macroalgal-dominated reefs may have more browsing herbivores. However, there was no consistent relationship for 10 fish assemblage variables. Benthic change occurred along three main axes: coral to macroalgal cover (or vice versa); CCA to sand; 'other' macroalgae (e.g. *Dictyota*) to turf algal cover. These changes (both direction and magnitude of shift) were found to be associated with reciprocal changes in nine (of 13) aspects of the reef fish assemblage. High variation despite approximately zero benthic change at some sites was apparent. By broadening my focus to other components of the benthos, my findings emphasize the need to consider multi-group assemblages in predictive assessments.

Species richness is an assemblage-level measure and conceals individual relationships between and within functional groups of species. Some functional groups of species will have a net response to changes (e.g. corallivores) whereas others will not (e.g. excavating herbivores). Within a group, response diversity may be high (Pratchett et al. 2011a). For example, within the corallivores, *Oxymonacanthus longirostris* abundance increased between the two years, *Chaetodon melannotus*, a soft coral specialist, declined and there was no change in *Chaetodon zanzibarensis*. Nevertheless, I found that species richness is relatively predictable just from a reef's benthic condition along a continuum from coral to macroalgal-domination. There was an overall decline in species richness as reefs were positioned closer to the macroalgal-dominated end of the continuum, which may hinder functional processes (Cardinale et al. 2013), for example through reduction in response diversity (Elmqvist et al. 2003), loss of specialised species (Davey et al. 2013) or restricting the full range of required species (Rasher et al. 2013).

Corallivores have evolved to exploit a novel resource (Cowman et al. 2009; Bellwood et al. 2010), and losing this resource has highly detrimental effects for the species involved. Corallivores unequivocally responded negatively to loss of corals (c.f. Spalding and Jarvis 2002; Graham et al. 2007) but there were large fluctuations in their abundances between the two years. From predictions, the 2010 data tended to underestimate large abundances in 2012, indicating that corallivores may be recovering faster than expected, given the relatively small changes in coral cover, on reefs at the coral-dominated end of the continuum. Faster recovery could potentially arise because there were initial lag effects such as time taken for growth of either preferred coral prey or of the fish themselves to surveyable size, or for a reproductive population to re-establish from local extinction (Graham et al. 2006; Petitgas et al. 2010).

Browsing herbivores had the most tenuous of the statistically significant relationships with the benthos – explaining less than 20 % of the variance, and primarily driven by four reefs. Previous studies have also found limited response of herbivores to increasing macroalgae (Wismer et al. 2009; Johansson et al. 2010; Cheal et al. 2010, 2013). However, many of these browsing species are increasingly considered to be diver-shy and cryptic to survey (Fox and Bellwood 2008; Hoey and Bellwood 2009; Chong-Seng et al. 2014: Chapter 4). For example, up to 15 individuals of *Siganus* *canaliculatus* were observed on video footage from coral-dominated reefs, yet never recorded on any of 60 visual censuses (Fox and Bellwood 2008). Therefore, estimates of browsing herbivore abundances from visual census are likely to be underestimates. Moreover, the browsing herbivore group is relatively species-poor in comparison to other diet-based functional groups (Bellwood et al. 2006a; Hoey and Bellwood 2009). Of the seven browsing herbivore species in our study, two were relatively uncommon, represented by three individuals (*Calotomus spinidens, Naso brachycentron*). Five species can exhibit schooling behaviour and vary from solitary individuals to schools of over 20 individuals (Froese and Pauly 2011), which may contribute substantially to large fluctuations in abundance between years (c.f. apogonids; Messmer et al. 2011). Variation in browsing herbivore abundance was highest towards higher macroalgal cover, and a meta-analysis of response diversity found a mean positive response to habitat change (Pratchett et al. 2011a), indicating that the relationship is likely real. However, macroalgal browsers, while increasing with increased food availability, may be unlikely to reverse shifts to macroalgal-dominance because their macroalgal removal rates have been found to be very low on Seychelles reefs (Chong-Seng et al. 2014: Chapter 4).

Most aspects of the fish assemblage had no consistent relationship across time with the benthos. This may reflect the relatively weak associations that certain fish groups have with the benthos. Piscivores for example, may only depend on the live benthos indirectly as habitat for their prey (e.g. Hixon and Beets 1993), and may be large enough to be less reliant on refugia (Nash et al. 2013). Four fish functional groups (detritivores, omnivores, piscivores and planktivores) and total fish abundance had no significant relationship with the benthic continuum (coral to macroalgae) in 2010, but did in 2012, and vice versa for invertivores. Such inconsistencies indicate that spatial patterns sampled do not necessarily hold over time and therefore these groups cannot be predicted from the benthos alone. It is also possible that statistical power was weak, with the addition of more data (increasing *n*) likely to reduce some of the natural variation (Zar 1999). Relationships may be masked due to high natural variation in abundances of at least some of the fish metrics because they respond to reef-level changes in certain aspects of the benthos (e.g. detritivores; Table 5.3; Appendix D Fig. S2). Interestingly however, three fish assemblage metrics showed no response to any aspect of the benthos that was investigated – excavating and grazing herbivores and generalist carnivores. These groups may comprise more generalist species (e.g. *Thalassoma herbraicum*; Chong-Seng et al. 2012: Chapter 2), which can inhabit a wide range of environments. Alternatively, there may be high response diversity within these groups; a meta-analysis found fish responses to local coral loss was relatively evenly spread across the full range of responses for all three groups (Pratchett et al. 2011a). Nevertheless, these latter fish groups may be considered winners as reefs become increasingly stressed (c.f. van Woesik et al. 2011).

On local scales, stochastic variability is known to be high (Pickett 1989; Suding and Leger 2012), which may mask external effects (Arias-González et al. 2011; Chase and Myers 2011; Blois et al. 2013) or inhibit species-level predictions (Mumby and Steneck 2011). Nevertheless, natural variability is important to quantify and act as a yardstick against which to measure impacts of acute disturbances (Mumby and Steneck 2011). I found high variability in fish responses between the two years despite approximately zero benthic change for some sites, which may be useful for parameterising forecast models if it represents local stochasticity (although some may result from unaccounted variables; Bolker 2008). My study covered a two year time period, with no acute disturbance occurring in the interim. Nevertheless five aspects of the fish assemblage responded to specific adjustments in benthic condition, and four aspects of the fish assemblage responded to a combination of shifts in benthic condition. Certain groups of fish responded primarily to increases in sand cover rather than quantities of coral or macroalgal cover, unequivocally decreasing as sand cover increased. Surprisingly not among them, were the grazing and excavating herbivores, which have previously been shown to prefer more sediment-free surfaces (Bellwood and Fulton 2008, Goatley and Bellwood 2012). Other groups (e.g. omnivores) seemed to respond more to the magnitude rather than direction of change. Several of the relationships were driven by one reef (GP along PC1, CE along PC2), which shifted the most, so it is possible that changes at many sites were not large enough to initiate a direct response.

Coral reefs are among the world's threatened ecosystems, with many reefs severely degraded (Gardner et al. 2003; Bruno and Selig 2007; Ateweberhan et al. 2011), and projections looking grim (Hoegh-Guldberg et al. 2007; Riegl et al. 2013). This study demonstrates the diversity of responses to disturbances among reef communities, with multiple trajectories within a local system, emphasizing the complexity of predictability. The findings are phenomenological – pattern fitting using GAMs (Austin 2002), rather than testing or supporting an underlying mechanistic theory. However, these can be seen as first steps in developing a more mechanistic understanding of the system (Carpenter 2002). My results incorporate a key aspect of the coral reef ecosystem (primarily corals versus macroalgae) into predictions of future dietary-based reef fish assemblages, but perform surprisingly well for three aspects of the fish assemblage. It remains to be seen how ubiquitous these relationships are on reefs in other parts of the world. The need to understand which elements of the ecosystem are predictable through time is becoming more pertinent as management attempts to cope with an increasingly changing world.

CHAPTER 6

General Discussion

Degradation of ecosystems worldwide is necessitating more informed management and conservation initiatives, which ideally require predictions of ecosystem dynamics (Jackson et al. 2001; Hughes et al. 2005; Pressey et al. 2007; Pressey and Bottrill 2009; Cardinale et al. 2012). Central to our ability to predict ecosystem structures and assemblages is an understanding of how new conditions manifest and are maintained (Done 1999; Hughes et al. 2010; Nyström et al. 2012). The majority of research on alternative reef conditions to date are often restricted to benthic data and discussion (e.g. Hughes 1994; Bruno et al. 2009; Hughes et al. 2010), with little mention of the reefs' physical structure or associated biological communities. By comparing communities and processes within a system of disturbed coral reefs, this thesis identifies relationships among various reef communities (Chapters 2 and 5), and uncovers limitations in key ecological processes that may inhibit recovery of coral assemblages following major and widespread disturbances (Chapters 3 and 4). Ultimately the work goes beyond descriptions of ratios in coral-algae benthic cover and explores what reef condition means for other organisms, ecological processes and also therefore, ecosystem services.

6.1 Implications of alternative benthic conditions

Ecosystem processes are governed by interactions among ecosystem components (e.g. across trophic levels, competition; Nyström et al. 2012; Grime and Pierce 2012). These interactions generate feedbacks that reinforce particular aspects of coral reef conditions (Mumby and Steneck 2008; Hughes et al. 2010; Nyström et al.

2008, 2012). For example, Mumby and Steneck (2008) highlight algal grazing intensity, which if levels are high, reinforce coral-dominated conditions on reefs (given adequate supply of coral larvae). However, low grazing intensities could liberate algae, reinforcing macroalgal-dominated conditions instead. Some interactions amongst a selection of coral reef components are conceptualised in Fig. 6.1, which can vary in intensity and direction, with resulting effects through the system (Fig. 6.2).

Corals and algae are some of the best-studied interactions on coral reefs because their resultant ratios are fundamental to habitat quality (Barott et al. 2012; reviews by Birrell et al. 2008a; Chadwick and Morrow 2011; see Norström et al. 2009 for extensions to other benthic competitors). Depending on life history stage, corals and algae can compete or be inhibited by the other (e.g. Birrell et al. 2008b; Vermeij et al. 2009), and resultant coral cover is conditional on survival of earlier life stages. Moving up into the water column and/or through trophic levels, the benthic biota will interact with various fish functional groups directly, as habitat providers (e.g. coral-associated planktivores; Wilson et al. 2006) or food source (e.g. corallivores; Pratchett et al. 2008), or indirectly (e.g. as habitat for their prey; Randall 1967). In this work, the intensity and direction of possible interactions among the selected coral reef components (Fig. 6.1) were found to influence investigated ecosystem processes (coral survivorship; Chapter 3, macroalgal herbivory; Chapter 4), and may therefore be involved in the persistence of degraded conditions currently in place among inner Seychelles coral reefs. Using conceptual models, the following summarises my understanding of the interactions and resulting feedbacks, in contrasting reef habitats within the inner Seychelles (Fig. 6.2).

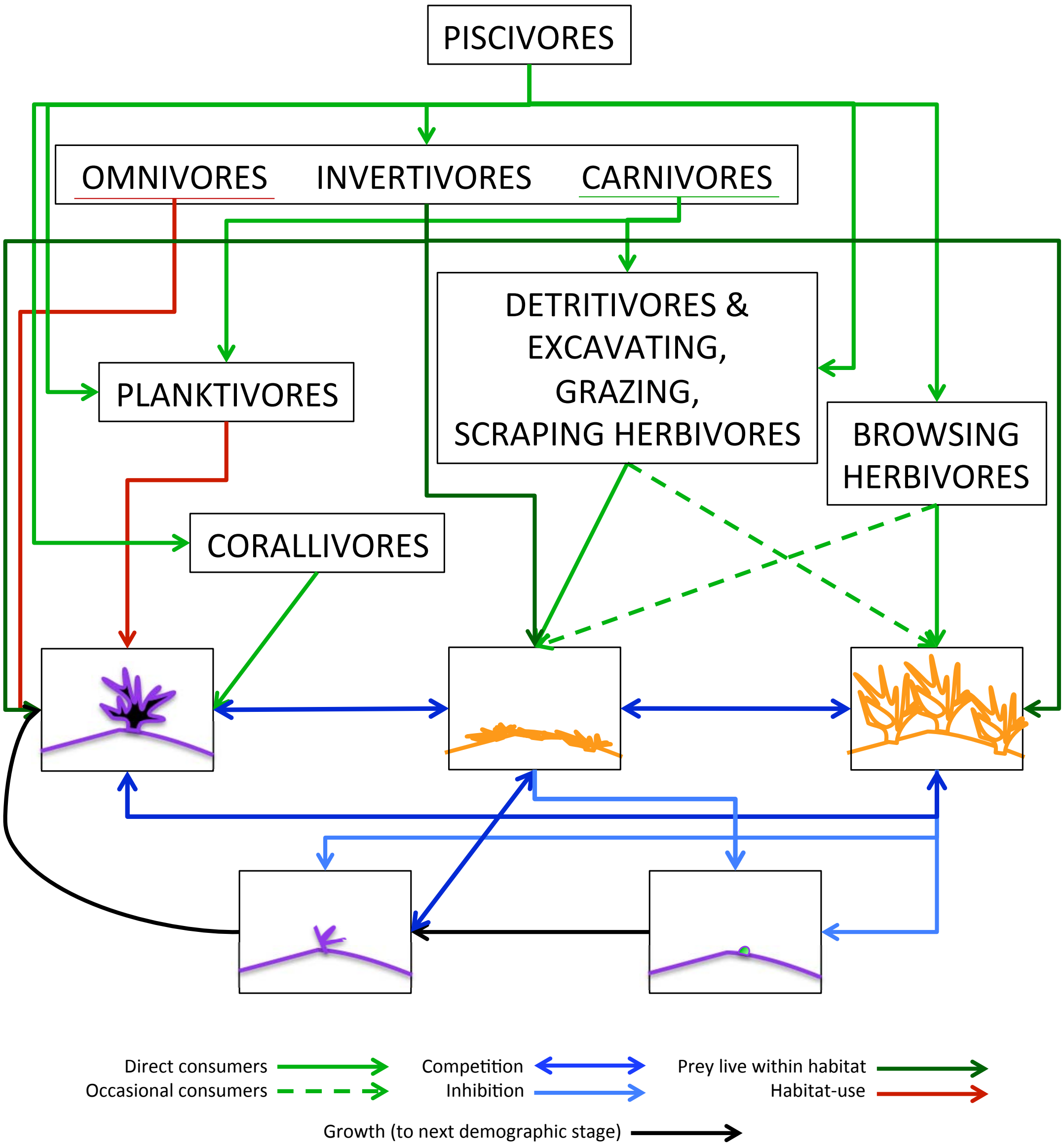

Fig. 6.1 Conceptual diagram of interactions among biological organisms on coral reefs. Arrows represent interactions, colour-coded following the key. Trophic groups consider fish primarily. Purple benthic organisms represent three coral life history stages (adult, juvenile (<5 cm diameter), recruit). Orange benthic organisms represent algae – the epilithic algal matrix, and macroalgae (primarily leathery macroalga such as *Sargassum*).

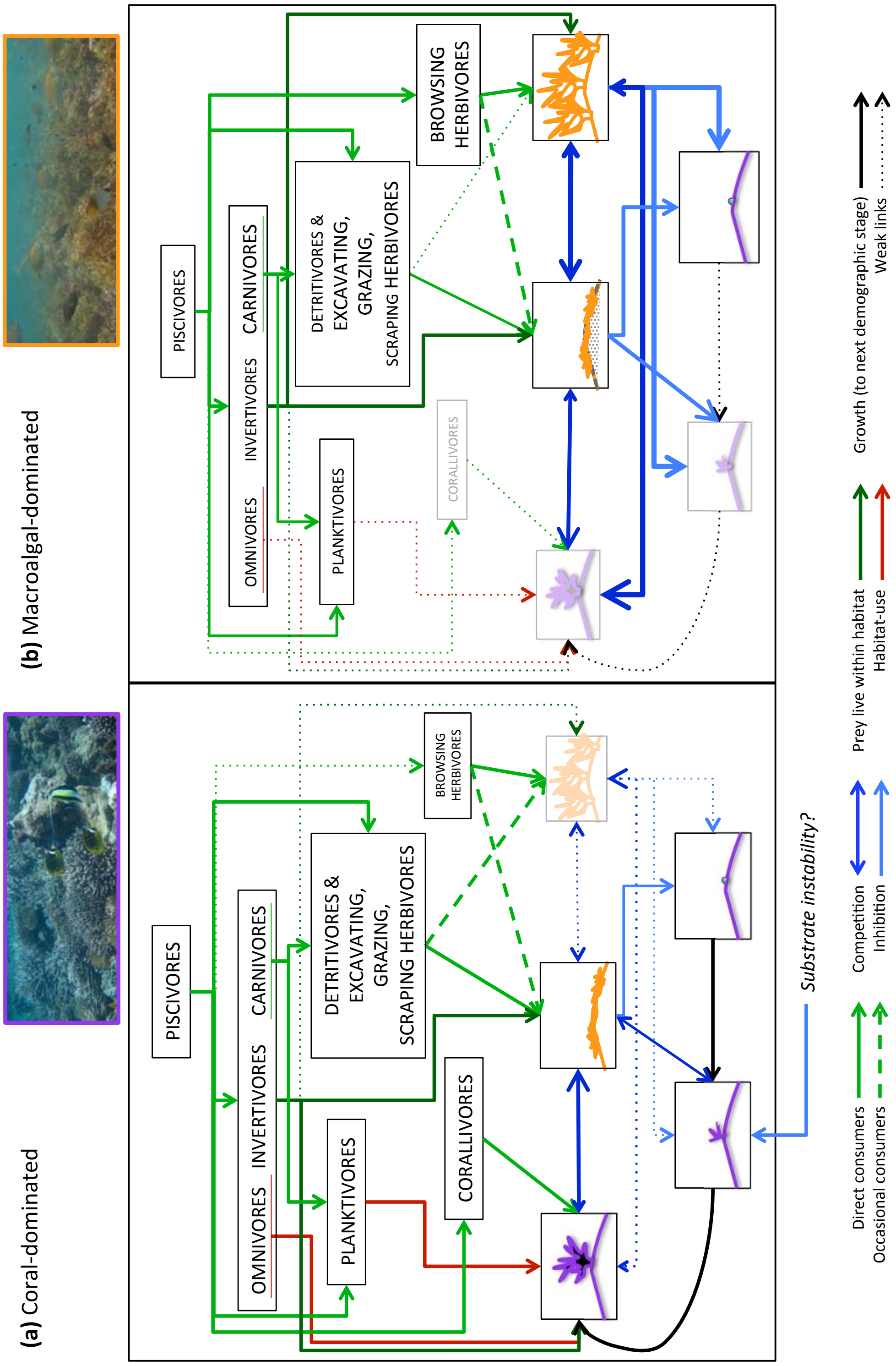

Fig. 6.2 Conceptual diagram of interactions among biological organisms on (a) coral-dominated, (b) macroalgal-dominated reefs. Size and colour intensity represent strength of interactions (larger and more vivid indicate stronger interactions). Trophic groups consider fish primarily. Benthic colours as for Fig. 6.1. Substrate instability is included as an external factor that affects particular nodes of the network, but with important ramifications (see text).

6.1.1 **Coral-dominated reefs**

Coral-dominated reefs are characterised by a diverse fish assemblage and minimal macroalgal cover (Steneck 1988; Knowlton and Jackson 2008; Sandin et al. 2008; Sale and Szmant 2012; Graham and McClanahan 2013; Chapter 2), so interactions involving macroalgae would be relatively weak (Fig. 6.2a). For example, incoming coral larvae on coral-dominated reefs would be arriving into a habitat where the benthos is characterised by either CCA or relatively sediment-free EAM, and therefore conducive to successful settlement (Birrell et al. 2008a; Ritson-Williams et al. 2009), providing beneficial conditions for recruits to survive to juveniles and then reproductive adults (Chapter 3; Fig. 6.2a). A variety of herbivorous fishes exert top-down control on macroalgal propagules within the EAM, boosting the competitive superiority of corals vs. algae in the fight for limited space on reefs (Diaz-Pulido et al. 2009; Chadwick and Morrow 2011) and therefore preventing their growth into mature macroalgae (i.e. ensuring low macroalgal cover; e.g. Arthur et al. 2006; Gilmour et al. 2013). The reduced number of browsing herbivores on coral-dominated reefs (Bellwood et al. 2006a; Johansson et al. 2013; Chapters 2 and 5; Fig. 6.2a) may be a result of limiting food resources, although Hoey and Bellwood (2010) suggested that these species might be highly efficient foragers, and these species may therefore be present but cryptic to survey (Fox and Bellwood 2008; Hoey and Bellwood 2009; Chapter 4). However, despite an apparent shortage of browsing herbivores, the potential for macroalgal herbivory to occur on these reefs appears to be equivalent to that occurring on macroalgal-dominated reefs (Fig. 6.2), yet with a different suite of species involved (Chapter 4). Some of the non-browsing herbivorous species were important consumers of mature macroalgae bioassays on these coral-dominated reefs (Chapter 4), despite avoidance of in situ macroalgae during feeding observations in their natural environment (Ledlie et al. 2007). Furthermore, these non-browsing herbivorous species have been observed consuming *Sargassum* assays on other coral-dominated reefs elsewhere, though to a lesser extent (Australian Great Barrier Reef; e.g. Hoey and Bellwood 2009, Ningaloo; Vergés et al. 2012, Fiji; Rasher et al. 2013). These findings suggest potential for functional plasticity amongst reef herbivores.

Adult coral colonies are important in a number of roles on reefs (e.g. Pratchett et al. 2008; Fig. 6.2a). Corals are essential for obligate corallivores, providing food and habitat (Pratchett et al. 2008). Branching coral species in particular, are important habitat providers for a range of organisms, including small-bodied fishes (e.g. gobies, planktivorous and omnivorous damselfish; Bellwood et al. 2006b, 2012a), invertebrates (Stella et al. 2011) and juveniles of many coral reef fishes (Jones et al. 2004). These coral-inhabiting species or ontogenetic stages are an important food source for many reef fish (piscivores, generalist carnivores, non-coral invertivores and omnivores; Randall 1967; Fig. 6.2a). Consequently, reef fish populations are highly dependent on the coral assemblage, as a demographic stepping-stone, habitat for prey, and as habitat themselves. A coral assemblage characterised by a range of habitat-providing species ensures a more diverse reef fish community (Wilson et al. 2006; Graham et al. 2006; Sandin et al. 2008; Johansson et al. 2013; Chapters 2, 4, 5).

6.1.2 ***Rubble-dominated reefs***

High cover of habitat-providing corals may, however, mean that the system is vulnerable to rubble formation, as a result of physical breakdown (e.g. storms; Harmelin-Vivien 1994, Connell et al. 1997) or bioerosion following coral colony mortality (e.g. bleaching episodes; Graham et al. 2006, Arthur et al. 2006). Reefs may avoid perpetuating further damage and rubble accumulation if there is enough water flow to immediately remove broken pieces (e.g. Arthur et al. 2006; Rasser and Riegl 2002). If rubble persists, instability of the underlying physical reef matrix can interfere with small coral colony survival (Fox et al. 2003; Arthur et al. 2006; Chapter 3; Fig. 6.2a), instigating an alternative trajectory in benthic condition with few macro-benthic organisms and low structural complexity (e.g. Fox et al. 2003; Graham et al. 2006; Birkeland et al. 2013). Benthic organisms such as crustose coralline algae are likely to be important for reef consolidation (e.g. Littler et al. 1995; Victor 2008; reviewed by Rasser and Riegl 2002), and although present on the rubble-covered study reefs, many of these reefs remain unconsolidated (Chapters 2, 3, 5). Rubble consolidation occurs in two main stages, requiring preliminary stabilisation (i.e. rubble remains stable during average wave conditions) prior to rigid binding, which is when crustose coralline algae may be most important (Rasser and Riegl 2002). Preliminary stabilisation can involve overgrowth by fast growing benthic organisms but may not always be permanent (e.g. soft corals such as *Xenia* cannot always withstand storms; Fox et al. 2003), which may be the case on the rubbly inner Seychelles reefs. Although there are extended periods of calm (Chapter 3), any preliminary stabilisation appears insufficient to prevent disruption following periodic high wave energy periods (cf. Birkeland et al. 2013).

6.1.3 ***Macroalgal-dominated reefs***

Differing from coral- or rubble-dominated reefs as a result of high macroalgal cover, macroalgal-dominated reefs are also characterised by lower fish species richness, low structural complexity and low to non-existent coral cover (Hughes 1994; Ledlie et al. 2007; Chapters 2 and 5; Fig. 6.2b). The loss of corallivorous species due to reductions in live coral (Graham et al. 2006; Pratchett et al. 2008; Fig. 6.2b) is the greatest component of decline in species richness on macroalgal-dominated reefs

(Chapters 2 and 5). There were also much lower abundances of other fish functional groups, except browsing herbivores, on macroalgal-dominated reefs when considering only extremes of the inner Seychelles habitat quality continuum (coral- vs. macroalgal-dominated reefs; Chapter 2; Fig. 6.2b). This is in comparison to Hoey and Bellwood (2011), who reported slight increases in predatory fish biomass around experimental plots with increased macroalgal density, and Wismer et al. (2009) who reported no correlation between browsing herbivores and macroalgal cover. While not explicitly analysed in this thesis, lowered abundances may be a result of fewer species making up the functional groups, and therefore indicators of reduced redundancy within functions (Folke et al. 1996; Nyström 2006). On inner Seychelles macroalgal-dominated reefs, 13 years after the 1998 bleaching event, reduced functional redundancy may imply that feedbacks reinforcing the macroalgal condition strengthen, because the species involved may be adapted to the macroalgal conditions and less likely to be influential in enhancing processes that may revert the system to coral-domination.

Increased macroalgae may be expected to influence the herbivorous reef fish population. However, turf and macroalgal herbivory appeared to remain relatively consistent across the Seychelles' continuum in habitat quality (Chapters 2, 4, 5; Fig. 6.2). There were no changes in abundances of excavating and grazing herbivores across the benthic gradient in condition, nor in response to shifts in benthic communities on individual reefs over time (Chapters 2 and 5). Mature macroalgae has often appeared unpalatable to non-browsing herbivorous fish groups (Bellwood et al. 2006a; Ledlie et al. 2007). Moreover, these non-browsing species have been shown to significantly reduce their grazing intensity on the substratum in areas with high macroalgal density (Hoey and Bellwood 2011). Despite significant reductions in intensity, grazing continued, indicating that while non-browsing herbivorous fish may preferentially avoid macroalgal-dominated habitat conditions, survival is possible as evidenced by their relatively consistent presence on all surveyed reefs (Chapters 2, 4, 5). For the browsing herbivores, there were apparent increases in abundances towards the macroalgal-dominated end of the continuum (Chapters 2 and 5). Nevertheless, quantitative estimates of macroalgal consumption were similar between macroalgal- and coral-dominated reefs (Chapter 4; Fig. 6.2). Minimal macroalgal-removal on macroalgal-dominated reefs may be because the feeding capacity of browsers is swamped by the amount of algae available (Williams et al. 2001) or that other processes, such as nutrient enrichment (Burkepile and Hay 2006), are driving macroalgal abundance. Further, fishing pressure is likely decreasing the abundance of important macroalgal-feeding species (Hicks and McClanahan 2012).

Minimal coral cover on macroalgal-dominated reefs is a characteristic that can be reinforced through various processes (Birrell et al. 2008a). A multitude of algal species can inhibit and thwart coral survivorship (e.g. Rasher and Hay 2010; Rasher et al. 2011), their effects worsened with increasing density or in concert with sedimentation and microbial communities (e.g. Arnold et al. 2010; Smith et al. 2006). Effects can be apparent throughout the coral life cycle; algae interfere with key phases in coral recruitment (Diaz-Pulido et al. 2010; Arnold et al. 2010; reviewed by Birrell et al. 2008a; Ritson-Williams et al. 2009; Chapter 3; Fig. 6.2b), and presumably, coral growth and reproductive capabilities as a result of increased energy spent in competition (Rasher and Hay 2010; Rasher et al. 2011; Barott et al. 2012; Bonaldo and Hay 2014; reviewed by Birrell et al. 2008a; Chadwick and Morrow 2011). However, on macroalgal-dominated reefs, the latter processes will likely become less prominent over time, because the former will have created a coral population bottleneck, preventing adult coral mortality (amplified by increased competitive interactions with macroalgae) from being replaced by corals growing from new recruits (Mumby and Steneck 2008; Chapter 3).

6.1.4 ***Reef degradation***

In comparison to reefs where coral recovery was prevented or delayed by limited larval supply (e.g. Williams et al. 2008; Gilmour et al. 2013), on inner Seychelles reefs 13 years after the 1998 bleaching event, larval survival seems to be the main bottleneck – either pre- or post-settlement, as a result of both biotic and abiotic factors (Chapter 3; cf. Nyström et al. 2012). Therefore, if coral recruit mortality continues to be high, more reefs may lose their adult coral cover, further decreasing reproductive output from the reefs. There is a danger that if too many local reefs become degraded, whole regions may become affected because feedbacks begin to operate at more extensive scales, eroding the resilience of remaining coral-dominated reefs (Elmhirst et al. 2009). For example, models based on dispersal of a generic broadcasting coral species by oceanographic controls (eddy-resolving ocean current data) have shown that the Seychelles region (including the Mascarene Islands and northern Madagascar) contributes to the coral larval supply of other reef systems (Wood et al. 2013). Therefore, depletion of coral larval production in the Seychelles may eventually feed through to other connected parts of the world.

Degradation involves changes, in particular, declines, in ecosystem services (Moberg and Folke 1999; Nyström et al. 2012). Fisheries and tourism are the two most important ecosystem services provided locally by Seychelles coral reefs (Gössling et al. 2002; Grandcourt and Cesar 2003). This thesis emphasized the ecological benefits of coral-dominated reefs, even those that may represent novel community compositions (Graham et al. 2014), over reefs that are further along the continuum in benthic habitat condition. Extending these ecological benefits to ecosystem services – tourism, in particular, the Seychelles' high-end marketing strategy as a pristine and exclusive eco-destination (Gössling et al. 2002) is unlikely to advance if reefs become macroalgal-dominated with lower fish abundance and diversity. Investigations into tourist preferences show that fish abundance and diversity play a major role in attracting and satisfying dive tourists (Shafer and Inglis 2000; Williams and Polunin 2000; Uyarra et al. 2005). Local artisanal trap fisheries are likely to be influenced by coral reef degradation, as some target species showed declines in abundance across the habitat gradients in this thesis (Grandcourt and Cesar 2003; Daw et al. 2011a; Chapter 2). Macroalgal-dominated reefs may still afford some benefits to the fishery, although less than coral-dominated reefs (Mumby et al. 2008). In the context of the broader western Indian Ocean region (e.g. Cinner et al. 2009a), relatively affluent areas such as the Seychelles are well placed for manipulative management experimentation to reverse macroalgal phase shifts (McClanahan et al. 2008).

6.2 Management and future directions

The oceanic Scott reef system off the coast of Western Australia has received important attention (Polidoro and Carpenter 2013) because it has recovered following the catastrophic 1998 bleaching event, despite local isolation (Gilmour et al. 2013). Recovery is attributed primarily to limited anthropogenic pressures, which enabled natural feedback responses to occur, such as increased herbivore densities following coral loss preventing release of algal growth into the newly available space (Gilmour et al. 2013). That is, conditions were favourable for regeneration and self-seeding from remnant coral populations, which were able to survive, recover and reproduce owing to the maintenance of key benthic characteristics (see also the Lakshadweep Islands;

Arthur et al. 2006) – low cover of macro-benthic competitors and stability of the underlying physical substrata. These conditions are ideal for coral recruit survival (see above, Chapter 3 and references within). However, although there are more examples of relatively unpopulated wilderness areas (e.g. Sandin et al. 2008; Graham and McClanahan 2013; Friedlander et al. 2014), the majority of reefs worldwide are not so free from anthropogenic influences (Hughes et al. 2003; Pandolfi et al. 2003; Bellwood et al. 2004). These reefs experience additional stressors to those driven by a globally changing climate (e.g. Fabricius 2005; De'ath et al. 2012), and there is a need to balance social, political and economic demands alongside the environment (Hughes et al. 2005; Cinner et al. 2009b; Graham et al. 2013).

Considering coral reefs as part of a broader social-ecological system embraces the need to alter human behaviour in order to protect ecosystems and ensure continued provision of services (Folke et al. 2004, 2005; Walker et al. 2004). Humans interfere substantially with the environment (e.g. Jackson et al. 2001; Halpern et al. 2008) and have variable priorities towards ecosystems and their conservation (e.g. Cinner et al. 2009a; Hicks et al. 2013). As a result, there are socioeconomic drivers that can alter ecosystem feedbacks (e.g. Cinner et al. 2009a) and vice versa, changes in the ecosystem, such as degradation, which can result in changes to society (e.g. management institutions and policy; Horigue et al. 2012; Nyström et al. 2012). Management practices need to be adaptive and supplemented with manipulative experiments to determine how much effort can be realistically expected from management agencies in terms of rehabilitative efforts (Graham et al. 2013, 2014).

Local scale management initiatives may improve a reef's resilience to the global changes over which we have minimal control. Marine protected areas (MPAs) are key management strategies, with benefits extending beyond relief from fishing pressure to ecosystem-wide amelioration (e.g. Stockwell et al. 2009; Rasher et al. 2013), and effective controls of other forms of human impact to marine and coastal systems – tourism, anchor damage (McCook et al. 2010; Green et al. 2014; cf. Edgar et al. 2014). It will be important to identify reefs with apparent resilience through time to boost existing MPA networks (e.g. Wilson et al. 2012). Predictions of future communities are therefore necessary, although complex, as a result of multiple stressors (Ban et al. 2014), multiple responses that alter through time (Chapter 5), and chaos (e.g. recruitment lottery; Mumby and Steneck 2011).

Depending on the condition of a site, tangible benefits from protected areas may take more or less time (i.e. a degraded habitat will take longer to respond to protection vs. one that has moderate resilience to begin with). Coral reefs can show non-linear responses to external drivers, in part, as a result of ecological and socio-ecological feedbacks (Scheffer et al. 2001; Hughes et al. 2010, 2013). The reversal of degradation in such cases is likely to require more than just protection. With more active interference, and uncertainty that all possible system interactions are known, ecological surprises are likely (Bakun and Weeks 2006). Nevertheless, carefully thought out restoration efforts, in synergy with other effective management strategies, should aid positive change (Bakun and Weeks 2006; Edwards 2010; Suding 2011). Two contrasting trajectories of reef degradation, with ecological feedbacks appearing to reinforce the degraded condition, were identified among inner Seychelles coral reefs – rubble- and macroalgal-domination (Chapters 3 and 4). Restorative efforts may be influential on some of these reefs, especially if feedbacks have not yet developed to fully stabilise new conditions (Graham et al. 2013); i.e. reefs not at extremes on the continuum of habitat quality (Chapters 2 and 5). Substrate instability was influential on rubble-dominated reefs (Chapter 3), which is a key area of reef restoration research that has achieved some measure of success (e.g. Fox et al. 2005; Edwards 2010). On reefs of the inner Seychelles, stabilisation may be a viable option and is likely to have a perceptible response because there is a good supply of incoming coming larvae and high recruit survivorship (Edwards 2010; Chapter 3). On macroalgal-dominated reefs, macroalgal removal is a lot more intensive (McClanahan et al. 2001, 2000, 1999), but periods of seasonal senescence may be exploited (e.g. Diaz-Pulido et al. 2009). However, it is only likely to be cost-effective for small-scale studies, on reefs that appear to have stabilised as macroalgal-dominated (cf. Pywell et al. 2007, 2011).

6.3 Concluding remarks

The results from this thesis augment knowledge, while at the same time revealing new gaps, highlighting the need to further our understanding of the ecology of degraded reef systems and how such degradation may be reversed (Graham et al. 2013). Clear differences in feedback intensity and direction altered important processes on reefs that had recovered coral cover post-disturbance compared to those with unstable rubble substrates, or that had become dominated by macroalgae. Caution is therefore required when extrapolating findings from ‘healthy’ or regenerating habitats to degraded systems. Although discrete states could be inferred at the extremes of the continuum in habitat quality, most reefs exist somewhere in transition along trajectories, complicating predictability. Nevertheless, spatial patterns in some fish groups remained consistent over time and may be used for predictions of reef responses to benthic change, although reef specific data may be required to implement necessary management plans (Westoby et al. 1989; Walker 1993). Clearly, prevention of further reef degradation through a reduction in anthropogenic pressures is of critical importance because the repercussions of declining habitat condition may be far reaching.

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Appendix A: Supplemental information for Chapter 2

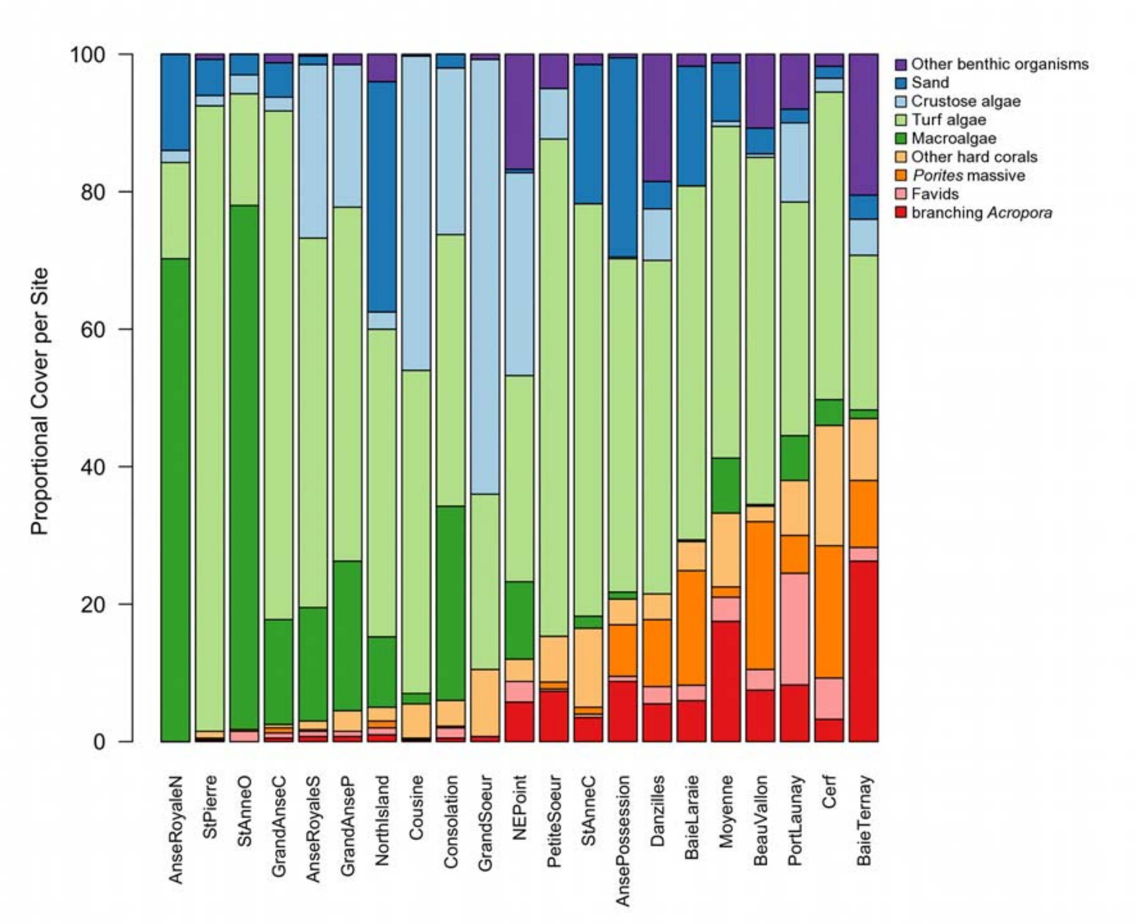

Fig. S1 Proportional cover of benthic biota per site

Appendix B: Supplemental information for Chapter 3

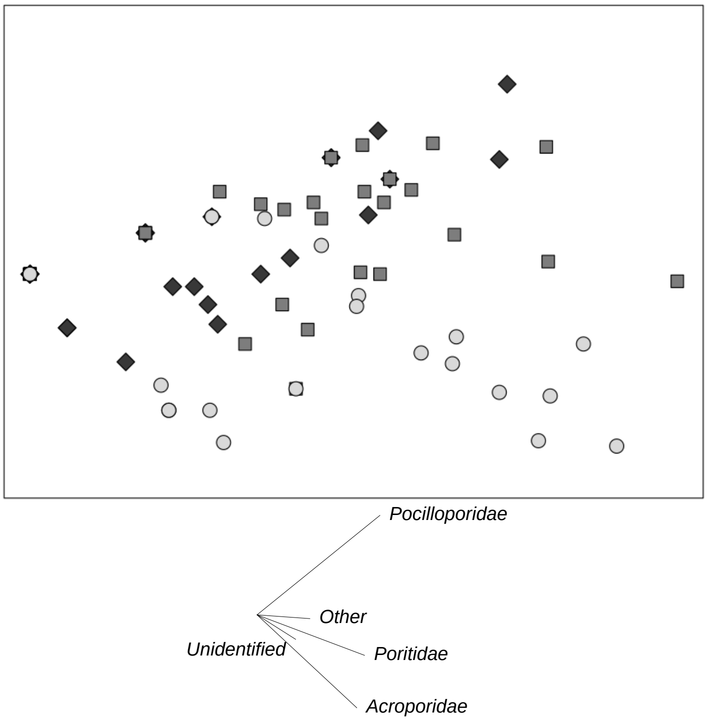

Fig. S1 Non-metric multi-dimensional scaling plot of the family-level composition of coral recruit assemblages. Each data point represents one artificial settlement tile with symbols as for Fig. 3.1. Vectors show the influence of the three distinguishable coral families, and two categories of unidentified corals (see methods). Stress = 0.1

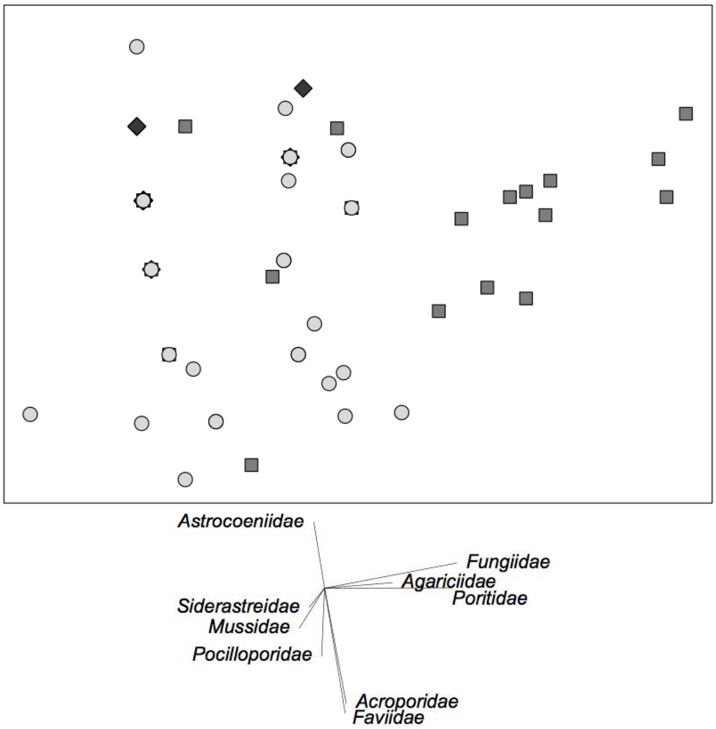

Fig. S2 Non-metric multi-dimensional scaling plot of the family-level composition of coral juvenile assemblages. Each data point represents one quadrat with symbols as for Fig. 3.1. Vectors show the influence of nine coral families recorded from the quadrats. Stress = 0.13

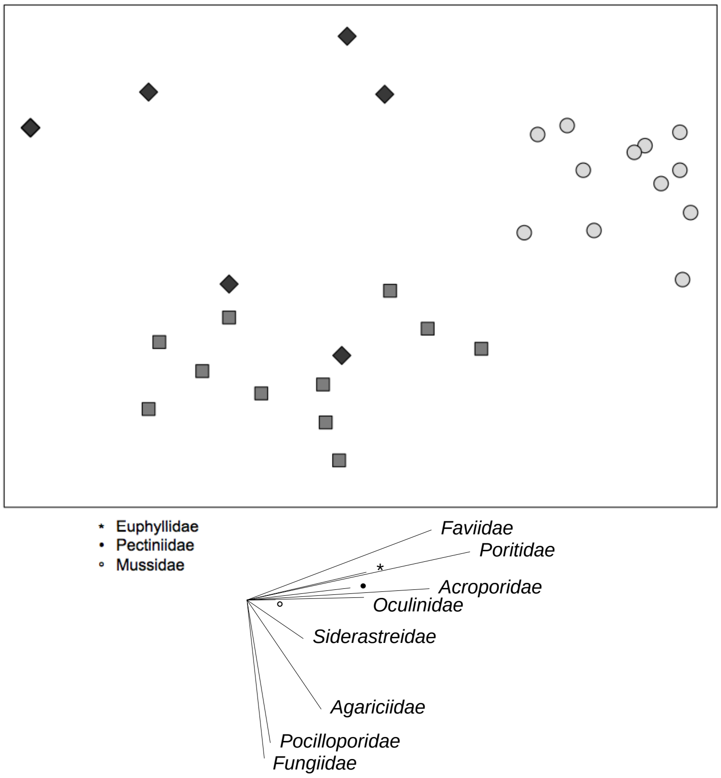

Fig. S3 Non-metric multi-dimensional scaling plot of the family-level composition of adult coral assemblages. Each data point represents one transect with symbols as for Fig. 3.1. Vectors show the influence of 11 coral families recorded from the transects. Stress = 0.11

Appendix C: Supplemental information for Chapter 4

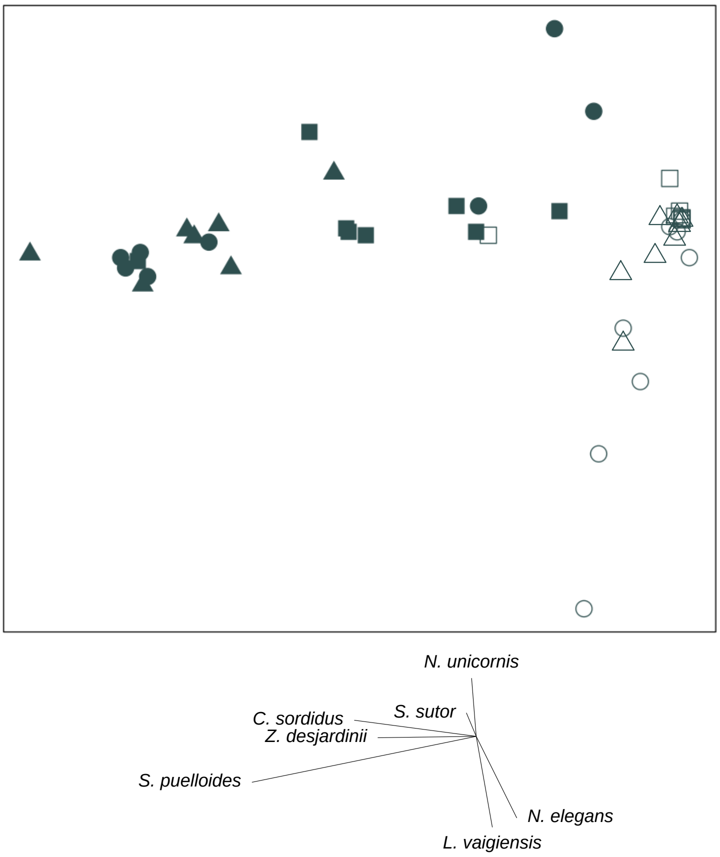

Fig. S1 Separation of the assays from the two reef conditions, based on the number of mass standardised bites taken by the fish assemblages recorded feeding on each of the assays. Filled symbols represent assays on coral- dominated reefs; triangles – C1, circles – C2, squares – C3. Open symbols represent assays on macroalgal- dominated reefs; circles – M1, squares – M2, triangles – M3. Vectors visualise the influence of the 7 fish species that took over 5% of the actual bites in each reef state; however, only *S. puelloides* (82% on coral-dominated reefs) and *N. elegans* (94% on macroalgal-dominated reefs) took > 5% of mass standardised bites. Stress = 0.1.

Table S1 PERMANOVA testing for variation among reef conditions (coral- and macroalgal-dominated), taking reef (nested in condition) and day (nested in reef and condition) into account, in the assemblage of fishes feeding on assays based on their number of mass standardised bites taken on the assays

Source of variation	df	MS	*Pseudo-F*	P
Condition	1	44779	7.344	**0.016**
Reef (Condition)	4	6106	1.493	0.126
Day (Reef | Condition)	6	4092	1.860	**0.005**
Residual	35	2201		

Significant probabilities are indicated in bold.

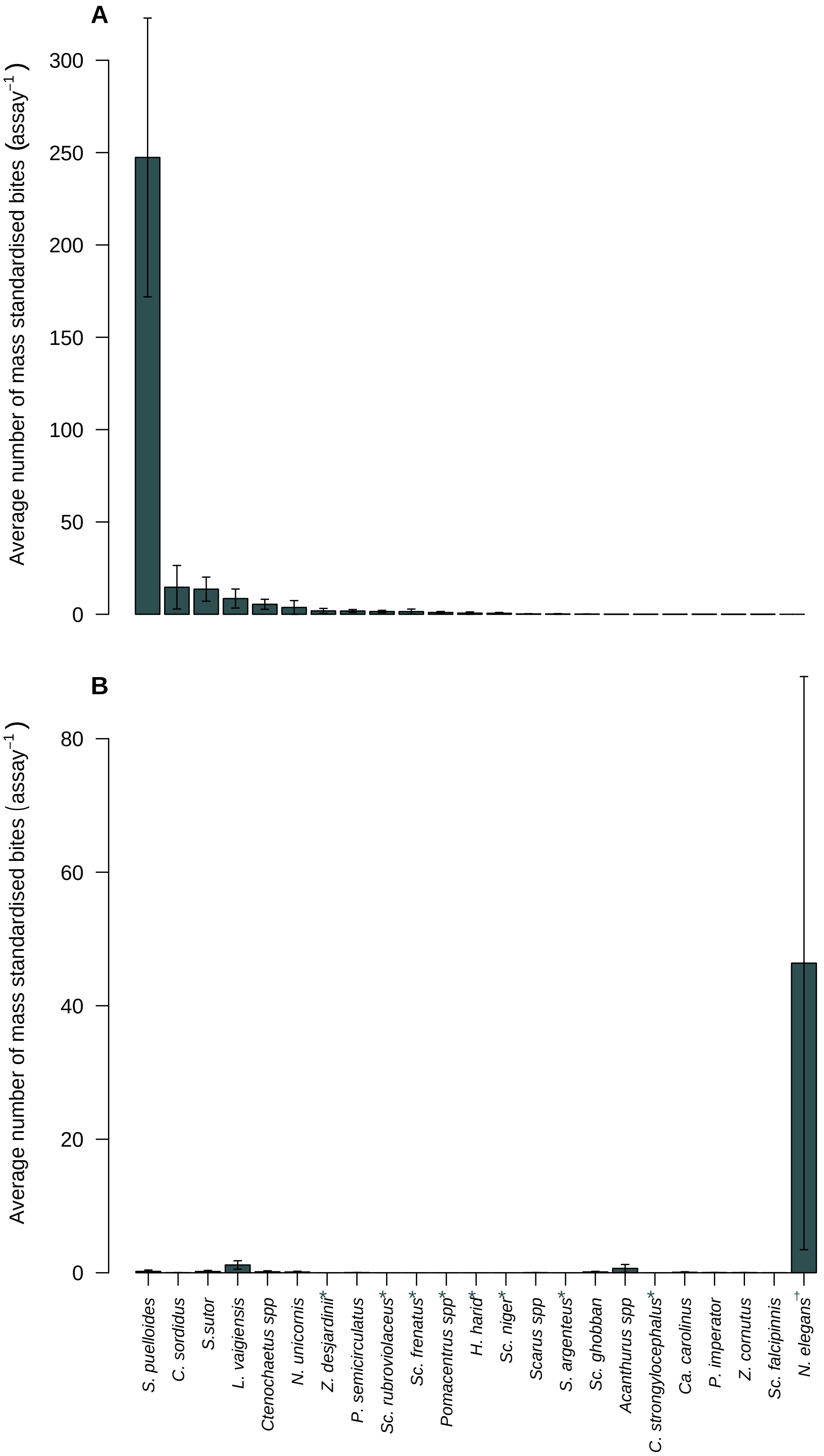

Fig. S2 Average number of mass standardised bites per assay taken by the 23 species recorded to feed on Sargassum assays placed in (A) coral- vs. (B) macroalgal-dominated reefs. '*' – Species that fed only on assays in coral-dominated reefs. '†' – Species that fed on assays only in macroalgal-dominated reefs. Genera: Ca – Calotomus; C – Chlorurus; H – Hipposcarus; L – Leptoscarus; N – Naso; P – Pomacanthus; S – Siganus; Sc – Scarus; Z – Zebrasoma.

Table S2 Relative influence of dominant macroalgal-feeding fishes on Sargassum loss in coral-dominated reefs based on the number of mass standardised bites taken

Source	Estimate	SE	t	p
C. sordidus	0.0016	0.0006	2.78	**0.012**
S. puelloides	0.0002	0.0001	1.98	0.064
S. sutor	0.0051	0.0010	4.92	**0.000**
Z. desjardinii	-0.0024	0.0050	-0.47	0.642
Sum of all other species	0.0020	0.0009	2.17	**0.043**

Significant probabilities are indicated in bold
$R^2_{adj} = 0.585, F = 7.5, df = 5,18, p = 0.001$

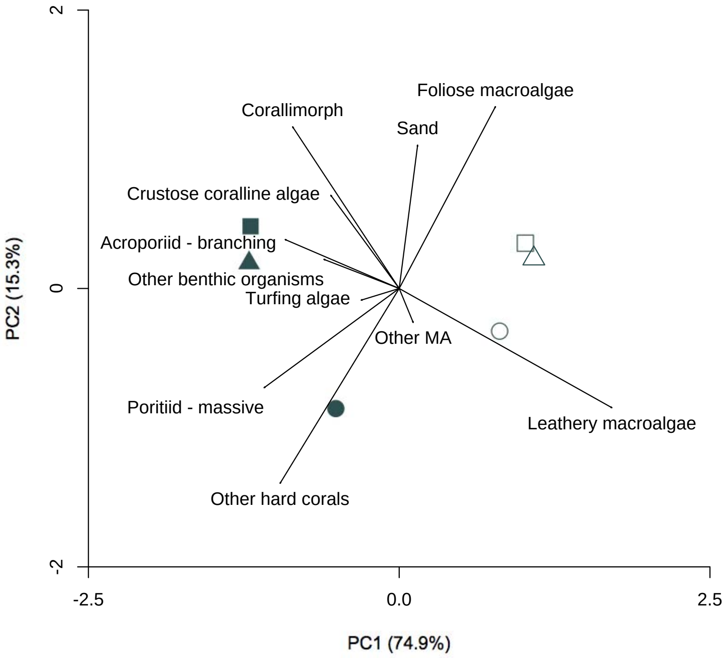

Fig. S3 Separation of the two reef types used for the bioassay comparison; based on correlation-based principal components analysis on Euclidean distances of the proportional benthic cover of each reef. Filled symbols represent assays on coral-dominated reefs; triangles – C1, circles – C2, squares – C3. Open symbols represent assays on macroalgal-dominated reefs; circles – M1, squares – M2, triangles – M3. ‘Other MA’ – other macroalgae

Table S3 Abundance of fishes on each of the study reefs (excluding C2): nominally herbivorous species and other species identified to feed on the _Sargassum_ bioassays

	C1t1	C1t2	C3t1	C3t2	M1t1	M1t2	M2t1	M2t2	M3t1	M3t2	M3t3
Acanthurus auranticavus	0	0	0	0	0	0	1	0	0	0	0
_Acanthurus dussumieri_*	0	1	3	0	0	2	14	11	0	0	0
Acanthurus leucosternon	0	0	0	0	1	0	0	1	0	0	0
_Acanthurus nigrofuscus_*	0	3	10	8	5	2	1	18	0	0	0
_Acanthurus spp_*	1	0	0	0	0	0	0	0	0	0	0
Acanthurus tennentii	0	0	1	0	0	0	0	4	0	0	0
Acanthurus triostegus	0	0	0	0	3	5	3	0	0	0	1
_Calotomus carolinus_*	0	0	0	0	1	2	0	0	0	0	0
Chlorurus atrilunula	0	0	0	0	3	18	3	2	0	5	0
_Chlorurus sordidus_*	**36**	**25**	**41**	**10**	**10**	**8**	**6**	**5**	**21**	**22**	**37**
_Chlorurus strongylocephalus_*	0	0	0	0	0	0	0	0	0	0	0
_Ctenochaetus binotatus_*	7	2	0	0	0	0	0	0	0	0	0
_Ctenochaetus striatus_*	1	2	2	0	1	0	3	0	0	0	0
Ctenochaetus truncatus	0	0	15	7	0	0	0	0	0	0	0
_Hipposcarus harid_*	0	0	0	0	0	1	0	1	0	0	0
_Leptoscarus vaigiensis_*	**0**	**0**	**0**	**0**	**5**	**7**	**3**	**4**	**4**	**4**	**1**
_Naso elegans_*	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
_Naso unicornis_*	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Platax orbicularis	0	1	0	0	23	0	0	0	0	0	0
Platax teira	0	0	0	0	0	0	1	1	0	0	0
_Pomacanthus imperator_*	0	0	0	0	0	0	0	1	0	0	0
_Pomacanthus semicirculatus_*	3	1	0	1	0	1	3	1	1	0	3
Scarus falcipinnis	35	0	0	0	0	0	0	0	0	0	0
_Scarus frenatus_*	0	0	0	0	0	0	0	0	0	0	0
_Scarus ghobban_*	0	14	5	2	0	1	6	2	1	4	8
_Scarus niger_*	3	1	14	8	1	3	0	0	2	5	1
Scarus psittacus	0	1	0	0	5	9	0	0	0	3	15
_Scarus rubroviolaceus_*	4	3	10	1	7	4	3	1	2	0	2
Scarus russelii	0	0	0	1	0	6	0	0	0	3	2
Scarus tricolor	0	0	5	0	0	0	0	0	0	0	0
_Siganus argenteus_*	0	0	0	0	3	2	3	10	0	0	3
Siganus corallines	0	0	0	0	1	0	2	0	0	0	0
_Siganus puelloides_*	**5**	**0**	**1**	**2**	**0**	**0**	**0**	**0**	**2**	**0**	**6**
Siganus stellatus	0	1	0	0	2	1	0	0	0	0	0
_Siganus sutor_*	**0**	**0**	**0**	**0**	**0**	**0**	**15**	**4**	**5**	**1**	**17**
_Zanclus cornutus_*	5	3	0	0	1	0	3	2	0	0	0
_Zebrasoma desjardinii_*	**1**	**2**	**4**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**1**
Zebrasoma scopas	0	0	3	2	0	0	0	0	0	0	0

* Species observed to feed on Sargassum _bioassays_

Dominant species involved in the removal of Sargassum _on reefs indicated in bold_

Appendix D: Supplemental information for Chapter 5

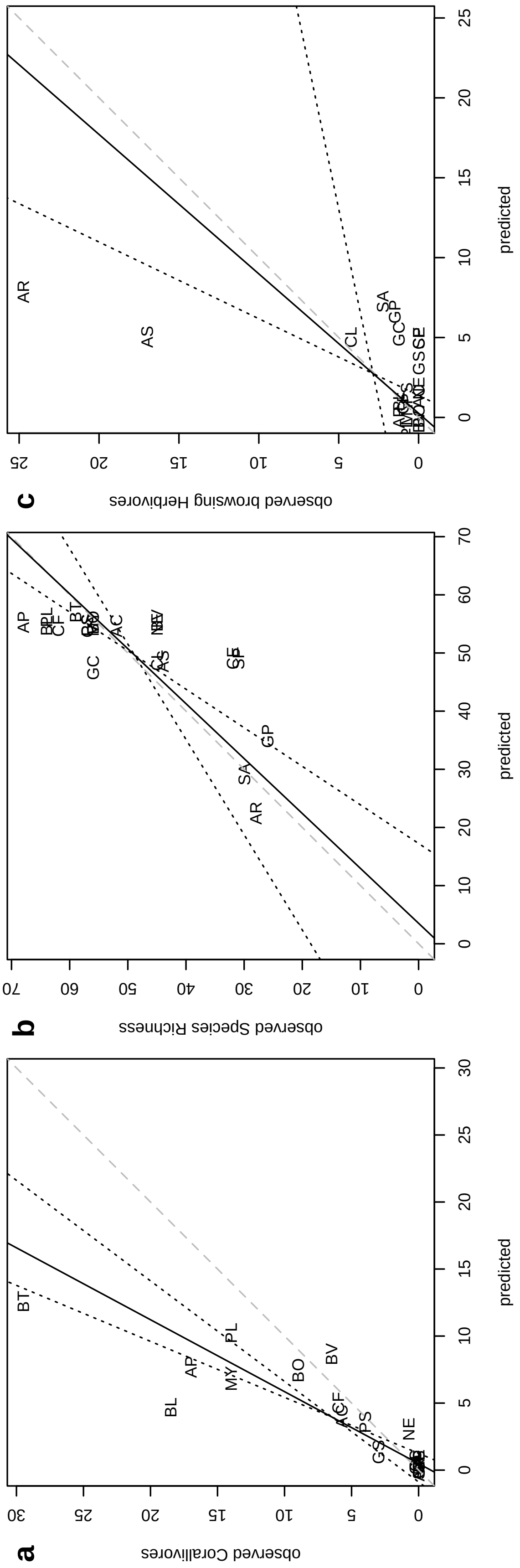

Fig. S1 Relationships between observed and predicted (a) corallivore abundance (b) fish species richness, and (c) browsing herbivore abundance in 2012. Dashed line represents the expected relationship should the model predictions be perfect (intercept = 0, slope = 1), solid line represents the predicted fit with dotted lines representing the 95% confidence intervals.

Table S1. Parameters and prediction accuracy of the significant GAM model based on 2010 data, estimating the relationship between three fish metrics and the gradient in benthic condition along PC1. Predictions based on observed changes in benthic condition in 2012 and compared with 2012 fish observations. Parameters of significant GAM model – D_{Null}: null deviance, D_{Expl}: proportion of explained deviance, Estimates of the parametric terms: model intercept (± SE), Smooth terms edf: estimated degrees of freedom of pc1 smooth function. Prediction accuracy of significant GAM model using linear regression to compare observations and predictions – R^2: goodness of fit, Intercept and Slope: estimates of the line of best fit, *RMSD*: root mean squared deviation (deviation of predicted values with respect to the observed ones measured in the same units as the fish metric in question; Piñero et al. 2008).

Fish metric	D_{Null}	D_{Expl} (%)	Parametric estimates (± SE)	Smooth terms edf	R^2	Intercept	Slope	*RMSD*
Species Richness	2714	66.1	51.0 ± 1.7	2.5	0.577	-3.7	1.1	8.7
Corallivore	232	89.3	3.5 ± 0.3	2.8	0.752	-0.9	1.9	5.9
Herbivore (browsing)	537	22.5	2.7 ± 1.1	1.0	0.268	-0.3	1.1	5.5

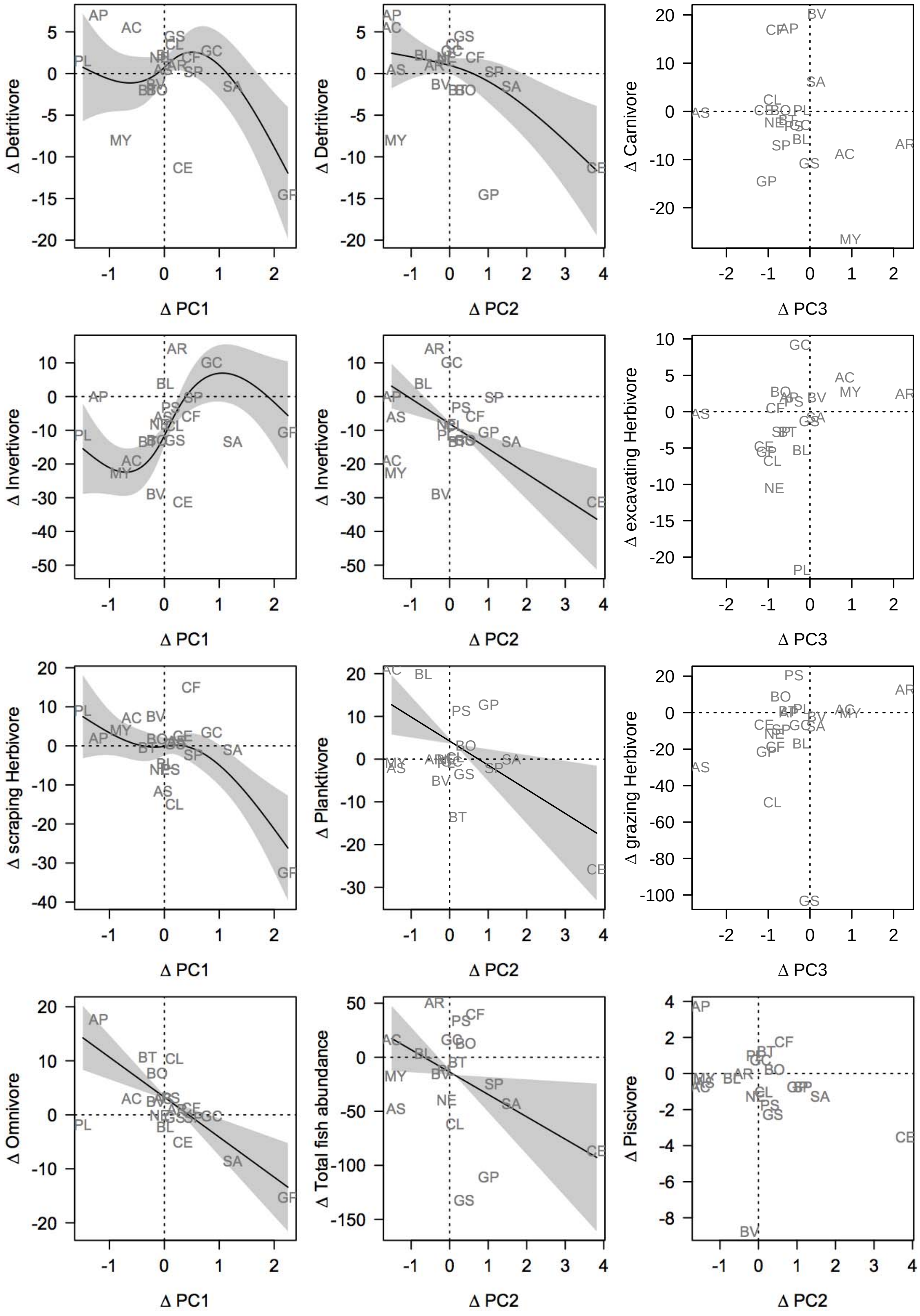

Fig S2 Magnitude and direction of changes in fish and benthic assemblages (see also Table 3). Dotted lines: zero change, Letters: reefs (see Fig. 1), Solid lines: significant GAM smoother, shaded region: 95% confidence intervals. Δ PC1: high coral cover and complexity (-) to low complexity and high leathery macroalgal cover (+), Δ PC2: high CCA cover (-) to high sand cover (+), Δ PC3: high ‘other macroalgae’ (-) to high turf cover (+).

Appendix E: Publications arising during candidature

Publications derived from thesis chapters

Chong-Seng KM, Mannering TD, Pratchett MS, Bellwood DR, Graham NAJ. 2012. The influence of coral reef benthic condition on associated fish assemblages. PLoS ONE 7: e42167.

Chong-Seng KM, Nash KL, Bellwood DR, Graham NAJ. 2014. Macroalgal herbivory on recovering versus degrading coral reefs. Coral Reefs 33:449-461

Chong-Seng KM, Graham NAJ, Pratchett MS. 2014. Bottlenecks to coral recovery in the Seychelles. Coral Reefs 33:409-419

Other peer-reviewed articles published during PhD candidature

Pratchett MS, Trapon M, Berumen ML, **Chong-Seng KM**. 2011. Recent disturbances augment community shifts in coral assemblages in Moorea, French Polynesia. Coral Reefs 30: 183-193.

Chong-Seng KM, Cole AJ, Pratchett MS, Willis BL. 2011. Selective feeding by coral reef fishes on coral lesions associated with brown band and black band disease. Coral Reefs 30: 473-481.

Wilson SK, Graham NAJ, Fisher R, Robinson J, Nash KL, **Chong-Seng KM**, Polunin NVC, Aumeeruddy R, Quatre R. 2012. Effect of macroalgal expansion and marine protected areas on coral recovery following a climatic disturbance. Conservation Biology 26: 995-1004.

Pratchett MS, **Chong-Seng KM**, Feary DA, Hoey AS, Fulton CJ, Nowicki JP, Dewan AK, Walker SPW, Berumen ML. 2013. Butterflyfishes as a model group for reef fish ecology: important and emerging research topics. In: Pratchett MS, Berumen ML, Kapoor BG, editors. Biology of butterflyfishes. Boca Raton, USA: CRC Press. p310-334.

Chong-Seng KM, Graham NAJ. (2014) Novel ecosystem futures for Seychelles coral reefs? Kapisen 16: 8-9.

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PLoS one

The Influence of Coral Reef Benthic Condition on Associated Fish Assemblages

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Abstract

Accumulative disturbances can erode a coral reef's resilience, often leading to replacement of scleractinian corals by macroalgae or other non-coral organisms. These degraded reef systems have been mostly described based on changes in the composition of the reef benthos, and there is little understanding of how such changes are influenced by, and in turn influence, other components of the reef ecosystem. This study investigated the spatial variation in benthic communities on fringing reefs around the inner Seychelles islands. Specifically, relationships between benthic composition and the underlying substrata, as well as the associated fish assemblages were assessed. High variability in benthic composition was found among reefs, with a gradient from high coral cover (up to 58%) and high structural complexity to high macroalgae cover (up to 95%) and low structural complexity at the extremes. This gradient was associated with declining species richness of fishes, reduced diversity of fish functional groups, and lower abundance of corallivorous fishes. There were no reciprocal increases in herbivorous fish abundances, and relationships with other fish functional groups and total fish abundance were weak. Reefs grouping at the extremes of complex coral habitats or low-complexity macroalgal habitats displayed markedly different fish communities, with only two species of benthic invertebrate feeding fishes in greater abundance in the macroalgal habitat. These results have negative implications for the continuation of many coral reef ecosystem processes and services if more reefs shift to extreme degraded conditions dominated by macroalgae.

Citation: Chong-Seng KM, Mannering TD, Pratchett MS, Bellwood DR, Graham NAJ (2012) The Influence of Coral Reef Benthic Condition on Associated Fish Assemblages. PLoS ONE 7(8): e42167. doi:10.1371/journal.pone.0042167

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Introduction

An ecosystem's ability to recover from degradation is eroded by increases in frequency, intensity and array of disturbances [1–4]. On coral reefs, increasing anthropogenic pressures (e.g. fisheries exploitation) and climate change, are compounding upon pre-existing disturbances (e.g. cyclones) and causing declines in coral cover and structural complexity [5,6], associated changes in coral and fish community composition [7–9], and shifts in the dominant benthic biota [10–12]. Documented shifts on coral reefs include changes to corallimorphs, sponges, or most often, macroalgae domination of the benthos [10–12]. Although these other benthic lifeforms are typical components of most reefs, scleractinian coral domination is considered preferable; corals function as the main provider of the complex structural habitat that is largely responsible for the high diversity of reef associated organisms, and the provision of a range of ecosystem services, such as vital food resources [13–15].

All major coral reef regions of the world have undergone declines in coral cover [5,16,17]. In conjunction with these reductions in coral cover, is an increasing documentation of shifts in the dominant benthic biota (reviewed by: [12]) that focus primarily on causes of the shifts, and subsequent changes in the benthic community composition. For example, although the causes attributed to the shift from coral to macroalgae on Jamaican coral reefs included overfishing of herbivorous fish, hurricane Allen and disease mediated collapse of urchin populations, the description was based solely on benthic composition [11]. How these changing benthic communities interact with underlying substrata, or influence the rest of the coral reef ecosystem, for example reef fish assemblages, is poorly understood.

Complex interconnections among organisms and with their physical environment, imply that changes to one aspect of the ecosystem may lead to a subsequent series of, often unanticipated, changes to the ecosystem's community assemblage [18–20]. Strong relationships exist between coral reef fishes and their habitat [21,22], although there is variability in the specific responses of different fishes, and of different ontogenetic stages, to changes in coral cover [9,23,24]. Live coral loss can trigger shifts in the entire fish assemblage [25,26], and prompt declines in abundance and diversity of fishes [27,28]. The potential for other benthic organisms to provide the necessary habitat for reef fishes has not been widely investigated, although Syms and Jones [29] showed that soft coral was not a favourable habitat replacement for hard corals. From non-marine ecosystems it appears possible that some organisms may provide habitat for an equally, or more diverse community, or alternatively, that changes in the habitat-providing organisms can be detrimental to diversity. As an example of the former, Brazilian forests contained 26 lizard species whereas the grassland alternative contained 30 species [30]. In contrast, lakes lose their high submerged macrophyte and animal diversity following shifts to turbid eutrophic waters [31], while shifts from rangelands to desert lead to much reduced diversity [32].

The interactions between the foundational structure upon which the live reef is built, the underlying substratum, and changes in the benthic community, may hinder essential ecosystem processes required for recovery, and perpetuate an alternative community. For example, coral recruit survivorship is considered an essential process for recovery [33,34] and can be inhibited by burial and damage of new recruits by highly mobile rubble substrata during storms [35–37]. The relationships between a reef's underlying substratum and dominant benthos are generally unknown, but knowledge of such relationships would further our understanding of the development and endurance of degraded conditions on coral reefs.

Coral reefs of the Seychelles archipelago offer a unique opportunity to assess differing benthic communities. The inner Seychelles islands are geographically isolated, were severely impacted by the 1998 mass bleaching event, and there is a good record of post-disturbance degradation [6,17,38,39]. Ten years after this major bleaching event, coral cover in the inner Seychelles ranged from <5% coral cover to >20% coral cover, which is amongst the lowest in the region [6,40]. Individual reefs have shown highly varied responses to disturbance, and there have been reports of benthic community shifts on some reefs [28,40]. However, detailed characterisation of the benthic condition of these reefs is lacking, along with the implications of benthic condition for other aspects of the reef community. We therefore quantitatively characterised the benthos, underlying substratum, and fishes of inner Seychelles reefs to investigate: 1) if there was a link between underlying substrata and benthic condition; and 2) the relationship between benthic condition and the taxonomic and functional composition of associated fish assemblages.

Materials and Methods

Ethics Statement

A research permit for this work was granted by the Seychelles government through the Seychelles Bureau of Standards; permit number A0347.

Study Site and Sampling Design

Twenty-one carbonate fringing reefs within a 3600 km^2 area around the inner Seychelles islands (4 30′S, 55 30′E) were surveyed in October 2010. Fishing practices in the inner Seychelles use non-destructive techniques (handlines, traps and octopus harpooning are the most widely used; [41]), and there is relatively low variability in fishing pressure along the shallow fringing reefs among the islands, with most fishing occurring in deeper water [42,43]. At each reef, four 50 m transects were laid at approximately 4 m depth, perpendicular to the reef slope. The following data were collected along each transect; 1) live benthic cover recorded at 0.5 m intervals, 2) underlying substratum quantified at 0.5 m intervals, 3) number and identity of all fish greater than 8 cm were recorded along a 5 m wide belt (to minimise disturbance, large, mobile species were counted as the transect was laid; [44]), and 4) structural complexity was recorded using both a 6-point scale and by estimating the number of small refuge holes, <10 cm diameter, along two 10×1 m sub-transects (following [45]). Scleractinian corals and macroalgae were identified to genus and/or morphological group, while other algae were identified to functional group. Other benthic organisms recorded included corallimorphs, sponges and zoanthids. For analyses, branching acroporids, massive *Porites*, and favids were differentiated from the rest of the coral genera (grouped as 'other hard corals') due to their high coverage. The underlying substratum, defined as the substratum below recorded benthic cover or the top 10 mm of sand/sediment, was categorised into loose dead coral rubble, consolidated rubble (rubble pieces that were showing visual and tactile signs of amalgamation), solid carbonate pavement, or bommie (isolated coral outcrops). Fish species were assigned to 8 functional groups based on the literature and FishBase: obligate corallivores, browsing herbivores, other herbivores (including scrapers, grazers, excavators, detritivores), planktivores, piscivores, non-coral invertivores (hereafter invertivores), omnivores (consume animal and plant material) and generalist carnivores (fish and invertebrate feeders). Additionally, the level of exploitation sustained by different fish species was assigned at four levels: primary targets, important by-catch, occasional by-catch and non-fished species [46].

Analyses

The data were organized into four matrices; i) benthic habitat (11 variables; including the two complexity measures) that was natural log transformed to improve the spread of the data, and normalised to standardize the contribution of variables measured as percent cover and those measured on different scales, ii) underlying substrata cover (4 variables), iii) fish functional group abundances (8 variables) that were square-root transformed to downweigh abundant groups [47], and iv) fish species abundances (152 species) that were also square-root transformed to downplay the influence of highly abundant species. The complexity measures were included with the benthic cover variables because these measures are thought, at least in part, to reflect the complexity provided by live benthic organisms (e.g. [6,48,49]). Within- and among-reef variation was assessed using ordination methods on dissimilarity matrices in the statistical software PRIMER; correlation-based principal components analysis (PCA) on Euclidean distances for the underlying substratum and benthic cover matrices (as the data is continuous and needed to be normalised; [47]), and non-metric multidimensional scaling (nMDS) on Bray-Curtis dissimilarities to account for high zero counts [47], for the fish matrices. Pairwise relationships between all variables within a matrix showed no collinearity ($r<0.7$; [50]). Groupings in the benthic cover PCA were assessed by overlaying slices from a hierarchical cluster analysis using group averaging of the same Euclidian distance matrix.

Relationship between Data Matrices

Variability in benthic composition among reefs was related to underlying substratum, and also the composition of fish assemblages, in two ways. First, data points (= transects) on the underlying substratum and fish assemblage ordinations were colour-coded according to groups identified from the benthic cover hierarchical cluster analysis to visualize relationships. Second, the BEST BIO-ENV routine was carried out using a Spearman rank correlation between the different similarity resemblance matrices to identify the variable or group of variables that best explained similarities among the data matrices [47]. The overall significance of the BEST routine was assessed using a permutation test under the null hypothesis of no linkage of variables between matrices (maximum permutations = 999; [51]).

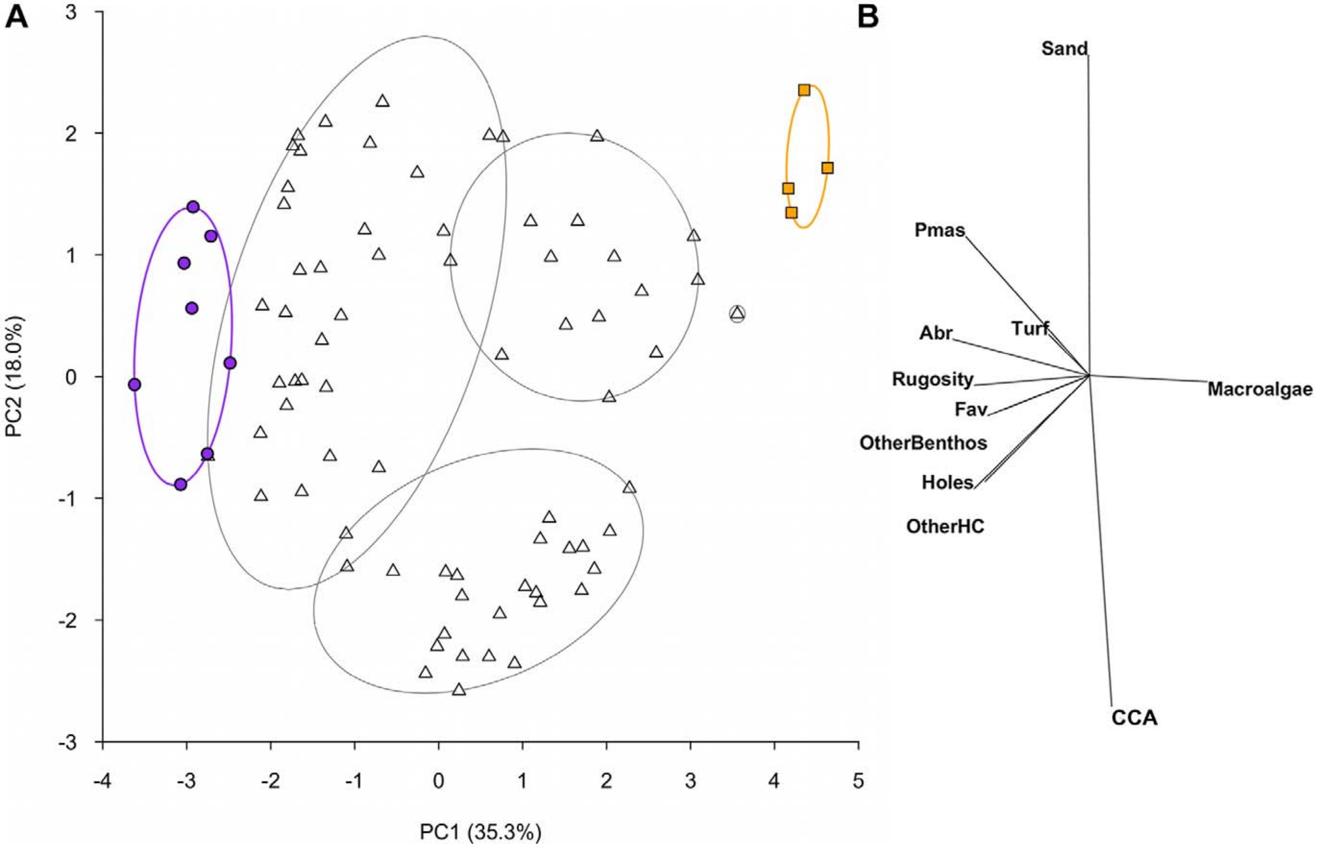

Figure 1. Principal components analysis of benthic habitat variables. (A) Spatial variation in benthic habitat on reefs at the transect level, shown for the first two components from a principal components analysis on natural log(x+1) transformed and normalised data. Ellipses show groupings calculated from a slice taken through a hierarchical cluster analysis at a Euclidean distance value of 4. Data symbols represent transects within reefs; filled circles and squares highlight transects within the extreme clusters for visualisation purposes. Purple circles and ellipse shows high complexity coral cluster consisting of 8 transects from 2 reefs; orange squares and ellipse shows low-complexity, high macroalgae cluster consisting of 4 transects from 1 reef; triangles are transects that fall within intermediate clusters. (B) The relative contribution of the 11 benthic habitat categories to the observed variation in reef benthic condition. Pmas – massive *Porites*; Abr – branching *Acropora*; Fav – favids; OtherBenthos – non-coral or algae benthic organisms; OtherHC – all other scleractinian corals; CCA – crustose coralline algae.
doi:10.1371/journal.pone.0042167.g001

Comparing Variables along a Gradient of Contrasting Benthic States

A combination of cluster analysis and ordination showed the presence of contrasting benthic assemblages along a gradient from coral to macroalgae. To investigate whether there were any fish species that typified either assemblage, we ran a similarity of percentages (SIMPER) analysis using a subset of the fish species matrix that reflected the two extreme clusters of transects identified by the slice through the benthic cluster diagram. This represented transects dominated by macroalgae versus transects with high coral cover and structural complexity. An index of the fish functional group diversity was calculated using the Shannon-Weiner diversity index, *H'*, which takes into account both abundance and the number of functional groups (maximum n = 8). The relationships between the benthic gradient (the benthic PCA's first principal component) and fish functional group diversity (*H'*), fish species richness, total fish abundance, and individual functional group abundances were examined using General Additive Models (GAM). GAMs incorporate the possibility of non-linear relationships between the response and predictive variables [50]. Reef was included as a random effect variable using restricted maximum likelihood estimation (REML) using the gam and gamm functions of the mgcv package in R.

Results

Benthic Reef Assemblages

Benthic cover of reef organisms was highly variable among the 21 reefs in the inner Seychelles. Live coral cover ranged from 0 to 47% (±5.1 SE) and macroalgae cover from 0 to 76% (±6.7 SE) per reef (Figure S1). The first principal components axis (PC1) of the benthic PCA differentiated transects along a gradient from high coral cover (up to 58% per transect) and structural complexity (rugosity score up to 4, and up to 1150 10 cm holes) at negative PC1 scores, to high macroalgae cover (up to 95%) and low structural complexity (rugosity score down to 0.5, and as few as 30 10 cm holes) at positive PC1 scores (Figure 1). A separation from sand and sediment-laden turf to crustose coralline algae was represented by PC2. A slice through a cluster analysis at a Euclidean distance of 4 represented six groupings in the data, including two groups at extreme ends of PC1, and four intermediate groups (Figure 1).

Underlying Substrata

The underlying substrata of the reefs varied from loose rubble to consolidated carbonate pavement. When highlighted on the underlying substrate PCA plot, transect groupings from the

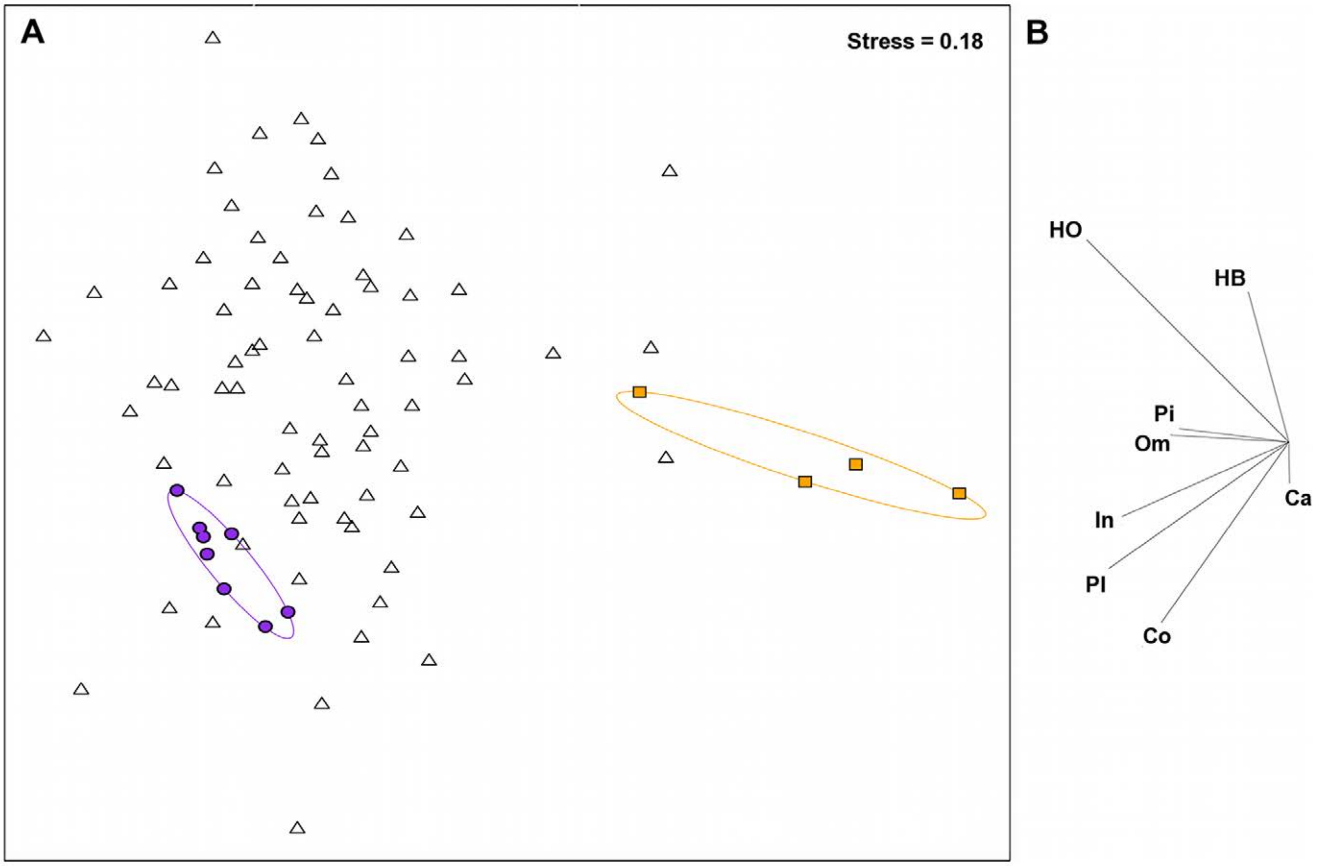

Figure 2. Non-metric multidimensional scaling analysis of fish functional groups. (A) Spatial variation in the reef fish functional group abundances on reefs at the transect level, assessed using a non-metric multidimensional scaling plot on square-root transformed data. Data symbols represent transects within reefs. For visualisation purposes, filled circles and squares, and ellipses highlight the transects within the extreme clusters calculated from a slice taken through the Benthic data's hierarchical cluster analysis at a Euclidean distance value of 4. Purple circles and ellipse shows high complexity coral cluster, orange squares and ellipse shows low-complexity, high macroalgae cluster. (B) The relative contribution of the 8 fish functional groups to the observed variation on reefs. HB – browsing herbivores; HO – non-browsing herbivores; Pi – piscivores; Om – omnivores; In – non-coral invertivores; Pl – planktivores; Co – obligate corallivores; Ca – generalist carnivores.
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benthic cluster analysis were not apparent, however reefs found at both extreme ends of the benthic PC1 were associated with more stable substrata. It is to be noted that the stress level of the MDS was fairly high, so although general patterns are robust, details need to be interpreted with some caution [47]. A BEST analysis ($r_s = 0.16$, $p<0.05$) corroborated this pattern, finding a weak but significant correlation between the benthic and underlying substrata distance matrices, specifying the presence of pavement rather than rubble as the principal cause of similarity.

Fish Assemblages

A total of 152 fish species were recorded from the study site, with 3 to 38 species observed per transect. All of the eight fish functional groups were more strongly associated with transects plotted on the left hand side of the MDS plot (Figure 2). Highlighting the transect clusters found by the benthic analysis, on the fish functional group MDS plot indicated that the more fish-depauperate reefs corresponded to reefs with the highest levels of macroalgae (BEST $r_s = 0.48$, $p<0.001$). Fourteen fish species, including planktivores, invertivores, an obligate corallivore and non-browsing herbivores (a bioeroder, a scraper and two detritivores) contributed to 70% of the similarity within the cluster of transects at the high coral cover, high complexity end (herein referred to as complex coral habitats) of the benthic PC1 (Table 1). These 14 species included a primary fishery target species, *Chlorurus sordidus*, and 3 important- and 3 occasional fishery by-catch species (Table 1). In comparison, only 3 species – *Thalassoma herbraicum* (an invertivore), *Cheilio inermis* and *Lethrinus harak* (both generalist carnivores, and the latter is an important fishery by-catch species), contributed to 70% of the similarity within the cluster of transects at the high macroalgae cover, low-complexity end (herein referred to as low-complexity macroalgae habitats) of the benthic PC1 (Table 1). One species, *T. herbraicum* was common to both groups. Sixteen species explained 49.3% of the dissimilarity between the complex coral and low-complexity macroalgae habitats and represent 5 of the 8 defined functional groups (Table 1).

The transition along the benthic gradient from complex coral to low-complexity macroalgae associated with PC1 (Figure 1), corresponded with a decline in fish functional group diversity ($r^2 = 0.375$, $p<0.001$; Figure 3a), overall fish species richness ($r^2 = 0.434$, $p<0.001$; Figure 3b) but not total fish abundance ($r^2 = 0.081$, $p>0.05$, Figure 3c) (Table 2). For the abundance of fish within functional groups, PC1 of the benthic PCA corresponded with a strong decline in obligate corallivore abundance ($r^2 = 0.754$, $p<0.001$, Figure 4a), a weak decline in invertivore abundance ($r^2 = 0.139$, $p<0.05$, Figure 4b), and a very weak

Table 1. Fish taxa contributing to the similarity within, and dissimilarity between, the extreme groups of low-complexity macroalgae and complex coral.

			Similarity		Dissimilarity
Species	**FG**	**FP**	**Macroalgae (49.5%)**	**Coral (46.8%)**	**(88.7%)**
Lethrinus harak	Ca	I	35.69		2.67
Cheilio inermis	Ca	N	30.91		3.21
Thalassoma herbraicum	In	N	14.68	6.02	2.11
Chromis atripectoralis	Pl	N		9.75	5.45
Chlorurus sordidus	HO	P		8.95	4.12
Chaetodon trifasciatus	Co	N		8.19	4.42
Plectroglyphidodon lacrymatus	HO	N		5.43	3.87
Pomacentrus sulfureus	Pl	N		5.29	3.92
Gomphosus caeruleus	In	O		5.09	3.11
Ambyglyphidodon leucogaster	Pl	N		4.08	3.33
Cheilinus trilobatus	In	I		4.03	1.63
Labroides dimidiatus	In	N		3.69	2.30
Scarus niger	HO	I		3.26	2.68
Halichoeres marginatus	In	O		2.73	2.23
Ctenochaetus striatus	HO	I		2.70	2.21
Halichoeres hortulanus	In	O		2.70	2.05
Pomacentrus trilineatus	Pl	N			2.24
Carangidae	Pi	P			2.00
Hemigymnus fasciatus	In	O			1.76
Halichoeres nebulosus	In	O			1.69
Zanclus cornutus	In	O			1.55
Stethojulis albovittata	In	O			1.53
Labrichthys unilineatus	Co	O			1.44
Macropharyngodon bipartitus	In	O			1.40
Oxymonacanthus longirostris	Co	N			1.32
Centropyge multispinis	In	O			1.30
Scolopsis frenatus	In	O			1.27
Lethrinus obsoletus	Ca	I			1.24
Chromis ternatensis	Pl	N			1.18
Zebrasoma scopas	HO	N			1.11
TOTAL % contribution			81.28	71.91	70.33

SIMPER analysis performed on square-root transformed abundance data. Cutoff for low contributions: 70%. Average similarity or dissimilarity reported in parentheses. Functional group (FG) acronyms defined in Figure 2 legend. Fishing pressure (FP) exerted on the species. P – primary target; I – important by-catch; O – occasional by-catch; N – not targeted.

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increase in browsing herbivore abundance ($r^2 = 0.066$, $p < 0.05$, Figure 4c)(Table 2). No relationships were found between the benthic habitat gradient and the abundances of the other five fish functional groups (Table 2; non-browsing herbivorous species also Figure 4d).

Discussion

This study found markedly different fish composition along a multivariate gradient of reef benthic conditions ranging from complex coral habitats to low-complexity macroalgae habitats. Very different fish assemblages were linked with the two habitat extremes, not only in terms of species present, but also richness and diversity at both species and functional group level. The strongest relationships with the habitat gradient were found at the overall fish assemblage scale, rather than at the individual functional group scales. Obligate corallivorous fishes were the exception, and are known for their dependence upon live corals [52]. The dependence of reef fish assemblages on the coral reef benthos has been demonstrated through numerous before-after studies of fish and benthic changes through disturbance events (reviewed by: [9,23]). In contrast, this study assesses the role of a broad array of benthic conditions following disturbance, on reef fish assemblages, providing useful insights into potential future compositions of reef fishes.

At the extreme ends of the benthic gradient, complex coral habitats support a higher number of fish species and functional groups than low-complexity habitats dominated by macroalgae. A major consequence for many ecosystems facing degradation is ecological homogenisation, whereby multiple specialist species or

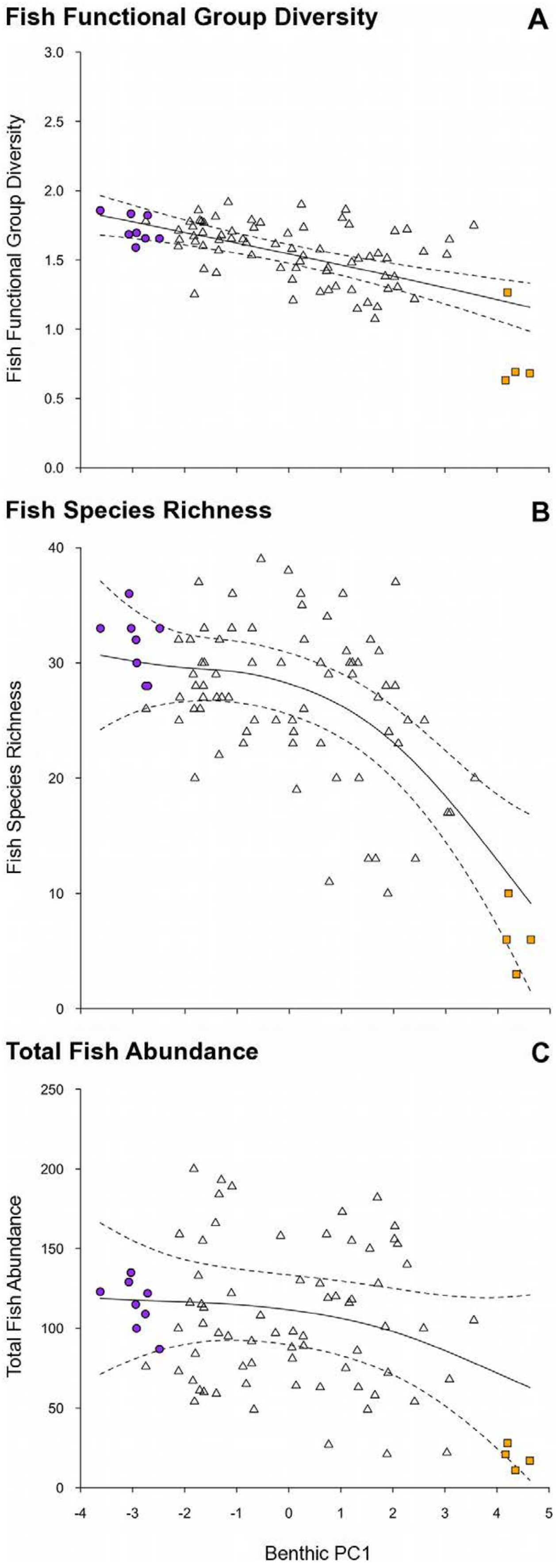

Figure 3. Relationships between the gradient in benthic habitat condition and fish assemblage metrics. Benthic habitat condition (PC1 axis): negative values – complex coral habitats; high values – low-complexity macroalgae habitats. Fish assemblage metrics: (a) fish functional group diversity (an index calculated using the Shannon-Weiner diversity index (H′) at the functional group level), (b) fish species richness, (c) total fish abundance. Plotted are fitted parameter estimates ±95% confidence intervals based on GAM with Reef as a random variable. Note that (c) represents a statistically non-significant relationship. Two extreme outliers were excluded from (C) to aid visual representation, but were included in the analysis. Symbols as in previous figures. Note different scales along y-axis.
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groups are replaced by fewer, more generalist species or groups leading to much simpler ecosystems [53,54]. Our results appear to support this theory with the low-complexity macroalgae habitats lacking many of the more specialised coral reef fish functional groups (e.g. obligate corallivores and coral-associated planktivores; [45,55]) and also the essential groups for the provision of key ecological processes (e.g. herbivores; [56–58]). While macroalgae provide 3-dimensional structure, in comparison to the often intricate and unyielding skeletal structures of scleractinian corals, it is a more homogeneous and flexible habitat that appears to be less favourable to reef fishes [59].

Macroalgal-dominated reefs have long been regarded as degraded reef states [11]. This study provides some empirical evidence that macroalgal-dominated reefs are unfavourable for the wider ecosystem's ecological communities and economic potential. Nevertheless, habitats with abundant macroalgae can be naturally occurring and provide important refuges for juvenile reef-associated fishes [60]. Juvenile *Cheilio inermis* for example, are present only in *Sargassum* stands in Western Australia [60]. Also, *Sargassum* and *Turbinaria* algal stands have been present on Seychelles coral reefs for some time [61,62], although the influence of human settlement on macroalgal presence is not known. Importantly, macroalgal cover has shown substantial expansion following the 1998 bleaching event [28] and is continuing to increase in cover [63]. Given the high cover of macroalgae

Table 2. Results of generalized additive mixed models (GAMM) used to model response variables with respect to the gradient in benthic habitat (Benthic PC1), with Reef as a random variable.

Response variable	*df*	*F*	*p*	r^2
Fish functional group diversity	1.15	26.024	**	0.375
Fish species richness	2.687	27.135	**	0.434
Total fish abundance	1.642	3.133	NS	0.081
Obligate corallivores	7.546	26.938	**	0.749
Browsing herbivores	1	2.789	*	0.066
Non-browsing herbivores	2.226	1.756	NS	0.094
Non-coral invertivores	1.775	4.963	*	0.139
Generalist carnivores	1	0.002	NS	−0.012
Omnivores	2.336	3.593	NS	0.104
Piscivores	1	3.523	NS	0.05
Planktivores	1	2.127	NS	0.08

df: estimated degrees of freedom for smooth term (Benthic PC1; 1 = linear).
p: $^{**}p<0.001$, $^{*}p<0.05$, NS $p>0.05$.
r^2: proportion of variation explained by the benthic habitat gradient (negative value = model is a worse representation than the Null model).
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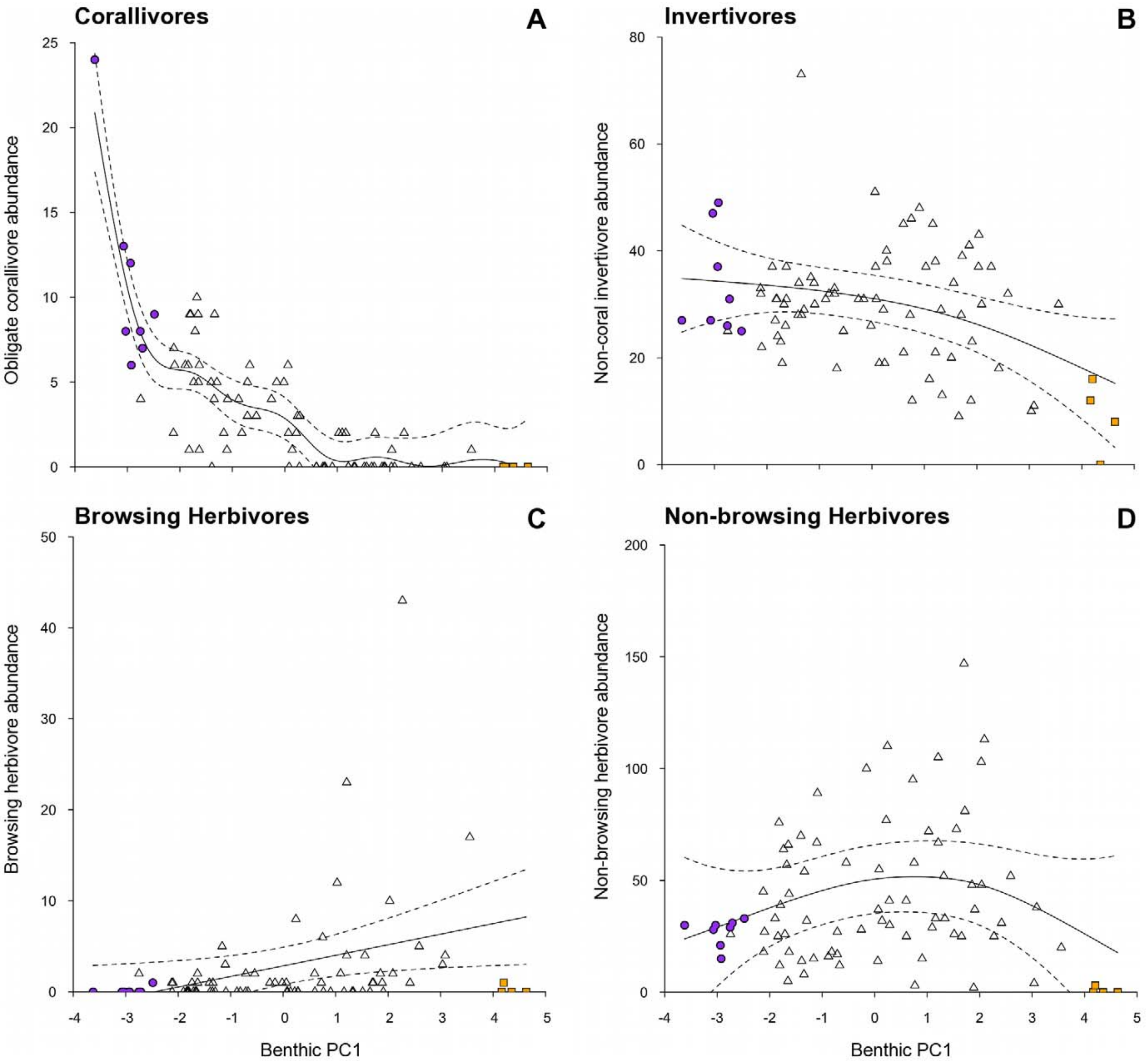

Figure 4. Relationships between the gradient in benthic habitat condition and abundances of fish functional groups. Benthic habitat condition (PC1 axis): low values – complex coral habitats; high values – low-complexity macroalgae habitats. Abundances of fish functional groups: (a) obligate corallivores, (b) non-coral invertivores, (c) browsing herbivores, and (d) non-browsing herbivores. Plotted are fitted parameter estimates ±95% confidence intervals based on GAM with Reef as a random variable. Note that (d) represents a statistically non-significant relationship. An extreme outlier was excluded to aid visual representation from (B), (C), and (D), but was included in the analyses. Symbols as in previous figures. Note different scales along y-axis.
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documented in our study, and the habitats surveyed, it is likely that some of the sites represented recently degraded reef states. Our study suggests that expansion of macroalgae on reefs will have substantial negative repercussions for associated fish diversity.

Herbivores are considered the most important functional group of fish on coral reefs through their role in mediating the competition for space between corals and algae [57,64,65]. Indeed, negative relationships exist between herbivore biomass and macroalgae cover [66–69], although a distinction has been found between herbivorous species that maintain low algal biomass, and browsing species that will consume mature macroalgae thalli [58,70]. Surprisingly therefore, there was no substantial increase in either of the two herbivorous functional groups along the benthic gradient found in this study. Similarly, a study of benthic changes across 7 countries in the Indian Ocean spanning the 1998 coral bleaching event found no increase in herbivore abundance in response to the increase in benthic space available for algal growth [6], while browsing species in Australia show no correlation with increasing macroalgal cover on the GBR [69] or Ningaloo reef [71]. Although browsing herbivores have been able to reverse phase shifts in small-scale experimental settings surrounded by intact reef [58], reefs with high fleshy macroalgal cover tend to have low functional redundancy amongst browsing herbivores [70], and dense macroalgal stands can inhibit herbivory [59]. Indeed, the ability of browsing herbivores to perform their vital function on macroalgae-dominated reef systems is very poorly understood.

The identified differences in the fish community with changing benthic condition are likely to have implications for ecosystem service provision [10,72–74]. Major ecosystem services associated with reef fishes include the provision of fisheries and tourism [13,75,76]. Therefore, as fish species richness and functional group diversity decreases across the benthic condition gradient, the multi-species fishery and substantial dive tourism industry of the Seychelles are likely to be negatively affected by shifts away from complex coral-dominated reefs [41,73,77]. Specifically, there was a 5-fold difference in fish abundances at the benthic extremes of our study: macroalgal-dominated reefs had an average of 19.3 (±3.6 SE) fish per 250 m^2 compared to 105.3 (±5.4 SE) fish per 250 m^2 at the reef with the highest overall coral cover and complexity. Moreover, two of the five primary fishing target species, and 19 important by-catch species [46] were present on reefs with highest overall coral cover and complexity compared to no primary target species, and only one important by-catch species on low complexity and macroalgae-dominated reefs. This 5-fold difference in total fish abundance and the reduction in target species, is likely to reflect a decline in fishery potential. This contrasts with results from the Caribbean where macroalgae-dominated reefs appeared to sustain high fish species richness [78]. Similarly, studies of tourist preferences show that fish abundance and diversity play a major role in attracting and satisfying dive tourists (e.g. [79–81]).

Although we predicted that the stability of the underlying substratum would interact with the condition of the benthos, with stable substrata having higher coral cover than mobile rubble reefs, we found only weak relationships. Studies in rubble-dominant locations, such as former dynamite fishing areas, have found substantially lower coral cover on rubble versus stable rocky sites [35]. Furthermore, other macro-benthic organisms such as reef sponges have been found to have decreased growth rates on mobile rubble substrata compared to stable rock substrata [37]. Our results showed that many of the rubble dominated transects did have low coral cover (where rubble was >80%, mean coral cover was 4.9% (±1.9 SE)). However, many other transects that had little rubble also had low coral cover (22/46 transects with <5% rubble had <10% coral cover), indicating that substratum stability was not the only variable influencing coral cover. Interestingly however, both the coral-dominated and macroalgal-dominated extremes were associated with more stable substrata, suggesting that substratum stability is important in enabling these macrobenthic organisms to survive to maturity.

The multivariate gradient of benthic conditions found in this study indicates a continuum of reef states. However, in the absence of long-term time series data and/or experimental manipulations it is not possible to establish the stability of our extreme benthic state categories [82]. Similarly, the reefs in the middle of the continuum may be fairly stable in their own right, or in transition (i.e. degrading or recovering) between different characteristic equilibrium states because of various natural disturbances or perturbations [8,32,33,83]. Regardless, it is clear that more degraded reefs, in terms of coral cover, diversity and structural complexity, host more depauperate reef fish assemblages.

As coral reefs continue to degrade due to a range of anthropogenic drivers, and alterations in community compositions occur, it is imperative that we understand how changes in one aspect of an ecosystem affect the rest of the ecosystem. From a management perspective, the fact that many reefs do not exist in discrete states means that few generalisations are possible, and reef specific data may be required to implement necessary management plans [32,84]. While many previous studies have linked loss of fish diversity with loss of coral cover, the lack of reciprocal increases in herbivorous fishes to counter increases in algal cover is alarming, with negative implications for the continuation of many coral reef ecosystem processes and services if more reefs shift to macroalgal-dominated states. Clearly, prevention of further reef degradation through a reduction in anthropogenic pressures, is of critical importance because the repercussions of declining habitat condition may be far reaching.

Supporting Information

Figure S1 Proportional cover of benthic biota per site. (TIF)

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Author Contributions

Conceived and designed the experiments: KMC NAJG MSP DRB. Analyzed the data: KMC. Wrote the paper: KMC TDM MSP DRB NAJG. Collected the data: KMC TDM.

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REPORT

Bottlenecks to coral recovery in the Seychelles

K. M. Chong-Seng · N. A. J. Graham · M. S. Pratchett

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Abstract Processes that affect recovery of coral assemblages require investigation because coral reefs are experiencing a diverse array of more frequent disturbances. Potential bottlenecks to coral recovery include limited larval supply, low rates of settlement, and high mortality of new recruits or juvenile corals. We investigated spatial variation in local abundance of scleractinian corals in the Seychelles at three distinct life history stages (recruits, juveniles, and adults) on reefs with differing benthic conditions. Following widespread coral loss due to the 1998 bleaching event, some reefs are recovering (i.e., relatively high scleractinian coral cover: 'coral-dominated'), some reefs have low cover of living macrobenthos and unconsolidated rubble substrates ('rubble-dominated'), and some reefs have high cover of macroalgae ('macroalgal-dominated'). Rates of coral recruitment to artificial settlement tiles were similar across all reef conditions, suggesting that larval supply does not explain differential coral recovery across the three reef types. However, acroporid recruits were absent on macroalgal-dominated reefs (0.0 ± 0.0 recruits tile^{-1}) in comparison to coral-dominated reefs (5.2 ± 1.6 recruits tile^{-1}). Juvenile coral colony density was significantly lower on macroalgal-dominated reefs (2.4 ± 1.1 colonies m^{-2}), compared to coral-dominated reefs (16.8 ± 2.4 m^{-2}) and rubble-dominated reefs (33.1 ± 7.3 m^{-2}), suggesting that macroalgal-dominated reefs have either a bottleneck to successful settlement on the natural substrates or a high post-settlement mortality bottleneck. Rubble-dominated reefs had very low cover of adult corals (10.0 ± 1.7 %) compared to coral-dominated reefs (33.4 ± 3.6 %) despite no statistical difference in their juvenile coral densities. A bottleneck caused by low juvenile colony survivorship on unconsolidated rubble-dominated reefs is possible, or alternatively, recruitment to rubble-dominated reefs has only recently begun. This study identified bottlenecks to recovery of coral assemblages that varied depending on post-disturbance habitat condition.

Keywords Scleractinian corals · Phase shifts · Larval supply · Recruitment · Degradation · Rubble · Macroalgae

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REPORT

Macroalgal herbivory on recovering versus degrading coral reefs

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Abstract Macroalgal-feeding fishes are considered to be a key functional group on coral reefs due to their role in preventing phase shifts from coral to macroalgal dominance, and potentially reversing the shift should it occur. However, assessments of macroalgal herbivory using bioassay experiments are primarily from systems with relatively high coral cover. This raises the question of whether continued functionality can be ensured in degraded systems. It is clearly important to determine whether the species that remove macroalgae on coral-dominated reefs will still be present and performing significant algal removal on macroalgal-dominated reefs. We compared the identity and effectiveness of macroalgal-feeding fishes on reefs in two conditions post-disturbance—those regenerating with high live coral cover (20–46 %) and those degrading with high macroalgal cover (57–82 %). Using filmed *Sargassum* bioassays, we found significantly different *Sargassum* biomass loss between the two conditions; mean assay weight loss due to herbivory was 27.9 ± 4.9 % on coral-dominated reefs and 2.2 ± 1.1 % on reefs with high macroalgal cover. However, once standardised for the availability of macroalgae on the reefs, the rates of removal were similar between the two reef conditions (4.8 ± 4.1 g m^{-2} h^{-1} on coral-dominated and 5.3 ± 2.1 g m^{-2} h^{-1} on macroalgal-dominated reefs). Interestingly, the *Sargassum*-assay consumer assemblages differed between reef conditions; nominally grazing herbivores, *Siganus puelloides* and *Chlorurus sordidus*, and the browser, *Siganus sutor,* dominated feeding on high coral cover reefs, whereas browsing herbivores, *Naso elegans, Naso unicornis*, and *Leptoscarus vaigiensis,* prevailed on macroalgal-dominated reefs. It appeared that macroalgal density in the surrounding habitat had a strong influence on the species driving the process of macroalgal removal. This suggests that although the function of macroalgal removal may continue, the species responsible may change with context, differing between systems that are regenerating versus degrading.

Keywords Ecosystem function · Phase shifts · Redundancy · Sargassum · Recovery · Degradation

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REPORT

Recent disturbances augment community shifts in coral assemblages in Moorea, French Polynesia

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Abstract Coral reefs are often subject to disturbances that can cause enduring changes in community structure and abundance of coral reef organisms. In Moorea, French Polynesia, frequent disturbances between 1979 and 2003 caused marked shifts in taxonomic composition of coral assemblages. This study explores recent changes in live cover and taxonomic structure of coral communities on the north coast of Moorea, French Polynesia, to assess whether coral assemblages are recovering (returning to a previous *Acropora*-dominated state) or continuing to move towards an alternative community structure. Coral cover declined by 29.7% between July 2003 and March 2009, mostly due to loss of *Acropora* and *Montipora* spp. Coral mortality varied among habitats, with highest levels of coral loss on the outer reef slope (7–20 m depth). In contrast, there was limited change in coral cover within the lagoon, and coral cover actually increased on the reef crest. Observed changes in coral cover and composition correspond closely with the known feeding preferences and observed spatial patterns of *Acanthaster planci* L., though observed coral loss also coincided with at least one episode of coral bleaching, as well as persistent populations of the corallivorous starfish *Culcita novaeguineae* Muller & Troschel. While climate change poses an important and significant threat to the future structure and dynamics coral reef communities, outbreaks of *A. planci* remain a significant cause of coral loss in Moorea. More importantly, these recent disturbances have followed long-term shifts in the structure of coral assemblages, and the relative abundance of both *Pocillopora* and *Porites* continue to increase due to disproportionate losses of *Acropora* and *Montipora*. Moreover, *Pocillopora* and *Porites* dominate assemblages of juvenile corals, suggesting that there is limited potential for a return to an *Acropora*-dominated state, last recorded in 1979.

Keywords Disturbance · Resilience · Coral reefs · *Acanthaster planci* · Bleaching · Pacific

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REPORT

Selective feeding by coral reef fishes on coral lesions associated with brown band and black band disease

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Abstract Recent studies have suggested that corallivorous fishes may be vectors for coral disease, but the extent to which fishes actually feed on and thereby potentially transmit coral pathogens is largely unknown. For this study, in situ video observations were used to assess the level to which fishes fed on diseased coral tissues at Lizard Island, northern Great Barrier Reef. Surveys conducted at multiple locations around Lizard Island revealed that coral disease prevalence, especially of brown band disease (BrB), was higher in lagoon and backreef locations than in exposed reef crests. Accordingly, video cameras were deployed in lagoon and backreef habitats to record feeding by fishes during 1-h periods on diseased sections of each of 44 different coral colonies. Twenty-five species from five fish families (Blennidae, Chaetodontidae, Gobiidae, Labridae and Pomacentridae) were observed to feed on infected coral tissues of staghorn species of *Acropora* that were naturally infected with black band disease (BBD) or brown band disease (BrB). Collectively, these fishes took an average of 18.6 (±5.6 SE) and 14.3 (±6.1 SE) bites per hour from BBD and BrB lesions, respectively. More than 40% (408/948 bites) and nearly 25% (314/1319 bites) of bites were observed on lesions associated with BBD and BrB, respectively, despite these bands each representing only about 1% of the substratum available. Moreover, many corallivorous fishes (*Labrichthys unilineatus, Chaetodon aureofasciatus, C. baronessa, C. lunulatus, C. trifascialis, Cheiloprion labiatus*) selectively targeted disease lesions over adjacent healthy coral tissues. These findings highlight the important role that reef fishes may play in the dynamics of coral diseases, either as vectors for the spread of coral disease or in reducing coral disease progression through intensive and selective consumption of diseased coral tissues.

Keywords Coral disease · Corallivores · Butterflyfishes · Feeding selectivity · Disease transmission

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Conservation Biology

Contributed Paper

Effect of Macroalgal Expansion and Marine Protected Areas on Coral Recovery Following a Climatic Disturbance

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Abstract: *Disturbance plays an important role in structuring marine ecosystems, and there is a need to understand how conservation practices, such as the designation of Marine Protected Areas (MPAs), facilitate postdisturbance recovery. We evaluated the association of MPAs, herbivorous fish biomass, substrate type, postdisturbance coral cover, and change in macroalgal cover with coral recovery on the fringing reefs of the inner Seychelle islands, where coral mortality after a 1998 bleaching event was extensive. We visually estimated benthic cover and fish biomass at 9 sites in MPAs where fishing is banned and at 12 sites where fishing is permitted in 1994, 2005, 2008, and 2011. We used analysis of variance to examine spatial and temporal variations in coral cover and generalized additive models to identify relations between coral recovery and the aforementioned factors that may promote recovery. Coral recovery occurred on all substrate types, but it was highly variable among sites and times. Between 2005 and 2011 the increase in coral cover averaged 1%/year across 21 sites, and the maximum increase was 4%/year. However, mean coral cover across the study area (14%) remained at half of 1994 levels (28%). Sites within MPAs had faster rates of coral recovery than sites in fished areas only where cover of macroalgae was low and had not increased over time. In MPAs where macroalgae cover expanded since 1998 there was no recovery. Where coral was recovering on granite reefs there was a shift in relative prevalence of colony life-form from branching to encrusting species. This simplification of reef structure may affect associated reef fauna even if predisturbance levels of coral cover are attained.*

Keywords: climate change, coral bleaching, coral reef resilience, ecosystem recovery, herbivory, marine reserves

Efecto de la Expansión de Macroalgas y Áreas Marinas Protegidas sobre la Recuperación de Coral Después de una Perturbación Climática

Resumen: *La perturbación juega un papel importante en la estructuración de ecosistemas marinos, y existe la necesidad de entender la manera en que las prácticas de conservación, como la designación de Áreas*

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Marinas Protegidas (AMPs), facilitan la recuperación después de una perturbación. Evaluamos la asociación de AMPs, biomasa de peces herbívoros, tipo de sustrato, cobertura de coral después de la perturbación y cambio en la cobertura de macroalgas con la recuperación de coral en los arrecifes marginales de las islas Seychelle, donde la mortalidad de coral fue extensiva después de un evento de blanqueo en 1998. Estimamos visualmente la cobertura bentónica y la biomasa de peces en 9 sitios en AMPs donde esta prohibida la pesca y en 12 sitios donde se permite la pesca en 1994, 2005, 2008 y 2011. Utilizamos análisis de varianza para examinar variaciones espaciales y temporales de la cobertura de coral y modelos aditivos generalizados para identificar relaciones entre la recuperación de coral y factores antes mencionados que pueden promover la recuperación. La recuperación de coral ocurrió en todos los tipos de sustrato, pero fue altamente variable entre sitios y tiempos. Entre 2005 y 2011, el incremento de la cobertura de coral promedió 1%/año en los 21 sitios, y el incremento máximo fue de 4%/año. Sin embargo, la cobertura promedio de coral en el área de estudio (14%) permaneció a la mitad de los niveles de 1994 (28%). Sitios dentro de las AMPs tuvieron tasas de recuperación de coral más rápidas que los sitios en áreas con pesca solo donde la cobertura de macroalgas fue baja y no había incrementado en el tiempo. No hubo recuperación en AMPs donde se expandió la cobertura de macroalgas desde 1998. En sitios con recuperación de coral sobre arrecifes de granito hubo un cambio en la prevalencia relativa de forma de vida colonial de especies ramificadas a incrustantes. Esta simplificación de la estructura del arrecife puede afectar a la fauna arrecifal asociada aunque se alcancen los niveles de cobertura de coral previos a la perturbación.

Palabras Clave: blanqueo de corales, cambio climático, herbivoría, recuperación de ecosistemas, reservas marinas, resiliencia de arrecifes de coral