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A Functional Analysis of Herbivory on Ningaloo Reef, Australia

Thesis submitted by

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for the degree of Doctor of Philosophy in Marine Biology
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Statement on the Contribution of Others

This thesis includes some collaborative work with my supervisors, Professor David Bellwood (James Cook University) and Dr Martial Depczynski (Australian Institute of Marine Science (AIMS)), Dr Andrew Hoey (Centre of Excellence for coral reef studies at James Cook University) and PhD-Candidate Ingrid van de Leemput (Wageningen University, the Netherlands). While undertaking these collaborations, I was responsible for the project concept and design, data collection, analyses and interpretation, and the final synthesis of results into a form suitable for publication. My collaborators provided intellectual guidance, equipment, financial support, GBR data, technical instruction, statistical advice and editorial assistance.

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Abstract

Roving herbivorous fishes play a key role in controlling the biomass of benthic algae on coral reefs. These fishes are examined here to provide insights into how the composition of herbivorous species and their ecological functions contribute to ecosystem resilience in a relatively un-impacted reef system, Ningaloo Reef in Western Australia. Atypical in the fact that it has very low levels of terrestrial run-off and or anthropogenic disturbance, this reef system provides a rare opportunity to study herbivory in its natural state. However, Ningaloo Reef has a very high natural presence of both macroalgae and sea urchins, both of which are often cited as being detrimental to some reef systems and key indicators of degraded coral reef systems. Between 2009-2012, visual censuses were used to quantify the distribution of these two indicators of reef decline, alongside those of four functional groups of herbivorous fish (browsers, excavators, grazers and scrapers), to provide a better understanding of the functional role that vertebrate and invertebrate herbivores play on coral reefs.

Extensive macroalgal beds present in the sandy lagoon and high densities of the sea urchin *Echinometra mathaei* recorded from the nearby reef slope were significant features of Ningaloo Reef. A marked cross-shelf variation in the composition of herbivorous fish functional groups was also found, with only the back reef and the reef slope supporting fish populations with high grazing rates (completely scraped every 43 and 59 days, respectively). To assess the relative importance and contribution of herbivorous fishes and urchins to grazing and bioerosion, feeding rates were quantified. Rates of bioerosion by fishes were low (1 and 2.3 kg m^{-2} yr^{-1} of $CaCO_3$) compared to those seen on the Great Barrier Reef, reflecting the lack of large excavating parrotfishes. However, the sea urchin *E. mathaei*, had an annual erosion capacity on the reef slope close to that of the most abundant excavating parrotfish, *Chlorurus sordidus* (0.4 and 0.54 kg m^{-2} yr^{-1} of $CaCO_3$, respectively), indicating that herbivory at Ningaloo Reef is divided between urchins and fishes. High, apparently natural, urchin and macroalgal

abundances on this relatively intact reef system highlight the need for caution when using these metrics for evaluating the condition of a reef ecosystem.

To investigate why Ningaloo Reef has such high densities of sea urchins, diurnal predation events on tethered *E. mathaei* were recorded using stationary underwater video cameras. Despite the densities of *E. mathaei* varying from 0.1 individuals 100m^{-2} in the lagoon to 219.7 individuals 100m^{-2} on the reef slope, the density and biomass of potential sea urchin predators did not differ among habitats. However, the predator assemblage on Ningaloo Reef differed markedly from those of other global regions suggesting that the composition of available urchin predators could be critical in determining the level of top-down control. Unlike many other studies on East African and Indo-Pacific reefs where balistids are dominant and active predators on sea urchins, labrids were the dominant sea urchin predators on Ningaloo Reef. The fact that labrids are the dominant predator in this system appears to reflect a lack of large balistid predators, suggesting that the predatory composition as well as bottom-up factors (e.g., water flow, food availability and habitat structure) may control densities and determine among-habitat distributions.

The effect of coral cover on herbivorous fishes was explored for each functional group over three size classes. Small excavating and scraping parrotfishes were found to have a strong dependency on live coral cover on the physically demanding exposed slope. Since coral tissue is not a part of the diets of small parrotfishes, this close association may instead allow these small and comparatively weaker swimmers to subsist and forage in strong water flows and avoid predation by utilizing the increased structural complexity of corals. In contrast, small schooling grazers on the slope were not constrained in the same manner, instead preferring areas with low levels of coral cover. While similar benefits to those provided by coral structure are gained by schooling, grazers can explore adjacent parts of the reef where the competition from coral promotes algal biomass. Although these contrasting relationships were evident on the slope, they were absent from protected back reefs. They were also restricted to the small

size classes. Significant loss of coral cover may therefore be particularly important for small non-schooling fishes, especially in high energy habitats.

Species richness, generic richness, abundance and reserve capacity (the capacity of the remaining species to functionally compensate for the loss of the most abundant species) were used to examine the functional redundancy of herbivorous functional groups across habitats on Ningaloo Reef and a comparison was made with the Great Barrier Reef. Marked variations in the composition of herbivorous functions were found among habitats. Despite extensive management and limited fishing, coastal habitats in both reef systems had particularly low levels of herbivory in all the above metrics compared with offshore habitats, suggesting that coastal habitats are less likely to resist disturbances. By utilising these four metrics, which can easily be applied to any fish abundance dataset, this approach provides a simple yet robust estimate of the potential capacity of functional groups and habitats to cope with change, and further highlights the spatial variation in potential sensitivity to declining reef health.

High densities of sea urchins and extensive macroalgae beds are present on Ningaloo Reef. However, these two commonly cited indicators of reef degradation appear to represent a natural state at Ningaloo Reef, highlighting the unique configuration of this system. However, with fewer species and genera, as well as lower abundances and reserve capacity, the inshore coastal habitats of Ningaloo Reef and the Great Barrier Reef appear to be more vulnerable to disturbance than offshore reefs as far as herbivory is concerned. This highlights the sensitive nature and importance of herbivory in the macroalgal dominated lagoon at Ningaloo Reef. Furthermore, high densities of sea urchins on the reef slope and the strong association of smaller size-classes of excavators and scrapers to live coral cover identify a further level of vulnerability at Ningaloo Reef. Despite some signs of vulnerability, in terms of herbivorous processes, Ningaloo Reef appears to be a unique and relatively healthy coral reef ecosystem.

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Chapter 1: General Introduction

Coral reefs are facing increasing exposure to anthropogenic disturbance (Hoegh-Guldberg, 1999, Hughes et al., 2003, Jackson et al., 2001). Climate change, overfishing, pollution and other stressors can undermine important ecological functions or processes (Bellwood et al., 2004, Graham et al., 2011). As a result, changes to ecosystem processes can weaken a coral reef's resistance to perturbations and reduce its capacity to cope with and reorganize after a disturbance event (ecological resilience) (Walker et al., 2004). Ecosystems with reduced ecological resilience are more susceptible to shifts in benthic community structure, where one dominant organism is replaced by another. They are also more likely to remain within this new altered state (Walker et al., 2004, Scheffer et al., 2001, Gunderson, 2000, Walker and Meyers, 2004). Such shifts change not only coral reef ecosystems and the way in which they function, but may also be detrimental to the people who depend on reefs for ecosystem goods and services (Hughes, 1994, Hughes et al., 2003).

'Healthy' coral reefs are commonly associated with high levels of coral cover and low densities of macro algae. One of the key components in ensuring the persistence of the 'healthy' state on coral reefs is herbivory. Herbivory is considered to be an important process in maintaining high coral cover on reefs by the continuous removal of macroscopic algae. Thus, herbivory is a key process in the continued well-being and management of coral reef ecosystems (Hoey and Bellwood, 2010b, Wismer et al., 2009, Burkepile and Hay, 2006, Smith et al., 2001). Fishes and urchins, are considered to be two of the most important primary herbivore groups in preventing coral-dominated reefs from shifting to algal domination (Hughes, 1994, Carpenter, 1986, Carpenter, 1988). Herbivorous fishes are, by far, the more diverse of the two groups, with a wide range of species feeding on a range of different algal types. When feeding, roving herbivorous fishes cover hundreds of meters of coral reef (Welsh and Bellwood, 2012b), compared to the more site attached territorial damselfishes and sea urchins which tend to feed within or in the vicinity of their territory or burrow (Vanderklift et al., 2009, Ogden et al., 1989). Fishes and sea urchins therefore contribute to herbivory at varying spatial scales. A thorough understanding of the identity and nature of species associated with grazing, and their consequences on algal productivity and biomass, are therefore important aspects in effectively managing and reducing the risk of coral reef system shifts (Hughes et al., 2005, Walker and Meyers, 2004, Nyström et al., 2012).

Roving herbivorous fishes can be divided into four main functional groups: browsers, excavators (bioeroders), grazers and scrapers (Steneck, 1988, Bellwood et al., 2004). These four groups can be categorised by both their food source and feeding mode (Bellwood and Choat, 1990, Choat et al., 2002). As a result, they are functionally distinct and complement each other via fine scale niche partitioning in their feeding mode and/or type of algae targeted (Green and Bellwood, 2009). For example, scrapers scrape turf algae off the reef substratum, while excavators use their strong jaws to bite into the reef matrix, thus contributing to bioerosion. These two groups not only control algal biomass but also ensure that there is open space on the reef substratum for settlement of marine organisms such as coral (Bellwood and Choat, 1990). Grazers on the other hand do not physically alter the substratum, but instead graze by cropping the top of turf algae. While excavators, grazers and scrapers all graze on turf algae, browsers are the only group capable of reducing the biomass of established macroalgae (Green and Bellwood, 2009, Hoey and Bellwood, 2010a). Additionally, research has shown that the feeding mode of herbivorous fish can change with ontogenetic development (Bellwood, 1988, Bonaldo and Bellwood, 2008, Lokrantz et al., 2008). Variations in diet both within and among species highlight the complexity of functional roles within a reef ecosystem. Overall, what this suite of species and their activities emphasise is that each functional group makes a different but collectively important contribution to the maintenance of coral reefs.

Sea urchins are also known to make an important contribution towards the control of algae on coral reefs and are further categorized by their significant bioeroding activities (McClanahan, 1998, Ogden and Lobel, 1978, Carpenter, 1986, Peyrot-Clausade et al., 2000).

Some species of sea urchins can therefore functionally replace herbivorous fishes as both algal browsers, grazers and bioeroders (Hughes, 1994). However, despite their interchangeable roles, the presence of large numbers of urchins has often been associated with declines in reef ecosystem health (McClanahan, 2000, Lafferty, 2004). Urchin populations have the capacity to rapidly increase in response to reduced top-down control from predators (McClanahan, 1995, Lafferty, 2004, Babcock et al., 2010, Uthicke et al., 2009). Under such circumstances, their beneficial ecological role as grazers and bioeroders may quickly change into one where bioerosion rates far exceed reef accretion rates (Hay, 1984, McClanahan and Muthiga, 1988, Sala et al., 1998) leading to significant reductions in topographic complexity (Alvarez-Filip et al., 2009). Some urchin species on coral reefs may thus represent a functional equivalent but undesirable alternative to fishes.

The capacity of herbivorous functional groups to act in response to the effects of a disturbance depends on multiple factors. These responses are determined by the type of disturbance itself, as well as the composition of species, their functional role, abundance, size (Lokrantz et al., 2008, Bellwood, 1988, Bonaldo and Bellwood, 2008), habitat distribution (Hoey and Bellwood, 2008, Cheal et al., 2012a) and the presence or absence of other herbivorous organisms in the system. In well-managed or low impact systems, the composition of species contributing to various ecosystem functions is likely to be regulated by a set of ecological factors such as recruitment, disease and predation. Hence, low impact coral reef ecosystems potentially hold a relatively intact or near ‘pristine’ functional assembly. The opportunity to investigate herbivory in a functional context in a low impact system can therefore provide valuable insights into the natural structure of an herbivorous fish community and within a system that is expected to have a high degree of resilience to disturbance events.

One such system is Ningaloo Reef. Ningaloo Reef is situated on the central west coast of Australia and is a large, low-impact, Indian Ocean coral reef system (Roberts et al., 2002). Ningaloo Reef is exceptional in that it supports the largest coral reef system on the west coast of any continent. It extends 290 km along the coast with the reef slope as close as 0.2-7 km from the coast, with an average distance of 2.5 km (Fig. 1.1) (Cassata and Collins, 2008). Here, the usual west-continental, upwelling-driven, nutrient-rich, cool waters are suppressed by the warm, south-flowing Leeuwin Current enabling Ningaloo Reef to support coral communities (Hanson et al., 2005, Woo et al., 2006, Furnas, 2007), exposing the reef slopes to strong currents and swells (Cassata and Collins, 2008). The continuous reef, with well-developed spur-and-groove morphology, is broken in parts by sandy passages connecting the ocean with the protected lagoon. The lagoon is covered with white calcareous sand, scattered coral bommies and macroscopic algae. Ningaloo Reef, situated within Ningaloo Reef Marine Park, has been subject to various levels of protection since the 1980s. The fishery is regulated within the marine park and no commercial fin-fishing activities are currently allowed within sanctuary zones. Additionally, Ningaloo Reef experiences minimal freshwater run-off due to the arid nature of the region in which it resides and extremely low human coastal development (Cassata and Collins, 2008). Disturbances to this reef system are dominated by natural events, such as high wave energy and cyclones (Collins et al., 2003). Ningaloo Reef, therefore, experiences little direct human impacts compared to other coral reef systems, including the Great Barrier Reef. The unusual characteristics of Ningaloo Reef present an opportunity to explore a relatively intact coral reef, and may provide insights to the benthic community structure and ecosystem processes in an extensive coastal reef system where direct human impacts are limited (Roberts et al., 2002).

Currently, there is limited understanding of the distribution and composition of herbivorous fishes and sea urchins on Ningaloo Reef. Similarly, it is unclear to what extent macroalgae represent a significant component of benthic communities. More knowledge of the functional breakdown and distribution of Ningaloo Reef herbivores may help identify the distinct characteristics of this reef system.

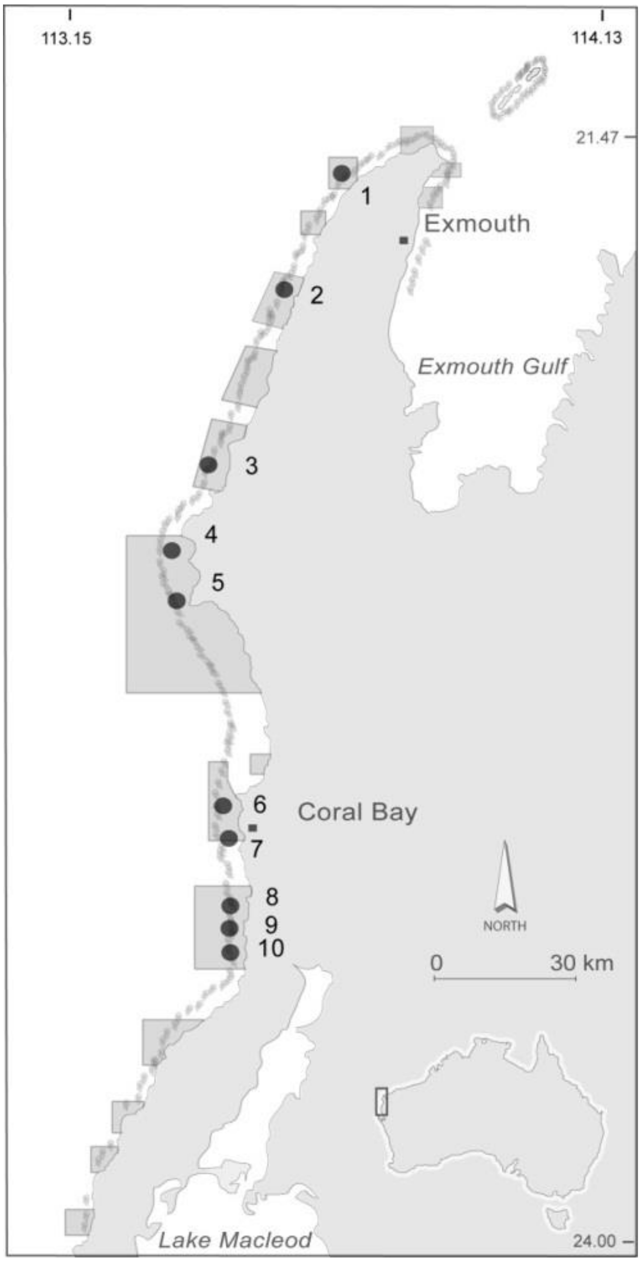

Fig. 1.1 Ningaloo Reef, Western Australia. The 10 study locations in which fish and benthic surveys and sea urchin experiements took place. Three habitats (slope, back reef and macroalgal lagoon) were surveyed at each location. Grey boxes represent Ningaloo Reef sanctuary zones.

Aims and thesis outline

The research for this thesis was conducted on Ningaloo Reef in Western Australia (Fig. 1.1), between 2009 and 2012. The remote location of this reef system offered a unique opportunity to study ecosystem processes on a coral reef with a limited number of human derived disturbances. This thesis defines and characterizes herbivory in a functional context within this low impact reef system by comparing herbivory across three habitats situated in zones closed to fishing: reef slopes, back reefs and reef lagoons (Fig. 1.2). More specifically, it describes the distribution and composition of herbivorous functional groups and potential mechanisms which explain the unique makeup of Ningaloo Reef's macroscopic algae, herbivorous fishes and sea urchins. Finally, this thesis provides a representative picture of the potential levels of ecological resilience available at Ningaloo Reef. Specifically, the research within this thesis is structured to answer the following questions:

1) What are the structural and functional characteristics of the herbivorous fish communities and two common indicators of reef degradation, macroalgae and sea urchins, across three relevant reef zones at Ningaloo Reef?
2) Do top-down predators or bottom-up processes control the intensive sea urchin population on Ningaloo Reef?
3) What is the relationship between live coral cover and herbivorous fishes, and can this help predict what effects coral loss will have on the herbivorous fish community of Ningaloo Reef?
4) What is the potential level of redundancy of the four functional groups of herbivorous fishes at Ningaloo Reef and how does that compare to other reef systems?

These questions are examined in four data chapters. **Chapter 2** examines the distribution of coral and macroalgae. Additionally, it evaluates the functional role and impact of bioeroding fishes and sea urchins within the context of these distributions. **Chapter 3** examines the distribution of sea urchins in detail and identifies their predators to address the question of whether sea urchin densities are subject to top-down control at Ningaloo Reef. **Chapter 4** focuses on the distribution and size-composition of fish herbivore functional groups in two reef habitats in order to understand patterns of ecosystem function. This chapter also identifies the likely effects of coral loss on the herbivorous fish community. **Chapter 5** uses species richness, generic richness, abundance and reserve capacity to obtain a complete picture of the potential level of redundancy available on two relatively low impact reef systems, Ningaloo Reef and the Great Barrier Reef off the east coast of Australia.

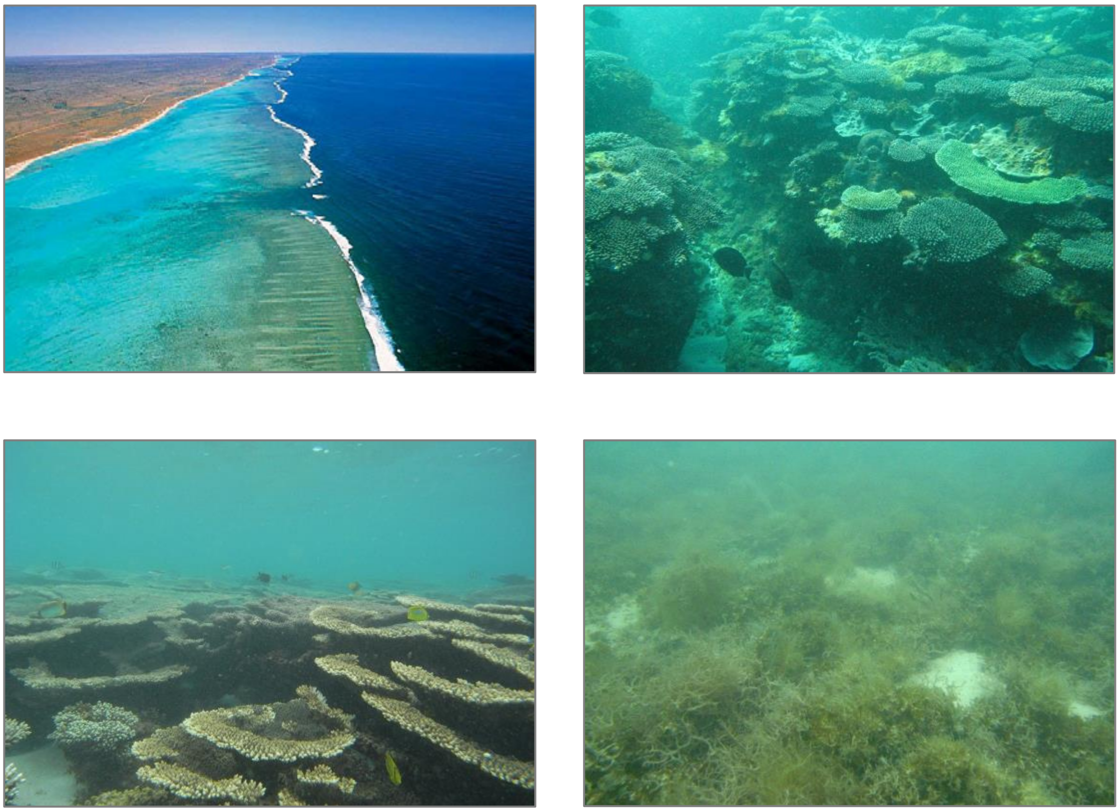

Fig. 1.2 Ningaloo Reef, Western Australia. Clockwise from top left: aerial photo of Ningaloo Reef, reef slope, macroalgal reef lagoon and back reef.

In answering the research questions outlined above, this thesis provides an in-depth examination of reef herbivores, both roving fishes and herbivorous sea urchins, in a low impact reef system. The research in this thesis provides valuable new knowledge which will contribute to the effective conservation and management of vital ecological functions at Ningaloo Reef. More specifically, this thesis stresses the potential utility of using a functional group approach, particularly for herbivory, when planning management and conservation efforts. Finally, this thesis emphasizes the importance of amending and adapting coral reef management, to consider potential variations in functional processes across habitats.

Chapter 2: Sea urchins, macroalgae and coral reef decline: a functional evaluation of an intact reef system, Ningaloo, Western Australia

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2.1 Introduction

The world's coral reefs are in decline (Pandolfi et al., 2003, Bellwood et al., 2004, Graham et al., 2007) and the pressure from human exploitation and climate change are having impacts on ecosystems that are difficult to predict (Lough, 2008, Nyström et al., 2008, De'ath et al., 2009). Numerous reefs around the globe are exhibiting various levels of degradation. Although some are considered to be healthy and well managed, others show clear signs of change in critical functions and processes (Wilkinson, 2008, Paddack et al., 2009). Nevertheless, the responses of reefs to various disturbance events tend to vary as a result of local and regional variation in ecosystem structure and processes (Hughes, 1994, Ledlie et al., 2007, Lokrantz et al., 2008, Nyström et al., 2008). Despite the diversity of responses to coral reef degradation, two widely recognized indicators of coral reef decline have been identified: macroalgal cover and sea urchin density (Hughes, 1994, McClanahan and Mutere, 1994, Jackson et al., 2001, McManus and Polsenberg, 2004). These two taxa tend to increase in abundance and biomass on degrading reefs and may create undesirable alternative states (Done, 1992, McClanahan and Mutere, 1994, McManus and Polsenberg, 2004, Bellwood et al., 2006b, Mumby et al., 2006, Norström et al., 2009).

In both intact and human-disturbed ecosystems, macroalgal biomass appears to be primarily regulated by the abundance and biomass of herbivores, especially fishes (McCook, 1996, McCook, 1999, Bellwood et al., 2006b, Burkepile and Hay, 2008). Algal biomass may also increase in response to the influx of nutrient-enriched terrestrial run-off. This is usually linked to agricultural land-use practices and human coastal development (Schaffelke, 1999, Done et al., 2007, De'ath and Fabricius, 2010). Similarly, increases in echinoid numbers have been identified as direct consequences of the overfishing of sea urchin predators (Hay, 1984, McClanahan, 1995), potentially increasing urchin densities and erosion by urchins to damaging levels. In both cases, overfishing of critical functional groups, i.e. key algal consumers and urchins predators, weakens and reduces the links and processes within the system (Bellwood et al., 2004, Mumby et al., 2006, Hughes et al., 2007b), and can potentially increase macroalgae and sea urchin populations to a state where high abundances are detrimental to the system and increase the possibility of ecosystem shifts (Norström et al., 2009).

It is widely accepted that there are two main drivers controlling macroalgae abundance on coral reefs: herbivores and nutrients. There is, however, considerable disagreement in the relative contribution of the two. Most evidence supports the dominant role of herbivory (McCook, 1996, Burkepile and Hay, 2008). Nevertheless, there is an ongoing argument that macroalgae are primarily influenced by water quality and/or a combination of low herbivory and reduced water quality, especially in areas where terrestrial inputs are present (Schaffelke, 1999, De'ath and Fabricius, 2010). To date, most macroalgal stands in coral reef ecosystems have been reported in areas with limited herbivore activity (Mumby et al., 2006, Wismer et al., 2009) and/or areas where macroalgal distributions have been linked to declining water quality (De'ath and Fabricius, 2010). However, it has also been suggested that macroalgal biomass is not necessarily influenced by human activity, but may be a natural characteristic of some coral reef ecosystems (Vroom et al., 2006, Bruno et al., 2009, Wismer et al., 2009, Vroom et al., 2010) and strongly related to coral cover (Williams et al., 2001).

Ongoing human pressure on coral reefs seems to be unavoidable and coral reef health is consequently measured against an increasing level of human-generated disturbance (Hughes et al., 2003, Pandolfi et al., 2003). In this context, the Great Barrier Reef is considered to be one of the healthiest and best managed reefs in the world (Pandolfi et al., 2003, Wilkinson, 2008).

However, the Great Barrier Reef has a long history of fishing (Jackson et al., 2001) and has experienced several outbreaks of Crown-of-thorn starfish (Hart and Klumpp, 1996). Furthermore, not only does it receive high levels of freshwater input, which deliver sediment and nutrient enriched waters to the inshore reefs (Done et al., 2007, De'ath and Fabricius, 2010), but it is also exposed to increasing natural disturbances like cyclones (Fabricius et al., 2008) and coral bleaching, as a result of climate change (Hughes et al., 2007b). The combined effects, however, are difficult to interpret. Considering the wide range of both natural and human induced impacts, the Great Barrier Reef may not be as healthy as once considered.

On the contrary, Ningaloo Reef has experienced limited fishing activity. One of the few documented cases of a commercial fin-fishery is for reef associated lethrinids from 1987 to 1992 (Moran et al., 1993). The fishery is regulated within the marine park and no commercial fin-fishing activities are currently allowed within the sanctuary zones. The remoteness of Ningaloo Reef, result in minimal exposure to anthropogenic disturbances, such as terrestrial run-off, fishing and pollution compared reef systems such as the Great Barrier Reef (Roberts et al., 2002). Ningaloo Reef therefore offers a unique opportunity to study the characteristics of a low impact reef system to understand the structure of various ecosystem processes and the benthic community. This system may thus reveal the nature of healthy fish, urchin and benthic populations across habitats and along the coast. The aim of the present study was to provide a preliminary quantitative evaluation of the structural and functional characteristics of Ningaloo Reef’s benthic and herbivorous fish communities, including two potential indicators of coral reef decline: macroalgae and sea urchins.

2.2 Materials and Methods

Study sites

Surveys were conducted in the central and northern parts of Ningaloo Reef Marine Park in April 2009. Ningaloo Reef is a narrow fringing reef system that stretches approximately 280 km along the central Western Australian coast between latitudes 21° 47’ and 24°S (Fig. 1.1). The shallow section of the slope, crest and flat are exposed to high wave energy, while the back reef and the lagoon are relatively protected. The slope falls gently from the crest to the continental shelf and has relatively low structural complexity near the reef edge (Collins et al., 2003). The back reef is relatively shallow, either patchy on sandy substrata or continuous, and receives a regular influx of oceanic waters coming over the crest and through passages into the lagoon. The lagoon stretches from the shore to the back reef and measures 0.5 to 6 km in width. It is predominantly sandy with patches of coral and/or macroalgal stands (Collins et al., 2003).

Five sites were selected along the northern and central part of Ningaloo Reef. Each site was located inside or on the border of three no-fishing sanctuary zones: site 1 (Jurabi Sanctuary (21° 51’S, 113° 59’E)), site 6 (Maud Sanctuary (23° 08’S, 113° 45’E)) and sites 8 - 10 (Pelican Sanctuary (23° 20’S, 113° 46’E)) (Fig. 1.1). For each site, three habitats were selected to quantify benthic cover and herbivore abundances. Wave activity reduced the accessibility to the reef crest and flat, and censuses were consequently restricted to the slope, back reef and lagoon. All dives were made during daylight hours between 09:00 and 16:00 h. All surveys on the slope were conducted between 6 and 10 m, on the back reef between 2 and 8 m, and in the lagoon between 3 and 5 m.

Benthic surveys

At each of the five sites, benthic cover was surveyed in each habitat using fifteen 10 m transects. Transects were only deployed on hard benthic habitat, i.e. not on open sand. The benthic transects were separated by 10 m and deployed parallel to the coast. Each transect was treated as a replicate giving a total of 15 replicates per habitat per site. The benthic substratum at points immediately under each 1 m interval and at 1 m to each side were recorded giving a total of 33 points per transect (the 33 points were used to estimate proportional cover for each replicate transect). The substrata were classified to the lowest level possible and then grouped into the following substratum categories: live coral, dead coral (recently dead coral, sand/rubble, epilithic algal matrix (EAM), pavement/matrix (P/M), macroalgae (> 15 mm), crustose coralline algae (CCA) and others.

Herbivore censuses

Prior to the benthic surveys, five 5 × 50 m transects were used to quantify fish abundance and biomass in each habitat at each of the five sites. The length of transects was measured by a second diver who followed close behind the fish observer to avoid negative impacts on fishes as a result of diver presence (Fulton et al., 2001). Each transect was separated by at least 10 m. Care was taken throughout the survey to account for the diver effect (Dickens et al., 2011) and not to count fish that were 'pushed along' transects or fish re-entering the field of observation. Prior to the survey the observer practiced underwater size estimations using fish silhouettes. Four main roving herbivore groups were surveyed: Acanthuridae, Kyphosidae, Siganidae and parrotfishes (Labridae). The total length (TL) of each individual was recorded in 5 cm size classes and only included individuals > 10 cm TL. Abundance estimates were later converted into biomass using published length–weight regressions supplemented by direct measurements (Table S1 in Appendix A). Prior to retrieval of the transect tapes, sea urchins were surveyed using the same five 50 m transects. Each urchin transect was 2 m wide and all crevices and overhangs were carefully examined, recording all individuals found to species level (where possible).

Functional roles

To quantify the extent of various ecological processes on Ningaloo Reef, fish were grouped depending on their feeding mode (Table S2 in Appendix A) into the following four functional groups: grazers/detritivores (herein called grazers), browsers, scrapers and excavators, following Green & Bellwood (2009). The physical impact on the substrata was estimated for two of these groups, bioeroding excavators (product of annual bite rate × bite volume × carbonate density × fish density) and scraping grazers (product of annual bite rate × bite area × fish density × proportion of bites on turf substratum), following Hoey & Bellwood (2008). Bite rates, bite volume and carbonate density were taken from the literature (Bellwood, 1995, Fox and Bellwood, 2007). Only individuals > 15 cm TL were included, at which size most species exhibit adult functional capabilities (Bonaldo and Bellwood, 2008, Lokrantz et al., 2008). The impact of excavating sea urchins on the substrata was also considered and their erosion estimated. Daily carbonate and algal removal rates for *Echinometra mathaei* and *Diadema* sp. were taken from the literature (Carreiro-Silva and McClanahan, 2001). Removal rates for *Diadema* sp. were based on average daily removal rates from *D. setosum* and *D. savignyi*. All values were estimated per transect to permit comparison among sites and habitats.

Data analysis

The relative cover of benthic substrata across the three habitats was examined as univariate data for the three major components (coral, macroalgae and CCA). The data met the requirements for normality and no transformation was needed. Differences in total community composition were also examined with a principle component analysis (PCA). A cluster analysis provided an objective delineation of the site groupings. These analyses were based on squared Euclidian distances of non-transformed data using Ward's cluster analysis. Significant variation among the clusters was evaluated using an analysis of similarity (ANOSIM).

A series of two-way ANOVA's were used to examine potential patterns in benthic cover, fish and echinoid abundance, fish biomass and scraping and bioerosion rates by fishes and sea urchins across the shelf. Data were 4th root transformed for benthic cover, abundance and biomass and 5th root transformed for bioerosion and scraping to improve normality and homoscedasticity. Tukey's post hoc tests were used to identify significant differences between habitats and sites. No biomass was calculated for echinoids.

Potential relationships between percent macroalgal cover and total herbivore biomass, and macroalgal cover and the biomass of each functional group, were examined individually using Pearson's correlations. Data were $\log_{10}$ transformed for total herbivore biomass to improve linearity. The biomass for separate analysis of grazers, browsers, scrapers and excavators needed no transformation. All statistical analyses were performed using Statistica 8.0 and Primer 5.0.

2.3 Results

Benthic community distribution across the shelf

There was a clear cross-habitat gradient in the benthic community composition, with three distinct habitats: slope, back reef and lagoon. The ANOSIM identified the three significantly different habitats (global $r = 0.941$, $p = 0.001$) based on their benthic community composition, as indicated by the PCA (Fig. S1 in Appendix A) and found a significant difference between the slope and lagoon ($r = 1.000$, $p = 0.008$), the back reef and lagoon ($r = 0.928$, $p = 0.008$) and the back reef and slope ($r = 0.896$, $p = 0.008$). Ningaloo Reef exhibited numerous locations dominated by macroalgae (i.e. with macroalgae being the most abundant benthic group). These areas were restricted primarily to the lagoon where macroalgae (*Sargassum*) comprised about 42 % total cover and were significantly different from the macroalgal cover found on the slope and back reef ($F_{2,15} = 37.185$, $p = < 0.001$; Fig. 2.1a, 2.3,Table S3 in Appendix A). Macroalgae were also recorded from the back reef, but to a much lesser extent (approximately 10 % cover). Live coral was the main benthic component on the back reef (38 %) and displayed a significantly higher cover on the back reef when compared to the lagoon and slope ($F_{2,15} = 25.352$, $p < 0.001$). The slope, in general, had low complexity with 18 % of the reef matrix covered by CCA; this was significantly more than in the other two habitats ($F_{2,15} = 7.802$, $p = 0.013$; Fig. 2.1b, c, Table S3 in Appendix A). No variation between sites was detected for any of the three main benthic components tested. Details of the ANOVA results and Tukey's HSD post hoc tests are given in the supplement (Tables S4a and S5a in Appendix A).

Variation in functional group distribution

The distribution of herbivorous or detritivorous functional groups reflected the changes in benthic community structure. The abundance of herbivores on the slope was dominated by sea urchins (representing 97 % of individuals), while fish were the numerically dominant herbivore on the back reef (69 % of individuals) and in the lagoon (99 % of individuals; Fig. 2.2a, b). A significant increase in total fish biomass was recorded from the lagoon to the slope ranging from 18 to 39 kg 100 m^{-2}, respectively ($F_{2,15} = 6.984$, $p = 0.018$; Fig. 2.2c; Tables S4b and S5b, c in Appendix A).

Sea urchins displayed a marked variation in abundance across the shelf. The slope had the highest abundance of sea urchins with more than 12 individuals per m^2. The total abundance of sea urchins was significantly different among habitats ($F_{2,15} = 74.139$, $p = <0.001$), with both the common sea urchin *E. mathaei* and *Diadema* sp. displaying highest numbers on the slope (Fig. 2.2a, 2.3).

The abundance of grazers also differed significantly among habitats ($F_{2,15} = 4.773$, $p = 0.043$), with the slope and back reef having a higher abundance than the lagoon. A similar pattern was seen for biomass ($F_{2,15} = 4.566$, $p = 0.048$), although the highest biomass was recorded on the slope (Fig. 2.2b, c). This pattern was explained by the presence of large grazing species (*Acanthurus dussumieri*, *A. nigricauda* and *A. olivaceus*) on the slope and high abundances of smaller species on the back reef (*A. triostegus*; Table S2 in Appendix A).

Significant variation in scraper numbers was also recorded across the Ningaloo Reef shelf ($F_{2,15} = 20.938$, $p < 0.001$). The highest abundance was found on the back reef and the lowest in the lagoon (Fig. 2.2b). Scraper biomass was also different among habitats ($F_{2,15} = 21.499$, $p = <0.001$), although the highest biomass was on the slope (Fig. 2.2c). This was a result of the presence of larger scraping species (*Scarus prasiognathus* and *S. rubroviolaceus*) on the slope and high abundances of smaller species on the back reef (*S. frenatus* and *S. schlegeli*; Table S2 in Appendix A).

For excavators, both the abundance ($F_{2,15} = 5.427$, $p = 0.034$) and biomass ($F_{2,15} = 5.371$, $p = 0.033$) was highest on the back reef (Fig. 2.2b, c; Table S4 in Appendix A). In contrast to all other groups, no significant differences were found in the abundance of browsers across the shelf ($F_{2,15} = 0.773$, $p = 0.493$), likewise for browser biomass ($F_{2,15} = 0.714$, $p = 0.519$; Fig. 2.2b, c). Details of all ANOVA results and Tukey's HSD post hoc tests for abundance and biomass are given in the supplement (Tables S4b and S5b, c in Appendix A).

Although a negative correlation between the biomass of scrapers and percent macroalgal cover was found ($r = -0.749$, $n = 15$, $p = 0.001$), we detected no correlation between the biomass of browsers and macroalgal cover ($r = 0.194$, $n = 15$, $p = 0.489$), excavators and macroalgal cover ($r = -0.323$, $n = 15$, $p = 0.240$), grazers and macroalgal cover ($r = -0.457$, $n = 15$, $p = 0.086$) or total herbivorous fish biomass and macroalgal cover ($r = -0.360$, $n = 15$, $p = 0.188$).

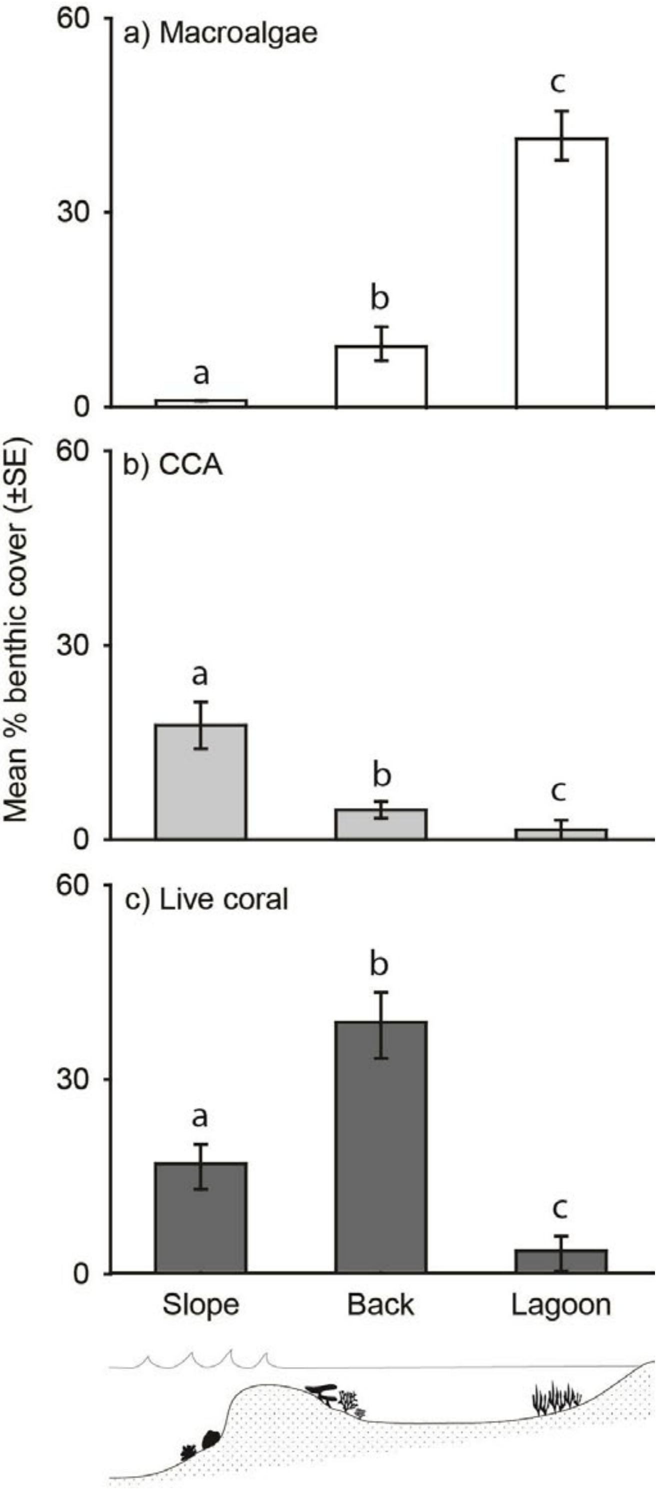

Fig. 2.1 Mean benthic cover (%) across 3 habitats on Ningaloo Reef for 3 benthic groups: a) macroalgae, b) CCA and c) live coral. SE is based on the 5 sites within each zone. Letters represent homogeneous groups identified by Tukey's HSD tests.

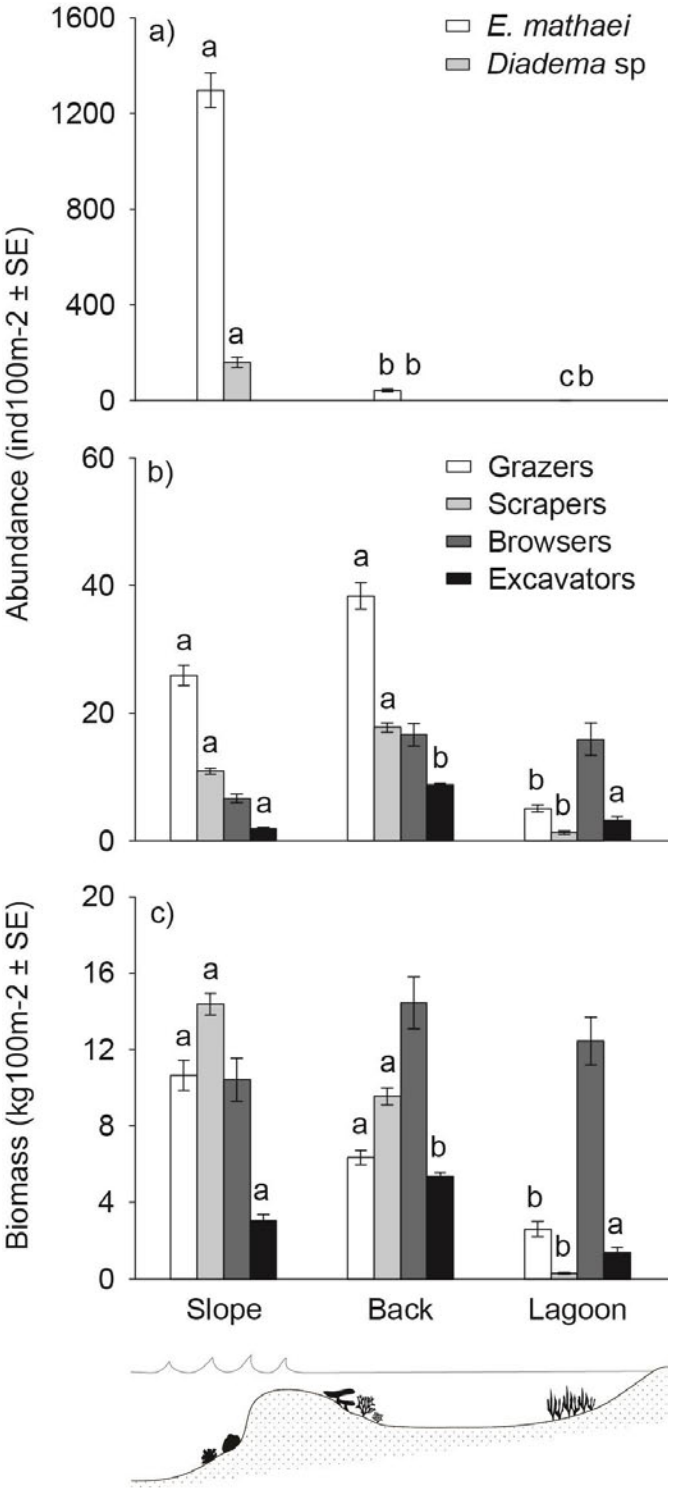

Fig. 2.2 Variation across 3 habitats on Ningaloo Reef for: a) mean abundance of sea urchin, b) mean abundance and c) mean biomass of 4 fish herbivorous functional groups. SE is based on the 5 sites within each zone. The functional groups are comprised of species in the families Acanthuridae, Kyphosidae, Labridae (scarids) and Siganidae. Letters represent homogeneous groups identified by Tukey's HSD tests.

Ecosystem processes among habitats

Rates for scraping on Ningaloo Reef reflect the patterns seen in abundance and biomass ($F_{2,15}$ = 22.919, p = < 0.001; Fig. 2.4a-c; Table S6 in Appendix A). On average, based on estimated scraping rates, scraping species would scrape each square meter of the back reef of Ningaloo Reef 40 times per year (every 8 d), compared to 30 times per year (every 11 d) on the slope and only twice per year (every 180 d) in the lagoon (Fig. 2.4a). The scraping rates estimated for the lagoon were significantly less than for the back reef and the slope, which were not found to differ (Fig. 2.4a; Table S5d in Appendix A). Annual erosion rates on Ningaloo Reef by excavating fishes were not found to be significantly different ($F_{2,15}$ = 3.474, p = 0.082), although *Chlorurus microrhinos* was the main species responsible for the erosion on the slope and in the lagoon (38 and 91 %, respectively), while *C. sordidus* was responsible for 85 % of the total erosion on the back reef (Fig. 2.4b). The impact from sea urchins also differed significantly between habitats ($F_{2,15}$ = 112.716, p < 001), and was over 90 % higher on the slope compared to the back reef and lagoon (Fig. 2.4c). The high abundance of *E. mathaei* resulted in markedly higher erosion rates when compared to *Diadema* sp. Details of all ANOVA results and Tukey's HSD post hoc tests are given in the supplement (Tables S4c and S5d in Appendix A).

2.4 Discussion

Distinct cross-shelf patterns in both benthic community structure and ecosystem function were found in the study areas of Ningaloo Reef. The three habitats; slope, back reef and lagoon, were clearly distinct; a pattern that was present at all sites surveyed. There were two particularly interesting results for this relatively undisturbed reef ecosystem that warrant further discussion: 1) the presence of widespread macroalgal stands in the lagoon and 2) the high abundance of sea urchins on the slope. The large stands of macroalgae were only found in the lagoon (Fig. 2.1a), mainly on sand-covered reef pavement and but also on a few more complex reef structures. In contrast, urchins were by far the most abundant herbivores on the slope, with numbers reaching more than 12 individuals per m^2 (Fig. 2.2a). Sea urchins were present in extremely low numbers on the back reef and in the lagoon. These areas were instead dominated by fishes which were responsible for high scraping rates, especially on the back reef (Fig. 2.4a).

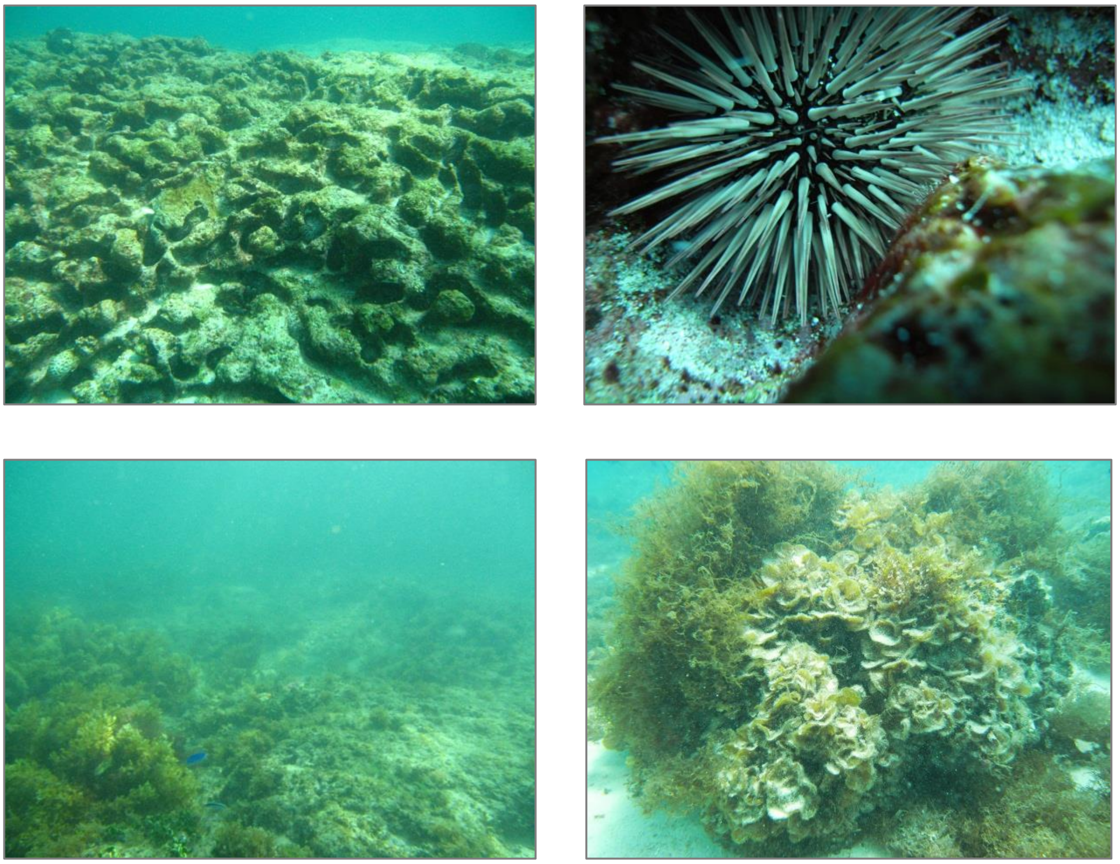

Fig. 2.3 Clockwise from top left: sea urchin burrows on the reef slope, the common sea urchin *Echinometra mathaei* in a burrow, extensive macroalgal beds in the reef lagoon, algae cover coral bommie in the lagoon.

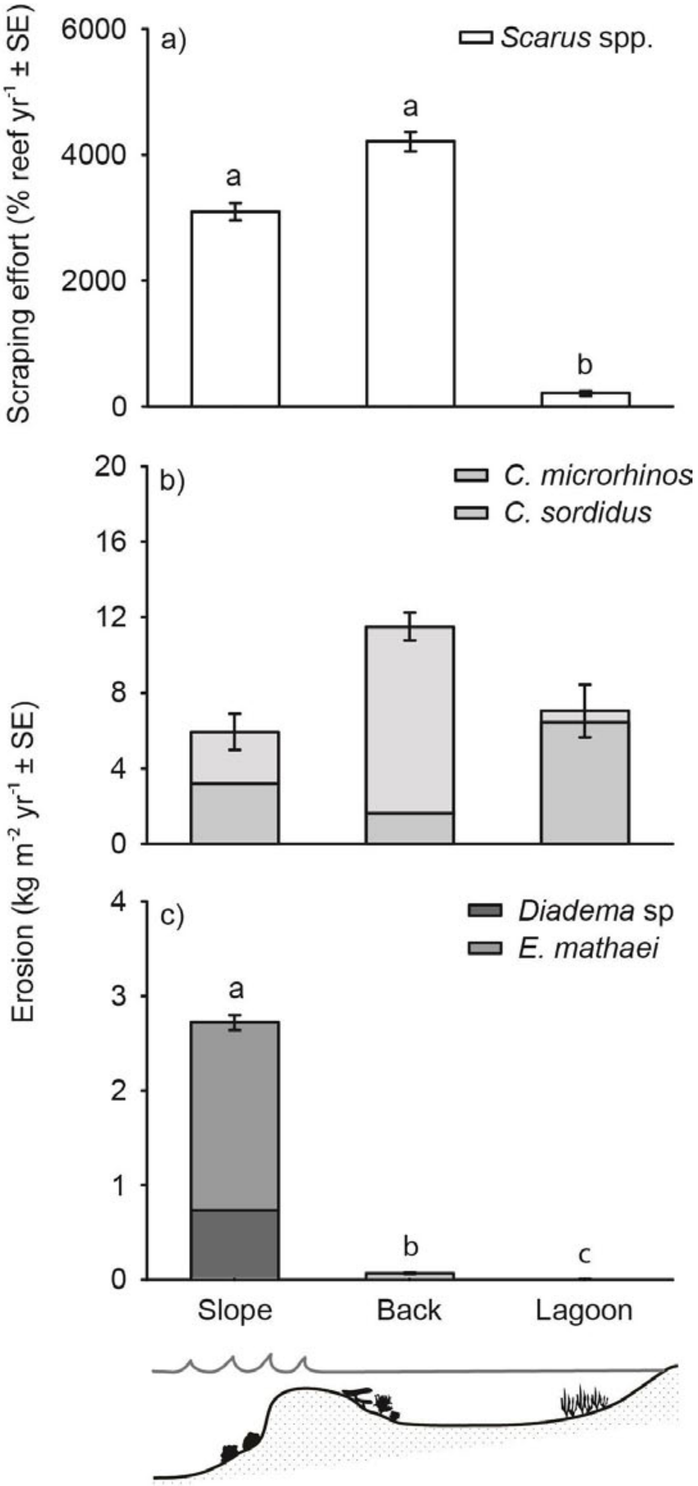

Fig. 2.4 Yearly physical impact across the shelf of Ningaloo Reef from: a) fish scraping, b) fish erosion and c) sea urchins erosion. Scraping effort estimates the area of reef scraped, expressed as the mean number of times a square meter of reef would be scraped per year (SE, n = 5). Letters represent homogeneous groups identified by Tukey's HSD tests.

Macroalgae

Currently, there are two views dominating the question of what is driving the biomass of macroalgae in coral reef ecosystems. The prevailing view is that variation in rates of herbivory is the primary determinant of macroalgal cover (McCook, 1996, Jompa and McCook, 2002, Bellwood et al., 2006b, Burkepile and Hay, 2006, Sotka and Hay, 2009). However, terrestrial run-off and nutrients are also believed to be significant factors shaping the distribution of macroalgal biomass (De'ath and Fabricius, 2010). In both cases, increases in macroalgal cover are often associated with degraded ecosystems as a result of anthropogenic disturbances, especially overfishing and eutrophication (Mumby et al., 2006, Burkepile and Hay, 2009, De'ath and Fabricius, 2010).

For ecosystems with low levels of anthropogenic disturbances, factors such as overfishing and eutrophication are less likely to be important. Natural variation in the resident herbivore populations is likely to be the primary factor shaping algal distributions. This appears to be the case for Ningaloo Reef. Due to the low levels of terrestrial input, the small resident human population and the isolation of Ningaloo Reef, terrestrially derived nutrients may be discounted as a significant factor enhancing fleshy macroalgal cover. However, the low abundance of herbivores in the lagoon probably allows for unimpeded growth and spread of macroalgae within the lagoon. This situation appears to be the natural status of this reef ecosystem. In this example, low herbivory within the lagoon is probably a natural phenomenon; a result of the lack of hard 3-dimensional reefal structures within the lagoon (McCook, 1997, Williams et al., 2001, Fox and Bellwood, 2007). The lagoon, therefore, provides adequate hard substratum for macroalgal growth, but insufficient 3-dimensional structure to support herbivore populations capable of limiting macroalgal development.

The abundant populations of herbivores on the back reef, as well as the negative correlation between scraper biomass and macroalgal cover, suggests that the herbivory on the back reefs of Ningaloo Reef is sufficient to suppress macroalgal growth in this zone. This highlights the potential importance of complex habitats on Ningaloo Reef for supporting herbivorous fish populations.

Sea urchins

High abundances of sea urchins (particularly *E. mathaei*) were found on the slope of Ningaloo Reef. Similar densities (> 12 individuals per m^2) have previously been recorded in what are considered to be degraded reef ecosystems, especially in sheltered habitats (Bak, 1990, Carreiro-Silva and McClanahan, 2001). The presence of *E. mathaei* on wave-washed dynamic reefs has been reported from rocky or temperate environments (Glynn et al., 1979, Vanderklift et al., 2009) and occasionally from shallow, wave-exposed tropical coral reefs (Russo, 1980). It is noteworthy that urchins on Ningaloo Reef are found in numbers that previously have been recorded primarily from degraded coral reefs. Furthermore, it is unusual to find them in such densities on the slope, the most exposed of the studied habitats. For Ningaloo Reef, two aspects are worth discussing: 1) predation pressure and 2) burrowing behaviour.

Echinometra mathaei is known for its ability to create burrows from feeding and spine abrasion that incorporate and protect the entire urchin from predation (McClanahan, 1988). Although abundances of urchin predators were not counted in the present study, this may be a significant factor controlling the distribution of sea urchins on Ningaloo Reef. Triggerfish (Balistidae) have been identified as the main urchin predator on coral reefs, but sparids, labrids, haemulids and lethrinids have all been shown to feed on sea urchins (McClanahan, 1995). However, given that fishing pressure on Ningaloo Reef is relatively low compared to other reefs and that all censuses were inside or on the border of sanctuary zones, it appears unlikely that the high densities of sea urchins are a result of overfishing of fish predators.

As *E. mathaei* creates its own protective burrows, it may be selectively advantaged in areas of low structural complexity. In these highly exposed and wave-swept environments it is essential for the sea urchins to stay within the crevices to avoid being dislodged. Ogden & Lobel (1978) and Vanderklift and colleagues (2009) have shown that under these conditions, sea urchins adopt a 'sit-and-wait' behaviour known as drift-feeding, where individuals feed primarily on food that accumulates in their burrows, only leaving their burrows for very short feeding events within their immediate neighbourhood. Given the high wave activity on Ningaloo Reef, the slope may provide a more energy-efficient environment where food availability in relation to energy loss is maximized.

The high numbers of sea urchins on the slope is most likely a combination of the above, where low predation pressure and high water movement on a carbonate reef base provide suitable territory for the maintenance of high sea urchin densities. The high abundance of sea urchins on the slope appears not to be an outbreak as a result of direct anthropogenic disturbance, but may well be an ecological and biological component adapted to this high-wave energy environment. Nevertheless, the importance of the impact from sea urchins clearly needs further investigation to fully comprehend their role on Ningaloo Reef.

Functional evaluations

Coral reefs around the world have shown that unsustainable human impacts and inadequate management can reduce the capacity of coral reefs to cope with various anthropogenic and natural disturbances, forcing them into alternative states (Jackson et al., 2001, Pandolfi et al., 2003, Bellwood et al., 2004, Norström et al., 2009). High macroalgal cover and high sea urchins densities have both previously been presented as indicators of degraded marine environments (Hughes, 1994, McClanahan and Mutere, 1994, Mumby et al., 2006). However, the present study suggests that in some locations, high macroalgae and sea urchins densities may represent a natural condition, and that they can act as important ecosystem components in less-impacted coral reef ecosystems. The highly abundant *E. mathaei* contributed to one-third of total erosion on the slopes of Ningaloo Reef. The rarity or absence of large excavating parrotfish species in this survey (e.g. *C. microrhinos* and the outer Great Barrier Reef excavator *Bolbometopon muricatum* respectively; Hoey & Bellwood 2008) makes urchin erosion a significant process on Ningaloo Reef.

Ningaloo Reef is unusual in three ways: 1) it supports the largest coral reef on the west coast of any continent; 2) the influence from the warm, south flowing Leeuwin Current is essential for its coral reef growth; and 3) Ningaloo Reef is relatively unaffected by human development and suffers little input from terrestrial run-off. These characteristics strongly suggest that this reef ecosystem is unusual. Additionally, the presence of vast macroalgal beds along the coast, and the importance of sea urchins for bioerosion on the slope, reflect the atypical functional configuration of this ecosystem. The findings of the present study have revealed another alternative state for a coral reef ecosystem, where macroalgae and sea urchins play important roles in ecological processes and where they are not necessarily bio-indicators of reef degradation. Although Ningaloo Reef is the only known fringing reef system of its size on the west coast of a continent in the world, it offers valuable insight into the potential diversity of ecosystem processes within and among coral reef systems.

Macroalgae and sea urchins do not appear to be bio-indicators of coral reef decline on Ningaloo Reef. Indeed, they may be important players in various ecosystem processes. While an increase in macroalgal cover or urchin densities can indicate ecosystem shifts and a move to a more degraded state, high abundances of the two taxa per se may not necessarily be indicators of human disturbance. While they may be characteristic features of degraded states they do not define this condition. It is the change in densities, not the densities per se that are important. Given the unusual functional structure of Ningaloo Reef, its proximity to shore and potential for human impact, Ningaloo Reef may be vulnerable. The inevitable increase in human impacts on this reef ecosystem will require careful management if we are to avoid jeopardizing the health of Ningaloo Reef.

2.5 Conclusion

The present study has highlighted the unusual benthic and functional composition of Ningaloo Reef. The results revealed unexpectedly high densities of sea urchins and macroalgae, two common bio-indicators of coral reef decline. Yet Ningaloo Reef is one of the least human-impacted large coral reef ecosystems in the world. At first glance (using traditional metrics for reef degradation) it appears that Ningaloo Reef is showing signs of decline. However, the high abundance of macroalgae in the lagoon and sea urchins on the slope may well be a natural feature of this ecosystem rather than another example of human induced decline. Nevertheless, Ningaloo Reef does face increasing pressure from human development and its unusual functional characteristics may make it particularly vulnerable. Careful management will be vital if we wish to maintain a resilient coral reef ecosystem in the face of increasing human activity.

Chapter 3: Top-down versus bottom-up control of the sea urchin *Echinometra mathaei* (de Blainville) in an intact reef system, Ningaloo Reef, Western Australia

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3.1 Introduction

Sea urchins are important consumers of benthic algae on coral reefs (Bak, 1990, Hart and Chia, 1990, McClanahan et al., 1996, Mills et al., 2000, Peyrot-Clausade et al., 2000), and mediate competition for space between corals and algae (Edmunds and Carpenter, 2001). In addition to their role as herbivores, sea urchins contribute to the bioerosion of reef substratum (Bak, 1994, Downing and El-Zahar, 1987) and the production and reworking of sediments (McClanahan and Muthiga, 2001). Despite playing an important role on coral reefs uncontrolled population growth of urchins (i.e., outbreaks) can severely reduce reef topography as rates of bioerosion exceed rates of reef accretion (Glynn et al., 1979, Uthicke et al., 2009). While at relatively low (or natural) densities sea urchins are viewed as key players in structuring coral reefs and their ecological function vital, at high densities sea urchins are a potentially destructive ecosystem component (Done et al., 1991, Eakin, 1996).

Sea urchin populations often respond strongly to variation in the densities of predatory fishes, suggesting that they are primarily structured by top-down control (e.g., Carreiro-Silva and McClanahan, 2001). Indeed, high densities of sea urchins in many regions have been related to overharvesting of predatory fishes (Hay, 1984, Hughes, 1994, McClanahan and Shafir, 1990), particularly those groups that are known to consume urchins, such as the Balistidae (McClanahan, 1995, McClanahan and Shafir, 1990, Young and Bellwood, 2012). The removal of potential urchin predators through fishing activities releases urchin populations from top-down control and may ultimately result in 'outbreaks' of urchin populations (Carreiro-

Silva and McClanahan, 2001). In turn, these marked increases in urchin densities may lead to overgrazing and/or destructive bioerosion of the reef substratum (Carreiro-Silva and McClanahan, 2001, Hay, 1984, McClanahan and Muthiga, 1988, Sala et al., 1998). While it is widely accepted that the removal of predatory fishes can lead to marked increases in urchin densities, the role of predators in structuring urchin populations in relatively intact reef systems is poorly understood.

Although top-down control is widely viewed as a major driver of sea urchin populations, it may not be the sole regulator of sea urchin communities. Marked variation in the densities of sea urchins across global, regional and local scales (Dumas et al., 2007, Glynn et al., 1979, Johansson et al., 2010, Kelso, 1970, McClanahan, 1988, Pearse and Phillips, 1968), and among reefs with various levels of exploitation (e.g., Hay 1984; McClanahan and Shafir, 1990), indicate that human-induced variation is set against a background of natural variation. This natural variation in population abundance across both global and local scales may arise from a range of processes, including variation in settlement and recruitment patterns (Watts et al., 1990), water flow and wave action (Ogden et al., 1989, Russo, 1977), burrow defence (Neill, 1988), position across the continental shelf (Khamala, 1971) and latitude (Watts et al., 1990). Furthermore, outbreaks of another echinoderm, the Crown-of-thorns starfish *Acanthaster planci*, have been hypothesised to be related to increased nutrients associated with flood events (Brodie et al., 2005). The relative importance of these factors in structuring urchin populations on coral reefs is yet to be established. While reductions in predation appears to be responsible for sudden shifts in abundances of urchins (McClanahan, 1994; Uthicke et al., 2009; for exception see Valentine and Edgar, 2010), the potential influence of bottom-up factors in shaping spatial patterns should not be overlooked.

To date, the majority of studies examining the role of predation in structuring sea urchin populations have been conducted on heavily impacted, or degraded reefs (e.g., Bak, 1990; McClanahan, 1994; McClanahan and Kurtis, 1991; Ogden et al., 1989) . Few studies have investigated the factors shaping urchin populations within intact reef systems. Recent research on a reef with relatively intact predator assemblages (Ningaloo Reef, East Indian Ocean) reported marked variation in the abundance of the sea urchin *Echinometra mathaei* among habitats, with *E. mathaei* being ten times more abundant on the wave-washed reef slopes than within the sheltered back reef habitat (Johansson et al., 2010). The presence of such among-habitat variability in a relatively intact reef system raises the question of the potential role of top-down and bottom-up processes in shaping these populations. The objective of the present study therefore, is to examine the relationship between the distribution of *E. mathaei* and its potential predators in a relatively intact reef system (i.e., with low levels of anthropogenic impact). We use both direct and indirect measures to test the hypothesis that reduced predation on adult urchins, as a result of low predatory fish abundances, is important in underpinning high urchin numbers on Ningaloo Reef. Specifically, our aims were to 1) identify potential predators of *E. mathaei* on Ningaloo Reef using a non-intrusive tethering experiment, 2) quantify the spatial variation in the abundance of potential predatory fish and *E. mathaei*, and 3) examine the relationship between the densities of *E. mathaei* and their potential predators.

3.2 Materials and Methods

The study was conducted in Ningaloo Reef Marine Park, Western Australia, in February 2010 and February 2011. Ningaloo Reef Marine Park covers approximately 290 km of fringing reef off the central western Australian coast (Fig. 1.1). This study consisted of two components. Firstly, a non-intrusive tethering experiment using stationary underwater video cameras was conducted to identify predators of *E. mathaei* on Ningaloo Reef (undertaken at sites 2 and 9; see Fig. 1.1). Secondly, we related the abundance of *E. mathaei* to that of its potential predators both along and across the reef (surveys at site 2-5, 7-10). Specifically, we censused the densities of *E. mathaei* and predatory fishes at seven sites spanning approximately

120 km of Ningaloo Reef, and three benthic habitats across the reef; the exposed reef slope (6-10 m), protected back reef (2-8 m) and macroalgal dominated lagoon (3-5 m).

Predation experiment

To identify the predators on adult *E. mathaei* on Ningaloo Reef, a tethering experiment was performed on the back reef, in two sectors of the park: the northern reefs in Mandu Sanctuary and the central reefs of Pelican Sanctuary (Fig. 1.1, sites 2 and 9). The strong hydrodynamic characteristics of the reef slope precluded this experiment from being replicated within that habitat. *E. mathaei* of typical adult size (maximum test diameter excluding spines: 3.30 - 6.35 cm) were collected from their burrows on the back reef or inner reef flat. The urchins were tethered (non-destructively) using fishing line (0.2 mm diameter) horizontally wrapped twice around the test and tied with a slipknot. Each *E. mathaei* was then attached to a dive weight, with 30 cm of fishing line to allow for some movement, and placed on the sandy bottom close to the reef edge (Fig. 3.1). Exposing *E. mathaei* on sand was selected as a method to prevent urchins from seeking shelter in the reef substratum and the close proximity of the tether to the reef to allow reef fish to safely approach the tether and attempt predation. To identify diurnal predators, the tethered urchins were filmed with stationary underwater video cameras during daylight hours (08:00-18:00 h). The cameras were always facing the reef and positioned approximately 2 m from the tethered sea urchin. Tethered urchins were separated by a minimum of 10 m and were not visible from other tethered replicates to avoid influence from activity at a neighbouring camera. Each camera recorded continuously for approximately 3 h. A total of 23 *E. mathaei* were filmed; six in the northern sector and 17 in the central sector. In order to identify nocturnal predators, six additional replicates were deployed in the northern sector at sunset (19:00 h). Cameras were set to night mode and two underwater LED torches were used to film the tethered sea urchin. The torches were equipped with a red filter (Lee^{TM} "Bright Red 026") to transmit red light in the wavelengths above the sensitivity of most marine fishes at night (Cappo et al., 2004, Michiels et al., 2008). No urchins escaped their tether during the experiment.

Fig. 3.1 Sea urchin predation on Ningaloo Reef. From top to bottom: tethered *Echinometra mathaei* in front of video camera, *Choerodon rubescens* predating on a tethered sea urchin, *Lethrinus atkinsoni* attempting predation on a tethered *Echinometra mathaei*.

The densities of potential sea urchin predators were quantified within the two sites used for the tethering experiment using 50 m belt-transects (n = 16 transects per site). All potential urchin predators greater than 10 cm total length (TL), were recorded within a 5 m wide belt. To reduce observer effects, fish were counted as the tape was deployed (Dickens et al., 2011). Fish were considered to be potential predators if they were identified during the tethering experiment or identified in previous studies as potential predators of fish predation of *E. mathaei* in Eastern Africa and the Great Barrier Reef (Table S7 in Appendix A). Closely related species within the same families were also considered to be potential predators.

Predator and sea urchin population structure

To quantify the abundance of *E. mathaei* and their potential predators within Ningaloo Reef, a series of visual surveys were conducted. Three habitats were surveyed along the west coast of Ningaloo Reef; the reef slope, back reef and macroalgal-dominated lagoon (see Johansson et al., 2010 for detailed habitat description). Seven sites spanning approximately 120 km of the reef were surveyed within each habitat (Fig. 1.1, sites 2-5, 7-8 and 10). At each site, five 50 m transects were deployed in each of the three habitats. All transects were parallel to the coastline. Along each transect all potential urchin predators were recorded in a 5 m wide strip as the tape was deployed. Individuals of *E. mathaei* were then recorded along the same transects as the predatory fishes. Each transect was systematically searched with all urchins identified and quantified within a 2 m wide belt. Overhangs and crevices were carefully inspected for concealed urchins. Fish were classified into 5 cm size categories (10-15, 15-20, etc.) and later converted to biomass using published length-weight relationships, with fish length taken as the mid-point of the respective size classes (following Hoey and Bellwood 2009).

Data analysis

To determine if densities and biomass of sea urchin predators varied among habitats or sites a series of nested analysis of variance (ANOVA) were performed with site nested within habitat. A separate analysis was performed for each family. Similarly, a nested ANOVA was used to determine if the density of *E. mathaei* varied among habitats or sites. Tukey's HSD post hoc tests were used to identify which means contributed to any significant differences detected. The analyses were based on the abundance or biomass per transect (n = 105). Density and biomass data were fourth root transformed to meet the assumptions of normality and homogeneity of variances.

Relationships between the densities of *E. mathaei* and their potential predators were examined using a series of Pearson's Product Moment correlations. The correlations were based on the mean densities of sea urchins and the mean densities or biomass of predators (by families) based on the five 50 m transects at each site (n = 7). Only the slopes and back reefs were examined as *E. mathaei* and predatory fishes were rare within the lagoonal habitat (i.e., no urchins and/or predators were recorded at five of the seven lagoon sites). Tetradontids were excluded from the analysis due to low numbers. The densities of *E. mathaei* and predators were square-root transformed on the slope and log transformed on the back reef.

3.3 Results

Predation experiment

The diurnal tethering experiment revealed a high instance of predation on tethered *E. mathaei*, with 20 of the 23 urchins being successfully predated. The observed predators belonged to seven fish species and five families: *Pseudobalistes fuscus* (Balistidae), *Cheilinus trilobatus*, *Choerodon rubescens* and *Coris aygula* (Labridae), *Lethrinus atkinsoni* (Lethrinidae), *Diodon hystrix* (Diodontidae) and *Arothron stellatus* (Tetradontidae). The most frequent predator on the tethered urchins was *C. aygula* accounting for 35 % (7/20) of the successful feeding events, followed by the endemic *C. rubescens* which accounted for a further 30 % (6/20) of the successful predation events (Fig. 3.1). In contrast, three species had just one successful predation event each; *C. trilobatus*, *P. fuscus* and *A. stellatus* (Fig. 3.2). On a couple of occasions small *L. nebulosus* and *L. atkinsoni* attempted predation on *E. mathaei* but were either unable to break the test of the urchin or were chased away by larger, and seemingly more dominant, predators (such as *C. aygula* and *C. trilobatus* during its one predation event). Interestingly the number of observed predation events did not appear to reflect the relative abundances of each of the predators at the study sites. For example, *L. atkinsoni* was the most abundant of the seven predatory species during the visual censuses (1.00 individuals 100 m^{-2}) but only accounted for 10 % of all predation (Fig. 3.2). Conversely, *C. rubescens* was relatively rare (0.04 individuals 100 m^{-2}) yet accounted for 30 % of all observed predation events. Of the potential predators recorded at each site the Labridae were the most abundant family (see Table S7 and Fig. S2 in Appendix A). No predation was recorded on the six nocturnal replicates.

All predators appeared to prey on tethered *E. mathaei* in a similar manner. Each predation event was initiated when the predator located and approached the urchin (some direct and others more cautiously). The fish then grabbed the urchin with their mouth and crushed the test before consuming it. Typically only a single predator was present during a successful predation attempt. The only exception was (on two occasions) when *C. aygula* and *C. rubescens* were chased away by the more aggressive predator *C. trilobatus*.

Several species also appeared to act as scavengers during the predation events. These species were curious and often came very close to the predatory fish during and immediately after a feeding event and included: *Chaetodon auriga* (Chaetodontidae), *Abudefduf sexfasciatus* (Pomacentridae), *Thalassoma lunare*, *Anampses* sp. and *Chelio inermis* (Labridae).

Overall the abundance and species richness of potential predators were greatest on the reef slope (0.64 individuals 100 m^{-2}, 13 species) and declined on the back reef (0.54 individuals 100 m^{-2}, 10 species) and lagoon (0.42 individuals 100 m^{-2}, 5 species). However, the high within-habitat variability in the density and biomass of predatory fishes precluded the detection of any significant variation among habitats (Fig. 3.3). The only exception to this was the labrids which had significantly higher density (ANOVA: $F_{2,84} = 3.73$, $p = 0.028$) and biomass (ANOVA: $F_{2,84} = 4.847$, $p = 0.010$) on the back reef compared to the lagoon. There was limited variation in the predators along the reef with only the density of labrids differing among sites (ANOVA: $F_{18,84} = 1.928$, $p = 0.024$). The densities of *E. mathaei* also varied among sites (ANOVA: $F_{18,84} = 15.912$, $p < 0.001$) and habitats (ANOVA: $F_{2,84} = 202.919$, $p < 0.001$) with more urchins being recorded on the reef slope (219.67 individuals 100 m^{-2}) compared to the back reef and the lagoon, 21.80 and 0.11 individuals 100 m^{-2}, respectively (Fig. 3.3). See Table S8 in Appendix A for further details of the ANOVA's.

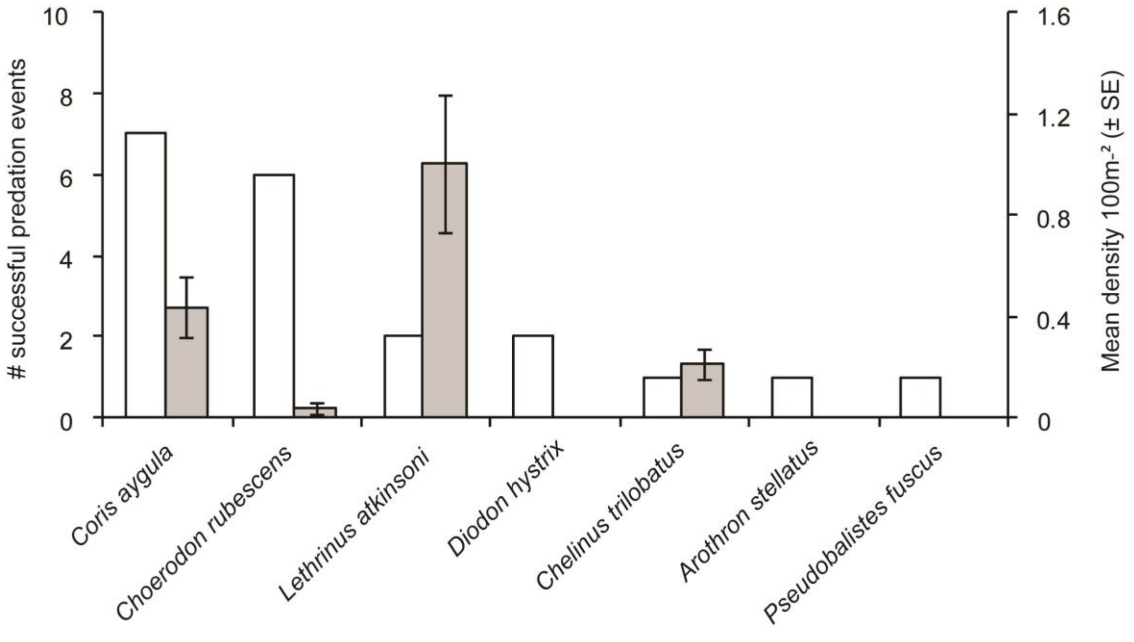

Fig. 3.2 Number of successful predation events on tethered *Echinometra mathaei* by identified sea urchin predators on Ningaloo Reef (open bars) and the mean density of each predator (individuals 100 m^{-2} ± SE) at the experimental sites (shaded bars).

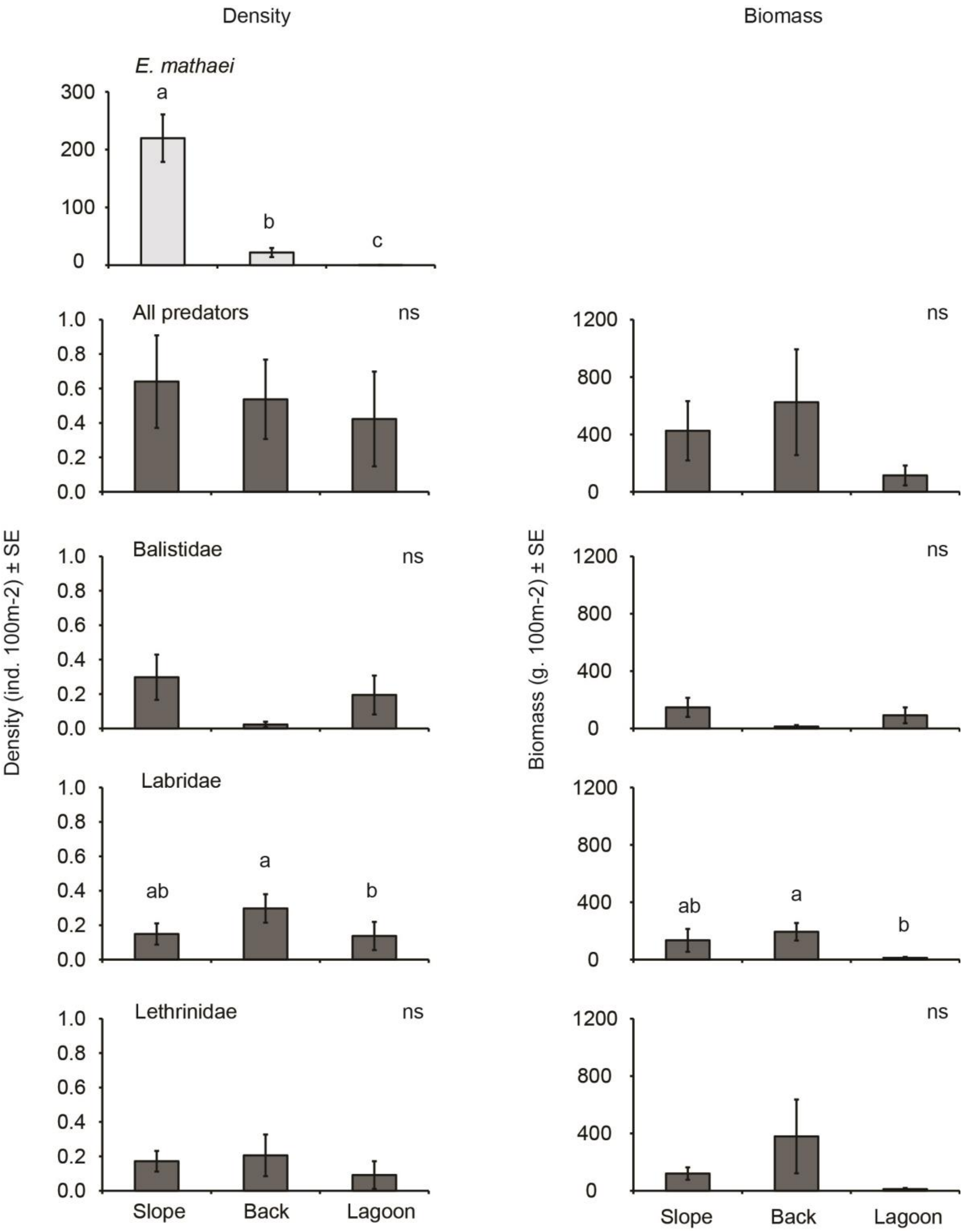

Fig. 3.3 Among-habitat variation in the the density of *Echinometra mathaei* and the density and biomass of potential predators, both collectively and for each of the predatory families independently on Ningaloo Reef.

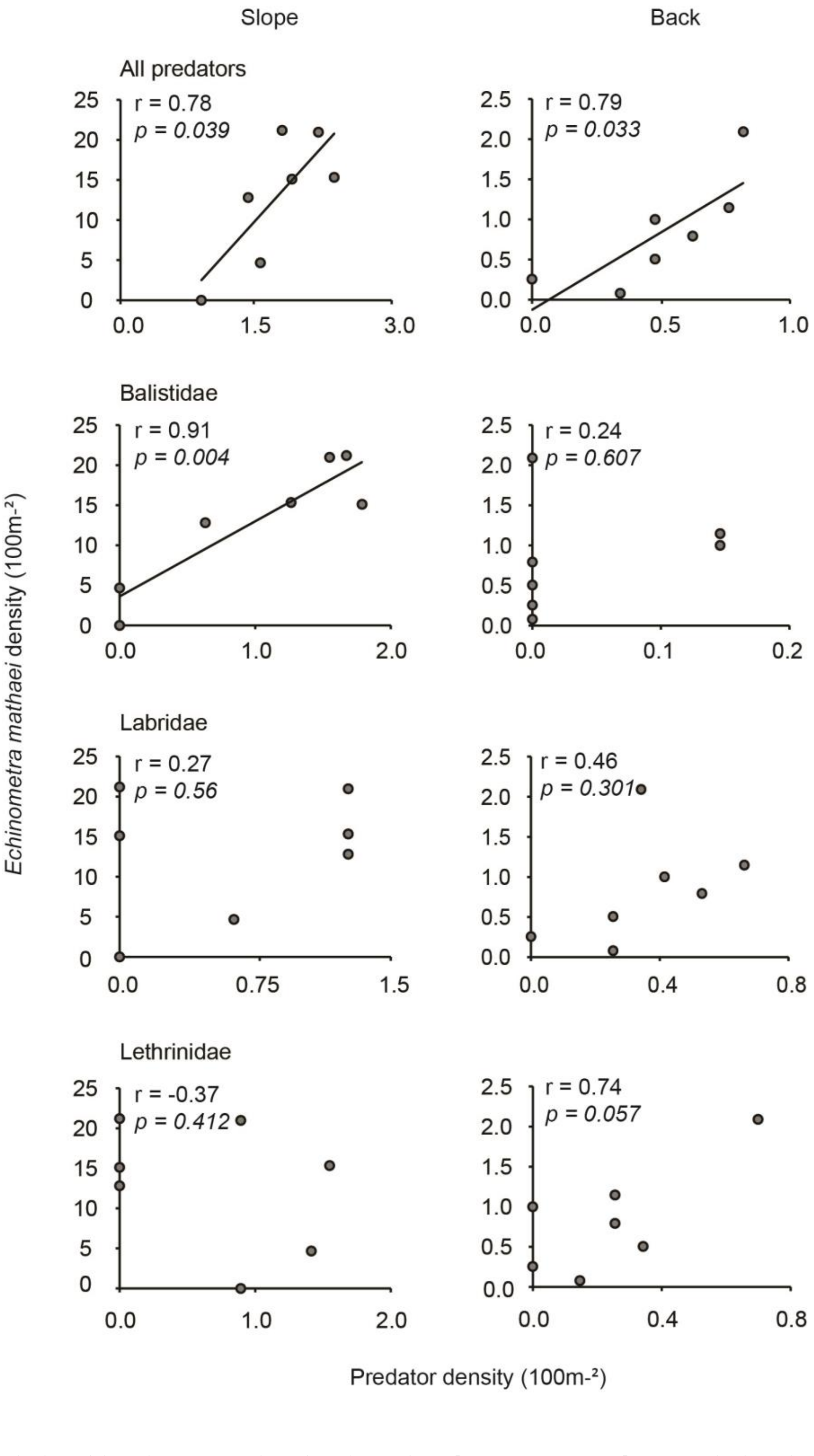

Fig. 3.4 Relationships between the density of *Echinometra mathaei* and the density of all predators collectively and each of the predatory families independently on the reef slope and the back reef. Correlations are based on mean densities per site (n = 7). All variables (both urchins and predators) on the slope were square root transformed and variables on the back reef were log transformed to meet the assumptions of normality.

The two most abundant potential predators were *Sufflamen chrysopterus* and *Rhinecanthus aculeatus* (Balistidae) accounting for 15 % and 11 % of total predator abundance, respectively (see Table S9 in Appendix A). Interestingly neither of these species were identified as predators during the tethering experiment. *Sufflamen chrysopterus* was most abundant on the reef slope where it accounted for 36 % of all predators recorded, compared to only 2 % and 0 % within the back reef and lagoon, respectively. In contrast, *R. aculeatus* was most abundant in the lagoon (40 %) compared to the back reef (2 %) and the slope (0 %). Of the seven predators identified in the tethering experiment only three were recorded during the fish censuses; *C. aygula*, *C. trilobatus* and *L. atkinsoni*. *Cheilinus trilobatus* was recorded in all three habitats, while *C. aygula* and *L. atkinsoni* were recorded on the reef slope and back reef only. Of these three species, *L. atkinsoni* was the most abundant predator on the reef slope (20 % of all predators recorded), whilst *C. aygula* was the most abundant predator on the back reef (21 %). Four of the predators identified in the predation experiment, *P. fuscus*, *C. rubescens*, *D. hystrix* and *A. stellatus*, were not observed during the visual surveys despite censusing over 2.6 hectares of reef (see Table S9 in Appendix A).

The density of *E. mathaei* was positively correlated with the density of all potential predators collectively on both the reef slope (r = 0.78, p = 0.039) and the back reef (r = 0.79, p = 0.033, Fig. 3.4) (table S10). The relationship on the reef slope was largely attributable to the density of balistids, which were positively related to the density of *E. mathaei* within that habitat (r = 0.91, p = 0.004). The density of *E. mathaei* was also positively correlated with both total predator and lethrinid biomass on the back reef (r = 0.81, p = 0.029 and r = 0.80, p = 0.031, respectively). No correlations were detected between the density of *E. mathaei* and the density or biomass of labrid predators.

3.4 Discussion

The relationship between sea urchins and their predators has been suggested to be an important indicator of the health of a reef ecosystem (McClanahan and Shafir, 1990, McClanahan, 1999), with high sea urchin numbers often regarded as an indication of low predator densities, overfishing, and reef degradation (McClanahan et al., 1996, McClanahan, 1995, McClanahan and Shafir, 1990, Hay, 1984). However, we found no evidence for the top-down control of *E. mathaei* populations either within or among habitats at Ningaloo Reef.

Despite the densities of *E. mathaei* varying by over an order of magnitude among habitats, the density and biomass of potential urchin predators did not differ among habitats. Furthermore, our results show positive correlations between the abundance of *E. mathaei* and that of their predators within two of the three habitats examined; the reef slope and the back reef. While our results suggest that the suite of urchin predators at Ningaloo Reef is having limited influence on *E. mathaei* populations, the potential role of predation should not be discounted. Several studies have reported large balistid species such as *Balistoides viridescens, Balistapus undulatus*, *Pseudobalistes flavimarginatus* and *P. fuscus* to be the dominant predators of urchins (e.g., McClanahan, 1995; Wachenfeld, 1993; Young and Bellwood, 2012). These species were conspicuously absent from our study sites and may have directly contributed to the high densities of *E. mathaei* on the reef slope. Alternatively, bottom-up factors such as food availability, habitat structure, availability of refuges, water flow and/or wave exposure may be influencing *E. mathaei* populations at Ningaloo Reef.

The densities of *E. mathaei* reported here for Ningaloo Reef (0.001 – 2.2 individuals m^{-2}) are high compared to other regions with relatively intact predator communities, but generally lower than those reported on many heavily fished or degraded Indo-Pacific reefs. On the Great Barrier Reef, one of the world's most intact reef systems, densities of *E. mathaei* range from 0 to 0.05 individuals m^{-2} (Done et al., 1991, Young and Bellwood, 2011). Similar densities have been reported within Marine Protected Areas (MPA) on the Kenyan coast (0.02 – 0.25

individuals m^{-2}, Carreiro-Silva and McClanahan, 2001; McClanahan and Shafir, 1990; McClanahan and Mutere, 1994). In contrast, the densities of *E. mathaei* are typically much greater on heavily fished reefs (e.g., Moorea: 7.4 individuals m^{-2}, Bak, 1990; Hawaii: 12.7 - 97.5 individuals m^{-2}, Russo, 1977; Kenya: 1.1 – 32.7 individuals m^{-2}, Khamala, 1971; McClanahan and Mutere, 1994; McClanahan and Shafir, 1990; Zanzibar 5.5 – 18.0 individuals m^{-2}, Wachenfeld, 1993) and have been reported to exceed 100 individuals m^{-2} in some locations (Persian Gulf: Downing and El-Zahar, 1987; Hawaii: Ogden et al., 1989). Interestingly, within these fished reefs the highest densities are typically recorded with the shallow reef flat and lagoon habitats, as opposed to the deeper reef slope habitat in the present study.

The marked differences in densities of *E. mathaei* between fished and protected reefs provide strong support for the role of predation in structuring these populations; however, we found no evidence of top-down control of *E. mathaei* either within or among habitats on Ningaloo Reef. Despite densities of *E. mathaei* varying 10 to 2000-fold among habitats there were no marked differences in the abundance of predators among habitats. The positive relationships between the density of potential predators and *E. mathaei* on both the reef slope and back reef suggest that the suite of predators at these sites were not exerting top-down control on urchin populations, but may be responding to similar environmental or habitat characteristics. Overall, the density (and biomass) of all potential predators was broadly comparable to those of previous studies on the Great Barrier Reef (Young and Bellwood, 2012) and within Kenyan MPA's (McClanahan and Muthiga, 1988, McClanahan and Shafir, 1990, McClanahan, 1994). Notably, densities of *C. aygula*, the dominant urchin predator in the present study, were 3 – 4 times more abundant on Ningaloo Reef than in similar habitats within Kenyan MPA's (McClanahan, 1994). The density of balistids on Ningaloo Reef, while greater than that reported for fished east African reefs (McClanahan and Muthiga, 1988, McClanahan and Shafir, 1990, Wachenfeld, 1993), was less than one-third of those recorded within Kenyan MPA's (McClanahan and Shafir, 1990, McClanahan, 1994, McClanahan et al., 2007). This variation in the density of balistids was attributable to the almost complete absence of large balistid species such as *B. viridescens* (75 cm max total length (TL)), *P. fuscus* (60 cm max TL), and *B. undulatus* (30 cm max TL) on Ningaloo Reef. While all of these species occur on Ningaloo Reef (Hutchings, 1994), none were recorded during the visual censuses of over 2.6 ha of reef.

Large balistid species have been identified as the dominant predators of *E. mathaei* and other urchins on Indo-Pacific reefs. Predation on tethered *E. mathaei* was dominated by *B. undulatus* on Kenyan reefs (McClanahan, 1995, McClanahan, 2000), by *B. viridescens* and *B. flavimarginatus* on Zanzibar reefs (Wachenfeld, 1993) and by *B. viridescens* and *B. undulatus* on the Great Barrier Reef (Young and Bellwood, 2012). Furthermore, Fricke (1971) reported that *B. undulatus* and *P. fuscus* were the dominant predators of another urchin *Diadema setosum* in the Red Sea. Smaller balistid species such as *Rhinecanthus* spp. and *Sufflamen* spp. have also been recorded to feed on *E. mathaei* under both natural and experimental conditions, however these predation events have been limited to small (< 20 mm test diameter) or juvenile urchins (McClanahan, 1995, Wachenfeld, 1993). Consequently their ability to consume adult urchins appears limited. This dichotomy is important and the dominance of large balistids as predators of adult urchins has led to suggestions that they are keystone predators on tropical coral reefs (McClanahan, 2000, Young and Bellwood, 2012). While the extremely low densities, or absence, of these fishes from our study sites may have contributed to the moderate-high densities of *E. mathaei* on Ningaloo Reef, they cannot explain the among-habitat variation.

While top-down predation is widely accepted as the key determinant of urchin populations on coral reefs (Hay, 1984, McClanahan, 1995), bottom-up factors (e.g., water flow, food supply, habitat complexity, and sedimentation) may have contributed to the distribution of *E. mathaei* on Ningaloo Reef. The high wave action and water flow on the reef slope may have directly contributed to the high densities of *E. mathaei* within this habitat. Hydrodynamic forces have been shown to limit habitat use and foraging of urchins in temperate systems (Kawamata, 2012, Lauzon-Guay and Scheibling, 2007). However, the habit of *Echinometra* spp. to stay within their burrows and feed on drift algae and detritus (Ogden and Lobel, 1978, Russo, 1977) makes them ideally suited for high wave energy environments. Russo (1977) found that the densities of two urchins in Hawaii (*E. mathaei* and *Echinometra oblonga*) were positively related to both water movement and food supply, but was unable to determine the relative importance of each factor as the supply of drift algae and detritus was a function of water flow. Furthermore, the elongated burrows, such as those of *E. mathaei* on the reef slope at Ningaloo Reef, maximize the accumulation of drift food while simultaneously providing shelter against predation (Grunbaum et al., 1978, Neill, 1988). Variation in structural complexity and hence availability of refuges among habitats may have also contributed to the observed patterns. Alternatively, the higher sediment loads within the back reef and lagoon may have limited the recruitment and survival of urchins (Burt et al., 2010, Walker, 2007) and contributed to the lower densities of *E. mathaei* within these habitats. Irrespective of the mechanism/s our results highlight the potential for bottom-up processes to influence the distribution of *E. mathaei* on coral reefs.

The present study, however, is not without its limitations. Tethering and exposing *E. mathaei* to diurnal predators on sand does not replicate natural predation events. However, this method facilitated the identification of the range of species that are capable of consuming exposed adult *E. mathaei* (i.e., potential predators) and is directly comparable to studies from other regions (e.g., McClanahan 1995; Young and Bellwood 2012). Direct observation of predation events also allowed potential predators to be distinguished from scavengers, as opposed to analyses of gut contents (e.g., Hobson, 1974). We acknowledge that all of the species identified as predators of tethered urchins may not be able to access and consume urchins that are concealed in their burrows. For example, Fricke (1971) reported that several labrid and lethrinid species were predators of *D. setosum* in the Red Sea but that they were only able to prey on solitary, exposed urchins. Unlike the larger balistids, the labrids and lethrinids were unable to prey on urchins that were in aggregations or concealed within crevices (Fricke, 1971). Nevertheless, gut content analyses of fishes from Ningaloo Reef supported our identification of potential urchin predators, with urchins being a common dietary component of *Lethrinus* spp. (including *L. atkinsoni*), *C. aygula*, *Choerodon* spp., and *A. stellatus* (Westera, 2003). By tethering urchins we were able to use remote underwater video cameras to record predation events, thereby avoiding any bias associated with diver presence (Dickens et al., 2011). Despite selecting a census technique to minimize 'diver-effects' and maximize detection of wary species (Dickens et al., 2011), there was a mismatch between the predators identified from the tethering experiment and visual surveys at the experimental sites. Several of the predators identified using tethered urchins were either underestimated (i.e., *C. rubescens*) or not recorded (i.e., *P. fuscus, A. stellatus,* and *D. hystrix*) during visual censuses within the experimental sites. Similar issues have been shown for herbivorous fishes on coral reefs, with species responsible for consuming fleshy macroalgae typically being underestimated in visual censuses (Bellwood et al., 2006b, Hoey and Bellwood, 2009).

3.5 Conclusion

Predation by fish is widely recognised as a key process shaping the distribution and abundance of *E. mathaei* populations on coral reefs (Brown-Saracino et al., 2007, McClanahan, 1995, McClanahan, 1999, Young and Bellwood, 2011), however, the factors controlling urchin populations on Ningaloo Reef appear more complex. While we found no evidence supporting the role of predation *per se*, the predator assemblage on Ningaloo Reef differed markedly from those of other regions. Labrids were the dominant predators of *E. mathaei* on Ningaloo Reef, yet large balistids, the dominant predators of urchins in other systems (e.g., McClanahan, 1995; Young and Bellwood, 2012), were conspicuously absent or rare. While far from conclusive, the lack of large balistids may have contributed to the moderate-high densities of *E. mathaei* on Ningaloo Reef. Balistids are not targeted by commercial or recreational fishers on Ningaloo Reef (Sumner et al., 2002), and consequently it is possible there were never sufficient densities of predators to control *E. mathaei* populations. Together with a lack of key predators, bottom-up factors (e.g., water flow, food availability, habitat structure) appear to be playing a significant role in determining among-habitat distributions. Irrespective of the mechanisms, moderate-high densities of *E. mathaei* can be a natural component of intact reef systems and should not be universally viewed as an indicator of reef degradation.

Chapter 4: The importance of live coral for small sized herbivorous reef fishes in physically challenging environments

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4.1 Introduction

Live coral cover on coral reefs is declining and is expected to exhibit further declines due to increasing impacts from ocean acidification, bleaching, coral disease and increased anthropogenic pressure (Hoegh-Guldberg et al., 2007, Hughes et al., 2003). Reductions in live coral cover and structural complexity have variable effects on fish communities, causing both increases and decreases in diversity and abundances (Cheal et al., 2010, Graham et al., 2006, Jones et al., 2004, Pratchett et al., 2008, Wilson et al., 2006). For example, many coral-dependent species have decreased in abundance following reductions in coral cover, while the relationship appears to be reversed for many herbivorous fishes (Wilson et al., 2009). Alterations to reef complexity, where the physical structure of the reef is reduced, can have even more severe impacts on fish communities, reducing the numbers of both coral-dependent and non-coral dependent species (Wilson et al., 2006). However, as reef complexity may be eroded for several years after coral mortality, the relationship between loss of live coral cover, structural complexity, and reef fish may not always be immediately apparent and may give rise to a lag-effect (Graham et al., 2007). The difficulty of predicting the long-term effects of coral loss and structural complexity on fish populations is further complicated by various responses and functional differences between adult and juvenile individuals.

The importance of herbivores as primary controllers of algal biomass, before, during, and after a disturbance, is vital for coral regeneration (Bellwood et al., 2004). While some small herbivores such as damselfish farm algae (Ceccarelli et al., 2011), other fishes (‘roving herbivores') have the potential to move between habitats and consume algae, thus reducing their biomass (Ceccarelli et al., 2006). The capacity of these roving herbivores to remove algae can be beneficial, even on exploited reefs (Bellwood et al., 2012). Lumping species into groups depending on their function is advantageous for management purposes, yet it is not straightforward, as species from the same family can exhibit vastly different functions (Green and Bellwood, 2009). Instead, species and size-specific traits needs to be acknowledged. Four main types of feeding behaviour (depending on how they feed and what algae they target) can be distinguished: browsing, excavating, grazing and scraping (Bellwood et al., 2004, Bellwood and Choat, 1990, Choat et al., 2002, Wilson et al., 2003). Excavators, grazers and scrapers all feed on the epilithic algal matrix (EAM). Grazers crop the algae, by scraping scrapers remove both algae and particulate material, while excavators bite into the substratum leaving a scar (Bonaldo and Bellwood, 2009, Fox et al., 2009). Browsing species feed on erect macroalgae (Hoey and Bellwood, 2009, Hoey and Bellwood, 2011). Excavating and scraping herbivorous fishes both exhibit ontogenetic changes during their life time (Bellwood, 1988, Bellwood and Choat, 1990) and perform different ecological roles depending on their body size (Bonaldo and Bellwood, 2008, Lokrantz et al., 2008). For example, juvenile parrotfish have an omnivorous diet and only develop a grazing function once the jaw musculature anatomy is capable of a scraping feeding mode (Bellwood, 1988, Bellwood and Choat, 1990, Bonaldo and Bellwood, 2008, Lokrantz et al., 2008). Using species richness, abundance or biomass of herbivores as sole measures of functional roles can therefore mask species-specific traits and potential functional implications related to body size. Using size-specific fish densities for each functional group of interest is therefore a crucial step when studying and managing coral reefs. Additionally, there is a need to understand how these various size classes within functional groups relate and react to changes in the benthic configuration of the reef.

Previous studies have investigated the impacts of the loss of live coral cover on fish densities and species richness (Pratchett et al., 2008, Wilson et al., 2006), but little is known about the consequences for different functional groups and how different size classes respond to coral loss (but see Wilson *et al.* 2010; Graham *et al.* 2007). In this study, we compare abundances of roving herbivorous fishes in two habitats, one sheltered from strong hydrodynamic processes (back reef) and one exposed to strong flow (slope), at sites with various levels of coral cover. Our aim is to investigate the relationship between various size classes of herbivorous fishes, in four functional groups, and spatial variation in live coral cover based on the hypothesis that higher complexity will support more species regardless of size. We then evaluate the extent to which these patterns can be used to predict the effect of coral loss on fish ecosystem functions.

4.2 Materials and Methods

This study was conducted within Ningaloo Reef Marine Park in Western Australia between 2009 and 2010. Ningaloo Reef stretches approximately 300 km along the central part of the coast (Fig. 1.1, site 1-10) and is the largest west-continental fringing reef ecosystem in the world (Cassata and Collins, 2008). It fringes a sandy and macroalgal covered lagoon, with a few scattered bommies, accessible only through a few passages. The slope is gentle and characterised by pavement (flat reef matrix), encrusting, table and branching corals. The reef flat and crest are only accessible during calm weather. The back reef sits off the flat and is dominated by table and branching corals. It borders the sandy lagoon which host large stands of macroalgae closer to land. The slope on Ningaloo Reef is subject to strong currents and surge with waves on the crest often exceeding 3 m during the winter. The flow over the crest and flat is predominantly wave-driven with flow rates between 10 and 30 cm^{-1} (Wyatt et al., 2010). Three habitats, lagoon, back reef and slope, were surveyed with ten sites sampled in each habitat: just below the surge zone on the slope at a depth of 6-10 m, on the back reefs at 2-5 m, and in the macroalgal meadows in the lagoon at 3-5 m.

Herbivorous fish were surveyed using visual censuses on SCUBA as transect tapes were deployed. At each of the 30 sites, five 50 m transects were deployed parallel to the reef edge (methods follow Johansson *et al.* 2010). Along each transect herbivorous fish were recorded in a 5 m wide belt. All fish species in the families Acanthuridae, Ephippidae, Kyphosidae, Labridae (parrotfish) and Siganidae were counted. Only individuals > 10 cm total length were recorded (to avoid cryptic and temporally more variable juvenile specimens). Fish surveys were conducted by one observer (CLJ), with extensive experience in size estimation and fish counts. Fish were placed in 5 cm categories (10-15, 15-20 etc) and later categorized into four functional groups: browsers, excavators, grazers/detritivores (from now on referred to as grazers), scrapers and three size groups (small, medium and large) (see Table S13 in Appendix A). These size groups were based on the maximum lengths of fish in each functional group recorded along transects (browsers, excavators and scrapers: small 10-20 cm, medium 21-40 cm and large > 40 cm, grazers: small 10-15 cm, medium 16-25 cm and large > 26 cm). Grazers are dominated by smaller species so the three basic divisions small, medium and large were appropriately reduced to emphasize the relative effect of size.

An estimate of live coral cover was obtained by conducting benthic surveys on the fish transects once the fish survey was completed to minimize disturbance to fish. At each site, ten 10 m benthic transects were surveyed, equalling two benthic transects per fish transect (at 10-20 m and at 30-40 m on the 50 m fish transect). The benthos was recorded at each 1 m interval and at 1 m on either side of the transect tape, resulting in a total of 33 points per transect (330 points per site). The benthos was categorized into the following eight substratum groups: live coral, recently dead coral, pavement (flat reefal matrix), epilithic algal matrix (EAM), macroalgae (> 15mm), crustose coralline algae (CCA), rubble, sand and others (sponge, soft coral etc). Dead coral, pavement and EAM were later grouped under EAM to represent substratum on which turfalgae predominate. Structural complexity was estimated using visual assessments of the topography for each site. Each site was assigned a value between 0 and 5, where 0 = no vertical relief, 1 = low and sparse relief, 2 = low but widespread relief, 3 = moderately complex, 4 = very complex with numerous fissures and caves and 5 = exceptionally complex with numerous caves and overhangs (following Wilson *et al.* 2007). This method has been shown to provide a representative measure of reef topography, comparable to the chain method (Wilson et al., 2007).

Any potential relationships between 1) topography and live coral cover and 2) abundance of herbivorous fish and live coral cover, fish and EAM, and fish and macroalgae, were tested using a series of Pearson's Product Moment correlations. Correlations were performed using topography category and proportion live coral cover per site, or the average density of fish (per size class in each functional group) and the proportion live coral, EAM or macroalgae per site. This resulted in 10 replicate sites each for the back reef and slope habitats for the two comparisons. Data were square root transformed for all size groups and coral cover to improve linearity. Topography categories were not transformed. Due to low coral cover in the lagoon, only the back reef and the slope were included in the analysis.

Statistical analysis

A series of one-way analysis of variance (ANOVA) was used to investigate 1) potential differences in the abundance of fish functional groups between the two habitats (back reef and slope), and 2) variations in abundance between size classes for each functional group and habitat separately. Potential differences in the abundance of fish functional groups between the two habitats were estimated using the abundance of each fish size class and functional group. Each transect was treated as a replicate within site resulting in 100 replicates per functional group (50 back reefs and 50 slopes). All variables were 4^{th} root transformed to meet the assumptions of normality and homogeneity. The assumptions were checked using normal probability plots and Levene's test. Due to low coral cover in the lagoon, only the back reef and the slope were included in the analysis.

4.3 Results

Live coral cover ranged between 10 and 61 % on the back reef and between 2 and 48 % on the slope (Table S11 in Appendix A). Coral cover was strongly correlated with topography for both the back reef and the slope ($r = 0.845$, $p = 0.002$ and $r = 0.913$, $p < 0.001$, respectively) (Fig. S3 in Appendix A). The relationship between coral cover and functional groups was examined in each habitat separately. Positive correlations were found between live coral cover and the density of small excavators ($r = 0.68$, $p = 0.031$) and small scrapers ($r = 0.81$, $p = 0.004$) on the slope (Fig. 4.1). In contrast, small grazers in the same habitat were strongly correlated with low levels of coral cover ($r = -0.85$, $p = 0.002$) (Fig. 4.1). The only other positive relationships were between medium sized excavators and scrapers and live coral cover on the back reef ($r = 0.76$, $p = 0.012$ and $r = 0.70$, $p = 0.025$, respectively); all other functional groups and size classes showed no correlation with live coral cover.

Correlations were also performed between fish vs. EAM and fish vs. macroalgae to identify potential association with food sources. Small grazers on the slope were positively correlated with EAM ($r = 0.91$, $p = 0.000$). Medium sized browsers on the back reef associated with sites hosting more macroalgae ($r = 0.65$, $p = 0.040$), while large and medium scrapers on the slope were negatively correlated with macroalgae ($r = -0.70$, $p = 0.025$ and $r = -0.77$, $p = 0.009$, respectively).

Significant differences were found in the densities of various size classes within each functional group between the back reef habitat and the slope habitat on Ningaloo Reef (Fig. 4.2; Table S12 in Appendix A). The back reef displayed significantly higher densities of small browsers and excavators, and medium excavators and scrapers. The highest densities of large grazers and scrapers were found on the slope. Both the slope and back reef had representation of each functional group and size group (small, medium and large), except for the absence of large excavators from the back reef (Table S13 in Appendix A).

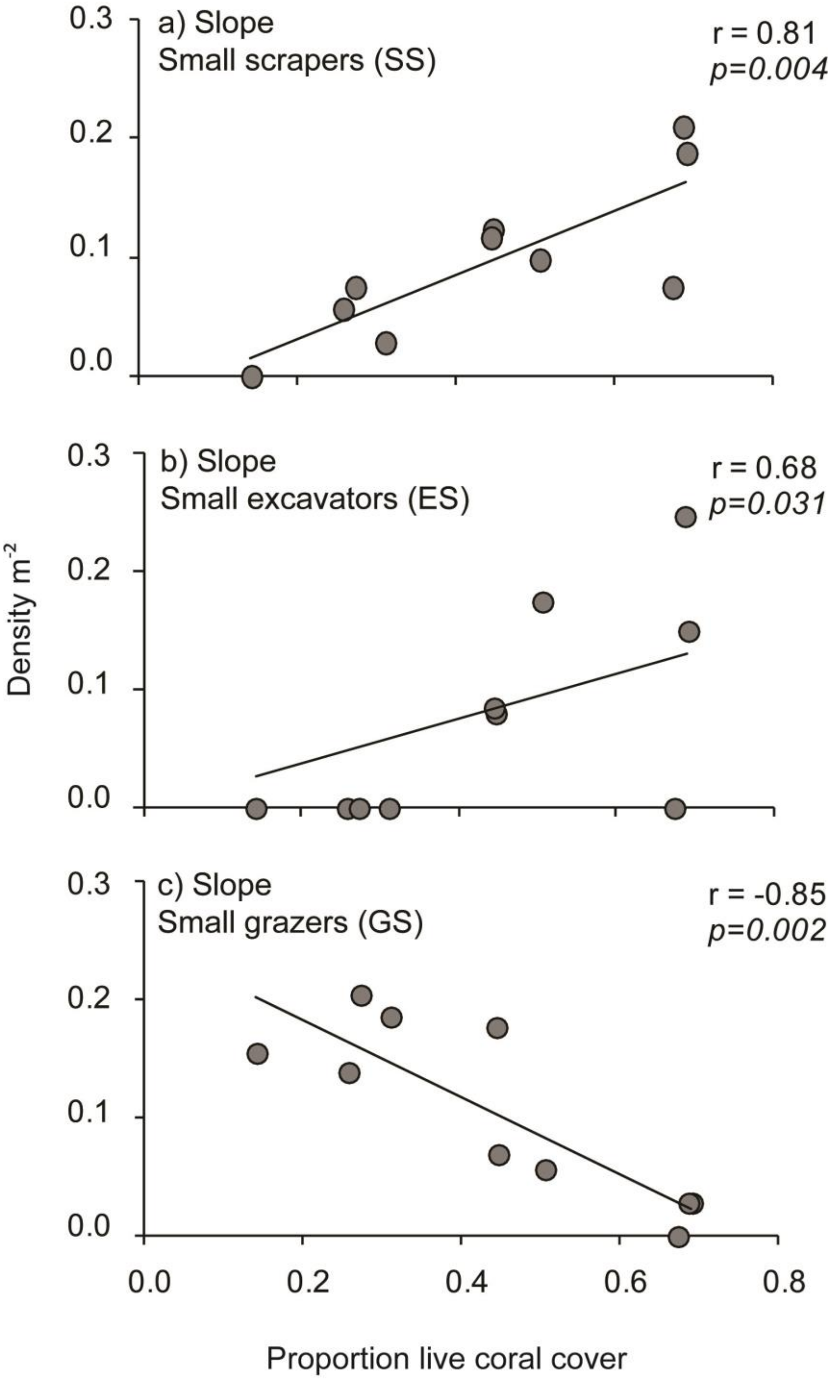

Fig. 4.1 Correlations between proportion live coral cover and densities of small scrapers, excavators, grazers and browsers (m^{-2}) on back reef and slope. Square root transformed data is shown to improve linearity.

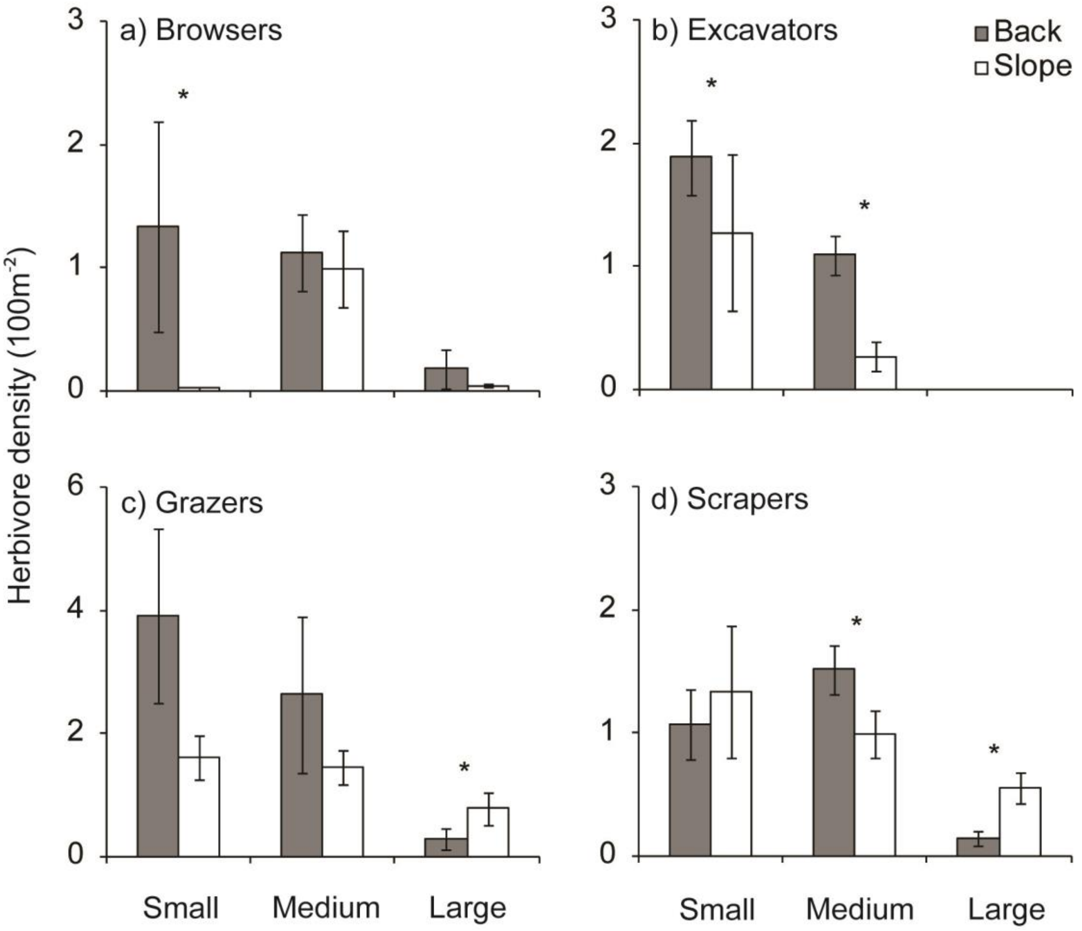

Fig. 4.2 Comparison of average density of fishes (100 m^{-2} ± SE) between three size groups (small, medium and large) for a) browsers, b) excavators, c) grazers and d) scrapers between the back reef habitat and the slope habitat. One-way ANOVAs were performed on transformed data to identify significant differences between habitats (marked with asterix).

Additionally, significant differences in abundance among size classes within functional groups were detected for both habitats (Table S14 in Appendix A). Browsers, grazers and scrapers on the back reef had significantly more small individuals compared to large (Tukey's HSD post hoc test: $p = 0.006$, $p < 0.001$ and $p = 0.001$, respectively) and more medium sized fish compared to large individuals ($p < 0.001$, $p < 0.001$ and $p < 0.001$, respectively). Scrapers also had more medium sized individuals compared to small ($p = 0.001$) on the back reef, while the slope had a higher abundance of medium sized browsers and grazers compared to large ($p < 0.001$ and $p = 0.048$, respectively). There were also significantly more large browsers compared to small browsers ($p < 0.001$). No other differences in abundance of fishes within each size class were detected.

The size frequency distributions showed that the smallest size range of herbivores was found in the lagoon, whilst the largest size range was encountered on the slope (Fig. S4 in Appendix A). Grazers had the overall smallest size range, 10-30 cm, which was a consistent pattern across habitats. Scrapers had the largest size range 10-70 cm of all functional groups and the largest individuals were found on the slope. The majority of small individuals were found in the lagoon for all functional groups, with the exception of grazers which had more small individuals on the back reef. For browsers and scrapers a clear shift from small individuals in the lagoon towards larger individuals on the back reef and slope was evident.

4.4 Discussion

Our results show a strong association between small herbivorous fishes and live coral cover on Ningaloo Reef, but only in exposed high energy habitats. On Ningaloo Reef, fishes on the slope appear to be particularly sensitive to a reduction in live coral cover (especially scrapers). Live coral cover appears to be important as a refuge for small scrapers and excavators in these energetically demanding habitats. As topography and coral cover were strongly correlated, distinguishing between the benefit of each of them is complicated. However, as live coral is not a dietary component of small herbivores, a structural role is likely to be the key factor. Hence, we suggest that the relationship with coral cover on the slope may be due to the challenging hydrodynamic nature of this habitat.

Fish swimming behaviour may be closely related to water movement on coral reefs (Fulton and Bellwood, 2004, Fulton et al., 2001) and the size of fish (Fulton and Bellwood, 2002). The utilization of complex structures in high flow environments can significantly reduce the energetic costs for fishes (Johansen et al., 2007). Therefore, using such energy conserving behaviours may explain why we find a correlation between the abundance of small parrotfish and coral cover in exposed high flow habitats, but not in sheltered habitats. Refuging behaviour increases the capacity of fish to lower their energy expenditure and sustain themselves in high-flow environments (Johansen et al., 2008) and will therefore provide fishes with substantial energetic advantages through a reduction in locomotor costs. On the other hand, habitats without refuges force fish to swim continuously, increasing the risk that small individuals or weak swimmers will become fatigued more quickly (Johansen et al., 2007). The frequency of refuge use is controlled on an individual level and can rapidly be adjusted by an individual in response to ambient flow. This allows weaker swimmers with well-developed refuge behaviour to inhabit environments with high flow (Johansen et al., 2008). Labriform swimming species (such as parrotfish) show clear ontogenetic development of the aspect ratio of the pectoral fins, suggesting that larger individuals have a different swimming mode (Fulton et al., 2001), which may allow them to cope more easily in high flow environments than smaller con-specifics (Fulton and Bellwood, 2002). Utilizing complex structures as an energy efficient behaviour may also yield additional benefits in terms of protection against predators.

Utilizing habitats and the benefits of their complexity does not only conserve energy, but also reduces the risk of predator exposure (Almany, 2004, Holbrook et al., 2006, Werner et al., 1983). The strong association with physical structures for small scrapers and excavators may also be a response to avoid predation. Habitats with more complex structures can offer recruits more protection against predators than bare habitats (Almany, 2004). The association with complex structures may therefore be a determining factor for fish abundance in predator-dense environments. The small scrapers and excavators on Ningaloo Reef were only found to associate with live coral on the slope and not on the back reef. One possible explanation could be that utilizing the protection from a complex structure will help the fish minimize the chances of being 'washed out' from its shelter and exposed to predators as the waves wash over the reef. Associating with coral structures on the slope is therefore likely to be a strategy to lower the risk of exposure to predators and reduce the cost of predation avoidance. While data on predator abundance is not available for these two habitats, larger predators are often associated with exposed reef slopes (Randall, 1997). The positive correlation between medium sized excavators and scrapers on the back reef is most likely related to the shelter provided by plate corals on the back reef (Kerry and Bellwood, 2011) and not water flow as these individuals are likely to be strong swimmers (Fulton et al., 2001).

The positive relationship between coral structure and small parrotfish was not found for small grazers. Instead, the negative correlation between small grazers and coral cover and the positive association with sites with more EAM, suggests that members of this functional group prefer to associate with open areas without corals but where algae may be abundant. The small grazers on Ningaloo Reef were dominated by *Acanthurus triostegus* (95 % of all small grazers). This species actively schools, presumably to minimize predation (Barlow, 1974) and conserve energy. Schools provide energetic advantages when swimming (Weihs, 1973), especially in labriform swimming like *A. triostegus* (Johansen et al., 2010) and reduced predation (Barlow, 1974, Brock and Riffenburgh, 1960, Overholtzer and Motta, 2000). These advantages may enable this acanthurid dominated group to exploit open areas on the wave-washed slope where food is abundant. *Acanthurus triostegus* association with low coral cover may therefore result from lower levels of competition for food resources with other herbivores at these sites given their reduced need for shelter.

While species' responses to loss of live coral cover can be both positive and negative (Bonin et al., 2011, Stockwell et al., 2009, Wilson et al., 2006), the underlying causes have yet to be resolved. The roving nature of many species suggests that behavioural responses may be hard to predict due to large home ranges, with habitat utilization being strongly affected by short-term diurnal patterns (Meyer and Holland, 2005), feeding behaviours (Fox et al., 2009, Wilson et al., 2008) and social interactions (Lawson et al., 1999). However, recent work has highlighted the small size of home ranges in some reef species (Fox and Bellwood, 2011, March et al., 2010, Meyer et al., 2010, Welsh and Bellwood, 2012a). Therefore, while some fish inhabiting an area exposed to decreasing coral cover may explore neighbouring parts of the reef or reefs outside their usual home range to increase chances of survival (Wilson et al., 2006), others may not. For instance, *A. triostegus*, the dominant grazer on the slope, may rely on its schooling behaviour to feed and reduce the risk of predation and is therefore able to migrate over larger areas and multiple zones in search for food (Barlow, 1974), while parrotfishes may be much more site attached even when schooling (Welsh and Bellwood, 2012b). Hence, the capacity to move/migrate may be a critical factor determining whether species will survive or become locally extinct following drastic habitat changes (Wilson et al., 2006). Furthermore, these changes may markedly alter the functional composition of the remaining fish faunas.

Our data show that neither species nor size distribution differ markedly between the back reef and the slope on Ningaloo Reef. In general, the back reef hosts higher abundances of most size classes of fishes among functional groups with the exception of large grazers, large scrapers and small scrapers. Large fishes generally have higher aspect ratios then small fish (Fulton et al., 2001), making larger individuals stronger swimmers with a greater capacity to sustain themselves in high flow environments such as the reef slopes (Johansen et al., 2007). Larger fish also experience less predation pressure compared to small and medium sized fish (Almany, 2004), hence can access habitats with less structural shelter. The physical characteristics of the exposed slopes could therefore benefit large fish and explain the association with high coral cover for small individuals on the reef slope, and the higher abundance of small and medium sized fish on the back reef.

While shelter appears to be a strong factor driving the spatial distribution of size classes, food availability is another factor which could restrict the abundance of some species or functional groups in some habitats. The higher percentage of macroalgae on the back reef compared to the reef slopes on Ningaloo Reef (Johansson et al., 2010), may make the back reef a preferred habitat for browsing fishes. The positive correlation between medium sized browsers and macroalgae on the back reef suggests that food availability could determine spatial preferences for some size classes in some functional groups. The spatial distribution of different size classes and species of herbivorous fish on Ningaloo Reef highlight the possibility that food and shelter may not only be important for small individuals but also for larger fishes.

Coral reef fishes can respond in multiple ways to the loss of coral and structural complexity, depending on the condition of the reef and various reef characteristics such as habitat and depth (Cheal et al., 2008, Graham et al., 2007, Wilson et al., 2009). Graham and colleagues (2007) showed that the loss of corals and complexity particularly affected small individuals. Our results offer support for this observation and we suggest that a loss of corals and structural complexity on the slope may have a greater effect on small herbivores than in other habitats. The abundance of important functional groups of herbivorous fish (scrapers and excavators) may be reduced, while grazing herbivores, especially *A. triostegus*, could benefit from a reduction in coral cover due to its non-dependency on complexity and an increase in algal cover. It is worth highlighting that the dominance of *A. triostegus* in our small grazer group may not reflect all small grazers; however, it is likely to be a common pattern on Ningaloo Reef. Species which depend more on complexity than the actual coral itself may not show a direct response to coral loss unless complexity is severely compromised. If complexity subsists after coral loss, fish may not show a response until complexity is reduced (Cheal et al., 2008, Graham et al., 2007, Stockwell et al., 2009). A potential loss of live coral, followed by a loss of structural complexity on Ningaloo Reef, could lead to a reduction in small herbivores, with long term implications for the structure of herbivore assemblages.

4.5 Conclusion

Here, we show that populations of small excavators, scrapers and grazers may display positive or negative responses to live coral cover in a physically challenging environment, the reef slope on Ningaloo Reef. These relationships were not detected for small individuals on the sheltered back reefs. We suggest that these patterns may be driven by size-dependent behavioural adaptations in fishes. The utilization of complex structures as a refuge to minimize predation and lower energy costs may be essential for small individuals to succeed in hydrodynamically challenging environments. A loss of live corals and other physical structures on the slopes of Ningaloo Reef can therefore have important consequences for scraping and excavating species and result in a reduction of both recruits and, later, adult individuals. The effects of coral degradation on strong relationships, such as those found here, suggest that some critical functional groups may be particularly vulnerable to potential future losses of corals on Ningaloo Reef.

Chapter 5: Key herbivores reveal limited functional redundancy on inshore coral reefs

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5.1 Introduction

Many of the worlds' ecosystems are in serious decline (Jackson et al., 2001, Walther et al., 2002, Hughes et al., 2003). The combined effects of climate change and anthropogenic disturbances have led to declines in the biodiversity, productivity and dynamics of ecosystems, with shifts to alternate assemblages of species becoming increasingly common (Scheffer et al., 2001). Coral reefs are one of the world's most productive and biologically diverse ecosystems, yet they are also one of the most threatened (Walther et al., 2002). Moreover, predicted increases in the diversity, frequency and severity of disturbances affecting coral reefs (Sheppard, 2003, Donner et al., 2005) are raising concerns over their long-term persistence. As coral reefs are increasingly exposed to multiple stressors, their ability to absorb shocks, resist change and/or reassemble after disturbances (i.e., resilience Holling, 1973) may gradually erode (Hughes et al., 2005). There is, however, high spatial variability in the resilience of coral reefs. Reefs in the inner Seychelles have displayed varying responses to large-scale coral mortality with some being overgrown by fleshy macroalgae while others have returned to coral-dominance (Graham et al., 2006, Chong-Seng et al., 2012). Similarly on the Great Barrier Reef, one of the world's most intact coral reef systems, several inshore reefs have transitioned from coral- to macroalgal-dominance (Done, 1992, Diaz-Pulido et al., 2009, Cheal et al., 2010, Hughes et al., 2010), yet other reefs, especially those further offshore have resisted change. Determining the factors that underpin this spatial variation in resilience is key to understanding the dynamics of these systems.

The ability of reefs to cope with environmental disturbances is strongly dependent on the species present, their functional roles, and their response to perturbations (Folke et al., 2004). A reduced number of species and functions, or a lack of variation in the responses of species to disturbance, can push a system closer to an ecosystem threshold, and reduce the chances of recovery (Walker et al., 1999). Herbivorous fishes perform a critical role on coral reefs (Bellwood et al., 2004, Burkepile and Hay, 2006). Collectively, herbivorous fishes control the biomass and distribution of benthic algae, minimise coral-algal competition, provide suitable substrata for coral settlement and, in doing so, promote the recovery of coral communities following disturbance (Steneck, 1988, Bellwood et al., 2004, Hughes et al., 2007a). There is, however, considerable variation in the functional impact among herbivorous species with four distinct functional groups (browsers, excavators, grazers and scrapers) performing different and complimentary roles: excavators erode dead coral skeletons; scrapers remove turf algae and sediment leaving surfaces clear for settlement; and grazers/detritivores (hereafter termed grazers) reduce turf algal biomass and/or associated detritus with no disturbance to the underlying reef surface (Green and Bellwood, 2009, Burkepile and Hay, 2010, Burkepile and Hay, 2011, Bellwood et al., 2012). While excavators, grazers and scrapers all harvest the epilithic algal matrix, browsers are the species capable of reducing the biomass of large algal turfs or fleshy macroalgae (Bellwood et al., 2006a, Hoey and Bellwood, 2009).

The importance of the four functional groups for ecosystem health is apparent. However, their ability to support ecosystem functions now, and into the future, depends on the level of functional redundancy within each group (i.e., the capacity of one species to functionally compensate for the loss of another species: Nyström et al. 2008, Bellwood et al. 2004). Functional redundancy not only requires a high diversity of functionally similar species but also that species within a functional group have dissimilar responses to ecosystem stressors (i.e., response diversity), preventing all species within a function being lost as a result of a disturbance (Elmqvist et al., 2003, Nyström, 2006, Thibaut et al., 2012). Response diversity often reflects the taxonomic or phylogenetic diversity of the taxa that make up a functional group (Elmqvist et al., 2003), where slightly different functional traits make some genera more or less susceptible to a given disturbance (Thibaut et al., 2012). Hence, species richness and generic richness may provide an indication of the number of functionally similar species and the level of potential response diversity available within a functional group, respectively. However, neither of these metrics incorporates a measure of species abundance.

To maintain and secure ecosystem functions, it is essential that individuals supporting critical functional roles are present in sufficient numbers to effectively deliver their functions (Rosenfeld, 2002, Hoey and Bellwood, 2009, Bellwood et al., 2012). Collectively the abundance of all species within a functional group provides an indication of the intensity or magnitude of that function and subsequently the vulnerability of the system to disturbances. As the overall abundance of species within a functional group declines the intensity of that function correspondingly weakens, potentially reducing the resilience of the system and increasing its sensitivity to ecosystem shifts. The resilience of a system is also influenced by the relative abundance of species within a functional group, in particular the proportion of numerically non-dominant species, herein termed reserve capacity (i.e., the number of individuals available to fulfil the function if the numerically dominant species is lost). If two species are equally abundant they may be clear substitutes. However, if one is rare, its capacity to effectively take over a functional role may be limited (Nyström et al., 2008). Each of these metrics: species richness, generic richness, and reserve capacity, thus provides a slightly different perspective on how likely it is that species are able to replace each other (i.e., functional redundancy). When combined, they act as potential indicators of functional redundancy, and, together with abundance, provide an indication of the vulnerability of a functional group to disturbances.

Using these four metrics (species richness, generic richness, abundance and reserve capacity) we investigate spatial patterns of potential functional redundancy in herbivorous fish assemblages in two of the world's most intact coral reef ecosystems, the Great Barrier Reef and Ningaloo Reef, Western Australia. Specifically, we examine potential functional redundancy in each of the four functional groups of herbivorous coral reef fish across a range of habitats spanning the continental shelf in each system. These two reef ecosystems are well managed and are likely to have relatively intact herbivorous fish assemblages; there is no recreational or commercial fishery for herbivorous fishes. We therefore hypothe that these reef systems should exhibit exceptionally high redundancy in all four metrics, although significant spatial variation within each system might be critical.

5.2 Materials and Methods

Spatial patterns of potential functional redundancy were quantified/estimated from visual censuses of herbivorous fish communities on the Great Barrier Reef on Australia's east coast, and Ningaloo Reef, Western Australia (Fig. 5.1). All nominally herbivorous fishes (Acanthuridae, Ephippidae, Kyphosidae, Labridae (parrotfishes), Pomacanthidae (pygmy angelfishes), and Siganidae) > 10 cm total length were censused in a range of habitats that spanned the continental shelf in each system. On the Great Barrier Reef the continental shelf is approximately 110 km wide at the study location, whereas on Ningaloo it is just 0.2 to 7 km wide (average = 2.5 km; Cassata and Collins 2008). On the Great Barrier Reef censuses were conducted in the Townsville region, with eight transects (ca. 590 m^2) being conducted in each of eleven cross-shelf habitats (i.e., three to four habitats [back reef, reef flat, crest and slope] on inner-, mid-, and outer-shelf reefs; see Wismer et al. 2009 for details). On Ningaloo Reef, ten transects (1250 m^2) were conducted in each of three cross-shelf habitats (reef slope, back reef and lagoon). Fish were categorised into four functional groups: browsers, excavators, grazers/detritivores (referred to herein as grazers) and scrapers (following Hoey and Bellwood 2011). The number of observed fish, species, and genera were recorded for each functional group for each transect within each habitat at each location (the Great Barrier Reef and Ningaloo Reef). Then, mean abundance (individuals 100 m^{-2}), mean species richness, and mean genera richness were calculated for each habitat at each location. Differences in transect areas preclude direct comparisons of species or genera richness among locations.

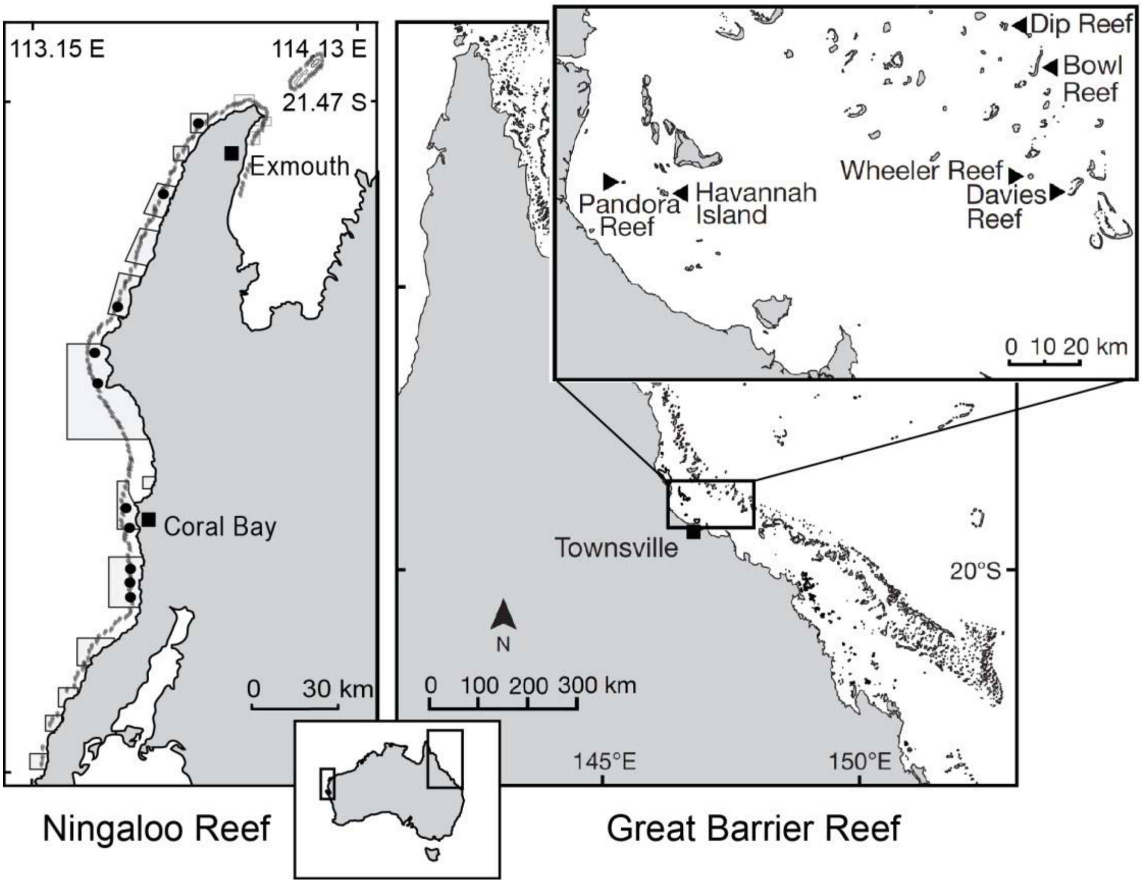

Fig. 5.1 Map showing the geographic location of Ningaloo Reef, Western Australia and the Great Barrier Reef off Australia's east coast. The location of the study sites on Ningaloo Reef (black circles) and the Great Barrier Reef (black triangles) are shown.

To assess reserve capacity we identified the most abundant species in each functional group on each transect as the numerically dominant species. Reserve capacity per transect was calculated as the proportion of fish that do not belong to this dominant species. The mean reserve capacity of each functional group in each habitat ($\overline{RC}$) was determined by the weighted average of the RC values per transect (e.g. weighted to fish abundance), which is simply the same as the proportion of all fish on all transects that do not belong to the dominant species:

$$\overline{RC} = \frac{\sum_{i=1}^{n}(RC_iA_i)}{\sum_{i=1}^{n}A_i} = \frac{\sum_{i=1}^{n}\left(\left(\frac{A_i - D_i}{A_i}\right)A_i\right)}{\sum_{i=1}^{n}A_i} = \frac{\sum_{i=1}^{n}(A_i - D_i)}{\sum_{i=1}^{n}A_i}$$

where A_i is the total fish abundance on transect i, D_i is the abundance of the numerically dominant species on transect i, and n is the total number of transects within each habitat. The weighted average was used, so that a reseve capacity value based on a transect with high total fish abundance is given a higher weight than a reserve capacity value based on a transect with low total fish abundance. Reserve capacity (rather than evenness) was used to emphasis the relative contribution of the numerically dominant species. Reserve capacity is more appropriate than other indices (e.g., evenness) as it quantifies the relative contribution of all numerically non-dominant species collectively rather than the relative contribution of individual species.

Among habitat variation in potential functional redundancy within each functional group and for all herbivorous fishes collectively was explored graphically for both reef systems. Namely, species richness was plotted against generic richness, and abundance was plotted against reserve capacity. A habitat with high species richness, generic richness, abundance and reserve capacity was considered to have higher potential functional redundancy.

Among habitat variation in mean species and generic richness and mean reserve capacity of each functional group in each reef system were analysed using generalised linear models. Species and generic richness are both discrete variables and were analysed using a Poisson regression. Reserve capacity was analysed using a logistic regression with the abundance of non-dominant species as ‘successes’, and the abundance of dominant species as ‘failures’. All regression models were performed in R using the glm package (R Core Team 2012). Variation in mean abundance of each functional group was compared among habitats within each reef system using an ANOVA. Abundance data were examined for normality and homoscedasticity using analysis of residuals, and no transformation was needed.

5.3 Results

Overall species richness and generic richness varied among functional groups, with grazers having the most species and genera on both Ningaloo Reef and the Great Barrier Reef (Table S15 in Appendix A). On Ningaloo Reef, a total of 44 species of herbivorous fishes were recorded, with 19 grazing, 13 scraping, 10 browsing and 2 excavating species. Grazing species belonged to five genera, scrapers to two, browsers to three, while excavators belonged to a single genus. On the Great Barrier Reef, 57 herbivorous fish species were recorded, consisting of 24 grazing, 18 scraping, 10 browsing, and five excavating species belonging to six, two, three and three genera respectively.

There were remarkably consistent cross-shelf patterns on both the Great Barrier Reef and Ningaloo Reef. Species richness, generic richness, abundance and reserve capacity of the four herbivore functional groups were all generally lower within inshore or coastal habitats compared to habitats further offshore (Fig. 5.2 and 5.3). These patterns were even more pronounced for herbivorous fishes as a whole (Fig. 5.4). On Ningaloo Reef the inshore habitat had significantly fewer species of browsers, grazers and scrapers than the offshore habitats (Table S16 in Appendix A). The number of excavating species was also lowest on the inshore Ningaloo Reef habitat, but only differed significantly from the mid-shelf habitat (Fig. 5.2c). Similarly, inshore habitats on the Great Barrier Reef generally had fewer species of scrapers and grazers than mid and outer-shelf habitats (scrapers: $p < 0.01$ for all pairwise comparisons; grazers: $p < 0.05$ for 22 of 24 comparisons; see Tables S17 and S18 in Appendix A for further details). Even within the species depauperate browsing and excavating groups the inner-shelf Great Barrier Reef habitats generally had fewer species than the mid- and outer-shelf habitats (Fig. 5.2b, d; Table S18 in Appendix A). Generic richness displayed broadly similar patterns with inshore habitats having fewer genera than the offshore habitats (Fig. 5.2), however, the limited number of genera within each functional group reduced the ability to detect significant differences. On Ningaloo Reef the inshore habitat had significantly fewer genera of grazers and browsers than the offshore habitats. Similarly, the number of genera within each of the

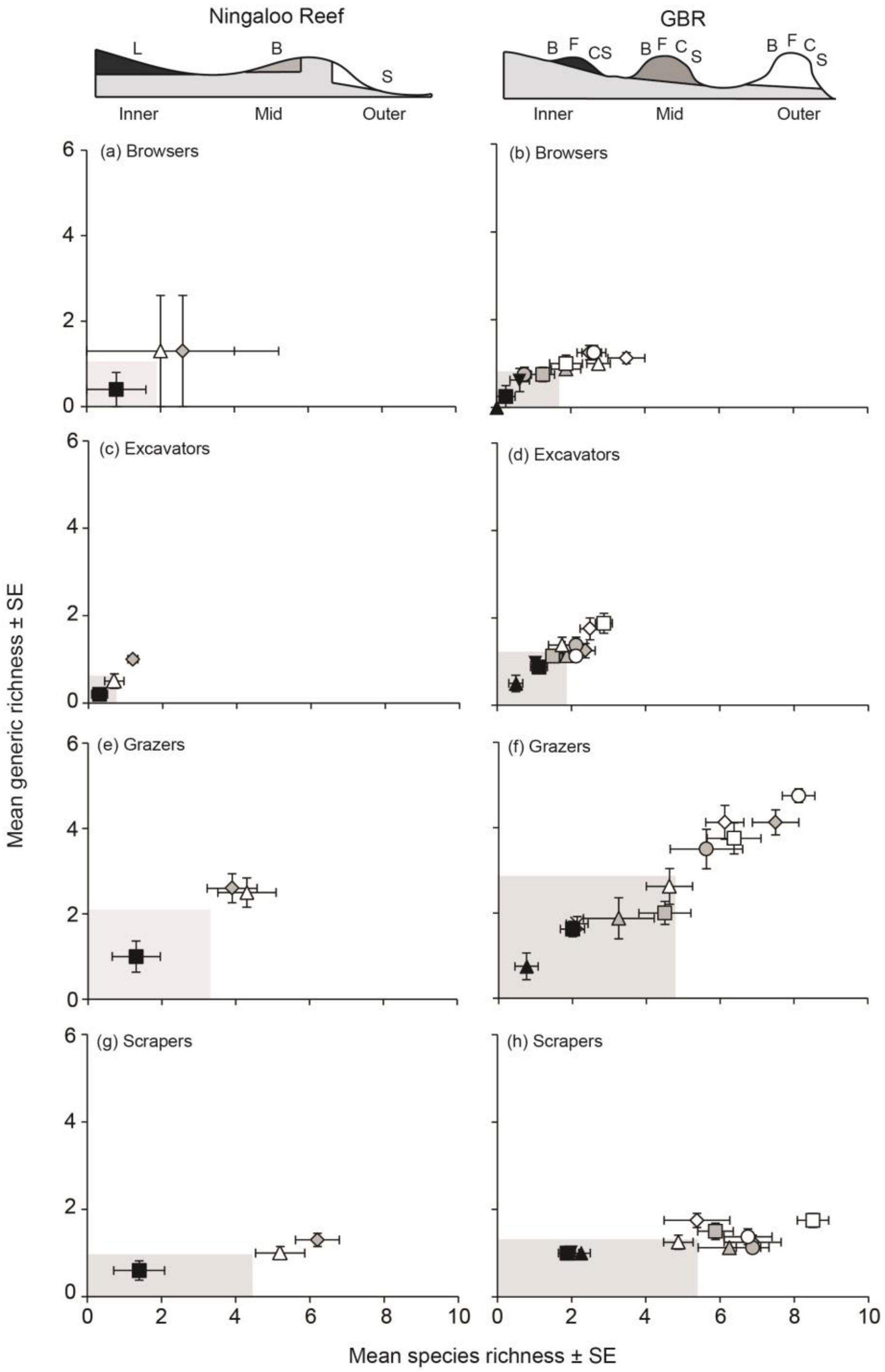

Fig. 5.2 Mean species richness and mean generic richness per habitat ± SE for four functional groups of roving herbivorous fish; a, b) browsers, c, d) excavators, e, f) grazers and g, h) scrapers, in different habitats within two reef ecosystems. Means are based on eight 590 m^2 transects on the Great Barrier Reef (GBR) and ten 1250 m^2 transects on Ningaloo Reef. For the Great Barrier Reef, symbols represent different habitats on the shelf locations: back (■), flat (▲), crest (♦) and slope (●), and crest/slope (▼). The colours of the symbols illustrate the different habitats (Ningaloo Reef)/shelf locations (Great Barrier Reef). The grey zones represent the species richness and generic richness below average for each functional group.

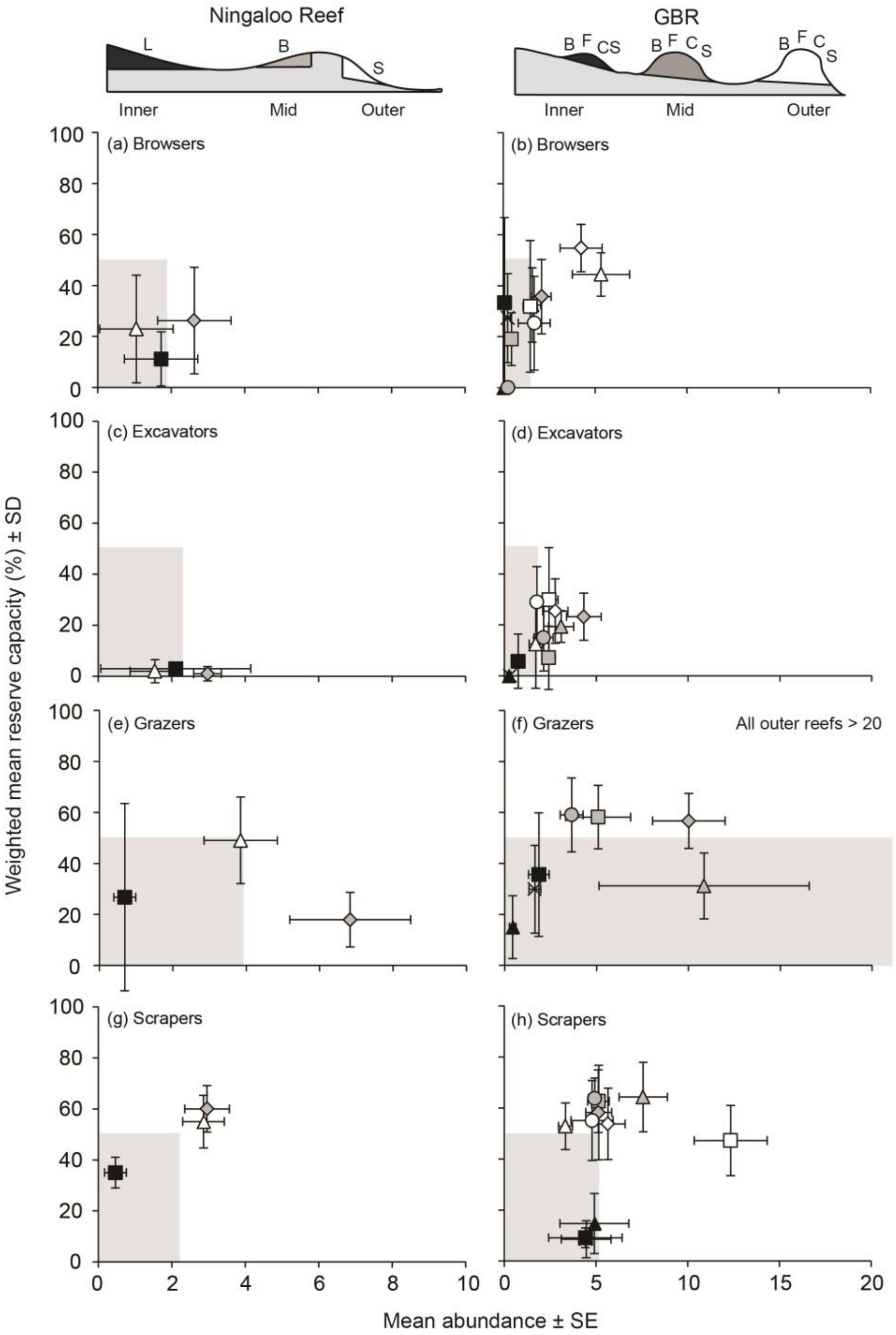

Fig. 5.3 Mean abundance (individuals 100 m^{-2}) ± SE and weighted mean reserve capacity (in %) ± SD for four functional groups of roving herbivorous fish; a, b) browsers, c, d) excavators, e, f) grazers and g, h) scrapers, in different habitats within two reef ecosystems, Ningaloo Reef and the Great Barrier Reef (GBR). Symbols and shading follow Fig. 5.2. The grey zones represent abundance below average, and reserve capacity below 50 %, indicating dominance by one species. Grazers on outer reefs have abundances greater than 20 individuals per 100 m^2 (see Fig. S5 in in Appendix A for full figure).

functional groups was consistently lowest within the inshore habitats on the Great Barrier Reef. With the exception of grazers ($p < 0.05$ for 16 of 24 comparisons), however, relatively few of these among-habitat differences were significant (Table S19 in Appendix A).

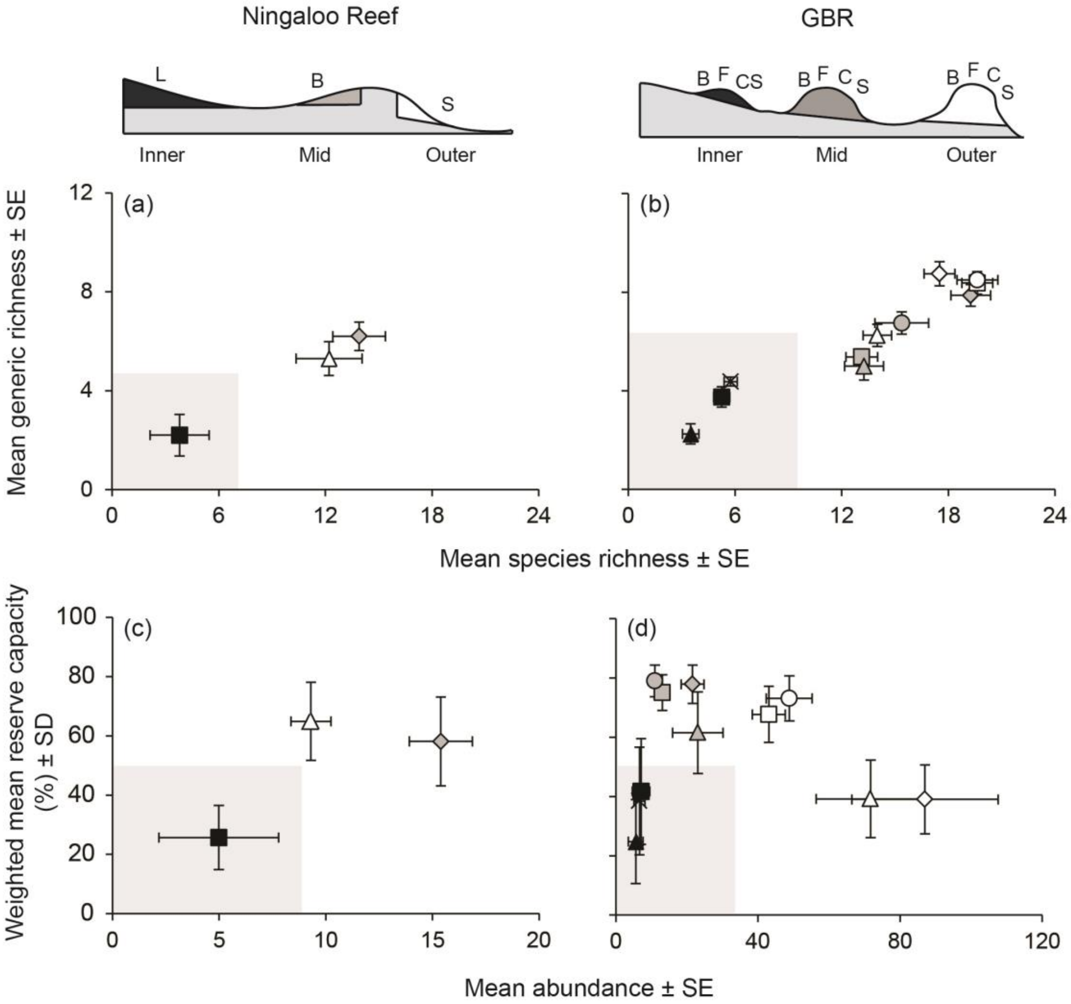

Fig. 5.4 Mean species richness and mean generic richness ± SE for the four functional groups of roving herbivorous fish combined; in different habitats within two reef ecosystems a) Ningaloo Reef and b) the Great Barrier Reef (GBR). And mean abundance (in number of observed individuals per 100 m^2) ± SE and weighted mean reserve capacity (in %) ± SD for the four functional groups of roving herbivorous fish combined; in different habitats within two reef ecosystems c) Ningaloo Reef and d) the Great Barrier Reef. Symbols and shading follow Fig. 5.2 and 5.3.

Abundance of fishes within each functional group varied significantly among habitats on both the Great Barrier Reef and Ningaloo Reef (Fig. 5.3; Table S20-21 in Appendix A). Abundances of each functional group were generally lowest on inshore habitats, however, high within-habitat variability limited the number of statistically significant differences detected (Table S20 and S22 in Appendix A). Reserve capacity was low (< 50 %) for the species depauperate browsers and excavators across most habitats in both reef systems (Fig. 5.3a-d). This was especially pronounced on inshore habitats (browsers: 0-33 %; excavators: 0-6 %) indicating that the processes delivered by these groups are dominated by a single species. Reserve capacity was more varied among the grazers and scrapers, with inshore habitats having significantly lower values than most offshore habitats on Ningaloo Reef and the Great Barrier Reef (Fig. 5.3e-h; Table S23-25 in Appendix A).

5.4 Discussion

Coral reefs, like many of the world's ecosystems, are in decline (Walther et al., 2002, Bellwood et al., 2004). Given the predicted increases in the frequency and severity of disturbances affecting coral reefs, the ability of reefs to persist into the future will depend, at least in part, on the level of functional redundancy within critical ecosystem process such as herbivory. Using four simple metrics that are inherent in most datasets (i.e., species richness, generic richness, abundance and reserve capacity) we estimated spatial variation in potential functional redundancy of herbivorous fishes on two of the world's most intact reefs systems; the Great Barrier Reef and Ningaloo Reef. Our results revealed remarkably consistent cross-shelf patterns in all four metrics for herbivorous fishes collectively, and the four functional groups (i.e., browsers, excavators, grazers and scrapers) independently. Strikingly, both potential functional redundancy and the intensity of each function were markedly reduced in coastal habitats of both reef systems suggesting that these habitats may be the most vulnerable to future disturbances. Coastal habitats consistently had the lowest species and generic richness, abundance and reserve capacity within each of the functional groups. The low levels of potential functional redundancy found among herbivorous fishes at these inshore locations indicate that the processes supported by these functional groups are not only dependent on a limited number of closely related species, but are also likely to have a limited ability to respond to disturbances. Indeed, the vulnerability of these reefs is highlighted by the transition of several inshore reefs on the Great Barrier Reef to macroalgal-dominance following disturbance (Done et al., 2007, Done, 1992, Diaz-Pulido et al., 2009, Cheal et al., 2010, Hughes et al., 2010).

Species richness has been widely used as a proxy for functional redundancy across a range of ecosystems (Jarvinen, 1982, Fraser and Currie, 1996, Gotelli and Colwell, 2001, Hope et al., 2003). While it provides an indication of the number of functionally similar species, species richness does not consider how the component species may respond to disturbances. Incorporating generic richness provides an additional dimension of redundancy by including a measure of potential response diversity (e.g., Pratchett et al. 2011). Collectively, species richness and generic richness provide valuable information on the number of species and genera contributing to a particular function and their potential responses to a disturbance event. However, they do not consider the relative contribution or importance of each species in performing the function. The number of individuals within a species or functional group can be reported either as absolute abundance, providing an indication of the intensity of the process, or as relative abundance of all non-numerically dominant species to the numerically dominant species (i.e., reserve capacity). Ecosystem processes with a strong numerical dominance of one species (i.e., keystone species) can be exceptionally sensitive to disturbances (Steneck et al., 2011). It is the abundance of species remaining, if the dominant species is lost, that might best indicate an abundance based capacity for redundancy. If the abundance of non-dominant species far exceeds that of the dominant species, redundancy is likely to be high. In contrast, where a process is supported by just one or two species (Bellwood et al., 2012, Hoey and Bellwood, 2009) the loss of just one species may equate to the local collapse of a crucial ecosystem process.

It must be noted, however, that the reserve capacity provides an instantaneous measure of the system's capacity to provide a specific function given the loss of the most abundant species, and an indication of the system's potential vulnerability. There remains the possibility of compensatory changes in the remaining species. With time, the remaining, previously uncommon, species may increase in abundance with the loss of the numerically dominant species (cf. Elmqvist et al. 2003; Folke et al. 2004). Alternatively, other groups may modify their functional status to exploit new opportunities (Bellwood et al. 2006). The capacity for compensatory changes depends on the nature and extent of response diversity within each functional group (Bellwood et al. 2004; Pratchett et al. 2011). A low reserve capacity merely indicates a limited short-term capacity to deliver the requisite function (although presenting a window of opportunity for outbreaks; Hoey and Bellwood 2011; Graham et al. in press) and a reduced likelihood of further compensatory change (given the lower number of species/individuals available to respond).

The combination of all four metrics; species richness, generic richness, abundance and reserve capacity has not been explored previously, yet each provides a different perspective of functional redundancy. The addition of reserve capacity, in particular, provides key information on the potential vulnerability of a location. Reserve capacity identifies functional groups that may appear resilient as a result of high abundances, but which may have a reduced capacity to cope with ecosystem disturbances due to the dominance of one species. In this situation high abundance of a single species should be recognised as a potential vulnerability (Steneck et al., 2011). Previous studies have identified vulnerable habitats or functional groups in coral reef ecosystems (Wilson et al., 2006, Bellwood et al., 2012). Studies on the Great Barrier Reef, for example, using species richness and abundance have inferred limited functional redundancy of herbivorous reef fishes on inshore reefs (Hoey and Bellwood, 2008, Cheal et al., 2012b, Cheal et al., 2012a). Our results support and expand these findings to show that inshore reefs on both Ningaloo and the Great Barrier Reef are likely to have more vulnerable herbivorous fish assemblages compared to offshore habitats or reefs, in terms of not only species richness and abundance but also generic richness and reserve capacity.

Our study identifies coastal habitats or reefs as areas of heightened vulnerability on both the Great Barrier Reef and Ningaloo Reef. Compared to habitats further offshore, coastal habitats displayed lower species and generic richness, lower abundance and reserve capacity across browsing, excavating, grazing and scraping fishes, and all herbivorous fishes collectively. Moreover, these critical ecosystem processes were all dominated by just one species within these coastal habitats. This raises the question why coastal reefs, in two protected reef ecosystems, appear to be so vulnerable. Interestingly, the coastal habitats on Ningaloo Reef and the Great Barrier Reef both exhibit fish assemblages with low functional redundancy and benthic communities with higher macroalgal cover compared to offshore habitats (Wismer et al., 2009, Johansson et al., 2010). On Ningaloo Reef, minimal coastal development suggests that these characteristics of inshore habitats are unlikely to be a result of direct anthropogenic impacts, and may be a natural feature of this system (Johansson et al., 2010). In contrast, inner reefs on the Great Barrier Reef have a history of compromised water quality due to terrestrial run-off (McCook, 1996, McCook, 1999, De'ath and Fabricius, 2010, Schaffelke et al., 2012) and these habitats with reduced water clarity appear to have a lower abundance of herbivorous fishes compared to off-shore habitats (Cheal et al., 2012a). The extent to which low herbivorous fish abundances are a natural feature of coastal Great Barrier Reef reefs or a result of anthropogenic stressors remains unclear. However, due to the low abundances and low levels of functional redundancy among herbivorous fishes, the capacity of coastal reef habitats to control algal outbreaks on Ningaloo Reef and the Great Barrier Reef appears to be limited.

5.5 Conclusion

Using four metrics to examine potential functional redundancy, in four key functional groups, across two coral reef systems: Ningaloo Reef and the Great Barrier Reef, we found remarkable congruence. In all metrics, groups, and systems, coastal habitats had less functional redundancy compared to non-coastal reefs, revealing considerable vulnerability to future disturbance. Coastal reef habitats on both Ningaloo Reef and the Great Barrier Reef may therefore have a reduced capacity to cope with change or to deal with macroalgal outbreaks. We suggest that this approach, combining four simple metrics that are inherent in most datasets; species richness, generic richness, abundance and reserve capacity, can act as a tool for estimating potential functional redundancy. Furthermore, in highlighting likely vulnerability for both functional groups and habitats, it offers a focus for areas of consideration when planning future management and conservation efforts.

Chapter 6: Concluding Discussion

The role of roving herbivorous fishes and sea urchins as algal mediators on coral reefs is well understood (Hoey and Bellwood, 2008, Bonaldo and Bellwood, 2009, Burkepile and Hay, 2006) but there is a pressing need to understand how these processes are distributed in the few intact reef systems remaining to successfully protect them. Ningaloo Reef, the largest west-coast continuous fringing reef in the world, is located in an arid region with minimal human development and anthropogenic disturbances and generally shares the same physical habitat characteristics to that of the Great Barrier Reef, albeit in a more compressed form (Cassata and Collins, 2008). The research in this thesis demonstrates unique coral reef characteristics for Ningaloo Reef, with large macroalgal stands and reduced levels of fish herbivory in the coastal lagoonal habitat coupled with high densities of sea urchins on the swell exposed reef slope, highlighting unexpected vulnerability in the lagoon and a potentially destructive sea urchin population on the slope habitat. Managing Ningaloo Reef to protect herbivores within the context of their diverse patterns of distribution, is essential to reduce the risk of Ningaloo Reef shifting from a coral dominated reef ecosystem to one dominated by macroscopic algae.

High densities of sea urchins and macroalgae have both historically been associated with degraded reef ecosystems and are hence often considered to be signs of reefs in decline (Mumby et al., 2006, Burkepile and Hay, 2009, Bak, 1990, Carreiro-Silva and McClanahan, 2001). Factors that tend to increase the biomass of algae, such as nutrient enrichment from terrestrial run-off (Schaffelke, 1999, De'ath and Fabricius, 2010), are not evident on Ningaloo Reef suggesting that high macroalgal cover may be a natural feature in this system. The research in this thesis demonstrates that both urchins and macroalgae can be widespread and highly abundant features of relatively undisturbed reef ecosystems (chapter 2). They may therefore not always be indicators of human impacts, declining reef health or degradation for this location. Surprisingly, only a handful of other studies have suggested that healthy coral reefs can have naturally high levels of macroalgae in close proximity to coral dominated reef habitats (Vroom et al., 2006, Vroom and Braun, 2010) highlighting the unusual benthic configuration of Ningaloo Reef. The presence of such widespread stands of algae could further directly influence the distribution of herbivorous fishes and how herbivory operates at Ningaloo Reef by providing shelter or food for certain species and functional roles. Further emphasising the unique characteristics of Ningaloo Reef is the high abundance of sea urchins on the reef slope. Given that all censuses were performed inside sanctuary zones, high urchin densities are unlikely to be a result of overfishing of known urchin predators. Instead, high urchin densities seem to be another natural feature of Ningaloo Reef. The high presence of sea urchins and macroalgae in a healthy reef system, therefore, suggests strongly that caution is needed when using them as indicative signs of reef degradation, especially in this system. However, their extensive presence at Ningaloo may be indicative of a heightened level of vulnerability to change. Based on this, Ningaloo Reef emerges as a rather unique reef system, with unusual benthic compositional characteristics.

The lack of top-down control of sea urchins by predators can significantly increase sea urchin populations (Lafferty, 2004, Carreiro-Silva and McClanahan, 2001). As seen in the Caribbean, relying on sea urchins as the sole organism responsible for herbivory can have catastrophic implications for the reef community and result in macroalgal dominance (Hay, 1984, Hughes, 1994). The high abundance of one dominant species of herbivorous urchins on Ningaloo Reef may therefore signal a potentially vulnerable system not driven by a lack of predators *per se* but possibly a lack of the ‘right predator’ (chapter 2). The absence of well-known pivotal balistid species from the present surveys on Ningaloo Reef, may well explain their low presence in the tethering experiment and the contrasting finding of labrids being the main predatory family on tethered *E. mathaei* at Ningaloo Reef compared to balistids as identified in both Great Barrier Reef and East African tethering experiments (Young and Bellwood, 2012, McClanahan, 1995, Wachenfeld, 1993). Although the high abundance of urchins is not a consequence of ecosystem degradation on Ningaloo Reef, their abundance and distribution should be carefully monitored. While urchins may have a functionally similar role to some herbivorous fishes on Ningaloo Reef (chapter 2), relying on sea urchins to functionally replace herbivorous fishes is not optimal due to the unpredictable nature of sea urchin populations.

Ningaloo Reef has distinct features which contrast sharply with many other coral reef ecosystems. Understanding the level of overlap within each functional group of herbivorous fishes within each habitat can therefore provide vital information about the potential capacity of these functional groups to cope with change on Ningaloo Reef. As chapter 5 reveals, the four metrics of herbivore presence; species richness, generic richness, abundance and reserve capacity, provide a highly detailed overview of the potential level of redundancy available within each herbivorous functional group in each habitat at Ningaloo Reef and the Great Barrier Reef. These metrics have previously never been combined to look at the level of redundancy until now. While independently important as evaluation tools to assess system redundancy, combined they provide an unprecedented detailed understanding of the level of redundancy available in a system, revealing ecosystem strengths, vulnerabilities and highlighting areas of particular sensitivity where conservation efforts should be concentrated. For example, reserve capacity identifies potentially vulnerable habitats by identifying functional groups that may appear resilient as a result of high abundances, but which may have a reduced capacity to cope with ecosystem disturbances due to an overwhelming dominance of a single species. The use of the four metrics revealed weakened herbivorous fish populations in coastal habitats on both Ningaloo Reef and the Great Barrier Reef in all metrics and for all functional groups. The coastal vulnerability found on the Great Barrier Reef is consistent with other studies, where low levels of herbivory and benthic shifts, from a coral dominated reef to one dominated by macroalgae, have been identified on inshore reefs (Cheal et al., 2012b, Cheal et al., 2012a, Hoey and Bellwood, 2008, Diaz-Pulido et al., 2009). Whether low herbivorous fish abundances are a natural feature of coastal reefs on the Great Barrier Reef or a result of anthropogenic stressors remains unclear. However, for Ningaloo Reef, this type of coastal vulnerability to disturbance is more likely to be a natural characteristic of the system. The low levels of herbivory and the extensive macroalgal beds present in this coastal habitat suggests that even a low-impact system, such as Ningaloo Reef, has a certain amount of inherent ‘fragility’.

Species and functional groups on coral reefs show varying degrees of dependency or association with different benthic habitats (Huijbers et al., 2011, Pratchett et al., 2011, Johansson et al., 2012). These habitat associations are likely to determine what species or functional groups might be more susceptible to disturbances, such as loss of live coral cover. While a wide range of responses have been recorded in herbivorous fishes following coral loss (Wilson et al., 2006, Graham et al., 2007, Pratchett et al., 2011, Cheal et al., 2008), the results in this thesis show that predicting responses to coral loss is complicated. Specific size-class differences between and among functional groups seem to depend on the varying levels of live coral, the corresponding structural complexity and other habitat characteristics (chapter 4). The strong association of small scrapers and excavators with live coral cover was clearly evident in the physically challenging slope habitat. In habitats where strong hydrodynamic processes are present, small fishes, with weaker and less developed physical characteristics can benefit from utilizing areas with reduced water movement (Johansen et al., 2008) and/or more complex habitats which provide a higher level of protection from predators (Almany, 2004). Other roving herbivorous fishes can, by schooling, gain the same benefits as provided by the habitat complexity of live coral (Barlow, 1974). The large, often single species, schools formed by the small grazer *A. triostegus* on Ningaloo Reef indicate a contrasting pattern to that seen in small scrapers and excavators which tend to forage in quite small groups on the slope. In this challenging environment, schooling provides an opportunity to increase mobility and hence foraging range perhaps explaining the reverse results found with live coral cover. The apparent breakdown of this pattern in calmer habitats for all functional groups of any size-class is interesting because it suggests that herbivorous fishes have no obvious dependency on coral for their survival. The results on Ningaloo Reef therefore highlight that the distribution of herbivores on reef systems is complex and dependent on each functional group, size-classes within these and environmental conditions.

The scarcity of large, pristine reef ecosystems makes the research in this thesis on Ningaloo Reef pertinent to our understanding of baseline herbivory and other reef processes. Overall, what this thesis shows is that factors often associated to reef degradation can be present and highly abundant in apparently healthy reef systems (chapters 2 and 3). High densities of sea urchins and macroalgae appear to be a natural characteristic of Ningaloo Reef, indicating that the presence of common signs of reef degradation may not always be cause for alarm. However, vulnerability of coastal areas was detected for all functional groups of herbivorous fishes at both Ningaloo Reef and the Great Barrier Reef, and levels of vulnerability should be considered when planning management strategies for coral reef resources. Maintaining coral systems in a coral dominated state is an often-stated management priority. It follows that careful consideration should therefore be given to the mechanisms and players that regulate benthic algae. A functionally strong and complete assemblage of herbivores is more likely to have the capacity to cope with disturbances and maintain appropriate levels of benthic algae, both pre- and post-disturbance. Managing for healthy herbivorous populations therefore increases the resilience of a reef ecosystem and subsequently reduces the chances of benthic shifts.

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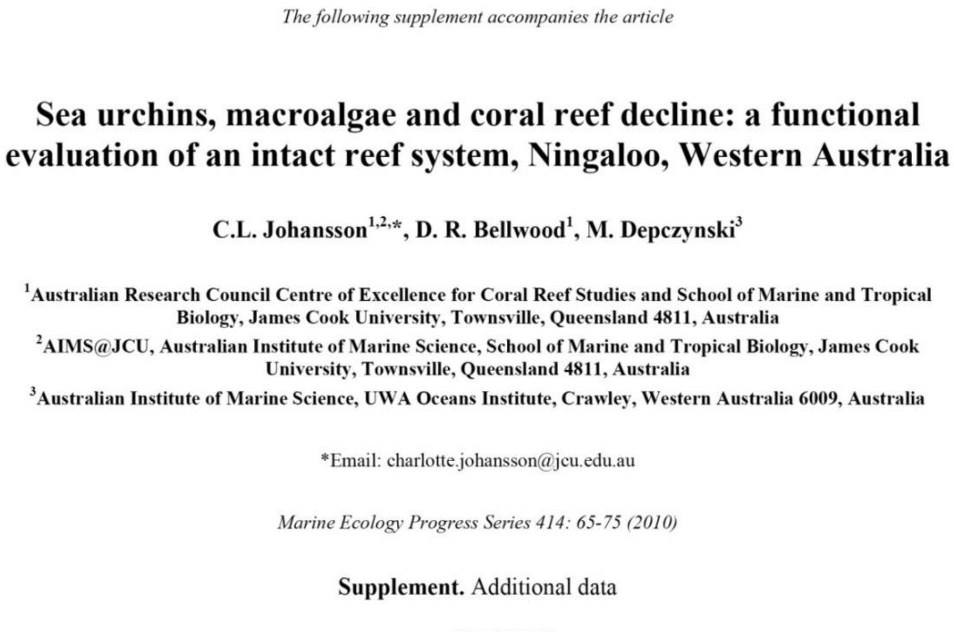
Appendix A: Supplementary Materials



The following supplement accompanies the article

Sea urchins, macroalgae and coral reef decline: a functional evaluation of an intact reef system, Ningaloo, Western Australia

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Supplement. Additional data

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SUPPLEMENTARY MATERIAL

Top-down versus bottom-up control of the sea urchin *Echinometra mathaei* (de Blainville) in an intact reef system, Ningaloo Reef, Western Australia

C. L. Johansson [a, b*], D. R. Bellwood [a], M. Depczynski [c] and A.S. Hoey [a]

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SUPPLEMENTARY MATERIAL

The importance of live coral for small sized herbivorous reef fishes in physically challenging environments

Johansson, C. L [1, 2*], Bellwood, D. R [2] and Depczynski, M [3]

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SUPPLEMENTARY MATERIAL

Key herbivores reveal limited functional redundancy on inshore coral reefs

Charlotte L. Johansson [1, 2*], Ingrid A. van de Leemput [3], Martial Depczynski [4],

Andrew S. Hoey [2] and David R. Bellwood [2]

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Appendix B: Publications arising from thesis

Sea urchins, macroalgae and coral reef decline: a functional evaluation of an intact reef system, Ningaloo, Western Australia

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The distribution of the sea urchin *Echinometra mathaei* (de Blainville) and its predators on Ningaloo Reef, Western Australia: The implications for top-down control in an intact reef system

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The importance of live coral for small-sized herbivorous reef fishes in physically challenging environments

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REPORT

Key herbivores reveal limited functional redundancy on inshore coral reefs

**C. L. Johansson · I. A. van de Leemput ·
M. Depczynski · A. S. Hoey · D. R. Bellwood**

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