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The effect of recreational fishing on targeted fishes and trophic structure, in a coral reef marine park

Mark B. Westera
Edith Cowan University

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The effect of recreational fishing on targeted fishes and trophic structure, in a coral reef marine park.

This thesis is presented for the degree of Doctor of Philosophy at Edith Cowan University

June 2003

Submitted by

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B. Sc. (Hons) Murdoch University, Western Australia
Abstract
Recreational line fishing is highly targeted at predatory fishes, making them vulnerable to overfishing. These same fishes play a role in trophic structure by regulating prey species. Despite increasing numbers of fishers, few studies have investigated the potential effects of recreational fishing on fish populations and subsequent trophic effects. This project investigated whether there were differences in fishes and benthos between unfished and recreationally fished areas, and whether the removal of targeted fishes influenced trophic structure. The study was conducted at the Ningaloo Marine Park, Western Australia, which had Sanctuary (no-take) and Recreation (recreationally fished) Zones. Data were collected from three regions (Mandu, Osprey and Maud) and replicated over time. Fish assemblages, benthos and trophic interactions were compared between zones at each region.

At Ningaloo the lethrinids (emperors) are a top-order predatory fish and the preferred target of recreational anglers. The algal-grazing urchin *Echinometra mathaei* comprised 51% of macroinvertebrate abundances and was heavily preyed upon by lethrinids, being recorded in 50% of the guts of sampled fish.

In all regions, Sanctuary Zones had a greater biomass of lethrinids than Recreation Zones, but there were no differences in non-targeted fishes between zones. Despite the consistent effect on lethrinids, there were inconsistencies among regions in the predator-prey relationships. At Mandu, *Echinometra mathaei* abundances were inversely related to lethrinid biomass, suggesting a strong predator-prey interaction. In the Recreation Zone, the abundances of *E. mathaei* were four times greater, and macro-algal cover was half, that of the Sanctuary Zone. Furthermore, algal composition differed between zones, and this was driven by fucoid brown algae, which dominated the diets of *E. mathaei*. This was interpreted as evidence of a trophic cascade resulting from the removal of lethrinids at the Recreation Zone.

At Maud, different results were recorded. Abundances of *Echinometra mathaei* and lethrinids were both higher in the Sanctuary Zone, than the adjacent Recreation Zone. *E. mathaei* reside in the crevices of rock, dead coral or *Echinopora* coral, which provided refuge from predation and this habitat was more available in the Sanctuary Zone. It is suggested that the availability of this habitat confounded the effects of predation. Macro-algal cover was lower in the Sanctuary Zone indicating a grazing effect from *E. mathaei*. At Osprey there was higher cover of *E. mathaei* habitat in the Sanctuary than the Recreation Zone. However, there were no differences in macro-algal cover, which was consistent with a lack of difference in *E. mathaei* abundances. The effect of *E. mathaei* grazing was unlikely to have been confounded by fishes that graze macro-algae, as they did not differ between zones at any region.
These results indicate that recreational fishing reduced fish populations below that of adjacent protected areas at Ningaloo Marine Park, and in one region this resulted in a trophic cascade. This may be the first study that has recorded evidence of a trophic cascade where recreational line fishing is the only means of extraction. However, the results also show that this is not a consistent response to reduced fishing pressure; in other regions, changes in predatory fish abundance did not result in differences in the abundances of their prey, suggesting no trophic cascade. The studies have contributed towards an understanding of fish-habitat interactions and provide a baseline for future monitoring of the Ningaloo Marine Park. They also have important implications for marine park managers in terms of defining their expectations when implementing Sanctuary Zones. The results also show that Sanctuary Zones have the potential to be effective tools for fisheries management.
Declaration

I certify that this does not, to the best of my knowledge and belief:

incorporate without acknowledgement any material previously submitted for a degree or diploma in any institution of higher education; contain any material previously published or written by another person except where reference is made in the text; or contain any defamatory material.

Signed .................................................................
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CHAPTER 1 - INTRODUCTION

1.1 THE ROLE OF MARINE PROTECTED AREAS AND MARINE RESERVES

A marine protected area (MPA) is an area of land and/or sea especially dedicated to the protection and maintenance of biological diversity, and of natural and associated cultural resources, and managed through legal or other effective means (IUCN, 1994). Objectives of MPAs are often set to: conserve biodiversity; preserve habitats; maintain essential ecological processes and life support systems; preserve genetic diversity; ensure the sustainable utilisation of species and ecosystems; and achieve sustainable fisheries (Colman and Simpson, 1998; Kelleher, 1999; National Research Council, 2001; Environment Australia, 2002; Airame et al., 2003). Numerous MPAs have been established worldwide, but many lack suitable protection for the biota within their boundaries, as extractive activities such as fishing are still permitted (Alder, 1996; Attwood et al., 1997; McClanahan, 1999a). However, some MPAs contain areas where extractive activities are excluded, known as marine reserves, sanctuary zones, no-take zones, no-fishing zones or marine harvest refugia.

Marine reserves, where fishing is excluded, have been successful in meeting some of the above MPA objectives. Studies have shown: increases in the abundance, biomass and size of fishes in reserves over time (Roberts, 1995a; Russ and Alcala, 1996a; Wantiez et al., 1997; Edgar and Barrett, 1999; Davidson, 2001) [and see reviews by Roberts et al. (2000) and Ward et al. (2001)]; differences between fished areas and reserves (Ferreira and Russ, 1995; Watson et al., 1996; Babcock et al., 1999; Chapman and Kramer, 1999; McClanahan et al., 1999; Chiappone and Sealey, 2000); and recovery of habitat when destructive fishing practices were halted (Badalamenti et al., 2002). Thus, some objectives have been met in terms of conserving species diversity and habitat. However, examples of marine reserves meeting other conservation objectives are less common (Turner et al., 1999).

If marine reserves are to maintain ecological processes, as is often stated in their objectives, performance measures are needed to assess whether this is being achieved. To ‘maintain’ implies that the system might stay the same, and there appears to be a presumption by marine reserve managers that this occurs, rather than empirical evidence demonstrating it. So how might a system respond ecologically when extractive activities are stopped? Babcock et al. (1999) recorded a complete shift in community structure over time due to the removal of fishing pressure in a marine reserve and McClanahan et al. (1989; 1994) showed changes in predation
and grazing regimes marine reserves. If the goal is to return a system to a more "natural" state then perhaps this is being met, however we would rarely know what the natural state was prior to it being exploited. Marine reserves may alter ecological processes so objectives may need to be broad enough to accommodate changes in marine systems. From both a management and an ecological perspective, therefore, a greater understanding is needed of how ecological functioning might change in marine reserves.

Despite fisheries management being an objective of marine reserves, there are few studies that have shown their effectiveness in enhancing fish stocks in adjacent fished areas (Roberts and Hawkins, 2000) as opposed to within their boundaries. There are two principle mechanisms by which marine reserves can enhance fish stocks in adjacent fished areas. Firstly, they can be expected to serve as a source of eggs and larvae due to increases in the abundance of mature fishes (Bohnsack, 1992; Roberts, 1997), and secondly, a spillover of fishes may occur as their abundances build up to a carrying capacity and they move across boundaries to fishable areas (Roberts and Hawkins, 2000; Ward et al., 2001). However, these processes are likely to be dependent on a number of factors, including currents that might distribute eggs and larvae (Jones et al., 1999; Chiappone and Sealey, 2000), the locomotory abilities of larvae (Armsworth et al., 2001; Leis and Carson-Ewart, 2001), and density-dependent factors (Kramer and Chapman, 1999). Spillover has been shown in some studies (Russ and Alcala, 1996b; McClanahan and Mangi, 2000) and another has shown increases in catches adjacent to reserves (Roberts et al., 2001) but due to the complexities of conducting studies on the dispersal of eggs and larvae, examples of this are difficult to find (Carr, 2000; Russ, 2001).

Emphasis on the potential of marine reserves as fisheries management tools has been growing (Rowley, 1994; Bohnsack, 1998) in parallel to, and perhaps because of, the overexploitation and collapse of many fish stocks worldwide (Myers et al., 1996; Botsford et al., 1997; Guenette and Pitcher, 1999). Overfishing has resulted from a combination of poor management (Ulltang, 1998; Russ, 2001) and improved technologies such as global positioning system and high powered boats that improve access to fisheries (Goni et al., 2000). Traditional fisheries management often relies on a single species approach (Castilla, 2000; National Research Council, 2001) and fails to recognise ecosystem complexity (Caddy, 2000), for example the removal of fishes influencing marine systems through changing predation, grazing or bioerosive regimes (McClanahan, 1997; Moellmann and Koester, 1999; Carreiro-Silva and McClanahan, 2001). However, fisheries managers may be sceptical of marine reserves as fisheries management tools, as they are often established for conservation purposes (Agardy, 1994; Ramos-Espla and McNeill, 1994) and may be located in areas of high biodiversity where fish densities may also be higher. Without well planned monitoring, comparisons of these and
adjacent fished areas may yield unrealistic results as differences in fish populations may be confounded by habitat or other artefacts from before the reserve was established. Fisheries managers may also claim that migratory species are unlikely to be protected by marine reserves, but this may be solved by creating them at aggregation sites or physical migration bottlenecks (Roberts and Hawkins, 2000).

Marine reserves also serve as experimental manipulation tools where we can increase our understanding of how undisturbed systems might function. The manipulation is the removal of humans from one experimental treatment (marine reserves), allowing populations of otherwise exploited prey to exist. Under these conditions, interactions between different levels of the biota may be compared with areas where exploitation continues. Without marine reserves, we would be unable to study undisturbed systems and to improve our understanding of sustainable management, resilience, recovery and other processes (Dayton et al., 2000).

1.2 THE VULNERABILITY OF FISHES TO RECREATIONAL FISHING

Most of the differences between marine reserves and fished areas have been shown where fishing pressure was from commercial or artisanal fishers and when a range of fishing methods was used including nets, spears, traps and lines (Russ and Alcala, 1989; McClanahan and Kaunda Arara, 1996; Rakitin and Kramer, 1996; Babcock et al., 1999; Chiappone et al., 2000). It is difficult to find studies that have examined the effect of recreational line fishing in coral reefs, probably because there are few areas where this is the only activity permitted. Exceptions from temperate waters are Davidson (2001), who recorded increases in the abundance of cod (*Parapercis colias*) when recreational fishing ceased and Bennett and Attwood (1991), who recorded improved catches of fish following establishment of a marine reserve.

Recreational fishing is increasing (Kearney et al., 1996), thus its potential to impact fish stocks will also increase. Recreational fishers are using advanced tools such as global positioning systems and echo sounders to increase their efficiency. Unlike many other forms of fishing, recreational line fishing relies on fishes taking bait from a hook and, therefore, focuses on carnivores. Fishers are driven by a desire to fish rather than a necessity and can afford the time to be selective. They generally target the most prized and palatable fishes such as lethrinids, serranids, haemulids and lutjanids (Cappo and Brown, 1996; Looby, 1997; Sumner et al., 2002). These fish are high in the trophic structure (tertiary consumers) of reefs (Hiatt and Strasbourg, 1960), but they are also vulnerable to overfishing as they have low rates of natural mortality, growth and recruitment (Russ and Alcala, 1998b). Overfishing of these fishes, therefore, has
the potential to affect lower trophic groups as reductions in the level of predation may allow prey species to increase.

Recreational fishing is a popular past time in developed countries. In Western Australia, there are approximately 643,000 people who partake in recreational fishing each year (Recfishwest, 2003) from a population of 1.9 million. In the USA, there were more than 17 million marine recreational anglers in 2001 who caught 455 million fishes and kept 41% of this catch weighing 121,000 tonnes (NOAA, 2003). This form of fishing has the ability to significantly impact fish stocks. For example, in 1997, intensive recreational fishing of snapper (Pagrus auratus) stocks in Shark Bay, Western Australia, lead to recruitment over-fishing (Department of Fisheries, 2002) and a decimation of fish stocks. A total fishing ban was implemented in 1998 and still remains while recovery is being monitored.

The impact of recreational fishing may be difficult to manage without information on the total amount of fishes caught. Commercial fishers are usually bound by mandatory reporting requirements and details on the amount and species caught can be used in future estimates of maximum sustainable yield. In comparison, data on total recreational catch relies on creel survey estimates that are often collected on an ad-hoc basis and may not accurately reflect long-term trends in total recreational catch. Comparisons of marine reserves and recreationally fished areas provide one of the few opportunities to assess whether recreational fishing has impacted fish stocks and the possible consequences on trophic structure. To date this has not been done and our understanding of the impact of recreational fishing remains debatable.

1.3 THE TROPHIC EFFECTS OF FISHING

A consequence of reductions in predators may be an increase in the population size of their prey through changes in the intensity of predation. In the marine context, this relationship has been shown for piscivorous fishes and fish prey (Beukers and Jones, 1998; Connell, 1998; Moellmann and Koester, 1999), invertivorous fishes and urchins (McClanahan and Muthiga, 1989; Sala and Zabala, 1996; Carreiro-Silva and McClanahan, 2001) and lobster and urchins (Mann, 1982b; Shears and Babcock, 2002). In each case, the decline in predators was due to overfishing. These predator-prey relationships are often driven by keystone species, i.e. species whose impact on their community, or an important component of it, is disproportionately large relative to their abundance (Power et al., 1996).

Logically, any changes in predator-prey relationships could have a flow-on effect to the food source of the prey, usually primary producers. This phenomenon, known as a trophic cascade
(Strauss, 1991; Pinnegar et al., 2000) has been shown in marine (Ruttenberg, 2001; Daskalov, 2002; Shears and Babcock, 2002), aquatic (Agrawal, 1998; Pace et al., 1998; Bell et al., 2003) and terrestrial (Dyer and Letourneau, 1999; Schmitz et al., 2000; Ripple et al., 2001) systems. One of the best known examples of a trophic cascade was the reduction of sea otters through hunting, that lead to an increase in the abundance of their prey, grazing urchins, and a loss of kelp forests (Estes and Palmisano, 1974). In a terrestrial case, the reintroduction of wolves in Yellowstone National Park altered the grazing behaviour of elks and lead to changes in the structure of aspen (Ripple et al., 2001). Marine reserves in MPAs provide the experimental basis for detection of trophic cascades in marine systems, as they allow comparisons between fished and adjacent unfished zones (Pinnegar and Polunin, 1999; Castilla, 2000). This was the situation in a New Zealand marine reserve where increases in predatory fishes and lobster reduced the abundance of grazing urchins through predation (Babcock et al., 1999; Shears and Babcock, 2002; 2003). Urchin barrens, which were previously dominated by crustose coralline algae, changed to macro-algal dominated habitat due to reduced grazing in the reserve.

Predator-prey interactions, and trophic cascades, may not always be predictable. Sala (1998a) stated that other processes may be important in regulating algal assemblages, including the availability of refuges, recruitment processes, pollution and disease. McClanahan et al. (1998) also showed the importance of crevices in the reef substrate in providing refuges for urchins from predators and mediating the effect of predation.

1.4 THESIS AIMS AND OVERVIEW

There is a lack of studies that compare unfished and recreationally fished areas, despite an increasing number of recreational fishers and their potential to affect fish stocks and trophic structure. Changes in trophic structure have been shown in marine systems where commercial or artisanal fishing is the dominant type of fishing (McClanahan and Muthiga, 1989; Babcock et al., 1999; Moellmann and Koester, 1999; Daskalov, 2002), possibly because of the intensity of fishing, mismanagement, or a lack of regulations that resulted in overfishing. However, recreational fishing also has the potential to affect trophic structure if the intensity of fishing is high and keystone species are targeted. There is a need to improve our understanding of the effects of recreational line fishing on targeted fishes and their associated benthic communities, and whether recreational fishing affects trophic structure. Other researchers have also cited the need for more studies to improve our understanding of interactions between fishes and their habitats, particularly in the eastern Indian Ocean (Roberts, 1995; McClanahan, 1997; Jones and Syms, 1998; Pinnegar et al., 2000).
The aim of this project was to investigate whether there were differences in fish assemblages and benthos between unfished areas and those areas where recreational line fishing was the only form of extraction, and to determine whether the removal of targeted fish species under this type of fishing regime influenced trophic structure and lead to a trophic cascade.

Examining trophic cascades requires a stepwise approach, starting with the removal of humans as top-level predators. Marine reserves and fished areas provide the comparative areas that allow us to examine the effect of humans on targeted fishes. If differences in fish populations existed, as a consequence of recreational fishing, the next questions would be: had there been a flow-on effect to their prey, and had changes in their prey affected their food source? The research presented in this thesis took advantage of an opportunity to address these questions using established marine reserves in a Marine Park (Ningaloo Marine Park) where the only extraction in adjacent areas was by recreational line fishing.

The research was constructed, and is presented as three discrete papers. The aim of Paper I (Chapter 2) was to test whether there were differences in populations of targeted fishes between marine reserves and recreationally-fished areas where: size and bag limits were applied; regulatory compliance was high; and recreational line fishing was the only form of extraction permitted. In Paper II (Chapter 3) the aim was to test whether there were different levels of predation between unfished and recreationally-fished areas and whether differences in the degree of predation by invertivorous fishes was reflected in the populations of dominant prey types. Paper III (Chapter 4) outlines investigations into interactions between grazing prey and primary producers. It relates these back to predator and prey abundances and whether these provide evidence of a trophic cascade as a result of recreational fishing. These papers are followed by a discussion section (Chapter 5) that synthesises the work and provides conclusions and recommendations for management based on the research. The study also provided the opportunity to examine whether there had been a build-up of fishes at a marine reserve. This was not an original objective of the project, but a resultant short communication (Chapter 6) has been attached to this thesis as it provided information on the most targeted fish family in the region and how it had changed over time at one of the study sites.

As this thesis has been constructed as a compilation of papers, some repetition was inevitable. Each paper required an introduction to marine protected areas and draws on the research of others to define specific hypotheses. References for all papers have been placed in one section at the end of the thesis.
1.5 THE NINGALOO MARINE PARK

A suitable area to conduct this study was the Ningaloo Marine Park in Western Australia, which had Sanctuary Zones that were closed to fishing and Recreation Zones where recreational line fishing was the only extractive activity allowed. Compliance with bag and size limits was very high (Sumner et al., 2002). Beach netting and spearing were permitted in some small designated areas, but were generally not allowed. Under these circumstances, it was possible to compare unfished and recreationally fished areas, where differences may be restricted to larger legal-sized predators that could be captured by line. There were no published comparisons of fish or benthic assemblages from Sanctuary and Recreation Zones at Ningaloo when this project commenced.

Ningaloo Marine Park is in the Indian Ocean on the Northwest Cape of Western Australia (21°40'S to 23°30'S and 113°45'E). It spans approximately 260 kilometres of coastline (Figure 1.1) and has been defined by the World Conservation Union (IUCN) as a coral reef of international significance. The Western Australian state waters (to three nautical miles offshore) are protected under the Conservation and Land Management Act 1984. The Commonwealth waters (to approximately 10 nautical miles offshore) are protected under the Environment Protection and Biodiversity Conservation Act 1999. This project was conducted in the state waters of Park.

Three regions of the Marine Park (Mandu, Osprey and Maud) were selected to conduct this study (Figure 1.1). These regions were chosen as each had comparative coral lagoon areas in a Sanctuary Zone and an adjacent Recreation Zone. Recreation Zones in each region were also subject to higher levels of fishing pressure than other regions and might therefore be the first to show an effect of fishing on fish assemblages. Other Sanctuary Zones in the region were not suitable as they were gazetted for a special purpose or were remote and not subject to comparatively high levels of fishing pressure.

The Marine Park was established in 1989 and Sanctuary Zones were implemented in 1991. However an isolated fishing exclusion zone has been in place at Coral Bay since 1984. Anecdotal evidence indicated that the Ningaloo region was heavily fished prior to the Marine Park's establishment (Weaver, 1998). There was a reduction in bag limits for some species in 1994 that may have relieved pressure on targeted fish stocks, but due to an increasing number of fishers visiting the region (Shaw, 2000) fishing pressure is likely to increase.

Much of the Marine Park is a lagoon with areas dominated by algae, coral or sand. There are long shore gutters and a fringing back reef between 200 m and 6 km offshore and a reef flat
generally less than 150 m wide (CALM, 1989). Tidal range is approximately 2 m and water
temperature ranges from 22.6°C in July to 30.7°C in January (pers. ob.). In some locations,
the coral reef is only tens of metres from shore, making it highly accessible to fishers and
tourists. The region is prone to cyclone activity between December and April, and in 1999,
suffered one of the most powerful cyclones to hit Australia. Fortunately there was no obvious
large-scale damage to corals in the lagoon areas that were examined in this study.

Corals at Ningaloo escaped the large scale bleaching suffered by other Australian coral reefs
such as Scott Reef and the Great Barrier Reef (Wilkinson, 2002). However, Ningaloo Reef was
subject to an outbreak of a corallivorous snail, Drupella cornus, in the 1980s which caused a
widespread loss of live corals, particularly in the northern parts of the Marine Park (Forde,
1994). Speculation arose about the role of predation in regulating populations of D. cornus with
some people from the region believing that the increases in Drupella were due to overfishing.
One fisher stated that lethrinids were full of Drupella shells when he gutted them (Weaver,
1998).
Figure 1.1: Location of study sites (●) in the Ningaloo Marine Park, Western Australia. Note the Mandu, Osprey and Maud Sanctuary Zones, which are shaded.
CHAPTER 2 - DIFFERENCES IN RECREATIONALLY TARGETED FISHES BETWEEN PROTECTED AND FISHED AREAS OF A CORAL REEF MARINE PARK.

Abstract

Many comparisons have been made between Sanctuary (no fishing) and fished areas, where fishing pressure is exerted by artisanal or commercial fishers, but few have examined the effect of recreational fishing on fish assemblages in coral reef habitats. In this study, comparisons were made of assemblages of targeted fishes from coral reef habitats in marine reserves and recreationally fished zones of a marine protected area. Surface visual census (SVC) transects were conducted two times, at three regions, to compare the composition of predatory fish assemblages and the abundance, biomass and size of the most commonly targeted fishes. Baited remote underwater video (BRUV) was used to make relative counts of fishes between zones. Benthic cover and rugosity were also measured as they may influence fish assemblages. ANOSIM revealed significant differences in the composition of fish families/genera targeted by fishers (Lethrinidae, Lutjanidae, Haemulidae, Serranidae and the genus Choerodon of the family Labridae) in terms of biomass ($P < 0.01$) and abundance ($P < 0.05$). The most consistent trends were recorded for biomass and this was supported by clustering of replicates in nMDS ordinations. SIMPER analysis indicated that the family Lethrinidae accounted for 73% (as abundance), and up to 69% (as biomass), of the dissimilarity between zones. Three-factor ANOVA highlighted significantly greater biomass, size and abundance of legal-sized lethrinids (the most targeted family in the region) in Sanctuary Zones, but no differences in other families/genera. Results of BRUV supported SVC with greater relative counts of lethrinids ($P < 0.01$) in sanctuaries, but no significant differences for other families. Cover of Acropora coral and hard substrate differed between zones at some regions but differences were inconsistent. There were no significant differences in algal cover or rugosity between zones. Given the inconsistency in benthic cover, the similarity of rugosity between zones, the consistently greater biomass of lethrinids in sanctuaries, and the abundance of large lethrinids in sanctuaries, the cessation of fishing in Sanctuary Zones appears responsible for observed differences in the populations of these fishes. These results demonstrate that recreational fishing pressure may be sufficient to deplete fish populations below that of adjacent protected areas and that the effect of recreational fishing in coral reef habitats may be greater than previously thought.
2.1 INTRODUCTION

A common objective of Sanctuary or unfished zones in marine protected areas (MPAs) is to help maintain viable fisheries in adjacent areas by reducing collapses of fish stocks, increasing the density and sizes of fish and providing centres for dispersal of individuals and larvae (Kelleher, 1999). Many studies have demonstrated a recovery of fish populations after fishing exclusion zones have been declared (Roberts, 1995a; McClanahan and Kaunda Arara, 1996; Russ and Alcala, 1996a; Wantiez et al., 1997) and fished and unfished areas have been shown to differ in abundance, biomass and numbers of species of fish (Watson and Ormond, 1994; Rakitin and Kramer, 1996; Roberts and Hawkins, 1997; Babcock et al., 1999; McClanahan et al., 1999; Chiappone et al., 2000). Differences have, however, usually been detected when fishing included: a number of methods such as spears, nets, traps and lines that may affect a range of species; intense fishing pressure; little or no regulation; or pressure exerted by commercial or artisanal fishers. Fewer studies have compared fished and unfished coral reef areas where there are only recreational line fishers. Line fishing may have a different effect because it is: selective for particular species; less intensive than netting or trapping; influenced by the abilities of the fisher; and controlled by recreational desire rather than economic necessity. Differences between areas may be smaller where line fishing is the major method.

The aim of this study was to test whether there were differences in the populations of targeted fishes between Sanctuary and fished areas where: size and bag limits were applied; regulatory compliance was high; and fishing pressure was exerted by recreational line fishers only. A further aim was to test whether Sanctuary areas preserved or enhanced the biomass of mature sized fishes. A suitable location for the study was Ningaloo Marine Park in Western Australia. This region had areas closed to fishing (Sanctuary Zones), minimum size and bag limits for predatory fishes, and fishers appeared to comply with regulations. Beach netting and spearing were permitted in some small designated areas, but were generally not allowed. Recreational fishing, but not commercial fishing, was permitted in Recreation Zones. Fishing pressure along the reef varied (CALM, 1999; Sumner et al., 2002) due to variable access. In some locations, the coral reef is only tens of metres from shore, making it highly accessible to fishers and tourists. Under these circumstances, it was possible to compare fished and unfished areas where differences may be restricted to larger legal-sized predators that could be captured by line. The Marine Park was established in 1989 and Sanctuary Zones were implemented in 1991. Anecdotal evidence indicated that the region was heavily fished prior to this time (Weaver, 1998).

Three hypotheses were posed to test whether there were differences in targeted fishes between Sanctuary and recreationally fished areas in fringing coral reef habitats of Ningaloo Marine
Park: (1) there was a difference in the composition of fish families between zones; (2) the abundance, biomass and size of fishes was greater in Sanctuary Zones; and (3) the abundance of legal-size fishes was greater in Sanctuary Zones. Habitat characteristics in Sanctuary and fished zones were compared, as they may confound any observed differences in fish assemblages (Garcia-Charton and Perez-Ruzafa, 1999). As Sanctuary Zones may lead to increases in both the density and average size of individuals, fish assemblages were compared using abundance, biomass and size measures. Measures of abundance were used to address questions of density differences, and biomass allowed a greater comparative contribution from larger individuals. Before vs. after comparisons could not be made, as no data had previously been collected. Given this lack of information, the study will also serve as a baseline, enabling future monitoring and performance assessment of Sanctuary Zones in the Ningaloo Marine Park.
2.2 METHODS

2.2.1 Study areas and experimental design

Ningaloo Marine Park is in the Indian Ocean on the Northwest Cape of Western Australia (21°40'S to 23°30'S and 113°45'E) (Figure 2.1). Much of the Marine Park is a shallow lagoon with deeper long shore gutters and a fringing back reef between 200 m and 6 km offshore, with the reef flat generally less than 150 m wide (CALM, 1989).

Fish assemblages were compared between Sanctuary and Recreation Zones in the Mandu, Osprey and Maud regions of the Marine Park (Figure 2.1). These were the only regions that could be used, as it was imperative that each had broadly comparable habitats between zones to reduce any confounding effects. The regions were also chosen as they were subject to a comparatively high level of fishing pressure (in Recreation Zones) than other parts of the Marine Park (CALM, 1999; Sumner et al., 2002) and would most likely be the first to show an effect of fishing. Creel survey data (Sumner et al., 2002) identified the Lethrinidae as the most targeted in the region (Table 2.1).

Figure 2.1: Location of study sites (•) in the Ningaloo Marine Park, Western Australia. Note the Mandu, Osprey and Maud Sanctuary Zones.
Table 2.1: Fish families targeted, within the Ningaloo region, and caught from locations at or near (< 2 km from) the study sites (from Sumner et al. 2002). "Others" include species not common at the study sites (e.g. Carangidae, Scombridae, and Platycephalidae) that may frequent sand or deeper waters beyond the reef crest.

<table>
<thead>
<tr>
<th>Targeted families</th>
<th>Percentage of overall catch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Targeted</td>
</tr>
<tr>
<td>Lethrinidae</td>
<td>43</td>
</tr>
<tr>
<td>Serranidae</td>
<td>2</td>
</tr>
<tr>
<td>Lutjanidae</td>
<td>1</td>
</tr>
<tr>
<td>Haemulidae</td>
<td>0.2</td>
</tr>
<tr>
<td>Choerodon spp.</td>
<td>0.2</td>
</tr>
<tr>
<td>Others</td>
<td>54.6</td>
</tr>
</tbody>
</table>

The sampling sites at zones within each region were comparable in terms of general habitat type (i.e. coral lagoon), depth, distance from shore and proximity to channels. Depth at the study sites was 1.5-2 m. Sampling was repeated in January and July 2000 to test whether patterns in fish assemblages between zones were consistent over time. Zones within each region were sampled one day apart and at the same time of the day to minimise any confounding effects from changes in tide, lunar phase or weather. The locations were not common dive sites where fishes may have become tolerant of divers. Comparisons of fishes were made at the family or genus level as it had been noted that fishers would keep any individual species from a particular family or genus they were targeting.

2.2.2 Census of the fish community

Surface visual census (SVC)

Predatory fishes were censused by swimming on the surface along four haphazardly located transects of 250 x 10 m in each zone and region. Orientation of transects was determined using randomly generated compass bearings. Fishes were counted, identified to species level and their size was estimated to within 10 cm. The accuracy of size estimates was tested using objects of known length. SVC was used to reduce any effects of fishes interacting with SCUBA divers, as larger predatory fishes were wary of SCUBA during pilot trials. The width and length of transects was determined using markers and global positioning system. To minimise bias, the same observer (M. Westera) conducted all fish censuses. Plots of species abundance against area sampled indicated that 90% of all species were recorded in the first two (of four) transects.
Underwater visual census (UVC) and SVC methods were compared on the most common serranid in the region, *Epinephelus rivulatus*. As this species hides under ledges and coral plates, it was possible that SVC might underestimate its abundance. However, there was no significant difference between methods (t-test, \( P > 0.05, n = 4 \)) and SVC was considered suitable.

The mean size of the dominant fish family was calculated to determine whether fishes were smaller in fished areas. The mean size was calculated for each transect \((n = 4)\), using the equation: \[ \Sigma (\text{midpoint of each size class} \times \text{number of fish in that size class}) / \Sigma (\text{total number fish in each size class}). \]

The abundance of under-size and legal-size lethrinids (those that can and cannot be legally taken by fishers) was compared between zones. Length at maturity corresponded with legal-size for *Lethrinus lentjan* (Lacepède), *Lethrinus atkinsoni* (Seale) and *Lethrinus laticaudis* (Alleyne and Macleay), i.e. 28 cm. *Lethrinus nebulosus* (Forsskål) matures at 38 cm (Moran et al., 1993; Agbayani, 2002) but the legal-size is 41 cm. Fish abundances were split between size-classes that corresponded to the legal-size. For *L. lentjan*, *L. atkinsoni* and *L. laticaudis*, 80% of the 20-30 cm size class was added to the under-size fish and 20% was added to the legal-size fish (i.e. 20-28 cm fish were under-size and 28-30 cm were legal-size). Similarly, for *L. nebulosus*, 10% of the 40-50 cm size class was added to the under-size fish and 90% was added to the legal-size fish. It was assumed that there was an even distribution of fishes within the size classes that were split.

**Baited Remote Underwater Video (BRUV)**

Video cameras were placed on the seabed in haphazardly chosen locations, similar to other studies (Bortone et al., 1991; Cappo and Brown, 1996; Babcock et al., 1999; Willis et al., 2000). A bag containing bait was placed in front of the camera and the activity of fishes was recorded for 30 minutes at 12 replicate locations in each zone. During filming, divers and the boat vacated the area. Footage was viewed on a television screen and the number of fishes that entered the field of view was counted. Lengths of fishes were estimated by placing the bait bag 1.5 m from the camera and calibrating the focal width at that distance. BRUV provided relative counts of fishes between zones, overcame any observer biases or interactions with fishes and validated the findings of SVC. There was the potential to make duplicate counts of fishes, but it was assumed that behavioural patterns of each species did not differ between zones. BRUV was not conducted at Osprey on either trip or Mandu in July due to time and weather constraints.
Spatial comparisons of abundances of fishes may be confounded by short-term temporal variations in weather, time of day, tidal or lunar effects (Kingsford and Battershill, 1998). To account for such effects, short-term variability was measured by repeating the BRUV survey at the Mandu Recreation Zone, three days apart. There was no significant difference in the counts of any of the five major fish families/genera (Lethrinidae, Lutjanidae, Haemulidae, Serranidae or Choerodon spp.) between days (t-test, $P > 0.05$), indicating that short-term variability was negligible. Due to the availability of cameras, four replicates were used for this test, whereas 12 replicates were used for between zone comparisons.

**Biomass of fishes**

Length-weight relationships were determined for Lethrinidae, Lutjanidae, Serranidae and Haemulidae using the equation: biomass = constant x length$^{\text{exponent}}$. Greater than 10 individuals in each family were weighed and measured but length-weight relationships from Kulbicki et al. (1993) were used for Choerodon spp. due to their low abundance in the study areas. Due to the low number of fishes captured, biomass estimates were also calculated using the length-weight relationships of Kulbicki et al. (1993), which yielded almost identical results.

**2.2.3 Description of habitat**

Benthic cover was measured to determine whether any observed differences in fish variates were related to differences in habitat. A video camera was held 50 cm above the substrate and moved along eight replicate 50 m transects in each zone and region. Transects were haphazardly placed in the same area as the SVC transects. From the video footage of each transect, 50 randomly-selected frames were analysed and substrate cover was grouped into five broad categories: Acropora coral cover; other coral cover; turfing algae (fine filamentous species); algal assemblage (all algal species except turfing such as Sargassum, Turbinaria, Dictyota, Hypnea, Caulerpa and Lobophora species); and total hard substrate cover. Video footage was viewed on a computer screen to determine the substrate cover type under 10 points on each frame. Plots of categories against area sampled indicated that 22 frames with 10 points per frame were sufficient to capture all categories. Fifty frames were analysed from each transect amounting to a total of 500 points per transect (4000 points per zone in each region). Algal and coral collections were used to verify identifications.

Rugosity was estimated by measuring the depth at the surface of the substrate, every metre along each benthic transect. A contour distance was calculated using the difference in depth at
each metre along the transect. Rugosity was analysed as the straight-line distance divided by
the contour distance (McClanahan and Shafir, 1990; Friedlander and Parrish, 1998) and
compared among transects and regions as an index of spatial relief.

2.2.4 Statistical analyses

Analyses were conducted to examine spatial trends in the composition of fish families/genera
and benthic cover between zones and among regions, and to identify which fishes, or types of
benthic cover, were driving any observed differences. This approach required the use of
multivariate and univariate techniques.

Multivariate analyses

Multivariate analyses were conducted using the PRIMER statistical package (PRIMER-E Ltd,
2000). Non-metric multidimensional scaling (nMDS) (Field et al., 1982) was used to examine
spatial patterns. Two-way crossed analysis of similarity (ANOSIM) (Clarke and Warwick,
1994) was used to determine the significance of spatial trends (for each time sampled) in fish
family composition (abundance and biomass) and benthic cover (percentage cover) between
zones and among regions. The tests were based on a Bray-Curtis rank similarity matrix,
calculated using square root transformed data. Time was not factored into multivariate analyses
as it was expected that fish assemblages would change over the 6-month study period
(Letourneur, 1996a; Rooker et al., 1997). The study was primarily focussed on differences in
fish composition between zones, not with changes between the two times sampled. One-way
ANOSIM was also used to determine the significance of any clustering of replicates, within
each region, in nMDS ordinations. Similarity percentages (SIMPER) (Clarke, 1993) were used
to examine individual contributions to any observed differences in fish composition or benthic
cover.

Univariate analyses

A three-factor orthogonal, mixed model, analysis of variance (ANOVA) (time, region and zone
as factors) was used to compare the abundance, biomass and size of the dominant fish
families/genera and benthic cover. Two-factor ANOVA was used to compare rugosity
measurements between regions and zones for one time. Interactions between factors were
analysed using multiple comparisons with the test slices function in the SAS statistical
Sampling time was treated as a random factor. As mentioned, only certain regions could be used for this study. Regions were chosen that had comparable habitats in Sanctuary and adjacent Recreation Zones and that also had a high level of fishing pressure compared with other Recreation Zones at Ningaloo. Zones were chosen to represent fished (Recreation) and unfished (Sanctuary) areas. Given that the choices of region and zone were not random, they were treated as fixed factors. BRUV data were compared between zones using T-tests. Data were tested for homogeneity of variance using Cochran's test and transformed if they were heterogeneous $[\log_{10}(x+1) - \text{fish data}; \text{arcsine and } \log_{10}(x+1) - \text{benthic cover data}]$. Student-Newman-Kuels post-hoc testing was used to determine what was driving differences in ANOVA.
2.3 RESULTS

Twenty-three species of recreationally targeted fishes were recorded in the SVC and BRUV (Table 2.2), the most common being *Lethrinus nebulosus*, *L. lentjan*, *L. atkinsoni*, *Lutjanus fulviflamma* (Forsskal), *Plectorhinchus chaetodontoides* (Lacepède) and *Choerodon schoenlenii* (Valenciennes).

2.3.1 Surface visual census

Multivariate analyses

Replicate samples for fish composition (Lethrinidae, Lutjanidae, Haemulidae, Serranidae and *Choerodon* spp.) from Sanctuary and Recreation Zones did not appear to separate in nMDS ordinations when all regions were considered. However, there was a separation within regions based on abundance and biomass data for Mandu, and on biomass data for Osprey and Maud (Figure 2.2). Two-way crossed ANOSIM highlighted significant differences between zones for abundance data in January and biomass data in January and July (Table 2.3). There were also significant differences between regions.

Fish composition was analysed using one-way ANOSIM to determine which regions were driving differences observed in two-way crossed ANOSIM. There were significant differences between the Mandu Sanctuary and Recreation Zones for abundance data in July, and for biomass data at both times ($P < 0.05$) (Figure 2.2; Table 2.4). Despite separation of replicates at Osprey and Maud using biomass data (Figure 2.2), one-way ANOSIM values were weaker ($P = 0.057$ and 0.086; Table 2.4). There were, however, only 35 permutations available for this test. SIMPER demonstrated that significant composition differences where being driven by the family Lethrinidae (Table 2.4).
Table 2.2: Fish families and species (in order of dominance) recorded in surface visual census (SVC) and baited remote underwater video (BRUV), January and July 2000.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Common name</th>
<th>Method</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lethrinidae</td>
<td><em>Lethrinus nebulosus</em> (Forsskal, 1775)</td>
<td>Spangled emperor</td>
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<td><em>Lethrinus lentjan</em> (Lacepède, 1802)</td>
<td>Pinkear emperor</td>
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<td><em>Lethrinus atkinsoni</em> (Seale 1910)</td>
<td>Yellowtailed emperor</td>
<td>SVC, BRUV</td>
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<td><em>Lethrinus latiaudis</em> (Alleyne and Macleay, 1877)</td>
<td>Blu-lined emperor</td>
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<td><em>Lutjanus lemniscatus</em> (Valenciennes, 1839)</td>
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<td>Serranidae</td>
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<tr>
<td>(Genus Choerodon)</td>
<td><em>Choerodon rubescens</em> (Gunther, 1862)</td>
<td>Baldchin groper</td>
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<td><em>Choerodon anchorago</em> (Bloch, 1791)</td>
<td>Anchor tuskfish</td>
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<td><em>Choerodon cephalotes</em> (Castelnau, 1875)</td>
<td>Purple tuskfish</td>
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Figure 2.2: NMDS ordinations of the abundance and biomass of targeted fishes (SVC) from Sanctuary Zones (open symbols) and Recreation Zones (black symbols) at all regions (January and July 2000) (n = 4). MNS - Mandu Sanctuary Zone, MNR - Mandu Recreation Zone, OS - Osprey Sanctuary Zone, OR - Osprey Recreation Zone, MS - Maud Sanctuary Zone, MR - Maud Recreation Zone.

Table 2.3: Two-way crossed ANOSIM R-values and significance levels, for the composition of targeted fish families/genera (in terms of abundance and biomass) (SVC). Data were square root transformed. 999 permutations used. Bold indicates significant differences.
Table 2.4: Results of SIMPER analysis and one-way ANOSIM (R-values and significance levels) on the abundance and biomass of targeted fish families/genera from surface visual census for Sanctuary (SZ) and Recreation (RZ) Zones at each region (January and July 2000). Bold indicates significant differences, 35 permutations was the maximum possible number for ANOSIM.

| Region/date | Jan 2000 | | | July 2000 | | | |
|---|---|---|---|---|---|---|---|---|
| | Average | Average | Contribution | Average | Average | Contribution | |
| **ABUNDANCE** | abundance | dissimilarity | Ratio | % | abundance | dissimilarity | Ratio | % |
| Mandu | | | | | | | | |
| Lethrinidae | 36.8 | 30.8 | 22.3 | 1.2 | 62.7 | 53.0 | 24.8 | 1.5 | 24.8 | 15.9 | 25.8 | 1.2 | 72.8 |
| Lutjanidae | 1.0 | 7.8 | 8.3 | 0.7 | 23.3 | 9.0 | 2.8 | 0.9 | 2.8 | 5.9 | 0.9 | 16.6 |
| Haemulidae | . | 2.2 | 3.5 | 1.6 | 10.0 | 0.2 | 2.5 | 0.9 | 2.5 | 9.6 | 0.9 | 8.1 |
| *Choerodon* spp. | 0.2 | 0.8 | 1.2 | 0.8 | 3.4 | . | . | 0.2 | 0.2 | 0.3 | 0.5 | 0.8 |
| Serranidae | . | 0.2 | 0.2 | 0.5 | 0.7 | . | . | 0.5 | 0.6 | 0.9 | 0.9 | 1.7 |
| Osprey | | | | | | | | |
| Lethrinidae | 48.8 | 27.2 | 29.5 | 1.7 | 90.4 | 44.8 | 19.2 | 40.5 | 1.5 | 76.5 |
| Lutjanidae | 1.5 | 0.2 | 1.5 | 1.5 | 4.6 | 3.2 | 0.8 | 4.3 | 1.1 | 8.2 |
| Haemulidae | 1.0 | . | 0.9 | 1.0 | 2.8 | 3.5 | 1.2 | 6.2 | 0.9 | 11.6 |
| *Choerodon* spp. | 0.8 | . | 0.7 | 0.6 | 2.1 | 0.8 | . | 1.2 | 0.9 | 2.3 |
| Serranidae | . | . | . | . | 0.2 | 0.2 | . | 0.6 | 0.7 | 1.3 |
| Maud | | | | | | | | |
| Lethrinidae | 18.8 | 14.2 | 31.8 | 1.7 | 74.1 | 42.25 | 35.75 | 10.6 | 1.5 | 64.5 |
| Haemulidae | 1.8 | 0.5 | 5.8 | 0.8 | 13.6 | 2.0 | . | 2.2 | 1.2 | 13.2 |
| Lutjanidae | 1.8 | 0.2 | 4.6 | 1.0 | 10.6 | 2.2 | 1.5 | 2.6 | 1.2 | 15.5 |
| *Choerodon* spp. | 0.2 | . | 0.7 | 0.5 | 1.7 | 0.2 | . | 0.3 | 0.6 | 1.8 |
| Serranidae | . | . | . | . | 1.0 | 0.5 | 0.8 | 1.1 | 5.2 |
| **BIOMASS** | | | | | | | | |
| Mandu | | | | | | | | |
| Lethrinidae | 15.1 | 7.24 | 26.4 | 1.2 | 46.0 | 23.6 | 9.5 | 31.1 | 1.7 | 69.0 |
| Haemulidae | 1.8 | 3.15 | 11.2 | 2.0 | 19.5 | 0.2 | 2.1 | 5.1 | 1.4 | 11.3 |
| Lutjanidae | 0.6 | 4.1 | 9.9 | 0.7 | 17.3 | 4.09 | 1.1 | 6.2 | 1.0 | 13.8 |
| *Choerodon* spp. | . | 2.8 | 9.5 | 0.8 | 16.6 | . | 0.9 | 2.2 | 0.5 | 4.8 |
| Serranidae | . | 0.1 | 0.3 | 0.6 | 0.5 | . | . | 0.2 | 0.5 | 0.8 |
| Osprey | | | | | | | | |
| Lethrinidae | 11.6 | 6.8 | 29.4 | 4.4 | 73.3 | 16.8 | 5.9 | 35.8 | 1.7 | 59.5 |
| Haemulidae | 1.2 | . | 4.2 | 0.9 | 10.5 | 4.5 | 0.6 | 14.3 | 1.4 | 23.8 |
| Lutjanidae | 0.9 | 0.1 | 3.2 | 1.4 | 8.0 | 1.4 | 0.3 | 3.7 | 2.3 | 6.1 |
| *Choerodon* spp. | 1.0 | . | 3.3 | 0.6 | 8.2 | 1.4 | . | 5.6 | 0.8 | 9.3 |
| Serranidae | . | . | . | . | . | 0.1 | 0.1 | 0.8 | 0.7 | 1.3 |
| Maud | | | | | | | | |
| Lethrinidae | 23.9 | 8.5 | 40.5 | 1.6 | 71.7 | 43.5 | 16.4 | 30.5 | 1.8 | 76.7 |
| Haemulidae | 4.3 | 0.5 | 11.9 | 0.9 | 21.0 | 4.3 | 0.3 | 5.5 | 1.1 | 13.8 |
| Lutjanidae | 0.9 | 0.1 | 2.1 | 1.2 | 3.7 | 1.1 | 0.8 | 1.9 | 0.9 | 4.7 |
| *Choerodon* spp. | 0.9 | . | 2.0 | 0.6 | 3.5 | 1.3 | . | 1.8 | 0.5 | 4.6 |
| Serranidae | . | . | . | . | . | . | 0.1 | 0.1 | 0.5 | 0.2 |
Univariate analyses

ANOVA yielded interactions between factors using biomass data (time x zone and region x zone). Analysis of the interactions showed that there was a greater biomass of lethrinids in Sanctuary Zones, than in Recreation Zones, in January (P < 0.05) and July (P < 0.01) and that differences were significant for each individual region (Table 2.5, Figure 2.3). There was also a difference between Sanctuary Zones in the regions with greater biomass at Maud than at Mandu or Osprey (P < 0.05) (Figure 2.3; See Table 2.4 for relative abundance and biomass values). There were no significant differences in the overall abundance of lethrinids or the abundance or biomass of other taxa of fish.

The mean size of lethrinids was greater in Sanctuary Zones than Recreation Zones and there was a significant difference among regions (both P < 0.05), with the greatest mean size at Maud, followed by Mandu and Osprey (Table 2.5, Figure 2.3). The abundance of legal-size lethrinids was significantly greater in Sanctuary Zones (Table 2.5, Figure 2.4) and there was interaction between time and region. Subsequent analysis revealed a significant difference between regions in July, and between times at Mandu and Maud. There were no significant differences in the abundance of under-sized lethrinids.

Baited remote underwater video

Differences in lethrinid populations recorded using SVC were confirmed with BRUV. T-tests highlighted greater counts of lethrinids in the Mandu and Maud Sanctuary Zones (P < 0.01) (Figure 2.5). There were no significant differences in the counts of other targeted fishes.
Table 2.5: Results of three-factor ANOVA on lethrinid measurements (overall abundance, biomass, mean size, abundance of legal-size and abundance of under legal-size) (SVC), with sampling time (January and July 2000), region (Mandu, Osprey, and Maud) and zone (Sanctuary, Recreation) as factors. Mean size and legal-size data transformed [Log$_{10}$ (x + 1)]. Significant interactions have been analysed using multiple comparisons. Bold indicates significant differences.

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<th>P value</th>
<th>Mean Square</th>
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<th>P value</th>
<th>F Ratio</th>
<th>P value</th>
<th>F Ratio</th>
<th>P value</th>
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Tests for significant interactions

**Biomass**

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Figure 2.3: The abundance, biomass and size of lethrinids (± S.E.) (SVC) from Sanctuary and Recreation Zones at all regions in January and July 2000, n = 4. Horizontal bars indicate those regions that were not significantly different (Student-Newman-Keuls post-hoc test).
Figure 2.4: Mean abundances (SVC) of legal-size and under-size lethrinids (± S.E.) from Sanctuary and Recreation Zones, for each region and time. Horizontal line indicates those regions that were not significantly different (Student-Newman-Kuels post-hoc test).

Figure 2.5: Mean counts (BRUV) of targeted predatory fishes (± S.E.) recorded at Sanctuary and Recreation Zones in the Mandu and Maud regions. Data were transformed [Log_{10}(x + 1)]. Note significant differences (t-test) ** P < 0.01, *** P < 0.001, n = 12.
2.3.2 Habitat measurements

Multivariate analyses

Two-way crossed ANOSIM highlighted a significant difference in the benthic cover between zones and among regions in both January and July (Table 2.6). NMDS ordinations, used to examine trends within each region and time, showed variable patterns. At Mandu and Osprey there were significant patterns using one-way ANOSIM in July and January, respectively (Table 2.7, Figure 2.6). Trends at Maud were consistent over time with a clear separation between zones. SIMPER analysis (Table 2.7) indicated that Acropora coral and total hard substrate cover were primarily responsible for dissimilarity between zones. Contributions from algal assemblage, turf algae and other coral types were generally much lower.

Table 2.6: Two-way crossed ANOSIM R-values, and significance levels for benthic cover (%). Data were square root transformed. 999 permutations used. Bold indicates significant differences.

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Table 2.7: Results of SIMPER and one-way ANOSIM (R-values and significance) for benthic cover (%) from Sanctuary (SZ) and Recreation (RZ) Zones at each region in January and July 2000. Bold indicates significant differences. 999 permutations used.

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<td>Average</td>
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<td>Average</td>
</tr>
<tr>
<td></td>
<td></td>
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<td>dissimilarity</td>
<td>%</td>
<td></td>
<td>abundance</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
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<tr>
<td>Mandu</td>
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<td></td>
<td></td>
<td></td>
<td>R = 0.214 (P = 0.014)</td>
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<td>58.0</td>
<td>7.6</td>
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<td>45.6</td>
<td>72.9</td>
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<tr>
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<td>28.2</td>
<td>28.6</td>
<td>5.0</td>
<td>1.5</td>
<td>30.1</td>
<td>31.2</td>
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<tr>
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<td>2.1</td>
<td>1.3</td>
<td>12.5</td>
<td>8.8</td>
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<td>1.3</td>
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<td>9.5</td>
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<td></td>
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<td>R = 0.042 (P = 0.625)</td>
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<td>4.9</td>
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<td>3.3</td>
</tr>
<tr>
<td>Turf algae</td>
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<td>1.2</td>
<td>1.8</td>
<td>3.2</td>
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</table>
Figure 2.6: Benthic cover (%) nMDS ordinations from Sanctuary ■ and Recreation ▲ Zones for each region in January and July 2000, n = 8. Note: ANOSIM R-values and significance levels; and * = significant differences.

Univariate analyses

ANOVA revealed a significant difference between regions for turf algae and significant interactions between region and zone for Acropora coral cover, and total hard substrate cover (Table 2.8, Figure 2.7) (See Table 2.7 for relative cover values). Analysis of interactions showed: a significantly greater cover of Acropora coral and total hard substrate at the Maud Recreation Zone than at the Sanctuary Zone; and a significant difference in Acropora coral cover between Sanctuary Zones at each region. Analysis of rugosity measurements showed a significant difference between regions (P < 0.01) with Mandu and Maud being more rugose than Osprey (Student-Newman-Kuels PLSD post-hoc: P < 0.01) but there was no significant difference between zones.
Table 2.8: Results of ANOVA on benthic cover (%) variables with time (January and July 2000), region (Mandu, Osprey, and Maud) and zone (Sanctuary, Recreation) as factors. Data were transformed [arcsine and Log \(_{10}(x + 1)\)]. Alpha was reduced to 0.01 for other coral and algal assemblage as variances were heterogeneous after transformation. Bold indicates significant differences.

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<thead>
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<th>Source</th>
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<th>Hard substrate</th>
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<td>F Ratio</td>
</tr>
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<td>0.002</td>
<td>1.04</td>
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Tests for significant interactions

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<table>
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<td>Recreation Zone</td>
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Figure 2.7: Mean benthic cover (% ± S.E.) for Sanctuary and Recreation Zones from each region in January and July 2000, n = 8.
2.4 DISCUSSION

2.4.1 Species composition and family level differences

This study has provided a rare comparison of targeted fish assemblages in Sanctuary and fished areas, where recreational line fishing is the only pressure exerted on fish stocks. Under these circumstances, Sanctuary Zones studied at Ningaloo Marine Park supported a different composition of targeted fish to adjacent Recreation Zones. Differences in fish composition between fished and unfished zones have been demonstrated in other coral reef MPA comparisons (Jennings et al., 1996b; Rakitin and Kramer, 1996; Roberts and Hawkins, 1997; Wantiez et al., 1997; Chiappone and Sealey, 2000), but where fishing pressure was exerted by commercial or artisanal fishers. This study has shown that recreational line fishing alone may, in some cases, be sufficient to alter the composition of targeted fishes.

Trends in the composition of fishes were stronger in terms of biomass than abundance. Mandu showed the greatest difference between zones of the three regions. Although not significant, there was a separation in nMDS ordinations between zones for biomass at Osprey and Maud. Differences in assemblages were driven by lethrinids, which constituted approximately 78% of all fishes censused and differed between zones in terms of biomass, mean size and abundance of legal-sized fishes. There were no significant differences in other families/genera (Lutjanidae, Haemulidae, Serranidae and Choerodon spp.) between zones. The mean size of lethrinids was smaller in the fished zones, which may be the result of recreational fishers removing the larger legal-sized fishes. This was supported by the fact that legal-sized lethrinids were significantly more abundant in the Sanctuary Zones, i.e. where there was no fishing pressure. There was also a greater abundance of legal-sized lethrinids at the Maud region, than at Mandu or Osprey (Figure 4). Differences in the abundance of under-sized lethrinids were not significant, but they tended to be more abundant at the Mandu and Osprey regions, than at Maud. A number of factors may have influenced these findings, including the duration of protection and the level of fishing pressure. These factors varied between the regions sampled but were not controlled in the design of this study.

Other researchers have noted vulnerability of lethrinids to overfishing, with significant differences in abundances between fished and unfished zones (Letourneur, 1996c; Russ and Alcala, 1998b). Watson and Ormond (1994) recorded mean abundances of Lethrinus spp. within an unfished marine park that were over 500 times higher than on an apparently identical reef that was fished artisanally. The results from Ningaloo Marine Park indicate that
recreational fishing has reduced the biomass, mean size and abundance of legal-sized lethrinids in the fished zones of the study areas.

2.4.2 Habitat structure

In this study, there was a possibility that the observed differences in fish assemblages between zones, were a consequence of factors other than fishing pressure such as the influence of benthic cover (Galzin et al., 1994; Jennings et al., 1996a) and topographic complexity (Ohman et al., 1997; Connell and Kingsford, 1998) on fish assemblages. These factors are discussed below.

In multivariate analyses of benthic cover, Acropora coral appeared to be influencing between zone differences, and tended to be greater in the Recreation Zones at Osprey and Maud, and very similar between zones at Mandu. Significant differences in overall hard substrate cover were also inconsistent and there was no difference in rugosity between zones within any region in this study. Greater abundance, biomass and species richness of coral reef fishes have been associated with more topographically complex habitats (Letourneur, 1996b; Friedlander and Parrish, 1998) and greater coral cover (Chabanet et al., 1997). Other researchers have shown no such relationship between these variables (Roberts and Ormond, 1987; Roberts, 1995a), but still recorded greater abundance and biomass of fishes in no-fishing zones. Ayling and Ayling (1987) noted that Lethrinus nebulosus were most common at Ningaloo in areas where sandy substratum was associated with coral patches. This sand and coral habitat was typical of all locations in this study. The inconsistent differences recorded in habitat, and the similarity of rugosity measures, do not explain the differences in fish assemblages between the zones studied at Ningaloo.

Algal cover may provide a structural habitat (Sala, 1997) or food source (De Ridder and Lawrence, 1982; Babcock et al., 1999) for invertebrates, which are in turn preyed on by fishes (Hiatt and Strasbourg, 1960; Hobson, 1974). Thus, differences in algal cover might influence predatory fish populations. There were no significant differences in algal assemblage cover between zones, but it tended to be higher in the Recreation Zone at Maud (driven by Dictyota and Lobophora spp.) and the Sanctuary Zone at Mandu (driven by extensive seasonal growth of Turbinaria ornata.) Cover of algal turf did not differ significantly between zones. Other researchers have noted relationships between the cover of algal turf and the abundance of herbivorous fishes (Polunin and Klumpp, 1992) and invertebrates (Morrison, 1988), the potential prey of the targeted predatory fishes censused (Randall, 1967; Jones et al., 1991). However, there were no similar patterns between algal cover and the targeted fish populations in the regions studied.
It was possible that observed differences between zones were an artefact of habitats or fish assemblages prior to implementation of Sanctuary Zones. A criterion for determining Sanctuary Zones in the Ningaloo Marine Park was that, “Representative areas of high biological and structural diversity have priority” (CALM, 1989). However, comparative zones in each region were similar in terms of bathymetry, proximity to channel areas and distance from shore, and the aforementioned benthic cover results confirm that there were no consistent differences between zones. It therefore seems unlikely that pre-Sanctuary zoning effects influenced the targeted fish assemblages in this study.

The aforementioned differences in habitat structure are unlikely to explain the different composition of fish families and the greater biomass, size and abundance of legal-sized lethrinids in Sanctuary Zones. The consistent findings from this census of targeted fishes across three regions of the Ningaloo Marine Park, suggest that the cessation of fishing in these Sanctuary Zones exerts an over-riding influence on targeted fish assemblages and particularly lethrinids.

2.4.3 Sanctuaries for the protection of targeted fishes

The Sanctuary Zones examined at Ningaloo have, to some extent, met the management objective of preserving higher numbers of mature sized fishes, and thus potential spawning stock. For a Sanctuary to have achieved this, the proportion of spawning age/size fishes should be greater than adjacent fished areas, as was the case at the regions studied. Theoretically, larval export from the Maud Sanctuary should be greater than the Mandu or Osprey sanctuaries, given the greater abundance of large lethrinids. However, this was not reflected in high numbers of juvenile fishes in the Maud Recreation Zone, perhaps due to eggs and larvae being transported to other areas or density dependant effects on recruitment.

Sanctuary Zones at Ningaloo may be preserving higher numbers of potential spawning fishes, but it is not known whether the spawning fishes were sufficient to replenish fished areas, whether they actually spawn within the Sanctuary Zones, or how and where eggs and larvae are dispersed. D’Adamo and Simpson (2001) reported that circulation within the lagoons at Ningaloo is driven by a wave pumping effect with water coming over the reef crest, and flowing out via channels in the back reef. Consequently, some eggs and larvae may be dispersed in the lagoons, but lagoon flushing times are rapid (six hours to five days depending on wave, tide and wind conditions) and eggs and larvae may also be dispersed by passing oceanic currents. D’Adamo and Simpson (2001) suggest that Ningaloo may act as a source of eggs and larvae to reefs in the Monte Bello Islands and Dampier Archipelago (proposed marine reserves 250 km
and 400 km to the north of Ningaloo, respectively) during summer, with their transport facilitated by the north flowing Ningaloo current. However, there is debate in the literature on the mobility of fish larvae and oceanographic transport mechanisms. Some authors have rejected the assumption that settlement stage reef fishes larvae are passive (Leis and Carson-Ewart, 2001). But, larval mobility increases with age (Fisher et al., 2000) and, during earlier developmental stages (pre-settlement), larval dispersal may depend more on oceanographic conditions than swimming. Recent studies have demonstrated both passive and active dispersal among different fish species (Tilney et al., 1996; Smith, 2000).

### 2.4.4 Conclusion

This study is unique in that it has highlighted differences between fished and unfished areas of a fringing coral reef marine park that is subject only to recreational line fishing. The results from this study demonstrate differences in predatory fish assemblages between Sanctuary and Recreation Zones in three regions of the Ningaloo Marine Park. Differences appeared to be due to the removal of fishing pressure from the Sanctuary areas and could not be explained by habitat variables. The data suggest that fishing of legal-sized lethrinids in Recreation Zones has depleted their numbers to levels below that in Sanctuary Zones. The greater abundance of lethrinids in the Sanctuary Zone at Maud (compared with Mandu and Osprey) may be due to its size or the duration of protection but these factors need to be investigated.

These findings highlight the need for managers to understand that recreational fishing may significantly affect populations of targeted fishes. The study has implications for the management of marine parks and recreational fishing, and assessment of the importance of Sanctuary areas for protecting fish stocks. These findings may be of particular relevance in developed countries where recreational fishing is popular and MPAs are being established for fisheries management and conservation purposes. Western Australia has a population of 1.9 million and coastline of 12500 kilometres. Despite this sparse population the potential effects of recreational fishing on targeted fishes seemed apparent. A greater effect could be expected in more densely populated regions.

Future studies that would be universally applicable to marine parks, should investigate larval transport and spillover of mature fishes from Sanctuary Zones, under a recreational fishing regime. The effect of removing predatory fishes on other reef biota has been shown elsewhere (McClanahan, 1997; Rosado Solorzano and del Proo, 1998; Babcock et al., 1999), but generally under a commercial or artisanal fishing regime. Potential trophic effects that may arise from recreational fishing should therefore also be investigated.
CHAPTER 3 - FISH PREDATION ON INVERTEBRATES FOLLOWING EXCLUSION OF RECREATIONAL FISHING: REGIONAL DIFFERENCES IN A CORAL REEF MARINE PARK

Abstract
Comparisons of marine protected areas (MPAs) and adjacent fished areas have revealed increases in invertebrate populations, when their fish predators are reduced through the effects of commercial or artisanal fishing. Few studies have examined this phenomenon when recreational line fishing was the only method of extraction. Responses by benthic macroinvertebrate prey to predation from fishes were examined by comparing unfished and recreationally fished zones of the Ningaloo Marine Park. A previous study at Ningaloo had identified lethrinids (emperors) as the most common predatory fishes targeted by fishers. Lethrinids made up 96% of targeted invertivorous fishes and their populations were higher in unfished zones. In this study, measured variables included: the biomass of non-targeted invertivorous fishes; the abundance, biomass and size of the dominant benthic macroinvertebrates (the urchin *Echinometra mathaei* and the corallivorous gastropod *Drupella cornus*); the diet of invertivorous fishes; and substrate cover and rugosity as indicators of refuge availability for invertebrates. A tethering experiment was also conducted to determine rates of survival of prey from predation. Urchins and juvenile *D. cornus* were recorded in the gut of 50 and 6% of lethrinids respectively. The tethering experiment revealed that *E. mathaei* and *D. cornus* were preyed upon at the study sites and numerous lethrinids were observed preying on urchins in the unfished zones. The main predator in fished zones was *Coris aygula*. There were no differences in non-targeted invertivorous fishes between zones. Habitat (refuge availability) differed between zones in some regions but differences were inconsistent. At the Mandu region there was no difference in *E. mathaei* habitat between zones but *E. mathaei* abundance, biomass and size were significantly greater in the fished zone, indicating a response of prey to reduced predation. In the Maud unfished zone the cover of habitat for *E. mathaei* was higher than in the adjacent fished zone and appeared to over-ride the effect of predation, as high biomass of lethrinids was recorded with high abundance, biomass and size of *E. mathaei*. There were no significant differences in *D. cornus* abundances between zones. This study indicates that *E. mathaei* populations at the Mandu fished zone have increased in response to a reduction in invertivorous fishes and that differences are likely to be due to recreational fishing. Monitoring in MPAs must include measures of dominant predators, their prey and habitat availability, if managers are to understand the potential trophic effects of fishing and/or the exclusion of fishing.
3.1 INTRODUCTION

Marine protected areas (MPAs) are being used increasingly as conservation and fisheries management tools (Boersma and Parrish, 1999; Halpern, 2003). Marine reserves within MPAs, where no fishing or other types of harvesting are permitted, have been shown to be effective in increasing populations of crustaceans (Cole et al., 1990; Edgar and Barrett, 1997; Kelly et al., 2000), molluscs (Edgar and Barrett, 1999; Manriquez and Castilla, 2001) and fishes (Bennett and Attwood, 1991; Roberts, 1995a; McClanahan and Kaunda Arara, 1996; Russ and Alcala, 1996a; Wantiez et al., 1997) where these biota would otherwise have been exploited. Predatory fishes, in particular, have been shown to benefit from marine reserves as their low rates of mortality, recruitment and growth make them vulnerable to overexploitation (Russ and Alcala, 1998b). There are also many examples of greater abundance, biomass and size of predatory fishes in marine reserves, when comparisons have been made with adjacent areas (Watson and Ormond, 1994; Jennings et al., 1996b; Letourneur, 1996c; Chapman and Kramer, 1999) [and see reviews (Roberts et al., 2001; Ward et al., 2001)]. Fished areas in these comparisons were generally subject to commercial or artisanal fishing. A consequence of these differences in predatory fishes between fished and unfished areas may be an effect on the populations of their prey through changes in the intensity of predation. Thus, fished and unfished zones in MPAs give us an opportunity to examine relationships between predators and their prey.

Many fishes prey on herbivorous or corallivorous invertebrates (Hiatt and Strasbourg, 1960; McClanahan and Muthiga, 1989; Gochfeld and Aeby, 1997) and overexploitation of these fishes can reduce predation (Shears and Babcock, 2002) and lead to an increase in abundance and size of their invertebrate prey (McClanahan and Muthiga, 1988; McClanahan, 1999b). The most straightforward relationships between fish predators and their prey involve a decrease in prey populations under high levels of predation or the converse situation when predation is reduced. For example, declines in cod [Gadus morhua (Linnaeus, 1758)] from overfishing were associated with an increase in population size of their preferred prey, sprat [Sprattus sprattus (Linnaeus 1758)] (Moellmann and Koester, 1999). Similarly, declines in the wrasse, Thalassoma duperrey (Quoy and Gaimard, 1824) were shown to reduce the populations of a nudibranch prey, Phestilla sibogae (Bergh) in coral reef environments (Gochfeld and Aeby, 1997). Furthermore an increase in the abundance of fish predators, following establishment of no fishing zones in a temperate marine reserve, lead to reduced abundances of their urchin prey (Cole and Keuskamp, 1998; Babcock et al., 1999). Extensive work on relationships between predatory fishes and invertebrate prey, has been conducted by McClanahan et al. (1989; 1990; 1996; 1998). They recorded lower abundance and biomass of urchins in areas protected from
fishing, due to higher predation from balistids, labrids and lethrinids. The mean size of urchins
was also greater in fished areas as predators were smaller and could not consume large prey.

Differences in predator-prey interactions between fished and unfished areas may be confounded
by habitat characteristics (Hixon and Menge, 1991; Sala and Zabala, 1996; McClanahan, 1998).
Habitat structure may allow prey species to avoid predation, even when predator numbers are
high. However, this can be accounted for in the design of a study, by measuring benthic cover
and topographic complexity (rugosity), which may provide an indication of habitat availability
for invertebrates and fishes (Chabanet et al., 1997; Friedlander and Parrish, 1998; Aburto-
Oropeza and Balart, 2001).

In the Ningaloo Marine Park, Western Australia, differences were recorded in the assemblages
of predatory fishes between Sanctuary Zones (marine reserves, where fishing is not permitted),
and adjacent Recreation Zones where recreational (but not commercial) fishing was permitted
(Chapter 2). Sanctuary Zones had greater biomass, size and abundance of legal-sized lethrinids
than Recreation Zones. Lethrinids were the dominant predatory fishes and comprised 78% of
the biomass of targeted fishes recorded in census work. Preliminary studies had revealed that
the urchin *Echinometra mathaei* (Blainville) and a corallivorous gastropod *Drupella cornus*
(Roding) were the dominant benthic macroinvertebrates in the region. Historical and anecdotal
evidence, from Ningaloo Reef and elsewhere, suggests that lethrinids and other predatory fishes
prey on urchins and *Drupella cornus* (Walker, 1978; Forde, 1994; Weaver, 1998). Thus, there
was the potential that the observed differences in the populations of predatory fishes between
unfished and recreationally fished zones, could have lead to differences in the populations of
their prey. Studies of predator-prey relationships in areas subject only to recreational line
fishing are rare and there was an opportunity, at the Ningaloo Marine Park, to address the
paucity of these studies.

The aim of this study was to test whether there were different levels of predation between
unfished and recreationally fished areas and whether predation by invertivorous fishes had
affected populations of dominant prey types. The specific hypotheses were: (1) there are
differences between Sanctuary and Recreation Zones in the abundance of *Echinometra mathaei*
and *Drupella cornus* and the mean size and biomass of *E. mathaei*; and (2) predation of *E.
mathaei* and *D. cornus* by lethrinids and other invertivorous fishes is higher in Sanctuary Zones,
where biomass of targeted invertivorous fishes is higher. Targeted fishes are those sought by
recreational line fishers at the study regions. In order to interpret the findings with respect to
these hypotheses, the biomass of non-targeted fishes was also compared between Sanctuary and
Recreation Zones.
3.2 METHODS

Predator, prey and habitat characteristics were measured in Sanctuary and Recreation Zones in the Ningaloo Marine Park. In each zone, the following variables were measured: the abundance, biomass and size of non-targeted invertivorous fishes; the abundance and mean size of the most common benthic macroinvertebrates in the study areas; the cover of live and dead coral as a measure of invertebrate habitat; the predation intensity on these invertebrates; and fine-scale rugosity, as an indicator of refuge provision for these invertebrates. Samples of invertivorous fishes were collected opportunistically throughout the project for dietary analysis.

The study was conducted at three regions in the park (Figure 3.1): Mandu, Osprey and Maud. Each region had one Sanctuary Zone where no fishing was permitted, and for comparison a site was selected in the adjacent Recreation Zone where recreational line fishing was permitted. The two sites in each region were similar in terms of depth, distance from shore and proximity to channel areas.

![Figure 3.1: Location of study sites (*) in the Ningaloo Marine Park, Western Australia. Note the Mandu, Osprey and Maud Sanctuary Zones, which are shaded.](image-url)
3.2.1 Abundance, biomass and size of invertivorous fishes

Data on the abundance, biomass and size of targeted invertivorous fishes were taken from Chapter 2. Non-targeted invertivorous fishes were measured using underwater visual census (UVC) transects of 50 x 5 m in August 1999, January 2000 and July 2000. Traditional UVC methods that involve using a slate to record data have been shown to have limitations (Bohnsack and Bannerot, 1986; Kulbicki, 1998), so a combination of audio and video was used, as recommended by Bortone et al. (1991). A full face ARGA mask with a microphone was hooked up to an underwater video so that verbal counts of fishes could be recorded on the videotape. This method minimised the possibility of making duplicate counts of fishes by allowing the observer to watch the transect rather than a slate and, where necessary, the video footage was used to validate fish identifications. Fishes were counted and their size was estimated to within 10 cm, on eight haphazardly located transects (a pilot trial had indicated that no new invertivorous species were recorded after six transects). The same observer (M. Westera) was used for all UVC work, as inter-observer bias has been shown to confound the results of UVC (DeMartini and Roberts, 1982; St. John et al., 1990; Watson and Quinn, 1997; Harvey et al., 1998).

To calculate the biomass of fishes, individuals of a variety of sizes were caught at the study sites and their lengths and weights were recorded to derive relationships of the form: biomass = constant x length$^{exponent}$. These relationships were then applied to the length data to generate biomass estimates for the transects. Due to the low number of individuals captured for some families, biomass estimates were also calculated using the length-weight relationships of Kulbicki et al. (1993), which yielded almost identical results.

3.2.2 Diets of invertivorous fishes

Invertivorous fishes (both targeted and non-targeted) were captured using lines and spears and their guts removed and stored in ethanol. Guts were weighed after they had been dried on absorbent paper and the contents were separated into identifiable categories. The proportion of each food category was expressed as a relative percentage of overall stomach contents (Hyslop, 1980). Prey that could not be identified were assigned to broader categories (e.g. bivalve, gastropod, echinoid etc). To reduce the number of fishes killed, the frames and guts of filleted fishes were obtained from fish cleaning areas at campsites along the coast. Qualitative feeding observations were made by placing whole and broken Echinometra mathaei and Drupella cornus in open areas and using video to record fish feeding activity.
3.2.3 Measurement of invertebrate assemblages

The species richness and abundance of benthic macroinvertebrates was recorded in 1 m$^2$ quadrats that were randomly located within hard substrate, along the transects used for UVC (n = 40). Studies were focussed on the grazing sea urchin *Echinometra mathaei* and the corallivorous gastropod *Drupella cornus*, as pilot studies had shown them to be the dominant benthic macroinvertebrates at the study sites (51 and 37% of abundance respectively). Abundance data were collected in August 1999, January and July 2000 and July 2002 for *Echinometra mathaei*, and in July 2000 and July 2002 for *D. cornus*. To determine whether predation had affected the mean size of *E. mathaei*, urchin tests were measured, from anus to mouth, using vernier calipers, in July 2002. Measurement was made of the urchin closest to the bottom left-hand corner of each quadrat used for abundance counts. To calculate the biomass of *E. mathaei*, fifty individuals were collected from the study sites ranging in size from 3.2 – 32 mm. They were wet weighed and their test size was measured. A size-weight relationship was calculated using the equation: biomass = constant x size$^y$ (y = 2.4839; R$^2$ = 0.9601) and expressed per square metre of hard substrate. The regression was applied to all *E. mathaei* to estimate biomass in each transect. The size of *D. cornus* was not compared between zones as only mature individuals (> 30 mm) were recorded. It is likely that smaller individuals of *D. cornus* existed, but these were probably not recorded as they live in different microhabitats of the coral reef (Forde, 1994).

3.2.4 Predation on invertebrates

An experiment was conducted at the Mandu and Maud regions to test for different levels of predation by invertivorous fishes in Sanctuary and Recreation Zones. *Echinometra mathaei* were tethered to the seabed using the methods of McClanahan and Muthiga (1989). *Drupella cornus* were tethered by drilling a hole through their shells below the operculum, through which monofilament line (10 kg breaking-strain) was looped and tied. In a pilot trial, four *E. mathaei* and *D. cornus* were caged for a 24-hour period to confirm that they survived the tethering process. *E. mathaei* were separated into two size classes, less than and greater than 20 mm, to determine whether predation would be greater on smaller individuals that could be more easily consumed. Sizes were not separated for *D. cornus* as all non-cryptic individuals were greater than 30 mm.

Tethered invertebrates were attached to pegs that were driven into bare sediment between the corals. *Echinometra mathaei* and *Drupella cornus* were tethered to the same pegs to determine whether there was any preferential feeding. Twenty *E. mathaei* (10 in each size class) and 10
were tethered at each site. Similar to other studies (McClanahan and Muthiga, 1989; Shears and Babcock, 2002) pegs were checked at 24-hour intervals, for 3 days, to count the number of individuals that survived. This was to be used as a comparison of survival rate between Sanctuary and Recreation Zones. However, after only 24 hours, more than 95% of the \textit{E. mathaei} (and 10% of \textit{D. cornus}) had been removed in each zone. Therefore, it seemed inappropriate to calculate predation rates for \textit{E. mathaei} from this method, but the results still provide evidence that fish prey on \textit{E. mathaei} and \textit{D. cornus} at the study sites. Future tethering studies may need to check experiments at shorter time scales and/or use remote videography to record feeding activity. McClanahan (1998) noted that this tethering method is not good at distinguishing sites with high levels of predation as \textit{E. mathaei} is very susceptible to predators and may not persist for 24 hours.

3.2.5 Rugosity, habitat and refuge provision

Rugosity was measured to assess potential refuge provision for invertebrates. Ten metres of chain was draped in a straight line over the substrate, taking care to follow the contour of corals and rocks \((n = 60)\). Rugosity was calculated as \(1 - \frac{d}{L}\) where \(d\) was the horizontal distance and \(L\) was the contour distance (McClanahan and Shafrir, 1990; Aronson and Precht, 1995; Friedlander and Parrish, 1998). These measures were made on a single occasion (July 2002) and resultant values were compared among regions and zones.

Measurements were made of the percent cover of habitats that \textit{Echinometra mathaei} and \textit{Drupella cornus} inhabited, to determine the influence of habitat on their abundances. Pilot trials, revealed that \textit{E. mathaei} was mainly found in dead coral, rock and corals of the genus \textit{Echinopora} that each provided crevices in which the urchins could hide. \textit{E. mathaei} habitat was therefore defined as “dead coral, rock and \textit{Echinopora} cover”. Mature \textit{D. cornus} reside on or under live corals (pers. ob.) and their habitat was defined as live coral cover. Relationships between the proposed habitat types and invertebrate abundances were examined using correlations.

To measure habitat cover, a video camera was held 50 cm above the substrate and moved along each of the UVC transects. From the video footage of each transect, 50 randomly-selected frames were analysed and substrate cover was grouped into categories: \textit{Acropora} coral; \textit{Echinopora} coral; other coral genera; dead coral; macroalgae; turf algae; sand; and total hard substrate cover. The footage was viewed on a computer screen to determine the substrate cover type under 10 points on each frame. Preliminary analyses indicated that 22 frames were sufficient to capture all categories. Therefore 50 frames were analysed yielding a total 4000
points per zone in each region. Habitat cover was expressed as a percentage of overall cover of hard substrate, as *E. mathaei* and *D. cornus* did not inhabit sand areas at any of the sites.

### 3.2.6 Statistical Analyses

Three-factor mixed model analysis of variance (ANOVA) with time, region and zone as factors, was used to compare the abundance and biomass of non-targeted fishes, the abundance of *Echinometra mathaei* and *Drupella cornus*, percent cover of live coral (*D. cornus* habitat) and the percent cover of dead coral, rock and *Echinopora* coral (*E. mathaei* habitat). Percent cover data were arcsine transformed prior to analyses. Rugosity data, and the size and biomass of *E. mathaei*, were measured in July 2002, and were compared using two-factor ANOVA with region and zone as factors. Rugosity data were arcsine transformed as they were proportions (Fowler and Cohen, 1990). All data were tested for homogeneity of variances using Cochran's test and transformed \[
\text{Log}_{10} (x + 1)\] where necessary. Where variances were heterogeneous after transformation, alpha was reduced to 0.01 (Underwood, 1981), and the untransformed data were analysed, as ANOVA is robust and can still operate well with heterogeneous variances, as long as there is a balanced sampling design (Glass et al., 1972). Interactions between factors were analysed using multiple comparisons with the test-slices function in the JMP statistical package (SAS Institute Inc., 2000). Time was treated as a random variable as sampling times were chosen to observe the generality of any trends. The choice of regions was dictated by previous work (Chapter 2) that had identified regions with different assemblages of predatory fishes in Sanctuary and adjacent Recreation Zones. Zones (Sanctuary and Recreation) were chosen to represent fished and unfished areas. Consequently region and zone were treated as fixed variables.
3.3 RESULTS

3.3.1 Abundance, biomass and size of invertivorous fishes

Fourteen species of non-targeted invertivorous fishes were recorded at the study sites in census work, in addition to the eight targeted invertivores recorded in Chapter 2 (Table 3.1). These were from the Labridae (wrasses), Balistidae (triggerfish), Tetraodontidae (pufferfish) and Diodontidae (porcupinefish) families. The most abundant species were *Coris aygula* (Lacepède) (Humpheaded wrasse) and *Rhinecanthus aculeatus* (Linnaeus) (Whitebarred triggerfish). Other common predatory families from the region, such as Mullidae (goatfish) and Nemipteridae (breams), were not included in this study as they do not feed on large benthic macroinvertebrates such as urchins and *Drupella* species (Hiatt and Strasbourg, 1960; Randall, 1967; Hobson, 1974) that were the focus of this study.

There were no statistically significant differences in the abundance or biomass of non-targeted invertivorous fishes between zones (Table 3.2; Figures 3.2 and 3.3). Previous work had shown that the biomass, size and abundance of legal-sized lethrinids (those large enough to be legally taken by fishers) were greater in Sanctuary Zones than Recreation Zones (Chapter 2) (Figure 3.2). Lethrinids comprised 96% of the biomass of targeted fishes (lethrinids and *Choerodons*) that prey on benthic macroinvertebrates such as *Echinometra mathaei* and *Drupella cornus*. Lethrinids included *Lethrinus nebulosus* (Forsskål) (Spangled emperor), *Lethrinus lentjan* (Lacepède) (Pinkeared emperor), *Lethrinus atkinsoni* (Seale) (Yellowtail emperor) and *Lethrinus laticaudis*, (Alleyne and Macleay) (Blue-lined emperor). There were no differences in *Choerodons* (Chapter 2).
Table 3.1: Targeted and non-targeted invertivorous fishes (listed in order of dominance by family and then by species within each family) recorded UVC transects. Details on targeted fishes from Chapter 2.

<table>
<thead>
<tr>
<th>Family / species</th>
<th>Common name</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Labridae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Coris aygula</em> (Lacepède, 1802)</td>
<td>Humpheaded wrasse</td>
</tr>
<tr>
<td><em>Hemigymnus melapterus</em> (Bloch, 1791)</td>
<td>Thicklipped wrasse</td>
</tr>
<tr>
<td><em>Cheilinus trilobatus</em> (Lacepède, 1802)</td>
<td>Tripletail maori wrasse</td>
</tr>
<tr>
<td><em>Cheilinus fasciatus</em> (Bloch, 1791)</td>
<td>Banded maori</td>
</tr>
<tr>
<td><em>Cheilinus chlorurus</em> (Bloch, 1791)</td>
<td>Yellow-dotted maori wrasse</td>
</tr>
<tr>
<td><em>Novaculichthys taeniurus</em> (Lacepède, 1802)</td>
<td>Carpet wrasse</td>
</tr>
<tr>
<td><strong>Balistidae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Rhinecanthus aculeatus</em> (Linnaeus, 1758)</td>
<td>White barred triggerfish</td>
</tr>
<tr>
<td><em>Sufflamen chrysopterus</em> (Bloch and Schneider, 1801)</td>
<td>Black triggerfish</td>
</tr>
<tr>
<td><em>Melichthys vidua</em> (Solander, 1844)</td>
<td>Paddlefin triggerfish</td>
</tr>
<tr>
<td><em>Pseudobalistes fuscus</em> (Bloch and Schneider, 1801)</td>
<td>Yellowspotted triggerfish</td>
</tr>
<tr>
<td><strong>Tetraodontidae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Arothron stellatus</em> (Schneider, 1801)</td>
<td>Starry pufferfish</td>
</tr>
<tr>
<td><em>Arothron manillensis</em> (de Proçè, 1822)</td>
<td>Narrow-lined toadfish</td>
</tr>
<tr>
<td><em>Arothron hispidus</em> (Linnaeus, 1758)</td>
<td>Stars and stripes toadfish</td>
</tr>
<tr>
<td><strong>Diodontidae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Diodon lituratus</em> (Shaw, 1804)</td>
<td>Porcupine fish</td>
</tr>
<tr>
<td><strong>Targeted invertivorous fishes</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Lethrinidae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Lethrinus nebulosus</em> (Forsskål, 1775)</td>
<td>Spangled emperor</td>
</tr>
<tr>
<td><em>Lethrinus lentjan</em> (Lacepède, 1802)</td>
<td>Pink emperor</td>
</tr>
<tr>
<td><em>Lethrinus atkinsoni</em> (Seale 1910)</td>
<td>Yellowtailed emperor</td>
</tr>
<tr>
<td><em>Lethrinus laticaudis</em> (Alleyne and Macleay, 1877)</td>
<td>Bluelined emperor</td>
</tr>
<tr>
<td><strong>Labridae (Genus Choerodon)</strong></td>
<td></td>
</tr>
<tr>
<td><em>Choerodon schoenlenii</em> (Valenciennes, 1839)</td>
<td>Blackspot tuskfish</td>
</tr>
<tr>
<td><em>Choerodon rubescens</em> (Gunther, 1862)</td>
<td>Baldchin groper</td>
</tr>
<tr>
<td><em>Choerodon anchorago</em> (Bloch, 1791)</td>
<td>Anchor tuskfish</td>
</tr>
<tr>
<td><em>Choerodon cephalotes</em> (Castelnau, 1875)</td>
<td>Purple tuskfish</td>
</tr>
</tbody>
</table>
Table 3.2: Results of three-factor ANOVA on the abundance and biomass of non-targeted invertivorous fishes (Balistidae, Diodontidae, Labridae and Tetraodontidae) from UVC, with sampling time (August 1999, January 2000 and July 2000), region (Mandu, Osprey and Maud) and zone (Sanctuary and Recreation) as factors. Data were transformed [Log_{10}(x + 1)].

<table>
<thead>
<tr>
<th>Non-targeted fishes</th>
<th>Abundance</th>
<th>Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Source</td>
<td>DF</td>
</tr>
<tr>
<td>Time</td>
<td>2</td>
<td>0.374</td>
</tr>
<tr>
<td>Region</td>
<td>2</td>
<td>0.255</td>
</tr>
<tr>
<td>Zone</td>
<td>1</td>
<td>0.039</td>
</tr>
<tr>
<td>Time*Region</td>
<td>4</td>
<td>0.041</td>
</tr>
<tr>
<td>Time*Zone</td>
<td>2</td>
<td>0.311</td>
</tr>
<tr>
<td>Region*Zone</td>
<td>2</td>
<td>0.033</td>
</tr>
<tr>
<td>Time<em>Region</em>Zone</td>
<td>4</td>
<td>0.065</td>
</tr>
<tr>
<td>Residual</td>
<td>126</td>
<td>0.063</td>
</tr>
</tbody>
</table>

Figure 3.2: The biomass of targeted and non-targeted fishes that prey on *Echinometra mathaei* and *Drupella cornus* from Sanctuary and Recreation Zones (mean ± S.E. averaged over sampling times and regions). Notes: significant difference between zones from three-factor ANOVA (* = P < 0.05, ns = not significant); data on targeted fishes from Chapter 2; and biomass of non-targeted fishes was standardised to 2500m² for the figure.
3.3.2 Gut contents of invertivorous fishes

The guts contents of 61 lethrinids were analysed, of which 10 were empty. Of those that contained food, 35% had consumed *Echinometra mathaei* and a further 15% contained digested urchin remains that could not be identified to species (Table 3.3). On a volume basis, the gut contents of all lethrinids contained a mean of 40% urchin remains. *Lethrinus lentjan* were the most specific predators of *E. mathaei*. Lethrinids also preyed on xanthid crabs, chitons, small *Haliotis* sp., as well as other crustaceans and gastropods that could not be identified. Juvenile *Drupella cornus* were recorded in the gut contents of three lethrinids. The guts of the three *Choerodon* spp. caught, contained some urchin remains, xanthid crabs, unidentified mollusc fragments and Clypeasteroida (sand dollars). *Choerodon rubescens* (Gunther) is highly targeted but unfortunately only one gut sample could be obtained due to their very low abundances. This contained the remains of two mature *Drupella cornus* shells.

Predation on urchins by lethrinids varied between legal-sized (*n* = 33) and under-sized (*n* = 18) fishes. Of the under-sized fishes (i.e. *Lethinus atkinsoni*, *Lethinus laticaudis* and *Lethinus lentjan* < 28cm and *L. nebulosus* < 41cm) only 16% contained urchin remains, while 75% of the...
larger legal-sized lethrinids contained urchin remains. Smaller fishes preyed more on small gastropods and crustaceans.

The low sample size of the *Choerodon* spp. and some species of non-targeted fishes sampled was representative of their low abundance at the study sites. *Coris aygula* was the most common non-targeted predator and consumed mainly gastropods and other molluscs that had been crushed beyond recognition. *C. aygula* were also observed eating whelks (Family Nassaridae) that contained hermit crabs (pers. ob.). Balistids consumed xanthid crabs and bivalves. *Rhinecanthus aculeatus* had consumed some algae, but they are known to be omnivorous (Hiatt and Strasbourg, 1960).

The families Serranidae (cods), Haemulidae (sweetlips), and Lutjanidae (seaperch) are not thought to be predators of benthic macroinvertebrates such as urchins and *Drupella cornus*. However, to ensure this was consistent with the study sites, five of each of the most common of these fishes were analysed and had no large invertebrates in their guts. As they were not intended as part of this study, the particular results are not presented.
Table 3.3: Dietary composition of invertivorous fishes captured in the Ningaloo Marine Park (August 1999 to July 2002). Data are means of n number of fishes. The low numbers of some species are indicative of their low abundances at the study sites. FL = fork length.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>FL (cm)</th>
<th>Size range</th>
<th>Mean % of gut content by volume</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Echinoderm</td>
<td>Unidentified</td>
</tr>
<tr>
<td><strong>Targeted</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lethrinus atkinsoni</td>
<td>17</td>
<td>19.8-33</td>
<td>9</td>
<td>2</td>
</tr>
<tr>
<td>Lethrinus laticaudis</td>
<td>7</td>
<td>25.3-39.4</td>
<td>14</td>
<td>29</td>
</tr>
<tr>
<td>Lethrinus lenjan</td>
<td>11</td>
<td>25.3-34.6</td>
<td>62</td>
<td>2</td>
</tr>
<tr>
<td>Lethrinus nebulosus</td>
<td>16</td>
<td>16.0-66</td>
<td>23</td>
<td>19</td>
</tr>
<tr>
<td>Choerodon spp.</td>
<td>3</td>
<td>32-66</td>
<td>20</td>
<td>7</td>
</tr>
<tr>
<td><strong>Non-targeted</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arothron hispidus</td>
<td>1</td>
<td>23</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arothron stellatus</td>
<td>1</td>
<td>54</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cheilinus chlorosus</td>
<td>1</td>
<td>23.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coris aygula</td>
<td>5</td>
<td>28.9-46.5</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Diodon liturosus</td>
<td>1</td>
<td>44</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hemigymnus melapterus</td>
<td>1</td>
<td>31.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Novaculichthys taeniurus</td>
<td>1</td>
<td>26.9</td>
<td></td>
<td>20</td>
</tr>
<tr>
<td>Pseudobalistes fuscus</td>
<td>1</td>
<td>41.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhinecanthus aculeatus</td>
<td>6</td>
<td>20.1-25.2</td>
<td>2</td>
<td>65</td>
</tr>
</tbody>
</table>
3.3.3 Measurement of invertebrate assemblages

There was a statistically significant interaction between region and zone for *Echinometra mathaei* abundance, biomass and size (Table 3.4). Analysis of the interactions revealed the same result for each measure, i.e. values were significantly higher in the Recreation Zone at Mandu and the Sanctuary Zone at Maud, than in adjacent zones in each region (Figures 3.4 and 3.5). There were no statistically significant differences at the Osprey region despite an appearance of higher abundances in the Sanctuary Zone. The greatest mean abundance and biomass of *E. mathaei* were recorded in the Maud Sanctuary Zone (6.4 individuals m\(^{-2}\) and 83 grams m\(^{-2}\), respectively). The greatest mean size of *E. mathaei* was 25 mm in the Mandu Recreation Zone. The maximum abundance and size of *E. mathaei*, in any one quadrat, was 22 individuals and 34 mm respectively. There were no statistically significant differences between time, region or zone for *D. cornus* abundance (Table 3.5; Figure 3.6).

### Table 3.4: Results of three-factor ANOVA on the abundance, biomass and size of *Echinometra mathaei* with sampling time, region (Mandu, Osprey and Maud) and zone (Sanctuary and Recreation) as factors. Abundance data (n = 40) are from August 1999, January 2000, July 2000 and August 2002; biomass (n = 40) and size (n = 20) data are from August 2002. Alpha was reduced to 0.01 for abundance and biomass as data were heterogeneous after transformation. Significant interactions were analysed using multiple comparisons. Bold = statistically significant differences.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Mean Square</th>
<th>F Ratio</th>
<th>P value</th>
<th>Tests for interactions</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ABUNDANCE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time</td>
<td>3</td>
<td>32.58</td>
<td>3.21</td>
<td>0.3274</td>
<td>Region*Zone</td>
</tr>
<tr>
<td>Region</td>
<td>2</td>
<td>173.45</td>
<td>10.47</td>
<td>0.0111</td>
<td>Osprey</td>
</tr>
<tr>
<td>Zone</td>
<td>1</td>
<td>338.44</td>
<td>44.78</td>
<td><strong>0.0068</strong></td>
<td>Maud</td>
</tr>
<tr>
<td>Time*Region</td>
<td>6</td>
<td>16.57</td>
<td>1.19</td>
<td>0.4210</td>
<td>Sanctuary Zone</td>
</tr>
<tr>
<td>Time*Zone</td>
<td>3</td>
<td>7.56</td>
<td>0.54</td>
<td>0.6720</td>
<td>Recreation Zone</td>
</tr>
<tr>
<td>Region*Zone</td>
<td>2</td>
<td>868.24</td>
<td>62.08</td>
<td><strong>&lt;0.0001</strong></td>
<td></td>
</tr>
<tr>
<td>Time<em>Region</em>Zone</td>
<td>6</td>
<td>13.98</td>
<td>1.52</td>
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Alpha was reduced to 0.01 for abundance and biomass as data were heterogeneous after transformation. Significant interactions were analysed using multiple comparisons. Bold = statistically significant differences.
Figure 3.4: Mean abundance of *Echinometra mathaei* (± S.E.) from Sanctuary ■ and Recreation ■ Zones for each region and time, n = 40.

Figure 3.5: Mean biomass and size of *Echinometra mathaei* (± S.E.) from Sanctuary ■ and Recreation ■ Zones for each region in July 2002, n = 40. Note significant differences from ANOVA: ** P < 0.01; *** P < 0.0001; and ns = not significant.
Table 3.5: Results of three-factor ANOVA on the abundance of *Drupella cornus* with sampling time (July 2000 and August 2002), region (Mandu, Osprey and Maud) and zone (Sanctuary and Recreation) as factors, \( n = 40 \). Alpha was reduced to 0.01, as data were heterogeneous after transformation.

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Figure 3.6: Mean abundance of *Drupella cornus* (± S.E.) from Sanctuary and Recreation Zones for each region and time, \( n = 40 \). Note: *D. cornus* abundance data not collected in August 1999 or January 2000.
3.3.4 Predation on invertebrates

Videography of the tethered *Echinometra mathaei* showed immediate attacks by lethrinids (Lethrinus nebulosus, L. lentjan and L. atkinsoni) and the wrasse *Coris aygula*. In the Maud Sanctuary Zone, approximately 80 lethrinids waited while the tethering experiment was being setup. Divers were placed elsewhere in the water to distract the fishes but this failed. As the experiment was left, the lethrinids and two *C. aygula* attacked the tethered urchins. However, in the Maud Recreation Zone no fishes were observed attacking tethered invertebrates. The situation was similar at Mandu with approximately 25 lethrinids and five *C. aygula* in the Sanctuary and four lethrinids and five *C. aygula* in the Recreation Zone. Tethered *Drupella cornus* were taken in the mouth but then released. Three *D. cornus* were not recovered from the tethering experiment. In other videography, *E. mathaei* were taken from their refuges and placed in the open to observe predation. They were quickly consumed by lethrinids and *C. aygula*. *D. cornus* were inspected by these fishes but not consumed.

The tethering experiment demonstrated that *Echinometra mathaei*, and to some extent *Drupella cornus*, were preyed upon at the study sites. However, as mentioned in the methods, it failed to be useful to compare the level of predation on *Echinometra mathaei* between Sanctuary and Recreation Zones. To infer levels of predation, the measurements from Chapter 2 were used, which showed that the biomass, size and abundance of legal-sized lethrinids were significantly greater in Sanctuary Zones, than adjacent Recreation Zones, at all three regions. This inference was supported by videography and observations of feeding.

3.3.5 Rugosity, habitat and refuge provision

Analysis of rugosity measurements yielded a statistically significant interaction between region and zone (Table 3.6). Analysis of the interaction highlighted that the Maud Recreation Zone was more rugose than the Maud Sanctuary Zone (P < 0.0001) (Table 3.6; Figure 3.7). This measure of rugosity was largely influenced by the cover of tabulate corals such as *Acropora hyacinthus* (Dana). Tabulate corals provided a large elevated surface area that increased the contour distance measured using the chain and tape method (see methods section).

There was an interaction between region and zone for the cover of dead coral, rock and *Echinopora* coral (*Echinometra mathaei* habitat) (Table 3.7). Habitat cover was significantly greater in the Sanctuary Zones at Maud and Osprey than adjacent Recreation Zones (P < 0.01 and P < 0.05, respectively), but not different between zones at Mandu (Figure 3.8). The cover of *Drupella cornus* habitat (live coral) was significantly higher in the Recreation Zones than the
Sanctuary Zones (P < 0.01) (Table 3.7 and Figure 3.8) and there was a difference among regions with less live coral cover at Osprey than at Mandu and Maud.

There was a modest correlation between the abundances of *E. mathaei* and the cover of *E. mathaei* habitat (dead coral, rock and *Echinopora* sp.): \( y = 0.0007x^2 - 0.0192x + 1.4794, R^2 = 0.1532 \) (R = 0.3914) (P < 0.0001). The correlation between percent cover of live coral and *D. cornus* abundance was not significant: \( y = 0.0002x^2 + 0.0042x + 2.3922; R^2 = 0.016 \) (R = 0.1265) (P = 0.1693).

Table 3.6: Results of two-factor ANOVA on rugosity measurements for July 2002, with region (Mandu, Osprey and Maud) and zone (Sanctuary and Recreation) as factors, n = 60. Alpha was reduced to 0.01 as data were heterogeneous after transformation. Significant interactions were analysed using multiple comparisons.

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Tests for significant interactions

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<td>Maud</td>
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</tr>
<tr>
<td>Recreation Zone</td>
<td>19.08</td>
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</tr>
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</table>
Table 3.7: Results of three-factor ANOVA on % cover of *Echinometra mathaei* habitat and *Drupella cornus* habitat (live coral) with time (August 1999, January 2000 and July 2000), region (Mandu, Osprey and Maud) and zone (Sanctuary and Recreation) as factors. Data were transformed [arcsine and Log$_{10}(x+1)$], n = 8. Significant interactions were analysed using multiple comparisons.
Figure 3.8: Mean percent cover of *Echinometra mathaei* habitat and live coral (*Drupella cornus* habitat) (± S.E.) from Sanctuary and Recreation Zones for each region and time, n = 8.
3.4 DISCUSSION

3.4.1 Predator - prey and habitat relationships of *Echinometra mathaei*

Where abundances of invertivorous fishes have been reduced due to fishing, we may expect urchins to increase in abundance and size. This relationship between fish predators and urchins has been demonstrated in comparative studies (McClanahan and Muthiga, 1989; McClanahan and Shafir, 1990; Cole and Keuskamp, 1998), but some authors have highlighted that factors such as habitat and recruitment may affect urchin abundances (Sala and Zabala, 1996; McClanahan, 1998; Sala et al., 1998a). The three regions studied at Ningaloo all had a higher level of predation in the Sanctuary Zones (in terms of the biomass, size and abundance of legal-sized lethrinids), as fishing had reduced assemblages of invertivorous fishes in comparative recreationally fished zones (Chapter 2). Despite this, the study has shown inconsistencies in predator-prey relationships between three regions of the Ningaloo Marine Park. Habitat (i.e. refuge provision) appeared to mediate the effect of predators on prey populations. However, where habitat did not differ between a recreationally fished zone and an unfished Sanctuary Zone (at Mandu), urchin abundance, biomass and size were significantly different, indicating different responses of prey to predation between zones. There were no differences in non-targeted invertivorous fishes that might have confounded these results. Each of the three regions will be discussed below.

Mandu fits the aforementioned predator-prey prediction. Where the biomass of lethrinids was lowest, in the Recreation Zone (Chapter 2), the abundance, biomass and size of *Echinometra mathaei* were greater, which probably reflects reduced predation by lethrinids. In comparison, *E. mathaei* variates in the Sanctuary Zone were lower, probably due to comparatively higher predation by lethrinids. Thus, the differences in lethrinid assemblages due to recreational fishing (Chapter 2) appear to have had a flow-on effect to their prey. The tethering experiment showed that *E. mathaei* were consumed at the study sites, and this was confirmed with videography that showed high predation in the Sanctuary Zone from lethrinids. In the Recreation Zone, the predators were fewer and consisted mainly of *Coris aygula*, which consumed mainly molluscs. Fifty percent of the lethrinid guts examined, contained urchins confirming the fact that they are a major urchin predator. Lethrinids were the most common invertebrate predators at the study sites (Chapter 2) and a creel survey had revealed that they comprised 90% of the fish that were targeted, and 48% of fish that were caught, by fishers at or near the study sites (Sumner et al., 2002).
The results provide strong indirect evidence of the effect of predation by lethrinids, on the abundances of their invertebrate prey (the grazing urchin *Echinometra mathaei*), at the Mandu region of the Ningaloo Marine Park. However, the results from the Maud region contrast those at Mandu. At the Maud region, predation in terms of the biomass, size and abundance of legal-sized lethrinids (Chapter 2) was greater in the Sanctuary Zone than the Recreation Zone. As for Mandu, videography and in situ observations confirmed that lethrinids were the dominant predators in the Sanctuary Zone and no predators were observed preying on tethered urchins in the Recreation Zone. So how can the higher abundance, biomass and size of *Echinometra mathaei*, that were recorded in the Maud Sanctuary Zone, be explained? This region appears to provide evidence that availability of suitable habitat can mediate the effects of predation by invertivorous fishes on invertebrates. Urchins often employ a crevice dwelling behaviour to avoid predation (Tsuchiya and Nishihira, 1984; Sala and Zabala, 1996; Cole and Keuskamp, 1998; McClanahan, 1999b) and *E. mathaei* only inhabited the crevices of dead coral, rock and *Echinopora* corals at the study sites. At Maud, there was significantly greater cover of dead coral, rock and *Echinopora* corals (*E. mathaei* habitat) in the Sanctuary Zone than the Recreation Zone. *E. mathaei* also erode the reef structure (Carreiro-Silva and McClanahan, 2001) and could have enhanced and increased the availability of refuges (Tsuchiya and Nishihira, 1984; Neill, 1988) at the Maud Sanctuary Zone. Rugosity was higher in the Recreation Zone, but high rugosity was dictated by cover of tabulate Acropora corals, such as *A. hyacinthus*, which were not inhabited by *E. mathaei* at the study sites. Therefore, rugosity was not a good measure of *E. mathaei* habitat in this study.

At Osprey, as for Mandu and Maud, the biomass, size and abundance of legal-sized lethrinids were greater in the Sanctuary Zone than the adjacent Recreation Zone (Chapter 2). However, no predator-prey response was evident, in the form of differences in *Echinometra mathaei* abundance, biomass or mean size between zones. This could be explained by a combination of two factors. Firstly, there was significantly greater cover of habitat for *E. mathaei* in the Sanctuary Zone, which may have provided refuge from predation, and secondly, the Osprey Sanctuary had the lowest biomass of lethrinids of the three regions examined (Chapter 2), which may have equated to comparatively lower predation.
3.4.2 Predator - prey and habitat relationships of *Drupella cornus*

*Drupella cornus* were included in this study as they proliferated at Ningaloo in 1980s and caused a widespread loss of live corals, particularly in the northern parts of the Marine Park (Forde, 1994). Speculation arose about the role of predation in regulating populations of *D. cornus*. An oral history of the region noted that, in the past, many octopi (potential gastropod predators) were poisoned along the reef to be used as bait. Some people also believed that the rise in *D. cornus* numbers was due to overfishing. One fisher stated that lethrinids were full of *Drupella* shells when he gutted them (Weaver, 1998). Forde (1994) also observed *Coris aygula* preying on *D. cornus* at Ningaloo.

The results for *Drupella cornus* are inconclusive with respect to any predator-prey relationships with invertivorous fishes. Six percent of the lethrinids that were sampled had consumed juvenile *D. cornus* and the one *Choerodon rubescens* had consumed mature *D. cornus*, but, due to the high variability among samples, there were no significant differences in *D. cornus* populations.

3.4.3 A hypothetical conceptual model of interactions between predators, prey and habitat

This study does not strictly allow for discussion of what caused the differences in *Echinometra mathaei* populations between regions, as there was no replication of the different levels of the cover of *E. mathaei* habitat within each region. Future studies that aim to examine predator-prey relationships may wish to incorporate this level of replication, but such designs will require a large amount of time and resources. However, a hypothetical model has been proposed based on what appears to be a gradation of effect of predation on *E. mathaei*, between the regions sampled (Figure 3.9). This model depicts: habitat cover using dead coral heads; the biomass of invertivorous fishes using lethrinids; and *E. mathaei* using urchins. Where habitat cover is comparable between areas that have high and low levels of predation (Box 1 - Mandu Sanctuary and Box 2 - Mandu Recreation Zone, respectively), there will be a measurable response of prey to different levels of predation. This may be in the form of reduced abundances of urchins. However, where habitat cover differs between areas, this may mediate predation pressure. Where habitat cover is high (Box 3 - Maud Sanctuary Zone), urchins will be higher in abundance and biomass, and larger in size, than areas where habitat cover is low (Box 4 - Maud Recreation Zone), despite the higher predation pressure. This is due to the crevice dwelling behaviour of urchins such as *E. mathaei* that afford them refuge from predation. In other words, the absence of habitat (in a Recreation Zones) makes the low number of predators a more
effective "predation pressure" than the higher density of predators in the Sanctuary Zones. The Osprey region was not depicted as there was not a statistically significant predator-prey response.

The effect of predation would depend on the types of predators (i.e. predators such as octopus or crustaceans may be able to remove urchins from their crevices), but the effect of habitat is likely to override the importance of predation, where fishes are the main form of predator. This argument is strengthened by the significant positive correlation between urchin abundances and urchin habitat taken from all Sanctuary and Recreation Zones in this study. The Osprey region fell between Mandu and Maud as there were no differences in prey variates. This may have been due to higher cover of habitat in the Sanctuary Zone, providing refuge from predation.

3.4.4 Implications for managers and ecologists

In this study, habitat and refuge provision in different zones of a marine protected area appeared to exert an over-riding influence on *Echinometra mathaei* abundance, biomass and size. Recent reviews have cited a lack of empirical studies on the effects of marine reserves (Sala and Zabala, 1996; Russ, 2001; Ward et al., 2001). The study helps to address this and provides information on the role of habitat in predator-prey relationships. This study recorded a predator-prey response where recreational line fishing was the only form of fishing permitted.

The effect of the Mandu, Osprey and Maud Sanctuary Zones at Ningaloo appeared to be consistent across space with respect to the dominant fish populations (lethrinids). However, indirect effects, such as relationships between predators and their prey, were highly variable and dependent upon habitat. Baseline monitoring plans in MPAs must therefore include measures of keystone species, their prey and habitat characteristics of prey, if they hope to understand the potential trophic effects of fishing and/or the exclusion of fishing. In this study, the dominant biota were recognised in a pilot study as the invertivorous Lethrinidae and the urchin *Echinometra mathaei*. Without data on habitat and its role in refuge provision conclusions could not have been drawn about the likely cause of differences in predator-prey relationships between zones.

Gut analyses indicated that larger lethrinids that can be legally taken by fishers, were far more likely to prey on urchins than under-sized lethrinids, indicating an ontogenetic shift in diet. Thus, removal of these large fish may allow *Echinometra mathaei* populations to increase. As *E. mathaei* graze algae (De Ridder and Lawrence, 1982), a consequence of overfishing may be
reduced algal cover. It is therefore likely that targeting of large lethrinids would have a greater effect on urchin assemblages than removal of a variety of sizes of fish. Perhaps maximum size limits should be adopted in addition to minimum size limits for these fish.

_Echinometra mathaei_ also bioerode reef substrate (Mokady et al., 1996; Mills et al., 2000; Peyrot-Clausade et al., 2000) and the rate of bioerosion by urchins increases with body size (Carreiro-Silva and McClanahan, 2001). Urchin bioerosion can equal or exceed carbonate production (McClanahan and Kurtis, 1991) and bioerosion by large _Echinometra_ urchins, with a test size of 30-40mm, has been shown to be 5-10 times higher than that of urchins half that size (Bak, 1994). Thus, increases in urchin abundance and size will increase reef bioerosion and reduce the accretion of calcium carbonate (Carreiro-Silva and McClanahan, 2001), which is the primary reef building process. Potential flow-on effects may then be a reduction in available substrate for colonisation by recruiting corals or algae and a consequent loss of physical habitat structure. In this study, the mean size (as well as the abundance and biomass) of _E. mathaei_ was greater in the Recreation Zone at Mandu, compared with the Sanctuary Zone, presumably because the smaller predators in the fished areas were not capable of consuming large urchins. Other studies have also noted this relationship between urchin size and predation (McClanahan, 1998; Shears and Babcock, 2002). Bioerosion could therefore have increased in the Recreation Zone at Mandu. This has implications for how fisheries might be managed if managers wish to ensure that overfishing does not allow populations of prey species, such as urchins, to increase.
CHAPTER 4 - THE TROPHIC EFFECTS OF FISHING EXCLUSION ON THE COVER AND COMPOSITION OF ALGAE IN A CORAL REEF ENVIRONMENT.

Abstract
A consequence of the loss of predators, through fishing, may be shifts in the population structure of their prey and flow-on effects to primary producers (i.e. trophic cascade). Comparisons of unfished and fished zones can provide the experimental basis that allows for detection of trophic cascades. Sanctuary (unfished) Zones in three regions of the Ningaloo Marine Park, Western Australia (Mandu, Osprey and Maud) supported higher biomass of predatory fish (lethrinids), than adjacent Recreation (recreationally fished) Zones. Lethrinids, the dominant predatory fish, preyed heavily on the grazing urchin *Echinometra mathaei*, which appeared to have been reduced by predation in the Mandu Sanctuary Zone. However, at the Maud Sanctuary Zone, habitat had appeared to have provided refuge from predation. In this study, the diets of fish and urchin grazers and the cover and composition of algae were analysed to determine whether differences in abundances of *E. mathaei* at these sites had affected algal cover and lead to a trophic cascade. At the Mandu Recreation Zone, the cover of macro-algae was half, and the abundances of *E. mathaei* four times greater, than the adjacent Sanctuary Zone. There were differences in algal composition between zones that were driven by fucoid brown algae such as *Sargassum* and *Turbinaria*, which also dominated the diet of *E. mathaei*. A trophic cascade may have resulted from the removal of lethrinids at the Mandu Recreation Zone region and there appeared to be no other explanation for the persistent differences in macro-algal cover. At the Maud region, where greater refuge is likely to have mediated the effect of predation, there was still a grazing effect from *E. mathaei* despite a high biomass of predators. The Osprey region did not differ in terms of *E. mathaei* abundances or macro-algal cover between zones. Differences were unlikely to have been caused by fishes that graze macro-algae, as their biomass did not differ between zones. These data suggest that a trophic cascade may have resulted from the effects of fishing at Mandu and that *E. mathaei* grazing reduces algal cover. The results are consistent with other studies but this may be the first study that has recorded evidence of a trophic cascade where recreational line fishing is the only means of extracting fishes. There was a predictable response of macro-algal cover to grazing by urchins. However, trophic interactions were not predictable among regions and differed on a scale of <15 kilometres.
4.1 INTRODUCTION

A consequence of the loss of predators, through hunting or fishing, may be shifts in the population structure of their prey and flow-on effects to primary producers. This phenomenon, known as a trophic cascade (Strauss, 1991; Pinnegar et al., 2000), has received much attention in the literature with examples derived from marine (McClanahan and Shafir, 1990; Ruttenberg, 2001; Shears and Babcock, 2003), freshwater (Pace et al., 1998; Drenner et al., 2002) and terrestrial systems (Ripple et al., 2001). A classic example of a trophic cascade was the reduction of sea otters through hunting, that lead to an increase in the abundance of their prey, grazing urchins, and a loss of kelp forests (Estes and Palmisano, 1974). In a terrestrial example, the reintroduction of wolves in Yellowstone National Park altered the grazing behaviour of elks and lead to changes in the structure of aspen (Ripple et al., 2001). Trophic cascades are being increasingly detected in marine systems, particularly when fishing exclusion zones in marine protected areas (MPAs) are compared to areas that are fished (Pinnegar and Polunin, 1999; Castilla, 2000). A marine trophic cascade was demonstrated in a New Zealand MPA (Babcock et al., 1999; Shears and Babcock, 2002; Shears and Babcock, 2003), where increases in predatory fishes and lobster reduced the abundance of urchins through predation. Urchin barrens, which were previously dominated by crustose coralline algae, changed to macro-algal dominated habitat due to reduced grazing in the reserve.

Manipulative experiments have been used to examine trophic cascades (Moran and Hurd, 1998; Pace et al., 1998; Drenner et al., 2002). But comparative studies in MPAs, between fished and unfished zones, can provide the experimental basis or manipulation that allows detection of trophic cascades. The manipulation is the removal of humans as predators from one of the experimental treatments, allowing populations of otherwise exploited prey to exist. Under these conditions, trophic interactions between different levels of the biota may be used as a baseline to compare with areas where exploitation continues. Thus, MPAs can be useful tools to determine the effects of predator removal on herbivorous prey and consequent effects on primary producers.

A previous study, in three regions of the Ningaloo Marine Park, Western Australia showed higher abundance, biomass and size of the dominant predatory fish family, Lethrinidae, in unfished Sanctuary Zones, compared with nearby Recreation (recreationally fished) Zones (Chapter 2). A creel survey had shown that 90% of fishers in the region targeted lethrinids and these were also the most caught genera comprising 48% of the catch by recreational fishers at or near the study sites (Sumner et al., 2002). Lethrinids also comprised 78% of the biomass of
targeted fish censused. Although lethrinids were shown to prey heavily on the grazing urchin *Echinometra mathaei* (Chapter 3), differences in urchin abundances between Sanctuary and Recreation Zones were not consistent among regions. At one region, higher abundance, biomass and size of *E. mathaei* in the Recreation Zone, compared with the Sanctuary Zone, appeared to have resulted from reduced predation. But *E. mathaei* populations were greater in the Sanctuary Zone at another region, a result that was attributed to higher cover of habitat (dead coral, rock and *Echinopora*) that provided refuge from predation. Although predation played a role in structuring the grazing invertebrate community, refuge provision appeared to have an over-riding influence. The possibility existed that differences in the abundances of herbivorous invertebrates at these sites would have affected algal cover. If this was the case, a trophic cascade may be evident where high predator abundance corresponded with low urchin abundance. There was also the possibility that herbivory from fishes might confound any effect of herbivory from urchins. There is a lack of studies on trophic cascades where recreational line fishing is the only extractive practice. Pinnegar et al. (2000) also noted a lack of studies on trophic cascades in the East Indian Ocean which includes the Ningaloo region.

The main aim of this study was to determine whether differences in *E. mathaei* populations, between Sanctuary and Recreation Zones of the Ningaloo Marine Park, had lead to differences in algal cover and hence a potential trophic cascade due to recreational fishing in the fished zones. A further aim was to test whether there were differences in herbivorous fishes between zones that may also have influenced algal cover and composition, and could have confounded any results of differences attributed to urchin herbivory. The aim of this study was therefore to test whether: (1) differences in *Echinometra mathaei* populations, due to differences in predation and habitat (Chapter 3), had changed algal cover and composition through grazing; and (2) differences between protected and unprotected areas in terms of herbivorous fish assemblages may confound the effects of grazing by *Echinometra mathaei*. 
4.2 METHODS

This study was conducted at three regions in the Ningaloo Marine Park (Mandu, Osprey and Maud) as per Chapters 2 and 3 (Figure 4.1). In each region the fish and algal assemblages were compared between a Sanctuary Zone where no fishing was permitted and an adjacent Recreation Zone where the only extractive activity permitted was recreational line fishing. The two zones in each region were similar in terms of depth, distance from shore and proximity to channel areas. Data on the biomass of predatory fishes; the abundance, biomass and mean size of *Echinometra mathaei*; and the habitat availability for *E. mathaei* were taken from Chapters 2 and 3.

Figure 4.1. Location of study sites (*) in the Ningaloo Marine Park, Western Australia. Note the Mandu, Osprey and Maud Sanctuary Zones, which are shaded.
4.2.1 Census of herbivorous fishes

Herbivorous fish assemblages were measured using underwater visual census (UVC) transects of 50 x 5 m (250 m² per transect) (n = 8). A combination of audio and video was used, as recommended by Bortone et al. (1991) which overcame the limitations of using a slate to record fish data (Bohnsack and Bannerot, 1986; Kulbicki, 1998). A full face ARGA mask with a microphone, was attached to an underwater video camera and verbal counts of fishes were recorded on a videotape. Inter-observer bias has been shown to confound the results of UVC (DeMartini and Roberts, 1982; St. John et al., 1990; Watson and Quinn, 1997; Harvey et al., 1998), so the same observer (M. Westera) was used for all UVC work. Fishes were counted and their size was estimated to within 10 cm. Eight transects were used, as a pilot study indicated that no new species were recorded after eight of ten transects. The accuracy of estimates of fish size were tested using objects of known length underwater prior to surveys. The biomass of herbivorous fishes was calculated using methods outlined in Chapter 3.

Reef fish assemblages may vary on short-term temporal scales (Kingsford and Battershill, 1998), thus differences in samples taken 1-2 days apart at different sites may be confounded by within site temporal changes. To test for short-term temporal variability in the biomass of herbivorous fishes, UVC transects were repeated at the Maud Sanctuary Zone three days apart in January 2000. There were no significant differences in the abundance or biomass of turf-algal grazing fishes or macro-algal grazing fishes (T-tests) and no significant difference in composition of herbivorous fishes (ANOSIM).

4.2.2 Algal cover

To measure the percent cover of turf- and macro-algae, a video camera was held 50 cm above the substrate and moved along the same transects used for UVC. Fifty randomly selected frames were extracted from the footage of each transect and viewed on a computer screen to determine the percent cover of turf-algae (fine filamentous types) and macro-algae (all larger erect genera such as Dictyota, Sargassum and Turbinaria) under 10 points on each frame. A total of 500 points per transect were analysed (4000 points per zone in each region). Algal cover was expressed as a percentage of substrate that could be colonised by algae. For turf- and macro-algae this included dead coral, rock and rubble, but for macroalgae this also included areas colonised by turf-algae.

Macroalgae were collected from 0.25 m² quadrats placed randomly along each of the benthic video transects. Turf algae were not harvested due to their low profile (< 1 cm) and being well
attached to the substrate. Algal biomass was reported as the wet weight of functional groups (e.g. fucoid browns, foliose browns, erect fleshy reds). Functional groups were used, as dietary information indicated that herbivorous fishes and urchins would be unlikely to distinguish between different species or genera of algae that are of a similar morphology (Hiatt and Strasbourg, 1960; Herring, 1972; Dart, 1975; Vanderklift, 2003). Species-area curves were used to ascertain the number of quadrats required. No new functional groups were recorded after nine quadrats. Therefore 12 were used in August 1999, but this was increased to 16 in January and July 2000 due variability in biomass. Only eight samples were available for Mandu in August 1999.

4.2.3 Diets of herbivorous fishes and invertebrates

Herbivorous fishes were caught using spears and their guts were removed and stored in 70% ethanol. Guts were dried on absorbent paper, weighed and the contents separated into algal functional groups. The proportion of each group was expressed as a percentage of overall stomach contents (Hyslop, 1980). Herbivorous fishes were classified as turf-algal feeders or macro-algal feeders, based dietary information in the literature (Hiatt and Strasbourg, 1960; Randall, 1967; Jones, 1968; Hobson, 1974; Choat, 1991; Choat et al., 2002) which was confirmed with feeding observations and preliminary samples of gut contents at the study sites. No attempt was made to identify algal species from scarids as they generally graze fine turf algae (Hobson, 1974; Choat, 1991) which they grind, making identification difficult without high power magnification (Choat et al., 2002). *Echinometra mathaei* diets were determined by analysing the guts of 30 individuals ranging in test size from 2 to 33 mm. Each urchin was opened with a hacksaw, to remove the gut after which its contents were sorted and classified into the above functional groups.

4.2.4 Statistical analyses

Three-factor mixed model analysis of variance (ANOVA) with time, region and zone as factors, was used to compare the biomass of herbivorous fishes, and the percent cover of macro- and turf-algae. Three-factor interactions were analysed using multiple comparisons with the test-slices function and the LSMeans Student's-t contrast function in the JMP statistical package (SAS Institute Inc., 2000). Ryan's procedure was used to control for any increase in Type I errors (Underwood, 1997). Data were tested for homogeneity of variance using Cochran's test and Log₁₀ (x + 1) transformed where necessary. If variances were heterogeneous after transformation alpha was reduced to 0.01 (Underwood, 1981) and analysis performed on
untransformed data, as ANOVA is robust and can operate with heterogeneous variances, as long as there is a balanced sampling design (Glass et al., 1972). Time was treated as a random factor as sampling times were chosen to observe the generality of any trends. The choice of regions was dictated by previous work (Chapters 2 and 3) that had identified different assemblages of predatory fishes and *Echinometra mathaei* in Sanctuary and adjacent Recreation Zones. Zones (Sanctuary and Recreation) were chosen to represent fished and unfished areas. Consequently, region and zone were treated as fixed factors. Spearman’s correlation coefficients were used to explore relationships between *Echinometra mathaei* abundances and macro-algal cover.

Multivariate analyses were conducted using the PRIMER statistical package (PRIMER-E Ltd, 2000), to compare assemblages of herbivorous fishes and macro-algae between zones and to determine which fish or functional groups of algae might be driving differences in univariate analyses. Non-metric multidimensional scaling (nMDS) (Field et al., 1982) was used to examine spatial patterns and two-way crossed analysis of similarity (ANOSIM) (Clarke and Warwick, 1994) was used to determine the significance of trends (for each region) between zones and over time. Two-way crossed ANOSIM was split by region as previous work had shown differences between regions in terms of *Echinometra mathaei* abundances and the habitat that provided them with refuge from predation (Chapter 3). Tests were based on a Bray-Curtis rank similarity matrix, calculated using square root transformed data. One-way ANOSIM was also used to determine the significance of any clustering of replicates, within each region, in nMDS ordinations. Similarity percentages (SIMPER) (Clarke, 1993) was used to examine individual contributions to any observed differences in the composition of herbivorous fishes or functional groups of algae.
4.3 RESULTS

4.3.1 Herbivorous fish assemblages

Thirty-nine species of herbivorous fishes were recorded from the families Acanthuridae, Scaridae, Pomacentridae, Siganidae, Pomacanthidae and Kyphosidae (Table 4.1). The most dominant species were *Acanthurus triostegus* (Linnaeus), *A. grammoptilus* (Richardson), *Scarus psittacus* (Forsskål), *S. sordidus* (Forsskål), *S. ghobban* (Forsskål) *S. rivulatus* (Valenciennes) and *Abedefduf sexfasciatus* (Lacepède).

ANOVA showed that there were no significant differences in the biomass of fishes that graze macro-algae between times, regions or zones (Table 4.2). This included the families Siganidae and Kyphosidae and the genus *Naso* of the family Acanthuridae (Table 4.1). Their biomass was highly variable among times, regions and zones ranging from 0.04 to 4 kg 250 m⁻² (i.e. per transect) (Figure 4.2). The biomass of turf grazing fishes was significantly higher in Sanctuary Zones than Recreation Zones (Table 4.2, Figure 4.2). These were mainly acanthurids and scarids, but also included members of the pomacentrids and pomacanthids. The biomass of turf-grazers was approximately five times that of macro-algal grazers (Figure 4.2) and ranged from 7.5 to 32.7 kg 250 m⁻² in Sanctuary Zones and from 2.5 to 12.4 kg 250 m⁻² in Recreation Zones.

Assemblages of herbivorous fishes (both turf- and macro-algal grazers combined) differed significantly between zones and times (Two-way crossed ANOSIM – Table 4.3). NMDS ordinations showed some separation of replicates from Sanctuary and Recreation Zones (Figure 4.3). Trends were strongest at Mandu with significant differences for each time (one-way ANOSIM) but at Osprey and Maud differences between zones were significant for two of the three times sampled. SIMPER revealed that differences between zones at all regions were being driven mainly by *Scarus sordidus* *S. psittacus, S. ghobban* and *Acanthurus triostegus* with a contribution from *Abedefduf sexfasciatus* at Mandu, all of which are turf grazers (Table 4.4). Differences at Maud were also driven by *Naso unicornis*. Elsewhere, contributions from macro-algal grazers (siganids, kyphosids and the genus *Naso*) were generally low.
Table 4.1: Herbivorous fishes recorded in UVC transects, in order of dominance by family. Note food types (TA = filamentous turf-algae; MA = macro-algae; DD = detritus and diatoms).

<table>
<thead>
<tr>
<th>Family / species</th>
<th>Common name</th>
<th>Food types</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Acanthuridae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acanthurus dussumieri (Linnaeus, 1758)</td>
<td>Ornate surgeonfish</td>
<td>TA</td>
</tr>
<tr>
<td>Acanthurus grammoptilus (Richardson, 1843)</td>
<td>Ring-tailed surgeonfish</td>
<td>TA</td>
</tr>
<tr>
<td>Acanthurus nigricans (Linnaeus, 1758)</td>
<td>White cheeked surgeonfish</td>
<td>TA</td>
</tr>
<tr>
<td>Acanthurus nigricauda (Duncker and Mohr, 1929)</td>
<td>Blackstreak surgeonfish</td>
<td>TA</td>
</tr>
<tr>
<td>Acanthurus olivaceus (Bloch and Schneider, 1801)</td>
<td>Orange-spot surgeonfish</td>
<td>TA</td>
</tr>
<tr>
<td>Acanthurus triostegus (Linnaeus, 1758)</td>
<td>Convict surgeonfish</td>
<td>TA</td>
</tr>
<tr>
<td>Acanthurus xanthopterus (Valenciennes, 1835)</td>
<td>Yellowfin surgeon fish</td>
<td>TA and DD</td>
</tr>
<tr>
<td>Naso fageni (Morrow, 1954)</td>
<td>Blunt unicornfish</td>
<td>MA</td>
</tr>
<tr>
<td>Naso lituratus (Bloch and Schneider, 1801)</td>
<td>Stripe-face unicornfish</td>
<td>MA</td>
</tr>
<tr>
<td>Naso tuberosus (Lacepede, 1802)</td>
<td>Humphead unicornfish</td>
<td>MA</td>
</tr>
<tr>
<td>Naso unicornis (Forsskål, 1775)</td>
<td>Brown unicornfish</td>
<td>MA</td>
</tr>
<tr>
<td>Zebrasoma scopas</td>
<td>Blue lined tang</td>
<td>TA</td>
</tr>
<tr>
<td>Zebrasoma veliferum (Bloch, 1797)</td>
<td>Sailfin tang</td>
<td>TA</td>
</tr>
<tr>
<td><strong>Scaridae</strong></td>
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<td></td>
</tr>
<tr>
<td>Cetoscarus bicolor (Ruppell, 1828)</td>
<td>Red speckled parrotfish</td>
<td>TA</td>
</tr>
<tr>
<td>Hipposcarus longiceps (Bleeker, 1862)</td>
<td>Longnosed parrotfish</td>
<td>TA</td>
</tr>
<tr>
<td>Scarus chameleon (Choat and Randall, 1986)</td>
<td>Chameleon parrotfish</td>
<td>TA</td>
</tr>
<tr>
<td>Scarus dimidiatus (Bleeker, 1862)</td>
<td>Saddled parrotfish</td>
<td>TA</td>
</tr>
<tr>
<td>Scarus frenatus (Lacepede, 1802)</td>
<td>Sixbanded parrotfish</td>
<td>TA</td>
</tr>
<tr>
<td>Scarus ghobban (Forsskål, 1775)</td>
<td>Blue barred parrotfish</td>
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</tr>
<tr>
<td>Scarus microhinos (Bleeker, 1854)</td>
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</tr>
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<td>Scarus oviceps (Valenciennes, 1839)</td>
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<td>TA</td>
</tr>
<tr>
<td>Scarus prasognathus (Valenciennes, 1839)</td>
<td>Dusky parrotfish</td>
<td>TA</td>
</tr>
<tr>
<td>Scarus psittacus (Forsskål, 1775)</td>
<td>Palenose parrot</td>
<td>TA</td>
</tr>
<tr>
<td>Scarus rivulatus (Valenciennes, 1840)</td>
<td>Surf parrotfish</td>
<td>TA</td>
</tr>
<tr>
<td>Scarus rubroviolaeus (Bleeker, 1849)</td>
<td>Ember parrotfish</td>
<td>TA</td>
</tr>
<tr>
<td>Scarus schegeli (Bleeker, 1861)</td>
<td>Schlegel's parrotfish</td>
<td>TA</td>
</tr>
<tr>
<td>Scarus sordidus (Forsskål, 1775)</td>
<td>Greenfinned parrotfish</td>
<td>TA</td>
</tr>
<tr>
<td><strong>Pomacentridae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abedelfah seafasciatus (Lacepede, 1802)</td>
<td>Scissortail sergeant</td>
<td>TA</td>
</tr>
<tr>
<td>Abedelfah vaigienis (Quoy and Gaimard, 1825)</td>
<td>Sergeant major</td>
<td>TA</td>
</tr>
<tr>
<td>Abedelfah bengalensis (Bloch, 1787)</td>
<td>Narrow-banded sergeant major</td>
<td>TA</td>
</tr>
<tr>
<td>Diastodus prosopotaenia (Bleeker, 1852)</td>
<td>Honeyhead damsel</td>
<td>TA</td>
</tr>
<tr>
<td>Pomacentrus vaigiensis (Jordan and Seale, 1906)</td>
<td>Princess damsel</td>
<td>TA</td>
</tr>
<tr>
<td>Stegastes nigricans (Lacepede, 1802)</td>
<td>Dusky gregory</td>
<td>TA</td>
</tr>
<tr>
<td><strong>Siganidae</strong></td>
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<td></td>
</tr>
<tr>
<td>Siganus dolatus (Cuvier, 1830)</td>
<td>Doublebar spinefoot</td>
<td>TA and MA</td>
</tr>
<tr>
<td>Siganus fuscuscens (Houttuyn, 1782)</td>
<td>Pearly spotted rabbitfish</td>
<td>TA and MA</td>
</tr>
<tr>
<td>Siganus triolius (Woodland and Allen, 1977)</td>
<td>Threespot spinefoot</td>
<td>TA and MA</td>
</tr>
<tr>
<td><strong>Pomacanthidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Centropyge tibicen (Cuvier, 1831)</td>
<td>Keyhole angelfish</td>
<td>TA</td>
</tr>
<tr>
<td><strong>Kyphosidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kyphosus biggii (Lacepede, 1802)</td>
<td>Southern drummer</td>
<td>TA and MA</td>
</tr>
<tr>
<td>Kyphosus corneli (Whitley, 1944)</td>
<td>Western buffalo bream</td>
<td>TA and MA</td>
</tr>
</tbody>
</table>
Table 4.4: Results of SIMPER analysis and one-way ANOSIM (R-values and significance levels) on the biomass of all herbivorous fishes (i.e. macro-algal and turf grazers) separated by species, from Sanctuary (SZ) and Recreation (RZ) Zones for each region and time. Bold indicates significant differences, 999 permutations used.

<table>
<thead>
<tr>
<th>Date</th>
<th>August 1999</th>
<th>January 2000</th>
<th>July 2000</th>
</tr>
</thead>
<tbody>
<tr>
<td>Region</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Average biomass</td>
<td>Average dissimilarity</td>
<td>Contribution%</td>
</tr>
<tr>
<td>Mandu</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. psittacus</td>
<td>3.8 0.4</td>
<td>15 1.2</td>
<td>20 0.2</td>
</tr>
<tr>
<td>S. sordidus</td>
<td>2.0 0.6</td>
<td>12 1.4</td>
<td>16 0.3</td>
</tr>
<tr>
<td>A. triostegus</td>
<td>1.5 1.4</td>
<td>9.1 1.1</td>
<td>13 0.8</td>
</tr>
<tr>
<td>A. sexfasciatus</td>
<td>0.4 1.6</td>
<td>8.8 1.2</td>
<td>12 0.2</td>
</tr>
<tr>
<td>S. ghobban</td>
<td>0.5 0.6</td>
<td>4.4 0.7</td>
<td>6.0 0.3</td>
</tr>
<tr>
<td>S. rivulatus</td>
<td>. .</td>
<td>. .</td>
<td>. .</td>
</tr>
<tr>
<td>N. tuberosus</td>
<td>. .</td>
<td>. .</td>
<td>. .</td>
</tr>
<tr>
<td>Osprey</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. triostegus</td>
<td>4.4 1.4</td>
<td>15 0.9</td>
<td>23 1.2</td>
</tr>
<tr>
<td>S. psittacus</td>
<td>2.8 1.2</td>
<td>12 1.1</td>
<td>19 3.9</td>
</tr>
<tr>
<td>S. sordidus</td>
<td>2.8 1.9</td>
<td>9.0 1.1</td>
<td>14 1.0</td>
</tr>
<tr>
<td>S. ghobban</td>
<td>2.0 0.9</td>
<td>8.0 1.0</td>
<td>13 0.7</td>
</tr>
<tr>
<td>A. grammoptilus</td>
<td>0.4 0.2</td>
<td>2.1 1.2</td>
<td>3.4 0.1</td>
</tr>
<tr>
<td>Maud</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. sordidus</td>
<td>4.4 1.0</td>
<td>24 2.0</td>
<td>32 4.9</td>
</tr>
<tr>
<td>S. psittacus</td>
<td>2.4 1.0</td>
<td>11 1.8</td>
<td>15 4.6</td>
</tr>
<tr>
<td>S. ghobban</td>
<td>1.6 0.1</td>
<td>10 1.2</td>
<td>14 0.6</td>
</tr>
<tr>
<td>A. triostegus</td>
<td>1.3 0.1</td>
<td>7.6 1.1</td>
<td>10 0.7</td>
</tr>
<tr>
<td>S. frenatus</td>
<td>0.8 0.1</td>
<td>4.3 0.5</td>
<td>5.8 0.9</td>
</tr>
<tr>
<td>N. unicornis</td>
<td>. .</td>
<td>. .</td>
<td>. .</td>
</tr>
</tbody>
</table>

4.3.2 Algal cover and composition

ANOVA of macro-algal cover yielded a significant interaction between times, regions and zones (Table 4.5) indicating variability in macro-algal cover at each region over time, and also between zones for each time. Multiple comparisons showed contrasting results in the Mandu and Maud regions (Table 4.5, Figure 4.4). Macro-algae covered nearly 50% of the available substrate at the Mandu Sanctuary Zone in August 1999 and, despite falling to just over 20% (in January and July 2000), it was consistently higher than cover in the Recreation Zone. The opposite trend was evident at Maud. Macro-algal cover remained low in the Sanctuary Zone...
ranging from 5 to 9%, while in the Recreation Zone it ranged from 15 to 33% (Figure 4.4). There were no significant differences in macro-algal cover between zones at Osprey. Turf-algae covered approximately 15 to 45% of available substrate among the regions and zones but were not significantly different for any of the factors tested (Table 4.5; Figure 4.4).

Macro-algal composition was dominated by 19 species, which belonged to nine functional groups (see Section 4.3.3 below). The dominant functional group was the fucoid browns. Species composition of macro-algae was dominated by *Turbinaria ornata*, *Lobophora variegata*, *Hypnea pannosa* and *Laurencia papillosa*. Turf-algae was dominated by Chlorophyta, such as *Cladophora* spp. but also included genera from other phyla such *Hypnea*, *Sphacelaria*, *Centrocerus* and *Giraudia*.

Two-way crossed ANOSIM on the composition of macro-algae (as functional groups) highlighted significant differences between zones and times, within each region. However, Clarke’s R-values for time groups were greater than for zone groups, indicating that differences between times were greater than differences between zones (Table 4.6). NMDS ordinations of macroalgal biomass data showed some clustering of replicates from Sanctuary and Recreation Zones within each region and time, but a lack of separation between zones (Figure 4.5). However, one-way ANOSIM revealed that there were significant differences between Zones at Mandu for all three times, at Osprey on two times and at Maud on only one occasion.

SIMPER analysis indicated that fucoid brown algae accounted for 63-96% of between zone differences at Mandu (Table 4.7). This group consisted of erect brown “leathery” algae such as *Sargassum* spp., *Turbinaria ornata* and *Hormophysa triquerta* (Table 4.8). Biomass of fucoid brown algae was always higher in the Sanctuary Zone at Mandu, than the Recreation Zone and differed greatly between times ranging from 365 g. 0.25 m$^2$ (i.e. per quadrat) in August to 14 g. 0.25 m$^2$ in January. This trend was driven largely by *Turbinaria ornata*. Biomass of erect fleshy reds (e.g. *Hypnea* and *Laurencia*) was also consistently greater in the Sanctuary Zone than the Recreation Zone at Mandu. Fucoid browns made up a large proportion of the macro-algal composition at Osprey and Maud, but there were no clear trends between zones.
Table 4.5: Results of three-factor ANOVA on percent cover of macro- and turf-algae with sampling time (August 1999, January 2000 and July 2000), region (Mandu, Osprey and Maud) and zone (Sanctuary and Recreation) as factors. Data were transformed [arcsine and $\log_{10}(x + 1)$], $n = 8$. Alpha was reduced to 0.01 for turf-algae, as variances were heterogeneous after transformation. Significant three-factor interaction was analysed using multiple comparisons and Ryan’s procedure reduced alpha to 0.01 for this analysis. Bold indicates significant differences.

<table>
<thead>
<tr>
<th>Source</th>
<th>Macro-algae percent cover</th>
<th>Turf-algae percent cover</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DF</td>
<td>Mean square</td>
</tr>
<tr>
<td>Time</td>
<td>2</td>
<td>0.018</td>
</tr>
<tr>
<td>Region</td>
<td>2</td>
<td>0.026</td>
</tr>
<tr>
<td>Zone</td>
<td>1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Time*Region</td>
<td>4</td>
<td>0.007</td>
</tr>
<tr>
<td>Time*Zone</td>
<td>2</td>
<td>0.005</td>
</tr>
<tr>
<td>Region*Zone</td>
<td>2</td>
<td>0.047</td>
</tr>
<tr>
<td>Time<em>Region</em>Zone</td>
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<td>0.004</td>
</tr>
<tr>
<td>Residual</td>
<td>126</td>
<td>&lt;0.001</td>
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</tbody>
</table>

Students-t contrasts at each region for three-factor interaction - macro-algae percent cover

<table>
<thead>
<tr>
<th></th>
<th>F Ratio</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mandu</td>
<td>17.18</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Osprey</td>
<td>2.28</td>
<td>0.0821</td>
</tr>
<tr>
<td>Maud</td>
<td>22.48</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
Table 4.7: Results of SIMPER analysis and one-way ANOSIM (R-values and significance levels) on the biomass of macro-algae separated by functional groups, from Sanctuary (SZ) and Recreation (RZ) Zones at each region and time. Note significant differences *, 999 permutations used.

<table>
<thead>
<tr>
<th>Date</th>
<th>August 1999</th>
<th>January 2000</th>
<th>July 2000</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SZ</td>
<td>RZ</td>
<td>SZ</td>
</tr>
<tr>
<td><strong>Region</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Average biomass</td>
<td>Average dissimilarity</td>
<td>Ratio</td>
</tr>
<tr>
<td><strong>Mandu</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fucoid browns</td>
<td>365</td>
<td>122</td>
<td>63</td>
</tr>
<tr>
<td>Erect calcified reds</td>
<td>3.9</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>Erect fleshy reds</td>
<td>2.8</td>
<td>0.6</td>
<td>0.8</td>
</tr>
<tr>
<td>Dictyotales</td>
<td>1.2</td>
<td>0.8</td>
<td>0.4</td>
</tr>
<tr>
<td>Foliose browns</td>
<td>1.2</td>
<td>1.5</td>
<td>0.6</td>
</tr>
<tr>
<td><strong>Osprey</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fucoid browns</td>
<td>303</td>
<td>335</td>
<td>30</td>
</tr>
<tr>
<td>Erect fleshy reds</td>
<td>13</td>
<td>11</td>
<td>2.8</td>
</tr>
<tr>
<td>Erect calcified greens</td>
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<td>3.4</td>
</tr>
<tr>
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<td>6.3</td>
<td>1.0</td>
</tr>
<tr>
<td>Foliose browns</td>
<td>1.2</td>
<td>0.3</td>
<td>0.2</td>
</tr>
<tr>
<td>Dictyotales</td>
<td>.</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td><strong>Maud</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fucoid browns</td>
<td>30</td>
<td>14</td>
<td>32</td>
</tr>
<tr>
<td>Dictyotales</td>
<td>1.0</td>
<td>10</td>
<td>18</td>
</tr>
<tr>
<td>Erect fleshy reds</td>
<td>4.2</td>
<td>3.6</td>
<td>10</td>
</tr>
<tr>
<td>Foliose browns</td>
<td>3.2</td>
<td>3.0</td>
<td>6.5</td>
</tr>
<tr>
<td>Erect calcified reds</td>
<td>0.2</td>
<td>.</td>
<td>0.6</td>
</tr>
</tbody>
</table>
4.3.3 Herbivore diets

Large schools of acanthurids and scarids were regularly observed grazing on areas of fine filamentous turf-algae on the reef. Gut analysis confirmed that the diet of these genera comprises a substantial proportion of turf-algae. The guts of *Acanthurus triostegus* and *Abedeuf sexfasciatus* contained an average of 75 and 60% turf-algae respectively (Table 4.8). Scarids contained a slurry of carbonate material, which was presumably eroded rock and dead coral that had been ingested when they grazed on epilithic algal turfs. *Acanthurus xanthopterus* consumed erect red algae and filamentous turfing algae amongst large amounts of sediment, which contributed 90% to the dietary biomass. Of the macro-algal grazers, *Naso* spp. consumed a large proportion of erect fleshy red algae (85%) as well as fucoid browns, foliose browns and Dictyotales (Table 4.8). The most common siganid (*Siganus fuscescens*) consumed erect fleshy reds (30%), Dictyotales (30%) and fucoid browns (10%).

*Echinometra mathaei* consumed mainly fucoid browns (63%) followed by foliose browns and Dictyotales (24%); erect filamentous reds (6%) and fine filamentous turf-algae (7%) (Table 4.8). Most urchins also contained balls of calcareous material, which had presumably been bioeroded from the reef substrate. There was a negative correlation between *E. mathaei* abundance and the percent cover of macro-algae ($R = -0.4268; P < 0.0001$).
Table 4.8: Algal functional groups and the dominant species recorded in algal collections, and percentages of each functional group recorded in guts of *Echinometra mathaei* and herbivorous fishes. 

Note: Foliose browns and Dictyotales are grouped for *Echinometra mathaei* as they could not be distinguished in the gut samples. See Table 4.7 for algal biomass figures.

<table>
<thead>
<tr>
<th>Number of samples</th>
<th>Echinometra mathaei</th>
<th>Abductella bengalensis</th>
<th>Acantharion triquetrum</th>
<th>Acantharens sedentarius</th>
<th>Narao tuberosus / tenerrimus</th>
<th>Scrobis praeceps / rivulatus / veligera</th>
<th>Sigmatomassa fuscovirens</th>
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<tr>
<td>Algal functional groups and species</td>
<td>30</td>
<td>4</td>
<td>9</td>
<td>5</td>
<td>4</td>
<td>10</td>
<td>3</td>
</tr>
<tr>
<td>Fucoid browns</td>
<td>63</td>
<td>10</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hormumphya triquerta</em></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><em>Sargassum</em> spp.</td>
<td></td>
<td></td>
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<tr>
<td><em>Turbinaria ornata</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>3</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lobophora variegata</em></td>
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<td></td>
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<tr>
<td><em>Padina australis</em></td>
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<tr>
<td><em>Stypopodium flabelliforme</em></td>
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<tr>
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<td>3</td>
<td>30</td>
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<td></td>
<td></td>
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<tr>
<td><em>Dictyota bartayresii</em></td>
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<tr>
<td>Erect fleshy green</td>
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<td></td>
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<tr>
<td><em>Caulerpa nummularia</em></td>
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<tr>
<td><em>Caulerpa racemosa</em> var. <em>clavifera</em></td>
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<td>85</td>
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<td><em>Hyphnea pannosa</em></td>
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<td><em>Laurencia papillosa</em></td>
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<td>Erect calcified green</td>
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<td><em>Amphirooa fragilissima</em></td>
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<td><em>Jania adhaerens</em></td>
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</tr>
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<td>60</td>
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<td><em>Cladophora socialis</em></td>
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<td><em>Giraudia</em> sp.</td>
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<td><em>Sphaceles</em> sp.</td>
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<td>Other food types</td>
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<td>Sediment and ground algae</td>
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<td>Plankton</td>
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</tr>
</tbody>
</table>


4.4 DISCUSSION

The data in this study provide evidence that a trophic cascade may have resulted from the removal of lethrinids at the Mandu Recreation Zone but not at the Osprey or Maud Recreation Zones. The three Sanctuary Zones studied at the Ningaloo Marine Park (Mandu, Osprey and Maud) supported higher biomass and abundance of legal-sized lethrinids than adjacent Recreation Zones, where recreational fishing was permitted (Chapter 2). Since lethrinids prey heavily on the grazing urchin *Echinometra mathaei* and were the dominant urchin predators (Chapter 3), there was the potential for a trophic cascade from fishing activities in the Recreation Zones. Figure 4.6 has been compiled to synthesise this data. At the Mandu region, the lower biomass and size of lethrinids in the Recreation Zone, compared to the adjacent Sanctuary Zone, corresponded with higher abundance, biomass and size of *E. mathaei* (Figure 4.6). The percent cover of macro-algae was lower in the Recreation Zone (Figure 4.6), where *E. mathaei* abundances were higher and differences in macro-algal composition were driven mainly by lower biomass of fucoid browns in the Recreation Zone. Since this algal group dominated the diets of *E. mathaei*, it is likely that the lower biomass of these algae reflect the higher grazing pressure from urchins. Other studies have also shown that sea urchin grazing alters algal cover and composition (Himmelman and Nedelec, 1990; Keats, 1991; Andrew and Underwood, 1993; Babcock et al., 1999).

Other factors that could have contributed to differences in macro-algal cover and composition between zones at Mandu include grazing by herbivorous fishes (Bythell et al., 2000; Williams and Polunin, 2001), differences in habitat characteristics that might have influenced predator-prey interactions (Hixon and Menge, 1991; McClanahan and Kurtis, 1991; Sala and Zabala, 1996) and differences in substrate availability for algal recruitment. However, these did not appear to confound the results as there were no significant differences in either the biomass of macro-algal grazing fishes, the cover of habitat that *E. mathaei* use to take refuge from predators (dead coral, rock and *Echinopora* corals) (Chapter 3) (Figure 4.6) and the availability of hard substrate for algal attachment (Chapter 2) between the Sanctuary and Recreation Zones.

The only extractive activity permitted in Recreation Zones of the Ningaloo Marine Park is recreational line fishing. This differs from other studies that have recorded trophic interactions involving predatory fishes, urchins and algae (Mann, 1982a; McClanahan and Shafir, 1990; Babcock et al., 1999; Shears and Babcock, 2002), as fishing pressure was from commercial or artisanal fishers using a number of fishing methods such as nets, traps and lines. It appears that this study may be the first that has recorded evidence of a trophic cascade where recreational line fishing was the only means of extracting fishes. Recreational fishers frequently target the most palatable and prized predatory fishes such as Lethrinidae, Serranidae and Lutjanidae.
(Polunin and Roberts, 1993; Sumner et al., 2002), however these fishes are highly vulnerable to overfishing as they have long life spans and low rates of natural mortality, recruitment and growth (Russ and Alcala, 1998b). These same fishes may fulfil a “keystone” role in the trophic structure of a reef community. Lethrinids at Ningaloo fit the definition of “keystone species” (Jennings and Kaiser, 1998), as they are a targeted predator that selectively feeds on a species of urchin, which otherwise dominates the herbivore community. The results of this study, combined with Chapters 2 and 3, highlight the potential effect of recreational fishing and the need to ensure that stocks of keystone predatory fishes are not depleted.

An equally significant finding of this study, in addition to a potential trophic cascade, was the inconsistency of results between regions. In contrast to Mandu, *E. mathaei* abundances were greater in the Maud Sanctuary Zone, where the biomass of lethrinids was greater (Figure 4.6). There was also greater cover of *E. mathaei* habitat (dead coral, rock and *Echinopora* corals) in the Maud Sanctuary Zone (Figure 4.6) and it is possible that this mediated the effect of predation by lethrinids on this urchin. The higher cover of habitat provided crevices in which *E. mathaei* resided and could avoid predation (Chapter 3), a behaviour that has been noted in other studies (Tsuchiya and Nishihira, 1984; McClanahan and Muthiga, 1988; Sala and Zabala, 1996). The low cover of macro-algae in the Maud Sanctuary Zone (approximately 20% of that recorded in the Recreation Zone) may have been due to heavy grazing by *E. mathaei*. *E. mathaei* forage at night (Mills et al., 2000), presumably to avoid predators, and this may have allowed them to graze algae without being preyed upon. The inverse relationship between abundances of *E. mathaei* (macro-algal grazers) and macro-algal cover at Maud and Mandu (Figure 4.6) was supported by a negative correlation between these variables over all regions and zones sampled. This grazing effect was unlikely to have been confounded by fishes that graze macro-algae, as the biomass of these fishes did not differ between the Sanctuary and Recreation Zones.

At the Osprey region there were no significant differences in *E. mathaei* abundances between Zones (Chapter 3) despite populations of lethrinids being greater in the Sanctuary Zone. This may have been due to higher availability of habitat in the Sanctuary Zone as was recorded at Maud (Figure 4.6) that allowed *E. mathaei* to take refuge from predation. The lack of a difference in *E. mathaei* abundances may explain why there was no obvious grazing effect in the form of a difference in macro-algal cover.

In this study, the availability of refuge (habitat), may be the over-riding factor that reduced the effect of predators on prey abundances (Chapter 3). This has implications for management particularly in terms of conservation. When an MPA is established, what do managers expect to happen? Chapter 2 showed that there may be an increase in targeted fishes and this has
commonly been shown in other studies [see reviews (Roberts et al., 2001; Ward et al., 2001)]. However, changes in the next trophic level (in this case grazers) may be more difficult to predict, and it is the grazers that might change benthic structure through their effect on primary producers. If managers wish to maintain or restore ecological processes or habitats, as is often an objective of MPAs (Goni et al., 2000; National Research Council, 2001; Environment Australia, 2002), they can not assume a classic trophic response to the removal of fishing pressure. MPA objectives may need to be flexible enough to allow for this unpredictability. Management should include monitoring that will identify whether objectives are being met and expand our knowledge of how ecosystems may respond to the removal of fishing pressure. Differences among regions, in the trophic effects of fishing, may be normal rather than exceptional.

Acanthurids and scarids are often the largest groups of turf grazers on coral reefs (Hiatt and Strasbourg, 1960; Jones, 1968). In this study, these were the dominant genera of grazing fishes and their biomass was greater in Sanctuary Zones at all regions. However, there was no obvious effect of grazing on turf-algal cover. It is unclear what mechanisms may have driven the differences in turf grazing fishes. These fishes rarely take bait from a hook and are therefore not generally captured by fishers at Ningaloo (Sumner et al., 2002) so protection from fishing is unlikely to explain their high biomass in Sanctuary Zones. Steneck and Dethier (1994) proposed that when there was intense grazing from herbivorous fishes, this may be compensated by increases in algal productivity that may increase the trophic carrying capacity of a region. Thus, despite no difference in the cover of turf-algae between zones, there may have been greater productivity in areas where biomass of turf grazers was high. Russ (2003) found that the biomass of large grazing herbivorous fishes was correlated with algal production, but not with algal biomass. Further work is required to determine why the biomass of turf grazing fishes was higher in Sanctuary Zones at the study sites.

This study adds to the growing literature that highlights the value of marine reserves for conducting comparative studies between fished and unfished zones (McClanahan, 1997; Sala and Boudouresque, 1997; Castilla, 1999; Shears and Babcock, 2002). The fished and unfished zones of the Ningaloo Marine Park allowed us to examine the effects of removing fishes in one chain of the trophic structure i.e. predators > prey > algae. Future studies may reveal more complex interactions.
Marine reserves are often established with broad objectives such as to conserve biodiversity, preserve habitats, maintain or restore ecological processes, and ensure the sustainable utilisation of species and ecosystems (Colman and Simpson, 1998; Kelleher, 1999; National Research Council, 2001; Environment Australia, 2002; Airame et al., 2003). Marine reserves also serve as experimental tools as they allow us to compare exploited and unexploited areas. The studies from the Ningaloo Marine Park (Chapters 2, 3 and 4) provide examples of a marine reserves meeting some of these objectives. Sanctuary Zones (marine reserves) and Recreation Zones (where recreational line fishing was the only extractive activity) were compared in the Mandu, Osprey and Maud regions of the Marine Park. The aim of this project was to test whether recreational line fishing had affected targeted fish assemblages and whether there were flow-on effects to other levels of the trophic structure, through predator-prey relationships, that might have lead to a trophic cascade.

The outcome of comparisons between Sanctuary and Recreation Zones was consistent for top-level predatory fishes. The exclusion of fishing resulted in higher biomass, size, and abundance of legal-sized lethrinids, the most targeted fishes in the region (Chapter 2). This demonstrated the effect of fishing as a direct and measurable impact on the most targeted fishes in the study regions. Investigations were then made to determine whether the larger populations of lethrinids were associated with changes in their prey (Chapter 3). Gut analysis showed that the grazing sea-urchin *Echinometra mathaei* were the favoured prey of lethrinids and census work showed that *E. mathaei* were the dominant macroinvertebrate grazers on the reef. A tethering experiment demonstrated that lethrinids and other predators preyed on *E. mathaei* at the study sites and observations suggested that predation was higher in Sanctuary Zones where there were more predators. At the Mandu Recreation Zone, the abundance, biomass and size of *E. mathaei* was greater where the number of predators was lower, compared with the Sanctuary Zone, and this was attributed to reduced predation. Similar relationships between predatory fishes and urchins have been shown elsewhere (McClanahan and Muthiga, 1989; Shears and Babcock, 2002). Urchins usually reside in crevices of the reef (Tsuchiya and Nishihira, 1984; Sala and Zabala, 1996) to avoid predation (McClanahan and Muthiga, 1988; Sala and Zabala, 1996), but there were no differences between zones in the cover of habitat that provided these refuges (dead coral, rock and *Echinopora* corals) that might have influenced *E. mathaei* assemblages.
The effect of predators on prey observed at Mandu was not consistent across all regions. At Maud, high abundances of *Echinometra mathaei* prevailed in the Sanctuary Zone despite the higher biomass and size of predatory fishes than in the Recreation Zone. At Maud, the Sanctuary Zone was characterised by the cover of dead coral, rock and *Echinopora* corals that provided refuge for *E. mathaei*. It is likely that this difference in habitat availability mediated the effects of higher predation in the Sanctuary Zone. At the Osprey region there were no significant differences between zones in *E. mathaei* abundances despite potentially higher predation from lethrinids in the Sanctuary Zone, possibly because of a greater availability of refuges in the Sanctuary Zone.

Investigations of this study were then focussed on whether *Echinometra mathaei* had reduced algal cover through grazing (Chapter 4), and whether there was a trophic cascade as a consequence of reduced numbers of lethrinids in the Mandu Recreation Zone. The diets of *E. mathaei* were dominated by fucoid brown algae such as *Turbinaria* and *Sargassum*. At the Mandu region the cover of these algae was lower in the Recreation Zone where the abundance, biomass and size of *E. mathaei* were higher, compared with the Sanctuary Zone, indicating that a trophic cascade may have resulted from the removal of lethrinids. At Maud there was an effect of grazing in the Sanctuary Zone, as high abundances of *E. mathaei* were associated with low macro-algal cover, but there was no trophic cascade as both lethrinids and *E. mathaei* were in higher numbers than the Recreation Zone. At Osprey there were no differences in macroalgae between zones and this was consistent with the fact that *E. mathaei* abundances did not differ significantly. The effect of *E. mathaei* grazing was unlikely to have been confounded by fishes that graze macro-algae (Siganidae, Kyphosidae and the genus *Naso* of the family Acanthuridae), as they did not differ between zones at any region. Sampling revealed inconsistencies in benthic cover, and consequently grazing regimes, between regions on relatively small spatial scales (i.e. between Osprey and Mandu that were less than 15 km apart). The biomass of turf grazing herbivorous fishes was greater in Sanctuary Zones at all regions but this could not be explained by differences in habitat or algal cover. Neither could this have been due to fishing as these turf-grazing fishes are rarely captured.

From a conservation perspective, the Sanctuary Zones at Ningaloo were successful in enhancing fish populations, in terms of the dominant predatory fishes and turf-algal grazing fishes. However, it is difficult to assess whether the common conservation objective, to maintain or restore ecological processes (Colman and Simpson, 1998; Kelleher, 1999; National Research Council, 2001; Environment Australia, 2002; Airame et al., 2003), has been met. To “maintain” implies that a system might stay the same after fishing pressure is removed, but this may not always be the case. Although there were no time series data, the results from Chapter 4 suggest
that the removal of fishing pressure at Mandu allowed algal cover to increase by increasing the number of predatory fishes that kept grazing urchins in check. Thus, ecological processes may have been altered rather than maintained. This process has been shown in other studies where the removal of fishing pressure resulted in large-scale ecological changes over time, such as urchin barrens shifting to macroalgal dominated habitat (Babcock et al., 1999) and changes in predation and grazing regimes (McClanahan and Muthiga, 1989; McClanahan, 1994). At Maud, the removal of fishing pressure and increase in fish predators was not sufficient to reduce urchins through increased predation. Sanctuary Zoning may have had different effects in different regions, depending on the ecological processes that were operating prior to their establishment. A marine reserve is unlikely to "maintain" a system as removal of fishing pressure may alter ecological processes. This may return or "restore" a system to a more "natural" state or there may be over-riding factors such as habitat and refuge provision that impede ecological change. A greater understanding is needed of how marine reserves might change ecological functioning over time.

Figure 5.1 graphically represents how predatory fishes, urchin abundances and refuge provision may have changed over time, how this may have influenced grazing regimes and algal cover, and why there were differences between the Mandu and Maud regions at Ningaloo. It draws on the findings of this research and other studies. Fish abundances are likely to decrease due to fishing (Christensen et al., 2003) (Figure 5.1A and B: Point 1). This may lead to an increase in abundance of their prey, grazing urchins [(Chapter 3) and (McClanahan and Muthiga, 1988)] and a reduction in algal cover due to increased grazing (Morrison, 1988) (Figure 5.1A and B: Points 2 and 3). When Sanctuary Zones are established, and fishing pressure is removed, they might respond with an increase in stocks of predatory fishes (Wantiez et al., 1997) (Figure 5.1A and B: Point 4), an increase in predation from those fishes and a reduction in abundances of their prey (Shears and Babcock, 2002), (Figure 5.1A: Point 4) and a change in the food source of the prey (e.g. biomass or cover of algae) to some pre-exploited level (Figure 5.1A: Point 5). This may have occurred at Mandu, but at Maud there may have been over-riding effects that persisted from before the Sanctuary Zone was established.

The relatively high availability of *E. mathaei* habitat at the Maud Sanctuary Zone may have been a long-term condition at the site. However, it is possible that the earlier fishing pressure contributed to this habitat provision (Figure 5.1B: Points 5 and 6). *E. mathaei* bioerode reef substrate (Mokady et al., 1996; Carreiro-Silva and McClanahan, 2001) and in doing so excavate burrows and crevices in the reef (Tsuchiya and Nishihira, 1984; Neill, 1988) which may have enhanced the availability of refuges. Of the three regions studied, Maud was the most likely to have been heavily fished prior to establishment of Sanctuary Zones, as the Coral Bay township,
the only developed area of the Marine Park, is located on its shores. Under conditions of high fishing pressure, where its predators were removed, *E. mathaei* may have proliferated and, produced a proportionally large amount of refuges at Maud compared with other areas. As predatory fishes built up, after the Maud Sanctuary Zone was established (Figure 5.1B; Point 4), they may have preyed on *E. mathaei* that left their refuges but posed little threat to reducing overall abundances. *E. mathaei* populations have been shown to have genetic distinction on scales of less than 4 km (Watts et al., 1990), indicating in situ recruitment, and this might have further increased abundances. *E. mathaei* graze at night (Mills et al., 2000), presumably to avoid predation, and could have maintained low algal cover compared with areas where their abundances were lower. In essence, *E. mathaei* may have reached extreme densities due to removal of their predators through fishing, and the removal of fishing was not sufficient to reverse the situation (Figure 5.1B: Point 7). McClanahan et al. (1996) suggested that removal of sea urchins might aid reef restoration in areas that have been heavily fished, but added that without sufficient grazing, canopy forming algae may affect corals and turf algae through shading.

Trophic linkages have been shown in other studies involving similar trophic groups to those at Ningaloo (invertivorous fishes > invertebrates > algae) (Mann, 1982a; McClanahan and Shafir, 1990; Babcock et al., 1999; Shears and Babcock, 2002) and differences in habitat have been shown to confound the effects of predation (Cole and Keuskamp, 1998; Sala et al., 1998b). Fishing pressure in the aforementioned studies was exerted by commercial and artisanal fishers that used a variety of capture methods. No studies appear to have recorded trophic cascades where recreation line fishing was the only extraction permitted. Other researchers have cited the need for more studies to improve our understanding of interactions between fishes and their habitats, particularly in the eastern Indian Ocean (Roberts, 1995; McClanahan, 1997; Jones and Syms, 1998; Pinnegar et al., 2000). The research outlined in this thesis has contributed towards an understanding of fish-habitat interactions at Ningaloo Marine Park. The studies also provide a baseline against which future monitoring and performance assessment of the Ningaloo Marine Park may be gauged.
1. Fish abundances decrease due to fishing.

2. *E. mathaei* abundances increase due to reduced predation from fish.

3. Algal cover decreases due to increased grazing by *E. mathaei*.

Sanctuary Zone established

4. Fish abundances recover after cessation of fishing and increase in predation reduces *E. mathaei* abundances.

5. Decreased grazing allows algal cover to increase.

6. *E. mathaei* abundances not great enough to increase refuge availability through bioerosion.

--- Predatory fish

--- *E. mathaei*

--- Refuge

--- Algae

Fishing \hspace{1cm} No fishing

Time

--- Predatory fish

--- *E. mathaei*

--- Refuge

--- Algae

--- Predatory fish

--- *E. mathaei*

--- Refuge

--- Algae

Fishing \hspace{1cm} No fishing

Time

--- Predatory fish

--- *E. mathaei*

--- Refuge

--- Algae

Figure 5.1: Schematic diagram of possible relationships between fishing, predatory fishes, *E. mathaei* abundances, refuge for *E. mathaei* and algal cover. Effects are numbered in order of how they may change. The Mandu and Maud Sanctuary Zones from Ningaloo have been used as examples and referred to as A and B in the text.
5.1 THE POTENTIAL EFFECT OF RECREATIONAL LINE FISHING

The impact of recreational fishing on fish stocks is likely to grow due to an increasing number of fishers (Kearney et al., 1996; Fisheries Western Australia, 2000) and an increase in their efficiency through the use of advanced tools such as global positioning systems and echo sounders that enable pinpointing of fishing areas. Recreational line fishing is generally restricted to capturing fishes that will take bait from a hook and is highly selective towards prized and palatable fishes such as lethrinids, serranids, haemulids and lutjanids (Looby, 1997; Sumner et al., 2002). These fishes are the top-level predators in many marine systems (Hiatt and Strasbourg, 1960) and are vulnerable to overfishing due to their low rates of natural mortality, growth and recruitment (Russ and Alcala, 1998b). These fishes may also play a keystone role in ecosystem structure in terms of their predation effect (Chapter 3) and declines in their numbers may result in trophic cascades (Chapter 4). Thus, as recreational fishing pressure increases, more trophic cascades are likely to become evident.

Recreational line fishing may also have a greater impact on trophic structure than fisheries that capture a cross-section of trophic guilds. For example, in an artisanal fishery, Russ and Alcala (1998a) found no evidence of secondary effects of fishing in terms of increases in their prey due, in part, to the fact that the fishery was relatively non-selective. Commercial fishers also target a broader suite of trophic guilds than recreational fishers (Fisheries Western Australia, 2003). Therefore, total catch aside, recreational fishing may have a greater impact on trophic structure as it may remove a large proportion of top-level predators which could have a flow-on effect to their prey, as was the case at Ningaloo (Chapter 3).

The impact of recreational fishing may be difficult to manage due to a lack of knowledge on the total catch taken (Friedlander and Parrish, 1997; Looby, 1997). Commercial fishers in Australia are required to report their catch and effort to fisheries authorities and the time series of data can be used to estimate maximum sustainable yield. In contrast, total recreational catches are often difficult to obtain because, there are usually no mandatory reporting requirements. Creel survey estimates may be used, but these are collected on ad-hoc basis and may not accurately reflect long-term trends in total recreational catch. A total catch limit including both commercial and recreational fisheries may be needed. This has been proposed by Fisheries Western Australia (2000), but has not been implemented.

Many fisheries are being fully exploited or exceeding maximum sustainable yield (World Resources Institute, 1994; Kearney et al., 1996; Castilla, 2000). If estimates of maximum sustainable yield do not include accurate data on recreational catch, as well as commercial
catch, we risk an even greater level of overexploitation. A creel survey conducted in 1999 in the Gascoyne region in Western Australia highlighted that recreational catch comprised one third of the commercial catch (Sumner et al., 2002). As recreational fishing increases, so too will a gap in our understanding of the total catch unless regular creel surveys or mandatory reporting are adopted.

5.2 HOW SHOULD THE STUDIES AT NINGALOO INFLUENCE MANAGEMENT OF MARINE RESERVES AND FISHED AREAS?

If maintenance or restoration of ecological processes is a goal of marine park managers, they should not assume a classic trophic response to the removal of fishing pressure, i.e. increases in predatory fishes may not necessarily cause a change in the abundances of their prey, as predation may be mediated by habitat and refuge provision. The studies at Ningaloo (Chapters 3 and 4) showed differences between regions separated by <15 km in similar coral lagoon habitats. Objectives need to be flexible enough to allow for this unpredictability. Management should include monitoring that will identify whether objectives are being met and expand our knowledge of ecological responses to the removal of fishing pressure. Differences among regions in the trophic effects of fishing, or fishing exclusion, may be normal rather than exceptional.

Managers should consider reducing bag limits and imposing maximum size limits (in addition to the current minimum size limits) on fishes that play a keystone role in community structure. The studies at Ningaloo (Chapters 2, 3 and 4) not only showed that lethrinids fulfil a keystone role, but there also appeared to be an ontogenetic shift in their diet. Of the legal-sized lethrinids sampled (those that can be legally taken by fishers), 75% contained urchin remains (mainly *Echinometra mathaei*), but only 16% of under-sized lethrinids contained urchins. As *E. mathaei* graze algae and bioerode reef structure (De Ridder and Lawrence, 1982; Mokady et al., 1996; Carreiro-Silva and McClanahan, 2001), removal of their predators through overfishing may reduce algal cover, increase bioerosive processes and eventually reduce physical habitat structure. Reduced bag limits would allow a greater number of predators to "maintain ecological processes". Maximum size limits would increase the predatory effect of larger lethrinids and would also increase egg production. A high level of predation by lethrinids on *E. mathaei* appears to be important in controlling the effects of grazing and possibly bioerosion and therefore in maintaining habitat structure.
Habitats or areas of high conservation value should be protected by marine reserves rather than included in management areas where recreational fishing is permitted. The research in Chapters 2, 3 and 4, indicated that recreational fishing reduced fish populations and lead to a trophic cascade which can potentially compromise conservation or fish protection objectives. However, multiple-use zoning within a marine protected area is important. Without the Recreation Zones at Ningaloo, fished areas would likely have been subject to heavier fishing pressure from both commercial and recreational fishers. The multiple-use zoning at Ningaloo (i.e. Sanctuary and Recreation Zones) allowed studies of the effects of recreational fishing without other confounding extractive activities. Recreation Zones provided a management buffer between Sanctuary Zones and openly fished areas and bag limits were reduced. However, if managers wish to ameliorate the impacts of recreational fishing (Chapters 2, 3 and 4) further fishing restrictions are necessary in the Recreation Zones.

The size of marine reserves will influence their effectiveness in protecting targeted fishes and this will depend on the movement of these fishes. In a tag-recapture study of *Lethrinus nebulosus* at Ningaloo, 66% of recaptured fish (n = 60) had moved less than three nautical miles from their release point over 3-years (Moran et al., 1993). Thus, Sanctuary Zones that are six nautical miles or greater in diameter are likely to protect a proportion of this species. The Sanctuary Zones sampled in the Ningaloo studies are four to five nautical miles in length and one to two nautical miles wide, but they encompass only the shallow lagoon areas. They would provide some protection for *L. nebulosus* as was inherent in the results (Chapter 2) that showed differences in variates between zones for these fish. However, where these fish spawn and how eggs and larvae are transported in the region are matters for further investigation. It is highly probable that spawning takes place outside the current Sanctuary Zone areas. Fish spawning aggregations generally occur in channels or well defined promontories with high topographic complexity that are near deeper waters (Robertson, 1983; Johannes, 1988; Beets and Friedlander, 1998; Sancho et al., 2000), and that may be affected by tidal currents (Bell and Colin, 1986; Samoilys, 1997). These areas are generally not included in the current Sanctuary Zones. If managers wish to protect stocks of *Lethrinus nebulosus*, consideration should be given to increasing the size of Sanctuary Zones at Ningaloo and including deeper waters. This might account for the range of movement of *L. nebulosus* and where spawning may occur. Although fish movement patterns and spawning areas may be difficult to determine, attempts should be made to define them for inclusion in planning of marine reserves when objectives include protecting targeted fishes.

Marine park managers should monitor marine reserves over an extensive time-period. The studies at Ningaloo showed differences between Sanctuary and Recreation Zones in terms of
predatory fishes, herbivorous fishes, and invertebrates and habitat. As no data had been collected prior to these studies, nothing was known about how fish populations may have changed over the longer term. Long-term monitoring may have elucidated: the rate at which fishes build up; whether habitat changed over time periods due to trophic cascades and the effects of fishing; or whether there were shifts in community structure due to other events such as cyclones, El Niño or global warming. Increases in fish populations over time in both Sanctuary Zones and Recreation Zones might also suggest replenishment of fishes through spillover or dispersal of eggs and larvae and trigger more intensive investigations into these issues. Long-term monitoring is crucial to the sound management of marine reserves and other zones in marine protected areas.

To determine the effectiveness of marine reserves as conservation and fisheries management tools, and to examine the trophic effects of fishing, a number of factors should be monitored. Based on experience gained in these studies at Ningaloo, these should include: (1) pilot studies of all non-cryptic biota including fishes, invertebrates, benthic cover and composition, ensuring sufficient replication to determine sample sizes for later study; (2) identification of keystone species; (3) examination of predator-prey interactions; (4) dietary analysis of the dominant predators and prey; (5) measurements of habitat or refuge provision which may mediate predation; and (6) measurements of benthic cover and composition. Data could also be used in predictive trophic modelling packages such as ECOPATH / ECOSIM to examine trends over time (Christensen et al., 2000). Managers also need to be aware of the role of bottom-up effects (Caddy, 1993) such as anthropogenic nutrient inputs that might stimulate algal growth and influence cause-effect relationships. Where existing marine reserves have shown a build-up of fishes, they should be investigated in their potential to produce spillover and to disperse eggs and larvae that might recruit to other areas. Studies on the export of larvae from marine reserves may be difficult (Rowley, 1994; Russ, 2001) and may need to rely on a combination of oceanographic data (currents), fecundity of fishes, knowledge of spawning areas and modelling. Statistically rigorous monitoring is essential if we are to understand the role of marine reserves in a more applied approach to conservation and fisheries management.
5.3 HOW MIGHT TARGETED FISHES RESPOND TO PROTECTION FROM FISHING?

When a marine reserve is established, we may expect certain characteristics of targeted fish populations to change over time within its boundaries. Figure 5.2 graphically represents some of these potential changes, i.e. a build-up in the abundance and the spawning stock biomass of fishes to a carrying capacity where density dependent effects may cause, increased egg and larval production (Ward et al., 2001) and a spillover of fishes over time (Russ and Alcala, 1996; McClanahan and Mangi, 2000). This assumes that fishes have limited movement and that they spawn inside the marine reserve.

The spawning biomass and abundance of fishes should increase due to the cessation of fishing (Figure 5.2: Points 1 and 2) (Guenette and Pitcher, 1999; Chiappone and Sealey, 2000). As each year class matures it would be logical to expect an increase in egg and larval production (Figure 5.2: Point 3) (Polunin and Roberts, 1993). For example, *Lethrinus nebulosus* matures at 3.1-years (Agbayani, 2002), so by this stage all *L. nebulosus* that remained within the marine reserve should have reached maturity and there should have been a consequent increase in the production of eggs and larvae for this species. Egg production can increase at an exponential rate (Plan Development Team, 1990; Roberts and Hawkins, 2000) and may continue beyond the maximum length of fishes, albeit at a slower rate, due to gains in weight (Ricker, 1975). Increased egg and larval production may increase the abundance of fishes within a marine reserve, due to larval retention and *in situ* recruitment (Jones et al., 1999; Swearer et al., 1999) or in adjacent fished areas via dispersal (Ward et al., 2001) (Figure 5.2: Point 4). Dispersal of eggs and larvae to other areas is likely, but due to the complexities of conducting such studies, examples of this are difficult to find (Carr, 2000; Russ, 2001). Spillover may occur after several years, once fishes had built up to a carrying capacity (Figure 5.2: Point 5) at which point density dependent effects, such as resource limitation or competition (Sanchez Lizaso et al., 2000), might drive some fishes to other areas. Spillover has been shown after a periods of 9 to 11-years (Russ and Alcala, 1996; McClanahan and Mangi, 2000).
4. Potential dispersal of eggs and larvae, dependent on currents, larval mobility etc.

3. Egg production increases as each year class reaches maturity and spawning stock biomass increases.

1. Spawning stock biomass increases as fish are not removed at minimum legal-size (41cm).

2. Abundance increases due to the cessation of fishing.

5. Potential spillover after 9-10 years due to density dependent effects.

Figure 5.2: A graphical representation of how fishes might respond over time to protection from fishing, based on increases in abundance and biomass. The intersection of the x and y-axes represents the establishment of a marine reserve.

### 5.4 FUTURE RESEARCH

There are gaps in the literature that need to be addressed, particularly in examining how trophic interactions change over time in marine reserves and whether conservation goals are being met. Further research is also needed on the mechanisms of spillover, the dispersal of eggs and larvae, and how marine reserves should be designed to maximise these fisheries management objectives. Results may not be applicable across space due to differences in habitat, the size of marine reserves, the mobility of the fishes or larvae in question and the conditions that might disperse them. The most convincing results will come from replicated studies that commence before marine reserves are established and where temporal variation in fishes and benthic biota has been monitored. The consensus from marine ecologists is that we must take an ecosystem approach to conservation (Agardy, 1994; Carr, 2000) and fisheries management (Mann, 1982b; Bohnsack, 1998; Jennings and Kaiser, 1998; Caddy, 2000; Castilla, 2000; Dayton et al., 2000; Garcia Charton et al., 2000; Rosenberg et al., 2000) and marine reserves in marine protected areas could help us achieve this.
CHAPTER 6 - NOTE: AN INCREASE IN THE ABUNDANCE AND BIOMASS OF LETHRINIDS IN THE NINGALOO MARINE PARK, WESTERN AUSTRALIA, 18-YEARS ON.

6.1 INTRODUCTION

Marine Reserves (where fishing is excluded) are increasingly being used as fisheries management tools (Bohnsack, 1997; Boersma and Parrish, 1999) as they may benefit fished areas by providing a source of eggs and larvae and a spillover of fishes (Ward et al., 2001). Long-lived fishes such as those in the families Lethrinidae, Lutjanidae and Serranidae often benefit most from protection, that is provided by reserves, due to their vulnerable life histories (Russ and Alcala, 1998). These fishes are also highly targeted by fishers (Roberts and Polunin, 1992; Jennings et al., 1995; Kulbicki et al., 2000; Sumner et al., 2002) making them relevant to fisheries management. To fulfil fisheries management roles, populations of targeted fishes must first build-up in reserves and this has been shown in many studies [e.g. (Watson and Ormond, 1994; Roberts, 1995a; Letourneur, 1996; McClanahan and Kaunda Arara, 1996; Russ and Alcala, 1996a; Wantiez et al., 1997)]. Greater abundances of mature targeted fishes in reserves, than fished areas, should then provide an increase in eggs and larvae that may disperse to fished areas [see reviews (Roberts and Hawkins, 2000; Russ, 2001; Ward et al., 2001)].

Marine reserves may continue to enhance fish populations within their boundaries until a carrying capacity is reached, which can be defined as the maximum biomass of fishes that could be sustained by a reserve (Sharkey, 1970), and the longer a reserve has been established the closer it may be to reaching a carrying capacity (Roberts and Hawkins, 2000). As a carrying capacity is approached, density dependant effects are likely to retard increases in the abundance and biomass of targeted fishes. Resource limitation and competition might then cause emigration of targeted fishes from the reserve (Sanchez Lizaso et al., 2000). This point may also represent the maximum production of eggs and larvae from mature targeted fishes in the reserve. In essence, the reserve would be functioning at maximum capacity as a fisheries management tool.

Studies on the spillover of fishes from a Marine Reserve should commence before the reserve is established and include abundance and catch data from inside and outside the reserve.
boundaries, or fish tagging studies (McClanahan and Mangi, 2000). However, if such studies were not underway, this point of maximum capacity would represent an imperative to implement them, as this is conceivably when emigration (due to density dependence) would be greatest. Spillover from reserves has been shown after approximately 10 years (Russ and Alcala, 1996b), but studies on larval dispersal are rare (Russ, 2001). However, both may occur at any time during the history of a reserve due to currents dispersing eggs and larvae (Swearer et al., 1999) and random movements of fishes (Rakitin and Kramer, 1996). Information on changes in fish populations in long established reserves might enhance our understanding of when a maximum capacity is attained and provide an impetus for studies on spillover or larval dispersal.

The Ningaloo Marine Park in Western Australia has Sanctuary Zones where fishing is excluded and Recreation Zones where recreational fishing is permitted. The Maud Sanctuary Zone, in the Ningaloo Marine Park, had been protected from fishing for 16-years at the commencement of this study, but fish populations had not been censused until 2000, despite high levels of fishing pressure and tourism in the region (May et al., 1983; Shaw, 2000; Sumner et al., 2002). In 2000, fish assemblages and benthic cover characteristics were compared between Sanctuary and Recreation Zones at Maud (Chapter 2). This revealed significantly greater biomass, size, and abundance of legal-sized lethrinids, in the Sanctuary Zone. The differences could not be explained by habitat, rugosity or pre-zoning artefacts and were attributed to fishing pressure in the Recreation Zone. The opportunity arose to resample the Maud region in July 2002 and make temporal comparisons of fish assemblages spanning 2.5 years. This study tested whether a Sanctuary Zone with a 16 year period of protection from fishing, still showed signs of enhancing fish stocks through increases in the abundance, biomass and size of fishes that are commonly targeted in adjacent fished areas. Increases in these variates might imply that the Sanctuary Zone was still enhancing fish stocks, but a lack of temporal change might indicate that it had reached a carrying capacity.
6.2 METHODS

The study was conducted in the Maud Sanctuary Zone of the Ningaloo Marine Park, Western Australia (23°09'S, 113°45'E). Visual census techniques were used to measure the abundance, biomass and size of predatory fishes that are targeted by fishers, adjacent to the Sanctuary Zone, where fishing is permitted. Sampling was conducted in July 2002 and compared with data collected in January and July 2000 by (Chapter 2). Water depth at the study site was approximately two metres.

Observations indicated that the use of SCUBA startled larger predatory fishes, making them difficult to count as they fled from the diver. The census technique therefore involved swimming on the surface, which enabled the observer to get closer to fishes and conduct a more thorough census. The size and abundance of fishes was estimated and biomass was calculated using length-weight ratios from fishes caught in the Ningaloo region. The same observer (M. Westera) was used for all census work to minimise observer bias. Censuses were conducted on haphazardly chosen transects of 250 x 10 m (n = 4). Plots of species abundance against area sampled indicated that 90% of all species were recorded in the first two (of four) transects.

The overall abundance, biomass and size of fishes, and the abundance of mature fishes, were compared using ANOVA, with time as a random factor. Student-Newman-Kuels post-hoc testing was used to determine which times were driving any significant differences. Analyses were conducted at the family or genus level as it was noted that fishers in the region kept any fishes within a family that they were targeting. Thus, any benefits a no-fishing zone may provide to fish populations would also be at the family or genus level.
6.3 RESULTS AND DISCUSSION

A total of 11 species of targeted fishes were recorded in visual census work (Table 6.1). These were from the families Lethrinidae, Lutjanidae, Haemulidae, Serranidae and the genus *Choerodon* of the family Labridae. The most common of these were the lethrinids (*Lethrinus nebulosus* Forsskål, *L. lentjan* Lacepède and *L. atkinsoni* Seale).

The abundance and biomass of lethrinids increased significantly between January 2000 and July 2002 (P < 0.01 and P < 0.05, respectively) (Table 6.2; Figure 6.1), but there were no significant differences in other fish families. Lethrinids constituted approximately 78% of the fishes that were targeted in the region (Sumner et al., 2002) and between 84 and 96% of the total number of targeted fishes censused in the Maud Sanctuary Zone, so subsequent analyses were focused only on this family.

Increases in the abundance and biomass of lethrinids were only significant over 2.5 years i.e. between January 2000 and July 2002. There was a significant increase in the abundance of mature lethrinids between each of the sampling times (P < 0.001), but no significant differences in their mean size (Table 6.2; Figure 6.1). The size at maturity for these fishes corresponds closely with the minimum legal-size when they can be taken by fishers (Moran et al., 1993).

### Table 6.1: Targeted fish species recorded in census work at the Maud Sanctuary Zone, January 2000 to July 2003.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Common name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lethrinidae</td>
<td><em>Lethrinus nebulosus</em> (Forsskål, 1775)</td>
<td>Spangled emperor</td>
</tr>
<tr>
<td></td>
<td><em>Lethrinus lentjan</em> (Lacepède, 1802), <em>Lethrinus atkinsoni</em> (Seale 1910)</td>
<td>Pinkear emperor, Yellowtailed emperor</td>
</tr>
<tr>
<td></td>
<td><em>Lethrinus laticaudis</em> (Alleyne and Macleay, 1877)</td>
<td>Bluelined emperor</td>
</tr>
<tr>
<td>Lutjanidae</td>
<td><em>Lutjanus fulviflamma</em> (Forsskål, 1775)</td>
<td>Blackspot snapper</td>
</tr>
<tr>
<td>Haemulidae</td>
<td><em>Plectorhinchus chaetodontoides</em> (Lacepède, 1800), <em>Diagramma labiosum</em> (MacLeay, 1883), <em>Diagramma pictum</em> (Thunberg, 1792)</td>
<td>Many spotted sweetlips, Painted sweetlips, Yellowdot sweetlips</td>
</tr>
<tr>
<td>Serranidae</td>
<td><em>Epinephelus fasciatus</em> (Forsskål, 1775)</td>
<td>Black tipped cod</td>
</tr>
<tr>
<td>Labridae</td>
<td><em>Choerodon schoenlenii</em> (Valenciennes, 1839), <em>Choerodon rubescens</em> (Gunther, 1862)</td>
<td>Blackspot tuskfish, Baldchin groper</td>
</tr>
</tbody>
</table>
The proportions of lethrinid species changed over time and it appears that differences between times were due to an increase in the abundance of *L. lentjan* and *L. atkinsoni*. These two species combined, made up 32, 69 and 84% of the abundance of lethrinids censused in January 2000, July 2000 and July 2002, respectively. The differences over time may have been due to seasonal variability between January and July samples. Another possibility is that a recruitment event, provided an initial increase in abundance followed by an increase in biomass, as the recruits matured. *L. lentjan* and *L. atkinsoni* mature at approximately 1.4 and 2.3 years of age respectively (Agbayani, 2002), i.e. within the 2.5 year duration of this study. A large recruitment event may have occurred during the study and driven the observed differences.

The abundance and biomass of lethrinids increased significantly at the Maud Sanctuary Zone, over the period of this study, but the mechanisms by which they increased remain unknown. Chapter 2 showed that lethrinid populations were greater in the Maud Sanctuary Zone than the Recreation Zone and suggest that the current study has not simply measured a change that occurred in both fished and unfished areas. A probable reason for the increases in lethrinids at the Maud Sanctuary is the absence of fishing pressure.

The changes recorded in this long-established Sanctuary Zone (i.e. 16 to 18 years) highlight the potential of reserves to enhance fish stocks within their boundaries many years after their implementation. It is possible that a carrying capacity for lethrinids has not been reached in the Maud Sanctuary Zone, if we assume that populations will increase up to this point. The higher biomass of lethrinids in the Sanctuary Zone suggests it is continuing to enhance populations of targeted fishes. The increase in abundance of mature fishes indicates that it may still be increasing as a source of eggs and larvae. But what happened to the fish assemblages previously? Due to the lack of long-term temporal monitoring (i.e. from the prior to establishment of the Sanctuary Zone), a valuable opportunity has been missed to track changes in reef fish populations over time. Long-term monitoring of fish populations would have enabled us to clarify whether these observations were part of a long-term trend or natural variability. In addition to spatial comparisons of reserves and fished areas, it is imperative that rigorous long-term monitoring is implemented in marine reserves to improve our understanding of how they enhance fish populations.
References


