2010

Do different levels of fishing pressure, through spatial management, influence communities and ecological interactions in seagrass meadows in South Western Australia?

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Recommended Citation

Inostroza, K. (2010). *Do different levels of fishing pressure, through spatial management, influence communities and ecological interactions in seagrass meadows in South Western Australia?*. https://ro.ecu.edu.au/theses_hons/1345

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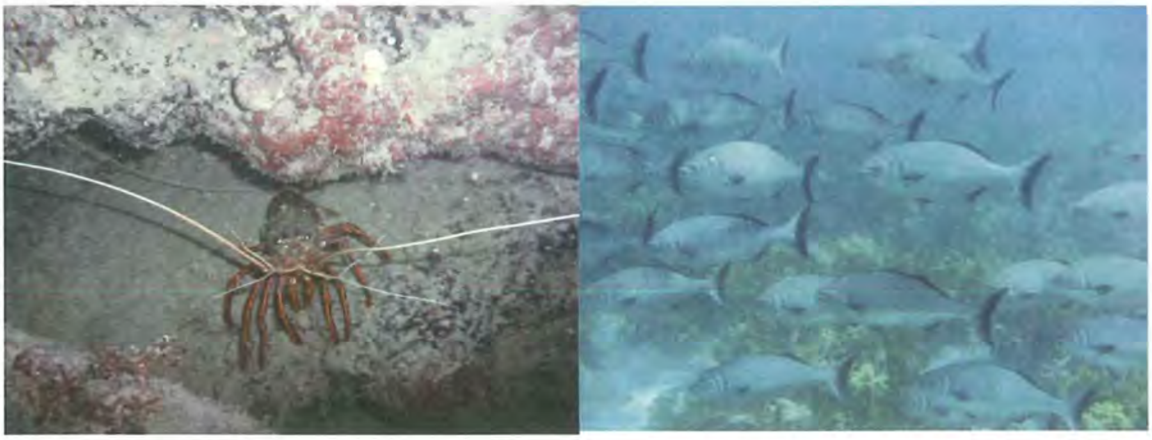

A thesis submitted in partial fulfilment of the requirements for the awards of

Bachelor of Science (Biological Sciences) Honours

At the School of Natural Sciences

Faculty of Computing, Health and Science

Edith Cowan University

Supervisors:

Associate Professor Glenn Hyndes

Dr. Pippa Moore

Date of Submission: 30th June 2010

Abstract

Marine Protected Areas (MPAs) are internationally recognised as a significant spatial management and cost-effective strategy to restore and conserve the marine ecosystems structure and function from human impact. MPAs have been declared with the aim to address a single or a set of management objectives in response to anthropogenic threats, such as fishing, which can have repercussions on biodiversity through indirect interactions or top-down control within an ecosystem or across ecosystems where consumers migrate to forage. However, this indirect impact of fishing remains poorly understood, and as a consequence, the effectiveness of MPAs in conserving those ecological processes and broader biodiversity is also poorly understood. Therefore, this study investigated the potential effects of sanctuary zones (no-take MPAs) on higher-order consumers and their effects on benthic assemblage structure both on the reef and in adjacent seagrass meadows. Consumer assemblages were examined using underwater visual census (UVC) on reefs and seagrass meadows at a range of sites in sanctuary and fished zones in Marmion Marine Park (MMP) and Rottnest Island Marine Reserve (RIMP) over three seasons between July 2009 and March 2010. Epibenthic fauna and flora were also sampled using quadrats on reefs and at set distances away from reefs in adjacent *Amphibolis* seagrass meadows over the same period.

Sanctuary zones had higher mean total abundance and biomass of fish compared to adjacent fished zones, and while not significant, there was also a trend of higher means rock lobsters abundance in sanctuary zones. However, there was a high degree of variability among sites nested in zone, and among seasons. Kingston Reefs sanctuary zone contained the highest rock lobster and fish abundance, biomass, and species richness across all seasons. In addition, there was a trend of decreasing mean abundance, biomass, and species richness of fish with increasing distance away from the reef in *Amphibolis* meadows. In terms of epibenthic fauna and flora assemblages, there was no significant difference in their abundances and taxa richness between zones, but as with consumers, there was high variability among sites within zone and among seasons. As sanctuary zones had substantially higher densities of consumers in close proximity to reefs than fished zones, it was expected that predation levels would be higher in sanctuary zones and would decrease with increasing distances away from the reef. However, there were no clear trends of decreasing epibenthic abundance and diversity with distance away from the reef. Furthermore, tethering experiments with gastropods, a major prey item for some consumer species, showed no significant differences in gastropod mortality between sites or with increasing distances away from the reef. Thus, a top-down effect caused by different abundances of consumers in sanctuary versus fished zones was not evident from the results.

Much of the variability in higher-order consumers and epibenthic assemblage could be due to site-specific characteristics, including the age, size, and the geographical location of sanctuary zones, and the structural complexity of the habitat. The detection of consumers' direct influence on prey abundance, richness, and distribution could be partly masked by their feeding habits, and the level of mobility of higher-order consumers. This study highlights the level of complexity of food web structures with consideration of other environmental and biological factors. It also provides important baseline of biological data on marine ecosystems in marine parks of southwest temperate waters of WA for future assessments of those marine parks. To meet a MPAs objective of biodiversity conservation, it is crucial for managers to acknowledge all natural variations in marine ecosystems, such as the life-history traits of individuals, when setting objectives for a MPAs performance, as protection may be suitable for some species and inadequate for others.

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Acknowledgements

This research would not have been possible without the help of many people. First and foremost, I would like to thank my supervisors Assoc. Prof. Glenn Hyndes, and Dr Pippa Moore for their endless help, continued guidance, and patience throughout the entirety of this project. Pippa, you provided me with opportunities to widen my skills, and challenged me in the field and I have become a better scientist through your supervision.

Special mention must be given to those who offered their time and assistance both in the laboratory and in the field throughout this project. These volunteers made this research possible and thoroughly more enjoyable, and would like to sincerely thank Candace Willison, Phong Nguyen, Steve Giles, Margie Mohring, Rob Czarnik, Peter Kiss, Aldo Turco, Geoff Purvis, Michael Pezzaniti, Pierre Bouvais, and Ariadne Macleod. Also to Geoff Atkinson, who spent hours in the shed making my aluminium fish templates.

I would like to thank the School of Natural Science and Rottnest Island Authority for your financial support. And finally, I thank my family and friends for your patience, unfailing support and belief in me that kept me going right to the end. Special thanks to my brother Alex, for helping me out in the laboratory and only complaining once about the seagrass smell.

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1. Introduction

1.1 Marine Protected Areas

For many centuries, humans have been closely associated with the marine environment, exploiting its resources for profit, and as a result, a large proportion of the world's fisheries are now considered unsustainable and overexploited (Jackson *et al.*, 2001; Lotze *et al.*, 2006; Byrnes *et al.*, 2007). In an attempt to prevent the collapse of marine ecosystems and to restore its former structure and function, systematic strategies for the conservation of marine ecosystems have been developed (Rodrigues *et al.*, 2004). Marine Protected Areas (MPAs) are spatially delimited areas of ocean that have been implemented and have gained international recognition as a significant spatial management and cost-effective strategy (Agardy, 1994; Bohnsack, 1998; Hooker & Gerber, 2004). MPAs have been declared with the aim to address a single or a set of management objectives in response to anthropogenic threats, whether for biodiversity conservation (Micheli *et al.*, 2004; Rodrigues *et al.*, 2004; Claudet *et al.*, 2008), the protection of spawning grounds of fish (West *et al.*, 2009), or recovering overfished targeted species (Palumbi, 2001).

To assess whether an MPA is successfully achieving its conservation objectives, research and monitoring of the marine ecosystem is vital. Before/after control/impact (BACI) designs have often been used to detect and assess changes in an ecosystem, through the collection of data before and after an ecological impact (Underwood, 1994; Schiel *et al.*, 2004; Henry *et al.*, 2006). Lack of historical data prior to the implementation of an MPA makes this method difficult to use. An alternative method is using a fished zone where fishing activities are permitted, as a reference area to compare with MPAs. Countless studies have used this approach, and have documented an increase in density (Chapman & Kramer, 1999; Shears & Babcock, 2002; Babcock *et al.*, 2007; Barrett *et al.*, 2007), average size (Micheli, 1997; Babcock *et* al., 1999; Guidetti& Sala, 2007; Pande *et al.*, 2008;Prado *et al.*, 2008; Linares *et al.*, 2010), and/or biomass (Denny *et al.*, 2004; Langlois *et al.*, 2005; McClanahan & Graham, 2005; Kramer & Heck Jr, 2007) of previously exploited fish and crustacean species within MPAs. Fewer studies have documented the failure of MPAs in meeting their objectives (Allison *et al.*, 1998) possibly due to the lack of suitable habitat

(Mayfield *et al.*, 2005), size issues (Le Quesne, 2009), the lack of reinforced management (Perera & Vos, 2007), or perhaps the benefits are too difficult to quantify and are often too slow to be realised (Agardy, 1994; Halpern & Warner, 2003). However, it is also possible that studies showing a lack of a response may reflect publication bias towards those studies showing a positive response of MPAs.

While many MPAs have been shown to provide a significant spatial refuge for fished species to increase in numbers, these protected areas may also benefit the broader fisheries outside those areas. Although not the primary goal of most MPAs (Edgar *et al.*, 2007, p.538), adjacent fisheries may benefit from these protected areas through a potential 'spillover' effect, and/or larval export. 'Spillover' effect describes the export of adults and juveniles of targeted species from MPAs to adjacent fisheries (Russ *et al.*, 2004; Goñi *et al.*, 2006; West *et al.*, 2009; Amargos *et al.*, 2010; Goñi *et al.*, 2010), whereas larval export is the net movement of propagules from MPAs into adjacent fished zones (Pelc *et al.*, 2009). A higher production of propagules (eggs and larvae) is expected following the protection and subsequent increase in biomass of targeted stock (Kelly *et al.*, 2002; Willis *et al.*, 2003). However, this concept of MPAs acting as a source of increased propagule production is debatable as it may also be due to an increased attraction of species to the MPA. Therefore, prior to understanding how systems respond to MPAs, it is crucial to grasp the fundamental concepts driving marine ecosystems.

1.2 Marine trophodynamics

Similar to terrestrial and freshwater ecosystems, marine ecosystems constitute a variety of organisms and processes that occur between the organisms and their associated habitat(s). Organisms can be broadly categorised into discrete trophic levels: primary producers forming the basis of a food web, followed by consumers that either feed on plant (herbivores) or animal (carnivores) material, or feed across trophic levels (omnivores), or feed on organic wastes or dead material of any trophic level (detrivores and scavengers) (Huntly, 1991). Many consumers may have close interactions to other trophic levels through important structuring processes such as competition, herbivory, recruitment, and predation (Huntly, 1991; Wilson, 1991). Marine ecosystems are generally open with high levels of connectivity among habitats (Hixon *et al.*, 2002; Edgar *et al.*, 2007, p.537), forming complex and interactive food webs. Therefore, a consumer's role, and the interactions it has with its associated food sources, is likely to influence other species within its community (Connell, 1975) through direct and indirect relationships.

Interactions in food webs have the potential to regulate a community's structure, either through bottom-up or top-down control (Hairston *et al.*, 1960; Power, 1992). Bottom-up control describes how predators are limited by the availability of prey (Power, 1992), whereas top-down control illustrates how lower trophic levels are limited by predation (Hairston *et al.*, 1960). Of particular focus, top-down control demonstrates how higher-order predators can shape the structure of the benthic assemblage by reducing two or more links such as herbivores and consumer numbers. This natural trophic cascade has been observed in coral reef systems (Graham *et al.*, 2003; Stallings, 2008), rocky reefs (Menge, 1995; Pinnegar *et al.*, 2000; Shears & Babcock, 2003; O'Gorman *et al.*, 2008), and in the open ocean (Frank *et al.*, 2005).

The level of complexity of a food web structure is crucial to understanding how ecological communities may respond to the effects of changes in consumer abundances (O'Gorman *et al.*, 2008). A simple linear food chain generally consists of three-tiers: primary producers, herbivores, and predators; however, these are not frequently observed in nature (Polis, 1991; Menge, 1995). Rather trophic interactions between species are typically dynamic, forming complex food webs involving four or more tiers (Polis, 1991; Pimm, 2002). Adding another level to the trophic system will shift the response in a trophic cascade, making it difficult to determine the species' response. A consumer's feeding mode further complicates this response. Unlike carnivores and herbivores that consume from a single trophic level, omnivores feed on a variety of trophic levels from primary producers to secondary consumers (Pimm & Lawton, 1978; Thompson *et al.*, 2007), making it difficult to determine whether or not omnivores have an impact on lower trophic levels (Ho & Pennings, 2008). Furthermore, unlike diurnally active species where their movement patterns can be observed, many individuals are nocturnally active and their activity patterns can go undetected (Nagelkerken *et al.*, 2000; Sheperd & Clarkson, 2001; Verweij *et al.*, 2006). These biotic factors, however, are often too complex to quantify or experimentally manipulate, making it difficult to link shifts in communities to changes in consumer abundances.

1.3 Impacts of fishing on marine biodiversity

Humans have dominated most marine food webs through the exploitation of marine resources primarily for human consumption through fishing (Jackson *et al.*, 2001; Dulvy *et al.*, 2003; Myers & Worm, 2003; Halpern *et al.*, 2008). This activity directly removes a wide range of species from multiple trophic levels, particularly higher-order consumers. As a result, the overall abundance and biomass of important targeted and by-catch species are drastically reduced (Ludwig *et al.*, 1993; Jennings & Kaiser, 1998; Myers & Worm, 2005; Byrnes *et al.*, 2007). The targeted species are often large carnivores (Jennings & Kaiser, 1998), which generally have prolonged lifespans, delayed reproduction, and low reproduction rates (Dayton*et al.*, 1995; Jennings *et al.*, 1999). Fishing activities also have the potential to manipulate genetic diversity, shift foraging behaviour, the age at which species mature, and reduce the average size of species (Policansky, 1993).

The direct loss of consumers through fishing potentially has repercussions throughout an ecosystem through indirect interactions or top-down control (Jackson *et al.*, 2001; Bascompte *et al.*, 2005). Several studies have shown that over-harvesting of high-order predators can lead to an increase in intermediate prey and indirectly structured lower trophic levels on rocky reefs (Shears & Babcock, 2002; Clemente *et al.*, 2008; Barrett *et al.*, 2009; Sonnenholzner *et al.*, 2009), coral reefs (Harborne *et al.*, 2009; Stallings, 2009), kelp forests (Estes *et al.*, 1998; Babcock *et al.*, 1999), and in seagrass meadows (Gloeckner & Luczkovich, 2008; Moksnes *et al.*, 2008). Changes in species composition, abundance, and distribution of lower trophic levels (e.g. marine benthos) has also been evident in other fisheries such as bottom fishing for scallops and shrimp through destructive dredging (Kaiser *et al.*, 2000; Bradshaw *et al.*, 2002; Morsan, 2009). Therefore, several components within a food web are influenced in response to a trophic cascade in individual systems.

The response of a marine system is dependent on its food web complexity. The restructuring of entire marine systems through trophic cascades has been documented for simple systems containing only a few interacting species (Estes & Duggins, 1995). Complex food webs containing many taxa and their direct and indirect effects can play a significant role in the community stability, however there is continued uncertainty about the mechanisms driving the cascading effects (Schmitz *et al.*, 2004;Dunne *et al.*, 2005; Frank *et al.*, 2005; O'Gorman& Emmerson, 2009). Studies on trophic cascades have generally focused on high-order carnivores within a single habitat. However, consumers can move across habitat boundaries, and any removal of consumers in one system via fishing may have a trophic cascade effect in adjacent systems where the target species forages.

1.4 Habitat connectivity

Some consumers are strongly associated with a particular habitat, while others move considerable distances into other habitats. This spatial movement between multiple habitats presents an important trophic link between consumers and prey across habitats in a marine landscape (Sheperd & Clarkson, 2001; Callaway & Hastings, 2002; Heithaus *et al.*, 2002; Bonfil *et al.*, 2005; Valentine *et al.*, 2007). Foraging movements across habitat boundaries may involve a consumer shifting from a structurally-complex shelter habitat (e.g. rocky reefs) to another structurally complex habitat (e.g. seagrass meadows) or a less structured habitat (e.g. unvegetated areas) as seen in the nocturnal movements of rock lobsters (Ogden *et al.*, 1976; Cox *et al.*, 1997; MacArthur *et al.*, 2008) and fish (Grober-Dunsmore *et al.*, 2007; Nagelkerken *et al.*, 2008). The effects of foraging in neighbouring habitats can propagate through reductions in prey densities and shifts in overall assemblages (Huxel & McCann, 1998; Barros, 2005; Langlois *et al.*, 2005; Guidetti, 2006). Prey species have been shown to decline in densities immediately adjacent the reef and increase with distance away from the reef (Posey & Ambrose, 1994; Langlois *et al.*, 2005; Wernberg *et al.*, 2006; Valentine *et al.*, 2007; Vanderklift *et al.*, 2007).

The foraging movement of higher-order consumers across habitat boundaries highlights the complexities in trophic dynamics of marine ecosystems. Fishing activities, through the direct removal of a consumer from one system can, therefore, potentially affect associated prey in adjacent habitats (Valentine *et al.*, 2008). Unfortunately, this indirect impact remains poorly understood, and as a consequence, the effectiveness of MPAs in conserving those ecological processes is also poorly understood.

1.5 Significance and aims of study

Despite abundant published literature on the benefits of MPAs and top-down control globally, there is relatively little known about these ecological processes in temperate marine ecosystems in Western Australia (WA). The Perth metropolitan waters of southwest WA cover approximately 14,000km^2, and comprise a mosaic of habitats from limestone rocky reefs dominated by macroalgae to seagrass meadows and unvegetated areas (Phillips, 2001). *Amphibolis* spp. and *Posidonia* spp. are the dominant canopy-forming seagrasses in the region (Kirkman & Walker, 1989) and function as important habitats for invertebrates and vertebrate marine organisms, and acts as an important substrate for epiphytic algal diversity (Moncreiff & Sullivan, 2001). Seagrass-associated fauna includes amphipods, crustaceans, nematodes, echinoderms and small fish (Jernakoff & Nielsen, 1998).

The Leeuwin Current is the dominant current in the region, with its poleward flow transporting warm, oligotrophic waters along the continental shelf (Church *et al.*, 1989). This current is responsible for the tropical-temperate transition zone that has promoted a high level of species richness and endemism in the region (Hutchins & Pearce, 1994; Roberts *et al.*, 2002). This biodiversity hotspot has made it a highly desirable region for commercial and recreational fishing (Department of Fisheries, 2008; Bellchambers *et al.*, 2009). This southwest transition region also contains an extended chain of inshore lagoons that are considered important areas for benthic productivity and recruitment for a variety of marine species, including consumers species targeted by fisheries (Department of Environment and Water Resources, 2006).

As a consequence of continued exploitation of marine resources that has lead to significant decline in population stocks (Mitchell & Baba, 2006), 12 marine parks have been created under the vesting authority of The Marine Parks and Reserve Authority (MPRA) in WA. One of the 12 Marine Parks of interest lies within the Perth Metropolitan region, Marmion Marine Park (MMP), while an additional reserve, the Rottnest Island Marine Reserve (RIMR) has been gazetted and governed by the Rottnest Island Authority. The key objective of these MPAs is to have healthy and sustainable marine ecosystems through the conservation of biological diversity (MPRA, 2009). MPRA is a statutory body reporting to the Minister for the Environment, however, the Department of Environment and Conservation (DEC) is primarily responsible for the daily management of the vested waters, providing administrative support to the MPRA (MPRA, 2009). Marine Parks allow some level of activities to occur within different areas by implementing four management zones consistent with the conservation of the marine environment. These zones include general use, recreation, special purpose, and sanctuary zones. Sanctuary zones prohibit all forms of fishing.

Fish and the western rock lobster *Panulirus cygnus* are abundant consumers along the southwest WA coast, both forming important fisheries. The West Coast demersal scalefish fishery targets over 100 fish species (Fairclough *et al.*, 2009), and the western rock lobster is the largest single-species fishery in Australia, annually worth AUS$250-$400 million. The western rock lobster fishery is considered a sustainable fishery having been awarded the Marine Stewardship Council accreditation (de Lestang & Melville-Smith, 2006). However, due to the low puerulus settlement numbers, the rock lobster fishery has had to review their management strategies (Caputi *et al.*, 2008). Demersal scalefish and rock lobsters, which are carnivorous or omnivorous, occupy high-relief limestone reefs dominated by macroalgal canopies, primarily by laminarian (kelps) (Searle & Semeniuk, 1985; Howard, 1989; Phillips *et al.*, 1997; Connell & Irving, 2008) and move into the surrounding habitats in shallow (<10m in depth) coastal waters (MacArthur et al. 2008).

The broad aim of this study was to investigate the potential effects of sanctuary zones (or no-take zones as a form of MPAs) on higher-order consumer abundance and in turn their effects on benthic assemblage structure both on the reef and in adjacent seagrass meadows. It is reasonable to expect that a change in higher-order consumer abundance induced by fishing may lead to a restructuring of benthic assemblages through changes in the intensity of their foraging activities. Also, since those consumers display limited movement into adjacent seagrass meadows (Willis *et al.*, 2001; Edgar *et* al., 2004), the restructuring of benthic assemblages will diminish with increasing distance away from reefs. More specifically, my research tested the following three hypotheses:

1. The abundance, biomass and diversity of higher-order consumers would differ between sanctuary and fished zones;

2. The abundance and diversity of epibenthic fauna and flora would differ between sanctuary and fished zones, and would increase in abundance with increasing distances away from the reef; and

3. Relative predation levels on gastropods in seagrass meadows would differ between sanctuary and fished zones, with predation levels decreasing with increasing distances away from the reef.

This study will provide baseline data necessary to assess whether the MPAs in southwest temperate waters of WA are successfully meeting their objectives of biodiversity conservation. It will provide some insights into how ecosystems function in response to harvesting of higher-order consumers by humans and to protection through sanctuary zones, and how it may affect other trophic levels. These data would contribute to the judicious use and preservation of marine ecosystems.

2. Materials and Methods

2.1 Study sites

2.1.1 Pilot study

Prior to the selection of the sites, extensive pilot work was conducted at various locations around Rottnest Island and Marmion Marine Park in April 2009 (Figure 2.1).Sites were selected to represent similar habitat structure based on visual observations via drop-down video cameras, snorkel and SCUBA diver surveys, as well as existing and current knowledge from local residents and researchers. All sites chosen had extensive (approximately 200m in length and of appropriate width) *Amphibolis* spp. seagrass meadows adjacent to limestone rocky reef, in shallow waters (<10m depth), and exposed to similar wind and swell conditions.

2.1.2 Study sites and general design

The study was conducted at two Marine Protected Areas (MPAs): Marmion Marine Park (MMP) (31°49.4' S, 115°40' E) and Rottnest Island Marine Reserve (32°0`0 S, 115°30`0 E), which were both located within the metropolitan region of the southwest coast of Western Australia (Figure 2.1).

Marmion Marine Park (MMP) was gazetted in 1987, when it was classified as a Class A Marine Reserve to conserve the diverse marine communities and habitats representative of West Australia's mid-west coast (DEC, 1992). MMP protects 9498ha of numerous shore-parallel intertidal limestone reef systems of low relief reef, and complex assemblages of benthic communities, including seagrass habitats and sand. Three sanctuary zones (where fishing if prohibited) were implemented within the MPA in 1999 (Figure 2.1). These are 'Little Island' ($0.06km^2$), 'The Lumps' ($0.28km^2$), and 'Boyinaboat Reef' ($0.07km^2$), all nested within a larger fished zone, and comprises of approximately $0.42km^2$ or 0.44% of the total Park.

Rottnest Island is located 18km west of Fremantle, Western Australia. Due to its geographic isolation from the mainland and its close proximity to the Leeuwin Current, the marine waters of Rottnest Island are ecologically and biologically unique. Therefore, the coastal waters of Rottnest were declared a Class A Marine Reserve in 1917 with the aim to protect representative samples of entire marine habitats, and endemic West Australian species. The Marine Reserve (MR) covers an area of 3828ha that excludes recreational spear fishing within 800m from the shore and commercial rock lobster fishing out to 1600m from the shore. Within the MR, five sanctuary zones have been implemented, two of which have been gazetted since 1988 (Kingston Reefs 164ha, and Parker Point 89ha) and have since been extended, and the creation of three sanctuary zones (Armstrong Bay 82ha, Green Island 92ha, and West End 236ha) in 2007 (Figure 2.1).

At MMP, two sites of similar wave exposure and west to west-south oceanic swells were selected, one in the Boyinaboat Reef sanctuary zone (31°49'S, 115°43'E) and the other at an adjacent site, Wreck Rock (31°48`S, 115°43`E), a fished zone where fishing is allowed (Figure 2.1). Four sites were selected at Rottnest Island MR. A site in the Kingston Reefs sanctuary zone (31°59`S, 115°33`E) was paired with an adjacent fished site at Twin Rocks (32°00`S, 115°33`E). Both these sites were relatively exposed to south and southeast swells and wind. An additional site at Green Island sanctuary zone (32°01`S 115°29'E) was paired with an adjacent fished site at Rocky Bay (32°00`S, 115°28`E) (Figure 2.1) of which both sites were sheltered from southerly winds and swell. All these sanctuary zones differ in terms of size and the length of protection, despite having similar fishing restrictions. Therefore, it is expected that each sanctuary site was to exhibit different responses to protection compared to fished zones.

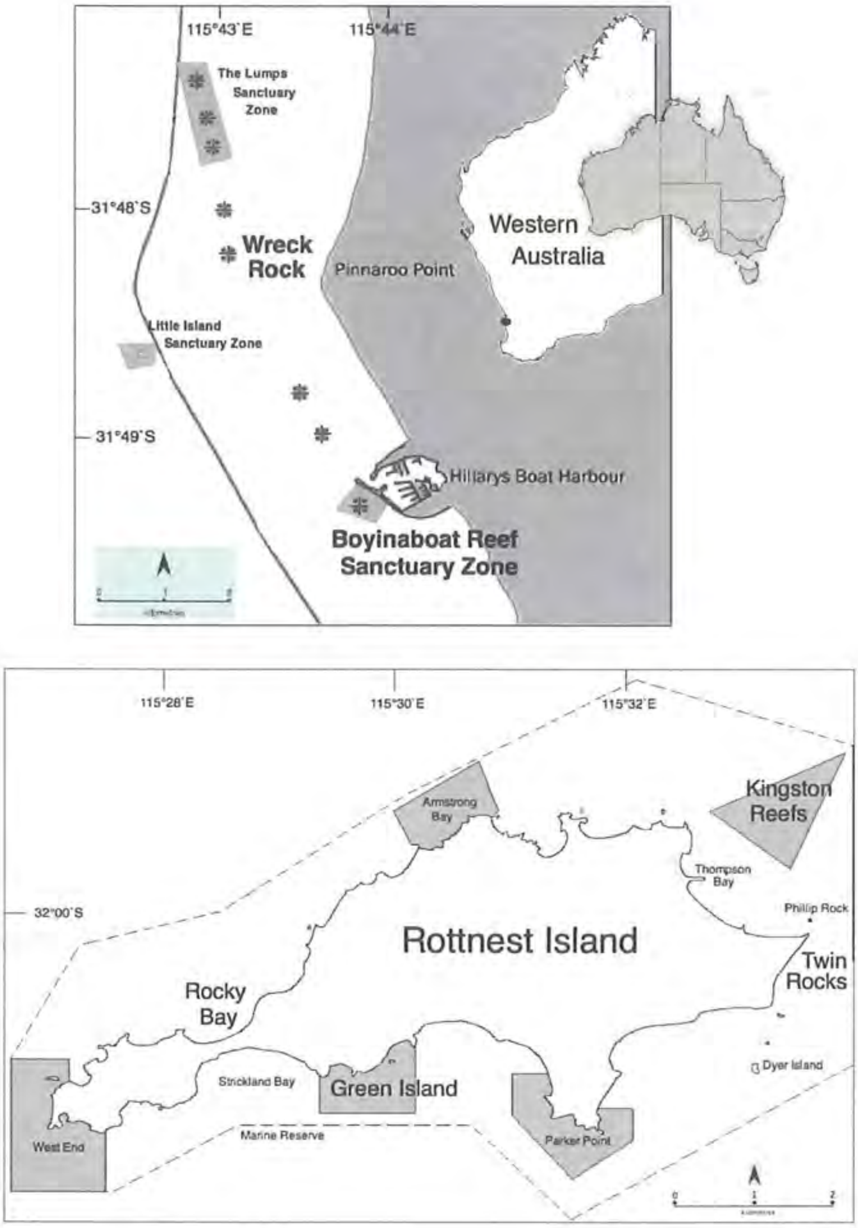


Figure 2.1. Locations of Marmion Marine Park (MMP) and Rottnest Island Marine Reserve (MR). Sanctuary zones are located at Boyinaboat Reef in MMP, and Kingston Reefs and Green Island in Rottnest Island MR; fished zones are located at Wreck Rock in MMP, and Twin Rocks and Rocky Bay in Rottnest Island MR.

The study design was based on three sets of paired sites (Figure 2.2). Within each pair, one site was located in a sanctuary zone where extractive activities such as fishing are prohibited and an adjacent reference site where extractive activities are permitted. All sites were located in shallow waters, generally with depths of 4-5.0m near the reef and gradually deepening with increasing distances away from the reef (4-10m). Twin Rocks fished zone was the exception, with depths gradually decreasing with distance (5.5-1.1m) from the reef. Sampling was conducted from late July 2009 to early-March 2010. This timeframe coincided with three different seasons, winter and spring 2009, and summer 2009-2010, respectively, and allowed me to compare open and closed western rock lobster fishing season, open from 15th November to 30th June.

The study design consisted of six sites however, only five were examined during the winter period (Figure 2.2). A fished site at Henrietta Rocks, located northeast of Parker Point, was initially paired with Green Island sanctuary zone. It was removed from further analysis as the reef was in close proximity to an adjacent reef, potentially confounding the overall data for higher-order consumers and benthic assemblage in seagrass meadows. Therefore, an unbalanced design was conceived.

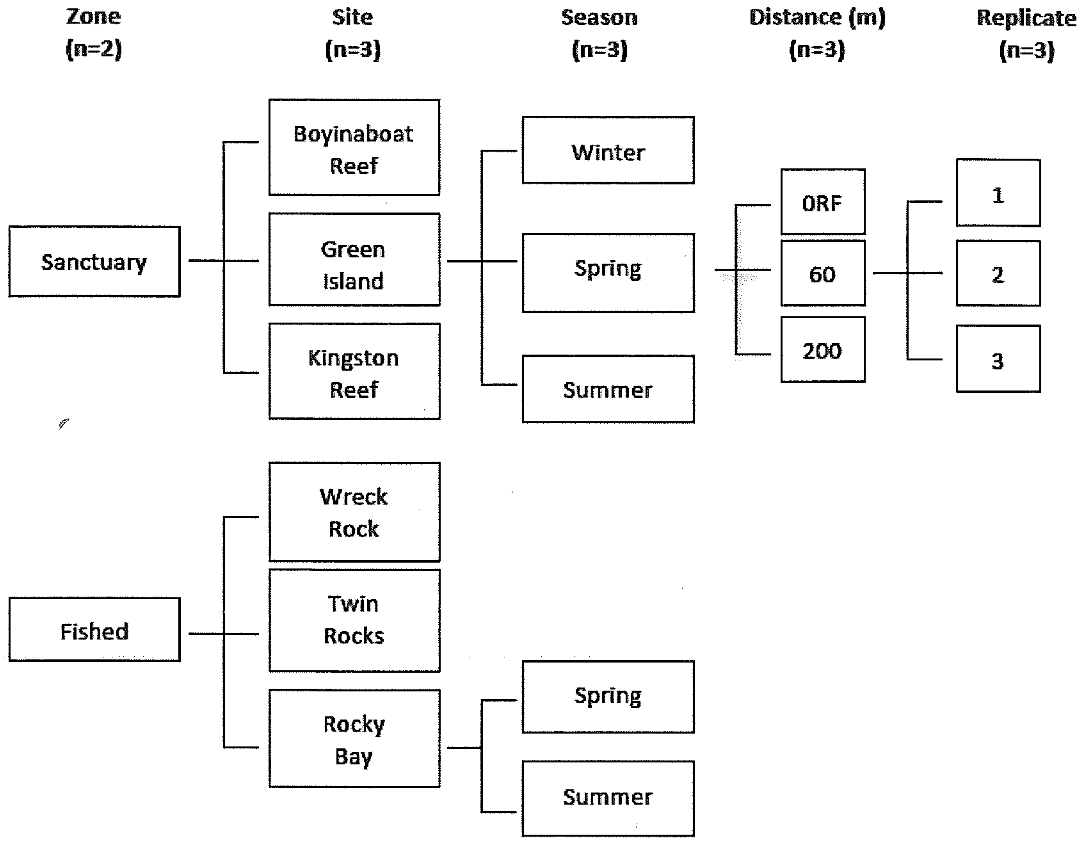


Figure 2.2. Experimental design to determine the abundance and diversity of higher-order consumers. 0RF: sampled at the reef.

2.2 Abundance of higher-order consumers

2.2.1 Pilot Study

A pilot study was conducted at Boyinaboat Reef (Figure 2.1) in June 2009 to practice visually estimating the lengths of fish species and rock lobsters accurately. To ensure the size estimates of each lobster was recorded accurately, the carapace length (CL) was first visually estimated to the nearest 5mm, then captured using a spring-loaded crayfish loop and measured using a ruler. A total of eight individual *P. cygnus* were caught. However, too few lobsters were caught to create a linear regression model on the association between the estimates and true measurement, therefore, lobsters were broadly categorised as legal (>77mm CL), non-legal (<77mm CL), or unknown (only antennae were observed). To ensure the total length (TL) of each fish was recorded accurately and could be applied to a wide variety of temperate demersal fish species, the observer (Inostroza, K.) used 2D aluminium fish figurines of known lengths (5, 10, 15, 20, 25, 30, and 40cm) (Westera *et al.*, 2003) as calibrations. Four randomly selected figures from the total seven known lengths were placed at the reef and in seagrass approximately 2.5m away to obtain a length estimate. This was performed for approximately 5-10 minutes prior to the commencement of every underwater visual census (UVC).

2.2.2 Relative abundance and biomass of fish species

To estimate the relative abundance and species richness of the fish assemblage within sanctuary and fished zones, underwater visual censuses were performed at the reef and two distances away from the reef edge: 0, 60, and 200m in adjacent *Amphibolis spp.* meadows (n=9) (Figure 2.2). These were conducted during daylight hours (between 0700 and 1200 hrs) and focused only on diurnally active non-cryptic fish species. Censuses were only conducted when visibility was >3m, and low swells to minimise potential risks and variations in results. Throughout the study, one observer (Inostroza, K.) conducted all UVCs to minimise error and bias (Samoilys and Carlos, 2000).

To avoid localised disturbances caused by the presence of divers after entering the water, both divers remained motionless on the seafloor for approximately 5-7 minutes to settle the behavioural responses of fishes (Shepherd and Clarkson, 2001). During this time, the observer practiced estimating and recognising fish size measurements through calibration using 2D aluminium figurines. Three 25m x 5m belt transect (length x width, respectively) five meters apart, were haphazardly placed parallel to whether the fish assemblages and abundances altered between two different habitats, as previous research has shown a greater abundance of fish species close to the reef than at greater distances away (Howard, 1989). For each transect, the primary diver followed a compass bearing to ensure that the transect did not deviate, while the second diver secured a tape measure at the beginning of the transect and followed closely behind the observer at a steady pace for 25m.To minimise bias in fish counts, both divers advanced at a rate of $25m^2$ per minute, completing each transect in approximately 12 minutes (Samoilys & Carlos, 2000).

All fish and schooling fish present within each transect were identified, counted and had their total length (TL) recorded to within 5cm. Fish were accurately identified to the lowest taxonomic level possible using photographic aids. Estimates of fish lengths obtained during UVCs were converted to biomass, using allometric length-weight conversion:

$$W=aL^b \qquad \text{(eq. 1)}$$

whereby W is weight in grams, L is total length in centimetres, and parameters *a* and *b* are constants, sourced from published length-weight relationship (Kulbicki *et al.*, 2005). For species where length-weight relationships were not available, the genus or higher taxonomic level were used, or the biomass were estimated by using a congener with a similar body size and shape.

2.2.3 Relative abundance of western rock lobsters

To estimate the relative abundance of western rock lobster *Panulirus cygnus*, four replicate 10-minute searches were conducted amongst reef, crevices, and reef edge at each site. Due to their nocturnal activities, *P. cygnus* generally seek shelter in reef crevices during daylight hours (Cobb, 1981; Jernakoff *et al.*, 1993). Each rock lobster observed was counted and assigned to three size classes: legal (>77mm carapace length CL), non-legal (<77mm CL), and uncertain. Those individuals were the carapace was not clearly visible but antennae were observed, were categorised as uncertain.

2.2.4 Statistical analysis

A 4 factor mixed-model design was employed to test for differences in fish abundance, diversity and biomass between: (1) zone (fixed factor; 2 levels); (2) site (random factor; nested within zone, 3 levels); (3) seasons (fixed factor; 3 levels); and (4) distance (fixed factor; 3 levels). Fish community structure, biomass, and species richness were examined using multivariate statistics as an unbalanced design. The data was not normally distributed following transformation due to the unequal sample size. As permutational multivariate analysis of variance (PERMANOVA; Anderson (2001)) is robust to data not meeting the assumptions of traditional ANOVA, it was used to investigate differences between dependent variables. To overcome heteroscadasticity, data were square-root ($\sqrt{x}$) transformed. All permutation analyses were conducted with 9999 permutations on residuals under a reduced model. Post-hoc *a prioiri* pair-wise comparisons (Monte Carlo) were used to test for differences among levels within significant factors.

Analyses of differences in fish assemblage structure were based on Bray-Curtis similarity indices, and data were square-root ($\sqrt{x}$) transformed to reduce the influence of extremely abundant fish species. Canonical analyses of principal coordinates (CAP) were undertaken. CAP plots allowed the examination of individual species that were likely to be responsible for any observed differences through correlations of taxa counts with the canonical axis. Data was constrained using two axes in a higher two-dimensional plot to separate the groups and visualise patterns. All multivariate analyses were made using PRIMER v6 with PERMANOVA+ add-on.

A 3-way mixed-model nested analysis of variance (ANOVA) was used to test for differences in legal-sized and total abundance of western rock lobster. The three factors were: (1) zone (fixed factor; 2 levels: sanctuary and non-sanctuary zones); (2) site (random factor; nested within zones; 3 levels: sanctuary Boyinaboat Reef, Green Island, and Kingston Reefs; fished Wreck Rock, Twin Rocks, and Rocky Bay); and (3) seasons (fixed; 3 levels: winter, spring, and summer). Cochran's test was used to test for homogeneity of variances. As data met the assumptions of ANOVA, data were not transformed. Student-Newman-Keuls (S-N-K) post-hoc tests were carried out where significant effects occurred ($p<0.05$). Analyses were performed using GMaV Statistical Analysis Program.

2.3 Impact of higher-order consumers on abundance and biomass of benthic assemblage

2.3.1 Experimental design and approach

The study design consisted of six sites, three sites nested within sanctuary zones and three sites nested within fished zones, examined over three seasons. Only five were examined during the winter period as previously mentioned (Section 2.1.2). The benthic assemblages were sampled at increasing distances from the reef at each site within sanctuary and fished zones (Figure 2.3). A tape measure was secured to the reef edge, and placed in *Amphibolis* spp. seagrass meadows adjacent to the reef out to approximately 200m. At increasing distances away from the reef (0RF on the reef, 0SG, 15, 30, 60, 120 and 200m in seagrass), three replicate $0.25m^2$ (0.5m x 0.5m) quadrats were placed haphazardly in the seagrass meadow (n=18) (Figure 2.3). Within each quadrat, all aboveground epibenthic and sessile fauna and flora were removed and carefully placed into calico bags and frozen once returned to the laboratory.

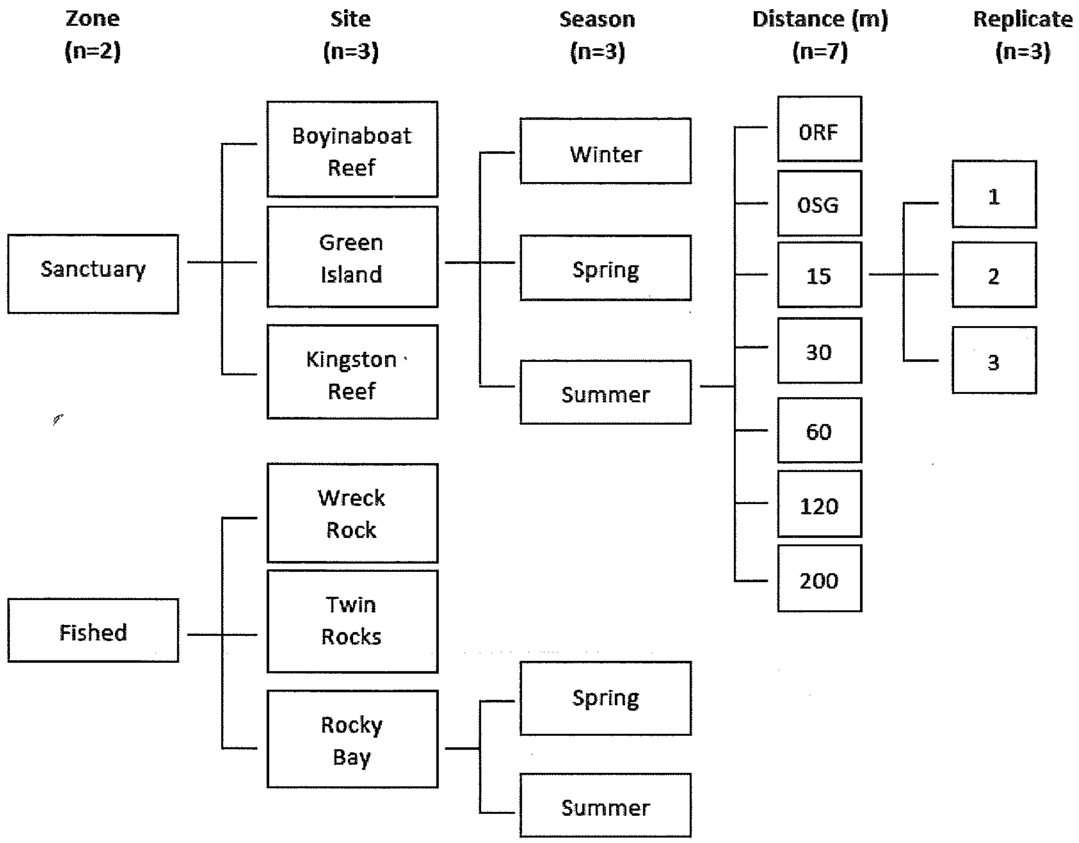


Figure 2.3. Study design to determine the abundance and biomass of the benthic assemblage. 0RF: sampled at the reef; and 0SG sampled in seagrass immediately following the reef.

2.3.2 Laboratory processing

Each sample was defrosted, rinsed in clean freshwater and passed through a 4mm and 0.5mm sieve to provide size-related abundance of broad taxonomic epifaunal invertebrate groups (Jernakoff & Nielsen, 1998). All fauna were identified to the lowest possible taxonomic level.

Seagrass were separated into species, and three shoots of each species were randomly selected from the sample, a substantial representation of the total sample (Phillips *et al.*, 1997). For *Amphibolis spp.*, all the leaf clusters were detached from the stems, and 10 individual leaves were selected at random. The total length of the stems were measured and cut into 20 equal portions. This allowed for the relative abundance of algae functional groups on seagrass to be obtained. These functional groups included: articulated and encrusting calcareous coralline, corticated terete and foliose, filamentous, and leathery algae (Steneck & Dethier, 1994). The algae were divided into simple polyphyletic groups based on anatomical and morphological characteristics. Using morphological attributes rather than species can: (1) assist in detecting patterns in community structure to make comparisons in space and time (Steneck & Dethier, 1994); (2) does not require a high level of taxonomic expertise; and (3) reduces sampling effort. These functional groups are readily consumed by *P. cygnus* (Edgar, 1990a; Jernakoff *et al.*, 1993) and by various temperate fish species (Edgar & Shaw, 1995; MacArthur & Hyndes, 2007).

The presence or absence of algal functional groups on all leaves and stems were recorded with the aid of a dissecting microscope. All algae were removed and separated into different functional groups. For each sample, the entire seagrass sample, selected leaves (n=10), stems (n=20), and each algal morphological group were weighed separately to the nearest gram, dried in a 60°C oven for 24 to 48 hours and weighed again to the nearest again to the nearest gram for dry weight (Jernakoff & Nielsen, 1998).

2.3.3 Statistical analysis

A 4 factor mixed-model design was employed to test for differences in relative abundance and total biomass of epiphytic algae on seagrass and benthic faunal assemblage between: (1) zone (fixed factor; 2 levels); (2) site (random factor; nested within zone, 3 levels); (3) seasons (fixed factor; 3 levels); and (4) distance (fixed factor; 7 levels). Benthic assemblages were examined using Permutational multivariate analysis of variance (PERMANOVA; Anderson (2001)) and post-hoc *a prioiri* pair wise comparisons (Monte Carlo) as previously mentioned above. SIMPER analyses were used to determine the contribution of each algal functional group to the average Bray-Curtis similarities between zones, sites nested within zones, seasons, and distances. This method identified the algal groups responsible for any differences that occurred between factors through the comparison of two factors at a time.

To visualise the maximum differences between zones and other factors, canonical analysis of principal coordinates (CAP) were undertaken. CAP plots allowed the examination of individual species that were likely to be responsible for any observed differences through correlations of taxa counts with the canonical axis.

2.4 Predation and its effect with increasing distance from reef edge

2.4.1 Pilot Study

A pilot study was conducted to test logistical problems associated with tethering, which was repeated twice. Gastropod death caused by tethering artefacts was of primary concern (Aronson & Heck Jr, 1995; Aronson *et al.*, 2001). The gastropods *Pyrene bidentata* (Collumbellidae) and *Cantharidus lehmanni* (Trochidae) were used for the pilot studies and the tethering experiments. Both are epifaunal species, common to south-western Australia coastal environments, and were selected because both occurred in high abundances at the reef and in seagrass meadows in the benthic assemblage studies. Numerous adult gastropods were collected from *Posidonia* spp. and *Amphibolis* spp. meadows at Wreck Rock in MMP. The species were transported to the laboratory in an esky and placed into an aerated seawater aquarium (20 x 15 x 10cm; length, width, and height, respectively), and fed on epiphytic *Posidonia* spp. and *Amphibolis* spp stems and leaves for two days prior to experimentation. This allowed them to acclimatised to the laboratory conditions with a 16°C room temperature, and reduce any stress levels.

To tether the gastropods, the outer shell of each individual was dried using paper towels, avoiding any contact with the soft body residing in the shell. A 15cm long monofilament line as suggested by Barbeau and Scheibling (1994), with a slipknot at each end was placed around the shell and glued using cyanoacrylate. A cable tie was placed at the other end of the line to act as a weight. For each gastropod species, one tethered and untethered individual were placed into a small tank (10 x 10 x 15cm; length, width, and height, respectively) (n=12). Three small tanks were then placed within a larger aerated aquarium (20 x 15 x 10cm; length, width, and height, respectively) (n=4), and fed *Amphibolis* spp. stems and leaves with epiphytes. Invertebrates were observed everyday for seven days to determine the number of surviving tethered individuals. Temperature and pH levels were observed once a day over this period, with minor fluctuations between 18-18.4°C and pH 8.01-8.07. Pilot work determined there were no mortalities for either tethered or untethered individuals for both species.

2.4.2 Experimental design

The tethering experiment was located at two sanctuary and two fished sites at Rottnest Island MR, since earlier UVCs at those sites had demonstrated a greater abundance and diversity of fish species and abundance of rock lobsters compared to sites in Marmion Marine Park (see Results). The four sites were located at Kingston Reefs and Green Island sanctuary zones, and Twin Rocks and Rocky Bay fished zones.

Adult *P. bidentata* and *C. lehmanni* individuals were collected from *Posidonia* spp from Twin Rocks in February 2010. Five individuals of each species were deployed at distances of 0 (reef), 15, 60, and 200m (n=160) in *Amphibolis* spp. seagrass meadows adjacent to limestone rocky reef. Each individual was tethered using a 15cm nylon monofilament line looped to a stainless steel tent peg, which was 16.5cm in height. Each tethered individual was left out for four days.

During the retrieval, not all tethers were located as a result of bad weather and therefore major changes were made to the objectives and overall statistical analysis. The tethered gastropods were classified into two broad categories: (1) dead (missing shell, with or without intact nylon loop attached); and (2) alive with intact and/or damaged shells (Barbeau & Scheibling, 1994).

2.4.3 Statistical analysis

A Kruskal-Wallis *H* test was employed to test for differences in predation and its potential effect with increasing distances away from the reef between: (1) site (4 levels); (2) distance (4 levels), and (3) gastropod species (2 levels). This non-parametric analysis was employed, as there was missing data, creating an unbalanced design and resulted in data not being normally distributed following transformation. Kruskal-Wallis test was used, as data does not need to meet the assumptions of normality or homogeneity of variance of traditional ANOVA. All univariate analyses were made using SPSS Statistical Package.

3. Results

3.1 Abundance and diversity of higher-order consumers

3.1.1 Legal-sized and total abundance of rock lobster

The mean relative abundance of legal-sized lobsters in sanctuary zones was 9.46 ± 1.38 individuals 10min^{-1}, compared to 1.58 ± 0.33 individuals 10min^{-1} in fished zones. Although a greater mean abundance of legal-sized rock lobsters was found in sanctuary zones compared to adjacent fished zones, statistics revealed no significant zone effect (F=3.05, $p>0.05$; Table 3.1). However, a difference in site nested within zone was found to be significant (F=21.48, $p<0.001$; Table 3.1). This was due to the variability between sites nested within sanctuary zones as indicated by SNK post-hoc tests. Kingston Reefs sanctuary zone had a significantly greater overall abundance of rock lobsters (16.75 ± 0.69 individuals 10min^{-1}), while Boyinaboat Reef sanctuary zone had the lowest overall lobster abundance (2.5 ± 0.18 individuals 10min^{-1}) (Figure 3.1A). There were no differences in the abundance of lobsters within fished zones (Figure 3.1A).

The mixed-model nested ANOVA also demonstrated a significant site nested within zone x season interaction (F=2.54, $p<0.05$; Table 3.1). Seasonal variability was observed within and between sites nested within sanctuary zones as shown by SNK post-hoc tests. Kingston Reefs sanctuary zone was the only site to show a significant seasonal effect, as a greater abundance of lobsters were observed in summer (21.25 ± 4.07 individuals 10min^{-1}) and spring (21.0 ± 1.08 individuals 10min^{-1}) compared to winter (mean 8.0 ± 2.48 SE individuals 10min^{-1}). All other sites nested within sanctuary and fished zones had relatively constant lobster abundance over the seasons. Seasonal variability between sanctuary zones was also observed, as Kingston Reefs displayed a greater abundance of legal-sized lobsters in summer (21.25 ± 4.07 individuals 10min^{1}), while Boyinaboat Reef had the lowest lobster abundance over all seasons (2.5 ± 0.18 individuals 10min^{-1}; Figure 3.1A). This demonstrated a high degree of spatial and temporal variability.

The mean relative abundance of all rock lobsters, including legal and below legal size, was 16.72 ± 2.20 individuals 10min^{-1} in sanctuary zones, compared to 3.0 ± 0.56 individuals 10min^{-1} in fished zones. Total abundance of lobsters showed a similar pattern to the legal-size lobster, as the legal-size lobsters made up a large proportion of the total abundances of lobsters. A greater mean abundance of rock lobsters were observed in sanctuary zones compared to fished zones, however, statistics indicated no significant zone effect (F=4.20, $p>0.05$; Table 3.1). There was however, variability between sites as highlighted by the significant site nested within zone effect (F=23.73, $p<0.001$; Table 3.1). This was primarily due to the variability between sites nested within sanctuary zones as demonstrated through SNK post-hoc analyses. Kingston Reefs sanctuary zone had a significantly higher relative total mean abundance of lobsters (28.75 ± 3.60 individuals 10min^{-1}; Figure 3.1B), whereas Boyinaboat Reef sanctuary zone had the overall lowest abundance of lobsters (5.67 ± 1.25 individuals 10min^{-1}; Figure 3.1B). No statistical differences in total mean abundance of lobsters were observed for sites nested within fished zones, as all fished sites showed relatively low abundances of lobsters (3.0 ± 0.56 individuals 10min^{-1}; Figure 3.1B).

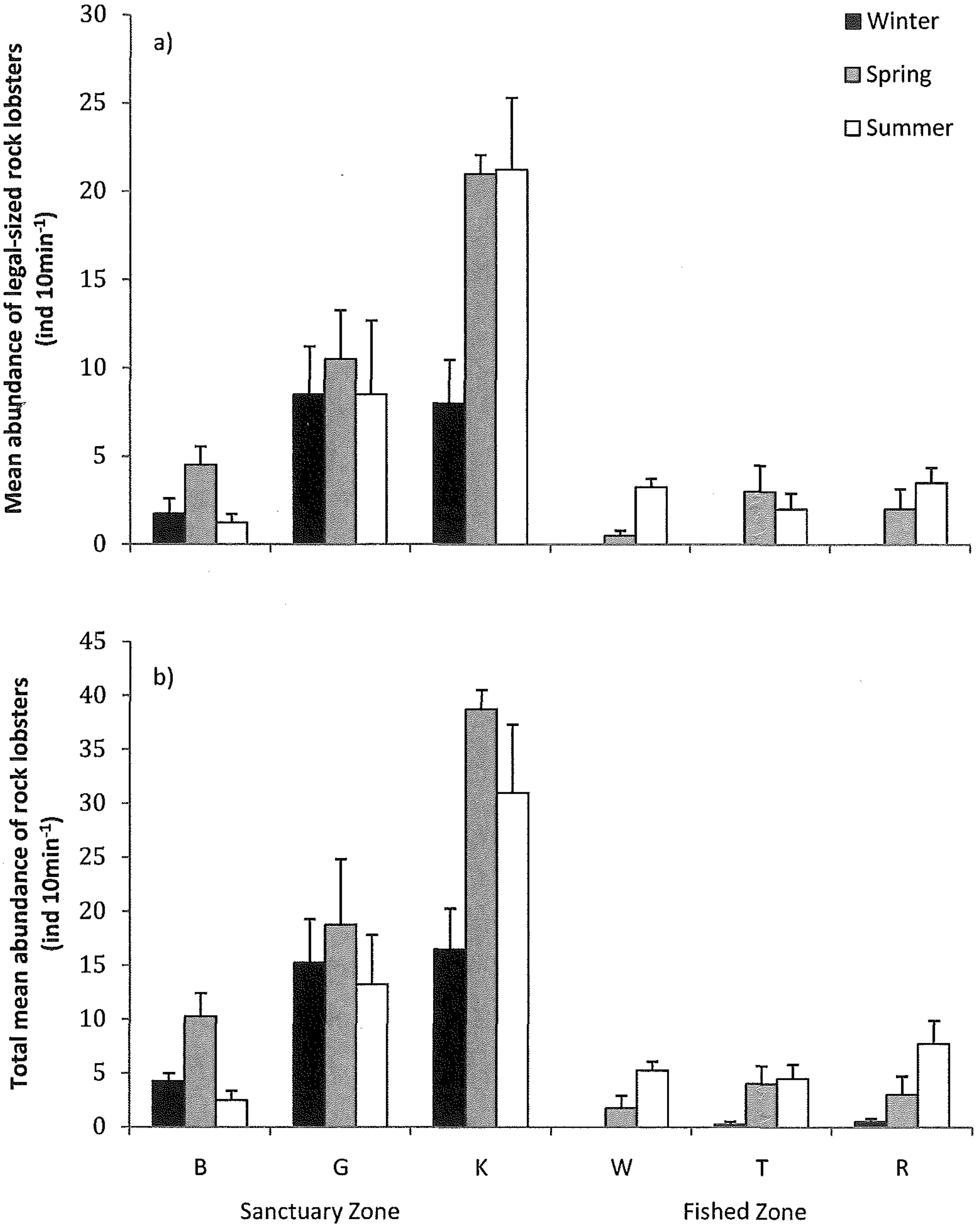


Figure 3.1. Mean (+S.E.) abundance of (a) legal-sized, and (b) total abundance of western rock lobster (*P. cygnus*) per 10 minute timed search in sanctuary zones: Boyinaboat Reef (B), Green Island (G), and Kingston Reefs (K), and in fished zones: Wreck Rock (W), Twin Rocks (T), and Rocky Bay (R).

Table 3.1. ANOVA comparing the mean abundances of legal-sized (>77mm CL; carapace length) and total abundance of rock lobsters (*P.cygnus*).Legal-size abundance *Cochran's test: C= 0.2745* not significant (ns). Total abundance *Cochran's test: C= 0.2626* ns. Z: zones, S(Z): sites nested within zone, and Se: seasons.

		Legal-size abundance (ind. 10min^{-1})			Total abundance (ind. 10min^{-1})		
Source	*df*	**MS**	**F**	*p*	**MS**	**F**	*p*
Z	1	1112.3472	3.64	0.1291	3389.3889	4.20	0.1097
S(Z)	4	305.7222	21.48	**0.0000*****	806.5556	23.73	**0.0000*****
Se	2	110.3889	3.05	0.1036	276.2639	4.09	0.0599
Z x Se	2	24.8889	0.69	0.5301	165.0139	2.44	0.1488
S(Z) x Se	8	36.1806	2.54	**0.0200***	67.6181	1.99	0.0654
Residual	54	14.2361			33.9907		
Total	71						

**p<0.05, **p<0.01, ***p<0.005*

3.1.2 Fish species abundance, biomass, and species richness

A total of 6,543 fish species belonging to 68 species and representing 30 families were recorded at the reef and in adjacent *Amphibolis* spp. seagrass meadows over the study period. The families occurring in greatest abundance over all sites and all three seasons were Labridae (45.5% of total individuals), Pomacentridae (15.4%), and Kyphosidae (13.1%). Families with the greatest number of species belonged to Labridae (15 species), and Kyphosidae (6 species). Numerically, the most abundant fish species observed over all sites were the western king wrasse *Coris auricularis* (Labridae, 0.08±0.94 individuals m^2; total 17.9%), brownfield wrasse *Halichoeres brownfieldi* (Labridae, 0.07±0.93 individuals m^2; 16.7%), brown-spotted wrasse *Notolabrus parilus* (Labridae, 0.05±0.44 individuals m^2; 10.9%), and the schooling carnivorous *Pempheris klunzingeri* (Pempheridae, 0.04±1.31 individuals m^2; 10.1%).

Mean fish abundances ranged up to 1.65 individualsm^{-2} across all sampling occasions. Species richness per site varied from 7 to 30 species (18.67±2.02) over three seasons. Fish biomass ranged up to 2,120.4 grams m^{2} across zones, sites, seasons, and distance from reef. Based on fish taxa, categorised into three different feeding modes, 16.18% of the total number of species were omnivores (11 species) and, 20.59% of species herbivores (14 species). Carnivorous species encompassed the greater proportion of total species (63.24%, 43 species), of which 16.18% was invertivores (11 species). Fish species were further categorised into fishing importance: 16 species were not targeted by fishermen (23.9% of the total), five were considered by-catch species (7.5%), 37 species were recreationally caught (55.2%), and nine were commercially targeted species (13.4%).

PERMANOVA demonstrated a significant multivariate interaction between the factors site nested within zone x season x distance for total mean abundance of fish (MS=3626.1, $p<0.001$; Table 3.2). The same complex interaction between the main factors was shown for fish biomass (MS=2.4294, $p<0.001$; Table 3.2) and fish species richness (MS=232.83, $p<0.05$; Table 3.2). This demonstrated the high degree of spatial and temporal variability, making it difficult to separate patterns from noise, however, some patterns were detectable as shown below.

A significant zone effect was detected (MS=14017.0, $p<0.05$; Table 3.2), however, this was masked over by a significant site nested within zone effect (MS=11147.0, $p<0.001$; Table 3.2). This was due to the high variability between all sites nested within sanctuary and fished zones. Although not figuratively clear, all fished zones had a greater abundance of fish (Wreck Rock 0.42 ± 1.26individuals m^{2}; Twin Rocks 0.39 ± 0.73individuals m^{2}; Rocky Bay 0.41 ± 1.34 individuals m^{2}) than adjacent sanctuary zones, with the exception of Kingston Reefs, which was the primary driver of fish abundance throughout all seasons (0.64 ± 1.79 individuals m^{2}; Figure 3.2). Boyinaboat Reef had relatively low total mean fish abundance over all seasons (0.19 ± 1.86 individuals m^{2}; Figure 3.2). The overall results were further complicated by the interactive terms with season. Rocky Bay was the main driver of fish abundance during the spring, while Wreck Rock dominated summer (Figure 3.2). The majority of the variation in the fish abundance among sites was due to large schools of fish including the skipjack trevally *Pseudocaranx wrighti*, buffalo bream *Kyphosus cornelli*, and rough bullseye *P. klunzingeri*,and solitary swimmers such as the rainbow cale *Odax acroptilus* and old wife *Enoplosus armatus*.

Statistics revealed a significant distance effect (MS=14351.0, *p*<0.01; Table 3.2). In general, there was a trend of decreasing mean abundance of fish with increasing distance away from the reef, as indicated through post-hoc Monte Carlo pair-wise comparisons (the reef and 200m, *p*=0.0186). In spring, Boyinaboat Reef sanctuary zone, Green Island sanctuary zone, Wreck Rock fished zone, and Twin Rocks fished zone displayed this pattern, however, this was not the case for Kingston Reefs sanctuary zone and Rocky Bay fished zone (Figure 3.2). Both Kingston Reefs and Rocky Bay had a significantly greater abundance of fish at 200m than 60m away from the reef (Figure 3.2). The same pattern of greater fish abundance at 200m was observed in summer for Twin Rocks and Rocky Bay (Figure 3.2). Both Green Island and Kingston Reefs had a greater abundance of fish at 60m away from the reef than at the reef (0m) and 200m away in *Amphibolis* spp. meadows (Figure 3.2). Therefore, fish species significantly differed in abundance with increasing distances away from the reef, however, this varied across sanctuary and fished sites and seasons.

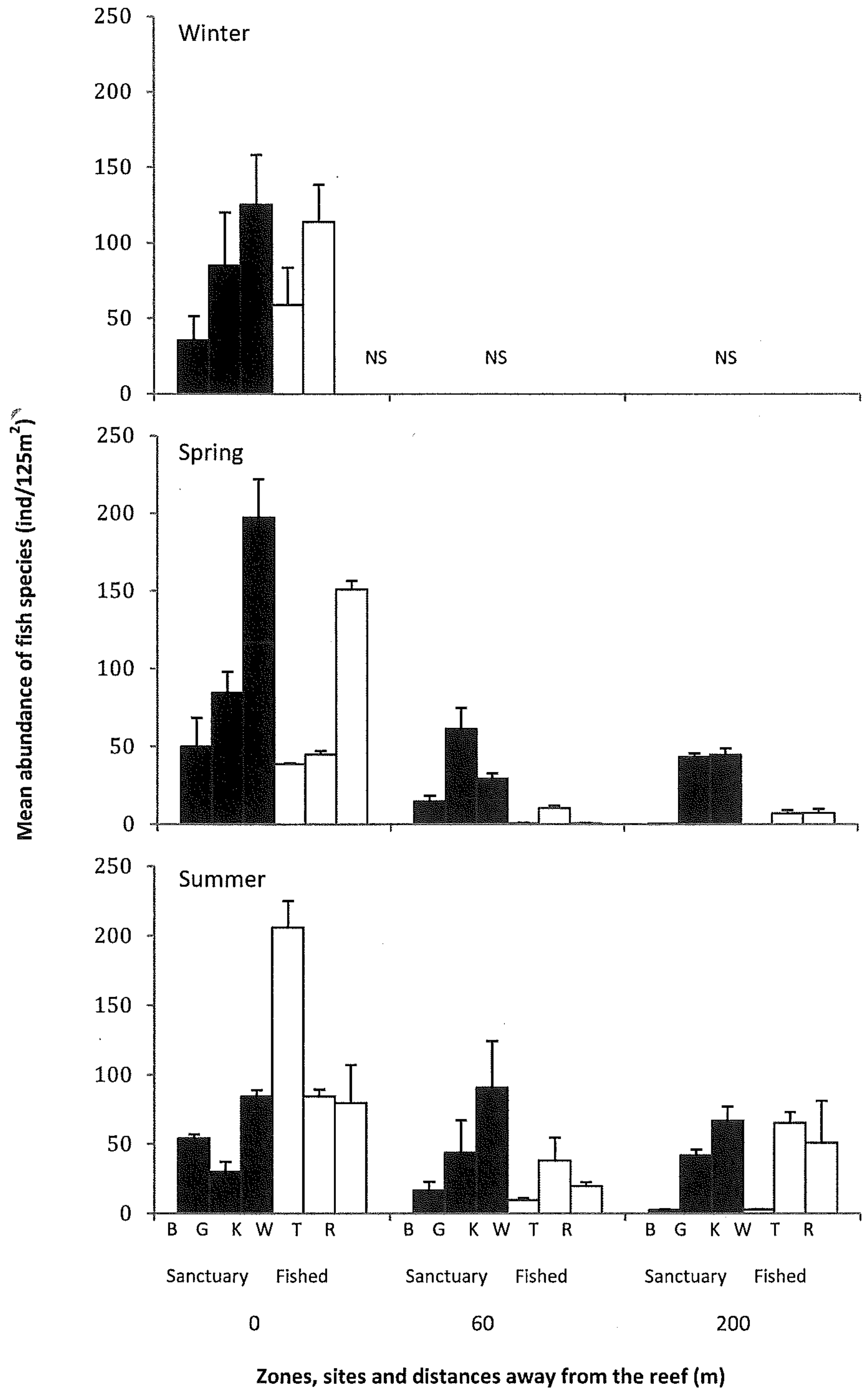


Figure 3.2. Mean (+S.E.) fish species abundance over three seasons in *Amphibolis spp.* meadows with proximity to the reef: 0 (on the reef), 60, and 200m, in sanctuary zones: Boyinaboat Reef (B), Green Island (G), and Kingston Reefs (K), and fished zones: Wreck Rock (W), Twin Rocks (T), and Rocky Bay (R). NS= not sampled.

There was a significant zone effect for fish biomass (MS=8702.4, $p<0.001$; Table 3.2) as sanctuary zones had a slightly greater biomass of fish (277.87 ± 7.26 grams m^2) than fished zones (217.27 ± 14.50 grams m^2). However, the separation between zones was unclear due to the high degree of variability between sites nested within zone (MS=3.48, $p<0.001$; Table 3.2). Twin Rocks had the greatest fish biomass during the winter, and Rocky Bay was the main driver for fished sites in summer (Figure 3.3). Kingston Reefs sanctuary zone had the greatest fish biomass over all seasons (520.33 ± 16.81 grams m^2), and is primarily responsible for driving the zone effect (Figure 3.3). Both MMP sites had relatively low biomass for fish (Boyinaboat Reef sanctuary zone 96.14 ± 2.89 grams m^2; Wreck Rock fished zone 78.22 ± 2.67 grams m^2). Majority of the variation in fish biomass among sites was due to large schooling fish, including herbivorous kyphosids *K.sydneyanus* and *K. cornelli.*

As previously seen in fish abundance, similar patterns were observed with total mean fish biomass and increasing distances away from the reef (MS=4.29, $p<0.001$; Table 3.2). The reef had a significantly greater biomass than 60m ($p=0.025$) and 200m ($p=0.0095$) away in *Amphibolis* spp. meadows, as indicated by post-hoc Monte Carlo pair-wise comparisons. This pattern was also observed for fish species richness. A change in fish biomass with proximity to the reef however, cannot be applied to all sites due to complex interactions between sites and distances. Statistics also show a significant variability in fish biomass with seasons (MS=2.40, $p<0.05$; Table 3.2). With the exception of Kingston Reefs sanctuary zone, spring demonstrated an overall relatively lower biomass (total mean 442.69 ± 39.94 grams m^2) than winter (1,654.36 ± 121.04 grams m^2) and spring (1,368.87 ± 74.46 grams m^2) however, there was difficultly disentangling patterns due to the complexity of interactions.

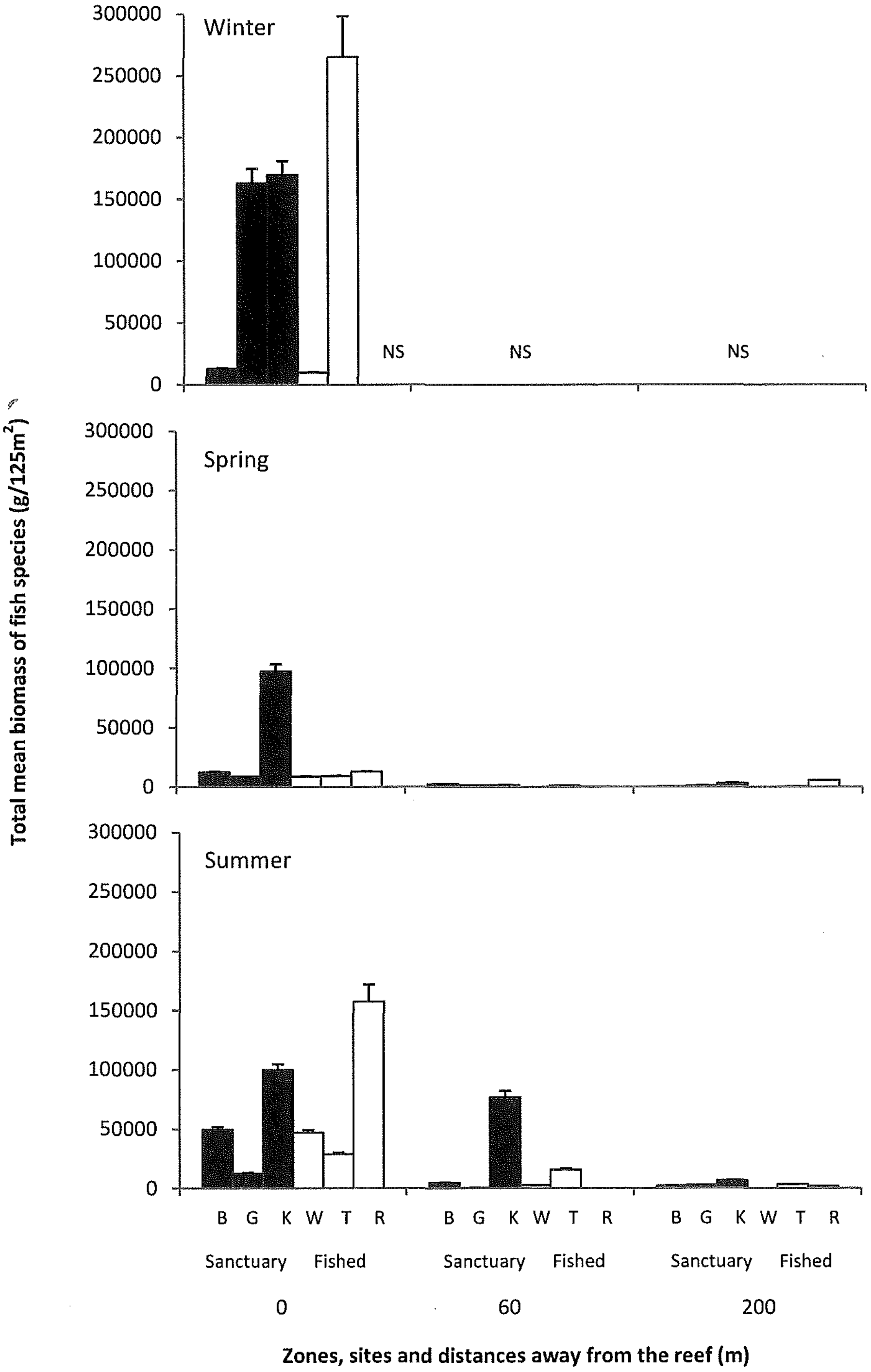


Figure 3.3. Total mean (+S.E.) biomass of fish species over three seasons in *Amphibolis spp.* meadows with proximity to the reef: 0, 60, and 200m, over six sites in sanctuary zones: Boyinaboat Reef (B), Green Island (G), Kingston Reefs (K), and in fished zones: Wreck Rock (W), Twin Rocks (T), and Rocky Bay (R). NS= not sampled.

Although there was no clear zone effect for species richness (MS=102.30; $p>0.05$; Table 3.2), PERMANOVA indicated a significant difference between sites nested within zones (MS=1147.10, $p=0.001$; Table 3.2). This was due to the high degree of variability in species richness between all sites nested within sanctuary and fished zones as indicated by post-hoc Monte Carlo pair-wise comparisons. All sites had relatively similar species richness (ranging from 0.13 to 0.15 species m^2), excluding both Kingston Reefs and Rocky Bay. Rocky Bay appears to be the main driver for fished zones (0.19 ± 0.03 individual species m^2) whereas Kingston Reefs was driving high species richness for sanctuary zones (0.18 ± 0.03 individual species m^2) (Figure 3.6). In general, there was no clear signal of increased species richness of fish in sanctuary zones.

Fish species richness was significantly influenced by increasing distances away from the reef (MS=7645.7, $p<0.001$; Table 3.2). In general, species richness was greatest at the reef and declined with increasing distances away from the reef. Although this was the outcome for most sites, this was not the case for Green Island and Rocky Bay during spring, and Green Island and Twin Rocks in summer. The same or greater species richness was observed at 200m away in *Amphibolis* spp. meadows than at 60m in seagrass (Figure 3.4). Furthermore, fish species richness fluctuated with seasons (MS=1698.80, $p<0.05$; Table 3.2), as post-hoc Monte Carlo pair-wise comparisons demonstrated a relatively lower total mean species richness in winter (0.05 ± 0.01 individual species m^2) and greatest in summer (0.17 ± 0.02 individual species m^2). This does not hold true for all sites, due to within site variability (Figure 3.4).

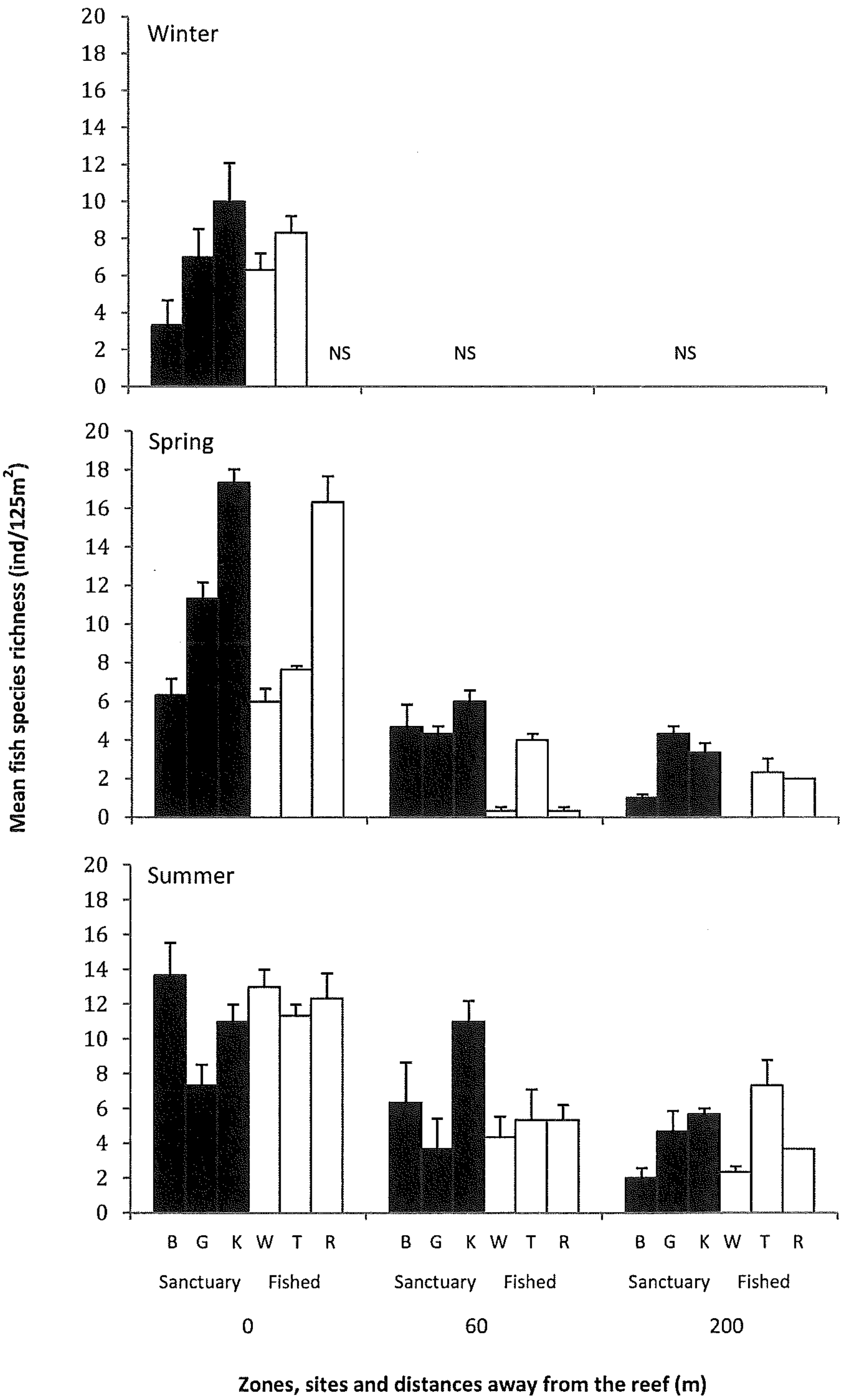


Figure 3.4. Mean (+S.E.) fish species richness over three seasons in *Amphibolis spp.* meadows with proximity to the reef: 0, 60, and 200m, in sanctuary zones: Boyinaboat Reef (B), Green Island (G), and Kingston Reefs (K), and fished zones: Wreck Rock (W), Twin Rocks (T), and Rocky Bay (R). NS= not sampled.

Table 3.2. Results of a PERMANOVA, examining mean fish species abundance, total biomass, and species richness. Analyses were conducted using Bray-Curtis similarity on square-root (√x) transformed data with 9999 permutations on residuals under a reduced model.

		Abundance (ind/125m²)		Biomass (g/125m^2)		Species richness (spp/125m^2)	
Source	*df*	**MS**	***p*(perm)**	**MS**	***p*(perm)**	**MS**	***p*(perm)**
Z	1	14017.0	**0.0248***	8702.4	**0.0001******	102.30	0.7935
S(Z)	4	11147.0	**0.0001******	3.4798	**0.0001******	1147.10	**0.0001******
Se	2	7066.3	0.0977	2.4013	**0.0132***	1698.80	**0.0192***
D	2	14351.0	**0.0047*****	4.2935	**0.0006******	7645.70	**0.0005******
Z x Se	2	7336.0	0.0748	1.0326	0.4507	482.97	0.2011
Z x D	2	4377.5	0.6227	1.1908	0.2889	418.09	0.3432
Se x D	2	2671.3	0.6971	1.238	0.3104	320.40	.0.2896
S(Z) x Se	7	4569.0	**0.0001******	2.6436	**0.0001******	261.08	**0.013***
S(Z) x D	8	5344.6	**0.0001******	2.9911	**0.0001******	365.98	**0.0005******
Z x Se x D	2	4448.3	0.2884	1.2441	0.3119	182.01	0.5612
S(Z) x Se s D	7	3626.1	**0.0001******	2.4294	**0.0001******	232.83	**0.0222***
Residual	75	1337.9				98.74	
Total	114						

3.1.3. Fish species assemblages

The canonical analysis of principle coordinates (CAP) ordination displayed no clear separation between zones, sites nested within zone, distances, or seasons, shown by the high degree of overlap in samples from the two types of zones based on fish abundances (Figure 3.5). Six species in particular, *P. klunzingeri, Parma mccullochi, K. cornelli, Austrolabrus maculatus, N. parilus,* and *C. auricularis*, were shown to be relatively higher contributors to mean fish abundance. This was indicated by their correlations (Pearson's r= 0.5) with the canonical axes, and the same correlation will be used throughout all CAP plots. *C. auricularis* and *N. parilus* appear to be the representative species at Kingston Reefs sanctuary zone, and *P. klunzingeri* was representative of Wreck Rock and Rocky Bay fished zone (Figure 3.5). The remaining three fish species, *P. mccullochi, K. cornelli,* and *A. maculatus* were found across various sites (Figure 3.5).

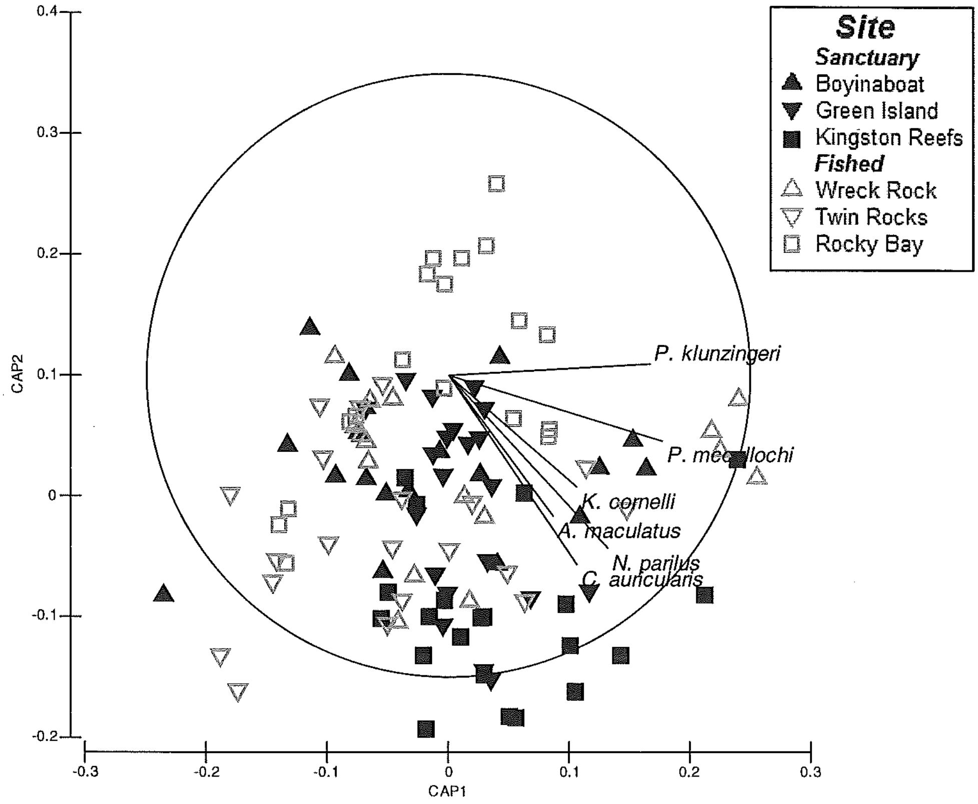


Figure 3.5. Canonical analysis of principle coordinates (CAP) ordination based on square-root (√x) Bray-Curtis similarities on mean fish species abundance across six sites nested within two zones, and over three seasons in *Amphibolis spp.* meadows with proximity to the reef: 0, 60, and 200m. A species correlation plot (Pearson correlation set at 0.5) is placed over the ordination.

The results of the CAP analysis on mean fish biomass further supported these complex interactive effects among between zones, sites, distance and season, as the canonical axes showed no clear separation between sites nested within zones, seasons, or distances (Figure 3.6). Five species in particular, *Dactylophora nigricans, K. cornelli, C. auricularis, N. parilus,* and *P. mccullochi,* were the overall biggest contributors. The mean fish biomass at Kingston was primarily driven by *K. cornelli, C. auricularis,* and *N. parilus*, whereas *P. mccullochi* appeared to be the key contributor of the biomass at MMP sites, Boyinaboat Reef sanctuary zone and Wreck Rock fished zone (Figure 3.6). The outlier (top-left corner) depicts Rocky Bay fished zone with a relatively low biomass of fish (2 species, *D. nigricans* and *Gerres subfasciatus*) during spring at 200m away from the reef (Figure 3.6).

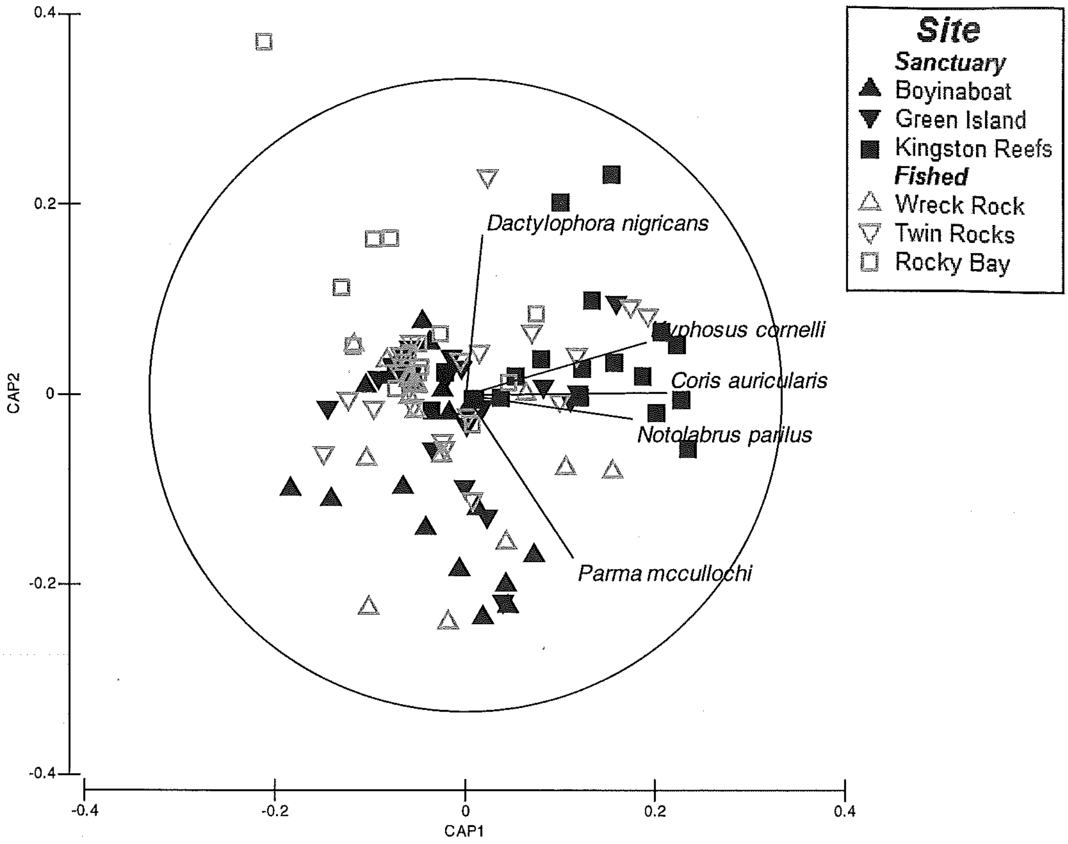


Figure 3.6. Canonical analysis of principle coordinates (CAP) ordination using Bray-Curtis similarities on fish species biomass across six sites nested within two zones, and over three seasons in *Amphibolis spp.* meadows with proximity to the reef: 0, 60, and 200m. A species correlation plot (Pearson correlation set at 0.5) is placed over the ordination. Data were square root (√x) transformed.

3.2 Benthic fauna

3.2.1 Abundance, biomass and family level richness benthic fauna

A total of 60 families of benthic taxa were observed over the study period, belonging to 18 classes from eight phyla. A wide range of invertebrate and vertebrate groups were recorded from polychaetes (Annelida) to crustaceans (Arthropoda) and sponges (Porifera). The most abundant macroinvertebrate fauna observed across all sites at the reef and in seagrass meadows were the gastropods (64.04% total mean abundance), ascidians (15.61%), and the malacostracans (13.27%). Mean benthic fauna abundance ranged from 0 to 143.7 individuals $0.25m^2$ across all sampling occasions (Figure 3.7), and the family level richness per site varied from 0 to 12 species over all three seasons (Figure 3.8).

PERMANOVA failed to detect a significant zone effect on the benthic assemblage (MS=19382.0, $p>0.05$), however, a significant difference among sites nested within zones was observed (MS=32284.0, $p<0.001$; Table 3.3). This was due to the high degree of variability between all sites nested within sanctuary and fished zones. Benthic faunal abundance was greatest at both sites within Marmion Marine Park (MMP), as Boyinaboat Reef appeared to be driving the faunal abundance of sanctuary zones whereas Wreck Rock was the primary driver of the fished zone over all three seasons (Figure 3.7). This was a result of malacostracans and gastropods occurring in high abundances at these two sites. Ascidians were also found to be consistently more abundant MMP sites and almost non-existent at Rottnest Island Marine Reserve (RIMR) sites. Despite the strong abundance patterns observed at MMP, no clear conclusions can be made considering the complex nature of interactions between the main factors (Table 3.3; Figure 3.7).

There was a significant interaction between the factors site nested within zone x season x distances for the benthic faunal assemblage (MS=2810.5, $p<0.001$; Table 3.3). This complex interaction was also observed for family level richness (MS=681.12, $p<0.05$; Table 3.3). It demonstrates the high degree of spatial and temporal variability causing difficulty in disentangling patterns from noise however, some patterns were detected.

Statistics demonstrated a significant distance effect (MS=7695.8, $p<0.05$; Table 3.3). Post-hoc Monte Carlo pair-wise comparisons indicated significant differences in the faunal abundance between seagrass immediately adjacent to the reef (0SG) and 60m (p=0.0279), 0SG and 200m (p=0.0278), and between 15m and 60m into the seagrass (p=0.0296). There was an overall decreasing trend of benthic faunal abundance with increasing distance away from the reef. This however was not clearly portrayed due to complex interactions between the main factors. For instance, Green Island, Wreck Rock and Rocky Bay showed the opposite trend in winter, as with Boyinaboat Reef and Twin Rocks in summer (Figure 3.7). In summer, Rocky Bay showed an increase in faunal abundance with increasing distances away from the reef primarily driven by *Cantharidus spp* (Trochidae) (Figure 3.7). Furthermore, there was a significant difference in the faunal abundances among seasons (MS=15053.0, $p<0.05$; Table 3.3). In general, summer had the greatest total mean faunal abundance (201.76 ± 6.18 individuals $0.25m^2$) in comparison to winter, which demonstrated the lowest abundance of fauna (71.71 ± 4.73 individuals $0.25m^2$) (Figure 3.7).

Table 3.3. Results of a PERMANOVA, examining benthic faunal abundance and family level richness. Analyses were conducted using Bray-Curtis similarity on square-root ($\sqrt{x}$) transformed data with 9999 permutations on residuals under a reduced model.

		Abundance (ind/0.25m^2)		Family level richness (spp/0.25m^2)	
Source	*df*	**MS**	***p*(perm)**	**MS**	***p*(perm)**
Z	1	19382.0	0.7471	376.60	0.896
S(Z)	4	32284.0	**0.0001*****	2226.00	**0.0001*****
Se	2	15053.0	**0.0482***	3538.10	0.3169
D	5	7695.8	**0.0116***	1436.50	**0.0091****
Z x Se	2	5129.6	0.7756	1462.00	0.7342
Z x D	5	3724.0	0.4464	747.19	0.3565
Se x D	10	2397.0	0.7958	733.63	0.3611
S(Z) x Se	7	7559.6	**0.0001*****	2762.90	**0.0001*****
S(Z) x D	20	3826.3	**0.0001*****	687.19	**0.0340***
Z x Se x D	10	1912.3	0.9740	808.95	0.2422
S(Z) x Se s D	34	2810.5	**0.0001*****	681.12	**0.0157***
Residual	189	1470.6		546.37	
Total	289				

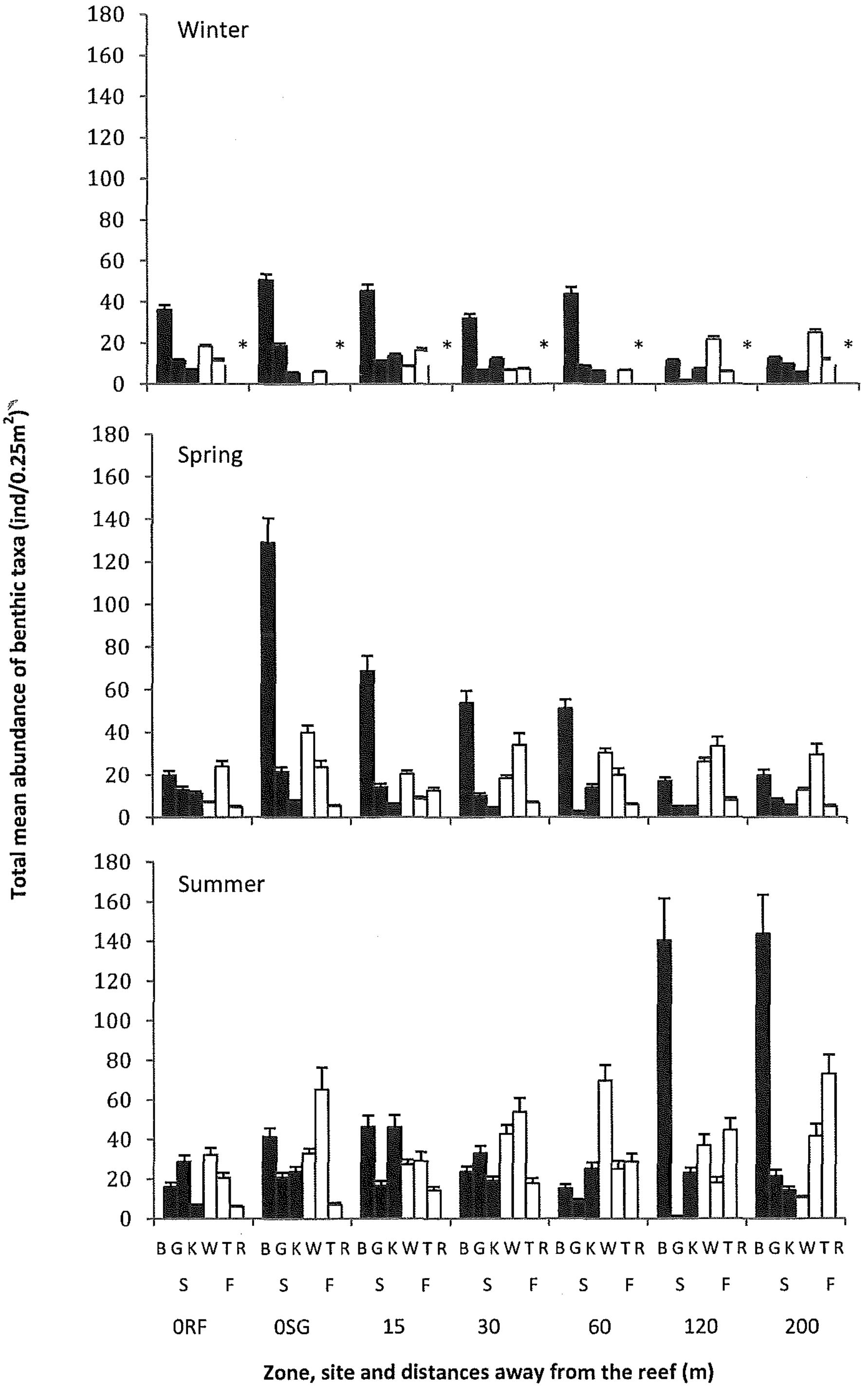
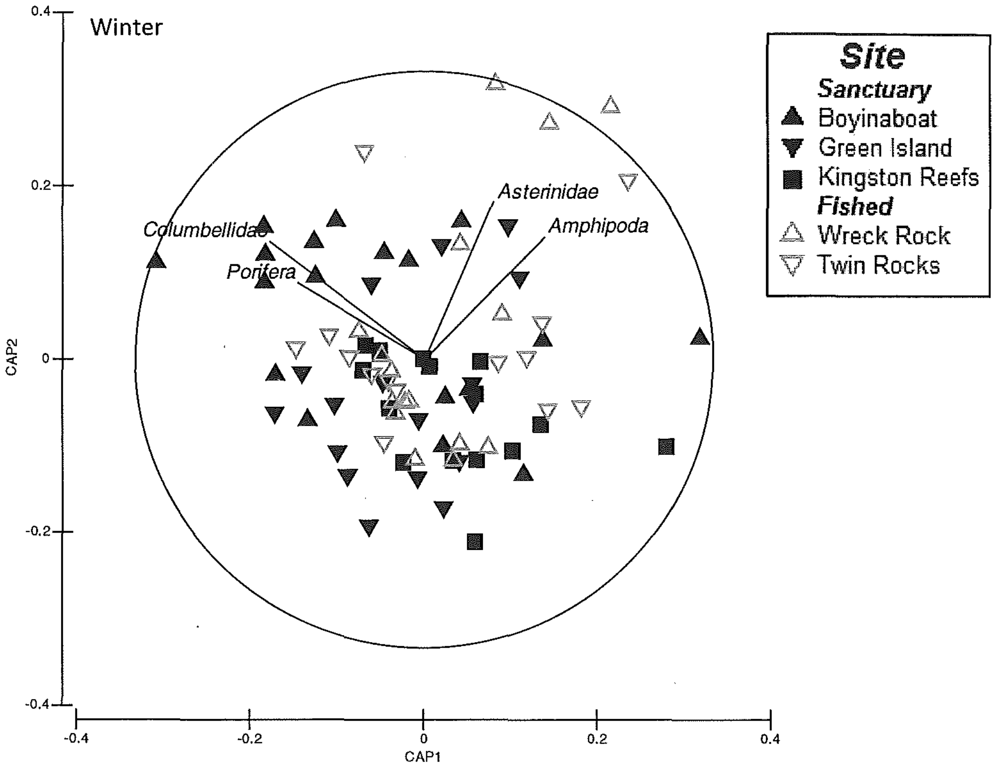
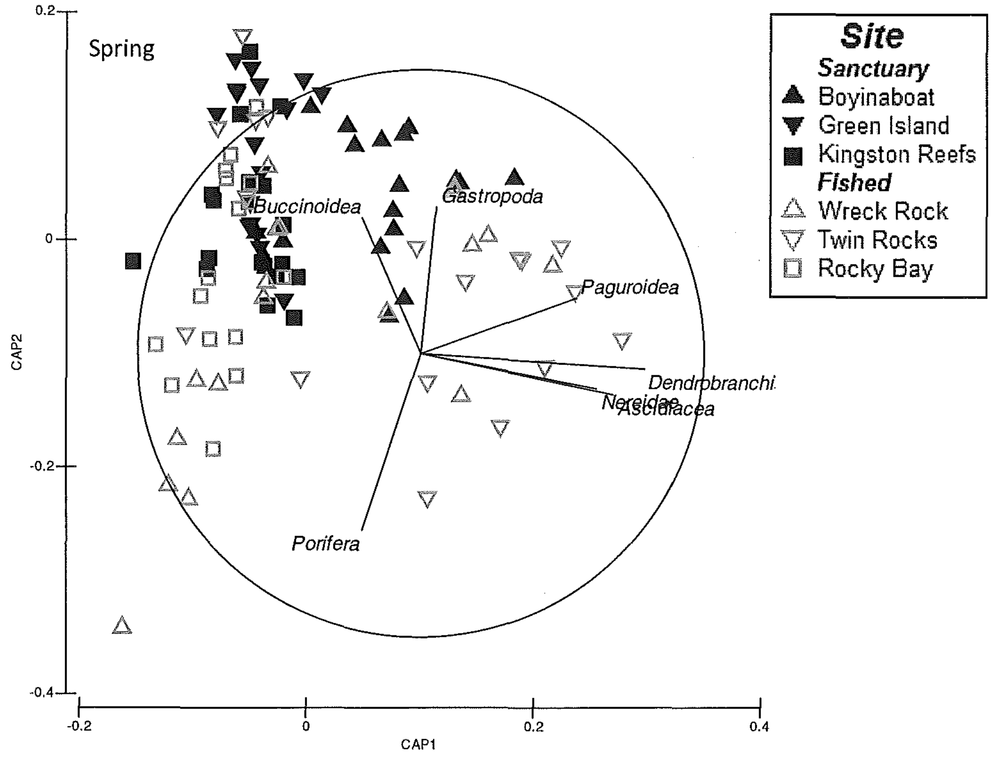


Figure 3.7. Total mean (+S.E.) abundance of benthic taxa over three seasons in *Amphibolis spp.* meadows with proximity to the reef: 0RF, 0SG, 15, 30, 60, 120, and 200m, in sanctuary zones: Boyinaboat Reef (B), Green Island (G), and Kingston Reefs (K), and in fished zones: Wreck Rock (W), Twin Rocks (T), and Rocky Bay (R). *= not sampled.

3.2.2. Benthic fauna assemblages

The CAP plots were separated into seasons as a result of the numerous data points, and the focus of the study was to establish patterns in benthic assemblages between sanctuary and fished zones, and among distances away from reefs. The CAP ordinations displayed no clear separation of the fauna samples between sanctuary and fished zones, and among sites nested within zones, and distances, for each seasons (Figure 3.8). In winter, sponges (Porifera) and dove shells (Columbellidae) were the high contributors to the faunal assemblages at Boyinaboat Reef sanctuary zone, however, no other patterns could be detected for this season (Figure 3.8). In spring, five groups in particular, hermit crabs (Paguroidea), prawns (Dendrobranchiata), polychaete worms (Nereidae), ascidians (Ascidiacea), and sponges (Porifera) appear to be contributing the greatest to the faunal assemblages at Wreck Rock fished zone and Twin Rocks fished zone (Figure 3.8). Gastropods showed a stronger correlation towards Boyinaboat Reef sanctuary zone than any other site (Figure 3.8). In summer, ascidians were the key contributing fauna in distinguishing Boyinaboat Reef sanctuary zone from other sites (Figure 3.8). Hermit crabs (Paguroidea) and turban snails (Turbinidae) formed the predominant faunal assemblage for both Wreck Rock and Twin Rocks fished zone (Figure 3.8).


Winter
0.4
0.2
0
-0.2
-0.4
CAP2
-0.4
-0.2
0
0.2
0.4
CAP1
Columbellidae
Porifera
Asterinidae
Amphipoda
Site
Sanctuary
▲ Boyinaboat
▼ Green Island
■ Kingston Reefs
Fished
△ Wreck Rock
▽ Twin Rocks


Spring
0.2
0
-0.2
-0.4
CAP2
-0.2
0
0.2
0.4
CAP1
Buccinoidea
Gastropoda
Paguroidea
Dendrobranchi
Nereidae
Ascidiacea
Porifera
Site
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▲ Boyinaboat
▼ Green Island
■ Kingston Reefs
Fished
△ Wreck Rock
▽ Twin Rocks
□ Rocky Bay

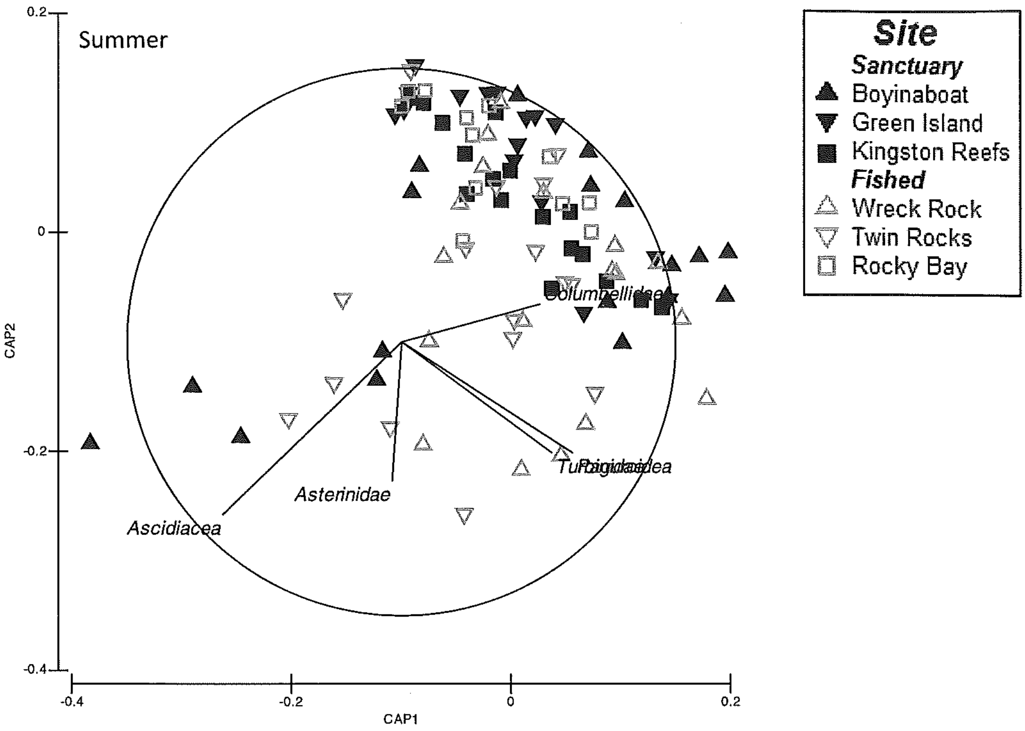


Figure 3.8. Canonical analysis of principle coordinates (CAP) ordination using Bray-Curtis similarities on benthic faunal abundances across six sites nested within two zones, and over three seasons in *Amphibolis spp.* meadows with proximity to the reef: 0SG, 15, 30, 60, 120, and 200m. A family-level correlation plot (Pearson correlation set at 0.5) is placed over the ordination. Data were square root ($\sqrt{x}$) transformed.

Zones or seasons had no significant effect on the benthic faunal richness as indicated by PERMANOVA (Table 3.3). There was a significant distance and sites nested within zones effect, and an interaction between sites within zone and season, and between site within zone and distance, implying a variable response of benthic richness across sites, distances and seasons (Table 3.3). Despite the significant distance effect (MS=1436.50, $p<0.01$; Table 3.3), no clear trend of decreasing taxa richness with increasing distance away from the reef was observed (Figure 3.9). Post-hoc Monte Carlo pair-wise comparisons further validated this lack of trend ($p>0.05$).

Benthic faunal richness varied across all sites. Both sites within MMP displayed an overall greater family level richness (Boyinaboat Reef sanctuary zone 6.77 ± 0.62 individual species 0.25m^2; Wreck Rock fished zone 7.33 ± 0.79 individual species 0.25m^2) compared to the relatively low benthic richness at sites at RIMR, which ranged from 2.99 to 4.12 individual species 0.25m^2 (Figure 3.9). Boyinaboat Reef was driving the high benthic richness in spring as was Wreck Rock in summer, though distinguishing this pattern across distances and seasons was difficult to visualise due to the interaction terms (Figure 3.9). Gastropod and malacostracan groups are likely responsible for the variation in faunal richness between sites. 96 different species of gastropods were found across all sites, while malacostracans had 25 species. Gastropods largely comprised three commonly observed species: *Pyrene bidentata* (Columbellidae), *Cantharidus lehmanni* (Trochidae), and an unknown gastropod species; while malacostracans were predominately hermit crabs, occupying empty *P. bidentata* shells.

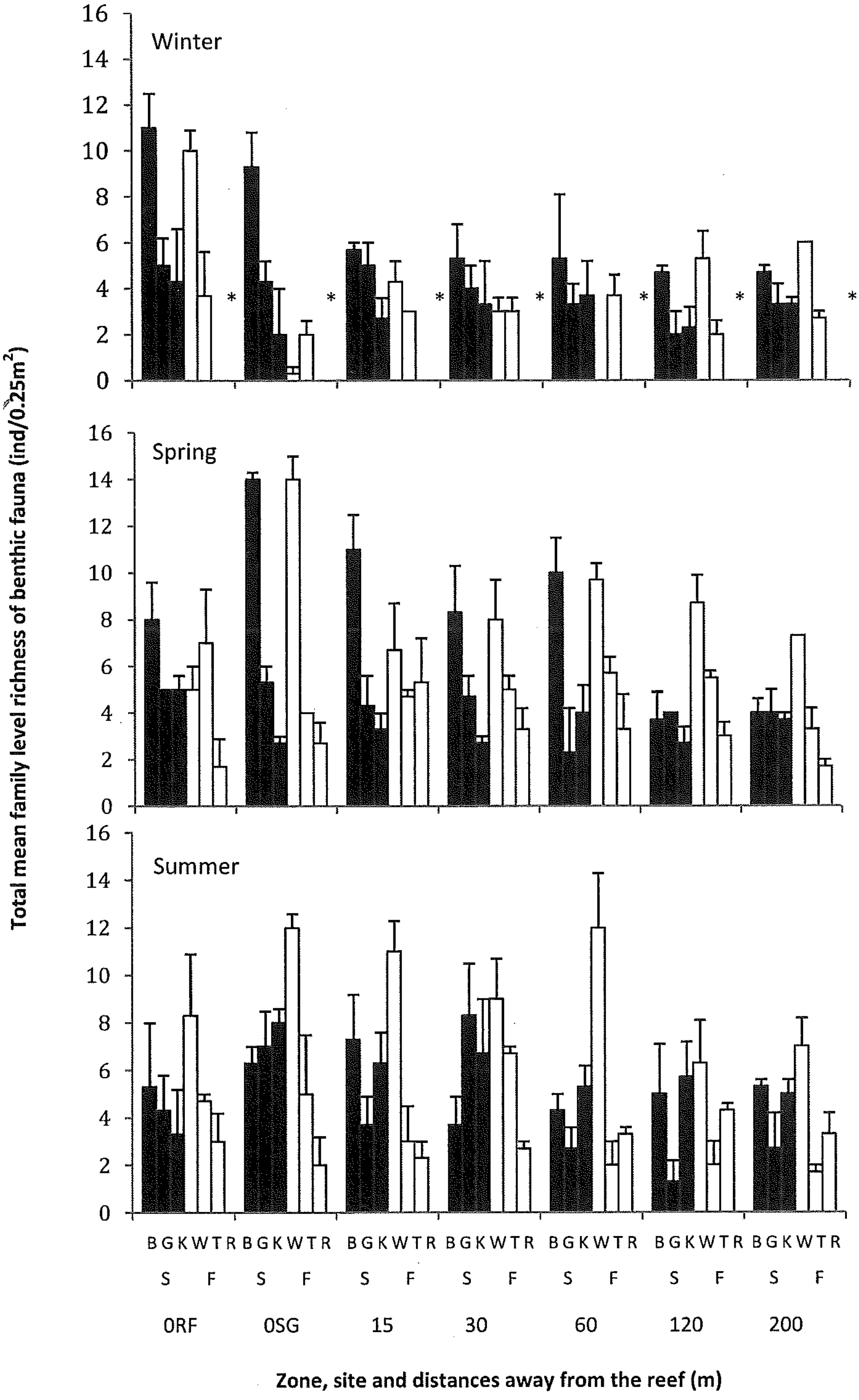


Figure 3.9. Total mean (+S.E.) family level richness of benthic taxa at family level over three seasons in *Amphibolis spp.* meadows with proximity to the reef: 0RF, 0SG, 15, 30, 60, 120, and 200m, in sanctuary zones: Boyinaboat Reef (B), Green Island (G), and Kingston Reefs (K), and in fished zones: Wreck Rock (W), Twin Rocks (T), and Rocky Bay (R). *= not sampled.

3.3 Benthic flora

3.3.1 Relative abundance, biomass and taxa richness of epiphytic algae

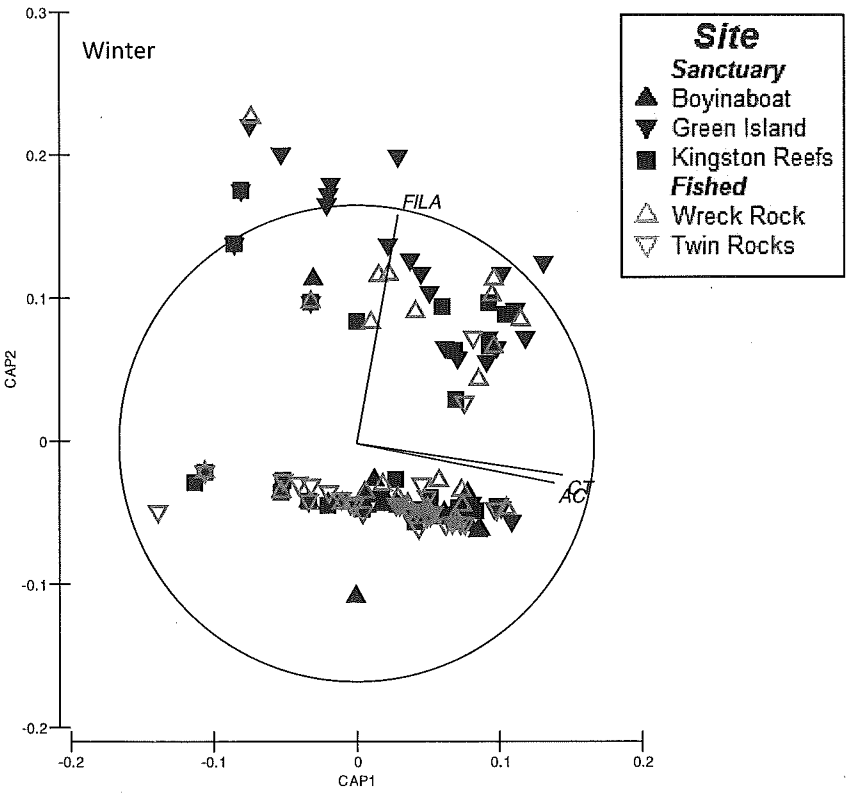
For percentage relative abundance of epiphytic algae, there was no zone, season, or distance from reef effect (Table 3.4), but there was a significant sites nested within zone effect (MS=6596.4; $p<0.001$; Table 3.4) which interacted with season (MS=1057.7, $p<0.05$; Table 3.4). This highlights the variability in the relative abundance of epiphytic algae over sites and seasons. All sites had a relatively high percentage relative abundance of encrusting calcareous algae on seagrass leaf blades. Corticated terete algae also demonstrated a similar pattern, however, its percentage abundance fluctuated over sites and seasons. Articulated calcareous algae were also observed over all sites excluding Boyinaboat Reef where it infrequently occurred. Articulated calcareous algae were the predominate epiphytic algae on *Amphibolis* spp. seagrass leaves at Green Island particularly in summer where a two-fold increase was observed since winter (25.69 ± 4.23% 0.25m^2 in winter to 50.14 ± 5.20% 0.25m^2 in summer). In winter and summer, both Boyinaboat and Kingston Reefs sanctuary zones had similar epiphytic abundances; while Wreck Rock and Rocky Bay fished zones had similar epiphytic algal abundances and remained the same throughout the seasons.

Table 3.4. Results of a PERMANOVA examining the percentage relative abundance and total mean biomass of epiphytic algal assemblage. Analyses were conducted using Bray-Curtis similarity on square-root ($\sqrt{x}$) transformed data with 9999 permutations on residuals under a reduced model.

	% Relative abundance (%/0.25m^2)			Biomass (g DW/0.25m)		
Source	***df***	**MS**	***p*(perm)**	***df***	**MS**	***p*(perm)**
Z	1	1382.9	0.8728	1	6547.4	0.7091
S(Z)	4	6596.4	**0.0001*****	4	12942	**0.0001*****
Se	2	1546.4	0.2467	2	7067.3	0.2944
D	5	116.5	0.9735	5	1577.9	0.3849
Z x Se	2	1144.2	0.4065	2	8863	0.2158
Z x D	5	590.9	0.1933	5	1272.3	0.6223
Se x D	10	398.4	0.2152	10	1092.6	0.3598
S(Z) x Se	7	1057.7	**0.0105***	7	5503.4	**0.0001*****
S(Z) x D	20	406.5	0.6386	20	1489.4	**0.0001*****
Z x Se x D	10	389.2	0.2313	10	1475.7	0.0539
S(Z) x Se s D	35	306.1	0.9838	35	1014.2	**0.0001*****
Residual	525	458.7		204	638.6	
Total	626			305		

3.3.2. Epiphytic algal assemblages

Similar to faunal assemblages, CAP analyses were carried out on data from each season separately. No clear separation can be made between zones, sites, seasons, or distances in the CAP plots due to the high degree of overlap (Figure 3.10). In winter, filamentous algae were the only distinguishable epiphytic algae to be contributing the greatest at Green Island sanctuary zone (Figure 3.10). A similar pattern was observed in spring, as filamentous algae was the key contributing epiphytic algae in Green Island sanctuary zone (Figure 3.10). No other patterns could be distinguished. The percentage relative abundance of epiphytic algae in summer also demonstrated a high degree of overlap, making it difficult to distinguish any patterns between sanctuary and fished zones (Figure 3.10).


Winter
Site
Sanctuary
▲ Boyinaboat
▼ Green Island
■ Kingston Reefs
Fished
△ Wreck Rock
▽ Twin Rocks
FILA
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0.3
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-0.2
-0.2
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0
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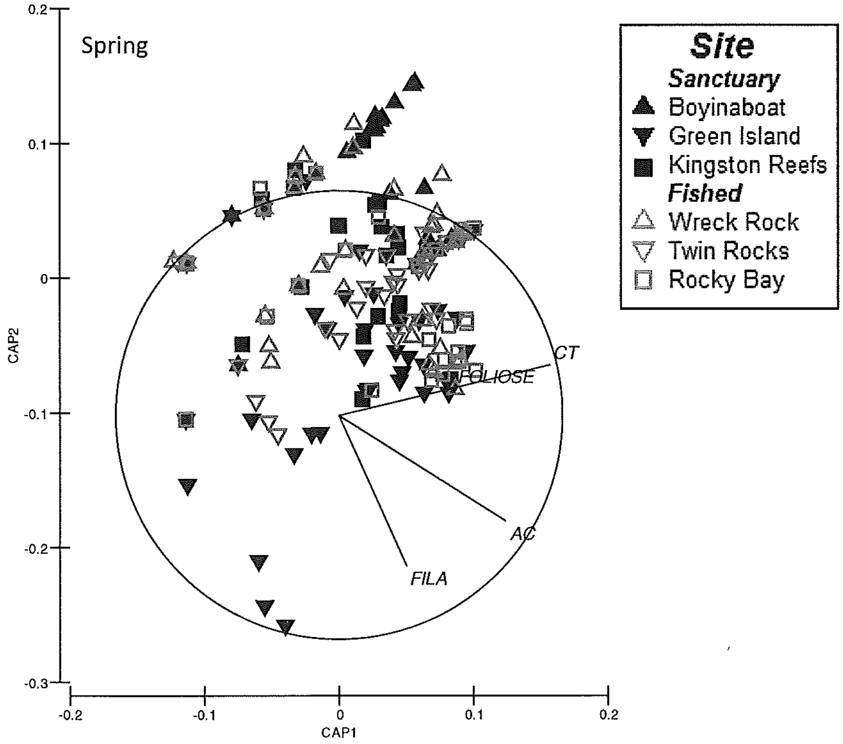
Spring
Site
Sanctuary
▲ Boyinaboat
▼ Green Island
■ Kingston Reefs
Fished
△ Wreck Rock
▽ Twin Rocks
□ Rocky Bay
CT
FOLIOSE
AC
FILA
CAP2
CAP1
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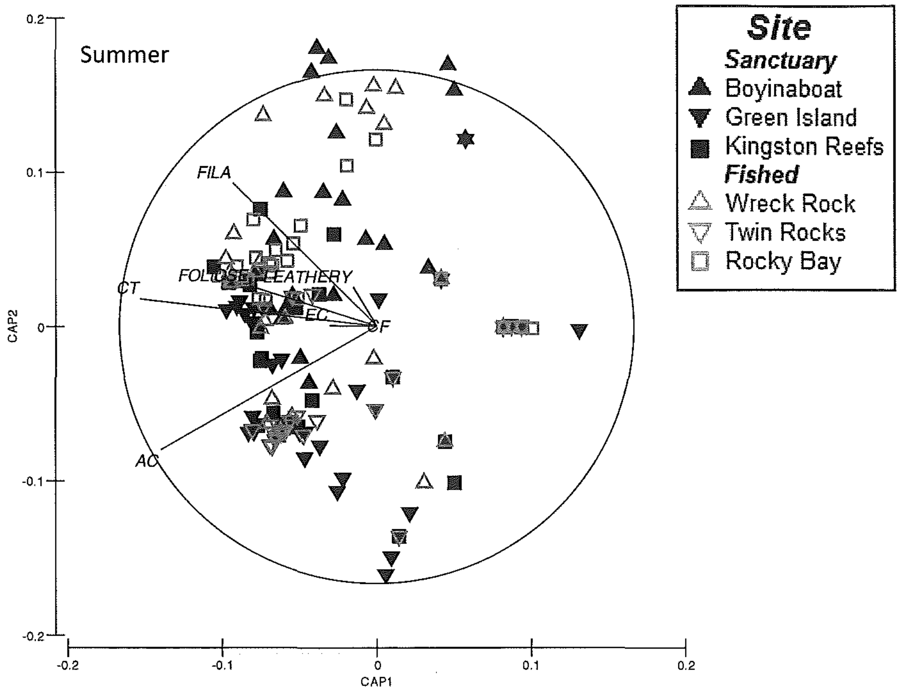


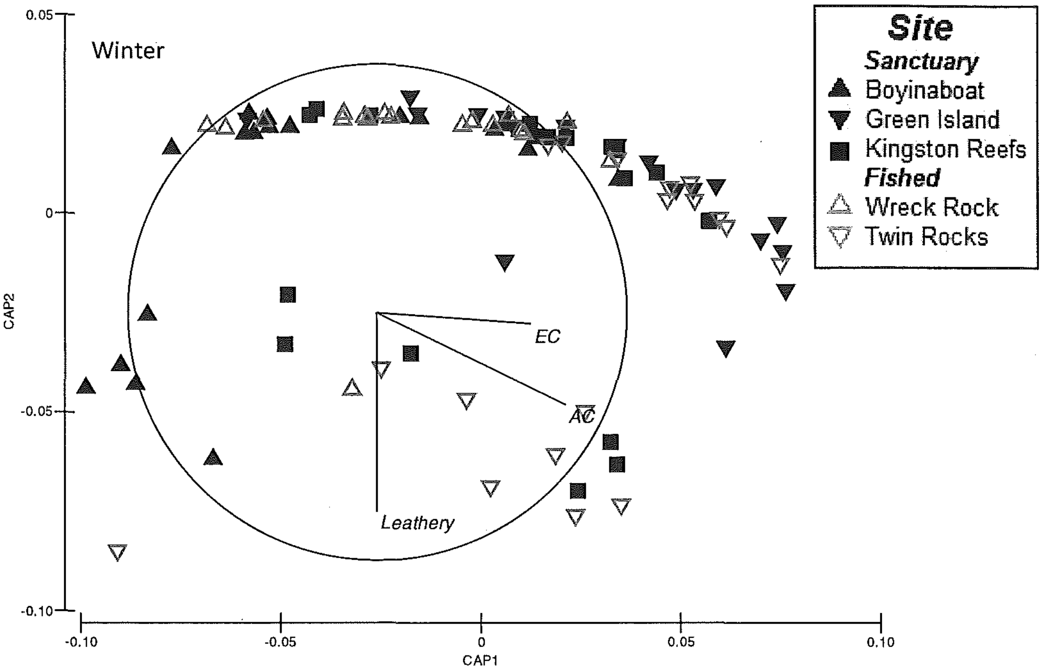
Figure 3.10. Canonical analysis of principle coordinates (CAP) ordination using Bray-Curtis similarities on the percentage relative abundance of epiphytic algae across six sites nested within two zones, and over three seasons in *Amphibolis spp.* meadows with proximity to the reef: 0SG, 15, 30, 60, 120, and 200m. A species correlation plot (Pearson correlation set at 0.5) is placed over the ordination. Data were square root ($\sqrt{x}$) transformed.

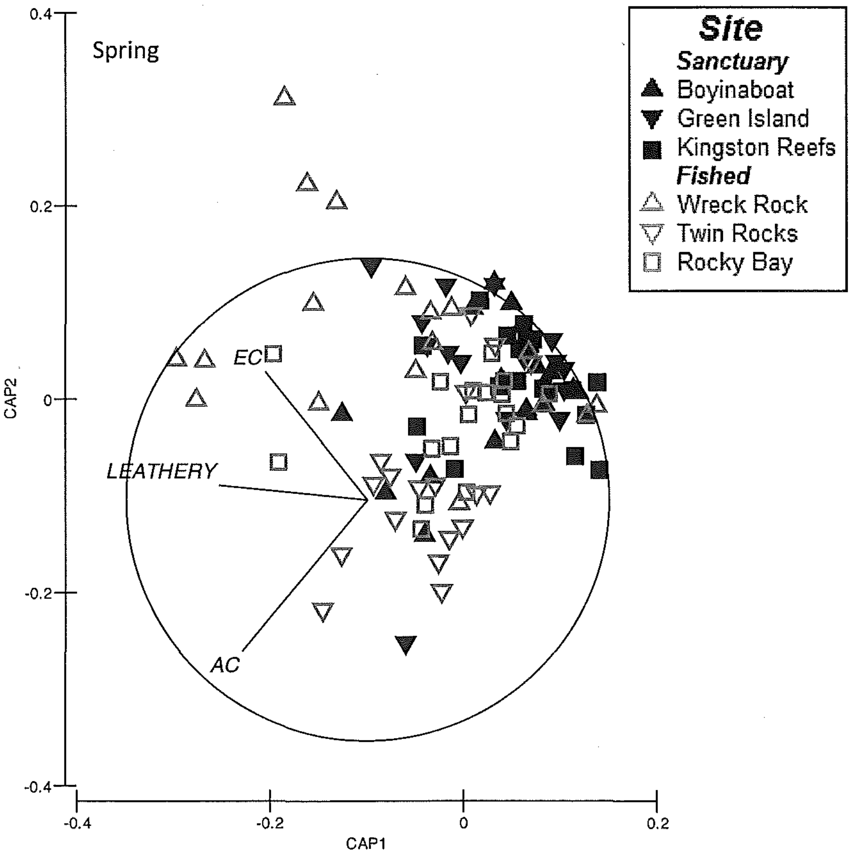
Similar to the relative abundance, there was no zone, season, or distance from reef effect, but there was an interaction between sites nested within zones and season for biomass of epiphytic algae, but in the case of biomass, there were also interactions between sites nested within zones and distance and among sites nested within zones, season and distance (MS=12942.0, $p<0.001$; Table 3.4). This indicates a high degree of variability in epiphytic biomass in seagrass meadows.

Encrusting calcareous algae was the main contributor to the overall biomass at most sites as indicated by SIMPER analyses, ranging from 34.69% at Rocky Bay fished zone to 54.67% at Boyinaboat Reef sanctuary zone. Twin Rocks fished zone was the exception, as articulated calcareous algae was the most influential algal group and accounted for the observed difference in biomass (579.35 ± 121.72 grams DW 0.25m^2; 52.52%). Articulated calcareous algae also contributed greatly to the overall biomass of Green Island and Kingston Reefs sanctuary zones. Corticated terete were also a discriminating algal functional group, contributing great biomass to all sites, ranging from 13.68% at Twin Rocks to 33.09% at Boyinaboat Reef.

The total mean algal biomass varied across seasons, as articulated calcareous algae was a key contributor to biomass in winter and summer, while corticated terete was greatest during the spring. Encrusting, articulated calcareous, and corticated terete were the dominant algal groups found at all distances away from the reef. Due to high degree of variability between sites and seasons however, no conclusions can be drawn to determine whether there is a difference in epiphytic biomass between sanctuary and fished zones.

The CAP plots displayed no similarities in epiphytic algal assemblages among factors, as the points for each sample from different zones and distances for each season were relatively indistinguishable (Figure 3.11). In winter, a separation occurred along the CAP2 axis, although no patterns could be distinguished. Articulated calcareous algae were the key contributors to Kingston Reefs and Twin Rocks, whereas encrusted calcareous algae was observed at all sites (Figure 3.11). The CAP plot for spring showed articulated calcareous algae to be the dominant algal assemblage for Twin Rocks and Green Island (Figure 3.11). Wreck Rock fished zone had a greater biomass of leathery algae, while encrusting calcareous algae were predominantly observed at Wreck Rock and Rocky Bay. The three outliers located on the top-left corner are the relatively low epiphytic biomass observed at 60m and 120m in *Amphibolis* spp. seagrass meadows at Wreck Rock (Figure 3.11). In summer, leathery algae were the key contributors of Wreck Rock, Boyinaboat Reef, and Green Island (Figure 3.11), while encrusting calcareous algae were regarded as relatively high contributors at Wreck Rock (Figure 3.11).


Winter
Site
Sanctuary
▲ Boyinaboat
▼ Green Island
■ Kingston Reefs
Fished
△ Wreck Rock
▽ Twin Rocks
EC
AC
Leathery
CAP2
CAP1
0.05
0
-0.05
-0.10
-0.10
-0.05
0
0.05
0.10


Spring
Site
Sanctuary
▲ Boyinaboat
▼ Green Island
■ Kingston Reefs
Fished
△ Wreck Rock
▽ Twin Rocks
□ Rocky Bay
EC
LEATHERY
AC
CAP2
CAP1
0.4
0.2
0
-0.2
-0.4
-0.4
-0.2
0
0.2

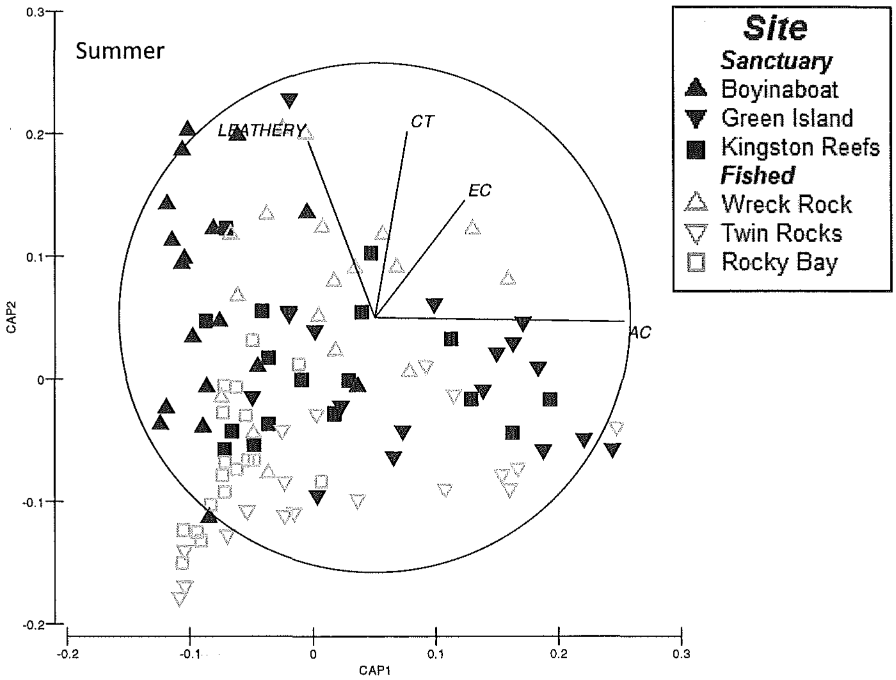


Figure 3.11. Canonical analysis of principle coordinates (CAP) ordination using Bray-Curtis similarities on the total mean biomass of epiphytic algal assemblages across six sites nested within two zones, and over three seasons in *Amphibolis spp.* meadows with proximity to the reef: 0SG, 15, 30, 60, 120, and 200m. A species correlation plot (Pearson correlation set at 0.5) is placed over the ordination. Data were square root transformed.

3.4Predation and its effect with increasing distance from reef edge

3.4.1 Predation and its effect with increasing distance from reef edge

The Kruskal-Wallis tests showed no significant site differences in gastropod mortality with increasing distances away from the reef, with the exception of Rocky Bay fished zone (N=40, $p<0.05$; Table 3.5). A greater number of gastropods were recorded alive 60m away from the reef (three *C. lehmanni* and four *Pyrene bidentata* were alive) compared to one live *P. bidentata* at the reef (Tukeys HSD test, $p=0.034$). Furthermore, gastropod mortality did not differ significantly between species across sites (Table 3.5).

Table 3.5. Results of the Kruskal-Wallis test examining the mortality of two gastropod species over four sites and at increasing distances away from the reef.

	Distance away from reef				Gastropod species			
	N	*df*	**Chi-Square**	*p*	N	*df*	**Chi-Square**	*p*
Green Island	30	2	2.231	0.3280	30	1	1.115	0.2910
Kingston Reefs	40	3	4.680	0.1970	40	1	2.080	0.1490
Rocky Bay	40	3	8.113	**0.0440***	40	1	2.444	0.1180
Twin Rocks	30	2	1.812	0.4040	30	1	0.518	0.4720

4. Discussion

The objectives of this study were to determine whether abundances, biomass, species diversity of higher-order consumers differed in sanctuary zones in response to protection from fishing, and to document the response of the epibenthic assemblage structure in relation to any changes in consumers. Such empirical data are useful in assessing the success, if any, of sanctuary zones with reduced fishing mortality, in addition to gaining a better understanding of the flow-on effect to lower trophic levels in marine food webs.

4.1. Abundance and diversity of higher-order consumers

The results from underwater visual censuses (UVCs) demonstrated that sanctuary zones had higher mean total abundance and biomass of fish compared to adjacent fished zones, although there was high variability among sites and seasons. Despite the lack of significance, there was a trend of higher means of rock lobsters in sanctuary zones than fished zones. Similar conclusions have been reached in numerous global studies examining the positive responses of fish and lobsters to MPAs (Shears & Babcock, 2002; Denny *et al.*, 2004; Langlois *et al.*, 2005; Babcock *et al.*, 2007; Pande *et al.*, 2008; Stockwell *et al.*, 2009). However, in this study, the effect of zone was dependent on site and season.

Although all sites were of similar structural complexity based on extensive pilot surveys, there were inevitable intrinsic differences among sites based on location and orientation to prevailing conditions, regardless of their level of protection from fishing. These environmental factors are likely to reflect patterns of fish assemblages and rock lobsters in temperate reef systems. Also, any effect of reserve protection will depend on a range of other factors, including the design, the size, and the length of protection of each sanctuary zone (Halpern & Warner, 2002; Graham *et al.*, 2003; Claudet *et al.*, 2008).

Larger sanctuary zones are likely to harbour more individuals because they encompass greater area in comparison to smaller sanctuary zones (Halpern, 2003). The degree in which a species is protected is dependent on their movement patterns, and the degree of compliance with MPA regulations. The sedentary nature of rock lobster may increase of legal and total mean abundance inside sanctuary zones. Using acoustic telemetry, MacArthur *et al.* (2008) reported nocturnally active *Panulirus cygnus* moving from reef crevices out to approximately 60m to forage in seagrass meadows. Other studies have recorded similar movements into surrounding habitats in *P. argus* (Bertelsen and Hornbeck, 2009), *P. elephas* (Follesa *et al.*, 2009), and *Jasus edwardsii*, with a small density of lobsters moving outside the reserve dependent on sex and size of the individual (Freeman *et al.*, 2009). Similar results have been documented for fish. While some temperate fish species display high site fidelity, such as the senator wrasse *Pictilabrus lacticlavius* (Edgar *et* al., 2004) and pink snapper *Pagrus auratus* (Willis *et al.*, 2001), many mobile fish demonstrate extensive and overlapping home ranges that venture beyond the sanctuary boundaries (Wetherbee *et al.*, 2004; Topping *et al.*, 2005; Kingsford & Carlson, 2010). This may help explain the low abundances and biomass of fish and lobsters observed at Boyinaboat Reef. Compared to both Green Island and Kingston Reefs sanctuary zones, which protect 92 and 164 hectares, respectively, Boyinaboat Reef located within the Marmion Marine Park (MMP) is a relatively small sanctuary zone protecting an area of 7.4 hectares. It would thereby offer a limited refuge to highly mobile species, crossing the reserve boundaries and potentially making them vulnerable to fishing pressures (Solandt *et al.*, 2003). Schooling fish species such as the skipjack trevally *Pseudocaranx wrightii* (Carangidae) were observed at Boyinaboat Reef and are particularly vulnerable to fishing mortality, as they are a highly mobile pelagic species displaying diel and seasonal movement between habitats (Afonso *et al.*, 2009). On the contrary, Kingston Reefs sanctuary zone offers a larger spatial protection that is closely associated with the relatively higher abundance of higher-order consumers. Adult male western blue gropers *Achoerodus gouldii* (Labridae) reaching lengths over one meter, and tarwhine *Rhabdosargus sarba* (Sparidae) were observed at this protected site, as they use protected inshore reefs and neighbouring islands as nursery habitats (Hesp & Potter, 2003; Shepherd & Brook, 2007; Coulson, 2008, p. 3). This suggests that small protected areas will only benefit individuals that restrict their movements to a localised home range during a part of their life cycle. Effective protection of mobile species such as lutjanids and carangids may be compromised in a small sanctuary zone due to their relatively large home ranges (Kramer & Chapman, 1999). It is difficult, however, to quantify their diel or seasonal movement patterns without acknowledging their individual characteristics and life histories.

The age of a sanctuary zone may also have an overriding influence on the current effect of those zones on consumer abundance and biomass, based on the recovery rate of consumers from previous fishing pressures. In my study, the sanctuary zones varied in age, as Green Island was established in 2007, Boyinaboat Reef in 1999, and Kingston Reefs was gazetted in 1988, making it the oldest of the three sanctuary zones. Some studies have documented a rapid increase in species biomass within one to three years after MPA establishment (Roberts & Hawkins, 1997; Halpern & Warner, 2002; Halpern, 2003; Denny *et al.*, 2004), while other studies have shown consumers to respond after longer time frames (Russ & Alcala, 2003; Barrett *et al.*, 2007; Pande *et al.*, 2008).

Slow-growing species with prolonged lifespan, and species with infrequent or highly variable recruitment levels, will more likely take longer to respond to reserve protection than short-lived, fast-growing species (Russ & Alcala, 1998; Jennings *et al.*, 1999; McClanahan *et al.*, 2006). For example, the results from this study showed that Kingston Reefs was the only sanctuary zone to have recorded the slow-growing and commercially important (McAuley & Simpfendorfer, 2003) western blue groper *Achoerodus gouldii.* With its no-take policy strongly enforced by the Rottnest Island Authority (RIA) since its establishment in 1988, a wide range of targeted species (both commercial and recreational) were observed at Kingston Reefs, including foxfish *Bodanius frenchii*, baldchin groper *Choerodon rubescens*, and Australian herring *Arripis georgianus*. These species have only been observed at Kingston Reefs compared to the other sanctuary zones that have been protected for shorter periods. These results however, are confounded by a combination of variables, such as the size of the sanctuary zone, and must therefore not be studied in isolation. This also highlights the importance of considering life-history traits when setting objectives for a MPAs performance, as protection may be suitable for some species and inadequate for others.

Fisheries generally exploit species high in the trophic food web, and a majority of these higher-order consumers are slow-growing carnivores. These species are therefore expected to respond slower to reserve protection compared to less targeted herbivores that respond faster to protection (Friedlander & DeMartini, 2002). Focusing solely on the response of targeted species to protection may not reflect a sanctuary zone's impact at a broader community scale, leading to possible bias and misinterpretation of data. It is, therefore, essential to observe the community as a whole as the intention of most MPAs is to protect biota at the community level rather than individuals species (Micheli *et al.*, 2004; Rodrigues *et al.*, 2004). Additional analyses were done separately on trophic groups' herbivores, omnivores, and carnivores, however, all trophic groups did not appear to respond clearly to protection in MPAs, and were therefore excluding from the Results.

The geographical location of a sanctuary zone may also influence patterns observed for higher-order consumers. Since this study was conducted over broad spatial scales, and results showed a high level of spatial variability in all parameters, population dynamics may respond to the different hydrodynamics along the west coast of WA. The study region is in a tropical-temperate transition zoning caused by the southward flowing Leeuwin Current. This may attribute to the transportation of larvae originating in warmer northern waters and dispersed to the southern region through the Leeuwin Current (Hutchin & Pearce, 1994).This may help explain the overall high fish diversity recorded at Kingston Reefs sanctuary zone and Rocky Bay fished zone. Of the 68 fish species recorded, only four were tropical, reef-associated species *Thalossoma lutescens* (Labridae), *T. lunare* (Labridae), *Scarus ghobban* (Scaridae), and *Anampses geographicus* (Labridae). These species were only recorded at Rottnest Island and in low abundances.

Much of the variability in higher-order consumers could also be explained by site-specific characteristics. Kingston Reefs is relatively exposed to southerly and easterly winds and swell, influencing the distribution of vegetation cover (Wernberg *et al.*, 2003, 2005). Low quantities of *Ecklonia radiata* (Laminariales) and other brown algae were recorded on the reef, which form an important food source for herbivorous species, including kyphosids (Clements & Choat, 1997; Morgan & Clements, 2002). The high structural complexity of the reefs that incorporates many crevices and cracks (García-Charton & Pérez-Ruzafa, 1998, 2001), offers more ecological niches for fish species, particularly labrids (Tuya *et al.*, 2009). Twin Rocks is another exposed fished site with relatively simple-structured reefs dominated by *E. radiata* canopies. Vast quantities of detached *E. radiata* were located at the base of the reefs, potentially attracting higher-order consumers through the increase of macroinvertebrates, as seen in wrack accumulation on the beach (Ince *et al.*, 2007). Both Green Island and Rocky Bay are relatively protected sites, but the reefs at Green Island are structurally complex, increasing the variety of microhabitats for inhabitants, as seen in coral reefs (Chabanet *et al.*, 1997). Greater habitat complexity is often associated with greater species richness and abundance, potentially reducing predation and competition (Côté *et al.*, 2001; Almany, 2004). Rocky Bay had *Caulerpa* spp. dominated, simple-structured reefs, and unlike all other sites examined, the water depth abruptly declined to 10-15m at the reef. This increase in depth may correlate with the higher fish abundance, diversity and biomass found at the reef, reflecting possible feeding and habitat preference (Buxton & Smale, 1989). Boyinaboat Reef is situated in close proximity to Hillarys Boat Harbour, a popular recreational destination. It is subjected to numerous and uncontrollable external stressors such as boat trafficking and fishing, as craypots were placed immediately adjacent to the sanctuary-zone boundary (K. Inostroza personal observation). Hence, the geographical location could be responsible for the overall lower high-order consumer biomass recorded at this site. Wreck Rock has a structurally complex reef offering numerous microhabitats, however it is subjected to recreational fishing pressures, having strong effects on the higher-order consumer population. This may reflect the variable abundances of rock lobsters and fish recorded at Wreck Rock. Habitat variables were not measured in this study, however, such differences in site characteristics (spatial patterns and habitat structure) may confound the effect of fishing protection.

4.2. Impact of higher-order consumers on benthic assemblage

Natural predation by consumers was expected to be substantially higher in sanctuary zones than fished zones following the cessation of fishing and would decrease with increasing distances away from the reef. This should then be reflected in the epibenthic assemblage and tethering experiment. However, as stated above, clear difference in consumer assemblages between sanctuary and fished zones were not clear, and there were also no clear differences in the epibenthic fauna and flora assemblages between zone types. Furthermore, although greater densities of fish and lobsters were found in close proximity to macroalgal-dominated reefs across all sites (Howard, 1989; Harman *et al.*, 2003; Kingsford & Carlson, 2010), no trends of decreasing epibenthic abundance and diversity were detected. The ability to detect a consumer's direct influence on prey abundance, richness, and distribution is difficult, due in part to their feeding habits. For instance, reef-associated herbivorous kyphosids feed on a wide range of macroalgae, predominantly phaeophtyes (*Ecklonia radiata*) (Clements & Choat, 1997; Morgan & Clements, 2002). Both *Kyphosus sydneyanus* and *K. cornelli* contributed the greatest biomass at the structurally complex reefs across all sites, potentially placing a vast amount of grazing pressure on macroalgae on the reef and epiphytic algae on adjacent *Amphibolis* spp. meadows. The negative influence carnivores or omnivores have on their prey will vary with species and their level of mobility (MacArthur & Hyndes, 2007). For example, lobsters are generalist consumers with small-scale foraging mobility (MacArthur *et al.*, 2008). A wide range of food sources have been detected through the analyses of lobster stomach content, ingesting large quantities of coralline algae, molluscs, and crustaceans (Edgar, 1990a,b; Jernakoff *et al.*, 1993). Equivalent studies on temperate fish species have shown that most mullids are carnivorous consuming decapods and amphipods (Platell *et al.*, 1998), while labrids are omnivorous, feeding on small epiphytic invertebrates including molluscans, crustaceans, and plant material (MacArthur & Hyndes, 2007). Labrids contributed substantially to the total abundance of fish in this study (45.5%), feeding on a range of prey species across different trophic levels, making their impact on the benthic assemblage difficult to detect. However, no distinct pattern could be detected in the epibenthic assemblage with increasing distances away from the reef. The lack of detection reflects the small-scale patchiness in benthic assemblages of temperate reef systems. This could have been overcome by increasing the number of replicate transects to incorporate this variability in the benthic assemblage. Furthermore, theory indicates that omnivores stabilise food webs (Krivan, 2000; Emmerson & Yearsley, 2004) through top-down and bottom-up processes, reducing the probability of trophic cascades (Bascompte *et al.*, 2005; Thompson *et al.*, 2007). This may help explain the lack of a significant zone effect on epibenthic faunal assemblages.

It was hypothesised that epibenthic abundances would increase with distance away from the reef since a greater concentration of consumers near the reef have limited mobility out into seagrass meadows to forage. This pattern in epibenthic assemblages did not match the results of this study, nor was it reflected in the tethering experiments with gastropods. Instead, the epibenthic abundances fluctuated over distances. These results are contrary to studies conducted by Langlois *et al* (2005) and Tuya *et al* (2010), which demonstrated higher predation of tethered prey in seagrass meadows adjacent to reef. Both studies concluded that this was likely to be due to greater abundances of predators near the reef. Predation intensity also varied considerably between molluscan prey species, *Cantharidus lepidus* and *Pyrene bidentata*, which can be strongly correlated with shell morphology (Edgar, 1990b). No differences in predation rates between gastropods *C. lehmanni* and *P. bidentata* were reported in this study, due to the experimental limitations including the lack of labelling. Green Island and Kingston Reefs in RIMR were the only sanctuary zones to demonstrate an overall lower abundance and family-level richness of epibenthic fauna. Since 60.09% of total fish species observed at Green Island, and 72.20% of fish species at Kingston Reefs were carnivores, these species may be driving the low epibenthic assemblage through foraging activities in *Amphibolis* spp. meadows. Contrary to my results, Langlois *et al.* (2006) confirmed this predatory pattern on bivalves through caging experiments, and tethering urchins (2005). A possible explanation for the lack of predatory interactions is the overlapping diets of many fish species (Edgar & Shaw, 1995).

Despite the numerous empirical studies demonstrating trophic cascades as a result of MPA protection (Estes *et al.*, 1998; Babcock *et al.*, 1999; Shears & Babcock, 2002; Clemente *et al.*, 2008; Gloeckner & Luczkovich, 2008; Moksnes *et al.*, 2008; Barrett *et al.*, 2009; Sonnenholzner *et al.*, 2009), this pattern was not obvious from my studies. An increase in higher-order consumer abundances was not reflected at lower trophic levels across seagrass meadows, demonstrating the complexity of food web structures (Polis & Strong, 1996). This may also be a result of examining the entire epibenthic assemblages rather than other studies that focus on a small subset of a community. For instance, Barrett *et al* (2009) examined the changes in macroalgal density in Tasmanian MRs in response to rock lobsters, urchins, and abalone abundances, while Tuya *et al* (2010) also demonstrated the predatory effects of fish species on a small selection of gastropod species. While these studies have shown possible trophic cascades in individuals groups, my study displayed no evidence of a trophic cascade over the entire epibenthic assemblage. Trophic cascades are assumed to be masked when entire communities are measured (Tessier & Woodruff, 2002). Therefore, to examine how the epibenthic assemblage responds to predation by higher-order consumers must take into account other environmental and biological factors.

4.3. Management implications

This study provides the type of baseline biological data on marine ecosystems that are necessary to assess whether the sanctuary zones in southwest temperate waters of WA are successfully meeting their objectives of biodiversity conservation. It also provides some insight into how ecosystems function in response to harvesting of higher-order consumers by humans in fished areas and to protection through sanctuary zones. Abundance and family-level richness for epibenthic fauna and algal epiphytes did not differ between fished and unfished zones, however, significant heterogeneity was observed across sites in this study, suggesting that each sanctuary zone functions in different ways. Therefore, in order to successfully meet the management objectives set for a sanctuary zone, further research is required on community demography and their physical and ecological processes that influence biodiversity across varying spatial scales.

To meet a MPAs objective of biodiversity conservation, managers must acknowledge the natural variations in marine ecosystems, including life history traits of individual species, daily or nocturnal or seasonal movements, recruitment patterns, and their trophic level in the food web. Taking these factors into consideration would provide realistic expectations concerning the conservation benefits of MPAs. A key determinant of differences in higher-order consumers in response to protection may be caused by the sanctuary zone design. The size and boundaries of a sanctuary zone needs to incorporate multiple habitats, whether used for shelter, nursery, and foraging that may form some part of an organism's life cycle. The size of the sanctuary zone, along with its time of protection and location, may influence the abundance and diversity of higher-order consumers, enhancing its usefulness in conservation and potentially for fisheries management. The objectives of some MPAs offer minimal benefits to fisheries management through a spillover of propagules and adults across the sanctuary boundaries following the cessation of fishing, however ,this still remains relatively unquantified and requires further research (Russ *et al.*, 2004; Goñi *et al.*, 2006; West *et al.*, 2009; Amargós *et al.*, 2010; Goñi *et al.*, 2010). With a lack of a long-term historical context of an ecosystem, further efforts should be employed in long-term and continuous monitoring over large-spatial scales. This will provide crucial temporal and spatial data to appreciate the impacts of fishing and how fishing may affect other trophic levels in a food web. This also emphasises the need for improved and enforcement of sanctuary zone status to ensure the judicious use and preservation of marine ecosystems.

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Appendix

Table 3.6. List of all fish species (in alphabetical order) recorded at all six sites within sanctuary and fished zones at the reef and at different distances in *Amphibolis spp.* meadows across three seasons.

Family	**Species**	**Fishing Importance**	**Trophic Level**
Aplodactylus	Aplodactylus westralis	R	H
Apogonidae	Apogon rueppelli	R	Z
	Apogon victoriae	B	C
Aracanidae	Anoplocapros amygdaloides	N	C
Arripidae	Arripis georgianus	C/R	C
Blennidae	Omobranchus germaini	N	O
	Paradennius intermedius	N	O
Belonidae	Hyporhamphus melanochir	C	O
Carangidae	Pseudocaranx dentex	C/R	Z/C
	Pseudocaranx wrightii	C/R	Z
	Pseudocaranx wrightii juveniles	C/R	Z
Chaetodontida	Chelmonops truncatus	N	C
Cheliodactylidae	Cheilodactylus gibbosus	N	O
	Cheilodactylusrubrolabiatus	R	C
	Dactylophora nigricans	R	O
Gerreidae	Parequula melbournensis	R	Z/D
	Gerres subfasciatus	R	C
Heterdontidae	Heterodontus portusjacksoni	R	C
Kyphosidae	Girella zebra	R	H
	Girella tephraeops	R	H
	Kyphosus sydneyanus	B	H
	Kyphosus cornelli	B	H

	Scorpis georgiana	R	Z
	Tilodon sexfasciatum	R	C
Labridae	Achoerodus gouldii	C	C
	Anampses geographicus	N	Z/C
	Austrolabrus maculatus	R	C
	Bodianus frenchii	C/R	C
	Choerodon spp.	R	C
	Choerodon rubescens	R	C
	Coris auricularis	R	C
	Coris auricularis juveniles	N	C
	Dotolabrus alleni	N	H
	Eupetrichthys angustipes	N	Z
	Halichoeres brownfieldi	N	C
	Thalassoma lutescens	R	C
	Opthalmolepis lineolata	R	C
	Pictilabrus laticlavius	R	C
	Pseudolabrus biserialis	R	C
	Notolabrus parilus	R	C
	Thalassoma lunare	R	C
Monacanthidae	Meuschenia hippocrepis	R	O
	Penicipelta vittiger	R	H
	Scobinichthys granulatus	R	O
Mullidae	Parupeneus signatus	R	Z
	Upeneichthys lineatus	R	C
	Upeneichthys vlagmingii	R	C
Odacidae	Odax acroptilus	R	O
	Odax cyanomelas	R	H
	Parodax caninis	N	H

Ostraciontidae	Aracana aurita	R	O
Pataecidae	Aetapcus maculatus	R	C
Pinguipedidae	Parapercis haackei	N	H
Pempheridae	Pempheris klunzingeri	R	C
	Pempheris multiradiata	B	C
Platycephalidae	Leviprora inops	R	C
Plesiopidae	Trachinops brauni	N	Z
	Trachinops noarlungae	N	Z
Pomacentridae	Chromis klunzingeri	B	Z
	Parma mccullochi	R	H
	Parma occidentalis	R	H
Scaridae	Scarus ghobban	R	H
Serranidae	Epinephelus armatus	C/R	Z
Sparidae	Chrysophrys auratus	C	C
	Rhabdosargus sarba	R	O
Terapontidae	Pelsartia humeralis	R	O
Tetraodontidae	Torquigener pleurogramma	N	H/D
Urolophidae	Urolophus testaceus	N	C