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Incorporating seascape ecology into the design and assessment of marine protected areas

Matthew John Rees
University of Wollongong

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**INCORPORATING SEASCAPE ECOLOGY INTO THE DESIGN
AND ASSESSMENT OF MARINE PROTECTED AREAS**

A thesis submitted in fulfilment of the requirements for the award of the degree

DOCTOR OF PHILOSOPHY

From

UNIVERSITY OF WOLLONGONG

By

Matthew John Rees BMarScAdv (Hons)

SCHOOL OF BIOLOGICAL SCIENCES

March 2017

CERTIFICATION

I, Matthew John Rees, declare that this thesis, submitted in partial fulfilment of the requirements of the award of Doctor of Philosophy, in the School of Biological Sciences, University of Wollongong, is wholly my own work unless referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution.

Matthew John Rees

24th March 2017

STATEMENT OF CANDIDATE CONTRIBUTION

The general introduction and four data chapters (i.e. Chapters 2, 3, 4 and 5) presented in this thesis have been prepared as manuscripts in collaboration with my supervisors Prof. Andy Davis and Dr Nathan Knott. Chapter 5 has been written for the following journal article.

- Rees, M.J., Knott, N.A., Fenech G.V. and Davis, A.R. (2015) Rules of attraction: enticing pelagic fish to mid-water remote underwater video systems (RUVS). *Marine Ecology Progress Series*, **529**: 213-218.

MJR, ARD and NAK developed the experimental approach; MJR collected the field data; MJR and GVF collected and processed the sound recordings; MJR performed the data analysis; MJR wrote the manuscript; MJR, ARD and NAK finalised the manuscript for submission.

As the primary supervisor, I, Professor Andy Davis, declare that the greater part of the work in each article is attributed to the candidate, Matthew John Rees. In each of the above chapters, Matthew led conceptual development, study design and was primarily responsible for the data collection, data analysis and data interpretation. The first draft of each manuscript was written by the candidate and Matthew was then responsible for responding to the editing suggestions of his co-authors. The co-authors were responsible for assisting with the study design, data collection, interpreting data and editing manuscripts where necessary. Matthew has been solely responsible for submitting the manuscript (Chapter 5) for publication in *Marine Ecology Progress Series*, and has been in charge of responding to the reviewers' comments.

Matthew John Rees

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24th March 2017

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PUBLICATIONS & PRESENTATIONS

In addition to the published manuscript listed above, during the course of my PhD I have published three journal articles and presented data from my thesis at national and international conferences. I have also co-organised and chaired a symposium on the application of remote video technology to study fish ecology. A summary of this activity is provided below.

Publications

Rees, M.J., Jordan, A., Price, O.F., Coleman, M.A. and Davis, A.R. (2014) Abiotic surrogates for temperate rocky reef biodiversity: implications for marine protected areas. *Diversity and Distributions*, **20**, 284-296.

Kelaher, B.P., Coleman, M.A., Broad, A., Rees, M.J., Jordan, A. and Davis, A.R. (2014) Changes in fish assemblages following the establishment of a network of no-take marine reserves and partially-protected areas. *PloS one*, 9(1), p.e85825.

Ferguson, A.M., Harvey, E.S., Rees, M.J. and Knott, N.A. (2015) Does the abundance of girellids and kyphosids correlate with cover of the palatable green algae, *Ulva* spp.? A test on temperate rocky intertidal reefs. *Journal of Fish Biology*, 86(1), 375-384.

Conference presentations

Rees, M.J., Davis, A.R., Jordan, A., Linklater, M. and Knott, N.A. (2016) Accounting for habitat structural complexity in the assessment of Marine Protected Area effectiveness. Australian Society of Fish Biology, 4th-7th September, Hobart, Australia.

Rees, M.J., Davis, A.R., Jordan, A., Linklater, M. and Knott, N.A. (2015) Seascape ecology and conservation: using habitat mapping to improve Marine Protected Area design. GeoHab Conference, 3rd-8th May, Salvador, Brazil.

Rees, M.J., Fenech, G.V., Knott, N.A. and Davis, A.R. (2015) Rules of attraction: enticing pelagic fish to mid-water remote underwater videos. Australian Society of Fish Biology, 12th-14th October, Sydney, Australia.

Rees, M.J., Fenech, G.V., Knott, N.A. and Davis, A.R. (2015) Rules of attraction: enticing pelagic fish to mid-water remote underwater videos. AMSA, 6th-10th July, Canberra, Australia.

Rees, M.J., Jordan, A., Price, O.F., Coleman, M.A. and Davis, A.R. (2014) Abiotic surrogates for temperate rocky reef biodiversity: implications for Marine Protected Areas. GeoHab Conference, 6th-8th May, Lorne, Australia.

Rees, M.J., Fenech, G.V., Knott, N.A. and Davis, A.R. (2013) Rules of attraction: enticing pelagic fish to mid-water remote underwater videos. EcoTas – 5th joint conference of the Ecological Society of Australia and New Zealand Ecological Society 24th-29th November, Auckland, New Zealand.

Symposia

Becker, A., and Rees, M.J. (2014) Application of video technology to the understanding of fish ecology and behaviour. Australian Society of Fish Biology conference, 12th-14th October, Sydney, Australia.

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ABSTRACT

Seascape ecology is an emerging sub-discipline of marine ecology, which examines the effect of spatial heterogeneity in marine ecosystems on ecological processes and species distributions. The opportunity to study seascape ecology in many coastal regions has been greatly assisted by advances in remote sensing technologies, which can acquire detailed habitat data over a range of spatial scales. This now allows quantification of spatial patterns in seascapes and the scientific examination of the ecological consequences of such patterns. Current research applying this approach has begun to demonstrate the importance of seascape connectivity and structural complexity in driving spatial variability of marine fish assemblages. Much of this research however, has focussed on tropical regions and as a result the effect of seascape patterning on temperate fishes remains poorly resolved. The aim of this thesis was to examine the seascape ecology of temperate fishes in two Marine Protected Areas (MPAs) in south-east Australian waters and also examine how this approach can aid in the design and assessment of MPAs. I achieved this by investigating spatial variability in temperate fish assemblages over three scales to examine the effect of i) three-dimensional reef structural complexity, ii) differences among habitat types (seagrass, rocky reef and unvegetated sediment) and iii) the seascape connectivity of habitats. I used baited remote underwater video systems (BRUVs) to survey demersal and mid-water fish assemblages in conjunction with existing habitat mapping to examine the relationship between fish and their habitats. In the Lord Howe Island Marine Park (LHIMP), reef structural complexity strongly influenced the abundance of yellowtail kingfish; *Seriola lalandi*. Despite being heavily targeted by fishers, a ‘conventional’ (GLM) assessment on the LHIMP revealed no difference in the abundance of *S. lalandi* between fished and unfished zones. However, on accounting for reef structural complexity in the assessment, I revealed substantially higher abundances of *S. lalandi* in unfished zones. This positive effect was only observed in their optimal habitat, reefs of high structural complexity. In the Jervis Bay Marine Park (JBMP), habitat type (seagrass, rocky reef and unvegetated sediment) was a strong and consistent predictor of the demersal fish assemblage but did not influence fishes in the mid-water environment. Although habitat influenced the abundance of many demersal fishes, some taxa from the

demersal assemblage displayed no affinity to underlying habitat type. Seascape composition and connectivity also appeared to strongly influence temperate fish assemblages. The abundance and diversity of temperate fishes was correlated with the area of rocky reef and seagrass within the surrounding seascape. The apparent importance of seascape connectivity was also noted in the LHIMP, where adult black rockcod (*Epinephelus daemeli*) were only recorded in areas adjacent to their nursery grounds. Finally, I sought to compare the effectiveness of attractants other than bait (sight and sound stimuli) to entice pelagic fishes to video systems positioned in the mid-water environment. I found the combination of sight, sound and scent attractants on mid-water remote underwater videos (RUVs) recorded a substantially higher abundance and shorter time of first arrival of pelagic fishes compared to RUVs with one or no attractant. I suggest future studies using this sampling method to survey pelagic fishes employ multiple attractants. My findings demonstrate that temperate fishes are influenced by patterns in seascapes and habitats at a number of spatial scales. They also have important implications for spatial conservation strategies such as MPAs, particularly in terms of their design, assessment and adaptive management. Representation of seascape variability over a number of spatial scales in MPA planning is likely to better represent temperate fish assemblages. Furthermore, I demonstrate that habitat classes and measures of structural complexity are appropriate surrogates for certain fishes, which is useful in MPA planning. Finally, I demonstrate that accounting for seascape variability in MPA evaluation is likely to provide a better assessment and clearer understanding of ecological change associated with this management action. In conclusion, integrating seascape ecology into MPA science will increase the usefulness of this conservation strategy to combat growing declines in global marine biodiversity.

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Chapter 1: GENERAL INTRODUCTION

Seascape ecology is an emerging sub-discipline of marine ecology, which applies the concepts of terrestrial landscape ecology to the marine environment. Progress in the application of seascape ecology has been hindered by the difficulties in acquiring habitat and species level data over a range of spatial scales (10's of square metres to 1000's of square metres). Recent improvements in remote sensing and sampling technologies now provide marine scientists the opportunity to explore seascape questions at multiple spatio-temporal scales. The current seascape ecology literature, although somewhat limited, highlights the importance of seascape patterns on ecological processes and species in marine systems. In this chapter, I review the current status of seascape ecology and highlight the conservation benefits of incorporating seascape ecology into the design and assessment of Marine Protected Areas (MPAs).

1.1 From landscapes to seascapes

A central aim in fundamental ecology and applied conservation research is to understand the relationship between species and their environment (Andrewartha and Birch 1954; Bell et al., 1991). Landscape ecology, first coined mid-20th century and conceptually developed during the 1980's, has revolutionised the way in which ecologists study species-environment relationships and conserve biodiversity (Urban 1987; Wiens 1993; Wiens 1995; Turner 2005a, b). Combining concepts from functional ecology with the spatial approach of geography, landscape ecology is the study of spatial heterogeneity and the effect of this heterogeneity on ecological

processes and species distributions (Fortin and Agrawal 2005). Although the definition of a landscape can vary, from an ecological perspective, landscapes are spatially heterogeneous areas which can be defined at a range of spatial scales depending on the process or question of interest (Forman and Godron 1981). Driving heterogeneity in the landscape are spatial components, or habitat patches, which are embedded within a relatively homogeneous matrix. The number and configuration of habitat patches influence landscape composition and spatial patterning (Forman and Godron 1981) (see Box 1.1). Landscape ecologists have developed a suite of indices to describe the spatial heterogeneity created by habitat patches over landscape scales (Forman and Godron 1981; O'Neill 1988; Riitters et al., 1995) (Table 1.1).

Importantly, such indices have been shown to display strong and informative links between landscape structure and ecological phenomena (see Turner 2005b for a detailed review). Consequently, landscape ecology has been incorporated into mainstream ecology, establishing itself as a popular interdisciplinary field, which has also significantly contributed to the design of terrestrial spatial conservation strategies worldwide (Pickett and Thompson 1978; Turner 2005b; Liu and Taylor 2002; Margules and Sarkar 2007).

Like terrestrial environments, marine systems display high degrees of spatial heterogeneity over similar spatial scales. Nearshore environments are complex mosaics governed by a range of natural processes including human activities, which operate through space and time (Pittman et al., 2011). Patterning of nearshore environments observed in the past include the zonation of mangrove forests along estuarine borders, dynamic patches influenced by disturbance within intertidal rocky shores (Levin and Paine 1974), the intricate mosaics of seagrass beds (Robbins and Bell 1994), the connectivity across mosaics comprised of nearshore patches (Ogden

and Zieman 1977; Parrish 1989) and the structural complexity of coral reefs (Sale and Douglas 1984). Similarly, the pelagic marine environment can be described as a dynamic, three-dimensional mosaic, which is composed of different water masses influenced by seafloor topography and oceanographic processes (Game et al., 2009; Hidalgo et al., 2016; Sayre et al., 2017).

The analogous spatial heterogeneity in marine systems can be conceptualized and quantified using a terrestrial landscape ecology approach (Wedding et al., 2011) (Box 1.1; Table 1.1). Despite the applicability of landscape ecology in marine systems, and the success of landscape ecology in terrestrial settings, the effect of broad-scale spatial heterogeneity on marine species and ecological processes remains poorly resolved (Pittman et al., 2011). Undoubtedly this lack of knowledge of the effect of landscape scale patterns in marine systems is an artefact of the inherent difficulties in acquiring habitat information over relevant spatial scales.

Glossary

Landscape: terrestrial spatially heterogeneous area composed of a cluster of interacting ecosystems usually defined at scales of 1-10's of km.

Seascape: analogous to landscape but applied to the marine environment.

Patch: a relatively homogeneous area with a definite shape, configuration and discrete boundary that differs from its surroundings. Sometimes referred to as a habitat patch.

Matrix: the most extensive and connected landscape or seascape element present. Also, a landscape or seascape element that surrounds a patch.

Mosaic: describes the pattern of patches and matrix that form a landscape or seascape.

Seascape patterns: the pattern of the seascape produced by patches and the matrix

Structural complexity: three-dimensional structural variability of the patch or habitat.

Grain: the resolution at which the landscape or seascape is viewed. A pixel in a digital image is analogous to a grain in a landscape.

Extent: the physical area or time scale that the landscape/seascape is viewed.

Spatial scaling: changing either grain or extent or both.

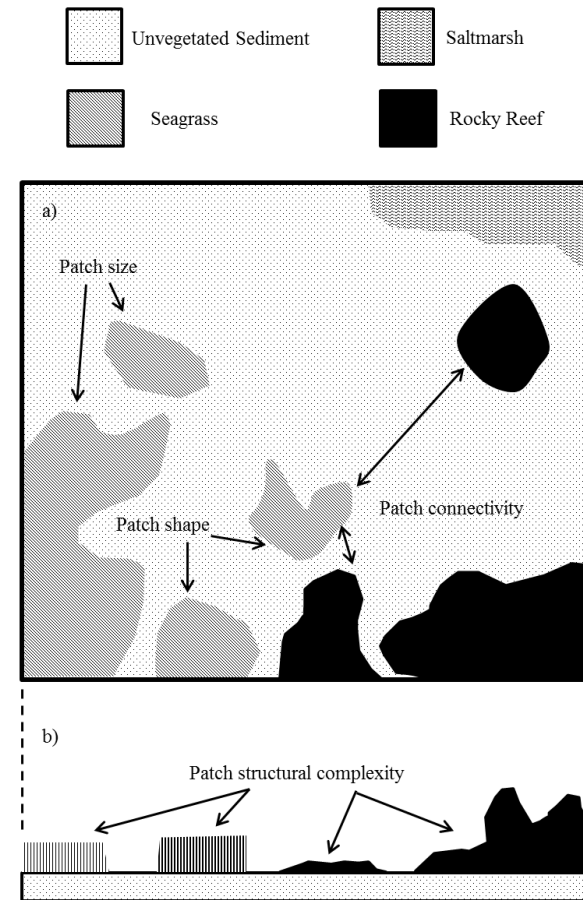
Pelagic fish: fish that live in the water column of the coastal and open ocean waters.

Demersal fish: fish that live near the benthos of coastal and open ocean waters.

Box 1.1 What is a seascape or landscape?

A seascape or landscape is an area that displays spatial heterogeneity which can be defined over a range of spatio-temporal scales based on the question or process of interest. Spatial heterogeneity is created by spatial components or ‘habitat patches’, which are usually embedded within a relatively homogeneous matrix. Patch size, configuration and connectivity drive the spatial patterning of seascapes and landscapes, while the variety of different types of patches influences seascape/landscape composition. Furthermore, patches may display within patch variability such as structural complexity. These attributes are scale dependent.

Figure 1.1a portrays a hypothetical seascape with patches of seagrass, rocky reef and saltmarsh embedded within an unvegetated sediment matrix. Patches vary in their size and shape. Seascape composition and configuration varies with patch diversity, spatial arrangement and connectivity. In addition, patches of seagrass, saltmarsh and rocky reef vary in three-dimensional structural complexity (Figure 1.1b). The practice of seascape/landscape ecology involves quantifying the configuration and composition of the seascape/landscape and understanding how these spatial patterns influence species and ecological processes. Landscape ecologists have developed a number of indices to quantify landscape structure (Table 1.1).



Recently, however, advances in remote sensing technologies are providing marine scientists with increasingly detailed information of marine habitats (Brown et al., 2011; Ierodiaconou et al., 2011). Consequently, the sub-discipline of “seascape ecology” has emerged, employing the concepts and tools from terrestrial landscape ecology to understand the effect of spatial patterns in marine systems (Hinchey et al., 2008; Pittman et al., 2011). However, the application of seascape ecology in marine spatial conservation strategies such as marine protected areas remains in its infancy, although the theory, tools and technology are now readily available (but see McNeill 1994, Engelhard et al., 2016 and Olds et al., 2016).

1.2 Practicing seascape ecology

Detailed habitat imagery of marine regions now provides marine scientists with the capability of producing detailed marine benthic maps, similar to terrestrial vegetation maps, which graphically display spatial heterogeneity in marine systems (Box 1.2). Understanding the effect of spatial heterogeneity on marine species and the processes that underpin pattern first requires quantification of the spatial structures within seascapes (Gustafson 1998). As spatial structure is relatively analogous between terrestrial and marine environments, the spatial tools and metrics developed by landscape ecologists can be used to determine the geometric properties of marine seascapes (Wedding et al., 2011). Landscape ecologists have developed a range of metrics that are used to examine the relationship between spatial heterogeneity, and species distributions and ecological processes (O’Neill 1988). These metrics can be broadly classified into three categories to determine; i) landscape composition, the abundance and diversity of habitat patches within the region of interest, ii) configuration, the spatial arrangement of the patches and

mosaics, and iii) structural complexity, e.g. the three-dimensional variability within habitat patches (Turner et al., 2001; Wedding et al., 2011) (Table 1.1). The quantification of these metrics can be derived from habitat maps using computer software programs including Geographic Information Systems (GIS) and the popular FRAGSTATS program¹.

Often landscape ecologists investigate relationships between spatial heterogeneity and species/ecological processes with an exploratory approach, examining a number of spatial metrics at a range of spatial scales (grains and extents). This approach is undertaken because landscape questions need to be scaled appropriately to the organism or process of interest (Wiens 1989; Wiens and Milne 1989; Turner et al., 1989), which is usually unknown *a priori*. For example, a territorial species that requires certain habitat qualities will respond to the same habitat at a different spatial scale compared to a transient habitat generalist. In the marine environment, knowledge of the appropriate spatial scaling is further confused by life histories of marine organisms, which operate over different spatial scales (Pittman and McAlpine 2003). The majority of marine invertebrates and fishes display a pelagic larval phase and undergo ontogenetic shifts in habitat use throughout their life history². Therefore, similar to terrestrial landscape ecology, an exploratory multi-scale and multi-metric approach is required to understand the effect of seascape patterning on marine species and processes (Pittman and McAlpine 2003).

¹ FRAGSTATS website (<http://www.umass.edu/landeco/research/fragstats/fragstats.html>).

² For example Snapper, *Pagrus auratus*, displays a pelagic larval duration of 3-5 weeks, followed by recruitment into nursery habitat followed by offshore migration as adults.

Table 1.1 A summary of commonly used metrics by landscape ecologists to quantify 1) landscape composition, 2) spatial configuration using two-dimensional vegetation or benthic maps, and 3) structural complexity from three-dimensional digital elevation models (DEM). Modified after Wedding et al., (2011).

Metric	Level	Type	Dimension	Description
(1) Landscape composition (abundance and diversity of habitat patches)				
Proportion	Mosaic	Structural	Two	Proportion of landscape occupied by cover type
Richness	Mosaic	Structural	Two	Number of patch types composing the mosaic
Evenness	Mosaic	Structural	Two	Relative abundance of different patch types
Diversity	Mosaic	Structural	Two	Composite measure of richness and evenness
(2) Spatial configuration (spatial arrangement and orientation of patches/mosaic)				
Contagion	Patch-based	Structural	Two	Distinguishes between overall clumped or dissected mosaic patterns
Patch area	Patch-based	Structural	Two	Total area of patch
Patch perimeter	Patch-based	Structural	Two	Perimeter of a patch
Perimeter:area ratio	Patch-based	Structural	Two	Index of patch shape complexity
Connectivity	Patch-based	Functional	Two	Average distance between patches
Proximity index	Patch-based	Structural	Two	Degree to which patches in landscape are isolated from other patches
Area-weighted average patch size	Patch-based	Structural	Two	Frequency distribution of patch sizes
Core area	Patch-based	Structural	Two	Area unaffected by the edge of the patch
(3) Structural complexity (three-dimensional across a gradient or continuum)				
Rugosity	Gradient/continuum	Structural	Three	Surface area over the planar area ratio
Slope	Gradient/continuum	Structural	Three	Maximum rate of change in bathymetry over a given scale
Mean depth	Gradient/continuum	Structural	Three	Bathymetric position relative to sea level
Variance in depth	Gradient/continuum	Structural	Three	Range in bathymetry within a given scale
Standard deviation of depth	Gradient/continuum	Structural	Three	Standard deviation in bathymetry at a given scale
Slope of slope	Gradient/continuum	Structural	Three	Maximum rate of maximum slope change at a given scale
Plan curvature	Gradient/continuum	Structural	Three	Rate of change in curvature across the surface highlighting ridges, crests and valleys

1.3 Statistical issues

Employing an explanatory approach to examine relationships between species and landscape patterning with no prior knowledge of the appropriate spatial scaling for the species or process of interest often results in statistical issues. Often, spatial scaling is underestimated, resulting in non-independence or positive spatial autocorrelation between survey points. Not accounting for spatial autocorrelation in landscape scale studies can seriously violate model assumptions and therefore compromise overall conclusions (Legendre and Fortin 1989; Legendre and Legendre 1998). Landscape ecologists and statisticians have developed a number of techniques and analyses to overcome the issues of spatially autocorrelated datasets. These include incorporating lag response variables or random effects into spatial models (Legendre and Legendre 1998), or using analyses, like machine learning techniques (e.g. boosted regression trees) that do not assume independence (Elith et al., 2006; Elith et al., 2008). Sophisticated modelling techniques such as these are necessary to deal with the issues of spatial data in studies of seascape ecology (Mellin et al., 2010; Young et al., 2015).

1.4 Seascape patterns in marine fishes

The effect of seascape patterning on marine fishes has been investigated at a number of spatial scales. Much of the previous research examining the relationship between marine fishes and seascape patterning can be broadly categorised into one of three hierarchical spatial scales. These include; i) a relatively fine-scale approach examining within patch variability such as structural complexity (i.e. rugosity); ii) a focal patch approach, examining metrics such as patch shape, size, edge effects and fragmentation; and iii) a broad-scale approach examining more than one patch type

and seascape attributes such as connectivity and composition (Box 1.1). The majority of previous research employing a seascape approach to understand spatial variability in fish assemblages has been conducted at relatively fine-scales, examining the effect of patch structural complexity, shape, size, edge effects and fragmentation (Boström et al., 2011). In contrast, fewer studies have examined the effect of seascape patterning of two or more patches on fish assemblages. The bias towards fine-scale studies is most likely a result of the inherent logistical difficulties in quantifying seascape metrics and surveying fishes over larger geographic areas. Despite this bias, previous research has demonstrated pronounced effects of seascape attributes on fish assemblages.

The influence of patch structural complexity on fish abundance and diversity over a range of different habitat types has been well documented (Box 1.1. and 1.2). Within seagrass patches, structural metrics such as shoot density, complexity, canopy height and cover has been demonstrated to drive spatial patterns in seagrass fish assemblages (Horinouchi 2007; Jelbart et al., 2007a, b). Similarly, in mangrove forests the structural complexity created by pneumatophore density influences species composition of fishes at fine spatial scales, which then may influence broad-scale patterns in certain species of fishes during adult life stages (de la Moriniere et al., 2002; Nagelkerken et al., 2008). The importance of structural complexity on reef fishes has been well documented in coral reef systems. Coral reefs that display high structural complexity have been shown to harbour a greater diversity and biomass of fish (Friedlander and Parrish 1998; Almany 2004; Gratwicke and Speight 2005). The positive response of fish assemblages to structural complexity has been attributed to structurally complex habitats providing a greater number of niches, resources and productivity compared to habitats of low structural complexity (Bell et al., 1991;

Friedlander and Parrish 1998). Furthermore, many studies have shown strong relationships between fish assemblages and reef structural complexity measures derived from remote sensing technologies. In Florida (USA), SW Puerto Rico, US Virgin Islands, Caribbean, Hawaii and the Chagos Archipelago, remotely-sensed structural complexity measures of coral reef habitat (e.g. rugosity) significantly correlated with fish species richness and abundance (Kuffner et al., 2007; Pittman et al., 2007; Purkis et al., 2008; Wedding and Friedlander 2008; Pittman et al., 2009). Meanwhile, similar patterns have been observed between remotely-sensed rocky reef structural complexity and fish assemblages in temperate regions (Monk et al., 2010; Monk et al., 2011).

The majority of research applying a seascape ecology approach to date has focussed on individual patches of a single patch type (i.e. seagrass), and examined how patch configuration (size, shape, edge effects and fragmentation) influences fish assemblages (Boström et al., 2011). For example, McNeill and Fairweather (1993) compared fish species richness on beds of seagrass of varying size. They found diversity was greater on several small patches compared to one large patch of the same area. In contrast, a number of studies have revealed positive effects of coral patch reef size on the abundance and diversity of fishes (Acosta and Robertson 2002; Chittaro 2004; Grober-Dunsmore et al., 2007). In temperate systems, the relationship between the size and shape of rocky reef habitat on fish assemblages remains relatively unclear. This is probably due to temperate reefs displaying a broader scale of continuity rather than a patch morphology. In South Eastern Australia, however, Rees et al., (2014) found a greater abundance and diversity of reef fishes on rocky reef habitat further from the unvegetated sediment boundary, indicating a positive relationship with distance from edge and reef size. More information on the

importance of patch size, edge effects and fragmentation on nearshore habitats on fish assemblages can be found in the extensive review by Boström et al., (2011).

In contrast to research focussed on one habitat type, fewer studies have examined the effect of seascape patterning involving two or more patch types on the spatial variability in fish assemblages. Those that have, often compared fish assemblages among discrete habitat patches such as seagrass, rocky reef and unvegetated sediment (Jenkins and Wheatley 1998; Guidetti 2000; La Mesa et al., 2011). Recently, however, there has been an increase in the number of studies examining the effect of seascape composition and patch connectivity on marine fishes. For example, in the US Virgin Islands, researchers revealed that coral reef fish density and diversity was positively correlated with amount of seagrass surrounding the coral reef sites. As much as 48-58% of the variation in mean and cumulative species richness was explained by areal coverage of seagrass, while 32% was explained for total abundance. When fish densities were explored at finer taxonomic resolutions relationships improved. Areal coverage of seagrass surrounding coral reef sites explained 57% and 50% of the variation in the commercially exploited Haemulid and Lutjanid families, respectively (Grober-Dunsmore et al., 2007). Other researchers in SW Puerto Rico (Pittman et al., 2007), Queensland, Australia (Pittman et al., 2004) and the US Virgin Islands (Kendall et al., 2003) have revealed supportive patterns at similar spatial scales, highlighting the importance of seagrass cover and proximity to coral reef fishes. In Moreton Bay, Australia, the area and position of both seagrass and mangroves were found to have a strong effect on the overall coral reef fish assemblage. Coral reef fish assemblages were primarily distinguished by isolation from mangrove habitat and secondarily by proximity to seagrass. Interestingly, these two indices displayed different effects on

the fish assemblage, with 25% of all species being influenced by mangroves and a different 25% being affected by seagrass (Olds et al., 2012b). In Belize, the effect of mangrove proximity on coral reef fish assemblages were examined by comparing atolls with scarce mangrove coastlines (mean perimeter = 3.9km) to atolls whose coastlines were dominated by mangroves (mean perimeter = 185km). Fish assemblages showed marked differences between mangrove-scarce and mangrove-rich reefs. Furthermore, the biomass of several commercially important fish species was more than double on coral reefs in close proximity to mangrove habitat (Mumby et al., 2004). Despite the growing evidence highlighting the importance of patch connectivity and context in structuring fish assemblages, no studies to my knowledge have employed this approach in temperate or polar ecosystems. This is concerning for temperate regions considering their high levels of biodiversity, including many endemic species, vulnerability to anthropogenic climate change and valuable ecosystem services (Bennett et al., 2016).

1.5 Seascape ecology and pelagic fishes

To date, the majority of studies employing a seascape ecology approach have focussed on demersal fishes, with little research examining the effect of spatial heterogeneity on pelagic fishes at seascape scales (1 – 10's km). Instead, most research on the spatial ecology of pelagic fishes has been undertaken at broad spatial scales (100 – 1000's km). The lack of research on pelagic fishes at seascape scales is likely a result of the assumption that pelagic fishes are highly migratory, have large home ranges with low residency, display little affinity to underlying habitat and comprise of one homogeneous stock across their geographic range (Sund et al., 1981). However, research examining the removal of fishing following MPA

declaration in Hawaii and the Philippines contradicts these assumptions, by finding increased abundance and biomass of carangids and other large pelagic fish inside the MPAs (Russ and Alcala 1998; Williams et al., 2006). Furthermore, acoustic telemetry research has demonstrated that Yellowtail Kingfish (*Seriola lalandi*), a species assumed to be highly migratory display relatively low levels of movement (<17 km) from their tagging site (Brodie 2016). Additionally, using a fine-scale scientific trolling method (km's), the relative abundance of three pelagic fish species was significantly related to the topographic complexity of the seafloor. From a total of 890 hours of trolling, eight distinct topographic features received 13.7% of the total fishing effort yet produced 43% of captures. Catch rates for Yellowtail Kingfish (*Seriola lalandi*), Australian Bonito (*Sarda australis*) and Skipjack Tuna (*Katsuwonus pelamis*) were 26, 6.59 and 2.47 times higher within 1km of topographic features compared to away from topographic features (Hobday and Campbell 2009). Employing mid-water baited remote underwater videos, a novel fishery independent sampling technique, ocean current speed at seascape scales (10's km's) was shown to strongly influence the pelagic fish assemblage within the Lord Howe Island Marine Park, Australia (Heagney et al., 2007). Similarly, using mid-water BRUVs, the distribution of two small pelagic fishes (*Trachurus novaezealandiae* and *Scomber australasicus*) in Jervis Bay Marine Park, Australia, were observed to be highly structured over fine spatial scales (100's of metres to kilometres). Yellowtail Scad, *T. novaezealandiae* showed a habitat preference of shallow areas close to reef with low current speeds, while *S. australasicus* a preference of deeper habitat further from reef with high current speeds (Heagney 2009). In both studies employing mid-water BRUVS, statistical issues were apparent due to the patchy distribution of pelagic fishes. More consistent estimates using mid-

water BRUVs could potentially be achieved using alternate attractants other than, or in combination with, bait. Future research is required to determine the optimal attractant for mid-water remote underwater camera surveys on pelagic fishes. Despite the difficulties in surveying pelagic fishes over seascape scales, the recent research highlights the potential to apply a seascape ecology approach to examine the spatial ecology of these fish and their linkages to benthic habitats.

1.6 Temporal scaling in seascape studies

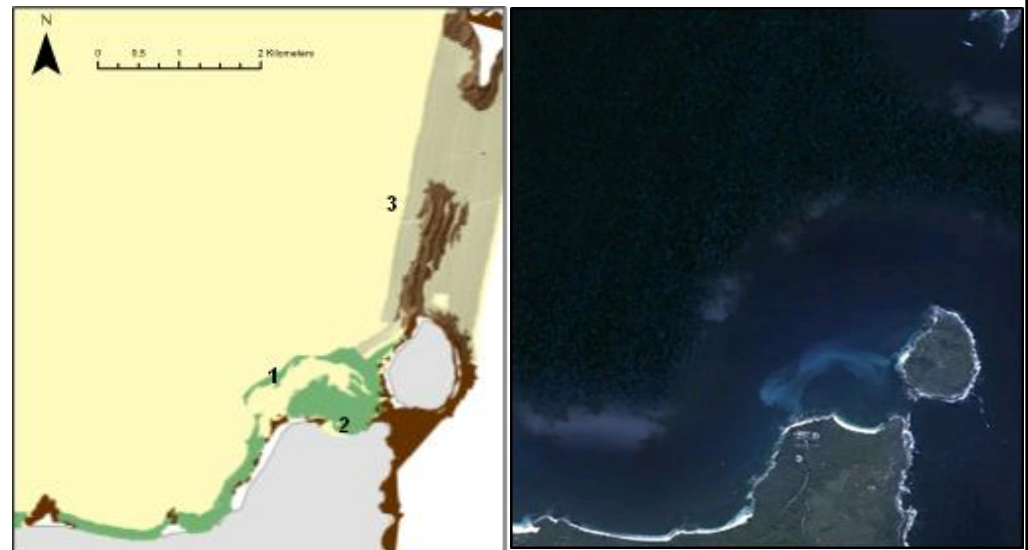
The temporal scaling of studies employing a seascape ecology approach usually provides a ‘snapshot’ of the relationship between spatial patterns and response measures in time. For generalities to emerge in the seascape literature this may prove problematic, as benthic habitats and their spatial patterns are dynamic, being strongly influenced by disturbance events (Levin and Paine 1974). Furthermore, fishes display high inter-annual fluctuations in recruitment, seasonal changes and daily variability in species abundance. Therefore, repeated sampling over a range of temporal scales is needed to provide a better understanding of seascape-fish relationships. The necessity for temporal replication is highlighted by strong interactions between response measures, time and landscape metrics for studies in seagrass habitat (Jelbart et al., 2006; Johnson and Heck Jr 2006).

1.7 Incorporating seascape ecology into Marine Protected Area design

Currently, MPA design in Australia and other parts of the world is based upon CAR principles (Roberts 2003; Jordan et al., 2005). The CAR principles ensure that newly established MPAs display i) comprehensiveness; including the full range of ecosystems across the bioregion, ii) adequacy; the size of reservation to ensure the

Box 1.2 Example of a coastal seascape: Jarvis Bay Marine Park, NSW, Australia

Jarvis Bay Marine Park is located on the south coast on New South Wales, Australia (35.09 °S, 150.80 °E) and provides an example of a coastal seascape. Subtidal patches of rocky reef (brown) and seagrass (green) within the bay create mosaics of patches embedded within a relatively homogenous matrix (unvegetated sediment). It is clear that seagrass patches display variability in patch attributes over a range of spatial scales. For example patch 1 is smaller and a corridor shape compared to patch 2, which is large and circular. Landscape metrics such as patch size and patch perimeter:area ratio will be different between the two patches which may influence associated fauna. Reef patches also vary in connectivity to seagrass. For example, reef near point 2 is connected to seagrass while reef at point 3 is isolated from seagrass habitat. Therefore landscape metrics such as connectivity and proximity indices will differ between the two reef patches. In addition, at a spatial scale of 500 metres point 2 contains three patch types; seagrass, reef and unvegetated sediment. In contrast, point 3 contains two patches; reef and unconsolidated sediment. Therefore landscape composite indices such as diversity, evenness, proportion and richness will vary between the two points. Increasing the spatial grain will increase the complexity of the benthic habitat map. For example the reef habitat may be further characterized by the benthic biota present. Finer scale reef habitat classes may include kelp forests, urchin grazed barrens and sponge gardens, etc. Finally, the three-dimensional structural complexity of the habitat patch may be quantified for certain habitat types. For example, point 3 highlights a reef patch characterized by high structural complexity derived from side-scan sonar imagery. In addition, the structural complexity of seagrass may be quantified examining shoot density or canopy height.



ecological viability and integrity of populations, species and communities, and iii) representativeness; areas included reflect the biological diversity of the marine ecosystem (ANZECC TFMPA 1998a, b). Due to the significant cost and time involved in sampling marine communities over the required spatial scales for MPAs, mapped habitat classes (e.g. rocky reef, seagrass, mangroves, unconsolidated sediments, etc.) have been increasingly used as surrogates to indirectly determine marine biodiversity and guide MPA boundaries (Ward et al., 1999; Jordan et al., 2005). Currently, in many parts of the world, MPAs are established by adequately representing each habitat class within the bioregion of interest. This design criterion has no consideration of the effect of broad-scale seascape patterning of these habitats on marine biodiversity. For example, when seagrass habitat is allocated to MPA protection, there is no consideration of patch shape, size, or whether the seagrass patches are connected or isolated from other habitats. Similarly, there is no consideration of within patch or habitat variability such as structural complexity (Rees et al., 2014), which is usually in response to a lack of *a priori* data.

As previous literature has demonstrated strong links between fishes and seascape composition and connectivity, incorporating this spatial heterogeneity into MPAs is likely to better represent and therefore protect local fish populations. Two recent studies have highlighted the synergistic effect of reserve protection and seascape patterning on marine biodiversity and ecological processes. In Moreton Bay MPA, Queensland, the effect of connectivity between coral reefs and mangrove habitat on fish assemblages was assessed inside and outside a marine reserve. Connectivity was shown to greatly improve reserve performance, with greater abundances of harvested fishes, piscivores and herbivores in reserves displaying

connectivity compared to similar non-reserve locations. In contrast, reserves that displayed no habitat connectivity showed no difference in fish densities when compared to similar non-reserve locations (Olds et al., 2012a). In a separate study completed in the same location, connectivity between coral reefs and mangroves has also enhanced herbivorous fish biomass and diversity in reserves compared to fished areas. Using grazing experiments, Olds et al. (2012c) found elevated herbivore biomass in reserves, resulting in greater grazing intensity which drove a trophic cascade reducing algal cover and enhancing coral recruitment and reef resilience inside reserved compared to unprotected areas. These two studies firstly emphasize the importance of seascape structure for marine ecological processes and biodiversity, and secondly, indicate that seascape patterning should be acknowledged in the MPA design process. Further research is required to examine the benefits of incorporating seascape patterning in MPA design, especially in temperate regions.

1.8 Incorporating seascape ecology into Marine Protected Area assessment

Accurate assessments of MPA effectiveness require robust designs capable of separating reserve effects from underlying spatial and temporal variability. A popular approach to assess MPAs while accounting for natural variability has been Before After Control Impact (BACI) designs. This method, however, requires biological data prior to the establishment of the MPA, which is rarely available. Instead, most assessments on MPA effectiveness use a Control Impact (CI) approach comparing reserves to adjacent unprotected areas at one point in time (Sciberras et al., 2013; Miller and Russ 2014). Differences between zones are then often attributed to a reserve effect. The CI method however, may provide misleading results, as differences may be due to underlying seascape variability, rather than MPA

protection. Few studies have taken into account the potential confounding effect of seascape composition and habitat structural complexity in MPA assessments, although these seascape features have been shown to influence marine biota. For example, Huntington et al., (2010), assessed the Glover's Reef Atoll Marine Reserve offshore of Belize both excluding and including natural seascape variability derived from high resolution IKONOS imagery. They found no reserve effects on the abundance and diversity of coral and fish assemblages when seascape variation was omitted from the assessment. However, when analyses were performed on reefs displaying similar seascape attributes, significant reserve effects became apparent. The lack of MPA assessments accounting for seascape variability is probably due to the inherent costs and difficulties in acquiring habitat data over the relevant spatial scales. Another potential reason is the insufficient awareness of the ecological importance of seascape patterning for MPA performance. Improvements in remote sensing technologies and increased affordability are likely to increase the opportunity of accounting for this variability in MPA assessments. Incorporating seascape variability, such as patch connectivity and structural complexity, will lead to more accurate assessments and better conservation outcomes.

1.9 Important knowledge gaps

The concepts of landscape ecology have not been extensively applied to marine systems, with most examples coming from relatively fine-scale studies focusing solely on seagrass habitat. However, recent advances in remote sensing technologies are now providing marine scientists the habitat information to explore seascape questions at multiple spatio-temporal scales. Recent studies applying a seascape approach have provided compelling evidence indicating the importance of

seascape patterning on species distributions and ecological processes in marine systems. However, further seascape ecology research is needed to i) establish the role and importance of seascape patterning for marine fishes and ecological processes (such as predator- prey dynamics) over a range of marine systems, including temperate regions and the pelagic environment; ii) determine the appropriate spatial scaling for seascape studies so specific hypotheses regarding seascape patterning can be explicitly tested; iii) examine the benefits of seascape patterning in MPA performance; and iv) examine the benefits of accounting for seascape variability in the assessment of MPA effectiveness. Demonstrating the value of these key research areas, seascape ecology will develop into an informative sub-discipline of marine ecology with strong implications for marine conservation science.

1.10 Thesis structure

The specific aims addressed by each chapter are:

Chapter 2 – *Does nearshore habitat type explain a significant amount of the spatial variability in coastal fish assemblages and can these habitats act as surrogates for Marine Park planning?* Based on previous literature, I predicted that there would be consistent differences in the demersal fish assemblages among habitats and therefore would be a suitable surrogate for conservation planning (Guidetti 2000). In contrast, I predicted that mid-water fish assemblages would show a weaker linkage to habitat type and therefore habitat would be an inappropriate surrogate for this assemblage. I also assessed the effect of habitat on the abundance of key species and families, to determine whether responses varied among taxa. Understanding habitat-assemblage relationships at lower taxonomic resolutions is

important to determine the usefulness of habitat surrogates for certain taxa. I assessed the influence of habitat on fish assemblages within four discrete seascapes. I predicted that differences in fish assemblages among seascapes would be due to seascape composition, specifically the area of rocky reef and seagrass.

Chapter 3 – *Is the current zoning arrangement of the Lord Howe Island Marine Park (LHIMP) adequately safeguarding the regions unique biodiversity?* In this chapter I evaluated changes in Lord Howe Island’s fish assemblage following approximately five and nine years since marine park zoning enforcement. As the LHIMP is relatively pristine, with low levels of anthropogenic impacts (for example no commercial fishing), I predicted that the abundance and diversity of fishes, as well as the abundance of common, endemic, near endemic and protected species would not differ between no-take SZs and HPZs, which allow some forms of fishing. Consequently, I predicted that the current LHIMP zoning arrangement would be adequately safeguarding the regions biodiversity within SZs and HPZs. In contrast, I predicted that species targeted by recreational and charter boat fishers would show an effect to MPA zoning with higher abundances inside SZs compared to HPZs where fishing is permitted.

Chapter 4 – *Does the inclusion of seascape variability into the evaluation of LHIMP efficacy improve the accuracy of the assessment?* In this chapter I test the effectiveness of no-take zones on a heavily exploited species; *Seriola lalandi* in the LHIMP with and without accounting for habitat structural complexity. To survey *S. lalandi*, I used baited remote underwater videos (BRUVs) at two sampling periods; 2009 and 2013. Without biological data prior to MPA implementation or quantifying seascape differences among MPA management zones, assessments on MPA efficacy

may be confounded. I predicted that incorporating a measure of habitat structural complexity, derived from high resolution multibeam bathymetry, would improve the assessment of the LHIMP. Furthermore, I predicted that the inclusion of seascape variability would improve the understanding of how spatial fishing closures affect the abundance of targeted species.

Chapter 5 - Mid-water baited remote underwater video systems (BRUVS) are becoming an increasingly popular tool for examining pelagic fish assemblages in a non-destructive, fisheries independent manner. As the technique is relatively novel, important methodological questions such as the most appropriate attractant for pelagic fish to mid-water RUVS remain unresolved. In this chapter I compared the relative effectiveness of four attractant treatments (sight: metallic reflectors, sound: bait fish recordings, scent: pilchards and their combination) on the time of first arrival, total abundance of pelagic fish and the relative abundance of three pelagic fish species: *Trachurus novaezelandiae*, *Sarda australis* and *Seriola lalandi*. Recordings were made using mid-water RUVS in the Jervis Bay Marine Park, Australia. I predicted that RUVS using a combination of all attractants would record the highest abundance and shortest time of first arrival of pelagic fish. This prediction was based on the notion that an array of sensory cues would enable pelagic fish to better detect the remote underwater camera.

**Chapter 2: SEASCAPE PATTERNS AND HABITAT DIFFERENCES
EXPLAIN SPATIAL VARIABILITY IN COASTAL FISH ASSEMBLAGES
WITHIN A TEMPERATE MARINE PROTECTED AREA**

This chapter has been prepared for submission to *Biological Conservation*.



Plate 2.1 A juvenile dusky whaler (*Carcharhinus obscurus*) recorded on a mid-water baited remote underwater video system in the Hare Bay Sanctuary zone, Jervis Bay Marine Park during a pilot study.

2.1 Introduction

Coastal marine ecosystems and the habitats within them are among the most productive and ecologically important worldwide (Costanza 1997; Waycott et al., 2009). Increasingly, coastal ecosystems and their associated biodiversity are under threat from a variety of anthropogenic activities such as overfishing, habitat degradation, pollution and urbanisation (Lotze et al., 2006; Diaz and Rosenberg 2008; Barnes et al., 2013). In the last two decades, Marine Protected Areas (MPAs) have been highlighted as one management approach to mitigate against some of these threats to coastal biodiversity (Halpern et al., 2010). Although many studies have demonstrated positive effects of MPAs on marine biodiversity and ecological processes (Lester et al., 2009), their establishment in coastal ecosystems is often met with objection related to socio-economic concerns. A solution to this problem has been to establish MPAs on an ecological foundation through CAR principles (ANZECC TFMPA 1998a, b); that is to have comprehensive, adequate and representative protected areas.

Designing Marine Protected Areas using CAR principles requires biotic information over relatively broad spatial scales (Jordan et al., 2005). Detailed spatial data on biological assemblages and individual species is, however, expensive to acquire and as a result, such information is rarely available. A cost-effective approach is to use habitat as a ‘surrogate’ to indirectly determine species distributions and abundances to guide the boundaries of protected areas (Sarkar et al., 2006; Rees et al., 2014). In response to the continued improvement of remote-sensing technologies, marine habitats can be mapped in high resolution at a range of spatial scales in an affordable manner (Brown et al., 2011; Ierodiaconou et al., 2011). Therefore, using habitat as a surrogate for MPA design may provide a rapid method

of estimating the biodiversity in an area (Zacharias and Roff 2000; Roff et al., 2003). In recent times, habitat classes (e.g. rocky reef, coral reef, seagrass, sand, etc.) are being increasingly used to provide an ecological foundation in MPA planning (Ward et al., 1999; Dalleau et al., 2010). Generally, this is because it is considered that different habitat classes support different biological communities, species, age classes and functional guilds. Hence, using a diverse range of habitat classes as a base for MPAs is believed to ensure adequate representation of the total biodiversity of the area (Ward et al., 1999; Roberts et al., 2003; Mumby et al., 2008; Dixon-Bridges et al., 2014). With an increasing movement towards habitat based surrogates in marine conservation planning it is important that we evaluate the basis of this planning approach. Specifically, whether habitat classes can reliably predict species distributions and abundances over scales relevant to spatial conservation planning. Without a quantitative and detailed understanding of these patterns, habitat surrogacy may be poorly representing local biodiversity and leading to undesirable planning outcomes.

In temperate coastal ecosystems, the design of MPAs is often guided by the distribution of the three habitat types; rocky reef, seagrass and unvegetated sediment. Studies on fish assemblages over these broad habitat types have often explored spatial variability within a particular habitat type (Curley et al., 2002; Garcia-Charton et al., 2004) or compared structurally complex habitats (e.g. rocky reef and seagrass) to adjacent unvegetated habitats with low structural complexity (Heck et al., 1989; Ferrell and Bell 1991; Connolly 1994; Gray et al., 1998; Williams and Bax 2001). There are a limited number of studies however, that have explicitly quantified differences in fish assemblages among seagrass, rocky reef and unvegetated sediment (see Jenkins and Wheatley 1998; Guidetti 2000 and La Mesa et al., 2011).

Therefore, the importance of habitat classes in structuring nearshore fish assemblages, and whether complexities exist with the use of habitat classes as surrogates for MPA planning remains poorly understood. In addition, all previous studies exploring fish-habitat relationships in coastal settings have investigated demersal fishes, with no research to our knowledge, testing the importance of nearshore habitats in structuring mid-water fish assemblages in coastal ecosystems (but see Costa et al., 2014 for a tropical example).

There is also growing evidence that broad-scale patterns of habitats (i.e. seascape patterning) may also play an important role in structuring nearshore fish assemblages (Boström et al., 2011; Pittman et al., 2011). This approach does not view habitats in isolation, but rather as non-independent patches influenced by the habitats surrounding them. In tropical environments larger coral reef patches harbour a higher diversity and abundance of coral reef fishes (Sale and Douglas 1984; Chittaro 2002). Meanwhile, previous research has shown positive correlations between coral reef fish assemblages and the amount of adjacent seagrass and mangrove habitat within the seascape (Grober-Dunsmore et al., 2007; Olds et al., 2012b; Olds et al., 2013). These findings have important implications for MPA planning, as they indicate habitat alone may not be an adequate surrogate for biodiversity and consideration may need to be given to spatial heterogeneity of the surrounding seascape (Olds et al., 2016). Despite growing evidence of the importance of seascape patterning in driving the abundance and distribution of fishes in tropical environments, very little research has employed a seascape approach to understand spatial patterns in temperate fishes (Jones and Andrew 1992).

In this study, we tested and quantified the influence of habitat classes; rocky reef, seagrass (*Posidonia australis*) and unvegetated sediment, in explaining the

spatial variability in temperate fish assemblages and examined whether these habitats could act as appropriate surrogates for MPA planning. To do this, I employed an hierarchical sampling design to explore the spatial variation in nearshore fish assemblages over three scales; i) among locations (> 5 km), ii) among habitats; rocky reef, seagrass and unvegetated sediment (~400 m), and iii) between sites within habitats (~200 m). Based on previous literature, I predicted that there would be consistent differences in the demersal fish assemblages among habitats across replicated experiment units (i.e. locations) and therefore, habitat would be a suitable surrogate for conservation planning. In contrast, I predicted that mid-water fish assemblages would show no affinity to habitat type and therefore habitat would be an inappropriate surrogate for this assemblage. We also assessed the effect of habitat on the abundance of key species and families, to determine whether responses varied among taxa. An assessment at lower taxonomic resolutions would provide conservation planners a more detailed understanding on the usefulness of habitat surrogates for certain taxa. To determine whether habitat classes were adequate surrogates, final models had to fulfil one of two criteria; i) the factor 'habitat' had to be a significant main effect with consistent differences among habitats across locations, or ii) if there was a significant habitat by location interaction, similar patterns among habitats between locations had to be observed. Furthermore, if the interaction between habitat and location was significant, indicating broad-scale spatial variability in the fish assemblage, we assessed whether these differences would be explained by the seascape attributes of the site.

2.2 Materials and Methods

This study was carried out in Jervis Bay, a temperate embayment in South-Eastern Australia and the central section of the Jervis Bay Marine Park (JBMP) between December 2013 to March 2014 (Fig. 2.1). The park covers an area of 220 km² comprising of a network of ‘no-take’ sanctuary zones, habitat protection zones and general use zones. The embayment contains three main benthic habitat types; rocky-reef, unvegetated sediments and the seagrass, *Posidonia australis* (Marine Parks Authority 2008). These habitat types are replicated throughout the Bay (Fig. 2.1), therefore the JBMP provides an ideal system to test habitat and seascape ecology related questions in relation to conservation management.

Fish assemblages were surveyed using mid-water baited remote underwater video systems (mBRUVS), as well as standard BRUVS positioned on the seafloor. Mid-water BRUVS were constructed following the design of Heagney et al. (2007) and Rees et al. (2015) but adapted so that the camera was positioned 0.5 m below the surface of the water. Both mBRUVS and BRUVS contained Canon HF20 video cameras within underwater camera housings constructed by SeaGIS Pty. The mBRUVS and BRUVS were deployed at 2 sites separated by 400 m on rocky-reef (RR), unvegetated sediment (US) and seagrass (SG) habitat across 4 locations (Murrays Beach, Callala Bay, Plantation Point and Hare Bay) within the JBMP. Locations were separated by between 5 and 8 km (Fig. 2.1). At each site, 2 mBRUVS and 2 BRUVS were deployed at least 200 m apart along the 5 m depth contour. Prior to deploying the systems, bait bags were replenished with 500 g of freshly crushed pilchards (Wraith et al., 2013). Both mBRUVS and BRUVS were deployed for 35 mins to achieve a 30 min sample. Previous studies have indicated that a 30 min deployment provides a representative sample of temperate demersal

fish assemblages (Harasti et al., 2015). Although unknown, I assume a 30 min deployment provides a representative sample of temperate mid-water fish assemblages.

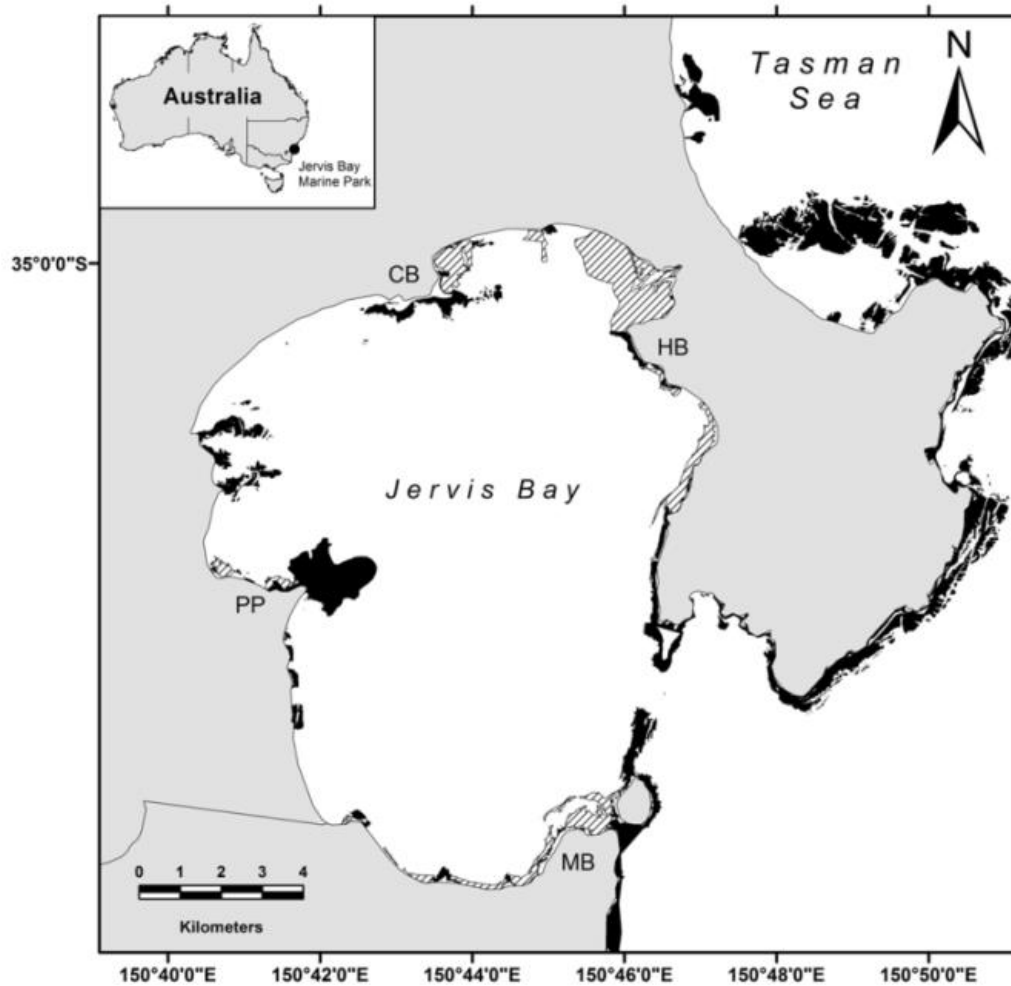


Figure 2.1 A habitat map of the Jervis Bay Marine Park. Dark areas indicate rocky reef, cross-hatched areas seagrass (*Posidonia australis*) and white areas unvegetated sediment. The four survey locations are indicated, Murrays Beach (MB), Plantation Point (PP), Callala Bay (CB) and Hare Bay (HB).

Footage from mBRUVs and BRUVs was analysed in the laboratory using Event Measure software (SeaGIS Pty). For each deployment, species richness and

relative abundance (Max N) was recorded. Species richness was the number of species of fish observed during the sample. The relative abundance of fishes, Max N, was the maximum number individuals of one species viewed at any one time during the sample (Cappo et al., 2004). Max N values for individual species were then summed to generate the overall relative abundance for each sample. Two species; *Trachurus noevazelandiae* and *Nelusetta ayraudi* dominated both the mid-water and demersal fish assemblage. A separate response measure of total fish abundance was analysed with these species removed.

Hypotheses about multivariate fish assemblages were tested using a 3 factor PERMANOVA (PRIMER Software, Plymouth Marine Laboratories) on Bray-Curtis dissimilarity values calculated from untransformed data (Anderson 2001). The factors were location (4 levels and random), habitat (3 levels and fixed; RR, US and SG) and site (2 levels nested within the location by habitat interaction and random). Non-metric multidimensional scaling (nMDS) was used to generate two-dimensional ordinations to illustrate patterns in mid-water and demersal fish assemblages. Species richness, total abundance and abundance data of numerically dominant individual species and families were analysed separately using a 3 factor ANOVA in GMAV 5 software (Underwood and Chapman 1984). Numerically dominant species and families were those that were observed in high abundances across all samples or within certain habitats (i.e. *Platycephalus spp.* on unvegetated sediment and *Hyporhamphus australis* in the mid-water environment). These analyses were completed with the factors as previously described for the multivariate analyses. Prior to analysis, data were visually assessed for normal distributions and Cochran's C test was used to test for departures from homogeneity of variances. If significant heterogeneity was present, data were transformed. The abundances of

Ophthalmolepis lineolatus, *Achoerodus viridis* and *Platycephalus spp.* were heterogeneous, but as analysis of variance is robust to heterogeneity in balanced experimental designs with large numbers of samples (Underwood 1997), these analyses were still performed. Student-Newman Keuls (SNK) tests were used for *post-hoc* comparisons. Following ANOVA, *post-hoc* pooling of the “location × habitat” interaction was performed if $P > 0.25$, in order to increase the power of the main tests (Underwood 1997).

To examine the relationship between seascape connectivity of seagrass and rocky reef habitats on nearshore fish assemblages, the amount of seagrass at each rocky reef site was calculated. Using Focal Statistics in *ArcGIS version 10*, the area of seagrass was quantified surrounding each BRUV deployment on rocky reef at a 50, 100, 150, 250, 500, 1000 and 1500 m radius. A multi-scale approach was used as the scale in which the fish assemblage was responding to seascape composition was not known *a priori*. Habitat mapping of Jervis Bay Marine Park’s subtidal features were derived from swath bathymetry, LADS and ADS40 aerial imagery (Williams et al., 2007; Creese et al., 2009). Simple linear regressions were performed in R (R Core Development Team, 2013) between several response measures of the rocky reef fish assemblage and the area of surrounding seagrass calculated at various spatial scales. Akaike information criterion (AIC) was used to determine which spatial scale best explained the variation for each response measure. Model residuals were checked for spatial autocorrelation using Moran’s I statistic. For all regressions no significant spatial autocorrelation was detected.

2.3 Results

A total of 8900 fish were observed, comprising 71 species from 41 families. Of the total number of individuals recorded, 50% were observed over rocky reef, 29% over seagrass and 21% over unvegetated sediment. Of the total number of species recorded, 57 species observed over rocky reef habitat, 37 species over seagrass and 21 species on unvegetated sediment. Only 2 species, *Hyporhamphus australis* and *Seriola rivolana* were recorded exclusively in the mid-water environment.

2.3.1 Effects of habitat on demersal fishes

Habitat had a significant effect on the demersal fish assemblage with a distinct composition of fishes observed among each habitat (Fig. 2.2a; Table 2.1). Rocky reef and seagrass habitat had a greater abundance of demersal fishes compared to unvegetated sediment (Fig. 2.3c; Table 2.2b). This result, however, was driven by two numerically dominant species; *Trachurus noevazelandiae* and *Nelusetta ayraudi*. When these species were excluded from the analysis, the abundance of demersal fishes was greatest on rocky reef, with no difference between seagrass and unvegetated sediment (Fig. 2.3e; Table 2.2c). Similarly, there was a general trend of rocky reef harbouring a higher diversity of demersal fish compared to seagrass and unvegetated sediment (Fig. 2.3a; Table 2.2a).

Many species contributed to the differences in the fish assemblage and total abundance among habitats. The abundance of Scorpidids and Labrids were clearly reef associated, effectively being observed on rocky reef habitat at each location (Fig. 2.4e, 2.5b; Table 2.3c, 2.4b). Two common Labrids; *Achoerodus viridis* and *Ophthalmolepis lineolatus* had greater abundances on rocky reef compared to other

habitats at all locations (Fig. 2.5c, d; Table 2.4c, d). Similarly, the abundance of *Trachurus noevazelandiae* in the demersal environment was greater on rocky reef and seagrass compared to unvegetated sediment (Fig. 2.4c; Table 2.3b).

Alternatively, individuals from the genus *Platycephalus* were only observed on unvegetated sediment (Fig. 2.5e; Table 2.4e). The Eastern Fiddler Ray; *Trygonorrhina fasciata* was similarly abundant on seagrass and unvegetated sediment, but displayed much lower abundances on rocky reef (Fig. 2.5f; Table 2.4f).

Only two taxa explored from the demersal fish assemblages were not influenced by habitat. The numerically dominant, *Nelusetta ayruadi* displayed considerable variability among habitats indicating no preference for any habitat type (Fig. 2.4a; Table 2.3a). Similarly, the abundance of individuals from the commercially important Sparidae displayed no clear pattern with habitat, however there were differences observed at certain locations (Fig. 2.5a; Table 2.4a).

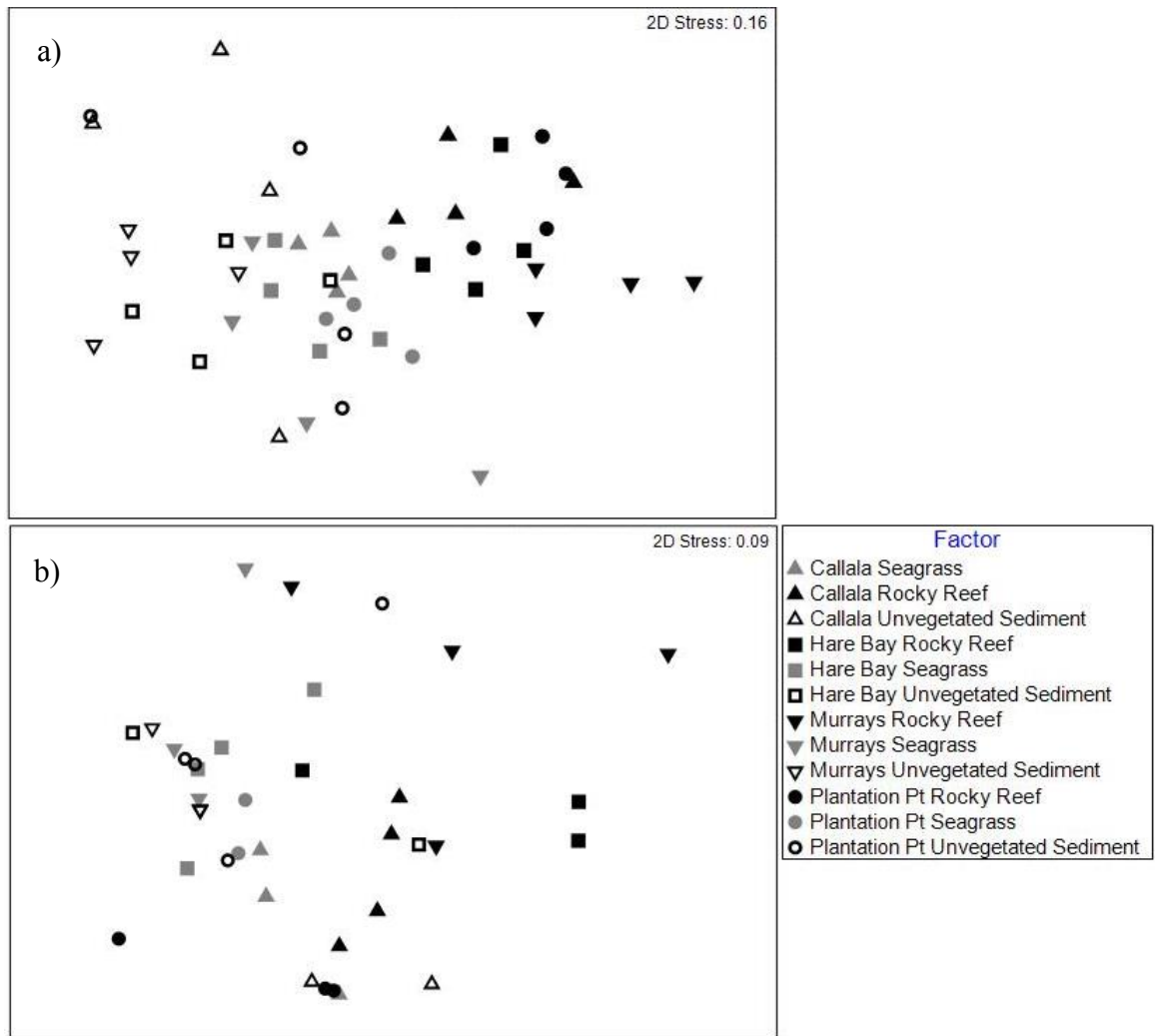


Figure 2.2 Non-metric multidimensional scaling (nMDS) ordination of a) the demersal and b) mid-water fish assemblage. Points closer together in ordination space represent sites with more similar species compositions.

Table 2.1 Results of a permutational multivariate analysis of variance (PERMANOVA) for a) demersal and b) mid-water fish assemblages. Factors were Habitat (H, fixed with 3 levels: rocky reef, seagrass and unvegetated sediment), Location (L, random with 4 levels: Callala Bay, Hare Bay, Murrays Beach and Plantation Point) and Site nested within the Habitat by Location interaction. Values in bold indicate statistical significance at $\alpha = 0.05$.

Source	df	MS	Pseudo F	P (perm)
a) Demersal				
Habitat	2	20342	10.12	0.001
Location	3	4028.8	2.425	0.002
H x L	6	2009.2	1.209	0.205
Site(H x L)	12	1661.3	1.366	0.032
Residual	24	1216.4		
Pairwise comparison: RR≠SG≠US				
b) Mid-water				
H	2	7529.6	1.89	0.085
L	3	6968.2	2.10	0.029
H x L	6	4002.9	1.22	0.243
Si(H x L)	9	3207.1	1.39	0.065
Residual	16	2311.2		

2.3.2 Effects of habitat on mid-water fishes

Unlike demersal fishes, habitat had no effect on the total abundance of mid-water fishes with and without the numerically dominant *Trachurus noevazelandiae* and *Nelusetta ayraudi* (Fig. 2.3 d, f; Table 2.2b, c). Similarly, habitat did not influence the diversity, or the assemblage structure of mid-water fishes (Fig. 2.2b, 2.3b; Table 2.1b, 2.2a). Although not significant, there was a trend for a higher abundance of *Nelusetta ayraudi* on unvegetated sediment and seagrass compared to rocky reef (Fig. 2.4b; Table 2.3b). The abundance of *Trachurus noevazelandiae* was extremely patchy in their patterns of distribution. Low abundances of this schooling species were recorded at all locations except Callala, where there was a substantially

higher abundance recorded on rocky reef compared to the other habitats (Fig. 2.4d; Table 2.3b). Habitat had no effect on the abundance of *Hyporhampus australis*, a species which was only recorded in the mid-water environment (Fig. 2. 4f; Table 2.3d).

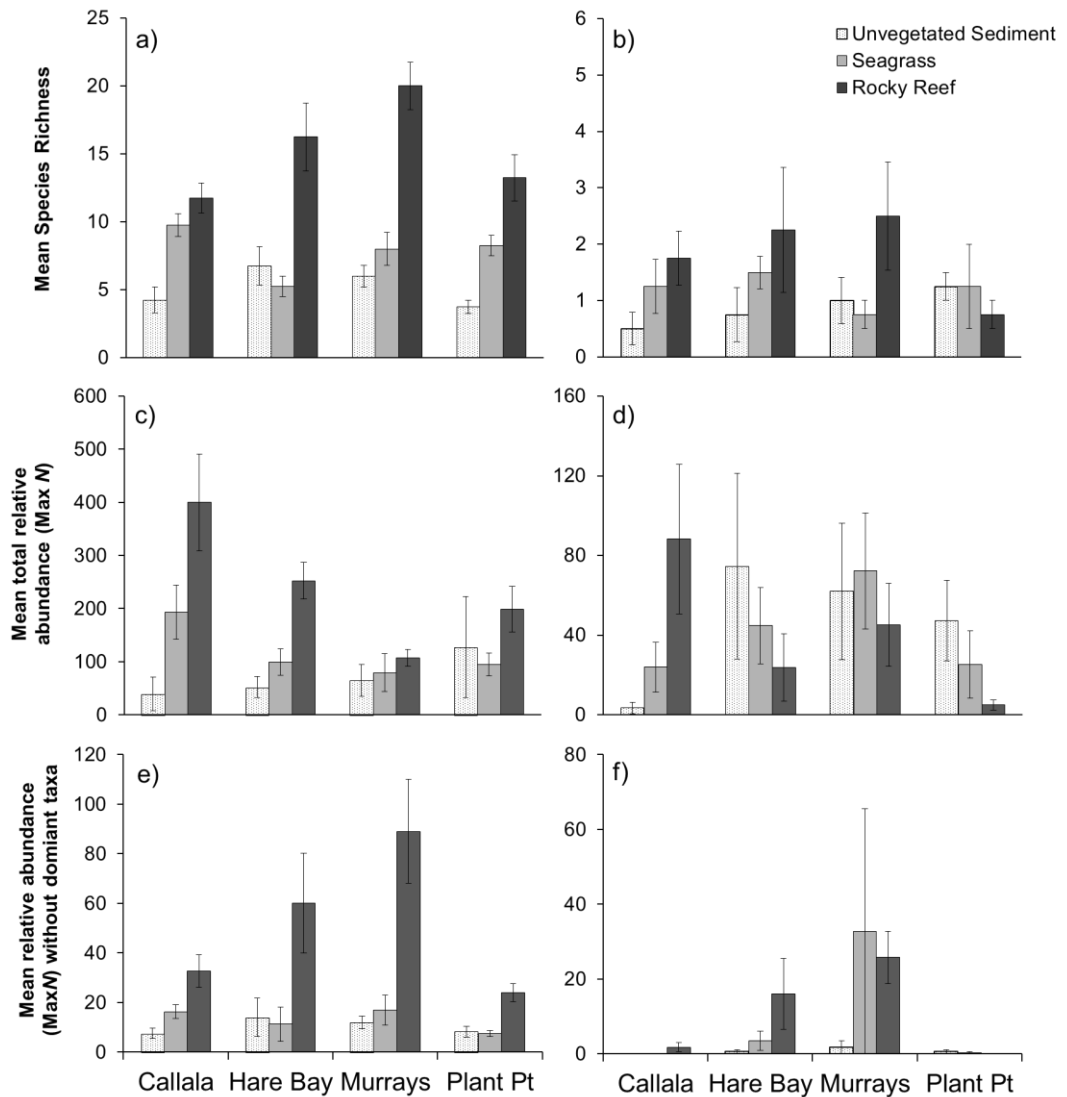


Figure 2.3 Mean (\pm SE) fish a) species richness, b) total abundance and c) total abundance without dominant taxa in demersal and mid-water environments ($n = 2$).

Table 2.2 Results for ANOVAs on a) species richness, b) total abundance and c) total abundance without two dominant taxa for demersal and mid water fish assemblages. Factors are the same as those listed in Table 2.1. Values in bold indicate statistical significance at $\alpha = 0.05$. Data stemming from pooling procedures outlined in Underwood (1997) referred to as 1-Pooled data; NS: not significant.

	Demersal				Mid-water			
	df	MS	F	P	df	MS	F	P
a) Species Richness								
Habitat	2	441.75	16.45	0.004	2	0.49	1.97	0.22
Location	3	21.47	3.13	0.037	3	0.05	0.18	0.90
H x L	6	26.86	3.92	0.004	6	0.25	0.79	0.60
Site(H x L)	12	7.44	1.09	0.401	12	0.31	1.61	0.16
Residual	24	6.56			24	0.20		
Total	47				47			
1-Pooled data	36	6.85						
Pairwise comparison:	CB: SS<SG=RR, HB: SS=SG<RR, MB: SS=SG<RR, PP: SS<SG<RR							
	Cochrans C (NS): 0.26				Cochrans C (NS): 0.34, Ln(x+1)			
b) Total Abundance								
H	2	13.06	10.43	0.011	2	49582.31	2.06	0.21
L	3	0.54	0.69	0.561	3	9178.41	0.38	0.77
H x L	6	1.25	1.62	0.170	6	24046.70	1.72	0.15
Site(H x L)	12	0.44	0.57	0.853	12	4120.31	0.29	0.99
Residual	24	0.94			24	18960.19		
Total	47				47			
Pairwise comparison:	SS<SG=RR							
	Cochrans C (NS) 0.27, Ln(x)				Cochrans C (NS): 0.27			
c) Total abundance minus dominant taxa								
H	2	10.54	29.70	0.000	2	4.38	1.84	0.238
L	3	1.26	3.17	0.034	3	6.04	2.54	0.153
H x L	6	0.40	1.13	0.36	6	2.38	2.17	0.069
Site(H x L)	12	0.31	0.88	0.58	12	1.03	0.94	0.520
Residual	24				24	1.13		
Total	47				47			
1-Pooled data	36	0.35			36	1.10		
2-Pooled data	42	0.35						
Pairwise comparison:	SS=SG<RR							
	Cochrans C (NS): 0.25, Ln(x+1)				Cochrans C (P<0.01): 0.44, Ln(x+1)			

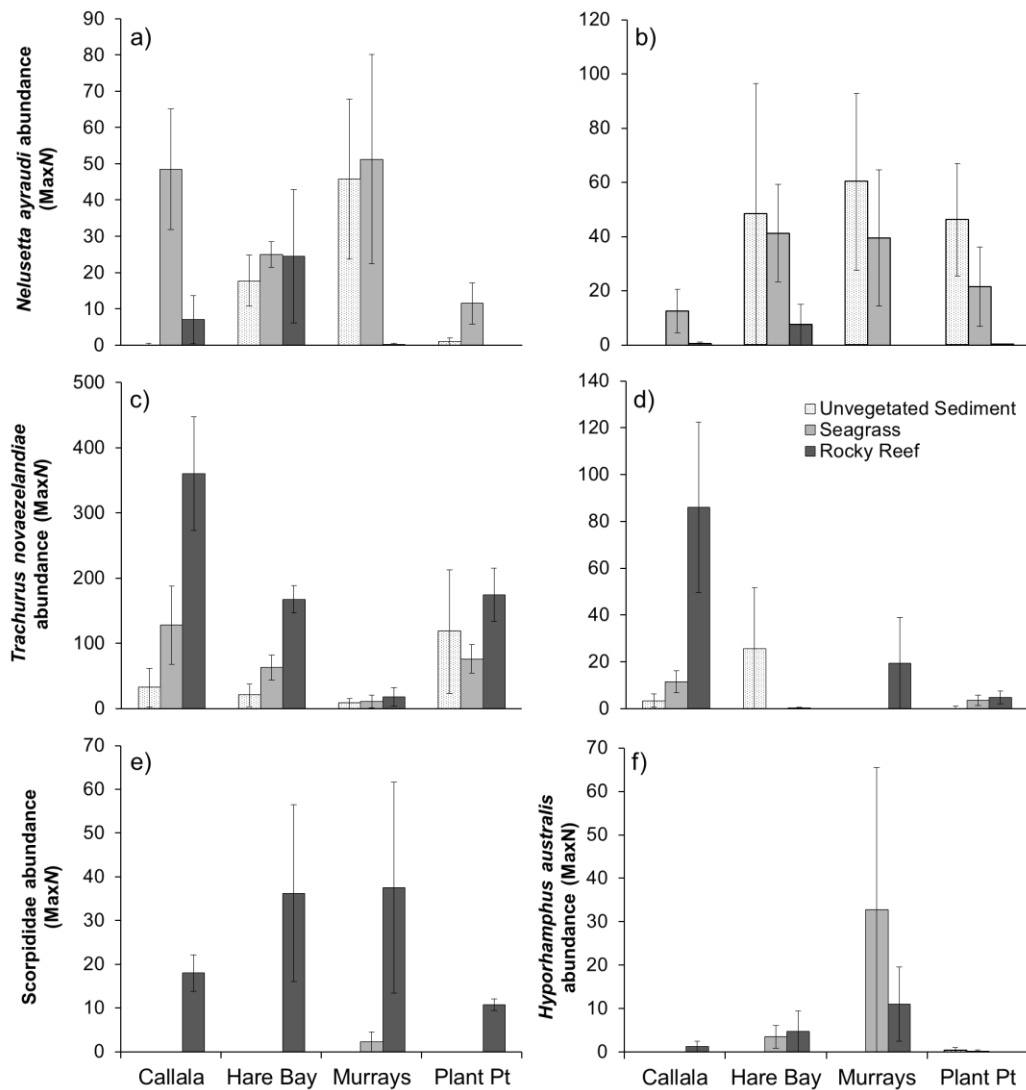


Figure 2.4 Mean (\pm SE) a) *Nelusetta ayraudi*, b) *Trachurus novaezelandiae* abundance in demersal and mid-water environments, c) Scorpididae abundance in the demersal environment and d) *Hyporhamphus australis* abundance in the mid-water environment (n = 2).

Table 2.3 Results for ANOVAs on the abundance of a) *Nelusetta ayraudi*, b) *Trachurus novaezelandiae* in the demersal and mid-water environments, c) Scorpididae in the demersal environment and d) *Hyporhamphus australis* in the mid-water environment. Factors are the same as those listed in Table 2.1. Values in bold indicate statistical significance at $\alpha = 0.05$. Data stemming from pooling procedures outlined in Underwood (1997) referred to as 1-Pooled data; NS: not significant.

	Demersal				Mid-water			
	df	MS	F	P	df	MS	F	P
a) <i>Nelusetta ayraudi</i> N								
Habitat	2	18.91	4.79	0.057	2	16.08	4.14	0.074
Location	3	7.78	5.22	0.004	3	3.83	0.99	0.460
H x L	6	3.95	2.65	0.031	6	3.89	0.90	0.525
Site(H x L)	12	1.46	0.98	0.487	12	4.32	1.87	0.094
Residual	24	1.51			24	2.31		
Total	47				47			
1-Pooled data	36	1.49						
Pairwise comparison:	CB: SS=RR<SG, HB: SS=SG=RR, MB: SS=SG>RR, PP: SS=SG=RR				Cochrans C (NS): 0.25, Ln(x+1)			
b) <i>Trachurus novaezelandiae</i> N								
H	2	27.46	14.74	0.005	2	19.42	1.28	0.344
L	3	19.91	6.72	0.007	3	24.34	1.60	0.285
H x L	6	1.86	0.63	0.705	6	15.17	3.04	0.017
Site(H x L)	12	2.96	1.61	0.155	12	4.10	0.82	0.628
Residual	24	1.84			24	5.44		
Total	47				47			
1-Pooled data					36	4.99		
Pairwise comparison:	SS<SG=RR				CB: SS=SG<RR, HB: SS=SG=RR, MB: SS=SG=RR, PP: SS=SG=RR			
	Cochrans C (NS): 0.26, Ln(x+1)				Cochrans C (NS): 0.32, Sqrt(x+1)			
c) Scorpididae N								
H	2	64.41	28.24	0.000	d) <i>Hyporhamphus australis</i> N			
L	3	1.56	0.69	0.57	2	1.68	1.52	0.230
H x L	6	0.94	0.41	0.87	3	1.56	1.41	0.252
Site(H x L)	12	1.10	0.48	0.92	6	0.71	0.64	0.695
Residual	24	3.21			12	1.14	1.03	0.438
Total	47				24	1.18		
1-Pooled data	36	2.50			36	1.17		
2-Pooled data	42	2.28			42	1.10		
Pairwise comparison:	SS=SG<RR				Cochrans C (NS): 0.42, Ln(x+1)			
	Cochrans C (NS): 0.33, Sqrt(x+1)							

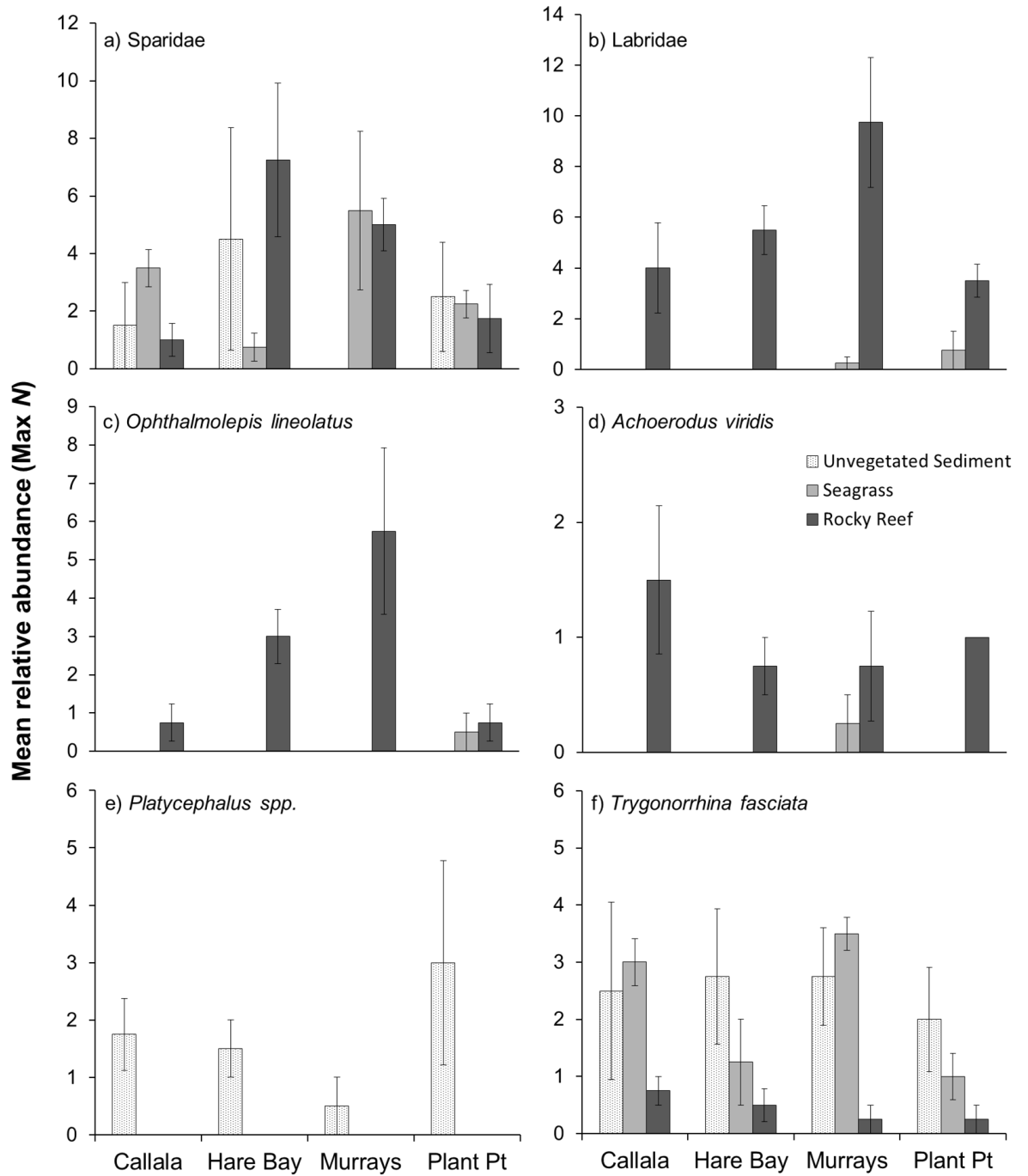


Figure 2.5 Mean (\pm SE) abundance of a) Sparidae, b) Labridae, c) *Ophthalmolepis lineolatus*, d) *Achoerodus viridis*, e) *Platycephalus spp.*, f) *Trygonorrhina fasciata* recorded in the demersal environment (n = 2).

Table 2.4 Results for ANOVAs on the abundance of a) Sparidae, b) Labridae, c) *Ophthalmolepis lineolatus*, d) *Achoerodus viridis*, e) *Platycephalus spp.*, f) *Trygonorrhina fasciata* on demersal BRUVs. Factors are the same as those listed in Table 2.1. Values in bold indicate statistical significance at $\alpha = 0.05$. Data stemming from pooling procedures outlined in Underwood (1997) referred to as 1-Pooled data; NS: not significant.

	df	MS	F	P	df	MS	F	P
	a) Sparid <i>N</i>				b) Labrid <i>N</i>			
Habitat	2	1.99	1.18	0.369	2	11.11	28.10	0.001
Location	3	0.21	0.32	0.809	3	0.37	1.38	0.296
H x L	6	1.68	2.62	0.033	6	0.40	1.48	0.265
Site(H x L)	12	0.68	1.06	0.422	12	0.27	2.54	0.025
Residual	24	0.62			24	0.11		
Total	47				47			
1-Pooled data	36	0.64						
Pairwise comparison:	CB: SS=SG=RR, HB: SS=SG, SS=RR, SG<RR, MB: SS<SG=RR, PP: SS=SG=RR				SS=SG<RR			
	Cochrans C (NS): 0.32, Ln(x+1)				Cochrans C (NS): 0.31, Sqrt(x+1)			
	c) <i>Ophthalmolepis lineolatus N</i>				d) <i>Achoerodus viridis N</i>			
H	2	3.01	18.05	0.000	2	1.88	26.05	0.000
L	3	0.14	0.82	0.449	3	0.02	0.25	0.862
H x L	6	0.14	0.82	0.559	6	0.05	0.78	0.551
Site(H x L)	12	0.05	0.30	0.985	12	0.09	1.25	0.282
Residual	24	0.23			24	0.07		
Total	47				47			
1-Pooled data	36	0.17			36	0.07		
2-Pooled data	42	0.17			42	0.07		
Pairwise comparison:	SS=SG<RR				SS=SG<RR			
	Cochrans C (p<0.05): 0.39, Ln(x+1)				Cochrans C (p<0.05): 0.38, Ln(x+1)			
	e) <i>Platycephalus spp. N</i>				f) <i>Trygonorrhina fasciata N</i>			
H	2	3.01	18.05	0.000	2	3.01	9.19	0.015
L	3	0.14	0.82	0.489	3	0.45	1.36	0.340
H x L	6	0.14	0.82	0.559	6	0.33	0.89	0.533
Site(H x L)	12	0.05	0.30	0.985	12	0.37	1.73	0.124
Residual	24	0.23			24	0.21		
Total	47				47			
1-Pooled data	36	0.17						
2-Pooled data	42	0.17						
Pairwise comparison:	SS>SG=RR				SS=SG>RR			
	Cochrans C (p<0.05): 0.39, Ln(x+1)				Cochrans C (NS): 0.19, Ln(x+1)			

2.3.3 Seascape effects

In addition to habitat, nearshore fish assemblages also displayed substantial variability among locations, which highlighted potential seascape effects.

Quantifying seascape composition at each sampling site, simple linear regressions confirmed significant positive relationships between four fish response measures and the amount of seagrass area surrounding each rocky reef habitat. First, mid-water fish abundance, mid-water fish cumulative richness, demersal fish abundance and finally Sparidae abundance recorded on rocky reef increased with increasing seagrass area in the seascape (Fig. 2.7; Table 2.5). Although not significant, there was a strong positive trend between demersal fish richness recorded on rocky reef and the area of surrounding seagrass (Fig. 2.7; Table 2.5).

Table 2.5 Simple linear regressions for various fish response measures recorded on rocky reef habitat with the areal coverage of seagrass within 1 or 1.5 km radius of each survey site.

Dependent variable	Independent variable	<i>F</i> -ratio	Model R ²	<i>p</i> -value
a) Demersal fish cumulative diversity	Seagrass 1000 m	5.36	0.38	0.06
b) Mid-water fish cumulative diversity	Seagrass 1500 m	14.5	0.66	0.009
c) Demersal fish abundance	Seagrass 1000 m	12.97	0.63	0.011
d) Mid-water fish abundance	Seagrass 1000 m	12.96	0.63	0.011
e) Sparid abundance	Seagrass 1500 m	6.67	0.45	0.042

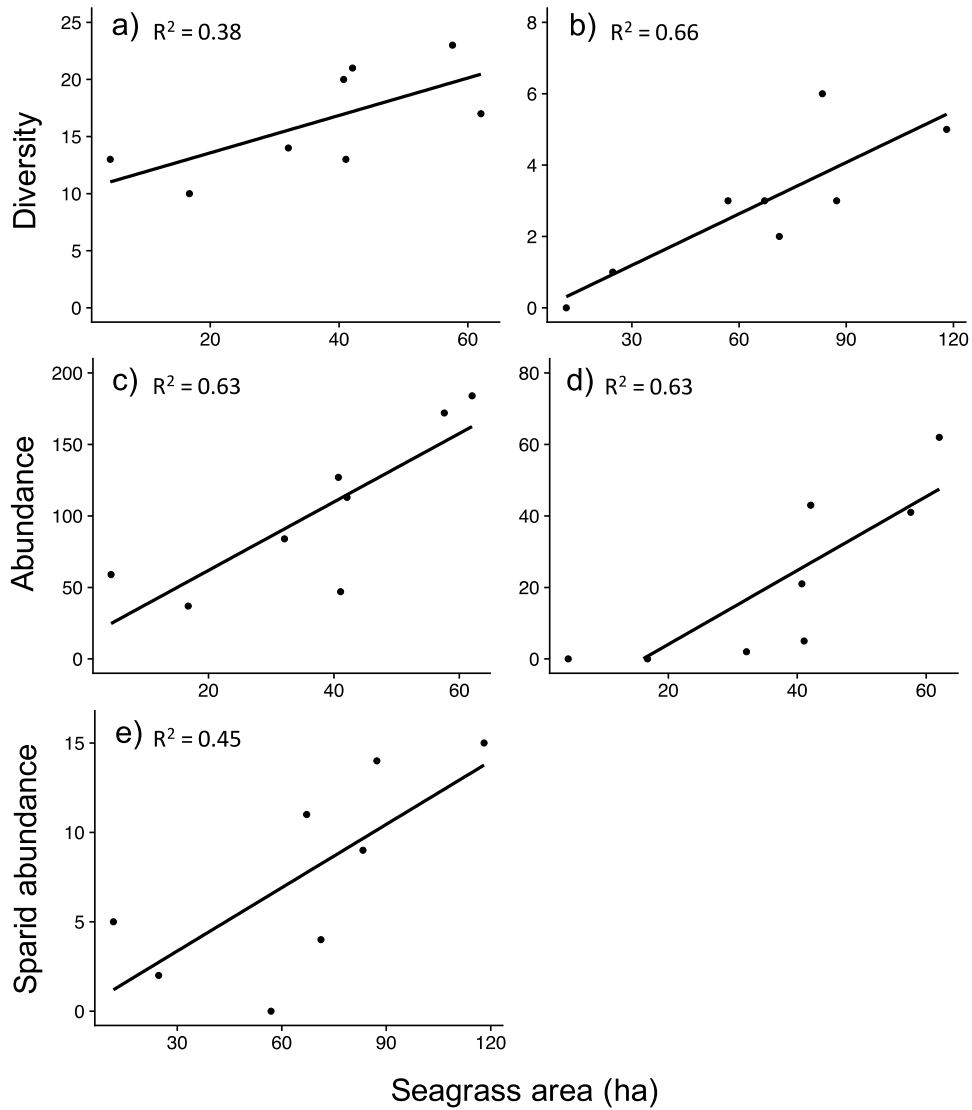


Figure 2.6 Relationship between a) demersal fish cumulative species richness, b) mid-water fish cumulative species richness, c) demersal fish abundance, d) mid-water fish abundance and e) Sparid abundance recorded on rocky reef and the area of seagrass habitat within the seascape.

2.4 Discussion

Our results demonstrate that habitat class is often a consistent and discrete predictor of spatial variability in the demersal fish assemblage. There were, however, substantial variations in patterns of fish abundance and distribution in regards to habitats. Some fishes showed no pattern among habitat classes, while others displayed similar abundances among two very discrete and different habitats (for example, unvegetated sediment and seagrass for *Trygonorrhina fasciata*). Furthermore, I have shown quantitative values for differences in the diversity and abundance of coastal fish assemblages among common nearshore habitats that can be used for conservation planning and fisheries management. Overall, the specific habitat elements we have investigated are appropriate surrogates for spatial conservation strategies such as MPAs, however, general species patterns also need to be considered.

Across all locations, habitat consistently influenced the structure of demersal fishes, with each habitat class comprising a distinct assemblage of fishes. This result was driven by differences in demersal fish diversity and total abundance (including and excluding dominant taxa), where rocky reef harboured a greater richness and abundance of fishes. Differences in demersal fish assemblages among habitats were also driven by a number of taxa displaying strong habitat preferences. Labrids and two species within this family; *Achoerodus viridis* and *Ophthalmolepis lineolatus*, as well as individuals from the Scorpididae, were almost exclusively recorded over rocky reef habitat. Meanwhile, individuals from the genus *Platycephalus* were only observed on unvegetated sediments. In contrast, certain species clearly preferred more than one habitat. For example, *Trachurus novaezelandiae* were more abundant over seagrass and rocky reef compared to unvegetated sediment, while

Trygonorrhina fasciata were more abundant over unvegetated sediment and seagrass compared to rocky reef. These strong, spatially consistent patterns indicate that the habitat classes investigated in this study may be appropriate surrogates for certain demersal fishes. As results varied among taxa however, our findings also highlight the importance of exploring fish-habitat relationships at finer taxonomic scales.

Habitat was not an important driver of the mid-water fish assemblage, with inconsistent and highly variable patterns in assemblage structure, abundance and diversity among habitats. Furthermore, the Eastern Sea Garfish; *Hyporhamphus australis*, a species observed exclusively in the mid-water environment displayed no preference for habitat type. Our findings demonstrate a clear decoupling of the mid-water fish assemblage from the underlying habitat class. This is despite mid-water BRUVS being positioned only approximately 4.5 metres above the seafloor. Therefore, we conclude that habitat classes would not be an effective surrogate for nearshore mid-water fish assemblages.

In response to the cost effectiveness and time efficiency of collecting remotely-sensed habitat information, mapped habitat classes (e.g. rocky reef, seagrass, mangroves, unvegetated sediments, etc.) are becoming increasingly used as surrogates to indirectly determine marine biodiversity and guide the design of MPAs (Jordan et al., 2005; Dalleau et al., 2010). This approach is based on the notion that different habitat types support different biological communities, species, age classes and functional guilds. Therefore, by representing habitat diversity within a protected area, it is assumed that biodiversity and ecological processes will also be captured. Little research, however, has critically evaluated or quantified how habitat influences nearshore fish assemblages and whether mapped habitat classes can act as adequate surrogates for the abundance and diversity of fishes. In this study, I observed mixed

effects of the influence of habitat classes on coastal fish assemblages. The distribution and abundance of some taxa were strongly influenced by habitat, while others showed no differentiation. This does not indicate that the broad habitat classes examined are not useful surrogates, but instead suggests that patterns may be species specific. In order to use habitat classes successfully as surrogates for spatial conservation planning, managers will have to consider this variation.

Previous studies comparing demersal fish assemblages among rocky reef, seagrass and unvegetated sediment have also observed effects of habitat. Notably, rocky reef, seagrass and unvegetated sediment each displayed a distinct assemblage of demersal fishes, which corroborates the findings of our study (Jenkins and Wheatley 1998; Guidetti 2000; La Mesa et al., 2011). Despite differences in the geographic location, species of seagrass investigated, and method to survey fishes, similarities between our findings and those of previous research suggest generalities for the importance of nearshore habitats structuring demersal fish assemblages. It also further underscores the potential of these habitats to act as surrogates for conservation on a broader scale than the one employed in this study. Strong species specific relationships were also observed among habitats by Jenkins and Wheatley (1998), Guidetti (2000) and La Mesa et al., (2011), further highlighting the need to explore such relationships at finer taxonomic levels.

Not all demersal fish taxa showed consistent differences in their patterns of abundance among habitat types. Most notable was the high variability in the abundance of the commercially and recreationally important Sparidae among habitats and locations. This outcome is consistent with them being habitat generalists or using specific habitats at different life stages. The latter is likely for Sparids, such as Snapper (*Pagrus auratus*), as they are known to undertake ontogenetic migrations

between nearshore habitats by first recruiting to seagrass and unvegetated sediments before taking up residence on rocky reef as adults (Hamer et al., 2006; Parsons et al., 2014). Measuring fish length, perhaps through use of stereo BRUVS, would provide an opportunity to determine whether rocky reef, seagrass and unvegetated sediments support different age classes on fishes. We suggest this as a future area of work in coastal seascapes.

Another key finding from our study was substantial spatial variability among locations, which highlighted the potential importance of broad-scale seascape connectivity on nearshore fish assemblages. Generally, sites within Murrays Beach and Hare Bay displayed a higher abundance and diversity of fishes compared to Callala Bay and Plantation Point. Sites within these locations also varied in their areal coverage of seagrass, with Murrays Beach and Hare Bay sites containing a greater area of seagrass compared to sites at Callala Bay and Plantation Point. Linear regressions confirmed the amount of seagrass in the surrounding seascape to significantly influence mid-water fish abundance, diversity, demersal fish abundance and Sparid abundance on adjacent rocky reef habitat. In all cases fish response measures were positively correlated with increasing seagrass area. Although not significant, similarly there was also a strong trend between demersal fish diversity and seagrass area. These findings are not surprising considering many species from families observed in this study (for e.g. Labrids, Girreids and Sparids), recruit into seagrass habitats before undertaking ontogenetic migrations to other habitat types (Curley et al., 2013). Furthermore, many species may undertake diel migrations between different habitat patches to seek refuge or utilise various habitat patches for foraging. Snapper (*Pagrus auratus*) from the Sparid family are known to prefer areas of greater patch diversity and complexity (coralline turf, mussel beds, sponges, pits

and burrows) (Kingett and Choat 1981; Parsons et al. 2014). Therefore, seascapes that display a high diversity of habitat patches are likely to facilitate a number of ecological processes and promote local biodiversity (Dunning et al., 1992). These findings also support previous research from tropical environments, which have highlighted the positive effect of connectivity between vegetated habitats such as seagrass and mangroves with coral reef habitat (Mumby et al., 2006; Grober-Dunsmore et al., 2007; Nagelkerken et al., 2012).

Although our findings are preliminary, we encourage future research to investigate the seascape ecology of temperate fishes, especially the role of connectivity between vegetated and rocky reef habitats. This is important, as many MPAs do not acknowledge or consider the seascape patterning in their design and as a result may not be protecting key seascape linkages important for ecological processes and species populations. A better understanding of the effect of seascape patterning on biodiversity and ecological processes such as ontogenetic species migration will better inform the design of spatial conservation management strategies in temperate regions (Olds et al., 2016).

2.5 Conclusions

Remotely-sensed benthic habitat maps have become a popular tool to guide the design of spatial conservation strategies like MPAs. Despite their use, there has been scant attention to whether nearshore habitat classes are appropriate surrogates for biological assemblages and ultimately their utility in MPA design. In this study, we found that nearshore habitats consistently explained the spatial patterns in demersal fishes in coastal environments. There were, however, some exceptions to this rule when relationships were explored at lower taxonomic resolution, which

planners should be aware of. In contrast, nearshore habitats did not influence mid-water fishes. I conclude that habitat classes can be a useful surrogate for demersal fishes, providing a cost effective and time efficient approach to designing MPAs on a firm ecological foundation. I also show that the surrounding seascape composition of rocky reef habitat, specifically the amount of seagrass, is important in explaining the abundance and diversity of nearshore temperate fishes. I propose that greater seagrass coverage facilitates ecological processes such as ontogenetic migrations, foraging behaviour and diel movements which results in disproportionate levels of biodiversity on reefs adjacent to large areas of seagrass. Future research, with larger sample sizes or employing technologies such as acoustic telemetry will strengthen the evidence of the importance of seascape connectivity for temperate fishes. As MPA design is often guided by socio-economic or political concerns, it is essential that future MPAs are developed on ecological grounds due to the rising threats to marine biodiversity, especially in coastal environments.

Chapter 3: ASSESSING THE EFFECTIVENESS OF THE LORD HOWE ISLAND MARINE PARK IN SAFEGUARDING THE REGION'S UNIQUE MARINE BIODIVERSITY

This chapter has been prepared for submission to *Aquatic Conservation: Marine and Freshwater Ecosystems*.



Plate 3.1 A large adult black rockcod (*Epinephelus daemeli*) recorded on the Lord Howe Island shelf using a baited remote underwater video system. Black rockcod are listed as vulnerable in New South Wales state waters.

3.1 Introduction

Remote oceanic islands represent areas of global biological significance as they often support disproportionate levels of biodiversity, including many endemic species (Allen 2008). Biodiversity associated with small remote oceanic islands are also more vulnerable to stochastic natural disturbances and anthropogenic threats as species often have restricted ranges and low abundances making them prone to extinction (Kier et al., 2009). Consequently, it is important that remote oceanic islands receive appropriate conservation management to protect their unique biodiversity and maintain ecosystem functioning (Edgar et al., 2010). Furthermore, established conservation strategies on remote oceanic islands, such as Marine Protected Areas (MPAs), require consistent and accurate assessments to determine whether management practices are adequately safeguarding biodiversity.

Lord Howe Island and its satellite island; Balls Pyramid fit the description of remote oceanic islands with unique biodiversity and natural history. Located 610 km off the east coast of northern NSW, Australia, at a latitude of 31°50'S in the South Pacific Ocean, the region lies on the Tasman Front; the oceanographic boundary between tropical and temperate water masses (Nilsson and Cresswell 1980). As a result, the region has a unique composition of tropical, subtropical and temperate marine biota, including the southernmost coral reef co-existing with abundant and diverse temperate macro-algal communities (Edgar et al., 2010). Owing to the islands isolation, the region also supports high levels of endemism among algae, fishes and marine invertebrates. For these biological attributes, Lord Howe Island received UNESCO World Heritage listing in 1982 (Environment Australia 2000).

In response to concerns over anthropogenic threats to Lord Howe Island's marine biodiversity, Marine Protected Areas (MPAs) have been established around

the island with an aim to protect biodiversity and maintain ecological processes (*Marine Parks Act, 1997*). In 1999 the NSW government proclaimed the Lord Howe Island Marine Park in state waters (<3 nm from land) and in 2000 the Commonwealth Marine Park was proclaimed by the federal government in the adjacent waters (3 nm – 12 nm) (*Marine Parks Act, 1997; Commonwealth Environment Protection and Biodiversity Conservation Act, 1999*). In an attempt to manage anthropogenic threats, two MPA management zones were established in the federal and state waters. The first, sanctuary zones (SZs), are strictly no-take marine reserves that prohibit extractive activities. The second, habitat protection zones (HPZs), are partially protected area allowing some forms of fishing (Kelaher et al., 2014), such as charter boat operations and recreational line fishing. Across the entire state and federal waters of the Lord Howe Island Marine Park (LHIMP), spearfishing and any form of commercial fishing, such as longlining and demersal trawling is banned. Enforcement of the zoning regulations came into effect in the state and federal waters in 2004 and 2002 respectively.

The LHIMP comprises a rich assemblage of fishes, with more than 490 species documented in its waters, most of which inhabit coastal inshore areas (Allen and Paxton 1974; Allen, et al., 1976; Francis 1991; Francis 1993; Francis and Randall 1993; Parker 1993). Most species are tropical with broad biogeographic ranges, however total biomass of fishes is heavily skewed towards temperate species (Edgar et al., 2010). Approximately 4% of the inshore fishes are endemic to the Lord Howe Island and Norfolk Island region, making it one of the world's most important regions for endemic fishes (Allen et al., 1976). The LHIMP fish assemblage also comprises of other species of special importance such as galapagos whalers (*Carcharhinus galapagensis*) and doubleheader wrasse (*Coris bulbifrons*) which are

listed as ‘near threatened’ and ‘vulnerable’ under the IUCN red list, respectively (Choat and Pollard 2010). Under the NSW *Fisheries Management Act*, 1994, 2 species of fish; black rockcod (*Epinephelus daemeli*) and ballina angelfish (*Chaetodontoplus ballinae*) are protected in state waters. Several species from Lord Howe Island’s fish assemblage are targeted by recreational fishers and commercial charter boat fishing operations. The predominant target species are yellowtail kingfish (*Seriola lalandi*) and silver trevally (*Pseudocaranx dentex*) which are sold by charter boat operators under a special fisheries arrangement to local restaurants on the island (effectively the sole providers of fresh fish to the island’s local and tourist population) (Figueira and Hunt 2012). To a lesser extent fishers target emperor (*Lethrinus spp.*), bluefish (*Girella cyanea*) and *C. bulbifrons* as well as seasonal pelagic fishes such as wahoo, tuna and billfish. Fishing activity is likely to result in by-catch of certain species; most notably galapagos whalers (*C. galapagensis*) that often depredate hooked catch (pers. Obs.). Although fishing pressure before and after the implementation of the LHIMP is likely to be low (Edgar et al., 2010), the potential impact of fishing on species abundances and ecosystem functioning has not been assessed (Neilson et al., 2010). Only one study has examined the effectiveness of the LHIMP management zones in safeguarding the regions fish assemblage which focussed on shallow-water inshore habitats (Edgar et al., 2010). No research has evaluated the LHIMP zoning on fish assemblages occupying the extensive shelf habitat (20 – 50 m) of Lord Howe Island and Balls Pyramid. Therefore, whether the LHIMP zoning is safeguarding biodiversity in this habitat type remains unknown. This is despite the shelf habitat being the most extensive habitat type protected in state waters of the LHIMP.

In this study we tested for differences in the fish assemblage between management zones within the LHIMP after approximately 5 and 9 years of the MPAs establishment. As the LHIMP is relatively pristine, with low levels of anthropogenic impacts (for example no commercial fishing) we predicted that the abundance of common (defined as >50% of survey replicates), endemic, near endemic and protected species would not be influenced by MPA zoning. Additionally, the LHIMP displays four of the five attributes found to increase the conservation benefits on MPAs (Edgar et al., 2014), that is the presence of no-take zones, strong enforcement, old age (>10 years) and isolated by deep water or sand. Consequently, we predicted that the current LHIMP zoning arrangement will be adequately safeguarding the regions biodiversity within SZs and HPZs. In contrast, we predicted that species targeted by recreational and charter boat fishers would show an effect of MPA zoning with higher abundances inside SZs compared to HPZs where fishing is permitted.

3.2 Materials and methods

Fish assemblages were surveyed using baited remote underwater video systems (BRUVS). BRUVS contained Canon HG21 video cameras within underwater camera housings constructed by SeaGIS Pty. Sixteen sites were sampled on the Lord Howe Island and Balls Pyramid shelf comprising coral reef, relict reef, rubble and rock habitat between the depth of 25 and 50 metres. Eight sites were in the Commonwealth Marine Park and eight sites in the state LHIMP, with an even sampling effort between SZs and HPZs (n = 8 per zone) (Fig. 3.1). At each site, 4 BRUVS were deployed at least 200m apart for a minimum of 35 minutes to ensure a 30 min sample. Previous studies have indicated that a 30 min deployment provides a

representative sample fish assemblages at this latitude (Harasti et al., 2015). Each site was sampled in 2009 and 2013 during daylight hours. In 2009, sampling occurred between 10th to 19th of November and in 2013 between 22nd to 30th April. For the 2009 sampling, bait consisted of 1 kg of crushed pilchards (*Sardinops sagax*); a highly effective bait (Wraith et al., 2013). Due to a limited supply of bait, the same kilogram of bait was re-used for up to 4 BRUVS deployments. In 2013, prior to deploying the units, the bait bags were replenished with 500g of freshly crushed pilchards.

Footage from BRUVS was analysed in the laboratory using Event measure software (SeaGIS Pty). For each deployment species richness and relative abundance (Max N) was recorded. Species richness was the number of species of fish observed during the each BRUVS deployment. The relative abundance of fishes, Max N, was the maximum number individuals of one species viewed at any one time during the sample (Cappo et al., 2004). Max N values for individual species were then summed to generate total relative abundance, Total Max N, for each sample.

Multivariate and univariate PERMANOVA analyses (Clarke 1993; Anderson et al., 2001) were carried out with the PRIMER-E v7 package using type III sums of squares with 9999 permutations. Multivariate differences in fish assemblages between management zones were tested using a 4 factor PERMANOVA on Bray-Curtis dissimilarity values calculated from fourth root transformed data. The factors were year (2 levels and random), zone (2 levels and fixed; SZ and HPZ), location (4 levels nested within zone and random) and site (2 levels nested within location and random). Non-metric multidimensional scaling (nMDS) was used to generate two-dimensional ordinations to illustrate patterns in the fish assemblage. Univariate analyses to examine differences in Total MaxN, species richness and the abundance

of key species were tested using 4 factor PERMANOVA's with the factors as previously described for the multivariate analyses. All univariate analyses were completed using Euclidian distance to create similarity matrices.

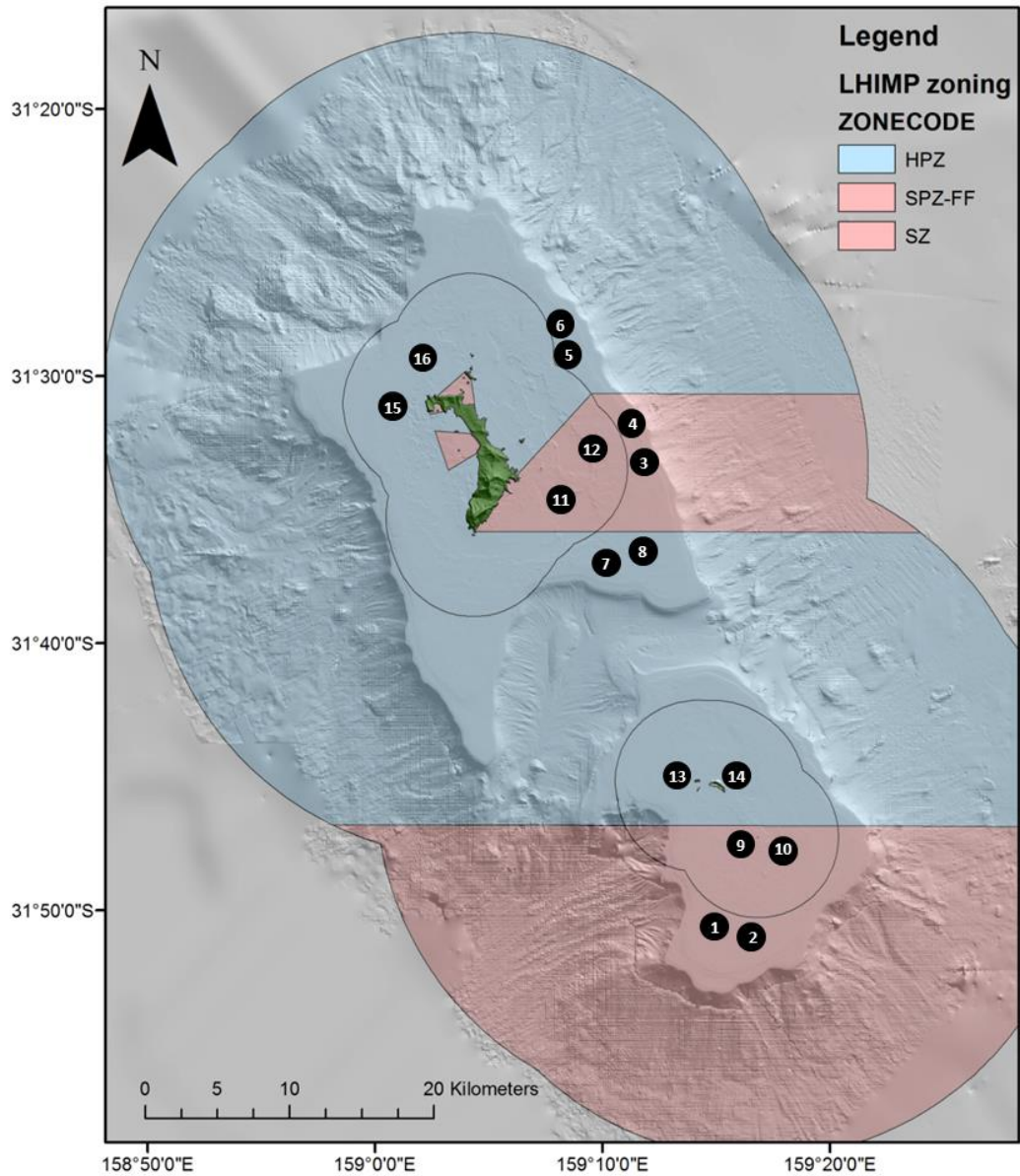


Figure 3.1 A map of survey sites in the Lord Howe Island Marine Park. The Lord Howe Island shelf is in the north and the Balls Pyramid shelf to the south. Regions in pink represent Sanctuary Zones (SZ) while regions in blue, Habitat Protection Zones (HPZ). Note the 2 sites within each location.

Key species included those that were common, targeted or caught as by-catch by fishers. We also included endemic, near endemic or protected fishes under the Fisheries Act of 1994. Common species were those recorded on >50% of deployments across both years (*Chaetodontoplus conspicillatus*, *Coris picta*, *Pseudolabrus luculentus*, *Sufflamen fraenatum* and *Thamnaconus analis*). Fished species were *Lethrinus nebulosus*, *Pseudocaranx dentex* and *Seriola lalandi* (Figueira and Hunt 2012). Galapagos whaler sharks; *Carcharhinus galapagensis* were also included in this category as they are often caught as by-catch and usually released alive by charter fishing operators (Figueira and Hunt 2012). Endemic and near endemic species included *Amphichaetodon howensis*, *Genicanthus semicinctus*, *Scorpaena cookii* and *Coris bulbifrons*. A number of endemic, near endemic and protected species displayed patchy distributions with low abundances making robust statistical analyses difficult. For these species; *Chaetodon tricinctus*, *Chaetodontoplus ballinae*, *Epinephelus daemeli* and *Girella cyanea*, patterns between management zones were described. *Post hoc* pairwise comparisons were made on terms of interest in the model that were statistically significant in the main PERMANOVA analysis. Monte Carlo random draws were used to obtain correct P-values where sufficient permutations (< 50) were not available in pair wise analyses (Anderson et al., 2008). Following PERMANOVA, *post-hoc* pooling of lower order terms was performed if $P > 0.25$, to increase the power of the main tests (Underwood 1997).

3.3 Results

In total, 6657 individuals from 106 species were recorded from BRUVS deployments in 2009 and 2013. The structure of the fish assemblages did not differ

between SZs and HPZs nor was there an interaction between zone and year (Table 3.1, Fig. 3.2). There were however, differences in the structure of the fish assemblage between years and among locations (Table 3.1; Fig. 3.2). Similarly to the multivariate analysis, there was no difference in total MaxN and species richness of fishes between SZs and HPZs (Table 3.2; Fig. 3.3). The abundance of fishes differed among sites between years (Table 3.2a; Fig. 3.3) and there were locational differences in fish diversity (Table 3.2b; Fig. 3.3).

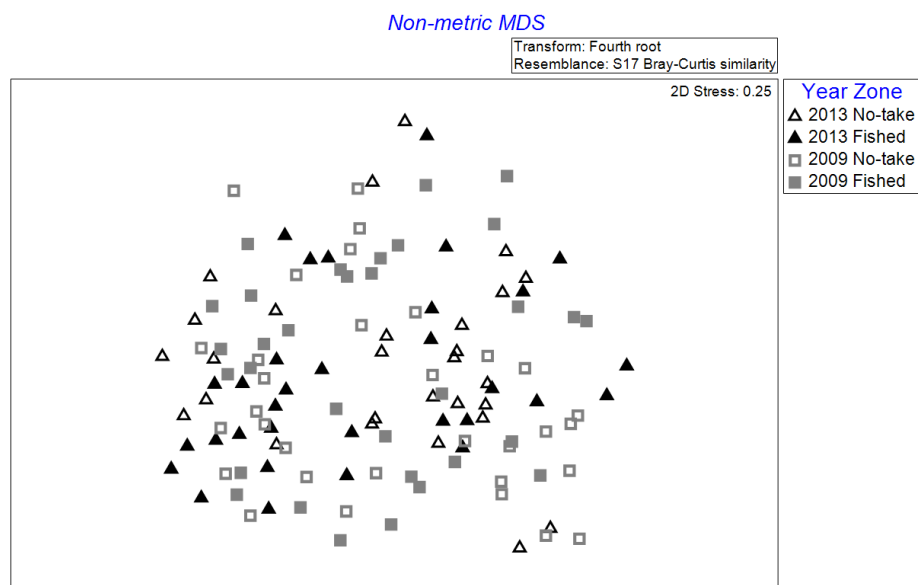


Figure 3.2 Non-metric multidimensional scaling (nMDS) ordination of Lord Howe Island fish assemblage. Points closer together in ordination space represent sites with more similar species compositions.

The abundance of common species; *Chaetodontoplus conspicillatus*, *Coris picta*, *Pseudolabrus luculentus*, *Sufflamen fraenatum* and *Thamnaconus analis* were not influenced by zone (Table 3.3; Fig. 3.4). In general, abundances were highly variable between years at the site level (Fig. 3.4). The abundance of *S. fraenatum* differed between years with a greater abundance observed in 2013 compared to 2009 (Table 3.3d, Fig. 3.4).

Table 3.1 Results of a permutational multivariate analysis of variance (PERMANOVA) comparing demersal fish assemblages between zones using Bray-Curtis similarity measures following fourth root transformations. Factors were: Year (Ye, random with 2 levels: 2009 and 2013), Zone (Zo, fixed with 2 levels: SZ and HPZ), Location (Lo, random with 4 levels nested in zone) and Site (Si, random with 2 levels nested in location). Values in bold indicate statistical significance at $\alpha = 0.05$.

Source	df	SS	MS	Pseudo-F	P(perm)
Ye	1	8694	8694	3.91	0.013
Zo	1	4541	4541	0.62	0.877
Lo(Zo)	6	50828	8471	2.15	0.004
YexZo	1	2590	2591	1.17	0.345
Si(Lo(Zo))	8	21695	2712	1.26	0.159
YexLo(Zo)	6	13373	2229	1.04	0.439
YexSi(Lo(Zo))	8	17170	2146	1.24	0.097
Res	92	159810	1737		
Total	123	279860			

The abundance of fished species; *Lethrinus nebulosus*, *Pseudocaranx dentex*, *Seriola lalandi* and *Carcharhinus galapagensis* did not differ between SZs and HPZs (Table 3.4; Fig. 3.5). Strong locational effects were observed for *C. galapagensis* and *S. lalandi* (Table 3.4a, d) while *L. nebulosus* and *P. dentex* differed among sites and times of sampling (Table 3.4b, c).

Although not significant, there was 2.3 times greater abundance of *S. lalandi* in SZs compared to HPZs but this was due to one location which consistently recorded high abundances of these individuals (Fig. 3.5). There was also a weak trend for higher abundances of *L. nebulosus* in SZs compared to HPZs in 2013 (Fig. 3.5).

Table 3.2 Results of a PERMANOVA comparing a) total MaxN and b) Species Richness between zones using Euclidian distance. Factors were as listed in Table 3.1. Values in bold indicate statistical significance at $\alpha = 0.05$.

Source	df	SS	MS	Pseudo-F	P(perm)	Source	df	SS	MS	Pseudo-F	P(perm)
a) MaxN						b) Species Richness					
Ye	1	3290	3290	0.86	0.377	Ye	1	25.2	25.2	0.52	0.493
Zo	1	7828	7828	0.83	0.563	Zo	1	0.4	0.4	0.19	0.945
Lo(Zo)	6	45289	7548	2.01	0.103	Lo(Zo)	6	610.4	101.7	1.58	0.043
YexZo	1	6502	6502	1.70	0.237	YexZo	1	149.2	149.2	3.09	0.133
Si(Lo(Zo))	8	31036	3880	0.49	0.834	Si(Lo(Zo))	8	287.6	35.9	1.14	0.341
YexLo(Zo)	6	22926	3821	0.48	0.810	YexLo(Zo)	6	291.1	48.5	1.54	0.171
YexSi(Lo(Zo))	8	63315	7914	2.06	0.044	Pooled	100	3146.7	31.5		
Res	92	352730	3834			Total	123	4561.0			
Total	123	533730									

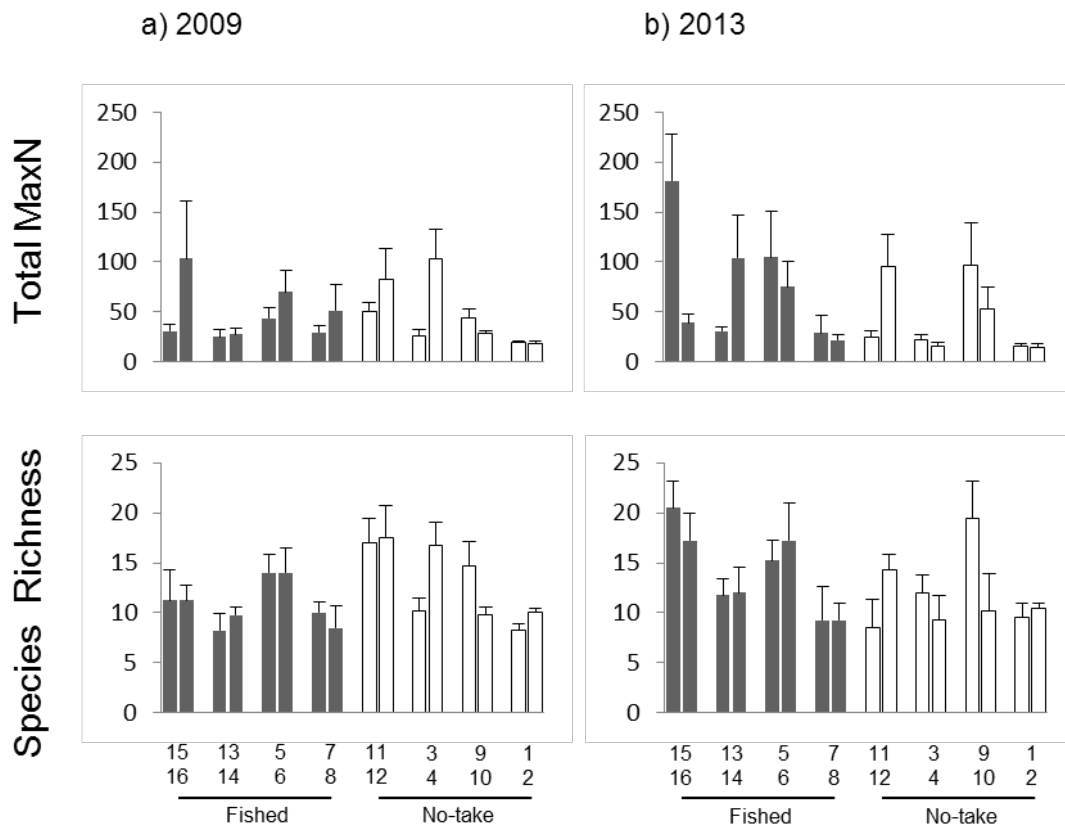


Figure 3.3 Mean (\pm SE) Total N and species richness between zones in 2009 and 2013 ($n = 4$). Shaded bars represent fished sites (HPZ) and clear bars represent no-take sites (SZ).

Table 3.3 Results of a PERMANOVA comparing the abundance of common species; conspicuous angelfish (*Chaetodontoplus conspicillatus*), comb wrasse (*Coris picta*), luculentus wrasse (*Pseudolabrus luculentus*), masked triggerfish (*Sufflamen fraenatum*) and darkvent leatherjacket (*Thamnaconus analis*) between zones using Euclidian distance. Factors are the same as those listed in Table 3.1. Values in bold indicate statistical significance at $\alpha = 0.05$.

Source	df	SS	MS	Pseudo-F	P(perm)	Source	df	SS	MS	Pseudo-F	P(perm)
a) <i>C. conspicillatus</i>						b) <i>C. picta</i>					
Ye	1	6.4	6.4	1.81	0.231	Ye	1	7.4	7.4	0.83	0.455
Zo	1	0.8	0.8	1.86	0.263	Zo	1	47.1	47.1	1.44	0.354
Lo(Zo)	6	12.8	2.1	0.64	0.362	Lo(Zo)	6	132.1	22.0	2.13	0.093
YexZo	1	0.2	0.2	0.06	0.806	YexZo	1	17.0	17.0	1.91	0.222
Si(Lo(Zo))	8	14.3	1.8	1.37	0.217	Si(Lo(Zo))	8	58.1	7.3	0.58	0.774
YexLo(Zo)	6	21.4	3.6	2.74	0.017	YexLo(Zo)	6	53.6	8.9	0.71	0.651
Pooled	100	130.0	1.3			YexSi(Lo(Zo))	8	100.5	12.6	1.93	0.064
Total	123	187.0				Res	92	599.1	6.5		
						Total	123	1040.7			
c) <i>P. luculentus</i>						d) <i>S. fraenatum</i>					
Ye	1	15.9	15.9	3.71	0.105	Ye	1	8.1	8.1	14.69	0.011
Zo	1	1.3	1.3	0.58	0.710	Zo	1	0.4	0.4	1.38	0.364
Lo(Zo)	6	47.4	7.9	1.49	0.232	Lo(Zo)	6	1.8	0.3	0.74	0.286
YexZo	1	1.8	1.8	0.41	0.538	YexZo	1	0.4	0.4	0.68	0.452
Si(Lo(Zo))	8	33.3	4.2	0.88	0.576	Si(Lo(Zo))	8	1.8	0.2	0.79	0.616
YexLo(Zo)	6	25.8	4.3	0.91	0.525	YexLo(Zo)	6	3.3	0.6	1.96	0.075
YexSi(Lo(Zo))	8	38.0	4.7	1.95	0.060	Pooled	100	28.1	0.3		
Res	92	224.0	2.4			Total	123	44.2			
Total	123	395.7									
e) <i>T. analis</i>											
Ye	1	3.3	3.3	3.28	0.118						
Zo	1	0.8	0.8	1.28	0.406						
Lo(Zo)	6	7.8	1.3	0.73	0.299						
YexZo	1	0.2	0.2	0.16	0.714						
Si(Lo(Zo))	8	13.7	1.7	2.46	0.017						
YexLo(Zo)	6	6.1	1.0	1.47	0.205						
Pooled	100	69.9	0.7								
Total	123	102.0									

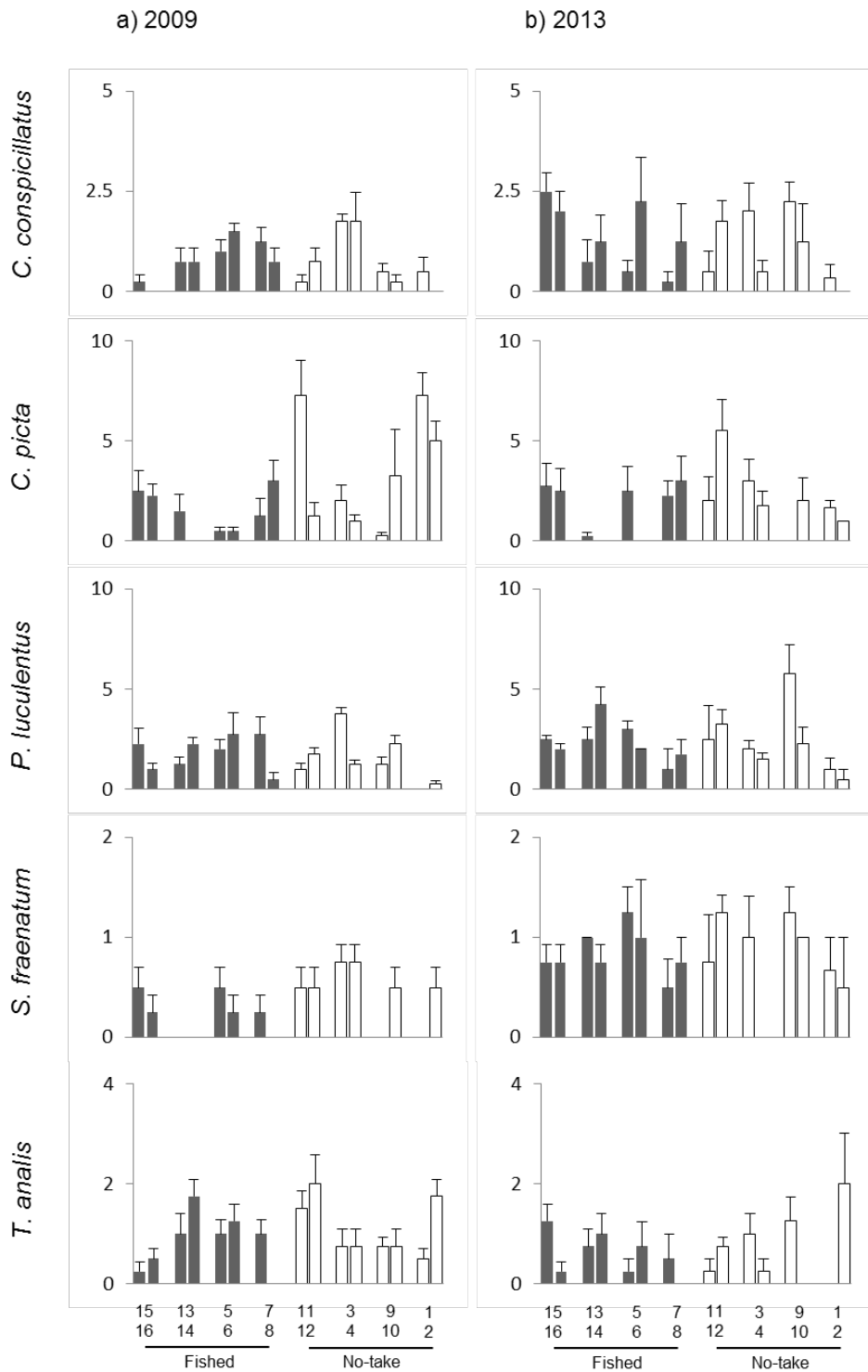


Figure 3.4 Mean (\pm SE) abundance of common species; Conspicuous Angelfish (*Chaetodontoplus conspicillatus*), Comb Wrasse (*Coris picta*), Luculentus Wrasse (*Pseudolabrus luculentus*), Masked Triggerfish (*Sufflamen fraenatum*) and Darkvent Leatherjacket (*Thamnaconus analis*) between zones in 2009 and 2013 ($n = 4$). Shaded bars represent fished sites (HPZ) and clear bars represent no-take sites (SZ).

Table 3.4 Results of a PERMANOVA comparing the abundance of fished and by-catch species; galapagos whalers (*Carcharhinus galapagensis*), spangled emperor (*Lethrinus nebulosus*), silver trevally (*Pseudocaranx dentex*) and yellowtail kingfish (*Seriola lalandi*) between zones using Euclidian distance. Factors are the same as those listed in Table 3.1. Values in bold indicate statistical significance at $\alpha = 0.05$.

Source	df	SS	MS	Pseudo-F	P(perm)	Source	df	SS	MS	Pseudo-F	P(perm)
a) <i>C. galapagensis</i>						b) <i>L. nebulosus</i>					
Ye	1	5.1	5.1	0.71	0.406	Ye	1	0.6	0.6	1.31	0.294
Zo	1	17.2	17.2	0.65	0.462	Zo	1	0.2	0.2	0.31	0.883
Lo(Zo)	6	159.7	26.6	3.73	0.001	Lo(Zo)	6	10.2	1.7	1.62	0.184
Pooled	115	819.7	7.1			YexZo	1	0.4	0.4	0.79	0.401
Total	123	1000.8				Si(Lo(Zo))	8	10.6	1.3	1.13	0.425
						YexLo(Zo)	6	2.7	0.5	0.39	0.876
						YexSi(Lo(Zo))	8	9.3	1.2	2.09	0.041
						Res	92	51.3	0.6		
						Total	123	85.4			
c) <i>P. dentex</i>						d) <i>S. lalandi</i>					
Ye	1	0.2	0.2	0.04	0.847	Ye	1	0.3	0.3	0.04	0.897
Zo	1	0.6	0.6	0.25	0.916	Zo	1	14.8	14.8	0.60	0.343
Lo(Zo)	6	64.0	10.7	1.27	0.260	Lo(Zo)	6	213.1	35.5	3.17	0.001
YexZo	1	9.9	9.9	2.20	0.178	YexZo	1	1.3	1.3	0.17	0.784
Si(Lo(Zo))	8	65.8	8.2	1.48	0.268	Si(Lo(Zo))	8	89.7	11.2	1.52	0.091
YexLo(Zo)	6	27.2	4.5	0.82	0.598	Pooled	106	782.3	7.4		
YexSi(Lo(Zo))	8	44.5	5.6	3.14	0.004	Total	123	1106.4			
Res	92	162.8	1.8								
Total	123	360.9									

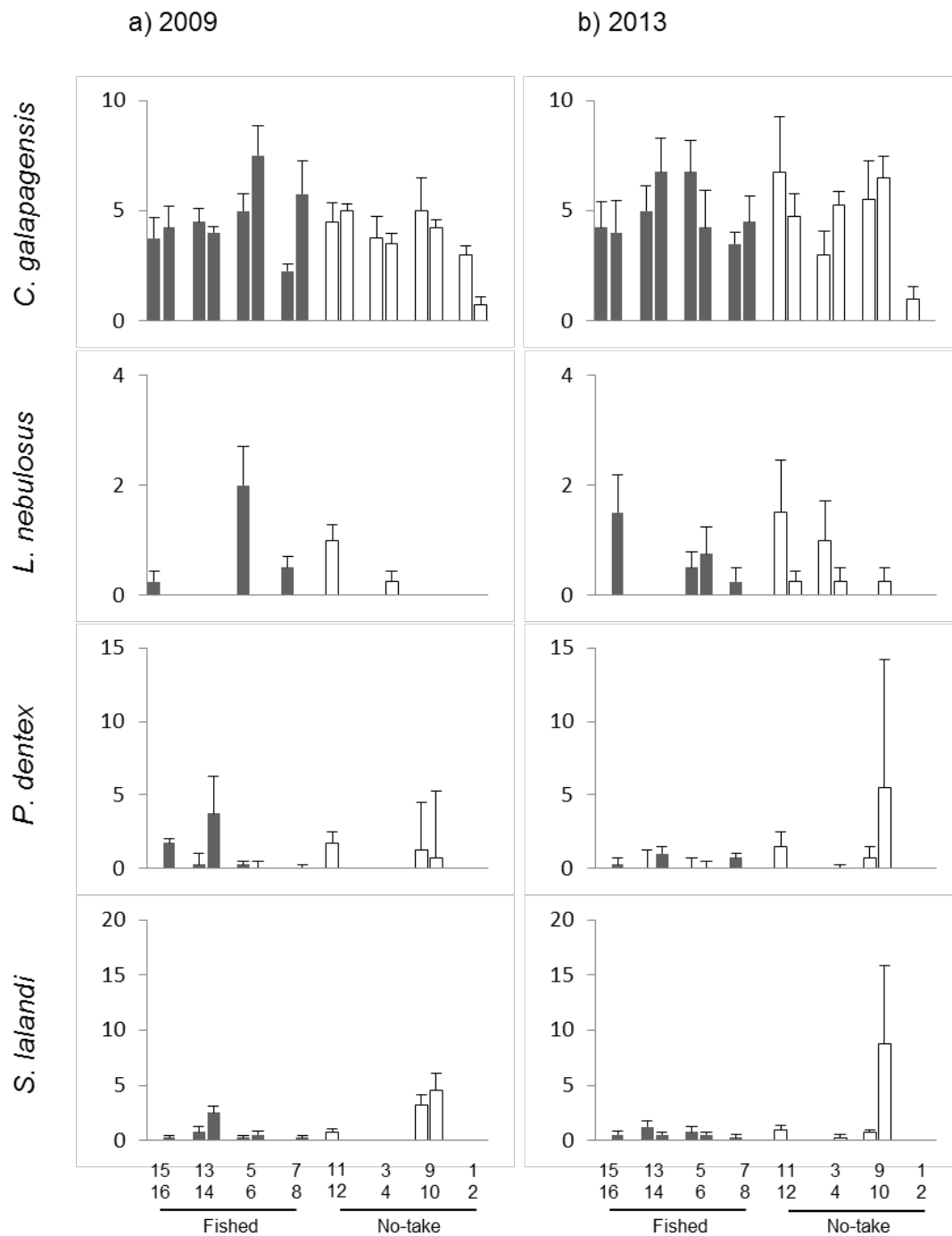


Figure 3.5 Mean (\pm SE) abundance of fished and by-catch species; galapagos whalers (*Carcharhinus galapagensis*), spangled emperor (*Lethrinus nebulosus*), silver trevally (*Pseudocaranx dentex*) and yellowtail kingfish (*Seriola lalandi*) between zones in 2009 and 2013 (n = 4). Shaded bars represent fished sites (HPZ) and clear bars represent no-take sites (SZ).

The abundance of endemic or near endemic species; *Amphichaetodon howensis*, *Genicanthus semicinctus* and *Scorpaena cookii* did not differ between management zones (Table 3.5, Fig. 3.6). The lord howe island butterflyfish; *A. howensis* exhibited strong spatio-temporal variation among sites and year while the abundance of *G. semicinctus* was strongly influenced by location (Table 3.5a, b; Fig. 3.6). There was a significant difference in the abundance of *S. cookii* among locations and between years, with a greater abundance observed in 2013 compared to 2009 (Table 3.5c, Fig. 3.6). The endemic, *Coris bulbifrons* differed between years but only in HPZ zones, where in 2013 there was a greater abundance compared to 2009 (Table 3.5d). There was a trend for more *C. bulbifrons* in SZs than HPZs in 2009, this however, was not statistically significant (Fig. 3.6).

Other endemic, near endemic and protected species displayed low abundances and patchy distributions among replicates, sites, locations and zones. Therefore, it is only possible to describe clear spatial patterns for these species. The abundance of *Chaetodon tricinctus* appears to be stable between years as individuals were observed at 5 sites in 2009 and 6 sites in 2013. In each year individuals were observed at 2 sites within SZs (Fig. 3.7). The ballina angelfish; *Chaetodontoplus ballinae*, exhibited a distinct pattern in their spatial distribution, observed only at one location (site 1 and 2) across both years (Fig. 3.7). There was an apparent decline in the number of individuals of the protected *Epinephelus daemeli* between years with 10 individuals observed in 2009 while only 6 in 2013. *E. daemeli* were only observed at one site within SZs in 2013 compared to 3 sites in 2009 (Fig. 3.7). A decline in the number of protected *Girella cyanea* was also apparent between 2009 and 2013, with 30 individuals observed in 2009 and just 7 in 2013 (Fig. 3.7). Additionally, *G. cyanea* were only observed at 2 sites in 2013 compared to 5 sites in

2009. The highest abundances of *G. cyanea* observed in both years were at the HPZ location containing site 5 and 6 (Fig. 3.7).

Table 3.5 Results of a PERMANOVA comparing the abundance of endemic, near endemic and protected species; lord howe island butterflyfish (*Amphichaetodon howensis*), halfbanded angelfish (*Genicanthus semicinctus*), cook’s scorpionfish (*Scorpaena cookii*) and doubleheader wrasse (*Coris bulbifrons*) between zones using Euclidian distance. Factors are the same as those listed in Table 3.1. Values in bold indicate statistical significance at $\alpha = 0.05$.

Source	df	SS	MS	Pseudo-F	P(perm)	Source	df	SS	MS	Pseudo-F	P(perm)
a) <i>A. howensis</i>						b) <i>G. semicinctus</i>					
Ye	1	0.1	0.1	0.29	0.604	Ye	1	0.2	0.2	0.05	0.835
Zo	1	0.0	0.0	0.08	0.995	Zo	1	0.3	0.3	0.04	0.892
Lo(Zo)	6	18.5	3.1	4.35	0.007	Lo(Zo)	6	52.4	8.7	2.14	0.040
YexZo	1	2.4	2.4	5.91	0.052	Pooled	115	469.0	4.1		
Si(Lo(Zo))	8	5.1	0.6	0.45	0.864	Total	123	522.1			
YexLo(Zo)	6	2.4	0.4	0.28	0.930						
YexSi(Lo(Zo))	8	11.4	1.4	2.45	0.017						
Res	92	53.5	0.6								
Total	123	94.2									
c) <i>S. cookii</i>						d) <i>C. bulbifrons</i>					
Ye	1	4.3	4.3	6.31	0.048	Ye	1	0.7	0.7	2.59	0.113
Zo	1	0.5	0.5	0.30	0.898	Zo	1	0.1	0.1	0.11	0.724
Lo(Zo)	6	9.3	1.6	2.30	0.012	Lo(Zo)	6	2.9	0.5	1.86	0.085
YexZo	1	2.4	2.4	3.57	0.112	YexZo	1	3.1	3.1	11.91	0.001
Si(Lo(Zo))	8	1.6	0.2	0.41	0.910	Pooled	114	29.9	0.3		
YexLo(Zo)	6	4.1	0.7	1.42	0.210	Total	123	36.7			
Pooled	100	48.2	0.5								
Total	123	70.5				pairwise comparison:		No-take: 2009=2013, Fished: 2009<2013			

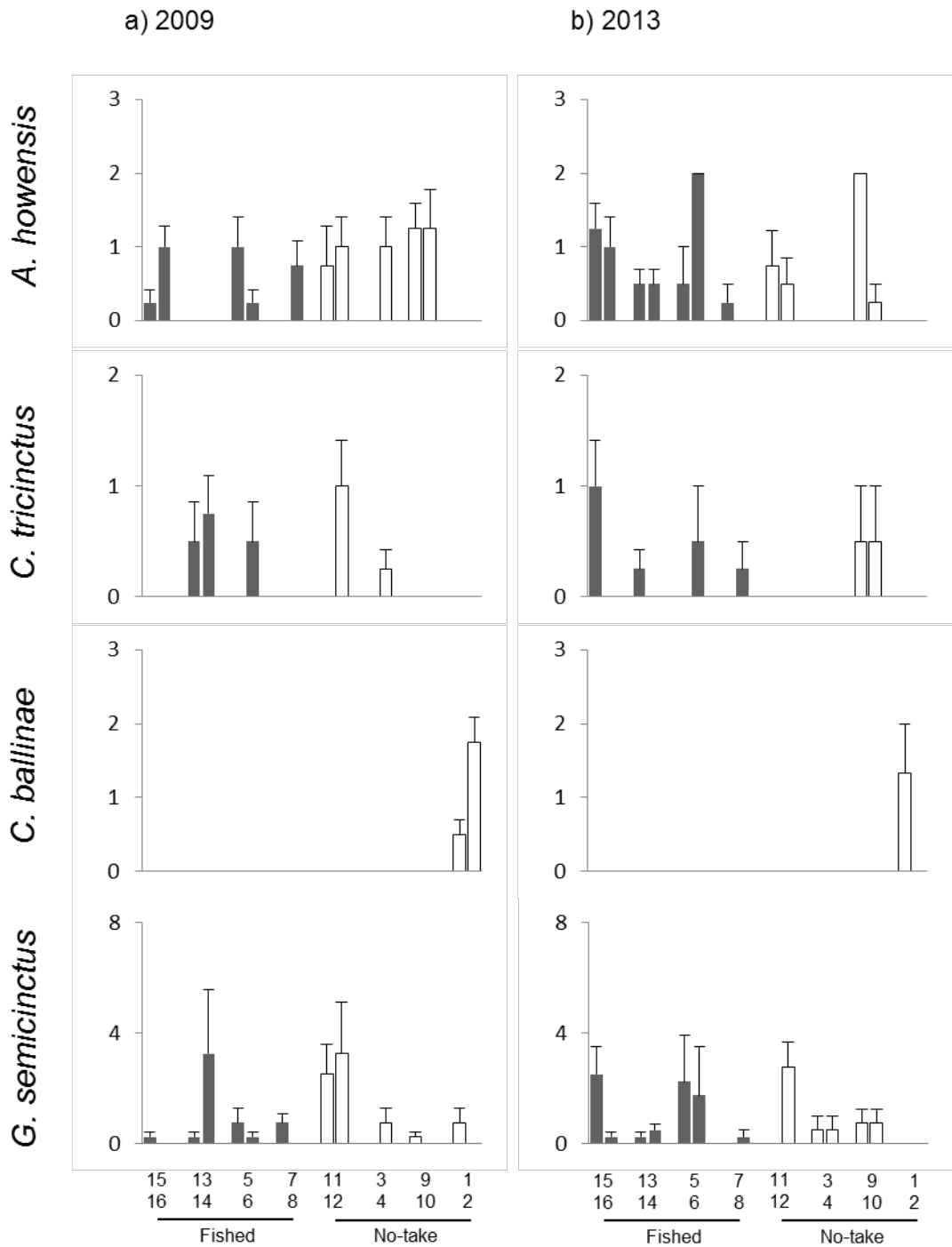


Figure 3.6 Mean (\pm SE) abundance of endemic, near endemic and protected species; lord howe island butterflyfish (*Amphichaetodon howensis*), threeband butterflyfish (*Chaetodon tricinctus*), ballina angelfish (*Chaetodontoplus ballinae*) and halfbanded angelfish (*Genicanthus semicinctus*) between zones in 2009 and 2013 (n = 4). Shaded bars represent fished sites (HPZ) and clear bars represent no-take sites (SZ).

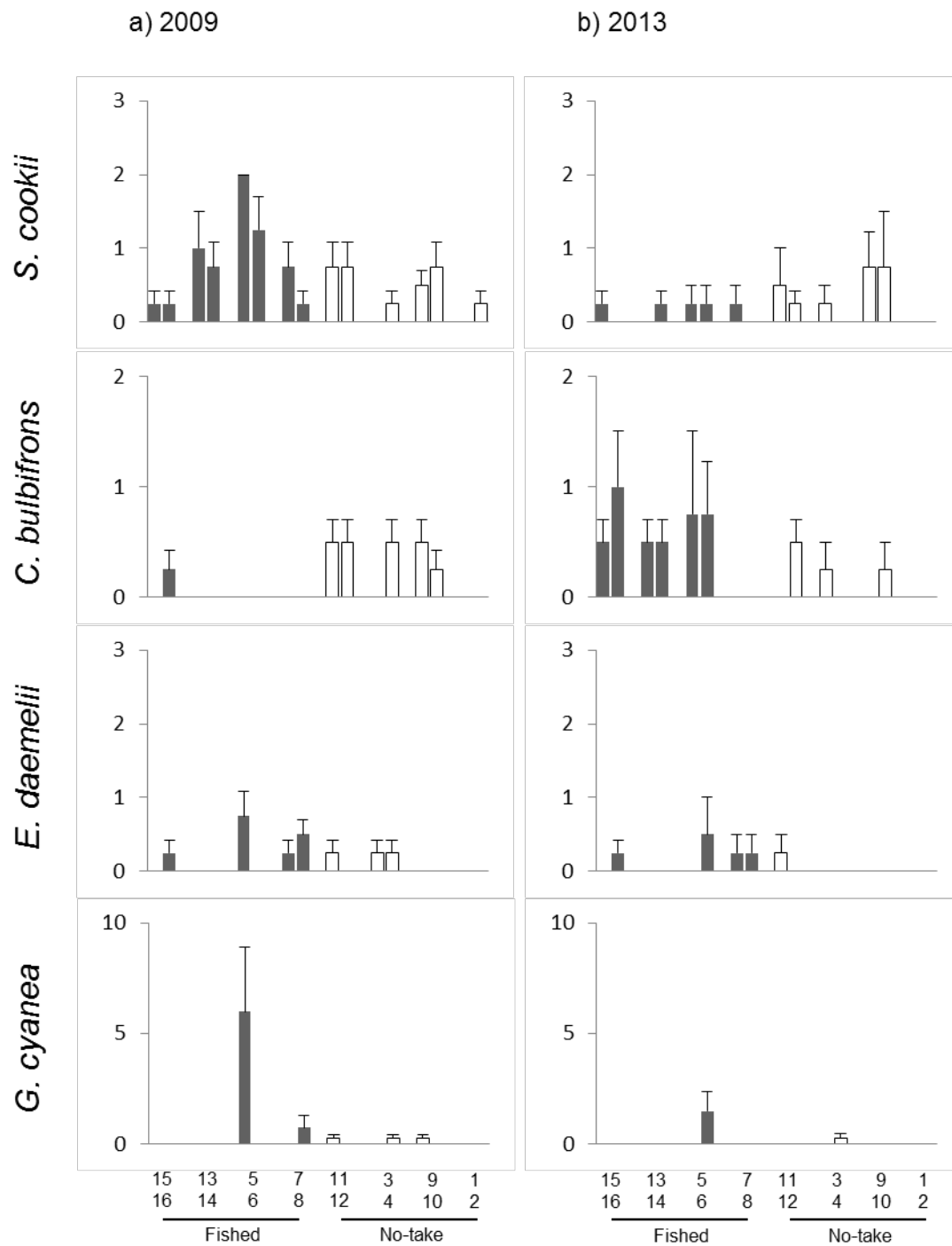


Figure 3.7 Mean (\pm SE) abundance of endemic, near endemic and protected species; cook's scorpionfish (*Scorpaena cookii*), doubleheader wrasse (*Coris bulbifrons*), black rockcod (*Epinephelus daemelii*) and bluefish (*Girella cyanea*) between zones in 2009 and 2013 (n = 4). Shaded bars represent fished sites (HPZ) and clear bars represent no-take sites (SZ).

3.4 Discussion

Our results reveal no effect of MPA zoning on the structure of Lord Howe Island's fish assemblage, total abundance, species richness and abundance of common species; *Chaetodontoplus conspicillatus*, *Coris picta*, *Pseudolabrus luculentus*, *Sufflamen fraenatum* and *Thamnaconus analis*. Similarly, endemic or near endemic species; *Amphichaetodon howensis*, *Genicanthus semicinctus*, *Scorpaena cookii* and *Chaetodon tricinctus* displayed no difference in abundance between management zones. The Doubleheader wrasse; *Coris bulbifrons* was the only species to show an effect of zoning, but surprisingly this was an increase in abundance within partially protected HPZs, rather than SZs in 2013. Of concern, two species protected in NSW waters; *Epinephelus daemeli* and *Girella cyanea* appear to be declining in their abundance and occurrence across the LHIMP over time. Contrary to our prediction, the cessation of fishing in no-take SZs had no effect on the abundance of targeted species *Lethrinus nebulosus*, *Pseudocaranx dentex*, *Seriola lalandi* and *Carcharhinus galapagensis*; a species caught as by-catch.

The lack of effect of MPA zoning might seem unexpected considering the LHIMP almost reaches the five criteria for a successful MPA as outlined by Edgar et al., (2014). Undertaking a global analysis on MPA effectiveness, Edgar et al. (2014) found conservation benefits of MPAs to increase exponentially with the accumulation of five attributes: the presence of no-take zones, large in size (>100 km²), strong enforcement, old age (>10 years) and isolated by deep water or sand. The LHIMP fits these criteria except for age, where at the time of the study, it was 9 and 10 years since establishment in state and federal waters respectively. Despite displaying these key attributes however, no effect of MPA zoning is unsurprising considering the relatively pristine condition of the LHIMP's marine environment and

minimal human impacts in the region. With no differences in most taxa explored between no-take and habitat protection zones through time, our results suggest that the LHIMP is adequately safeguarding the majority of the regions biodiversity.

Contrary to our hypothesis, fished species showed no response to the cessation of fishing with relatively similar abundances across management zones. This was unexpected, especially for *Seriola lalandi* and *Pseudocaranx dentex*, which are caught in high numbers by charter fishers for the local restaurant trade. No response of targeted species to MPA zoning contradicts some previous literature, such as Claudet et al., (2010) meta-analysis which indicates that commercially exploited species with relatively large home ranges can still show strong responses to protection. A likely explanation for the lack of differences between zones is sustainable levels of fishing operating within the LHIMP waters due to low fishing effort and strict fisheries regulations in catch size and bag limits. An alternate explanation, however, could be that our assessment of LHIMP efficacy for these species may have been confounded by underlying habitat variability (Huntington et al., 2010; Miller and Russ 2014). For example, one location in the Balls Pyramid sanctuary zone consistently recorded high abundances of *S. lalandi* and *P. dentex* across both years. These sites also displayed high reef structural complexity; a habitat attribute *S. lalandi* and *P. dentex* may preference. By inflating variance surrounding abundance estimates, underlying habitat differences among locations is likely to make detection of MPA zoning effects difficult. Future research accounting for habitat variability such as reef structural complexity, in the assessment of the LHIMP for *S. lalandi* and *P. dentex* will provide a more insightful evaluation of ecological changes associated with MPA zoning for these species.

The removal of fishing also did not influence the abundance of *Carcharhinus galapagensis* through time or space. As *C. galapagensis* is often incidentally caught as by-catch, this result suggests that the current level of fishing in the LHIMP is not a threatening process for this species. It is worth noting however, that this species is capable of moving large distances and consequently, results on spatial comparisons between management zones may need to be interpreted cautiously. Galapagos Whalers; *C. galapagensis* were the most prevalent species across the LHIMP being recorded on 96% of deployments. Compared to MPAs at similar latitudes on mainland Australia (Solitary Islands and Port Stephens-Great Lakes Marine Parks) the relative abundance of carcharinid sharks is substantially greater in the LHIMP (Malcolm et al., 2007). This is a promising finding given the global decline in shark numbers and their important trophic role in regulating marine ecosystems (Stevens et al., 2000; Dulvy et al., 2014). In fact, local opinion among fishers suggests that the number of *C. galapagensis* has increased dramatically in recent times (pers. comms). However, our findings do not support this observation as we recorded similar mean abundances between years (mean MaxN = 4.7 and 4.2 in 2013 and 2009, respectively) which are comparable to those observed by Speare et al., (2004) in the LHIMP's federal waters in 2004 (mean MaxN = 5).

Another key finding from the study was the discrete and consistent differences in the abundance of certain species among locations during both sampling periods. The protected *Girella cyanea*, were recorded in relatively high abundances at only one habitat protection zone location (site 5 and 6) through time. The result is likely to be driven by this location's shallower water and proximity to Lord Howe Island, as *G. cyanea* appear to be common in nearshore waters of the LHIMP (Edgar et al., 2010). During both sampling periods, the protected ballina

angelfish; *Chaetodontoplus ballinae*, also exhibited strong patterns in their spatial distribution, with individuals only being recorded at one location in the Balls Pyramid sanctuary zone. The presence of *C. ballinae* at this location is again likely to be related to depth, with sites at this location approximately 10 metres deeper compared to other locations. This observation confirms those by Speare et al. (2004) who recorded 12 individuals of *C. ballinae* on the deeper margins of the Lord Howe Island and Balls pyramid shelf (27 – 100 m) using BRUVS and towed video surveys. Therefore, it is likely that this species may be more common than previously thought and highlights the advantages of using remote survey techniques to sample biological assemblages at depths greater than conventional survey methods, such as SCUBA. Discrete and consistent differences among locations over time are important knowledge for the conservation management of the LHIMP, as it highlights the locations and their habitats that are representing and protecting biodiversity.

Most endemic, near endemic and protected species examined in this study displayed similar abundances between management zones and across time suggesting the LHIMP is providing adequate protection for these taxa. The endemic doubleheader wrasse; *Coris bulbifrons*, was the only species that appeared to respond to protection. Surprisingly, the abundance of *C. bulbifrons* increased in HPZs from 2009 to 2013. Across both zones, the number of individuals of *C. bulbifrons* observed doubled from 10 in 2009 to 20 in 2013, respectively. This is a promising finding given their restricted range, low abundances and their targeting by fishers in nearshore environments of Lord Howe Island (although catch and release is often practiced). Healthy numbers of *C. bulbifrons* is not surprising as recent genetic research has indicated that there are high levels of contemporary gene flow

between the populations in the LHIMP to surrounding islands (van der Meer et al., 2015). The abundance of the near endemic, *Scorpaena cookii*, was the only species in this category to significantly differ in their abundance over time, declining from an average of 0.6 ± 0.11 to 0.25 ± 0.08 individuals per deployment in 2009 to 2013 respectively.

Although the LHIMP appears to be safeguarding most of the regions biodiversity, the observed abundance of two protected species; *Epinephelus daemeli* and *Girella cyanea* declined between 2009 and 2013. This is potentially of concern particularly for *E. daemeli*, as Lord Howe Island is an important location for *E. daemeli*, which has a restricted distribution in the south-west Pacific, experienced overfishing (Pogonoski et al., 2002) and has low levels of recruitment (Harasti et al., 2014). Further research is needed to determine whether the decline in abundance of *E. daemeli* is a result of anthropogenic threats or natural temporal variability in population numbers. Patterns are unlikely to be due to temporal variability, however, as the species is very long lived (>50 years). We observed that the distribution of *E. daemeli* was exclusively restricted to the Lord Howe Island shelf and all individuals observed were adults. This observation is likely to be a result of the species life history, where larvae recruit into intertidal and shallow subtidal reef habitat then migrate onto deeper reefs with age (Francis et al., 2016). This may explain the prevalence of adults on the Lord Howe shelf and not the Balls Pyramid shelf and points to the important role of the Lord Howe Island lagoon and nearshore habitats in providing nursery areas for *E. daemeli*. This ontogenetic migration in *E. daemeli* also highlights the importance of cross shelf sanctuary zones in the LHIMP, especially as anecdotal evidence still suggests *E. daemeli* are subject to fishing pressure in the region due to accidental mortality during fishing (barotrauma and

shark attack) and misidentification (Neilson et al., 2010). Furthermore, zoning rearrangement in the LHIMP may benefit the *E. daemeli* population as abundances and detections are consistently higher at certain locations in HPZs compared to SZs. In contrast to *E. daemeli*, the decline in *G. cyanea* is unlikely to be of concern, as this species is more common in the nearshore habitats of Lord Howe Island, such as the lagoon (Hobbs et al., 2009). Differences between years are likely to be a result of their patchy distribution in deeper habitats and their schooling behaviour.

The temporal differences observed in the Lord Howe Island fish assemblages may not be indicative of changes in response to anthropogenic threats however, but rather due to natural variability or discrepancies in our sampling method between years. For example, the 2009 sampling was completed in November where the average sea temperature was 21°C compared to 23°C degrees in April when the 2013 sampling was undertaken (Allen et al., 1976). This is likely to impact the composition of tropical, subtropical and temperate species within the assemblage. There were also differences in the amount of bait and degree of bait replenishment between 2009 and 2013 which may have driven the observed changes in the fish assemblage between the two sampling periods. In 2009, 1 kg of pilchards was used as bait and on occasion this bait was re-used for up to 4 BRUVS deployments. In contrast, 500g of fresh pilchards was used during the 2013 sampling. Finally, changes in species abundances may be due to natural fluctuations in species abundances due to successful recruitment years for example. Such cyclic patterns in species abundances have been observed over a 12-year period in an Australian mainland MPA at similar latitude (Malcolm et al., 2015). Despite disparities in our sampling time and method, consistent patterns among locations for certain species suggests that such discrepancies had a minimal impact on the temporal patterns we

observed. We encourage future BRUVS monitoring in the LHIMP to standardise sampling season and the amount of bait used to help disentangle MPA effects from sampling artefacts and natural variability.

3.5 Conclusions

Overall, the fish assemblages and abundance of key species was not influenced by ~9 years of protection in the LHIMP. This is likely to be a result of the relatively pristine environment and minimal anthropogenic threats that exist currently and prior to the establishment of the MPA. One protected species; *E. daemellii* appears to be declining in abundance across the LHIMP. A targeted monitoring program to better estimate population numbers of *E. daemellii* is needed to determine whether this decline is of concern. Despite this finding, many species, including targeted, endemic, near endemic and protected species displayed consistent abundances between zones and time, suggesting the LHIMP is safeguarding the regions unique marine biodiversity. We encourage future BRUVS surveys in the LHIMP replicating our methods to better understand the effects of MPA zoning as well as the spatio-temporal variability in the fish assemblage.

Chapter 4: ACCOUNTING FOR STRUCTURAL COMPLEXITY IMPROVES THE ASSESSMENT ON MARINE PROTECTED AREA EFFECTIVENESS

This chapter is currently under review in *Journal of Applied Ecology*.

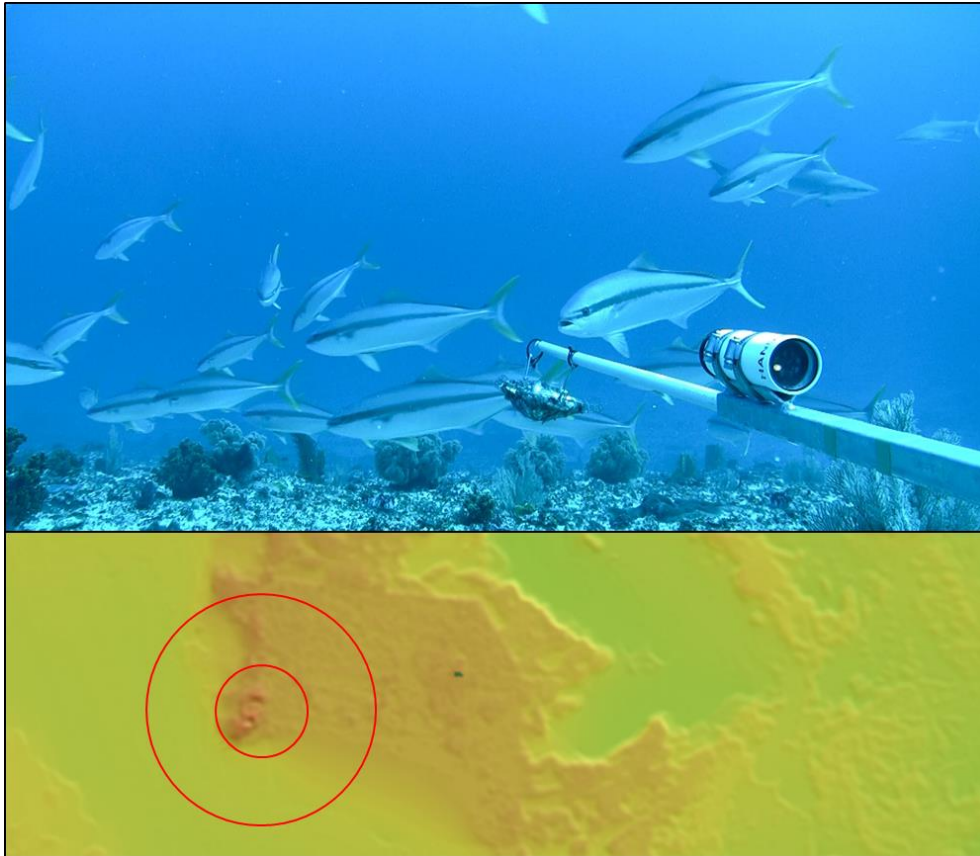


Plate 4.1 Top: A school of yellowtail kingfish (*Seriola lalandi*) recorded using a baited remote underwater video system in the Lord Howe Island Marine Park. Bottom: Bathymetric imagery of the Balls Pyramid shelf.

4.1 Introduction

Highlighted as an effective strategy to combat continued marine biodiversity loss, Marine Protected Areas (MPAs) have proliferated on a global scale in the last two decades (Halpern et al. 2010). To determine whether this management action is providing beneficial conservation outcomes, it is essential that MPAs are accurately assessed (McCook et al., 2010). Robust assessments on ecological change related to MPA management relies upon sampling designs capable of teasing apart the effects of protection on specific ecological attributes from underlying temporal and spatial variability (García-Charton and Pérez-Ruzafa 1999; García-Charton et al., 2000). If underlying natural variability is not accounted for, assessments on MPA effectiveness may be confounded, potentially providing misleading conclusions (Claudet and Guidetti 2000). A popular approach to date has been Before After Control Impact (BACI) experimental designs, which allow MPA effects to be separated from underlying natural variability (Underwood 1992). This methodology however, requires sampling of biological data multiple times prior to MPA establishment which rarely occurs (Halpern 2003). Instead, most studies use a Control Impact (CI) approach where biological assemblages within protected areas (preferably replicated areas) are compared to those in adjacent, or nearby, partially protected or unprotected areas (Lester et al., 2009; Sciberras et al., 2013; Miller and Russ 2014). Differences observed in biological assemblages among management zones are then inferred as evidence of an effect of MPA protection.

A potential issue for CI studies testing MPA effectiveness is that they may be confounded by seascape variability (Claudet and Guidetti 2010; Huntington et al., 2010; Osenberg et al., 2011). For example, in coral reef environments numerous studies have demonstrated the importance of habitat structural complexity as an

important driver of the diversity and abundance of fishes (Friedlander and Parrish 1998; Almany 2004; Gratwicke and Speight 2005). Previous research has demonstrated that coral reef habitat of greater structural complexity generally display a greater diversity and biomass of fishes compared to reefs of low structural complexity. This relationship is likely to be a result of structurally complex habitats providing increased abiotic variability, niches, resources and productivity (Bell et al., 1991; Friedlander and Parrish, 1998). Therefore, if structural complexity varies among management zones and is not accounted for in CI assessments on MPA effectiveness, there is a risk that incorrect conclusions may be drawn from such assessments (Young et al., 2016).

A possible solution to this issue is to include a measure of habitat structural complexity as a co-variate in statistical tests on MPA effectiveness. This approach would provide a more accurate and precise estimate on the effect of MPA protection, as variability associated with underlying seascape differences would be accounted for (Claudet and Guidetti 2010). In the past however, this has been problematic due to the difficulties and costs associated with collecting seascape data over the broad spatial scales that MPAs encompass. Recent advances in remote-sensing technologies now allow seafloor habitats to be mapped in high resolution over a range of spatial scales (Mellin et al., 2009; Brown et al., 2011). Consequently, marine ecologists have employed this technology to explore relationships between remotely-sensed seascape measures, such as structural complexity and biological assemblages in both coral and temperate rocky reef environments (Purkis et al., 2008; Pittman et al., 2009; Rees et al., 2014). As strong relationships between remotely-sensed measures and biological assemblages have been observed; habitat mapping has become increasingly used in guiding the design of MPAs (Pittman and

Brown 2011; Rees et al., 2014). Despite the applicability of this technology, the use of remote-sensing to account for potential seascape confounding in CI assessments is still in its infancy. This is most likely a result of the relatively high costs and limited availability of this technology throughout many regions of the world. However, as remote-sensing technologies become more cost effective and readily available (Mellin et al., 2009; Brown et al., 2011; Ierodiaconou et al., 2011), the application of this approach to aid MPA assessments is likely to become more feasible.

In this study, we tested the effectiveness of no-take marine reserves in the Lord Howe Island Marine Park (LHIMP) while accounting for underlying differences in habitat structural complexity. The LHIMP is located 610 km's off the east coast of Australia in the subtropical region of the South Pacific Ocean. For many reasons the LHIMP provides an ideal system to test reserve performance while accounting for seascape differences. First, Lord Howe Island and its surrounding waters have significant biological value, comprising the world's southernmost coral reef, a diversity of both tropical and temperate taxa that includes a suite of endemic species (Edgar et al., 2010). Consequently, Lord Howe Island received World Heritage Listing in 1982 (Environment Australia 2000). Second, the LHIMP is positioned in the subtropics; a region prone to the effects of climate change (Edgar et al., 2010) and the Marine Park's remoteness and relatively small size makes it vulnerable to ongoing and increasing anthropogenic pressures (Edgar et al., 2010). Therefore, it is important that conservation efforts are adequately and accurately assessed. Finally, the Lord Howe Island shelf has been extensively mapped with high resolution sonar (~5 m resolution) to understand the geomorphology of relict coral reefs formed 7000 to 9000 years ago (Brooke et al., 2010). As a result,

quantification of reef structural complexity across the entire LHIMP shelf habitat is possible.

To determine the importance of accounting for habitat structural complexity in CI assessments of MPAs, we performed two assessments on the effectiveness of the LHIMP. The first, a traditional CI assessment and the second, a CI assessment including a measure of reef structural complexity. Both tests compared the effect of protection on the abundance of yellowtail kingfish (*Seriola lalandi*); a heavily exploited species of bony fish in the LHIMP (Figueira and Hunt 2012). We predicted that remotely-sensed habitat structural complexity and MPA zoning would influence the abundance of *S. lalandi*. Consequently, we hypothesised that the model including habitat structural complexity would be more parsimonious compared to the model excluding habitat structural complexity, therefore leading to a better assessment of MPA effectiveness.

4.2 Methods

The Lord Howe Island Marine Park is a multi-use marine park located 610 km off northern NSW Australia at latitude 31°50'S. The marine park covers the state and federal waters which surround Lord Howe Island and Balls Pyramid. State waters are <3 nautical miles (nm) surrounding the islands while federal waters 3 nm to 12 nm offshore. The study was undertaken on the Lord Howe Island and Balls Pyramid shelf between depths of (25 – 50 m). At this depth, 2 different management zones are interspersed throughout federal and state waters. The first, sanctuary zones (SZs) which are strictly no-take marine reserves that prohibit extractive activities. The second are habitat protection zones (HPZs) which are partially protected area

allowing some forms of fishing, such as charter boat operations and recreational line fishing (Fig. 4.1). These will be referred to as “fished” zones.

The abundance of yellowtail kingfish; *Seriola lalandi*, was surveyed using baited remote underwater video systems (BRUVS) constructed by SeaGIS Pty with Canon HG21 video cameras BRUVS. This species was chosen as they are the most heavily targeted species by recreational fishers and charter boat operators within the Lord Howe Island fish assemblage. Catch by weight of *S. lalandi* has ranged from 16,904 kg to 24,313 kg per year between 2006 and 2011 (Figueira and Hunt 2012). Depredation of hooked and released individuals by Galapagos Whalers is a common occurrence in the LHIMP (authors pers. comms.), therefore fishing mortality is likely to be higher than what is reported. The majority of *S. lalandi* catch by charter boat operators occurs on the Lord Howe Island and Balls Pyramid shelf; the habitat assessed in this study (Figueira and Hunt 2012). In response to their high catch rates on the LHIMP shelf, *S. lalandi* are likely to show a positive response to the cessation of fishing (Claudet et al., 2010). In addition, the abundance and distribution of *S. lalandi* is likely to be influenced by habitat structural complexity at the scales explored in this study. Reefs of high structural complexity are potentially optimal habitat for *S. lalandi* within the LHIMP, providing increased prey such as baitfish and macroinvertebrates as well as favourable abiotic conditions such as variability in ocean current. Previous research has demonstrated increased catches of *S. lalandi* in areas of high structural complexity compared to areas of relatively low structural complexity (Hobday and Campbell 2009). As a result, the response of *S. lalandi* to MPA protected is likely to be influenced by underlying habitat structural complexity.

To estimate the abundance of *Seriola lalandi*, BRUVS were deployed at 16 sites within the LHIMP in 2009 (Neilson et al., 2010). Eight of these sites were in

areas open to fishing, while the other 8 sites in no-take SZs where fishing is prohibited. In 2013 the same 16 sites were resampled, however an additional 5 sites were surveyed (Fig. 4.1). Three of these sites were in fished zones while the remaining 2 sites in unfished areas. At each site 4 BRUVS were deployed

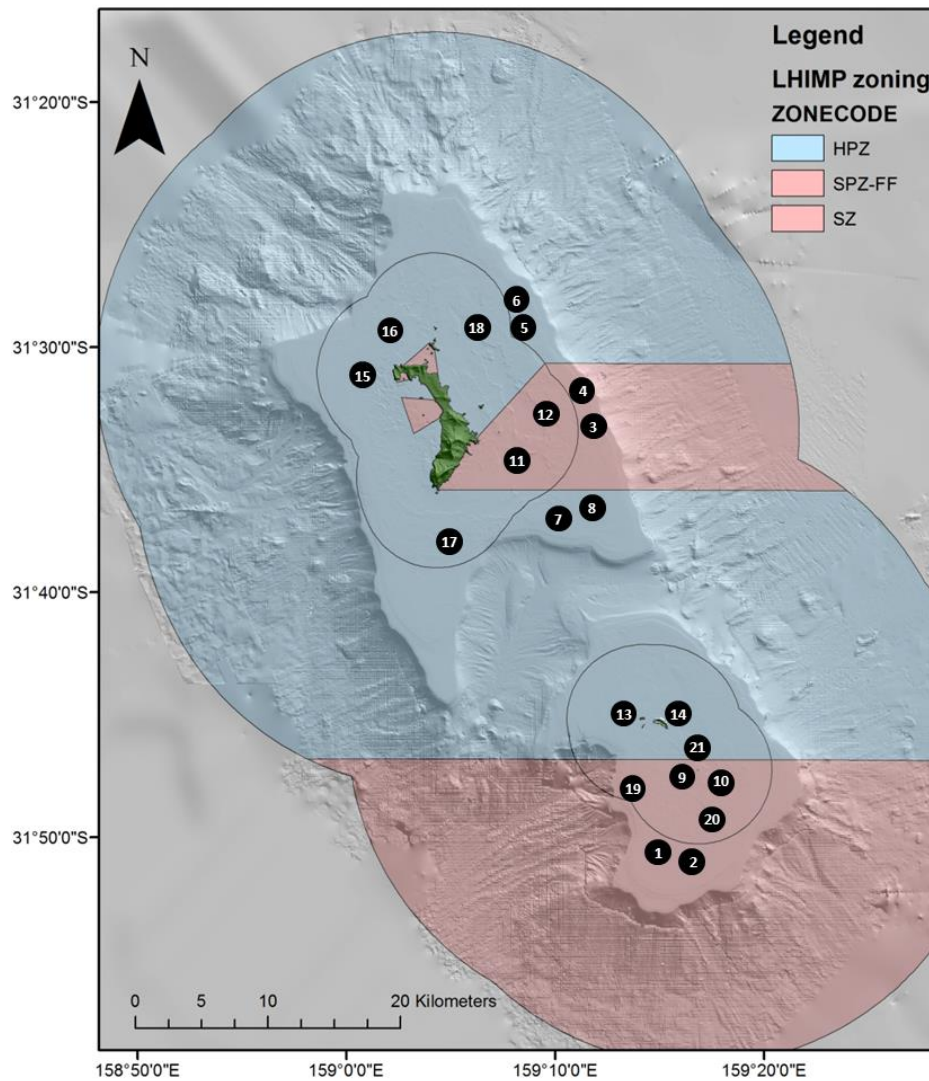


Figure 4.1 A map of survey sites in the Lord Howe Island Marine Park. The Lord Howe Island shelf is in the north and the Balls Pyramid shelf to the south. Regions in pink represent Sanctuary Zones (SZ) while regions in blue, Habitat Protection Zones (HPZ).

simultaneously (+/- 15 mins) at least 200 m apart. For the 2009 sampling period, bait consisted of 1 kg of crushed pilchards (*Sardinops sagax*). Due to a limited supply of bait, the same kilogram of bait was re-used for up to 4 BRUVS deployments. In 2013, prior to deploying the units, the bait bags were replenished with 500 g of freshly crushed pilchards (Wraith et al., 2013). BRUVS were deployed for a 35 min to ensure a 30 min sample. Previous research has demonstrated that a 30 min sample provides a representative sample of the fish at this latitude on the east coast of Australia (Harasti et al., 2015).

BRUVS footage was analysed using Event Measure software (SeaGIS Pty). For each deployment, the relative abundance (Max N) of *Seriola lalandi* was recorded. The Max N was the maximum number of individuals of *S. lalandi* viewed at any one time during the 30 minute sample. To determine the relative abundance of *S. lalandi* per site, the Max N of the four deployments was summed.

Multibeam data acquired around the Lord Howe Island and Balls Pyramid shelves were collated from multiple surveys on the shelf platforms, plains and slopes (Brooke et al., 2010, Mleczko et al., 2010, Linklater et al., 2015). World View II (2 m cell size) and Quickbird satellite images (2.4 m cell size) were used to infer depth in the shallow areas of the shelves, and these datasets were mosaicked together with the multibeam datasets to form a high resolution (5 m cell size) seamless grid of the region (Linklater 2016). Using the focal statistic function within *ArcGIS version 10*, the bathymetric data were used to calculate two measures of habitat structural complexity at a number of spatial scales surrounding each BRUV deployment (25 m, 50 m, 100 m, 150 m, 200 m and 500 m radii). The first measure, vertical relief (VR), was the range in bathymetry at a given scale. The second measure, bathymetric variance (BV), was the standard deviation in bathymetry at a given scale (Wilson et

al., 2007; Rees et al., 2014). These measures were averaged across the four deployments to estimate the vertical relief and bathymetric variance of each site. Larger values of vertical relief and bathymetric variance indicated reefs of greater habitat structural complexity.

A Generalised Linear Mixed Model (GLMMs) with a negative binomial distribution was used to test the effect of zone (fished versus areas unfished) on the abundance of *Seriola lalandi*. The sampling period, 'year' was included in the analysis as a random factor. To test the effect of zoning on the abundance *S. lalandi* while accounting for habitat structural complexity, a series of GLMMs including 'year' as a random factor were constructed including one of the structural complexity measures. All GLMMs were completed in the statistical software 'R' (R Core Development Team, 2013) using the package 'lme4' (Bates et al., 2014). The dredge function from the 'Mumin' package (Bartoń 2015) was used to determine what measure of habitat structural complexity (vertical relief or bathymetric variance) at what spatial scale (25m, 50m, 100m, 150m, 200m, 500m radii) best explained the spatial variability in *S. lalandi*. An exploratory multi-scale approach was used as the spatial scale that *S. lalandi* responds to reef structural complexity within the LHIMP was unknown. The most parsimonious model including a measure of structural complexity and 'zone' was determined by the lowest AICc. Similarly, the AICc was used to compare the models including and excluding habitat structural complexity.

4.3 Results

A total of 164 yellowtail kingfish; *Seriola lalandi* were observed during the study. The distribution of *S. lalandi* was patchy, with individuals only being observed on 35% of the BRUVS deployments across the two sampling periods.

Bathymetry of the Lord Howe Island and Balls Pyramid shelf, revealed considerable variability in seafloor structural complexity (Fig. 4.2). For example, at the largest spatial scale examined (500 m radii), the vertical relief ranged from a minimum of 2.64 m to a maximum of 19.8 m.

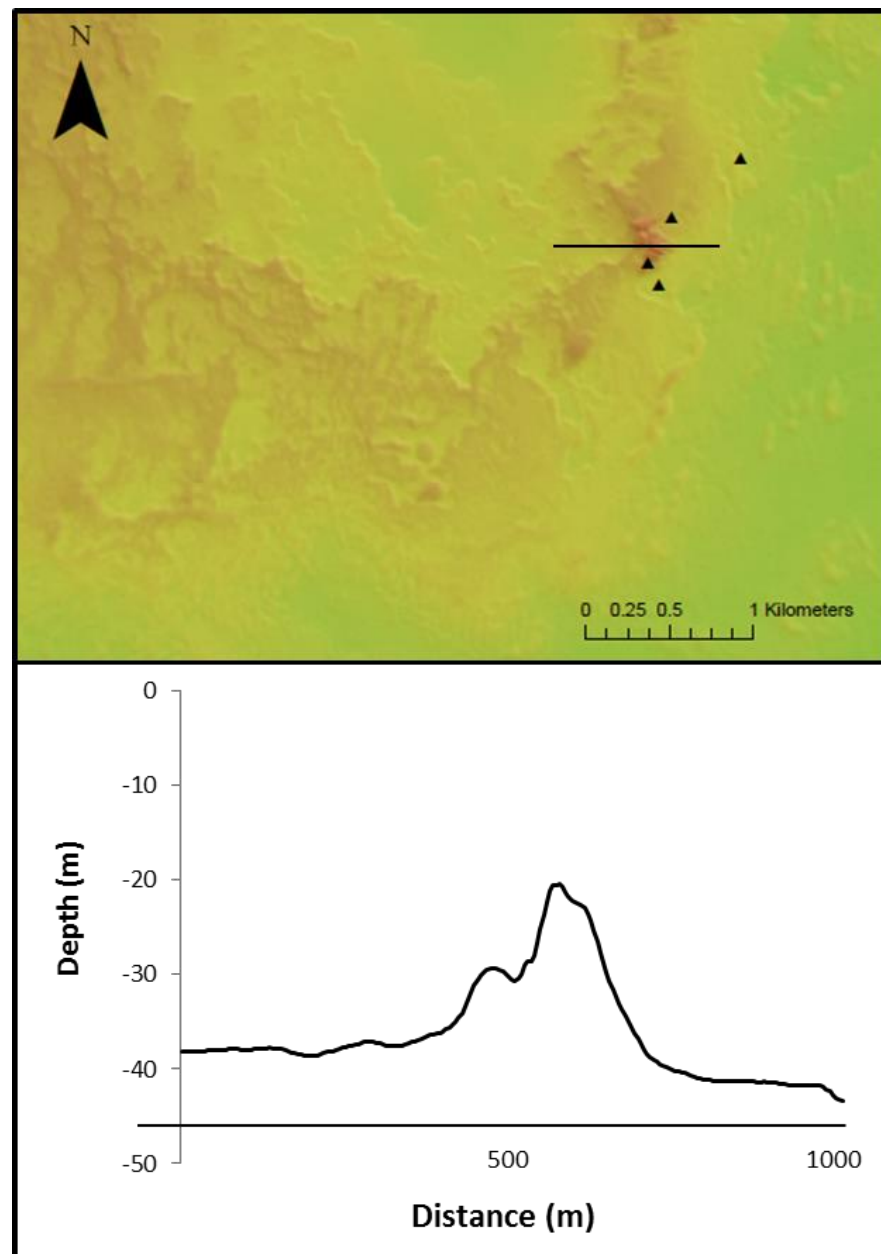


Figure 4.2 An image of the high resolution multibeam bathymetry at site 20 on the Balls Pyramid shelf in Lord Howe Island Marine Park. Below a bathymetric profile of the one kilometre transect bisecting the site.

On average, there were 2.7 times as many *Seriola lalandi* in no-take zones compared to adjacent fished areas (Fig. 4.3). Despite this, the model excluding a measure of habitat structural complexity revealed no effect of zone on the abundance of *S. lalandi* (Table 4.1). The lack of statistical significance between zones was in response to the substantial variability surrounding the mean abundance of *S. lalandi* in no-take zones; 6.5 ± 2.9 (± 1 SE) (Fig. 4.3).

Table 4.1 Results from negative binomial generalised linear mixed effects models comparing the abundance of *Seriola lalandi* between management zones with and without accounting for habitat structural complexity (bathymetric variance at the 100 m seascape scale, denoted as ‘BV100 m’).

Model and terms	Estimate	SE	z	p	AIC
a) <i>Zoning effects excluding structural complexity</i>					183.6
Intercept	0.88	0.38	2.33	0.020	
Zone	1.00	0.53	1.88	0.060	
b) <i>Zoning effects including structural complexity</i>					152.7
Intercept	1.54	0.42	-3.69	<0.001	
BV 100 m	-0.66	0.37	-1.78	0.075	
Zone	-4.38	0.85	-5.17	<0.0001	
BV 100 m x Zone	3.39	0.55	6.17	<0.0001	

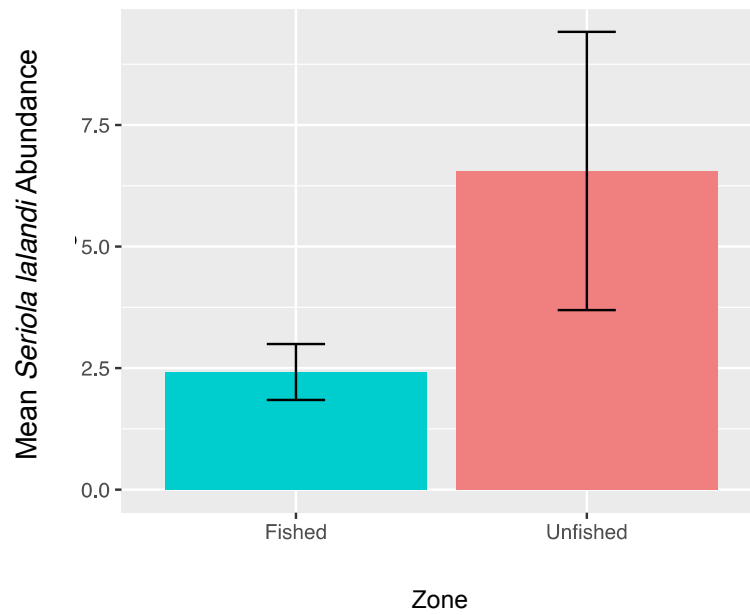


Figure 4.3 Mean (\pm SE) abundance of yellowtail kingfish (*Seriola lalandi*) between fished (HPZ) zones (n = 11) and unfished (SZ) zones (n = 10) across two sampling periods.

When habitat structural complexity was added to the model there was a significant interaction between zone and habitat structural complexity on the abundance of *Seriola lalandi* (Table 4.1). No-take zones had a greater abundance of *S. lalandi* but only at sites displaying high structural complexity (Fig. 4.4). There was no difference in the abundance of *S. lalandi* between no-take and fished zones in areas of low structural complexity (Fig. 4.4). Notably, both no-take and fished zones displayed a relatively even spread of sites that displayed low and high structural complexity (Fig. 4.4). There was no significant difference in average vertical relief between the two management zones ($t = 0.42$, $df = 19$, $p = 0.68$), hence the initial CI assessment was not necessarily confounded. The model including habitat however, was more parsimonious than the model excluding habitat, with an AICc value of 183.6 compared to 152.7 (Table 4.1).

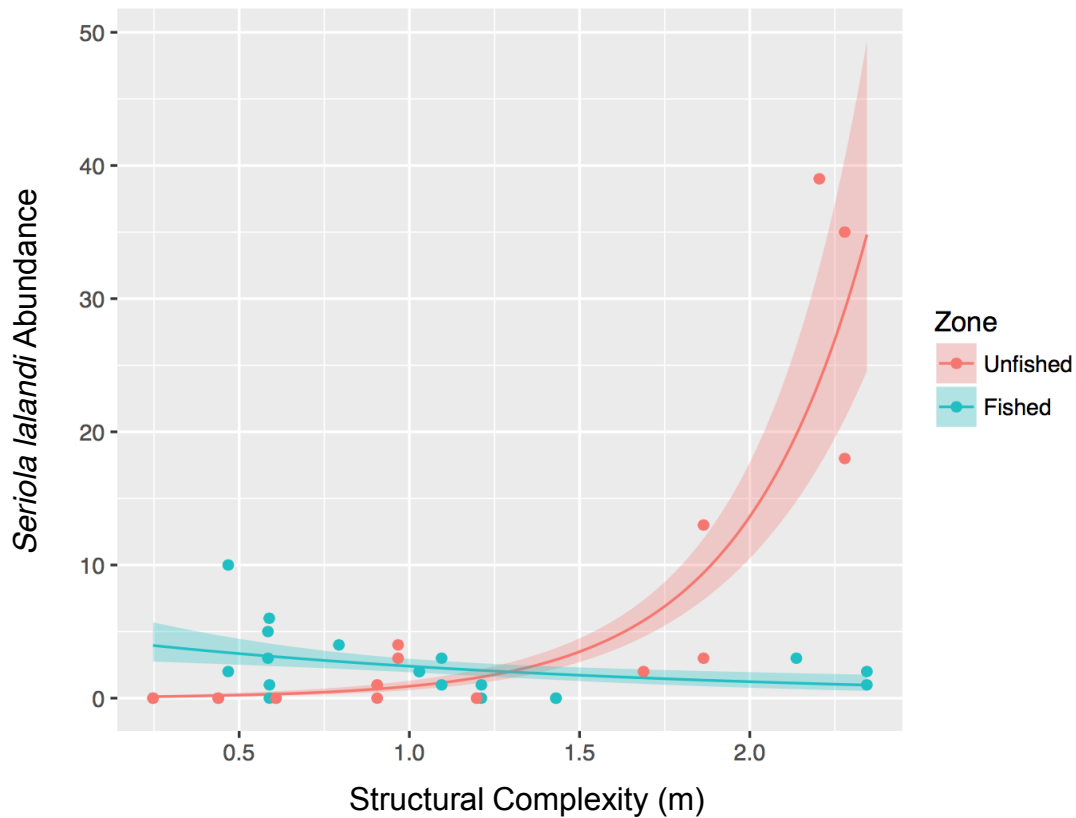


Figure 4.4 Relationship between the abundance of yellowtail kingfish (*Seriola lalandi*) and habitat structural complexity in fished zones (HPZ) and unfished zones (SZ) across two sampling periods. Habitat structural complexity is the bathymetric variance (standard deviation in depth) at a 100 m seascape scale. Trend lines constructed from the model using the ‘predict’ function in the ‘lme4’ package. Shaded areas represent ± 1 standard error.

The abundance of *Seriola lalandi* increased noticeably in no-take zones where the underlying reef exhibited a structural complexity (defined as bathymetric variance) greater than 2 at a 100 m radii scale. A habitat map demonstrates that areas displaying high bathymetric variance in reef structure are well represented in no-take zones on the LHIMP shelf habitat (Fig. 4.5). There is also a high density of this habitat type in areas open to fishing on the Lord Howe Island and Balls Pyramid shelf (Fig. 4.5).

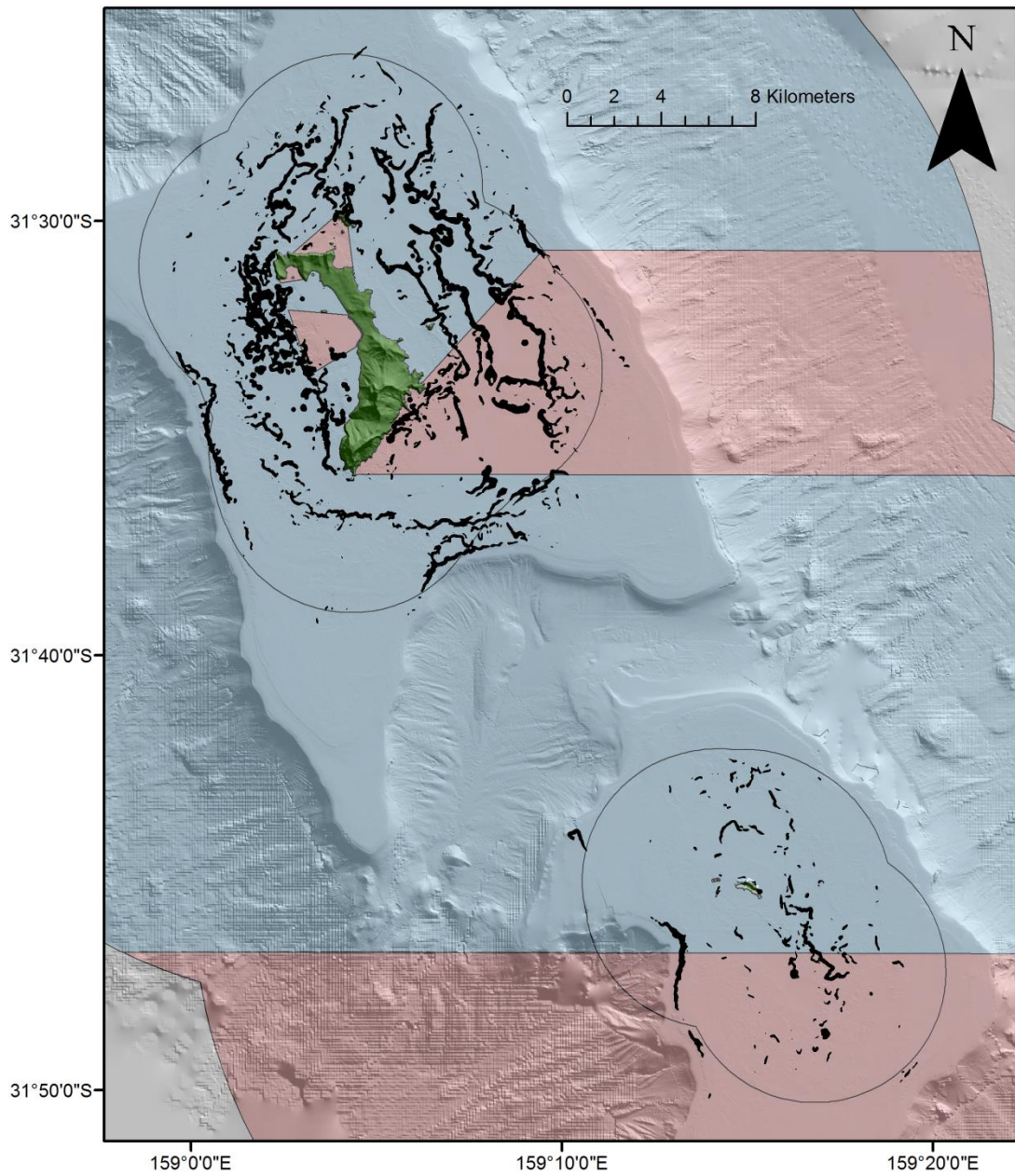


Figure 4.5 Map of the Lord Howe Island Marine Park and areas of shelf habitat (25 – 50 m) displaying structural complexity (bathymetric variance) greater than 2 m at a 100 m seascape scale. Regions in pink represent Sanctuary Zones (SZ) while regions in blue, Habitat Protection Zones (HPZ).

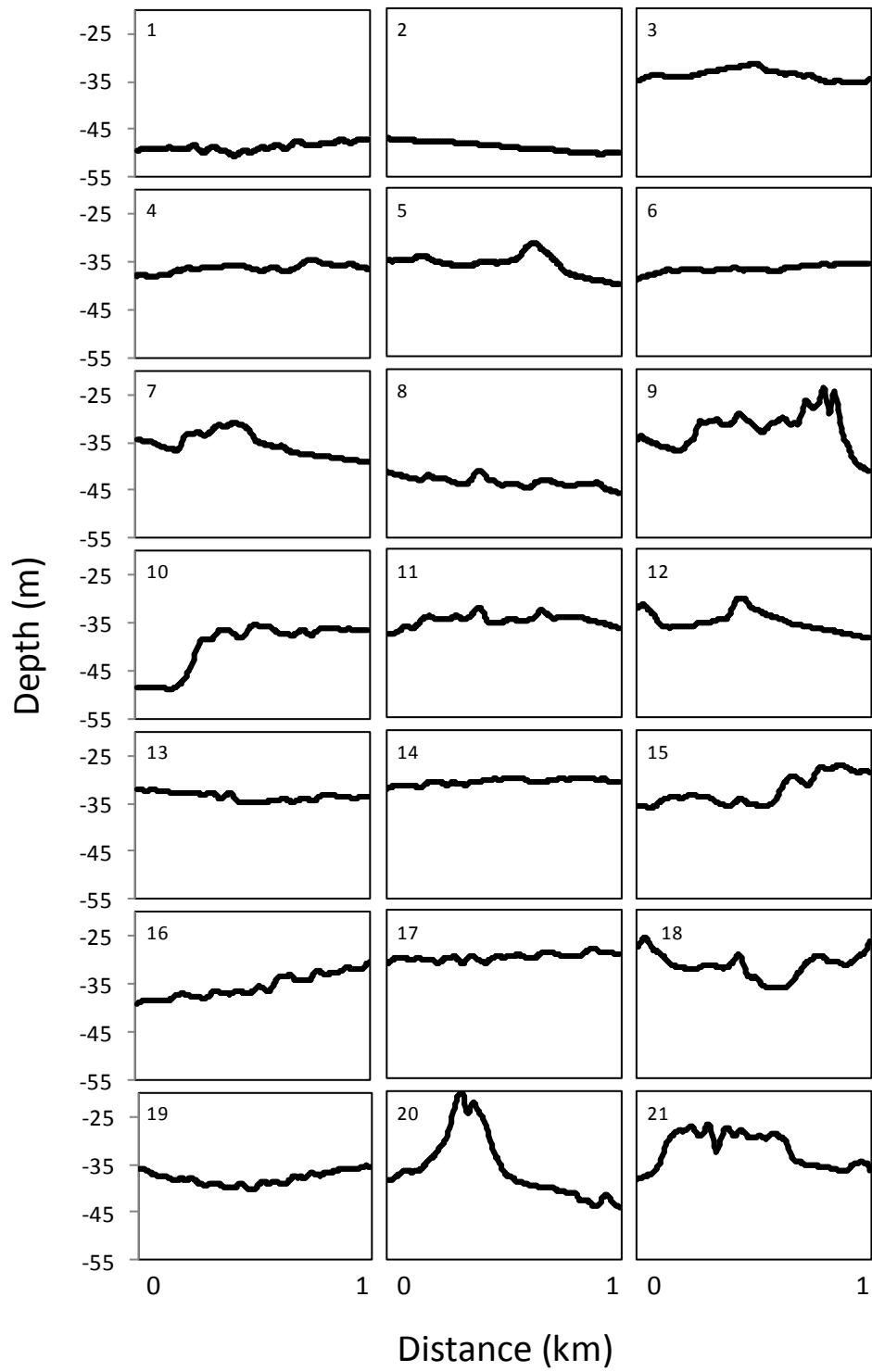


Figure 4.6 Depth profiles along a 1 km transect bisecting each survey site.

Table 4.2 Average vertical relief and bathymetric variance measures (m) at various seascape radii scales surrounding each survey site.

Site	Vertical Relief (VR)						Bathymetric Variance (BV)					
	20m	50m	100m	150m	200m	500m	20m	50m	100m	150m	200m	500m
1	0.78	1.74	2.67	3.11	3.65	4.38	0.21	0.41	0.61	0.66	0.74	1.25
2	0.23	0.62	1.19	1.62	1.96	2.64	0.05	0.14	0.25	0.34	0.42	0.91
3	0.42	0.89	1.96	3.22	4.20	6.50	0.11	0.21	0.44	0.68	0.91	2.20
4	0.62	2.03	4.51	7.08	8.76	13.01	0.16	0.43	0.91	1.46	1.91	4.23
5	1.23	2.81	4.72	6.12	6.80	8.40	0.34	0.70	1.09	1.36	1.46	2.14
6	0.76	2.14	4.68	6.58	8.25	11.78	0.20	0.50	1.03	1.47	1.89	3.92
7	1.18	2.79	4.94	7.40	9.28	11.08	0.34	0.68	1.21	1.71	2.17	3.50
8	1.04	1.70	2.44	3.24	3.96	5.32	0.27	0.47	0.59	0.69	0.84	1.44
9	1.99	4.56	6.57	9.85	11.19	14.28	0.49	1.30	1.86	2.48	2.79	4.03
10	3.27	5.60	7.05	8.80	10.40	13.20	0.96	1.77	2.28	2.52	2.80	4.21
11	0.71	2.07	4.83	6.84	8.67	14.51	0.18	0.48	0.97	1.36	1.77	4.73
12	1.17	3.20	4.75	5.68	6.36	7.75	0.30	0.76	1.20	1.31	1.39	1.91
13	0.99	2.01	2.67	3.10	3.60	4.23	0.23	0.48	0.58	0.72	0.78	1.19
14	0.51	1.16	2.41	3.88	4.57	5.83	0.12	0.23	0.47	0.80	1.06	2.00
15	1.89	3.99	5.59	7.07	8.43	9.14	0.53	1.08	1.43	1.66	1.91	2.85
16	2.54	6.42	9.44	10.60	11.25	13.72	0.65	1.60	2.34	2.85	3.22	4.03
17	1.20	2.52	3.65	5.41	6.51	8.42	0.30	0.62	0.79	1.02	1.25	2.09
18	2.46	5.80	8.52	11.15	13.75	16.52	0.66	1.45	2.14	2.56	2.87	4.09
19	0.58	1.41	2.76	3.58	4.61	6.60	0.15	0.35	0.59	0.77	1.02	2.14
20	2.14	5.42	10.36	14.94	17.44	19.83	0.53	1.28	2.20	3.16	3.78	4.10
21	1.44	3.76	7.25	9.35	10.56	13.43	0.37	0.83	1.69	2.36	2.68	4.12

4.4 Discussion

Using high-resolution bathymetric data, we demonstrate that coral reef habitat on the Lord Howe Island Marine Park (LHIMP) shelf exhibits substantial variability in three-dimensional structural complexity. We were concerned that such seascape variability may confound our Control Impact (CI) test on the effectiveness of the LHIMP, leading to an inaccurate assessment (Miller and Russ 2014). This was not the case however, as sites of high and low structural complexities were well represented among management zones. The inclusion of structural complexity into the test however, clearly resulted in a more complex and useful model, with higher

explanatory power compared to the test excluding structural complexity. Although the initial CI assessment revealed almost 3 times greater abundance of *Seriola lalandi* inside no-take zones compared to fished zones, this relationship was not statistically significant due to high variability surrounding mean estimates. Incorporating habitat structural complexity into the assessment revealed a positive effect of MPA protection on the abundance of *S. lalandi*, but this effect was only apparent over suitable habitat (i.e. reefs of high structural complexity). By controlling for differences in underlying seascape variability, we demonstrate with more certainty that there is a positive effect of the removal of fishing on the abundance of *S. lalandi*. Hence, we argue that accounting for seascape variability, such as structural complexity, may provide substantial improvements in the accuracy and strength of assessments on MPA effectiveness.

It is not surprising that the effectiveness of MPA protection on the abundance of *Seriola lalandi* was dependent on underlying habitat structural complexity. For *S. lalandi*, structurally complex reefs are likely to be optimal habitat, providing increased prey such as baitfish as well as favourable variability in abiotic conditions like ocean currents. Strong links between biota, such as pelagic fishes and topographic complexity has been observed in past literature (Bouchet et al., 2015). For example, Hobday and Campbell (2009) used a fine-scale scientific trolling method (km), to explore the importance of seafloor topography on the catch rates of three pelagic species including *S. lalandi*. They demonstrated that abundance of *S. lalandi* was significantly related to the topographic complexity of the seafloor. Catch rates of *S. lalandi* were 26 times higher over topographic features compared to away from topographic features. Furthermore, *S. lalandi* is the most heavily targeted species by charter fishing operations in the waters of the LHIMP, with an average

annual catch of approximately 20,000 kilograms (Figueira and Hunt 2012). Therefore, it is not surprising that there was a reduction in the abundance of Carangids in areas of high quality habitat open to fishing.

Given the breadth of literature indicating the importance of seascape variability in driving the spatial patterns in marine biological assemblages (Boström et al., 2011; Olds et al., 2016), we strongly recommend, if feasible, to quantify and account for such variability in MPA assessments. Previous studies have highlighted the need to standardise habitat type when assessing MPAs as differences in the diversity and composition of habitat types may confound comparisons between management zones (Friedlander et al., 2007; Harborne et al., 2008). To our knowledge only three studies have accounted for finer scale habitat variability (i.e. structural complexity, patch shape and size) when assessing MPA effectiveness over a single habitat type such as coral reef or temperate rocky reef. The first by Huntington et al., (2010), assessed the Glover's Reef Atoll marine reserve offshore Belize excluding and including natural seascape variability derived from high resolution IKONOS imagery. They found no reserve effects on the abundance and diversity of coral and fish assemblages when seascape variation was omitted from the assessment. However, when analyses were performed accounting for each sites seascape characteristics, significant reserve effects became apparent. The second study, by Young et al., (2016) tested the efficacy of a small marine reserve on southern rock lobster populations while using multibeam bathymetry data to characterise and account for variability in seafloor structure. The third study, by Russ et al. (2005) found that reserve effects were still apparent with the inclusion of structural complexity the assessment as a co-variate. Our findings accord with those of Huntington et al., (2010) highlighting the benefit of accounting for seascape

variability to better understand the complex responses of taxa to MPA protection.

We encourage future studies assessing MPA efficacy to, wherever possible, account for seascape differences, as it is likely to lead to more accurate assessments and ultimately better conservation management.

Not only did the inclusion of habitat structural complexity improve the test on MPA effectiveness, it also unravelled alternate findings, many of which have important conservation implications. As the abundance of *Seriola lalandi* exhibited a strong response to habitat structural complexity, our results lend support to the use of remotely-sensed abiotic variables as surrogates for marine biological assemblages (Pittman and Brown 2011; Rees et al., 2014). Furthermore, the outcome that no-take zones are only effective for *S. lalandi* over reefs of high structural complexity provides valuable information for the ongoing management of the LHIMP. Mapping suitable habitat of high structural complexity on the Lord Howe Island and Balls Pyramid shelf, we show that the current zoning arrangement of the LHIMP is adequately representing this habitat attribute within no-take zones. If the LHIMP zoning arrangement were to be reviewed, we stress the need to represent reefs of high structural complexity within no-take zones in order to protect *S. lalandi*.

Recently, the NSW state government has reduced the number of no-take zones in NSW waters and at this point in time marine reserves in commonwealth waters adjacent to the state LHIMP are under review. Therefore, a better understanding of the benefits and functioning of no-take zones in this region is important to ensure evidence based decisions are made in the future regarding the management of the LHIMP and its surrounding commonwealth waters.

In conclusion, amid the growing concerns of diminishing marine biodiversity, globally there has been an unprecedented increase in the establishment

of MPAs (Halpern et al., 2010). As many MPAs are developed on political or socio-economic concerns rather than a firm ecological basis, there is a possibility that current MPAs may not be reaching conservation targets (Roberts et al., 2003; Edgar et al., 2004). Therefore, it is important that MPAs are accurately assessed to objectives are being met. Without biological data collected prior to MPA establishment, however, it is difficult to tease apart effects of protection from underlying natural variability such as seafloor structural complexity (Garcia-Charton et al., 2000). In this study, we present an approach to account for structural complexity using remote-sensing technologies to better assess MPA effectiveness. Similarly, to Huntington et al., (2010) we propose that future CI assessments on MPA efficacy incorporate seascape variability to better identify and understand the effects of management. This approach, tying habitat information with ecological data will provide a better understanding of the effects of MPAs on marine biological assemblages, which will ultimately lead to improved conservation outcomes.

Chapter 5: RULES OF ATTRACTION: ENTICING PELAGIC FISH TO MID-WATER REMOTE UNDERWATER VIDEO SYSTEMS (RUVS)

A modified version of this chapter is published in *Marine Ecology Progress Series*.

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Plate 5.1 A black marlin (*Makaira indica*) recorded on a remote underwater video system using a sound attractant in the Jervis Bay Marine Park.

5.1 Introduction

Patchily distributed taxa present a challenge to adequately census (McDonald 2004; Barnes et al., 2006). Pelagic fish fit this description, as they are fast swimmers capable of avoiding conventional survey equipment, occupy challenging habitats and display high spatial and temporal variation in their patterns of distribution (Edgar and Barrett 1999; Freon and Misund 1999). As a result, ecological knowledge of pelagic fish has historically relied upon fisheries catch data, as well as tagging programs, which are often broad-scale, low in resolution and associated with sampling biases (Gillanders et al., 2001). In the absence of a cost-effective, fisheries independent sampling technique, information on the structure of pelagic fish assemblages over smaller spatial scales (e.g. seascape scales of 1–10 km) remains poorly resolved. Information on the basic ecology of pelagic fish is critical given their ecological importance in marine ecosystems (Freon et al., 2005) and their heavy exploitation by commercial and recreational fishers (Myers and Worm 2003). Therefore, cost-effective, fisheries independent sampling techniques are essential in understanding the ecology of pelagic fish.

Baited remote underwater video systems (BRUVS) have become a popular sampling method in recent years, providing robust estimates of demersal fish assemblages comparable to other techniques, in a fisheries independent and non-destructive manner (Murphy and Jenkins 2010; Kelaher et al., 2014; Mallet and Pelletier 2014). Evaluations of BRUVS methodology have focused on optimal length of deployment (Stobart et al., 2007; Gladstone et al., 2012), bait types (Wraith et al., 2013), quantities of bait (Harvey et al., 2007; Hardinge et al., 2013) and the influence of time of day (Birt et al., 2012). The success of BRUVS as a technique to sample demersal fish assemblages has led to the development and application of

mid-water BRUVS to survey pelagic fish assemblages (Heagney et al., 2007). Although the mid-water BRUVS technique is in its infancy, studies have evaluated the importance of soak time, replication, current speed and camera depth for assessing pelagic fish, as well as comparing the method to longline surveys (Heagney et al., 2007; Santana-Garcon et al., 2014a; Santana-Garcon et al., 2014c). However, no studies have examined the importance of attractant type on estimates of the diversity and abundance of pelagic fish, with all previous research using an oily bait (tuna oil and/or 100–1000 g of pilchards, *Sardinops sagax*), which is the standard attractant used in BRUVS surveys. Considering the biology of pelagic fish, many of which display schooling behaviour and are piscivorous predators, there may be an alternative attractant or combination of attractants which may provide better estimates of pelagic fish populations. Attractants other than bait, or a suite of attractants may reduce issues currently faced in using mid-water BRUVS, such as zero-inflated datasets and extreme variability in abundance estimates, which create problems for statistical analyses (Santana-Garcon et al. 2014a; Santana-Garcon et al. 2014c). Pelagic fish use vision, chemical senses (smell and taste) and sometimes hearing to locate fish schools, their prey, and fish aggregation devices (FADs) (Banner 1972; Freon and Misund 1999; Dempster and Kingsford 2003; Dempster and Taquet 2004). Therefore, attractants associated with sight and sound stimuli may offer potential alternatives, or complements to bait, thereby providing better estimates of pelagic fish populations.

In this study, we sought to test the effectiveness of 3 attractant types (sight, sound, scent), their combination and an unbaited control on the time of first arrival and the abundance of pelagic fish recorded using mid-water RUVS. We tested the null hypotheses that the time of first arrival, the total abundance of pelagic fish, and

the relative abundance of 3 common species - *Trachurus novaezelandiae* (Richardson), *Sarda australis* (Macleay) and *Seriola lalandi* (Valenciennes) - would not differ with the type of attractant used.

5.2 Materials and methods

5.2.1 Study site

The study was done in the Jervis Bay Marine Park (JBMP), located ~180 km south of Sydney, New South Wales (NSW), Australia. Jervis Bay is a 102 km² marine embayment characterised by 2 peninsulas (Fig. 5.1) that form coastal habitats with hydrographic conditions similar to those in the open ocean. As a result, pelagic fish are frequently observed close to shore in the open coast habitat of JBMP. The area between Point Perpendicular and the Tubes (see survey area, Fig. 5.1) in particular is regarded as one of the premier land-based game-fishing locations in NSW and was the focus area in this study (Lynch et al., 2004).

5.2.2 Mid-water RUVS

We constructed 5 identical, single camera midwater RUVS following Heagney et al., (2007) positioned 5 m below the water surface. We used video cameras (Canon HGF10) with wide angle lenses (Raynox HD Pro) and plastic camera housings constructed by SeaGIS Pty. All RUVS were fitted with a plastic bait container positioned 1.5 m horizontally from the camera housing. Each RUVS was assigned 1 of 5 treatments (outlined below).

5.2.3 Sampling design and experimental treatments

Each RUVS with its associated treatment was randomly deployed 18 times over 10 d between 21 February and 10 April 2013. Video systems were deployed over rocky reef ~20 m in depth, 50 m from the shore and were separated from one another by 400 m to achieve independence (Simpson et al., 2005). Video was recorded for 45 min at each deployment. Previous research has indicated that a 45 min deployment provides representative estimates of pelagic fish at this location (Heagney 2009; but see Santana-Garcon et al., 2014c).

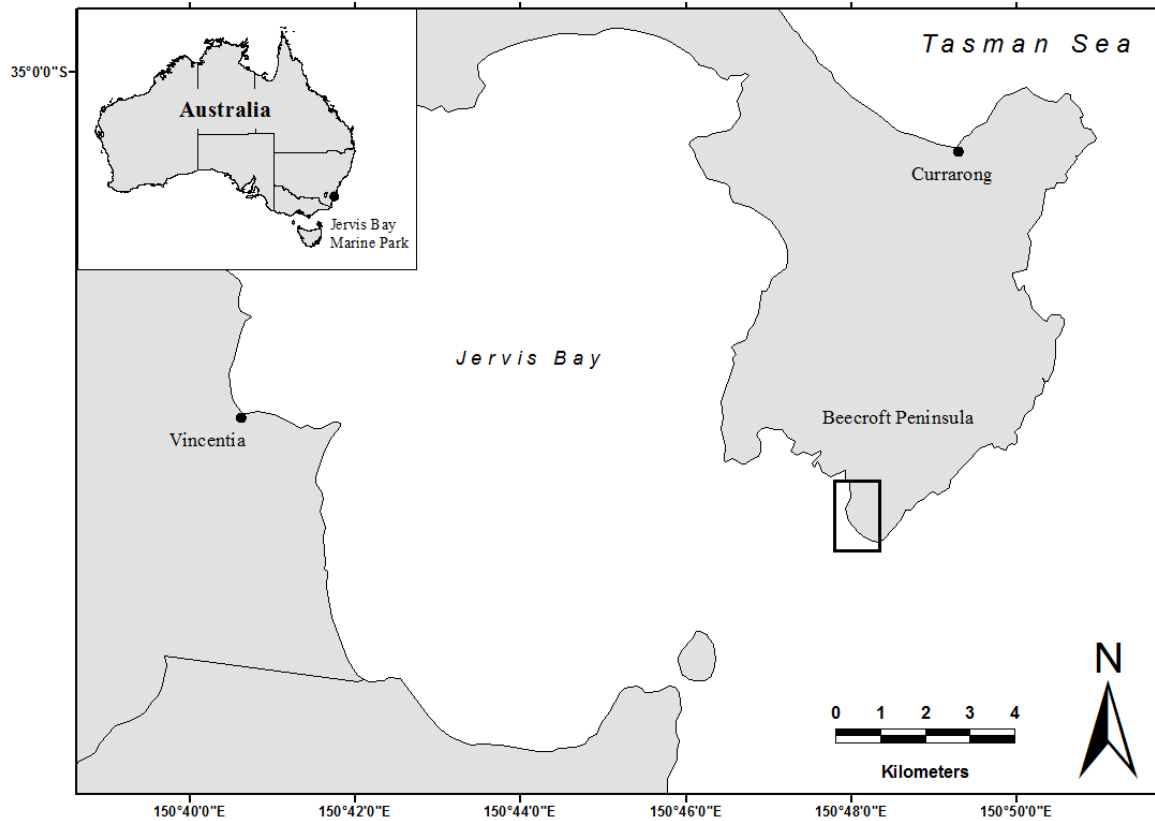


Figure 5.1 Survey area (□) within the Jervis Bay Marine Park. Inset map: location of Jervis Bay in Australia.

The sight treatment was a spearfishing 'PELAGIC swivel flasher' attached to the RUVS above the camera housing. It consisted of reflective material used by fishers to imitate bait fish.

The sound treatment was a play back of a bait fish recording through an underwater speaker located above the RUVS. The bait fish sound was previously recorded in close proximity to the study area. A combination of white bread and pilchards (*Sardinops sagax*) was used to attract blue mackerel (*Scomber australasicus*) and yellowtail scad (*Trachurus novaezelandiae*), 2 common live bait fish used by fishers targeting larger pelagic fish (Lynch et al., 2004). We recorded the swimming and feeding activities of the 2 species using a hydrophone (High Tech Inc-96-min) and a portable recorder (Zoom H4N). The raw sound files below 20 Hz and above 640 Hz were filtered to remove background interference (Banner 1972). The files were cut to create a 1 min continuous loop in mp3 format. All editing processes were completed in Pro Tools. The edited sound file was played back using an underwater speaker (Lubell UW30) connected to an amplifier (Kentiger) that was powered by a 60 amp 12 volt battery. The amplifier and battery were housed in a 60 litre plastic container on the surface of the water. The container was stabilised by surrounding it with an inflated inner tyre tube to ensure that the equipment did not tip and become waterlogged. The speaker was connected to the RUVS, set at a depth of 1.5 m below the water surface and was always positioned <2 m from the RUVS at any time during the deployment.

The scent treatment was 500 g of crushed pilchards (*Sardinops sagax*) placed in the bait container. This is the conventional attractant and quantity used in BRUVS surveys in NSW's marine protected areas (Kelaher et al., 2014). Bait was replenished prior to each mid-water RUVS deployment.

The ‘all’ treatment consisted of a RUVS with all 3 attractants (sight, sound and scent) attached as previously described. The control treatment consisted of a RUVS with no attractants. To prevent the absence of sound equipment from confounding our experiment, the sight, scent and control RUVS were equipped with identical floating containers of the same weight.

5.2.4 Analysis of video footage

A single experienced observer (M. J. R.) examined the video recordings on a computer screen using VLC media player. All pelagic fish species within the field of view were identified and quantified. The relative abundance of individual species was determined by recording the maximum number of fish (Max N) of each species viewed at any one time during the 45 min sample. Total relative abundance was determined by summing Max N s for each individual species during the 45 min sample. We also recorded the time of first arrival (t1st) of pelagic fish.

5.2.5 Statistical analysis

We used generalised linear models with a negative binomial distribution to test for differences in the abundance of pelagic fish among the attractant treatments. Analyses were performed in R using the MASS package (R Core Team 2013) following Zuur et al., (2009). No over-dispersion was apparent in models, except for *Seriola lalandi*. Therefore, we did not present statistical analyses for this species. To examine time of first arrival, we used only deployments that detected pelagic fish, and we compared the mean t1st observed on the treatment containing all attractants to the remaining treatments, using a t -test performed in R. Prior to analysis, data

were examined visually to ensure that the assumption of normality was met (Quinn and Keough 2002).

5.3 Results

A total of 2193 pelagic fish were observed, comprising 6 species from 4 families: Carangidae, Scombridae, Istiophoridae and Carcharhinidae. In total, 1412 *Trachurus novaezelandiae*, 669 *Sarda australis*, 108 *Seriola lalandi*, 2 *Makaira indica*, 1 *Seriola rivoliana* and 1 *Carcharhinus sp.* were recorded. *Posthoc* analysis revealed that the RUVS with all attractants recorded a significantly greater abundance of pelagic fish compared to the RUVS with one or no attractant (Table 5.1). In all instances, the RUVS with all attractants had >9-fold mean abundance compared to the RUVS with one attractant alone or the control treatment (Fig. 5.2a). Similarly, the mean time of first arrival of pelagic fish was significantly shorter on the RUVS with all attractants (17 ± 5 min mean \pm SE, $n = 7$) compared to the treatments with one or no attractant (31 ± 3 min, $n = 20$) ($t = 2.215$, $df = 25$, $p = 0.036$).

Mirroring the pattern in the total abundance of pelagic fish, the RUVS with all attractants recorded a significantly greater abundance of *Trachurus novaezelandiae* compared to the other RUVS (Table 5.1). The RUVS containing all attractants recorded a mean abundance that was 1 to 2 orders of magnitude higher than those with one or no attractants (Fig. 5.2b). Similarly, attractants had a significant influence on the relative abundance of *Sarda australis*, with the RUVS containing all attractants recording a significantly greater abundance compared to those with scent and sound (Fig. 5.2c). There was no significant difference in the abundance of *Sarda australis* recorded on the RUVS with all attractants compared to

the sight or control treatments (Fig. 5.2c; Table 5.1). Attractants had no clear effect on the abundance of *Seriola lalandi* (Fig. 5.2d).

Table 5.1 Parameter estimates, SEs and p-values from the *post-hoc* negative binomial model comparing the treatment with all attractants to the control, sight, scent and sound treatments. Significant values in **bold**.

Coefficient	Estimate	SE	p
Total pelagic fish abundance			
Control	-3.93	1.04	<0.001
Sight	-2.14	1.03	0.037
Scent	-4.69	1.06	<0.001
Sound	-2.16	1.03	0.035
<i>Trachurus novaezelandiae</i>			
Control	-4.86	1.16	<0.001
Sight	-7.16	1.50	<0.001
Scent	-6.06	1.26	<0.001
Sound	-2.47	1.12	0.028
<i>Sarda australis</i>			
Control	-3.02	1.60	0.059
Sight	-0.77	1.59	0.631
Scent	-4.12	1.63	0.012
Sound	-3.99	1.63	0.014

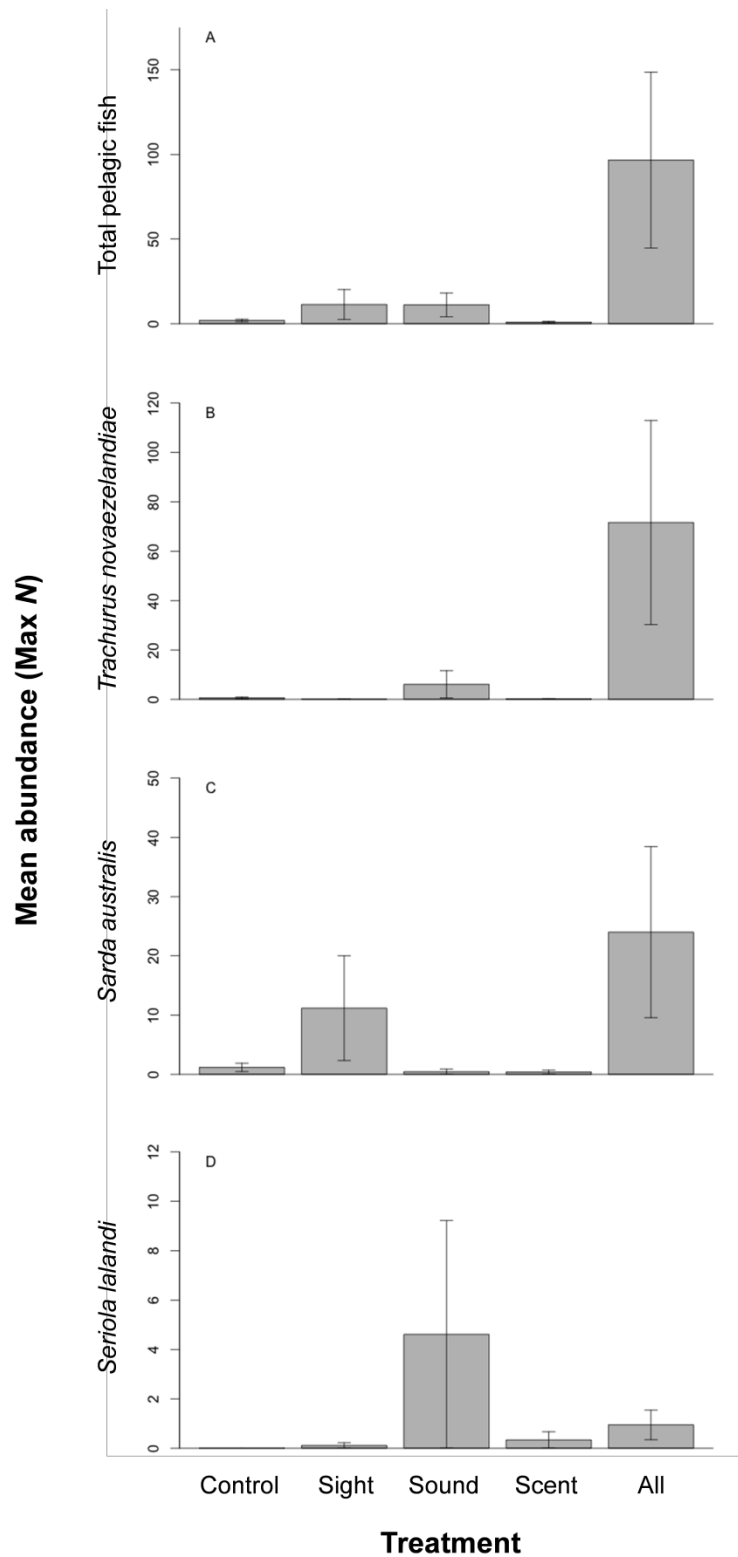


Figure 5.2 Relative abundance of (A) pelagic fish (Total Max N), (B) *Trachurus novaezelandiae*, (C) *Sarda australis* and (D) *Seriola lalandi* (mean \pm SE; n=18) estimated by mid-water remote underwater video systems with different attractant treatments.

5.4 Discussion

We reject our null hypothesis that the time of first arrival and the total abundance of pelagic fish do not differ with the type of attractant used. The total abundance of pelagic fish was markedly greater on the RUVS containing the combination of sight, sound and scent attractants compared to those containing one or no attractant. This result was primarily driven by the small zooplanktivore, *Trachurus novaezelandiae*, which displayed a striking preference for RUVS with all attractants. Similarly, the highest abundance of *Sarda australis* was recorded on the RUVS containing all attractants. In contrast, the attractants had no influence on the abundance of *Seriola lalandi*. This finding was unexpected, considering that ‘flashers’ are often used by spearfishers targeting *Seriola lalandi* (pers. obs.). To complement the abundance data, we also demonstrated that the type of attractant or attractants used had an effect on the time of first arrival of pelagic fish. The mid-water RUVS containing all attractants detected pelagic fish in almost half the time of RUVS with one or no attractant. It is noteworthy that in no instances were baited RUVS more effective than unbaited ones.

An array of sensory processes, such as sight, sound or vibrations, scent, touch and magneto-reception have been proposed to explain how pelagic fish detect and remain with floating structures (Dempster and Taquet 2004). In isolation, the sight, sound and scent treatments employed in this study were relatively ineffective. However, when combined, all attractants had a synergistic effect. Synergy is an important phenomenon in ecology, with multiple stressors and stimuli having a pronounced effect on organism fitness (Przeslawski et al., 2005) and behaviour (Raguso and Willis 2005). We encourage further research into the importance of synergistic interactions of multiple stimuli as a method of attracting fish to mid-

water and demersal RUVS. Whether the synergistic effect was due to the interaction of all 3 attractants or only a combination of 2 is unknown.

We propose that the mechanism behind the synergistic effect of multiple attractants is the difference in the spatial scale of operation of the different stimuli. In water, sound travels 5× faster, with lower attenuation compared to air, and propagates equally from the source in all directions (Slabbekoorn et al., 2010). Therefore, it is likely that sound is an important stimulus for pelagic fish to interpret their surrounding environment over broad spatial scales. Experiments have shown predatory chondrichthyan behaviour to be significantly influenced by playback of bait fish recordings through underwater speakers (Banner 1972), while research aiming to understand the homing behaviour of pelagic fish to FADs has indicated that sound is likely to be an important sensory cue (Dempster and Kingsford 2003). Recent work has shown that acoustic signals from FADs, primarily from fauna associated with them, are within the sensory range of many fishes (Ghazali et al., 2013).

The scale over which the other attractants (scent and sight) are effective is likely to be less than that of acoustic signals. For example, crushed pilchards may be an effective attractant over scales of up to 200 m (Heagney et al., 2007), while visual stimuli imitating schooling bait fish are effective over scales of up to 50 m (Freon and Misund 1999). We propose that the sound recordings may be attracting pelagic fish over a broad spatial scale (Kingsford et al., 2002) until they detect the bait plume (~200 m) and then visual stimuli (~50 m).

Contrary to expectations, bait alone was a poor attractant of pelagic fish. Since all previous research using mid-water RUVS to survey pelagic fish assemblages have solely used oily baits as an attractant (Heagney et al., 2007;

Santana-Garcon et al., 2014a, b, c, d), these studies may have underestimated the abundance of pelagic fish. The use of multiple attractants may also entice pelagic fish closer to mid-water RUVS, which may in turn aid in species identification, abundance estimates and length calculations. However, all previous work has been completed in tropical or warm-temperate waters, particularly coral reef environments harbouring a richer assemblage than the one observed in our study. It remains unclear whether our findings in the temperate zone apply to tropical and warm-temperate systems.

In conclusion, our findings highlight the importance of attractant type when surveying pelagic fish with mid-water RUVS. We demonstrate that multiple attractants associated with sight, sound and scent interact synergistically, recording greater total abundance of pelagic fish, earlier time of first arrival and elevated abundance for some species (*Trachurus novaezelandiae* and *Sarda australis*). We encourage the use of multiple attractants in future studies using mid-water RUVS to sample pelagic fish.

5.5 Acknowledgements

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contribution no. 315 from the Ecology and Genetics Group, University of
Wollongong.

Chapter 6: GENERAL DISCUSSION

One of the main aims in fundamental ecology and applied conservation research is to understand the relationship between species and their environment. Landscape ecology, has revolutionised the way in which terrestrial ecologists study species-environment relationships and conserve biodiversity (Urban 1987; Wiens 1993; Wiens 1995; Turner 2005a, b). The concepts of landscape ecology have not been extensively applied to marine systems. As a result, the importance of seascape ecology on a fundamental and applied level is poorly resolved. This has been in part due to the inherent difficulties in acquiring habitat and species data over the necessary spatial scales to test seascape ecology related questions. However, rapid advances in both remote-sensing (e.g. multibeam sonar) and biological sampling techniques (e.g. BRUVs) are now providing the opportunity to explore such questions (Brown et al., 2011; Ierodiaconou et al., 2011). Much research on seascape ecology however, has been heavily skewed towards the tropics and subtropics. Although, the importance of spatial habitat patchiness is well established in temperate nearshore ecosystems, most research has examined the effect of patch geometry of a single patch-type, such as seagrass, with less consideration directed towards understanding the effect of seascape patterning across multiple habitat patches. Similarly, most research in temperate systems on how habitat structural complexity influences biological assemblages has been investigated in a focal patch-type using relatively small scale field experiments. Compared to tropical settings, less research has examined the importance of structural complexity on temperate species distributions at larger spatial scales (1-100 km). As many temperate marine species use multiple habitat patches over a range of temporal scales, a seascape approach is likely to explain spatial variability in temperate species distributions and

ecological processes. Consequently, metrics quantifying seascape and habitat patch geometry as well as habitat structural complexity may provide suitable surrogates to indirectly predict ecologically important areas. If such seascape features can be easily mapped, their inclusion in spatial conservation strategies such as Marine Protected Areas may enhance their ability to protect biodiversity. Equally, differences in seascape features between MPA management zones may in certain circumstances cause issues such as habitat confounding, when assessing MPA performance. Quantify differences in seascape features among zones and accounting for this variability in performance tests is likely to improve the accuracy and precision of the evaluation. Despite the potential of seascape ecology improving MPA planning and assessment, limited research has investigated the benefits of this approach, especially in temperate regions.

I aimed to address a number of these knowledge gaps by using two model systems; Jervis Bay Marine Park (JBMP) and Lord Howe Island Marine Park (LHIMP), to explore questions on seascape ecology. First, I used a spatially hierarchical sampling design to examine differences in mid-water and demersal fish assemblages among common nearshore habitats and to determine whether habitat classes are adequate surrogates for these taxa (Chapter 2). I then explored the spatial variability in coastal fish assemblages at a broader scale to explore the effect of seascape composition, specifically patch area and connectivity (Chapter 2). I then performed an assessment on the Lord Howe Island Marine Park to examine changes in fish assemblages following 5 and 9 years of zoning enforcement (Chapter 3). Then, to improve this assessment, I incorporated a measure of seascape variability to avoid potential habitat confounding (Chapter 4). Finally, I tested the relative importance of attractant type (sound, scent and sight) to entice pelagic fishes to

remote underwater video systems (Chapter 5). Improving sampling methodologies of these taxa will hopefully encourage future studies to examine seascape ecology of pelagic fishes in coastal ecosystems.

6.1 Seascape patterns in temperate fish assemblages

Throughout my thesis I explored the effect of seascape patterning on fish assemblages at three scales within marine ecosystems. The first, examined differences in coastal fish assemblages among various habitat classes, or patches of habitat (Chapter 2). The second, examined broader scale patterns of seascape composition on fish assemblages (Chapter 2 and 3). The third, explored fine-scale habitat variability, in the form of reef structural complexity on the abundance of a targeted fish (Chapter 4).

6.2 Key findings

- The habitat patches; seagrass, rocky reef and unvegetated sediment displayed a unique assemblage of demersal fishes but not mid-water fishes.
- Many families and species of fish displayed spatially consistent differences in their patterns of abundance among habitat patches.
- Seascape composition, specifically the amount of seagrass in the surrounding seascape had a strong effect on the abundance and diversity of fishes recorded on rocky reef habitat.
- Habitat structural complexity had a strong effect on the abundance of yellowtail kingfish, where seafloor habitats of greater structural complexity displayed greater abundances compared to habitats of lower complexity.

Using Jervis Bay Marine Park as a model system, I demonstrated that habitat patches; rocky reef, seagrass and unvegetated sediment, had a strong and spatially consistent effect on the structure of demersal fish assemblages (Chapter 2). This result was driven by several species that displayed discrete patterns in their abundance among habitat types. Strong patterns in demersal fish assemblages and habitat patches are not surprising as many species are specialised to forage in particular patches over others (for example *Platycephalus* spp. on unvegetated sediments). As a result many demersal species are likely to be “residents” to particular habitat patches within seascapes. Not all taxa in the demersal fish assemblage however, displayed straightforward patterns among habitats. For example, some species, such as the Eastern Fiddler Ray (*Trygonorrhina fasciata*) consistently showed high abundances over two habitat types (seagrass and unvegetated sediment). This result may indicate that Eastern Fiddler Rays do not discriminate between unvegetated sediment and seagrass, and the two habitat patches can be substituted for one another. Alternatively, Eastern Fiddler Rays may prefer seascapes comprised of multiple habitat patches, where each patch type contains different resources, which in turn promotes abundances. For instance, unvegetated sediment may be their focal or residentiary patch type, but seagrass may be important for foraging and/or refuge. Such patterns have been well established in terrestrial landscape ecology and these processes are known as landscape complementation and supplementation (Dunning et al., 1992). In contrast, Sparids were highly variable in their abundance, displaying no affinity for a particular habitat type, indicating that each habitat may be important for these taxa. Again, this may be highlight the importance of landscape complementation and supplementation, indicating that certain species may require seascapes composed of multiple habitat

patches, rather than an independent or isolated habitat patch. As predicted, habitat had no influence on mid-water fishes, indicating a clear decoupling of this assemblage from the underlying benthos, even in relatively shallow water (i.e. 5 m). These findings support the few other studies which have quantitatively compared demersal fish assemblages among rocky reef, seagrass and unvegetated sediment in a standardised manner (Guidetti 2000; La Mesa et al., 2010). These previous studies have also noted substantial inconsistencies of the effect of nearshore habitats among taxa.

Another key finding from my thesis was the importance of seascape composition, or the connectivity of differing habitats patches, on temperate fish assemblages. A preliminary assessment examining the effect of seascape composition in the Jervis Bay Marine Park demonstrated that several response measures of fishes strongly correlate with the amount of seagrass area within the seascape (Chapter 2). On rocky reef habitats surrounded by a greater areal coverage of seagrass there was a greater abundance and diversity of fishes recorded in the demersal and mid-water environment. Additionally, Sparid abundance was strongly positively associated with the amount of seagrass area surrounding rocky reef patches. Similar to coral reef fishes, studies on the movements of temperate fishes (ontogenetic migrations, home range movements and spawning migrations) has demonstrated that many species of fish utilise multiple habitat patches over various temporal scales (Curley, et al., 2013). Therefore, it is not surprising that the spatial arrangement of habitat patches within temperate seascapes is an extremely important driver of the spatial variability observed in temperate fish assemblages. As many temperate fishes recruit into vegetated nearshore habitat patches such as seagrass (Curley et al., 2013), seascapes which contain nursery habitats adjacent to adult

habitats are likely to promote ontogenetic migrations and hence greater abundances. Also, it is likely that many temperate fishes make diel movements between multiple habitats to forage or seek refuge, and as a result, seascapes with high habitat patch diversity are likely to promote the species richness and abundance of temperate fishes. Consequently, seascapes composed of a diverse array of habitat patches are also likely to promote ecological processes such as herbivory, predation and movement of individuals. These findings support previous research in tropical regions showing strong effects of seagrass area and adjacency on species of coral reef fishes (Pittman et al., 2004; Grober-Dunsmore et al., 2007; Pittman et al., 2007; Olds et al., 2012b). Furthermore, these findings suggest that there may be generalities in the effect of seascape patterning among tropical, subtropical and temperate environments. Further evidence highlighting the importance of seascape patterning was detected within the Lord Howe Island fish assemblage. Over two sampling periods, the protected black rockcod was observed only on the Lord Howe shelf, with no individuals recorded on the Balls Pyramid shelf. This result is likely due to the seascape connectivity of important habitats for the ontogenetic migration of black rockcod on the Lord Howe Island shelf (Chapter 3). For example, black rockcod recruit into intertidal rockpools, and then occupy shallow subtidal reefs before migrating to deeper reefs as adults. The Balls Pyramid shelf lacks connectivity to these nursery grounds, which appears to be restricting their range from this habitat. Results from Chapter 2 and 3 support the growing evidence from coral reef literature about the importance of broad-scale seascape patterning on the spatial variability of fish assemblages.

Using high resolution bathymetry derived from multibeam sonar, I was able to quantify substantial variability in the three-dimensional structural complexity on

reef habitat of the Lord Howe and Balls Pyramid shelf (Chapter 4). This intra-habitat, or within patch variability, strongly influenced the abundance of *Seriola lalandi*; a heavily targeted species in the LHIMP. Strong relationships between fish assemblages and remotely-sensed structural complexity measures has also been observed in other studies, namely in coral reef environments (Kuffner et al., 2006; Pittman et al., 2007; Purkis et al., 2008; Wedding et al., 2008; Pittman et al., 2009). As structurally complex habitats display a greater number of resources (food, shelter, abiotic variability) compared to habitats of low complexity, it is not surprising that this fine-scale variability influences biological assemblages. This finding suggest that intra-habitat variability such as reef structural complexity should not be overlooked as another important seascape attribute that influences spatial variability in fish assemblages.

6.3 Incorporating seascape ecology in the design of Marine Protected Areas

Marine Protected Areas are spatial management strategies, which globally may differ in terms of their goals. Typically, however, they are implemented to either conserve biodiversity and/or aid fisheries management. Their design, including location, size, spacing and configuration can theoretically determine their effectiveness of reaching conservation or fisheries goals (Gaines et al., 2010). Previous research on MPA design has highlighted the need for networks containing fully protected zones that are large in size to gain conservation and fisheries benefits (Gaines et al., 2010). Often habitat representation within bioregions has been used to guide zoning arrangements (Dalleau et al., 2010; Malcolm et al., 2012; Malcolm et al., 2016). As different habitat classes are generally assumed to contain different

biological assemblages, a habitat representation approach uses habitat classes as building blocks to capture the regions' biodiversity.

There are a number of issues with using a habitat representation approach to guide the design of MPAs. First, whether habitat classes can act as appropriate surrogates for fish assemblages for MPA design has not been investigated in a standardised manner in many bioregions around the world. Rather, their use as effective surrogates has been inferred from observations or studies usually focused on one habitat type. In Chapter 2, I demonstrate the use of habitat classes as surrogates for temperate fishes does have some merit, as rocky reef, seagrass and unvegetated sediments each had a distinct assemblage of demersal fishes. Furthermore, most taxa from the demersal fish assemblage displayed strong patterns in their abundance among the habitat classes. These findings provide support for use of habitat-based surrogates to predict the distribution and abundance of certain taxa and therefore reliably inform spatial conservation planning. There were, however, exceptions evident for certain taxa, highlighting the need to use habitat-based surrogates with some degree of caution in MPA planning. For example, habitat classes were a poor predictor of the spatial distribution and abundance of the commercially and recreationally important Sparidae.

The second issue with the habitat representation approach for guiding MPA design is that it often neglects the connectivity of marine ecosystems and the importance of connectivity for maintaining biodiversity and ecological processes (Carr et al., 2003). Temperate fish populations are dependent on connectivity via dispersal of larvae and also the post-settlement movements by individuals within seascapes. Although, there has been wide acknowledgment of the importance of larval connectivity in the placement of MPAs, comparatively little consideration has

been placed on seascape connectivity and MPA design (but see Magris et al., 2014; Engelhard et al., 2016 and Weeks et al., 2017). This is especially the case for MPAs in temperate or Polar Regions. Many temperate fishes use multiple habitats over a range of temporal scales including diurnal movements, annual spawning migrations and at different stages during their life history (Curley et al., 2013). Therefore, seascapes with differing compositions and configurations of habitat patches are likely to be important for fishes and ecological processes in temperate regions. For example, nearshore vegetated sediments are important nurseries for many temperate fishes and their location in temperate seascapes is likely to facilitate ontogenetic migrations to adult habitats.

In chapter 2, I demonstrate that a significant proportion of the spatial variability in temperate fishes observed on rocky reef habitat was explained by the amount seagrass in the surrounding seascape. I propose that this is most likely due to seascape connectivity of nursery and adult habitats which promote increased abundances and diversity of fishes. However, rocky reefs surrounded by a large amount of seagrass could potentially be facilitating other processes such as foraging and seeking refuge, which in turn may be driving greater diversity and abundances of fishes in these areas. I also suggest that the abundance of adult black rockcod is likely to be influenced by seascape connectivity of nursery habitats (Lord Howe Island lagoon) and adult habitats (Lord Howe Island Shelf) which facilitate ontogenetic migration (Chapter 3). These findings suggest the need to incorporate the seascape connectivity into temperate MPA design, as a habitat representation approach may fail to identify such regions where these processes are operating. My findings, along with other research on the topic of seascape connectivity (Olds et al., 2012a; Olds et al., 2016) highlight the need to acknowledge and represent seascape

connectivity in MPA design. This is because highly connected habitats or patches within seascapes appear to disproportionately influence biodiversity and ecological processes compared to unconnected habitats or patches.

With the use of benthic habitat maps it is possible to incorporate seascape metrics such as connectivity into the design of MPAs. If seascape metrics strongly correlate to species diversity, abundances and ecological processes, using such metrics as surrogates offers a cost effective and time efficient procedure to guide the placement of reserve boundaries. In tropical settings, only a few studies have proposed ways to incorporate seascape connectivity in MPA design. These have included i) the use of algorithms to quantify connectivity between mangroves and coral reef habitats (Mumby 2006), ii) the use of network analyses to quantify connectivity across habitat mosaics for species with different home ranges then evaluate whether an existing MPA is adequately representing connectivity (Engelhard et al., 2016) and iii) more recently, using Marxan to identify seascape connectivity of nursery and adult habitats for conservation prioritisation (Weeks et al., 2017). There have been no studies to my knowledge that have used a conceptual approach to incorporate seascape connectivity in the design of MPAs in temperate regions. This is probably due to two main reasons. First, to incorporate seascape connectivity into MPA design, such metrics need to be appropriately scaled to the species of interest. In contrast to coral reef fishes (see Green et al., 2015) there is a paucity of accurate information on the home ranges of temperate fishes as well as their larger movements such as spawning and ontogenetic migrations. Second, historically, temperate marine environments are difficult to map and consequently, have not received as much attention as tropical regions. Both of these factors limit the ability to run theoretical simulations on how seascape connectivity may enhance

MPA functioning. However, with the increasing technological advances in acoustic telemetry and temperate habitat mapping this information will become available in the future, which will help managers incorporate seascape connectivity in MPA design. Nevertheless, acknowledging that seascape connectivity is likely to be important for temperate fishes, basic and easily accessible information on the distribution habitat patches in temperate systems (e.g. derived from aerial photography) can be used to quickly identify nursery habitats and highly connected seascapes in nearshore environments which could be prioritised in MPA planning. Although, more research needs to be completed to establish links between temperate fishes and seascape patterning, I believe any attempt to incorporate seascape connectivity is likely to improve the representation of temperate biodiversity and ecological processes.

Using a habitat class representation approach for MPAs planning also neglects the importance of intra-habitat variability such as structural complexity on biota. Many habitats that planners use to guide MPA design (e.g. seagrass, rocky reef and coral reef) can vary substantially in their three-dimensional structure which in turn can influence species distributions on those habitats. In chapter 4, I demonstrate that seafloor complexity strongly influenced the abundance of a targeted species of fish. Higher abundances of yellowtail kingfish were observed on structurally complex reefs compared to reefs of lower structural complexity. This finding highlights that all reefs within the Lord Howe Island Park are not of equal value to yellowtail kingfish, and to adequately protect this species, representation of complex habitats is required within reserve boundaries. Similar sentiments were made by Rees et al, (2014), who showed complex rocky reefs harboured higher abundance and richness of sessile invertebrates and therefore should be prioritised in MPA

planning. Therefore, when data exists on the structural complexity of seafloor habitats (e.g. digital terrain models), this variability should be represented in MPA boundaries to ensure that the biodiversity associated with these habitats is adequately protected.

6.4 Implications for the assessment of MPAs

The majority of MPAs around the world exist as single isolated marine reserves (Lester et al., 2009). Additionally, many MPAs worldwide have no data on the natural temporal and spatial variability of biological assemblages collected prior to their implementation. For MPAs that lack baseline data prior to their establishment and sufficient spatial replication of management zones, Control Impact (CI) assessments of their performance may be confounded by underlying seascape variability (Table 6.1). This is problematic as assessments that do not account for seascape differences may lead to false positive or false negative results on MPA performance. To overcome this issue, CI assessments on MPA efficacy should account for seascape differences by including a covariate in the statistical test, or be performed in areas displaying similar seascape attributes. For example, Friedlander et al., (2007) and Harborne et al., (2008) only revealed a positive MPA effect when comparisons between zones were made on the same habitat type. Similarly, Huntington et al., (2010) detected no reserve effect on coral reef fishes in the Caribbean Sea until the assessment standardised seascape connectivity. My findings support the previous literature highlighting the importance of accounting for underlying seascape differences in MPA assessments. By including a measure of habitat structural complexity into the assessment, I demonstrate that the accuracy and precision of the evaluation increased (Chapter 4). Furthermore, the addition of habitat structural complexity, revealed a more thorough understanding of the effect

of the cessation of fishing on targeted taxa. This finding emphasises that despite the costs and difficulties associated with obtaining high quality habitat mapping in MPAs, the benefits are likely to lead to substantially better conservation management and outcomes.

Table 6.1 Possible scenarios where seascape variability may potentially confound assessments of Marine Protected Area effectiveness.

Scenario	Likelihood of seascape confounding	Method to overcome potential confounding
1. A single marine reserve with no biological data collected prior to establishment and no habitat mapping used to guide the MPAs design.	High	<ol style="list-style-type: none"> 1. Ensure assessment is completed over similar habitat classes (rocky reef, seagrass etc) (Harborne et al., 2008). 2. An asymmetrical design with high replication of adjacent reference areas. This will increase the likelihood of sampling unprotected areas of similar seascape attributes. 3. High replication of an asymmetrically designed CI assessment through time. 4. Incorporate a measure of seascape variability during sampling campaign or via remote sensing. 5. Caution: seascape variability measure needs to be calculated at the appropriate scale for assemblage/taxa of interest.
2. A single marine reserve with biological data collected prior to establishment and no habitat mapping used to guide the MPAs design.	Moderate	<ol style="list-style-type: none"> 1. Ensure assessment is completed over similar habitat classes (rocky reef, seagrass etc) (Harborne et al., 2008). 2. An asymmetrical Before After Control Impact design (BACI) with high replication of adjacent reference areas. This will increase the likelihood of sampling unprotected areas of similar seascape attributes. 3. Incorporate a measure of seascape variability during sampling campaign or via remote sensing. 4. Caution: seascape variability measure needs to be calculated at the appropriate scale for assemblage/taxa of interest.
4. A single marine reserve with no biological data collected prior to establishment and habitat mapping has been used to represent seascape attributes evenly between protected and unprotected zones.	Low – depends on how well seascape attributes have been represented.	<ol style="list-style-type: none"> 1. Ensure assessment is completed over similar habitat classes (rocky reef, seagrass etc) (Harborne et al., 2008). 2. Asymmetrical design with high replication of adjacent unprotected reference areas containing similar seascape attributes as reserve. 3. High replication of an asymmetrically designed CI assessment through time 4. Caution: similarity of seascape attributes between zones is species dependent. 5. Incorporating a measure of seascape variability may still improve the accuracy and precision of the assessment.
4. A single marine reserve with biological data collected prior to establishment and habitat mapping has been used to represent seascape	Low – depends on how well seascape attributes have been	<ol style="list-style-type: none"> 1. Ensure assessment is completed over similar habitat classes (rocky reef, seagrass etc) (Harborne et al., 2008). 2. An asymmetrical Before After Control Impact design (BACI) with high replication of adjacent unprotected reference areas containing similar seascape attributes

attributes evenly between protected and unprotected zones.	represented.	<ul style="list-style-type: none"> as reserve. 3. Caution: similarity of seascape attributes between zones is species dependent. 4. Incorporating a measure of seascape variability may still improve the accuracy and precision of the assessment.
5. A network of marine reserves with no biological data collected prior to establishment and no habitat mapping used to guide the MPAs design.	Low	<ul style="list-style-type: none"> 1. Ensure assessment is completed over similar habitat classes (rocky reef, seagrass etc) (Harborne et al., 2008). 2. CI assessment with high spatial replication of marine reserves and unprotected reference areas. This will increase the likelihood of sampling unprotected areas of similar seascape attributes. 3. High replication of CI assessment through time. 4. Incorporate a measure of seascape variability when surveying response measures. 5. Incorporating a measure of seascape variability may still improve the accuracy and precision of the assessment. 6. Caution: seascape variability measure needs to be calculated at the appropriate scale for assemblage/taxa of interest.
6. A network of marine reserves with biological data collected prior to establishment and no habitat mapping used to guide the MPAs design.	Low	<ul style="list-style-type: none"> 1. Ensure assessment is completed over similar habitat classes (rocky reef, seagrass etc) (Harborne et al., 2008). 2. BACI assessment with high spatial replication of marine reserves and unprotected reference areas. This will increase the likelihood of sampling unprotected areas of similar seascape attributes. 3. Incorporating a measure of seascape variability is still likely to improve the accuracy and precision of BACI assessment.
7. A network of marine reserves with no biological data collected prior to establishment and habitat mapping has been used to represent seascape attributes evenly between protected and unprotected zones.	Low – depends on how well seascape attributes have been represented	<ul style="list-style-type: none"> 1. 1. Ensure assessment is completed over similar habitat classes (rocky reef, seagrass etc) (Harborne et al., 2008). 2. CI assessment with high replication of adjacent unprotected reference areas containing similar seascape attributes as reserve. 3. High replication of CI assessment through time. 4. Caution: similarity of seascape attributes between zones is species dependent. 5. Incorporating a measure of seascape variability may still improve the accuracy and precision of the assessment.
8. A network of marine reserves with biological data collected prior to establishment and habitat mapping has been used to represent seascape attributes evenly between protected and unprotected zones.	Very Low – depends on how well seascape attributes have been represented	<ul style="list-style-type: none"> 1. Ensure assessment is completed over similar habitat classes (rocky reef, seagrass etc) (Harborne et al., 2008). 2. BACI assessment with high spatial replication of marine reserves and unprotected reference areas containing similar seascape attributes as reserve. 3. High replication of BACI assessment through time. 4. Caution: similarity of seascape attributes between zones is species dependent. 5. Incorporating a measure of seascape variability may still likely to improve the accuracy and precision of the assessment.

6.5 Future directions

This thesis highlights several directions for future research on seascape ecology. More broadly, future research is needed to determine the importance of seascape patterning, composition and connectivity on marine biota in temperate and Polar Regions. Although, my preliminary findings suggest seascape connectivity to be a strong driver of the spatial patterns in temperate coastal fish assemblages, additional work, with a more directed experimental design (e.g. greater replication across multiple seascapes) is needed to better evaluate these relationships. Furthermore, my work has examined how patterns in seascape structural connectivity (spatial arrangement of patches) influence patterns in temperate fishes (Calabrese and Fagan, 2004). This represents a pattern-pattern approach (Pittman and Olds 2015) and future research should strive to quantify the functional connectivity (the actual movement) of temperate fishes across seascapes using methods such as acoustic telemetry. Determining whether seascape connectivity is an important driver of fish assemblages should also be a top research priority in other temperate regions around the world. For example, the Mediterranean region is similarly dominated by the three habitat classes; seagrass, rocky reef and unvegetated sediments in coastal areas (Guidetti 2000). Applying a seascape ecology framework in other temperate regions may provide evidence to support generality of the effect of seascape patterning on temperate fishes. Furthermore, if strong ties between seascape connectivity and fishes are uncovered in temperate regions, this would support the growing body of work from tropical regions demonstrating the importance of seascape connectivity.

The temporal scale of fish-seascape studies usually provides a ‘snapshot’ of the relationship between response measures and seascape patterning in time. To

achieve generalities in the seascape literature this may be problematic, as fishes display substantial temporal variability over a range of time scales. Furthermore, benthic habitats and their spatial patterning are dynamic as they are strongly influenced by disturbance events. In Chapter 4, I demonstrate that *Seriola lalandi* displayed the consistent responses to habitat structural complexity and MPA zoning for two time periods, thereby providing greater certainty around the effect of seascape patterning. Future research should strive, if possible, to do repeated sampling over a range of temporal scales to conclusively establish fish-seascape relationships. In addition, greater temporal replication of studies exploring seascape-fish relationships will provide opportunities to understand the impact of anthropogenic disturbances, such as climate change and habitat degradation, on such relationships (Pittman et al., 2011).

Another avenue for future research in seascape ecology in temperate systems is to better understand the relationship between species ontogenetic habitat use and seascape connectivity (Gillanders et al., 1997). For example, in Chapter 2 I found similar abundances of Sparid across rocky reef, seagrass and unvegetated sediments. I predict however, that the age class structure of Sparid among these habitats would differ, as juveniles of this family recruit onto seagrass and unvegetated sediments before migrating to deeper rocky reefs as adults. This could be tested by quantifying the age structure of Sparids among nearshore habitats using a method like stereo BRUVS. Future research could also use acoustic telemetry to track fish movements from their juvenile life stage to adulthood. Active or passive acoustic tracking could be employed to examine ontogenetic movements of fishes among habitats to better understand the value and importance of seascape connectivity for this family (Hitt et al., 2011; Ferguson et al., 2013; Fetterplace et al., 2016).

Future research using BRUVS to explore the relationship between seascape patterning and fishes should assess the benefits and limitations of using this survey technique. For example, by using bait to explore differences in fish assemblages among habitat classes in Chapter 2, fish may have been attracted from adjacent habitats resulting in a more homogenous assemblage. Therefore, the use of bait may have reduced the ability to detect an effect of habitat. In contrast, however, bait may be beneficial to understand the importance of seascape characteristics such as connectivity. For example, the use of an attractant such as bait, may improve the estimates of fish willing to move among different habitats. Future research should test the difference between BRUVS and unbaited RUVS to determine which approach is optimal for exploring seascape related questions in temperate systems.

Finally, recent research has indicated that the distribution of pelagic fishes in coastal environments may be structured at smaller spatial scales (1-10's km's) than previously assumed. As the pelagic environment is highly dynamic both temporally and spatially, the concepts of seascape ecology could be transferred to this system with the aim to better understand the spatial ecology of pelagic fishes. For example, a seascape ecology framework could be applied to examine abiotic heterogeneity in the pelagic environment such as oceanographic fronts and eddies on pelagic fishes. This approach however, has been hindered by the difficulties in surveying pelagic fishes in coastal environments. Due to the recent improvements in the methodology of using mid-water remote underwater video to sample pelagic fishes however (Chapter 5; Heagney et al., 2007; Santana-Garcon et al. 2014a; Santana-Garcon et al., 2014c), there is now the opportunity for future research to explore seascape related questions for pelagic fishes.

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APPENDIX 1: PUBLISHED MANUSCRIPTS

- Rees, M., Jordan, A., Price, O., Coleman, M. & Davis, A. (2014) Abiotic surrogates for temperate rocky reef biodiversity: implications for Marine Protected Areas. *Diversity and Distributions*. **20**, 284-296.
- Kelaher, B., Coleman, M., Broad, A., Rees, M., Jordan, A. & Davis, A. (2014) Changes in fish assemblages following the establishment of a network of no-take and partially-protected Marine Protected Areas. *PLoS ONE*. 9(1): e85825.
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Changes in Fish Assemblages following the Establishment of a Network of No-Take Marine Reserves and Partially-Protected Areas

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Abstract

Networks of no-take marine reserves and partially-protected areas (with limited fishing) are being increasingly promoted as a means of conserving biodiversity. We examined changes in fish assemblages across a network of marine reserves and two different types of partially-protected areas within a marine park over the first 5 years of its establishment. We used Baited Remote Underwater Video (BRUV) to quantify fish communities on rocky reefs at 20–40 m depth between 2008–2011. Each year, we sampled 12 sites in 6 no-take marine reserves and 12 sites in two types of partially-protected areas with contrasting levels of protection ($n = 4$ BRUV stations per site). Fish abundances were 38% greater across the network of marine reserves compared to the partially-protected areas, although not all individual reserves performed equally. Compliance actions were positively associated with marine reserve responses, while reserve size had no apparent relationship with reserve performance after 5 years. The richness and abundance of fishes did not consistently differ between the two types of partially-protected areas. There was, therefore, no evidence that the more regulated partially-protected areas had additional conservation benefits for reef fish assemblages. Overall, our results demonstrate conservation benefits to fish assemblages from a newly established network of temperate marine reserves. They also show that ecological monitoring can contribute to adaptive management of newly established marine reserve networks, but the extent of this contribution is limited by the rate of change in marine communities in response to protection.

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Introduction

Human activities, such as catchment development, overfishing, pollution and maritime industries, have degraded marine and estuarine environments [1,2]. Global concern for the health of marine systems has driven an unprecedented increase in marine protected area establishment over the last decade [3]. A small percentage of these marine protected areas are marine reserves where extraction of living marine resources is not permitted [4]. Many published studies have evaluated the responses of marine ecosystems to reserve establishment [5]. These include highlighting the types of species that do and do not benefit (e.g. [6,7]) cascading trophic responses (e.g. [8,9]), their influence on surrounding areas (e.g. [10,11]), their influence on invasive species (e.g. [12]) and the enforcement effort required for significant changes to occur [13,14].

While individual marine reserves provide conservation benefits, social and economic considerations often limit their size to a fraction of the bioregion whose biodiversity they are often designed to represent [4]. A limitation of most marine reserves is that they are not large enough to be completely self-sustaining

because their size is less than the average dispersal distance of key species [15]. Although this issue can be resolved by establishing much larger marine reserves, socio-economic pressures are likely to prevent this, particularly on densely populated coasts. In an attempt to scale up the benefits of individual marine reserves to broader regions, networks of marine reserves are increasingly being established [4,16]. Effective networks of marine reserves require adequate connectivity, such that each reserve can contribute and receive sufficient adults and larvae from adjacent reserves [4,17]. Theoretical models suggest that a network of marine reserves may synergistically increase conservation benefits relative to the sum of the benefits from unconnected individual reserves [15,18–20]. However, published data on changes in marine communities across marine reserve networks is limited relative to research on individual marine reserves and rigorous empirical tests of theoretical models optimizing marine reserve network designs are still in their infancy [4,21].

Partially-protected areas are typically marine protected areas with less restrictive regulations than marine reserves [22,23]. Depending on local objectives, they usually involve restrictions on particular activities, gear types, user groups, target species, or

extraction periods [23]. Partially-protected areas may also be used to limit foreshore developments that require marine infrastructure (e.g. marinas or discharge outlets) thereby further reducing environmental threats [24]. Relative to marine reserves, there is much less published information about ecological changes associated with the establishment of partially-protected areas [23]. A meta-analysis of 20 studies found that partially-protected areas maintain higher biomasses, density and richness of marine organisms than areas with less regulation, but do not provide the same level of ecological benefits as no-take marine reserves [23]. These conclusions are, however, limited by (i) major differences in fishing restrictions in partially-protected areas among the different studies and (ii) most comparisons within a region being based on a single marine reserve or partially-protected area (but see [25]).

The establishment of multiple-use marine parks with replicated, closely spaced marine reserves, partially-protected areas and open access areas provides the opportunity to test hypotheses about networks of marine reserves and make rigorous comparisons of change in marine communities associated with different levels of environmental protection [26]. Over the last decade, six such multi-zoned marine parks containing 115 individual marine reserves (i.e. no-take sanctuary zones) have been established in the state waters of New South Wales, Australia [27]. Built into the legislation administering these marine parks are statutory requirements to review and, if necessary, adaptively manage the zoning arrangements 5 years after establishment. Some species can display significant changes after only a few years of protection (e.g. <5 years [28]), while others may take decades [29,30]. Significant changes in marine community structure may take well in excess of 15 years [28,31]. It is uncertain, therefore, the extent to which marine environmental monitoring will contribute to evidence-based adaptive management of marine park zoning arrangements at a 5 year review.

To assess the recovery trajectory of a newly established marine reserve network, we tested the hypothesis that reef-associated fish assemblages in reserves will change significantly relative to fished areas within 5 years of establishment. Concurrently, we also tested the hypothesis that reef-associated fish assemblages vary with different levels of environmental protection by including partially-protected areas. We also evaluated the performance of individual reserves within the network and related this to reserve size and enforcement actions.

Materials and Methods

Study Area

This study was undertaken in the Batemans Marine Park, a ~85000 Ha multi-use marine park on the NSW South Coast, Australia (northern boundary = 35°31.086'S and southern boundary = 36°22.290'S) encompassing waters from the mean high tide mark to the limit of state waters (ca. 3 nm from land). The zoning plan for the marine park commenced in June 2007, after which activities (e.g. fishing, recreation, foreshore development, boating, pollution discharge, etc.) were regulated by the NSW Marine Parks Act (1998) and Regulations (1999, 2009), as well as a range of other legislation (e.g. Fisheries Management Act 1994, Coastal Protection Act 1979, Protection of Environmental Operations Act 1997, Threatened Species Conservation Act 1995, etc.). Marine park legislation specifically prohibits dredge and demersal trawling, mining and long-lining throughout the entire park.

As part of the objective to achieve conservation of biodiversity, the Marine Park was zoned into 4 types of areas: sanctuary zones, habitat protection zones, general use zones and special purpose zones, which represented 19.1%, 43.3%, 37.2% and 0.4% of the

entire park, respectively. The different zone types are interspersed throughout the marine park creating a network of marine reserves and partially-protected areas. Special purpose zones were not included in the hypotheses tested because they only represented <0.5% of the marine park and were created for a range of specific management purposes (e.g. oyster farming, foreshore development and cultural resource use).

Sanctuary zones are strict no-take marine reserves that allow for non-extractive activities. Habitat protection zones are partially-protected areas where the species that can be harvested and the fishing methods that can be used are prescribed by legislation. For example, lawful recreational fishing methods are allowed in habitat protection zones with a few exceptions, but commercial purse seining, lift netting, mesh-netting, estuary prawn and haul netting are not permitted. With only the overall park-wide prohibitions enforced, general use zones are the least restrictive partially protected areas in NSW Marine Parks. Lawful commercial and recreational fishing methods other than trawling and long-lining are permitted in general use zones in the Batemans Marine Park. More specific details about prohibited activities can be found in Read and West [24].

Sampling Methodology

Baited Remote Underwater Video (BRUV) was used to test hypotheses about changes in fish assemblages across the network of marine reserves and partially-protected areas. In many situations, BRUV units are preferred over other sampling techniques because they can be deployed in environments unsuitable for conventional diver based assessments [32], they are able to detect diver-shy species [33], they provide usable estimates of the relative abundance of economically-important species [33] and they provide a permanent visual record of surveys [32]. BRUV was particularly suitable for our study because it is a non-destructive sampling technique appropriate for high conservation areas (e.g. no-take marine sanctuaries) and survey depths often exceeded 30 m. Like all fish survey methods, BRUV only samples a subset of the fish community with a tendency towards sampling more predatory species than other methods on shallow reefs (e.g. underwater visual census [34]). The observed fish assemblage with BRUV systems can also be influenced by the presence of large predatory species (e.g. sharks [35]). Importantly, these issues did not systematically vary among zone types and, as such, did not influence the hypotheses that were tested here.

BRUV units were deployed on rocky reef at 12 sites in sanctuary zones, 6 habitat protection and 6 general use zones (Fig. 1). This design allowed for planned balanced comparisons between no-take and fished areas (12 sites vs 12 sites) and between the two types of partially protected areas (6 sites vs 6 sites) (see design below). The sanctuary zones included were between 2 km to 14 km apart, which is likely within the range of either larval or adult movements for many common reef fish species (e.g. [36] and references within), especially considering the East Australia Current [37,38]. Sites were haphazardly interspersed throughout the Marine Park from Brush Island (35°31.086'S) to Potato Point (35°06.172'S) (Fig. 1). Each site was dominated by rocky reef and was sampled in 2008, 2009, 2010 and 2011. In 2008, sampling occurred from January to May and for the following years it occurred from June to August. This change in timing was related to the implementation of a state-wide monitoring program and was not a major consideration for interpretation of results because there is often no clear seasonal signal in demersal fish assemblages in this region [39]. This likely stems from substantial spatial-temporal variation and relatively mild winters. Moreover, the key

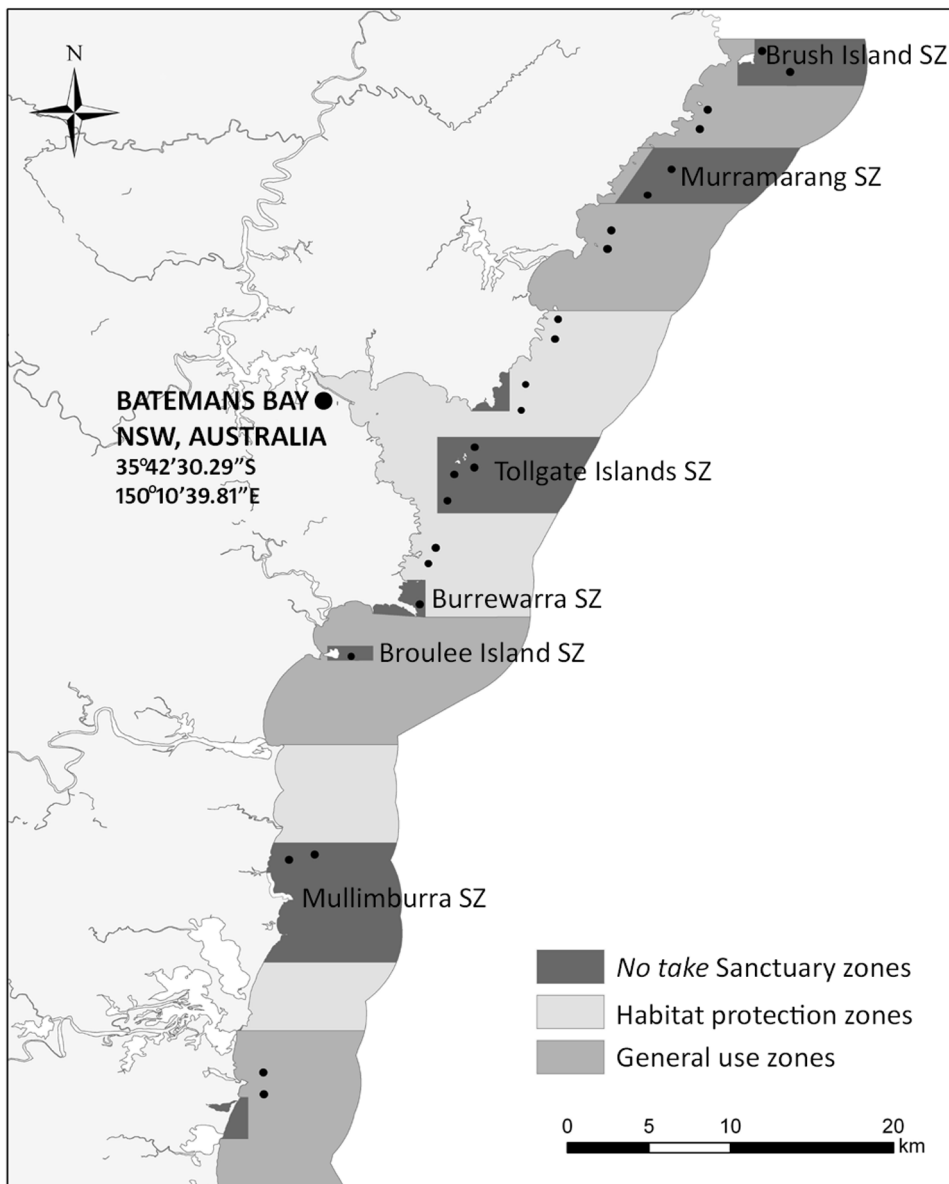


Figure 1. Map showing the configuration of zones in the part of the Batemans Marine Park (NSW, Australia) included in our study. The map highlights spatial arrangement of the network of no-take marine sanctuaries. ● indicates the location of each BRUV sites. doi:10.1371/journal.pone.0085825.g001

hypotheses of this study focused on differences between sanctuary zones and partially protected areas rather than temporal variation.

In each site, 4 BRUV units were deployed at approximately 200 m intervals onto reef habitat. The mean (\pm S.E.) depth of deployments was 26.0 (1.3) m, 26.3 (1.6) m and 26.6 (0.5) m for sanctuary, habitat protection and general use zones, respectively, and did not differ significantly among zones (PERMANOVA, *pseudo-F*_{2,21} = 1.48, *P* = 0.13). Each BRUV unit was constructed as per Malcolm et al. [40], which included a galvanized metal frame containing a video camera (mini DV SONY) pointed at a bait bag mounted horizontally at the end of a 1.5 m long bait arm. Cameras were housed within high-pressure polyvinyl chloride pipe with flat acrylic end-ports yielding a field of view of 110°. For each BRUV deployment, the bait bag was replenished with ~500 g of chopped pilchards (*Sardinops* spp.) and each BRUV unit was left on the bottom for 30 minutes. This bait type was determined to yield

the most consistent outcomes compared to others previously tested (e.g. abalone viscera or crushed urchin [41]). This bottom time was considered appropriate for sampling reef fish between 20–40 m because there is no significant differences among fish assemblages and the *max N* of many common species when deployment times of 30, 60, and 90 minutes were compared (D. Harasti, unpublished data). Furthermore, the replication levels of sites and camera deployments within sites provide adequate power to reliably detect significant differences between fish species richness and total *max N* in sanctuary zones compared to fished areas with mean differences of 30% and 100%, respectively (B. Kelaher, unpublished data).

Videos were analyzed in the laboratory using a field of view 2 m behind the bait bag, which represented a standardized area of 9.4 m³ [40]. For each replicate BRUV deployment, we determined species richness, total *max N*, and *max N* of each fish species. *Max N* for a species was the maximum number of individuals in

any frame and total *max N* was the sum of *max N*'s for each deployment [32]. When the abundances of families of fishes were analyzed, the *max N* value used for each replicate was the summed *max N* of each fish species in that family. Analyses were restricted to fin fish to avoid complications associated with extra protection of all but two species of elasmobranchs (i.e. *Mustelus antarcticus* and *Galeorhinus galeus*) in habitat protection zones.

Comparisons across a Network of Marine Reserves and Partially-protected Areas

Hypotheses about changes in fish assemblages across the network of no-take marine reserves and partially-protected areas were tested using 2 factor analyses with *zone type* (3 levels, orthogonal and fixed) and *years* since the commencement of the zoning plan (4 levels, orthogonal and fixed), with analyses based on site averages. To test for differences in fish assemblages between no-take sanctuary zones and fished areas a contrast was included to compare sanctuary zones against zones where fishing was allowed. To test for differences in fish assemblages between the two types of partially-protected zones a contrast was included comparing fish assemblages in habitat protection and general use zones.

Hypotheses were based on multivariate comparisons of fish assemblage structure and univariate comparisons of fish species richness and total *max N*. Hypotheses were also tested using the total *max N* of four numerically-dominant families, Carangidae, Kyphosidae, Labridae and Monacanthidae, which represented 17%, 29%, 14% and 7% of the overall total *max N*, respectively. Analyses were also conducted on fish species with a summed *max N* that totaled more than 300 individuals and are commonly-caught in NSW waters. Each species is currently assessed as either moderately fished, fully fished, growth overfished or overfished indicating that they are each under fishing pressure. These taxa were *Pagrus auratus* [snapper, growth overfished], *Pseudocaranx georgianus* [silver trevally, growth overfished], *Scorpius lineolata* [silver sweep, moderately to fully fished], *Ophthalmolepis lineolatus* [southern maori wrasse, moderately fished], *Trachurus novaezelandiae* [yellow tail scad, fully fished] and *Nemadactylus douglasii* [grey morwong, overfished] (see [42] for details). In Batemans Marine Park each of the above species is caught recreationally, as well as in the commercial ocean trap and line fishery. However, *T. novaezelandiae* is mostly caught in purse seine nets [42], which cannot be used in habitat protection zones.

Hypotheses about changes in fish assemblages and individual families and species were tested with non-parametric multivariate analysis of variance (PERMANOVA [43]). These non-parametric procedures are robust to variable ecological data commonly obtained from marine communities [44]. All univariate analyses were done using Euclidean distance to create similarity matrices. All multivariate analyses used the Bray-Curtis similarity coefficient [45]. Non-metric multidimensional scaling (nMDS) [46] was used to generate two-dimensional ordination plots which graphically illustrated multivariate patterns in fish assemblages.

Comparisons of the Performance of Individual Marine Reserves

The 12 sanctuary zone sites were located within six of the 10 offshore sanctuary zones in the Batemans Marine Park. From north to south, these were Brush Island, Murramarang, Tollgate Islands, Burrewarra Point, Broulee Island and Mullimburra (GPS co-ordinates of boundaries included in the NSW Marine Parks (Zoning Plan) Regulation 1999). These zones encompassed the smallest and largest offshore sanctuary zones in the marine park.

As well as size, these sanctuary zones varied across a range of marine park planning criteria (see Table 1 for details). To compare the individual performance of these 6 sanctuary zones since the commencement of the zoning plan, a ratio was established with $(x_{SZ}+1)/(X_{FA}+1)$, where x_{SZ} was the response variable from each sanctuary zone BRUV deployment and X_{FA} was the average of the closest two sites in areas where fish could be legally caught. This sanctuary zone/fished area ratio (hereafter called SZ/FA ratio) provided an indication of relative changes in fish assemblages in no-take and fished zones in a local area around individual sanctuary zones rather than across the network of reserves and partially-protected areas.

To test whether the performance of individual sanctuary zones was variable, a two factor PERMANOVA analysis was carried out on overall fish species richness, total *max N* and the total *max N* of four numerically-dominant families: Carangidae, Kyphosidae, Labridae and Monacanthidae with the factors *sanctuary zones* (SZ, 6 levels orthogonal and random) and *years* since zoning plan commencement (4 levels, orthogonal and fixed). These univariate analyses used Euclidean distance to create similarity matrices and were based on individual BRUV deployments.

The average direction of change of the six key fish outlined above (*Pagrus auratus*, *Pseudocaranx georgianus*, *Scorpius lineolata*, *Ophthalmolepis lineolatus*, *Trachurus novaezelandiae* and *Nemadactylus douglasii*) in each sanctuary zone was determined by calculating Pearson's correlation coefficient for the average SZ/FA ratio vs years since commencement of the zoning plan. These correlation coefficients were then averaged to determine a generalized direction of change (r_{av}) for each individual sanctuary zone with r_{av} being a value between -1 and 1 with positive and negative values indicative of positive and negative associations between SZ/FA ratio and time since establishment, respectively. To evaluate potential explanations for variation in individual sanctuary zone performance, the r_{av} for individual sanctuary zones were correlated using Pearson's correlation coefficient with the number of enforcement actions by marine park staff from 1 July 2009 to 30 June 2011 and the size of the sanctuary zone. To control for Type 1 error, the significance level of these correlations was corrected with sequential Bonferroni's technique [47]. Qualitative comparisons were also made between individual sanctuary zone performance and other important aspects of individual sanctuary zones, including whether they (i) terminated at the 3 nm limit maximizing cross shelf diversity, (ii) were directly linked to no-take estuarine areas facilitating connectivity, (iii) were buffered by habitat protection zones limiting accidental damaging activities or (iv) were adjacent to terrestrial reserves reducing land-based impacts (e.g. urban run-off).

Ethics Statement

This study was conducted with the permission of the NSW Marine Parks Authority and the NSW Department of Primary Industries. BRUV work was done under the auspices of the University of Wollongong animal ethics committee (approval number AE12/07). The study complied with the current laws of Australia.

Results

Comparisons across a Network of Marine Reserves and Partially-protected Areas

In total, 17,681 individuals from 89 species of fin fish were identified from the 384 BRUV deployments from 2008–2011. The structure of fish assemblages in no-take marine reserves (i.e. sanctuary zones) differed significantly from fished areas (Table 2,

Table 1. Average direction of association for the six abundant and commonly-caught fish species (see methods) since the commencement of the zoning plan and potential explanatory variables in six offshore sanctuary zones in the Bateman Marine Park.

	Brush Island	Murramarang	Tollgate Islands	Burrewarra	Broulee Island	Mullimburra	r	P
Direction of association since the establishment of the zoning plan								
Average Pearson's r for fish response variables	-0.07	-0.46	0.64	0.06	-0.19	-0.20		
Potential explanatory variables								
Enforcement actions	8	7	104	11	8	26	0.91	<0.01
Sanctuary zone area (ha)	1709	2449	3291	312	172	4542	0.12	0.82
Terminates at 3 nm boundary	Yes	Yes	Yes	No	No	Yes		
Directly Linked to estuarine sanctuary zones	No	No	No	No	No	Yes		
Buffered by Habitat Protection Zone	No	No	Yes	Part	No	Yes		
Adjacent to mainland National Park/Nature reserve	Yes	Yes	No	No	Yes	Yes		

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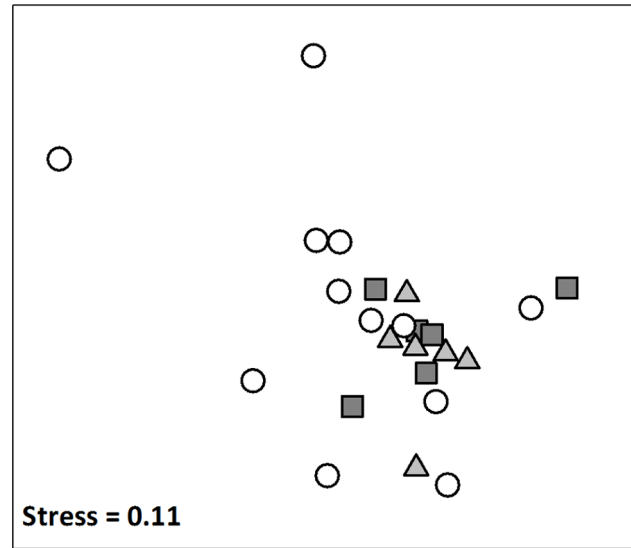


Figure 2. nMDS ordination of fish assemblages represented as centroids for each site within sanctuary (white circles), habitat protection (light grey triangles) and general use (dark grey squares) zones since the commencement of the zoning plan for the Batemans Marine Park. As there were no significant interactions between years and main effect contrasts (Table 1), points indicate site centroids averaged across years since establishment. doi:10.1371/journal.pone.0085825.g002

Fig. 2). In contrast, the structure of fish assemblages in habitat protection zones did not differ significantly from general use zones (Table 2, Fig. 2).

The richness of fish species was significantly greater in general use zones than in habitat protection zones, but did not differ significantly between sanctuary zones and fished areas (Table 2, Fig. 3). In contrast, the total *max N* of fishes was 37% greater in no-take marine reserves (i.e. sanctuary zones) compared to fished areas, which was significant (Table 2, Fig. 2). There was a trend towards more fish in general use zones compared to habitat protection zones ($P=0.053$, Fig. 3). Of the numerically-dominant families examined, the mean *max N* of kyphosids was significantly higher in no-take sanctuary zones compared to fished areas (Table 3, Fig. 3). For monacanthids, however, the differences in mean *max N* were significant between fished zones (Table 3, Fig. 3). The total *max N* of carangids and labrids did not differ significantly among zone types (Table 3).

In general, the *max N*'s of individual species were more variable than univariate community measures (i.e. species richness and total *max N*) or family groups, leading to fewer significant results. There was, however, a trend towards more *P. auratus* (snapper) in sanctuary zones than fished areas in 2008, 2010 and 2011 (Fig. 4). The *max N* of *P. georgianus* (silver trevally), *S. lineolata* (silver sweep), *O. lineolatus* (southern maori wrasse), *T. novaezelandiae* (yellow tail scad) and *N. douglasii* (grey morwong) did not vary significantly among zone types since the zoning plan's establishment (Table 4, Fig. 4). The average *max N* of *S. lineolata* increased in sanctuary zones with years since establishment.

Comparisons of the Performance of Individual Marine Reserves

There were significant differences in the SZ/FA ratio in the richness and total *max N* of fish assemblages among individual sanctuary zones (Table 5, Fig. 5). These ratios indicated a trend for

Table 2. PERMANOVA analyses comparing the structure of fish assemblages using multivariate data on the richness and abundance (total *max N*) of fishes among zone types and among years since the commencement of the zoning plan.

	df	(a) Fish assemblages			(b) Species richness			(c) Total <i>max N</i>		
		MS	<i>p-F</i>	<i>P</i>	MS	<i>p-F</i>	<i>P</i>	MS	<i>p-F</i>	<i>P</i>
Zone type	2	3926.20	2.16	<0.01	21.17	2.34	0.10	3210.50	5.61	<0.01
SZ vs FA	1	5352.00	2.96	<0.01	5.16	0.56	0.48	5188.40	9.22	<0.01
HPZ vs GUZ	1	2500.40	1.41	0.17	37.19	7.57	<0.01	1232.70	4.42	0.05
Years	3	4194.00	2.30	<0.01	47.52	5.26	<0.01	1978.90	3.46	<0.05
Zone type × Years	6	1058.90	0.58	0.99	3.86	0.43	0.86	228.44	0.40	0.88
Years × SZ vs FA	3	894.56	0.49	0.99	4.73	0.52	0.67	363.55	0.65	0.60
Years × HPZ vs GUZ	3	1223.20	0.69	0.92	2.98	0.61	0.60	93.32	0.33	0.79
Residual	84	1820.70			9.03			571.82		

Fish assemblages (a) used Bray-Curtis similarity measures following square root transformation while species richness (b) and total *max N* (c) used Euclidean distance to generate similarity matrices. Contrasts were included to compare sanctuary zones (SZ) with fished areas (FA) and habitat protection zones (HPZ) with general use zones (GUZ).

p-F = pseudo *F* ratio generated by PERMANOVA.
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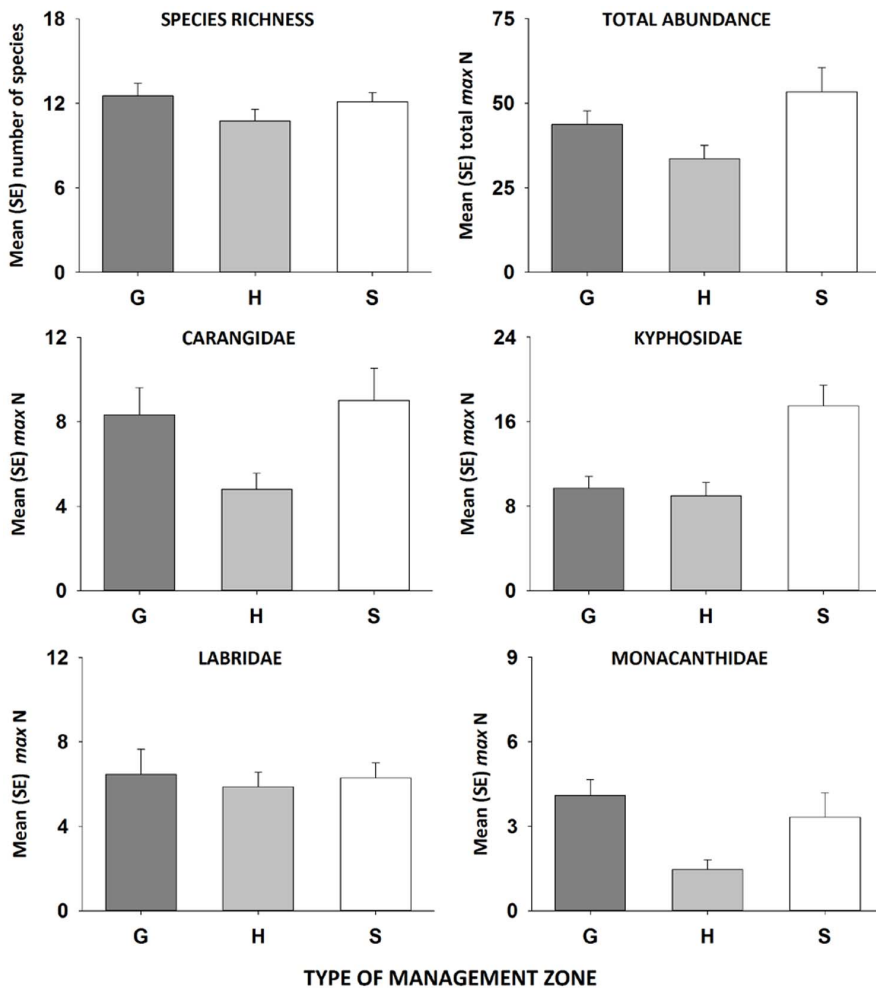


Figure 3. Mean (±1 SE) richness and total *max N* of fish assemblages and numerically-dominant family groups in general use (dark grey bars), habitat protection (light grey bars) and sanctuary (white bars) zones since the commencement of the zoning plan for the Batemans Marine Park.

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Table 3. PERMANOVA analyses comparing the total *max* N of the numerically-dominant families among zone types and among years since the commencement of the zoning plan using Euclidean distance.

	(a) Carangidae				(b) Kyphosidae		
	df	MS	<i>p-F</i>	<i>P</i>	MS	<i>p-F</i>	<i>P</i>
Zone type	2	146.12	1.32	0.29	803.43	6.03	<0.01
SZ vs FA	1	142.59	1.32	0.26	1600.70	12.37	<0.01
HPZ vs GUZ	1	149.64	2.11	0.17	6.20	0.14	0.70
Years	3	92.76	0.84	0.50	48.76	0.37	0.77
Zone type × Years	6	19.05	0.17	0.98	72.47	0.54	0.78
Years × SZ vs FA	3	15.91	0.15	0.93	81.74	0.63	0.58
Years × HPZ vs GUZ	3	22.19	0.31	0.84	63.20	1.38	0.26
Residual	84	110.57			133.24		
	(c) Labridae				(d) Monacanthidae		
	df	MS	<i>p-F</i>	<i>P</i>	MS	<i>p-F</i>	<i>P</i>
Zone type	2	2.27	0.42	0.65	44.87	5.12	<0.01
SZ vs FA	1	0.32	0.06	0.82	7.04	0.74	0.40
HPZ vs GUZ	1	4.23	0.99	0.32	82.69	9.94	<0.01
Years	3	63.84	11.71	<0.01	15.89	1.82	0.15
Zone type × Years	6	2.18	0.40	0.89	9.64	1.10	0.37
Years × SZ vs FA	3	1.14	0.21	0.88	12.15	1.27	0.31
Years × HPZ vs GUZ	3	3.21	0.75	0.53	7.14	0.86	0.46
Residual	84	5.45			8.76		

Contrasts were included to compare sanctuary zones (SZ) with fished areas (FA) and habitat protection zones (HPZ) with general use zones (GUZ).

p-F = pseudo *F* ratio generated by PERMANOVA.

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greater *max* N of fish in sanctuary zones (i.e. the probability (*P*) of 6 ratios greater than 1 = 0.059) and substantially richer fish assemblages in two of the six sanctuary zones sampled (i.e. where the mean plus standard error bar is greater than 1 on Fig. 4). However, the average number of fish species in the Mullimburra sanctuary zone plus one standard error was less than 1, indicating fewer fish species in this sanctuary zone relative to the surrounding fished area (i.e. mean plus standard error are less than 1 on Fig. 5).

The SZ/FA ratio of total *max* N for carangids, kyphosids and labrids also varied significantly among individual sanctuary zones demonstrating variation in individual reserve performance (Table 5, Fig. 5). For four out of six sanctuary zones, the SZ/FA ratio was close to one. For labrids, however, the average total *max* N plus one standard error was less than 1 in the Murramarang reserve indicating fewer of these fishes in this sanctuary zone than in the surrounding fished areas (Fig. 4). The SZ/FA ratio of total *max* N for carangids and monacanthids interacted significantly among sanctuary zones and years since establishment (Table 5). Post hoc tests (PHT) revealed that the patterns of average SZ/FA ratio for these fish taxa varied significantly among sanctuary zones in some years but not others (PHT: *P* < 0.05). For example, the SZ/FA ratio of carangids did not vary among individual sanctuary zones in 2008 and 2011, but was significantly greater at Mullimburra than other sanctuary zones in 2009 (PHT: *P* < 0.05) and significantly smaller than other sanctuary zones in 2010 (PHT: *P* < 0.05). The average SZ/FZ ratio for monacanthids and carangids indicated more of these fishes in 5 out of 6 and 3 out of 6 sanctuary zones than the surrounding fished areas, respectively (Fig. 4). The average SZ/FA ratio plus one standard

error for monacanthids at the Mullimburra reserve was less than 1 for each year of sampling (2008 SZ/FA ratio [SE] = 0.41 [0.08], 2009 = 0.32 [0.04], 2010 = 0.21 [0.03], 2011 = 0.51 [0.085]). Similarly, the average SZ/FA ratio plus one standard error of carangids in the Murramarang reserve, was less than 1 for three of the four years of sampling (2008 SZ/FA ratio [SE] = 0.67 [0.10], 2009 = 0.28 [0.06], 2010 = 0.11 [0.02], 2011 = 1.17 [0.61]).

The r_{av} for the six abundant species considered to be important for commercial and recreational fishing in NSW waters varied substantially among individual sanctuary zones (Table 1). The value of 0.64 for the Tollgate Island sanctuary zone was strongly positive with each of the six species having a positive association between SZ/FA ratio and the years since the zoning plan's commencement (Table 1). In contrast, the average direction of change at Murramarang ($r_{av} = -0.46$) and Mullimburra ($r_{av} = -0.20$) suggested limited performance in these marine reserves for the species we considered. For the remaining three sanctuary zones, there was no strong average directional association between SZ/FA ratio and the years since the zoning plan's commencement ($0.20 > r_{av} < -0.20$).

After *P*-values were corrected using sequential Bonferroni's technique, there was a significant correlation between the r_{av} for the six key fish species and the number of enforcement actions undertaken (Table 1), indicating a positive association between individual reserve performance and compliance activity. In contrast, there were no significant correlations between average directional association of the SZ/FA ratio for the six key fish species since the park's establishment (r_{av}) and the size of sanctuary zones (Table 1). With respect to key reserve attributes (Table 1),

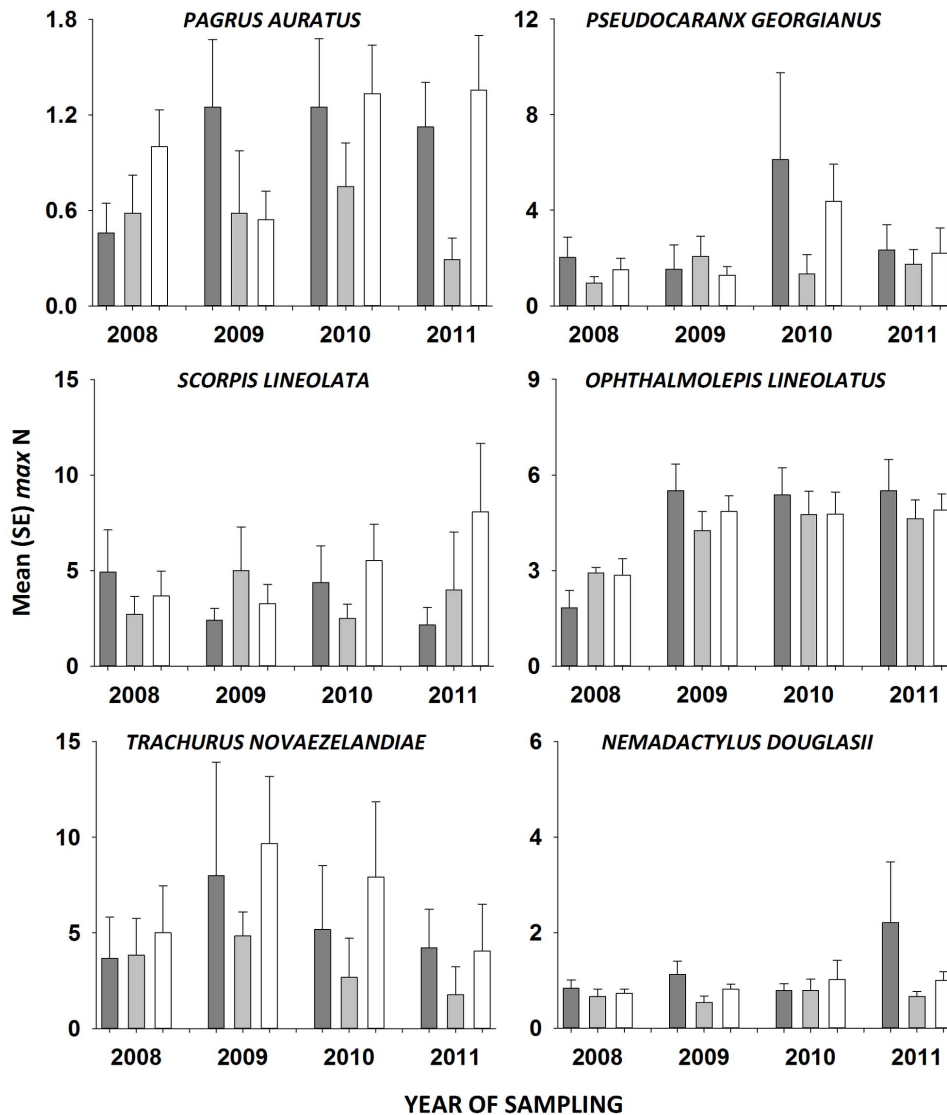


Figure 4. Mean (\pm SE) max N of fish species important to recreational and commercial fisheries in general use (dark grey bars), habitat protection (light grey bars) and sanctuary (white bars) zones in each year since the commencement of the zoning plan for the Batemans Marine Park.

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the large reserve at Mullimburra was the only one to have full coverage from the shore to the 3 nm limit of state waters, to be directly linked to estuarine sanctuary zones, to be buffered by habitat protection zones and to be adjacent to mainland National Parks. In contrast, the only key attribute possessed by the relatively small Broulee Island Reserve was that it was adjacent to a Nature Reserve. Moreover, the small Burrewarra reserve only had partial buffering from habitat protection zones. The reserves at Brush Island and Murramarang each terminated at the 3 nm limit and were adjacent to National Parks. The Tollgate Island Reserve ran out to the 3 nm limit of state waters and was buffered by habitat protection zones. As it commenced approximately 1 km offshore (Fig. 1), the Tollgate Island reserve could not link directly to estuarine sanctuary zones. It was, however, directly adjacent to the Clyde River Estuary that included several substantial no-take estuarine sanctuaries. Although the Tollgate Islands Reserve was adjacent to urban development, its distance from shore (Fig. 1) provided a substantial buffer from land-based impacts. The

Tollgate Islands themselves are Nature Reserves not accessible to the general public.

Discussion

On average there were 38% more fish in the network of marine reserves than in fished areas of the Batemans Marine Park. The largest contribution to this effect came from Kyphosids (drummers). Compared to global averages for individual reserves (e.g. 166%, $n = 124$ reserves [5]) the elevated fish abundances across the network of marine reserves was modest, but well within the spectrum of positive responses. This may, in part, be due to the marine park only being in place for 5 years (e.g. [30,48]) and previous fishing pressure being regulated by conventional fisheries management [42]. It may also stem from the fished areas being partially-protected such that even the most unprotected places in the marine park (general use zones) were free from potentially damaging activities such as demersal trawling and long-lining [24].

Table 4. PERMANOVA analyses comparing the *max N* of key fish species among zone types and among years since the commencement of the zoning plan.

	df	(a) <i>P. auratus</i>			(b) <i>P. georgianus</i>			(c) <i>S. lineolata</i>		
		MS	<i>p-F</i>	<i>P</i>	MS	<i>p-F</i>	<i>P</i>	MS	<i>p-F</i>	<i>P</i>
Zone type	2	2.20	2.95	0.07	13.20	1.06	0.37	31.73	0.81	0.45
SZ vs FA	1	1.76	2.32	0.15	0.15	0.01	0.92	63.38	1.67	0.22
HPZ vs GUZ	1	2.64	4.51	<0.05	26.26	1.96	0.18	0.08	0.01	0.95
Years	3	0.74	0.99	0.41	27.44	2.20	0.09	5.88	0.15	0.94
Zone type × Years	6	0.87	1.16	0.34	8.70	0.70	0.70	28.19	0.72	0.62
Years × SZ vs FA	3	1.21	1.59	0.19	1.38	0.11	0.95	37.98	1.00	0.41
Years × HPZ vs GUZ	3	0.53	0.90	0.44	16.02	1.19	0.31	18.40	0.96	0.44
Residual	84	0.75			12.48			39.20		
	df	(d) <i>O. lineolatus</i>			(e) <i>T. novaezelandiae</i>			(f) <i>N. douglasii</i>		
		MS	<i>p-F</i>	<i>P</i>	MS	<i>p-F</i>	<i>P</i>	MS	<i>p-F</i>	<i>P</i>
Zone type	2	1.04	0.31	0.74	92.33	1.07	0.36	1.86	1.87	0.13
SZ vs FA	1	<0.01	<0.01	1.00	137.16	1.65	0.19	0.07	0.06	0.85
HPZ vs GUZ	1	2.08	0.70	0.43	47.50	0.95	0.38	3.66	2.64	0.07
Years	3	31.49	9.37	<0.01	70.34	0.81	0.48	1.33	1.34	0.27
Zone type × Years	6	1.94	0.58	0.76	9.65	0.11	0.99	1.02	1.03	0.39
Years × SZ vs FA	3	0.69	0.21	0.90	12.79	0.15	0.93	0.51	0.49	0.77
Years × HPZ vs GUZ	3	3.20	1.08	0.40	6.52	0.13	0.95	1.53	1.11	0.33
Residual	84	3.36			86.55			0.99		

Contrasts were included to compare sanctuary zones (SZ) with fished areas (FA) and habitat protection zones (HPZ) with general use zones (GUZ). *p-F* = pseudo *F* ratio generated by PERMANOVA.

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Despite the total *max N* of fishes being significantly greater in marine reserves than in fished areas, there were no significant differences in the richness of reef fishes across the network of no-take reserves compared to fished areas. There was, however, greater richness of reef fish species in Brush Island and Burrewarra reserves compared to the adjacent fished areas. Similar to richness, there were also no significant differences in the abundances of some family groups and commonly-caught fish species among zone types. Large variation in the measurement of fish populations contributed to these results. For example, although there was 37% more Carangids in marine reserves than in fished areas, this comparison was not close to being significant due to substantial variation among zones and sites in fished areas. Nonetheless, it was to be expected that only the very large changes in fish assemblages would be detected because power analyses demonstrated that, for the levels of replication used, effects of 30% and 100% were required to reliably detect significant differences in the richness and *max N* between reserves and fished areas, respectively.

Another consideration for the non-significant results was the influence of time since reserve establishment. In comparisons of other temperate Australian marine reserves to fished areas from before to three years after establishment, Edgar et al [49] demonstrated few changes in the abundance of fish and invertebrates in the marine reserves compared to fished areas. They concluded that the three-year period studied after reserve commencement may have been insufficient to generate clear trends in fish population recoveries. The results from our study suggest that 5 years may also not be sufficient to detect change of some fish species whose abundances have been demonstrated to

recover in much older marine reserves (e.g. *Pagrus auratus*, snapper [28]). Similar conclusions were reached about fish populations on shallow subtidal reefs sampled using underwater visual census over the first five years following the establishment of the Batemans Marine Park [50].

An important consideration for interpreting positive effects of marine reserves on fish abundances is whether marine reserves were deliberately placed in areas with more fish. For the Batemans Marine Park this was not the case because, although some data was collected prior to the parks' establishment [31,51], detailed regionally specific data on reef fish assemblages and reef extent and complexity were not available to marine park planners prior to the marine parks establishment. Furthermore, there are two lines of evidence to support positive reserve effects: (i) the abundances of some species increased in sanctuary zones over time (e.g. *S. lineolata*, silver sweep) and (ii) sampling conducted prior to the zoning plan's establishment indicated that there were similar if not fewer fish in marine reserves compared to fished areas [48].

Given that all levels in the factor *zone type* were replicated with multiple sites and BRUV deployments were haphazardly located on reefs of similar structure, our study was of the form of a standard ecological field experiment where the manipulation was the implementation and enforcement of marine park regulations. While this sampling was sufficient for testing the proposed hypotheses about reserve effects, similar to most published field experiments, the ability to attribute treatment effects to the manipulation (e.g. conservation measures in this case) rather than site selection could be improved by the incorporation of pre-establishment data into comparisons (e.g. BACI-type experimental

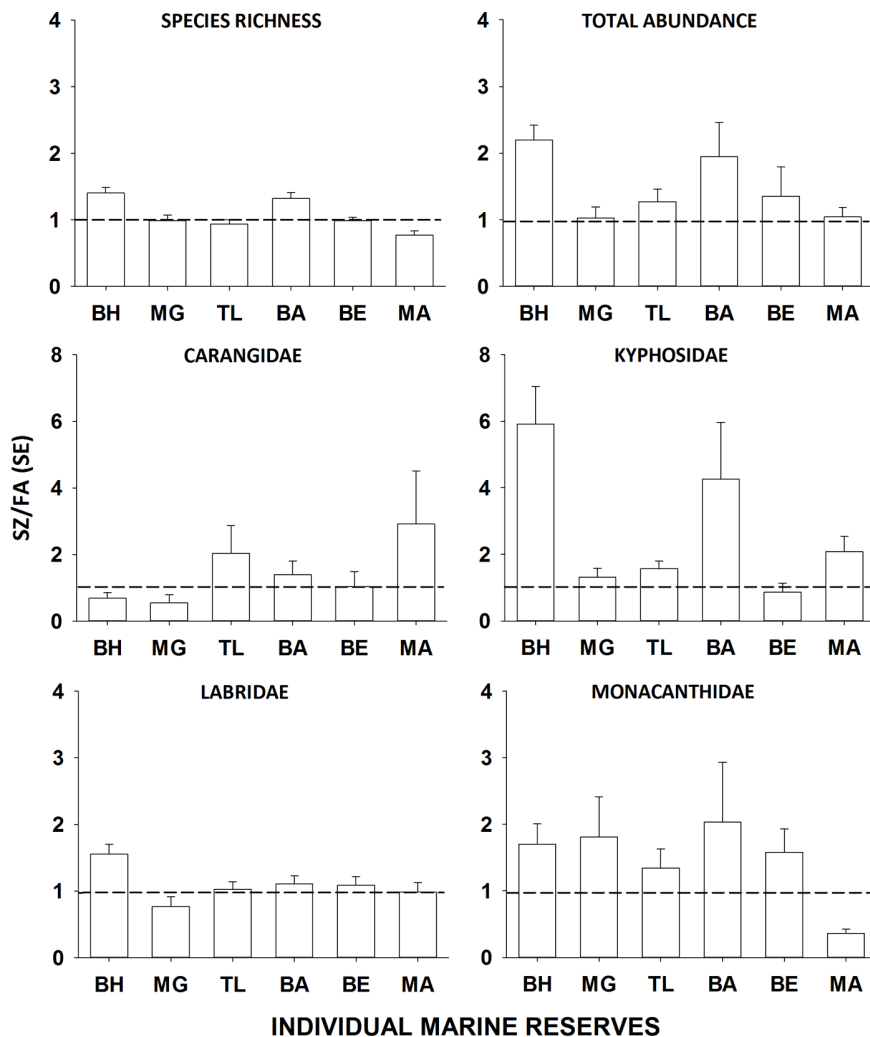


Figure 5. Mean (± 1 SE) sanctuary zone to local fished areas ratio (SZ/FA) for richness and total *max N* of fish assemblages and numerically-dominant family groups in the Brush Island (BH), Murramarang (MG), Tollgate Islands (TL), Burrewarra (BA), Broulee Island (BE) and Mullimburra (MA) sanctuary zones. Bars represent the main effects of sanctuary zone averaged across years since establishment.

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designs [52]). The marine park planning process is, however, not always conducive to implementation of robust BACI experimental designs. For the Batemans Marine Park, there was around 14 months between the declaration of the Park and the implementation of the zoning plan [27]. Most of this period was taken up with planning and public consultation, leaving only a few months between when the locations of the marine reserves were finalized and the zoning plan coming into effect. Consequently, there was insufficient time to collect the inter-annual pre-establishment data required for a temporally-replicated BACI-style experimental design.

In general, fish assemblages either did not differ between the partially-protected areas with different levels of protection or there were more species in general use zones than habitat protection zones. There was, therefore, no evidence that the additional restrictions associated with habitat protection zones, such as removal of commercial purse seining, lift netting and set lining, improved conservation outcomes for reef fish assemblages on offshore reefs after 5 years. Given that trawling and long-lining were removed from the entire Batemans Marine Park, the removal

of other less damaging commercial fishing activities from habitat protection zones probably had limited additional influence on fish communities. Furthermore, the designation of habitat protection zones could have attracted some increased recreational fishing effort, therefore reducing differences between the two different zones. This is because habitat protection zones are often promoted as enhancing recreational fishing opportunities through reduced commercial fishing effort, with similar types of areas in NSW estuaries (e.g. Recreational Fishing Havens) being perceived by recreational anglers as improving catch rates [53]. Management strategies that result in shifting recreational fishing effort towards partially-protected areas may limit the conservation benefits of these areas.

Although there was a general increase in overall fish abundance in marine reserves across the network, there was significant variation among the performance of individual reserves. The six commonly caught fish species in marine reserves at the Tollgate Islands showed the strongest positive trend over the 5 years of reserve protection (Pearson's $r = 0.64$). Although quantitative data on fishing effort was not collected consistently across the Batemans

Table 5. PERMANOVA analyses comparing the sanctuary zone to local fished area ratio (SZ/FA) for univariate measures of fish assemblages, numerically-dominant families and key fish species among sanctuary zones (SZ) and among years since the commencement of the zoning plan for the Batemans Marine Park.

	(a) Species richness				(b) Total abundance		
	df	MS	p-F	P	MS	p-F	P
SZ	5	1.70	16.15	<0.01	6.97	4.57	<0.01
Years	3	0.18	1.24	0.33	4.39	2.25	0.13
SZ × Years	15	0.15	1.47	0.13	2.03	1.33	0.21
Residual	168	0.11			1.52		
	(c) Carangidae				(d) Kyphosidae		
	df	MS	p-F	P	MS	p-F	P
SZ	5	26.72	3.38	<0.05	114.14	8.60	<0.01
Years	3	2.64	0.12	0.96	30.17	2.04	0.14
SZ × Years	15	25.65	3.24	<0.01	15.05	1.13	0.35
Residual	168	7.91			13.27		
	(e) Labridae				(f) Monacanthidae		
	df	MS	p-F	P	MS	p-F	P
SZ	5	2.18	6.77	<0.01	9.98	4.28	<0.01
Years	3	1.10	2.30	0.12	15.18	3.29	<0.05
SZ × Years	15	0.51	1.57	0.10	5.04	2.16	<0.05
Residual	168	0.32			2.33		

p-F = pseudo F ratio generated by PERMANOVA.
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Marine Park prior to its establishment, it was well known that the Tollgate Islands were heavily targeted by boat-based fishers prior to the enforcement of marine park regulations, as the islands are adjacent to the largest town and boating facilities in the region. This offshore reserve was also one of the most commonly patrolled because of its central location and proximity to a relatively safe ocean bar crossing. The substantial reduction in fishing effort combined with the greatest compliance effort would have contributed to the Tollgate Islands reserve showing the strongest positive responses to protection over the first 5 years.

Effective compliance cannot be underestimated in achieving positive marine conservation outcomes [13,14]. As expected, enforcement actions were positively associated with individual reserve performance in the Batemans Marine Park. As well as active enforcement, the Batemans Marine Park operational plan included priority actions aimed at increasing voluntary compliance. This included local education and awareness activities, programs to improve signage and zone markers as well as proactively restricting potentially harmful activities through permitting. In response to these strategies, we contend that public knowledge of the marine park zoning arrangements improved substantially since the parks establishment. For example, marine park awareness by tourists increased from 47% (n = 203) to 72% (n = 36) from 2008 to 2011 (Eurobodalla Shire Council and NSW Marine Park Authority, unpublished data). Public knowledge and support for marine reserves increases voluntary compliance, which can both improve the effectiveness of marine reserves and reduce

the costs of enforcement [54,55]. Greater consideration of compliance planning during establishment and adaptive management of marine reserve networks can enhance voluntary compliance and improve conservation outcomes [24].

Marine reserve size is generally regarded as a fundamental principle in effective marine reserve design with larger reserves often having greater conservation benefits [56]. By this criterion, the largest marine reserve in our study, Mullimburra, did not perform as well as smaller reserves in the network. Consequently, factors other than reserve size must have been driving this result. Importantly, the Mullimburra reserve had many characteristics considered important for effective reserve design (Table 1). Mullimburra marine reserve was adjacent to the Eurobodalla National Park minimizing potential land-based threats to the marine ecosystem [57,58]. It was also directly linked to no-take estuarine reserves ensuring undisrupted connectivity between juvenile and adult habitats [59,60]. Mullimburra marine reserve had cross-shelf coverage from the shore to the 3 nm limit of NSW state waters, maximizing reef habitat representation [61], which is known to be extensive in inner- and mid-shelf waters in the region [51]. It was also surrounded by extensive partially-protected areas (i.e. habitat protection zones) buffering it from unintentional commercial fishing activities [62].

Given all these key reserve attributes, it is not clear why the large reserve at Mullimburra did not perform as well as some smaller reserves, although it should be noted that the BRUV sites in fished areas adjacent to this reserve were further away than they were for other reserves. A more likely explanation is the influence of compliance levels because the least effective reserves, Murrarang and Mullimburra, also had the lowest number of enforcement actions per unit area. A review of compliance related issues from the Great Barrier Reef Marine Park suggests that even a small amount of poaching can have major ecological consequences [26]. Although there are no data available to discriminate between compliance efficacy and the amount of illegal fishing activity in the Batemans Marine Park, the significant relationship between enforcement actions and reserve performance suggests that quantitative monitoring of compliance and illegal activities should be prioritized to facilitate adaptive management to maximize marine conservation outcomes.

It is not possible from our results to determine whether the performance of individual marine reserves within the first 5 years will be a useful predictor of long-term reserve performance. This raises important questions about how much park-specific ecological monitoring can contribute to evidence-based adaptive management of marine park zoning arrangements at a 5 year review, as is currently required in NSW. Certainly, clear advice can be given that the network of marine reserves in the Batemans Marine Park had a positive influence on the abundance of fishes, particularly kyphosids, despite differences in the performance of the individual marine reserves we examined. In contrast, there were no consistent effects to validate the efficacy of habitat protection zones. Ongoing enforcement will also be required to maintain reserve efficacy and extra compliance attention should be focused on the large marine reserves at Mullimburra and Murrarang, which appear to be underperforming given their attributes (see Table 1).

Apart from this general advice, 5 years of ecological monitoring was insufficient to provide scientific evidence that would justify changing the current network of marine reserves and partially-protected areas in the Batemans Marine Park to improve long-term conservation of biodiversity. Nonetheless, the broader scientific literature about marine reserves will still have an invaluable contribution to the review process, with rigorous

assessments of reserve attributes (e.g. size, habitat linkages, buffering) from much older marine reserve networks being particularly informative. After the initial 5 year review, NSW marine parks are reviewed every 10 years. At the 15 year review, sufficient time should have passed for substantial changes in the structure of marine communities to have occurred [28,30]. At this point, the results from local ecological monitoring and other complimentary research will be in a much stronger position to drive evidence-based adaptive management to enhance long-term conservation objectives.

In conclusion, few studies have examined changes in fish assemblages across a network of marine reserves relative to fished areas with different levels of environmental protection. We show that after 5 years of protection, fish abundances were 37% greater across the network of marine reserves compared to partially-protected areas, although not all individual reserves performed equally and performance was temporally variable. These changes are relatively modest compared to some reserve networks (e.g. [63]), but still add to the growing weight of evidence that conservation outcomes from planned networks of marine reserves are greater than those from individual reserves [4,26]. Our results also provide insight into factors (e.g. past fishing effort and compliance) that promote early conservation benefits to fish in temperate marine reserves and thus should be carefully considered in marine reserve establishment and management. As coastal

population growth and associated development increases stress on marine environments, it is critical that networks of marine reserves are designed and adaptively managed to maximise their conservation objectives. Although local environmental monitoring can contribute to adaptive management of newly established marine reserve networks, the extent of this contribution will be limited by the rate of change in marine communities in response to protection. The adaptive management processes of newly established marine reserve networks could, therefore, be enhanced by rigorous assessment of the efficacy of ecological attributes and planning principles from much older networks.

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Author Contributions

Conceived and designed the experiments: BPK MC AB MR AJ ARD. Performed the experiments: BPK MC AB MR AJ ARD. Analyzed the data: BPK MC AB MR AJ ARD. Contributed reagents/materials/analysis tools: BPK MC AB MR AJ ARD. Wrote the paper: BPK MC AB MR AJ ARD.

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