

Relationships and interactions between temperate reef fish communities, physical habitat structure and marine protection.

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Abstract

Habitat heterogeneity and complexity are important factors responsible for structuring the associated faunal and algal compositions of temperate marine communities. Despite the efforts of traditional management approaches, the continued worldwide decline in commercial fisheries has led to a growing awareness and appreciation of ecosystem-based approaches as a potential means to sustainably managing and conserving the biodiversity of the World's oceans. Such an approach requires knowledge of the relevant environmental parameters, resources and habitats at multiple scales that are important in shaping the spatial distributions and abundances of marine communities. The magnitude of sampling effort required to sufficiently quantify marine biodiversity across whole ecosystems is generally prohibitive at broad management scales which has led to the need for more time and cost effective surrogate approaches utilising physical habitat data. Disentangling the separate importance of natural spatial and temporal habitat variability effects from those of spatial marine planning efforts is vital to ensuring successful management outcomes. To achieve this, scientists and managers first need to understand how specific aspects of the physical environment structure temperate reef-fish communities and at which scales they become relevant. The current availability of this information is limited across temperate marine environments of Southern Australia and Tasmania.

This thesis investigates patterns in the community structure responses of temperate reef fish communities along the South Australian and Tasmanian coasts in response to aspects of their surrounding habitat structure. The first and second chapters of this thesis investigate how fish community structure varies in response to variability in the physical characteristics, heterogeneity and complexity of reef habitat; and how these responses in fish community assemblage structure vary with the spatial scale at which they are measured. Across large,

inter-bioregional scales it is principally climatic and biogeographical differences between varying geographic positions which are important in structuring much of the temperate reef fish community structure around Australia, while at smaller, intra-bioregional and local scales, the importance of ecologically proximal physical variables, such as exposure, biogenic cover, refuge space and habitat substratum begin to come into effect suggesting an increasing importance of physical habitat heterogeneity and complexity towards finer ends of the scales investigated. The third chapter of this thesis investigates the potential of remotely sensed measures of habitat complexity (i.e. multibeam sonar derivative products) as surrogates to understanding how reef-fish community structure responds to the surrounding habitat. The bathymetry derived measures of habitat structure that were investigated were limited predictors of temperate reef fish community structure at fine resolutions with the most important variables identified being those acting as proxies of the predominant swell exposure. The final chapter attempts to disentangle the effects of natural community responses of reef-fish communities to their habitat structure from those related directly to marine protection. The results were largely uninformative but highlight the need for larger scale studies considering additional factors such as local anthropogenic pressure and recruitment variability in order to adequately apply this analysis approach across Tasmanian MPAs and maximise the ability to detect reserve effects. Overall, this thesis provides an improved understanding of the importance of physical structure in determining rocky reef marine assemblages and highlights some of the potential physical surrogate measures which should and should not be applied to predict spatial variability driven by such structure for use in all forms on marine spatial management.

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Chapter 1. Introduction

Coastal marine environments are often characterised by high structural heterogeneity, supporting a large diversity of species, ecological processes and habitat types (Choat and Schiel, 1982, Guidetti, 2000, Ruitton et al., 2000). The specific compositions of faunal marine assemblages are dictated by the spatial and temporal variability of complex interactions between the physical, chemical and biological factors present within their environments (Menge and Sutherland, 1987, Underwood, 2000, Valesini et al., 2004a). Therefore it is logical to surmise that areas within the same region, subject to similar environmental characteristics, might support similar faunal assemblages at any one time. This supposition formed the basis of the primary hypothesis behind this investigation, that quantifiable environmental characteristics can explain variations in the spatial patterns of fish assemblages and distributions observed across sub-tidal temperate reef habitats of Southern Australia and Tasmania.

1.1 Fisheries in peril

Natural ecological processes are not the only drivers dictating the biodiversity of marine systems. Anthropogenic influences have had considerable impacts on the World's oceans through resource exploitation and fishing (Pauly et al., 2005), pollution (Johnston and Roberts, 2009), invasive species introductions and climate change (Edgar et al., 2005). In 2008, the United Nations Food and Agriculture Organisation (UNFAO) reported that 52% of the world's fisheries were at that time fully exploited; producing catches that were at or close to their maximum sustainable limits, with no room for further expansion of the fishery (UNFAO, 2008). A further 28% of world stocks were categorised as over-exploited (19%), depleted (8%) or recovering from depletion (1%) while only around 20% were moderately

(18%) or under-exploited (2%) with the possibility of increased production. The same report highlighted the immediate need for effective and precautionary management for the majority of the world's fish stocks.

1.2 Ecosystem-based management

Worldwide decline in fisheries stocks has led to a renewed impetus to provide effective management techniques for commercially important fish species (Pauly et al., 2005). Due, in part, to the failings of traditional single species management approaches, ecosystem-based fisheries management is increasingly advocated as a means to restoring the world's fisheries (Garcia et al., 2003, Worm et al., 2009, Nevill, 2010). Ecosystem-based fisheries management approaches recognise the complexity of ecosystems and the interconnections among their component parts and attempts to manage them from a holistic perspective based on a thorough understanding of ecological interconnections and processes. The 2003 FAO 'Ecosystem approach to fisheries' report recommends that any effective ecosystem-based fisheries management approach requires adaptive management strategies based on scientific description of the ecosystem in terms of scale, extent, structure and functioning (Garcia et al., 2003).

1.3 Marine Protected Areas

Marine Protected Areas (MPAs) are being increasingly promoted as an effective ecosystem-based approach to sustainably managing and conserving the biodiversity and fisheries of the World's oceans (Murray et al., 1999, Halpern and Warner, 2002, Friedlander et al., 2003, Gell and Roberts, 2003, Halpern, 2003, Pauly et al., 2005, Ballantine and Langlois, 2008, Klein et al., 2008, Lester et al., 2009). They aim to achieve long term conservation of biodiversity, ecosystem processes and cultural value through a legal framework of sustainable utilisation, management and protection of the marine environment (UQTEC, 2009). The

Commonwealth of Australia's Oceans Policy (1998) commits all states and territories to the establishment of a National Representative System of Marine Protected Areas (NRSMPA) to ensure the long term conservation of Australia's marine biodiversity. The NRSMPA is managed through a system of zones of increasing protection ranging from strict 'no-take' nature reserves managed for science or wilderness protection, through national parks, habitat or species management areas, to areas managed for the protection and maintenance of biological diversity while providing a sustainable flow of natural products and services to meet community needs (Commonwealth of Australia's Oceans Policy, 1998).

Increasing numbers of MPAs are being established each year around the world with varying management outcomes in mind, be they conservation, resource management, scientific, recreational, or educational. MPAs and protection from fishing have been shown to have clear conservation benefits to marine faunal communities around the world, increasing relative total abundances (Mosquera et al., 2001), diversity (Côté et al., 2001, Halpern, 2003), and most prominently, the abundance and biomass of large bodied and commercially targeted species (Babcock et al., 1999, Côté et al., 2001, Halpern and Warner, 2002, Claudet et al., 2006, Barrett et al., 2007, Richards et al., 2012). A number of studies have successfully identified complex trophic cascade effects of protection from fishing (Shears and Babcock, 2003) and evidence is accumulating that supports the application of no-take MPA zones as effective means to managing marine fisheries resources (Halpern et al., 2009) however this is still a contentious area of debate (Kearney et al., 2012a). A large number of empirical studies have demonstrated that no-take MPAs significantly increase the abundance, diversity and biomass of a wide range of fished species within their boundaries (see Lester et al., 2009 for a synthesis of 124 peer-reviewed studies). Recent studies are also starting to suggest that MPAs have the potential to produce recruitment and adult spill-over benefits to the surrounding

local fisheries (Tupper, 2007, Halpern et al., 2009, Goñi et al., 2010, Díaz et al., 2011, Harrison et al., 2012, Kay et al., 2012).

Each new MPA constitutes a controlled experiment at an ecologically relevant spatial scale and provides important opportunity for scientific investigation. Studying MPAs furthers our understanding of anthropogenic effects on marine ecosystems by allowing us a baseline against which to make real-world comparisons (Ballantine and Langlois, 2008). They provide a local community recreation and education resource, a place where people of all ages and social circumstances can enjoy, experience and learn about the marine environment in close to natural conditions, helping to instill an appreciation and understanding of the conservation value of the wider marine environment. They support local tourism industries such as dive and wildlife tour operators by providing a natural attraction to a region and they are an important teaching resource for schools and universities. By way of example, field-visits to no-take MPAs in New Zealand have become important parts of the curriculum for students from primary to tertiary level (Ballantine and Langlois, 2008).

The varying management goals behind the establishment of MPAs consequently means that they vary greatly in the type, extent, species suitability and range of structure of the habitats that they protect. Targeting and protecting a wide and representative range of habitat structure and types which will maximise conservation value and safeguard over-exploited and threatened species, communities and systems is a major problem faced by policy makers and managers with the task of implementing effective MPAs (Babcock et al., 1999). Ultimately, understanding ecological processes and quantifying fish community responses to habitat structure is crucial for applied aspects of MPA planning and management, particularly if the goals of these particular management approaches are to maximise biodiversity (Garcia-Charton and Perez-Ruzafa, 1998). Understanding the habitat associations of organisms aids

conservation planning because of the potential for habitats and habitat structure to act as surrogate measures of biodiversity for rapid and cost-effective MPA selection (Ward et al., 1999). Complex habitats are generally expected to experience fastest and more intense responses to a release from fishing pressure (Barrett et al., 2007) and quantifying habitat structure and relating it to patterns of fish community structure will enable scientists to better understand biotic responses following the establishment of MPAs and assist in site selection that most effectively enhances the recovery of fish populations.

Various studies have considered the changes in reef communities in response to MPA declaration across temperate marine environments of Australia and New Zealand (Babcock et al., 1999, Edgar and Barrett, 1999, Shears and Babcock, 2003, Barrett et al., 2007, Barrett et al., 2009) but few studies have been carried out that specifically attempted to investigate the associations and interactions between components of the reef community, physical habitat structure and MPA effects. Alexander *et al.* (2009) have examined relationships between different metrics of reef habitat structure and the density of macro-invertebrates at different spatial scales inside and outside a MPA in Tasmania. Their work identified that protection from fishing greatly influenced most major components of the invertebrate reef community, while reef habitat structure appeared to have little interactive influence with MPA effects at the scales they investigated. The work of my thesis will be the first study to date to have quantitatively examined the relationships between fish assemblages, MPA effects and habitat structure across temperate reef habitats of Australia.

1.4 Environmental gradients and scales

Environmental variables that organisms respond to can be categorised into three general classes of indirect, direct and resource gradients (Austin, 1980). Indirect gradient variables do not tend to induce direct physiological effects on an organism or community (e.g. altitude,

latitude or longitude). Direct gradients have a proximal ecological effect on an organism or community (e.g. light, temperature or pH) while resource variables are directly consumed or utilised by an organism or community (e.g. food, nutrients or water). Organisms or communities often respond to these gradients in a hierarchical fashion resulting in different spatial patterns at different spatial resolutions and extents (Guisan and Thuiller, 2005).

Gradual patterns in species distributions over large scales and coarse resolutions tend to be correlated with indirect climatic gradients, whereas patchy, small scale distributions at fine resolution are more likely the result of direct environmental gradients and patchy resource distributions resulting from local topographic variation and habitat fragmentation (Guisan and Thuiller, 2005, Scott, 2002). Attempts to describe and understand habitat patterns in reef fish abundance and distribution need to consider the spatial, temporal and ontogenetic variability dictating these patterns (Morton and Gladstone, 2011).

Environmental variables can, alternatively, be considered by their influence or position in the chain of ecological processes that link them to their impact on an organism (Austin, 2002).

The most proximal ecological variables along this chain of processes determining an organism's local response will generally be direct or resource gradient variables while more distal variables tend to be indirect variables dictating broader scale pattern responses. In many cases, particularly across broad spatial scales, indirect variables can replace more ecologically proximal variables in a surrogate sense (Guisan and Zimmermann, 2000) but the type of environmental variables considered in an investigation will limit the applicable geographical extent and resolution across which species distribution models can be confidently applied without significant errors (Iampietro et al., 2008). Models based on ecologically proximal, direct and resource gradients will be the most robust and widely

applicable but caution should be applied when considering similar species and community responses across large regions exposed to differing environmental gradients.

Paradoxically, ecologically proximal, direct and resource gradient variables, although often more valuable in a modelling sense, are generally more difficult to understand and measure at fine, ecologically relevant resolutions. At present many ecologically proximal variables can only be measured accurately through direct field observations (if at all) making their use for broad-scale, predictive mapping of species distributions impractical. However rapid improvements in multibeam hydro-acoustics technology are now allowing broad scale continuous lateral assessment of physical marine habitats at finer and finer resolutions (i.e. across metre scales) (Purkis et al., 2008, Brown et al., 2011) at considerably lower costs and ease than the use of direct diver assessments of reef habitat structure over equivalent spatial scales. Concurrent advances and developments in GIS and other analysis tools are enabling various derivative metrics of habitat structure to be calculated from bathymetric digital elevation models (DEMs) providing researchers with a variety of potentially informative surrogate measures of biodiversity and species-specific environmental responses at very fine spatial resolutions (Guisan and Zimmermann, 2000). Chapter four of this thesis applies an approach of modelling reef fish community structure using surrogate measures of fine resolution physical habitat structure derived from broad scale, remotely sensed bathymetric data.

Syms (1995) examined changes in the composition of a guild of blennioid fishes relative to the scale at which their habitat was defined. At large geographic scales, characteristic blennioid assemblages could be detected according to the degree of wave exposure and geographical nature of sites. At intermediate scales the blennioid assemblage displayed strong

species-specific depth patterns and associations with macroalgal cover and at fine scales the degree of shelter afforded by topographic features, and the species habitat specialisations with them, best characterised the observed blennioid assemblages. In contradiction to this result Chittaro (2004) investigated the structure of reef fish communities across four spatial scales in the US Virgin Islands and showed that abundance and species richness correlated with specific habitat variables, independently of scale. However Chittaro's work also identified the widely varying body size and home range extent of reef fish considered in the study and the importance of investigating associations at multiscale levels in order to identify the spatial scales of relevance effecting particular fish species. Thus the precise influence of scale in determining reef fish responses to the physical structure of their environments is still largely unclear, however both authors conclude by emphasising that the strength of fish habitat associations can only be interpretable in the context of the scales at which they are measured and the importance of future ecological studies incorporating the examination of patterns at more than one spatial scale.

1.5 Defining and quantifying habitat structure

Habitat structure is a broad term which has been varyingly defined by ecological researchers (Bell et al., 1991, McCoy and Bell, 1991). It can include aspects of complexity and variability of the abiotic and biotic components of the environment and its effects manifest themselves varyingly depending on the spatial and temporal scales at which they are considered. Many ecological studies are theoretically underpinned by the hypothesis that structurally complex habitats provide greater niche availability and diversity of habitat 'opportunities' and thereby support greater biodiversity (Tews et al., 2004), however, historically the importance of habitat structure has generally been intuitively assumed and overlooked as a topic in itself. Studies focusing on the importance of habitat structure are under-represented in the study of community ecology and largely overshadowed by those considering other ecological aspects

such as resource availability, competition and predation and thus the potential ecological importance of habitat structure has probably been underestimated in most studies due to the complex interactions with these other ecological processes (McCoy and Bell, 1991).

Essentially, habitat structure can be defined as ‘the structure afforded by the arrangement of physical objects in space’ (McCoy and Bell, 1991) but in reality such simple definitions have little practical application when attempting to quantify habitat structure. Tews *et al* (2004) point out that definitions of habitat structure are entirely dependent on spatial resolution and taxonomic membership. For instance scales of structure can range from the architecture of a single leaf or plant up to landscape or bioregional scale heterogeneity and vary in relevance to the individual organisms depending on species and life-history stage. Beyond simple qualitative descriptions of habitat, any useful definition of habitat structure must be capable of quantifying the amount, composition and three-dimensional arrangement of biotic and abiotic physical matter within a defined location and time (Bell *et al.*, 1991) and importantly must possess ecological relevance to the study community or species of interest. A number of studies have attempted to conceive more precise definitions of habitat structure (Luckhurst and Luckhurst, 1978, Bell *et al.*, 1991, Halley *et al.*, 2004) but there is still no consensus on a single measure or scale capable of adequately characterising or extricating every facet of it (McCormick, 1994, Frost *et al.*, 2005, Wilding *et al.*, 2009). This has led to difficulty in general comparisons between taxon and location specific experimental studies. In response to this problem McCoy and Bell (1991) attempted to develop a general conceptual framework around which to facilitate future comparable studies of habitat structure based on three clearly defined aspects of structure; heterogeneity, complexity and scale. Heterogeneity in this respect was defined as the variation attributable to the relative abundance (per unit area) of different structural components. Complexity was defined as the absolute abundance (per unit area) of individual structural components and scale was defined as the variation

attributable to the extent or resolution of the area used to measure heterogeneity and complexity. In reality, distinguishing physical variables into one or other of these classifications of structure can be a somewhat ambiguous task.

Most research in the literature is focused on a limited number of physical variables describing habitat structure that are commonly identified as being important in structuring reef fish communities; substratum composition and diversity, variety of refuge spaces, rugosity, vertical relief and biogenic structure (Gratwicke and Speight, 2005a). The habitat structure afforded by substratum composition and diversity can vary markedly between environments. Tropical coral reefs are largely defined by the types and growth forms of the coral species present (Friedlander et al., 2003), while the substratum characteristics of temperate reef habitats are dictated by the forms and diversity of rock structures along a gradient from sand, gravel and cobbles, through varying boulders sizes up to consolidated, contiguous bedrock (Alexander et al., 2009). Substratum composition dictates the size and abundance of interstitial spaces and therefore is closely linked to the sizes and diversity of refuge spaces a habitat can provide (Chapman, 2002). Rugosity gives a representation of how physically convoluted the surface of a habitat is in the form of a ratio between the measured distance of the reef profile between two points and the linear distance between the same two points. Rugosity has been measured using a variety of direct and remotely sensed methods (Luckhurst and Luckhurst, 1978, Brock et al., 2004, Frost et al., 2005). A closely related measure of complexity is the fractal dimension; a number of reviews have examined the use of fractals in understanding habitat structure (Williamson and Lawton, 1991, Halley et al., 2004). Fractals are being increasingly considered in ecological investigations as a good ‘common currency’ when considering measures of complexity of a natural surface as they have the advantage of being able to describe complexity over a range of scales (Halley et al.,

2004, Frost et al., 2005). Fractal theory postulates that natural surfaces tend to be self-similar across different scales, which leads to the general hypothesis that the number of refuge spaces in a natural surface will decline with increasing scale. Measuring the fractal nature of a habitat allows a starting point from which to better understand the causal ecological processes structuring fish assemblages and their demographic structures with the physical patterns of reef complexity. For example, fractal effects of reef habitat structure will be expected to drive migration and mortality from predation due to a 'musical chairs' effect as individuals increase in size and compete for ever diminishing physical space and refuge availability relative to their individual body size. If the structure of a reef is fractal in nature, then this may be evident from experimental investigations of the relationships between the fractal measure of the reef surface and the demographic pattern of the associated fish assemblages (Caddy and Stamatopoulos, 1990). To date few studies have attempted to relate the fractal nature of temperate reefs to fish assemblage patterns.

1.6 The link between communities and their environments

An organism's distribution and abundance are not random across their environment. Reef fish communities are primarily influenced by stochastic recruitment events and subsequently the physical and biotic characteristics of their surrounding environments (Carr 1994; Guisan and Zimmermann 2000). A large number of studies from around the world have identified positive correlations between habitat structure and animal species diversity (see review by Tews et al. (2004)). Variations in the habitat structure of marine habitats have been shown to affect the composition of their associated faunal and algal communities (Choat and Ayling, 1987, Friedlander and Parrish, 1998, Andrew and O'Neill, 2000, Beck, 2000, Anderson and Millar, 2004, Toohey et al., 2007, Toohey and Kendrick, 2008). A large number of studies worldwide have investigated the physical characteristics that contribute specifically to habitat structure of sub-tidal tropical and temperate reefs and how they influence the associated algal

(Dahl, 1973, Harlin and Lindbergh, 1977, Ault and Johnson, 1998, Toohey et al., 2007, Toohey and Kendrick, 2008), invertebrate (Lapointe and Bourget, 1999, Beck, 2000, Alexander et al., 2009) and fish assemblages (Luckhurst and Luckhurst, 1978, Roberts and Ormond, 1987, Garcia-Charton and Pérez-Ruzafa, 2001, Harman et al., 2003, La Mesa et al., 2004, Gratwicke and Speight, 2005a, Gratwicke and Speight, 2005b).

Variation in the settlement of fish larvae onto reefs is thought to be important in determining the subsequent temporal and spatial variation in adult fish populations (Doherty, 1991, Levin, 1991). Habitat type and structure have both been identified as important factors influencing juvenile settlement and recruitment across temperate marine environments (Connell and Jones, 1991) but subsequent post-settlement processes such as competition, predation and disturbance are also considered to be important in structuring adult reef fish populations (Jones, 1991, Tupper and Boutilier, 1997). Connell and Jones (1991) determined that differences in the abundance of adult blennioid fish between habitats in New Zealand can be attributed to high juvenile mortality in low complexity habitats. Caley and St John (1996) examined the assemblage structure of tropical fishes on small, artificial reefs to determine if differences in predator refuge availability could modify the abundance and species richness of settling larvae. Refuge type did not appear to influence the patterns of settlement onto artificial reefs however post-settlement processes were found to be important in varying the later assemblages of resident fish on reefs. Similar results were obtained by Tupper and Boutilier (1997) for a commercially important temperate reef fish species of cunner, *Tautogolabrus adspersus*. Their results suggested that settlement was not affected by habitat type but that post-settlement survival and adult densities varied with habitat and were positively correlated with habitat structure. Other studies have advocated the use of artificial reef experiments to answer questions into the effects of habitat structure and other questions

related to settlement and post-settlement process effects (Gorham and Alevizon, 1989, Bohnsack, 1991, Garcia-Charton and Perez-Ruzafa, 1998).

A number of theories have been developed in relation to how aspects of reef habitat structure and ecological post-settlement processes may affect the structuring of adult reef fish communities. Most of these are based on two differing hypotheses relating to the mechanisms that increase fish abundance and species richness in response to habitat structure (Garcia-Charton and Perez-Ruzafa, 1998). The first relates to spatial habitat limitations and the effect of increasing structure leading to amplified space and resource availability and consequently an increase in a given area's carrying capacity. The second relates to increased structure leading to a diversification of resources and niche availability. Well designed and focused manipulative experiments are needed to discern between the possible effects of these various mechanisms and the relevant spatial scales at which they are operating on temperate reef fish communities.

Gratwicke and Speight (2005a) investigated the effects of habitat structure on Caribbean fish assemblages using sets of artificially constructed reefs. Their investigation identified that the percentage of hard substrata, number of refuge holes, rugosity and the variety of growth forms present were the most spatially relevant characteristics in determining fish abundance on Caribbean reefs. They also identified that the presence of habitat forming invertebrates (in this case a species of long-spined urchin, *Diadema antillarum*) were important in increasing observed fish species richness and abundance. Further studies have considered similar physical measures of habitat structure to explain patterns of reef fish assemblages (Risk, 1972, Luckhurst and Luckhurst, 1978, Roberts and Ormond, 1987, Garcia-Charton and Pérez-Ruzafa, 2001, La Mesa et al., 2004).

The proportion of hard substrata on a reef is thought to be an important limiting factor as attachment for the settlement of sessile algae and invertebrates (Dahl, 1973, Harlin and Lindbergh, 1977, Toohey et al., 2007) and therefore, theoretically the proportion of hard substrata in an area should be, to some extent, directly related to the abundance of invertebrates and in turn important in providing a range of potential food sources for fish as well as increasing habitat structure which will increase the variety of niche availability within a habitat (Carr, 1994, Gratwicke and Speight, 2005a). The size and availability of refuge spaces on reefs has been shown to be important due to the effect of reducing predation by providing permanent and transient predator free space (Hixon and Beets, 1993, Caley and St John, 1996).

Rugosity and substratum diversity are thought to be important in determining the numbers of fish an area can support as they will indirectly affect the availability of refuge spaces and areas of hard substrata availability. Increased substrata complexity is likely to determine the extent of interacting mechanisms affecting predator-prey interactions. Refuge space is important for reducing the physical access of predators to prey, reducing predator hunting efficiency and improving a prey species' ability to visually evade predators and increase its probability of survival (Savino and Stein, 1982, Caley and St John, 1996). Increased complexity and the resulting refuge spaces may influence reef community structure through a variety of other, interacting mechanisms such as providing shelter from wave exposure and currents (Gabel et al., 2011), intercepting suspended nutrients and food (Taniguchi and Tokeshi, 2004) and providing increased habitat space due to higher surface areas for nocturnal refuges and nesting sites (Nanami and Nishihira, 1999). Vertical relief will be likely to effect the structuring of adult reef fish assemblages due to the increased habitat structure associated with high relief reefs, and greater conspicuousness to aggregating pelagic fish and settling larvae (Harman et al., 2003). These processes are far from fully understood

but it is becoming increasingly clear from the findings of existing research that they interact with the physical structure of reef habitats in varied and intricate ways and dictate how communities assemble, function and persist.

It is a common conception that tropical coral reef systems support more diverse communities than temperate reefs. This belief is far from proven and in fact small-scale variation in habitat structure may be a more important determinant of community structure than large-scale latitudinal trends (McGuinness, 1990). Tropical coral reefs grow in shallow regions of ocean close to the equator where minimum winter water temperatures seldom drop below 20°C while temperate reefs are generally characterised by canopies of brown algae pole-ward of the 20°C winter isotherm. The two types of reef also differ in the composition of their hard substrata with temperate reefs generally consisting of various types of rock, with crevices, holes and promontories but lacking the micro-habitat surface complexity of coral reefs (Ebeling and Hixon, 1991). Besides physical reef structure the other major difference between tropical and temperate reef systems is the extent of macroalgal cover occupying temperate reefs. Temperate reefs often provide a temporally and spatially dynamic vertical dimension in the form of an algal canopy that coral reefs lack. This canopy provides habitat structure in addition to the structure of the physical substrata and is generally the major component of biogenic habitat structure on shallow temperate reefs. The bulk of the research into community-habitat associations appears to be focused on tropical reef systems, but a considerable number of studies have investigated the relationships between temperate reef communities of algae, invertebrates, and fishes and their associations with complexity, exposure, biogenic cover, substratum and refuge space (see Table 1.1).

Table 1.1. Temperate reef study examples of commonly identified relationships between environmental and community structure variables.

Habitat variable	Study focus	Studies
Depth	Fish community diversity and abundance	(Syms, 1995, Leathwick et al., 2006, Williams et al., 2008) (Goldberg and Kendrick, 2004)
	Algal species richness and biomass.	(Hill et al., In Review)
	Invertebrate distributions	
Physical complexity	Fish diversity and abundance	(Tupper and Boutilier, 1997, Garcia-Charton and Perez-Ruzafa, 1998, Garcia-Charton and Pérez-Ruzafa, 2001, García-Charton et al., 2004, Iampietro et al., 2008)
	Cryptic fish abundance	(Willis and Anderson, 2003, La Mesa et al., 2004)
	Algal and invertebrate diversity and abundance	(Lapointe and Bourget, 1999, Beck, 2000)
Biogenic structure	Fish and invertebrate diversity and abundance	(Choat and Ayling, 1987, Holbrook et al., 1990, Anderson, 1994, Levin and Hay, 1996, Ruitton et al., 2000, Hirst, 2008)
	Cryptic fish abundance	(La Mesa et al., 2004)
	Labrid abundance	(Tuya et al., 2009)
	Algal community diversity and abundance	(Kendrick et al., 1999)
Substratum composition/cover	Fish diversity and abundance	(Garcia-Charton and Pérez-Ruzafa, 2001)
	Cryptic fish abundance	(La Mesa et al., 2004)
Refuge density/diversity	Labrid abundance	(Tuya et al., 2009)
	Invertebrate diversity and abundance	(Alexander et al., 2009)
	Fish abundance and size	(Love et al., 2006)
Habitat type	Fish community diversity and abundance	(Anderson and Millar, 2004, Williams et al., 2008)
	Fish abundance	(Choat and Ayling, 1987, Tupper and Boutilier, 1997, Harman et al., 2003, Valesini et al., 2004a)
	Lobster distribution	(Lucieer and Pederson, 2008)
MPA status/ fishing pressure	Fish diversity and abundance	(Barrett et al., 2007, Claudet et al., 2010)
	Fish biomass, diversity and abundance	(García-Charton et al., 2004)
	Labrid size and sex ratios	(Shepherd et al., 2010)
	Invertebrate diversity and abundance	(Alexander et al., 2009, Barrett et al., 2009)
Wave exposure	Algal species richness and biomass	(Goldberg and Kendrick, 2004, Hill et al., 2010)

1.7 Modelling community responses to habitat structure

Predictive spatial habitat modelling of species distributions is becoming increasingly recognised as an important process in conservation planning and management of biodiversity (Austin, 2002, Love et al., 2006) and is becoming more commonly used in preference of direct survey data which is frequently incomplete or spatially biased (Guisan and Thuiller 2005). Development of ecological and statistical models which can accurately predict fish assemblage parameters, based on an understanding of the ecological processes operating between fish communities and their physical habitats, equips fisheries managers and policy makers with a powerful tool for managing coastal resources and MPAs effectively and sustainably. An understanding of the associations and ecological processes operating between fish communities and habitat structure in the functioning and recovery of MPA's around temperate Australia is lacking. This study addresses this deficit by investigating the relationships between reef fish communities and habitat structure and relates this understanding towards the development of explanatory models of fish assemblages based on physical reef metrics.

Species-habitat modelling relates spatio-temporal observations of a species or community to environmental conditions using quantitative techniques to explain and/or predict some measure of that species or community across a region, timeframe and/or range of environmental conditions (Roberts et al., 2010). Species-habitat modelling approaches have been used to investigate the habitat associations of many types of organism including marine mammals (Roberts et al., 2010), seabirds (Vilchis et al., 2006) and fish (Iampietro et al., 2008). A wide range of modelling approaches, often applied in combination with geographic information systems (GIS) and remotely sensed data are now available to ecologists (Guisan and Zimmermann 2000; Roberts et al. 2010; Wright and Heyman 2008). Guisan and

Zimmermann (2000) have reviewed a wide variety of modelling approaches available for predicting the distribution and abundances of species and communities (Guisan and Zimmermann, 2000). There are inherent limitations in the interpretations and application of spatial models across broader scales and locations due to unknown natural differences in the realised niches of separate communities. Ecological modelling implicitly assumes that a pseudo-equilibrium exists between organisms and their environments (Austin, 2002). This assumption risks inherent bias in the model interpretation because what is being modelled in nature is the response observed as a result of biotic interactions and stochastic responses of an organism specific to a particular time and region (i.e. the realised niche) rather than the full response of a species occupying all of its suitable habitat (i.e. the fundamental niche) (Guisan et al., 2002, Guisan and Zimmermann, 2000, Austin, 2002, Guisan and Thuiller, 2005). Since it is very difficult to be certain that a statistical model represents a good approximation of the fundamental niche, predictive models of a particular species or community response across different locations are difficult to compare. The predictive success of a model based on environmental predictors will vary depending on the degree to which the dispersal and disturbance history have defined a particular community assemblage. It is important therefore that investigators are specific about the ecological assumptions underpinning any model and the appropriate extent and accompanying levels of uncertainty with which their predictions can be accurately applied. True models of a species' fundamental niche require model development based on a solid theoretical and empirically derived understanding of a species response to its physical environment (Guisan and Thuiller, 2005).

Most predictive modelling efforts are based on the broad assumptions of niche theory which describes the response of a species to environmental gradients using the classic unimodal, symmetric bell-shaped curve relationship (Austin, 2002). There is a lack of evidence

supporting the classical niche theory assumptions underlying many attempts at species distribution modelling and a general lack of agreement around the specifics of individual species response shapes to environmental gradients (Austin, 2002), an issue which many predictive studies fail to address adequately when formulating their models. Conflicting theories consider competition and its potential to displace a species from its fundamental niche, altering its realised niches response curve to a variety of shapes from skewed to bimodal (Austin, 1999). The use of Ecological theory to underpin species distribution prediction is often neglected by investigators but is extremely important when selecting the most appropriate predictors, choosing ecologically realistic response curves to each predictor and selecting between competing model approaches (Guisan and Thuiller, 2005).

A number of studies have successfully explained fish species richness and biomass at relatively fine resolutions of 4 to 200 metres (Pittman et al., 2009, Wedding and Friedlander, 2008, Knudby et al., 2010) suggesting that environmental gradients at these scales can be important for predicting local variations in reef fish communities. Coarser scale environmental variables are likely to have a more uniform impact on fish communities at local scales and are therefore less likely to be important in explaining differences in reef fish community structure at local scales (Knudby et al., 2010). This highlights the importance of fine resolution remotely sensed data across large, management scale extents to ensure accurate predictive modelling of species and community responses to their physical environments. Various studies have attempted to develop models capable of characterising and predicting tropical (Luckhurst and Luckhurst, 1978, Roberts and Ormond, 1987, Friedlander and Parrish, 1998, Ferreira et al., 2001, Gratwicke and Speight, 2005a, Gratwicke and Speight, 2005b, Brokovich et al., 2006, Mellin et al., 2006, Pittman et al., 2007, Wedding and Friedlander, 2008) and temperate fish assemblages (Valesini et al., 2003, Francis et al.,

2005, Iampietro et al., 2008) on the basis of environmental variables but to date there have been few studies undertaken around temperate areas of Australia attempting to model patterns in fish assemblage against the physical habitat structure of reefs.

1.8 Project motivation and objectives

This PhD project formed part of the larger CERF Marine Biodiversity hub which aimed to improve the understanding of ecological processes linking environmental variables with patterns in biodiversity across Australia's marine environments. The hub project was a large scale, multi-habitat, investigation in collaboration between the University of Tasmania (UTAS), the Commonwealth Scientific and Industrial Research Organisation (CSIRO), Geoscience Australia, the Australian Institute of Marine Science (AIMS) and Museum Victoria which attempted to identify biological patterns and dynamics and determine the appropriate units and models to effectively predict Australia's marine biodiversity across a range of habitats. The project aim was to develop and deliver tools which aid the management of Australia's marine biodiversity and assist in effectively developing and implementing a National Representative System of Marine Protected Areas (NRSMPA).

The objectives of this study were three-fold. Firstly to identify important environmental and physical habitat variables capable of explaining patterns in temperate reef fish communities across Australia. Secondly to explain how these patterns vary across different spatial scales from bioregional to local fine scale (10s – 100s of metres). And finally to identify how physical reef habitat structure affects the recovery of temperate fish populations within MPA's following the cessation of fishing.

This thesis is divided into four main data chapters plus introduction and discussion chapters. The first data chapter, Chapter two, attempts to identify the influences of physical habitat structure and protection from fishing on the community structure of reef-fishes across

bioregional scales of temperate Australia. Chapter three investigates the components of physical habitat structure which best explain fish community similarity patterns, diversity and individual species distributions and abundance at scales from metres to kilometres across temperate coastal rocky reefs of southeastern Tasmania. Chapter four aimed to determine whether fine-scale bathymetric derivatives could be feasibly applied as surrogates to explain reef fish diversity and species-habitat associations in the absence of direct metrics of habitat and therefore identify an effective tool for spatial marine planning. And Chapter five attempted to disentangle the effects of protection on temperate marine reef fish communities from those of natural physical habitat variability.

The objectives of my research are closely aligned to the CERF project's overall aim in my attempt to identify patterns between fish community structure and habitat structure across shallow temperate reefs and generate subsequent hypotheses to link these patterns to causal ecological processes. By improving our understanding of the patterns and causal ecological processes dictating fish biodiversity on temperate reef systems it is hoped that scientists and spatial marine planners will be able to make informed decisions towards the development and implementation of MPAs which safeguard temperate reef ecosystems and better contribute to a National Representative System of Marine Protected Areas (NRSMPA) around Australia.

Effects of environmental variables and physical habitat structure on temperate reef fish community structure across inter and intra-bioregional scales of Australia.

2.1 Abstract

The responses of marine, reef-associated fish to environmental and habitat characteristics vary with the spatial resolution of the area considered. The ability to quantify habitat structure across the full range of scales relevant to a particular species or community and model the associations of species and communities with their habitats enables explanations and predictions of biodiversity patterns which are useful for marine spatial planning and management. This study attempted to identify the influences of physical habitat structure and protection from fishing on the community structure of reef-fishes across bioregional scales of temperate Australia. The findings suggest that across large, inter-bioregional scales it is principally climatic and biogeographical differences between varying geographic positions which are important in structuring much of the temperate reef fish community structure around Australia, while at smaller, intra-bioregional scales, the importance of ecologically proximal physical variables, such as biogenic cover, refuge space and habitat substratum begin to come into effect. Different habitat variables tended to explain community structure within each bioregion suggesting that habitat surrogates possess limited value in confidently predicting the spatial distribution and abundance of temperate reef fish outside of any one particular bioregion, even where communities are comprised of ecologically similar species. The variability of individual species responses to their physical habitat structure were largely species-specific in both the extent of responses and the particular types of habitat variables species respond to. The ability to identify reserve effects across the scale of this investigation was limited since they were probably masked by the overriding influence of other natural

sources of environmental variability. A notable outcome of the research was the detection of a likely effect of urchins on kelp barren formation between and within bioregions which warrants further research into the effects of altered biogenic habitat states and the causal mechanisms and interactions linking these effects to reef fish community structure. The results of this study lend support to the hypothesis that the structuring of temperate reef fish communities is dictated by a spatially hierarchical series of ecological processes ranging from latitudinal scale, indirect climatic responses through to localised influences of finer scale physical habitat structure affecting disturbance, competition and predation.

2.2 Introduction

The distributions of organisms and the structure of their communities are largely determined by the spatial and temporal variability of complex interactions between the physical, chemical and biological factors present within their environments (Menge and Sutherland, 1987, Underwood, 2000, Valesini et al., 2004a). Many studies from around the world have explained the structure of animal communities in relation to the physical structure of their habitats (Tews et al., 2004). The specific mechanisms behind species-habitat relationships are numerous but examples from studies of fish have revealed how habitat structure can influence many ecological processes in the marine environment, such as; recruitment and post-recruitment survival (Connell and Jones, 1991, Caley and St John, 1996, Tupper and Boutilier, 1997), prey availability (Warfe and Barmuta, 2004), predation and competition (Hixon and Beets, 1993, Johnson, 2006) home range size, and morphology and behaviour (Shumway, 2008). Spatial variability in the structure of various marine habitats have been shown to affect the composition of associated algal (Dahl, 1973, Harlin and Lindbergh, 1977, Ault and Johnson, 1998, Toohey et al., 2007, Toohey and Kendrick, 2008), invertebrate (Lapointe and Bourget, 1999, Beck, 2000, La Mesa et al., 2004, Alexander et al., 2009) and fish communities (Luckhurst and Luckhurst, 1978, Roberts and Ormond, 1987, Garcia-Charton and Pérez-Ruzafa, 2001, La Mesa et al., 2004, Gratwicke and Speight, 2005a, Gratwicke and Speight, 2005b, Anderson et al., 2009).

Consideration of the effects of habitat structure in marine spatial planning is important for ensuring that ecosystem resilience can be maximised by positively combining the effects of protection and the range of habitat structure present. For example it has been shown that the strength of fisheries-induced trophic cascades (FITC) can be reduced by the presence of available refuge space to reef fish communities (Salomon et al., 2010). Where prey are

vulnerable to predation, strong top-down control may result in unstable predator-dependant interactions, whereas where some level of protection to prey is afforded through available refuge space, systems are more likely to maintain a stable equilibrium. In this situation, the fisheries-induced trophic cascade impacts of high fishing pressure could be reduced by complimenting the protection effects of marine reserves with adequate levels of structural habitat diversity.

The response of marine organisms to habitat complexity and heterogeneity varies with the spatial resolution of the area considered (Claudet et al., 2010) and understanding the spatial distributions and community structure of fish species with respect to the physical characteristics of habitats relies on first understanding how these patterns vary across spatial scales (Wiens, 1989, Anderson and Millar, 2004). It is therefore important to be able to quantify habitat structure across the full range of scales relevant to a particular species or community (Morton and Gladstone, 2011). Identifying the appropriate scales at which to investigate the associations of species and communities with their habitats is one of the central problems of species-habitat modelling (Guisan and Thuiller, 2005). It is a well-established tenet within ecology that the distributions and abundances of species vary markedly over large latitudinal and longitudinal extents in response to large scale climatic gradients (Mora et al., 2003). What is less well understood are the underlying mechanisms dictating these patterns and the scales at which individual attributes of marine habitats begin to elicit a greater influence on community structure than geographic position. Additionally, little is known regarding whether widely different fish communities from different geographical localities, respond similarly to habitat structure or whether their responses are community specific.

Few studies have looked for general patterns of reef fish community structure in response to physical habitat heterogeneity and complexity across bioregional scales. Spatial location, particularly latitude is well known to determine large scale patterns of community structure and diversity (Willig et al., 2003) but little is understood about how communities vary in response to physical habitat structure across similar scales. Most studies which have explicitly investigated variation in the effects of habitat structure on reef fish species at different spatial scales have focused on small or intermediate scales of 10's to 100's of metres (Garcia-Charton and Pérez-Ruzafa, 2001, Chittaro, 2004). Where large scales have been investigated it is usually to consider a single species or limited groups of fishes (Syms, 1995) or variation in community structure across broadly differing habitat types (Anderson and Millar, 2004).

This study investigates the broad, bioregional scale community structure and individual species abundance and occurrence responses of temperate reef fish communities along areas of south-western and south-eastern coasts of Australia and Tasmania to aspects of the surrounding environment and habitat structure. A variety of direct and indirect environmental and habitat variables were investigated across a broad range of scales (100's – 1000's km) in an attempt to identify the variation in community structure due to differences in large scale geographic position from those due to the effects of physical habitat structure. Data were utilised from previous (and ongoing) marine reserve monitoring work obtained via underwater visual censuses of reef fish communities at sites being carried out across Australia (Barrett et al., 2007, Alexander, 2011b). This study took a hierarchical approach in considering temperate reef fish communities within and between their individual bioregions and in so doing allowed identification of general patterns of community response to habitat structure common across varying broad bioregional scales. This study attempted to test two

general hypotheses. Firstly that fish community structure will vary in response to variability in the physical characteristics, heterogeneity and complexity of the reef habitat and secondly that the physical variables important in explaining fish community assemblage structure will vary at scales between and within bioregions.

2.3 Methods

2.3.1 Study sites

One-hundred and twenty-two temperate reef sites were located across seven bioregions of South Australia, Western Australia and Tasmania, as defined by the Integrated Marine and Coastal Regionalisation of Australia (Commonwealth of Australia, 2006) . Physical reef structure and reef fishes were surveyed at 64 sites, across five bioregions around Tasmania (June 2006 – March 2007), 32 sites in the Central West Coast bioregion in Western Australia (October 2006) and 26 sites in the Batemans Shelf bioregion in New South Wales (May 2007) (Figure 2.1). Tasmanian sites are dominated by dolerite and granite geology, interspersed with areas of sandstone, quartzite and basalt. The average sea surface temperature in this region ranges from approximately 10 to 19 °C. Sites in Batemans Shelf were located around Jervis Bay and dominated by sandstone and siltstone bedrock geology, with sea surface temperatures ranging from between approximately 16 and 23 °C. Central West Coast sites were located around Jurien Bay, dominated exclusively by limestone geology with sea surface temperatures ranging from 18 to 23 °C.

2.3.1 Reef-fish assessment

Multispecies reef fish abundance data were collected between June 2006 and May 2007 across all one-hundred and twenty-two temperate reef sites. Non-cryptic reef fish were surveyed at each site along a 200 m transect within the five to ten metre depth contour. The abundance of reef fish was recorded by divers swimming at an average speed of 0.2 m/s⁻¹ along a five metre wide swathe either side of the line. A total 200 metre (4 x 500-m²) transect was thus surveyed at each site. Surveys were carried out in each case by a two to four person dive team using open circuit SCUBA. The number of all fishes sighted within 5 m of the line were recorded for each side of the transect line.

2.3.2 Physical reef assessment

Fourteen explanatory predictor sets were made up from twenty-five continuous and categorical variables measured at each site during the same 2006-2007 period as the reef fish surveys described above. Rugosity and refuge density were surveyed within eight randomly distributed 5 m² blocks along each 200 m transect and averaged for each site. Rugosity was sampled in each block using a 5 m lead core rope to measure the contour distance in relation to a fixed linear distance using the formula: $\text{rugosity} = 1 - (\text{linear distance} / \text{contour distance})$ (Risk, 1972, Harman et al., 2003).

Refuge space density was defined as an individual crevice, hole or other feature of the substratum that had the potential to provide fish some measure of protection from predation. Refuge densities within each 5 m² block were recorded for four size categories (1-5 cm, 6-15 cm, 16-50 cm, > 50 cm), which were based on an approximate log scale, rounded to lengths that could be easily estimated by a diver. The number of refuge size categories at a site was calculated as the mean of the number of size categories represented in each of the eight 5 m² blocks (0 – 4).

The fractal refuge index was calculated as the slope of the regression line for \log_4 (max bound of refuge size category) vs. \log_4 (number of refuges in the size category + 1) and describes the relative frequency of different sized refuges in a sample. A fractal index of around 0.5 indicates a size frequency distribution of refuges approximately following fractal expectations (ie. that the number of refuges declined with refuge size based on a log-log scale). An index close to 1 indicates that refuges in the block are numerically dominated by the smaller size category and a value close to 0 indicates equal numbers of refuges were present in each of the four size categories.

Biogenic cover was considered as the average percentage cover of canopy algae species (*Alariaceae*, *Cystoseiraceae*, *Durvilleaceae*, *Fucaceae*, *Lessoniaceae*, *Sargassaceae*, *Seirococcaceae*), sessile invertebrates (*Annelida*, *Brachiopoda*, *Bryozoa*, *Chordata* (*Ascidaceae*), *Cnidaria* (*Anthozoa*, *Hydrozoa*), *Mollusca* (*Bivalvia*, *Gastropoda*), *Porifera*) and bare, uncolonised or denuded rock, measured across twenty randomly placed 0.25 m² quadrats surveyed along the 200 m transect at each site. Percentages could be recorded in excess of 100% due to multiple layers to the canopy structure.

Exposure was recorded as a qualitative gradient estimate of predominant wave exposure at each site of 1 (sheltered), 2 (not directly exposed to oceanic swell but with considerable fetch >2 km), 3 (oblique and indirect exposure to oceanic swells and/or very large fetch length) and 4 (direct exposure to oceanic swells and very high wave energy).

Depth was not included as a variable as it would have required a stratified design requiring the need for much greater replication of transects and blocks which was unfeasible within the constraints of the project resources and time. Depth has been shown to be an important variable influencing marine fish community structure and diversity (Leathwick et al. 2006, Syms, 1995). Therefore by limiting sampling to the 5– 10 m depth contour it was assumed that any depth effects in structuring fish assemblages would be controlled. See Table 2.1 and Alexander (2011a) for further detailed explanations and survey methodology of the physical variables considered in this study. Appendix 1 displays the mean and standard errors for each of the physical variables plotted across the seven bioregions

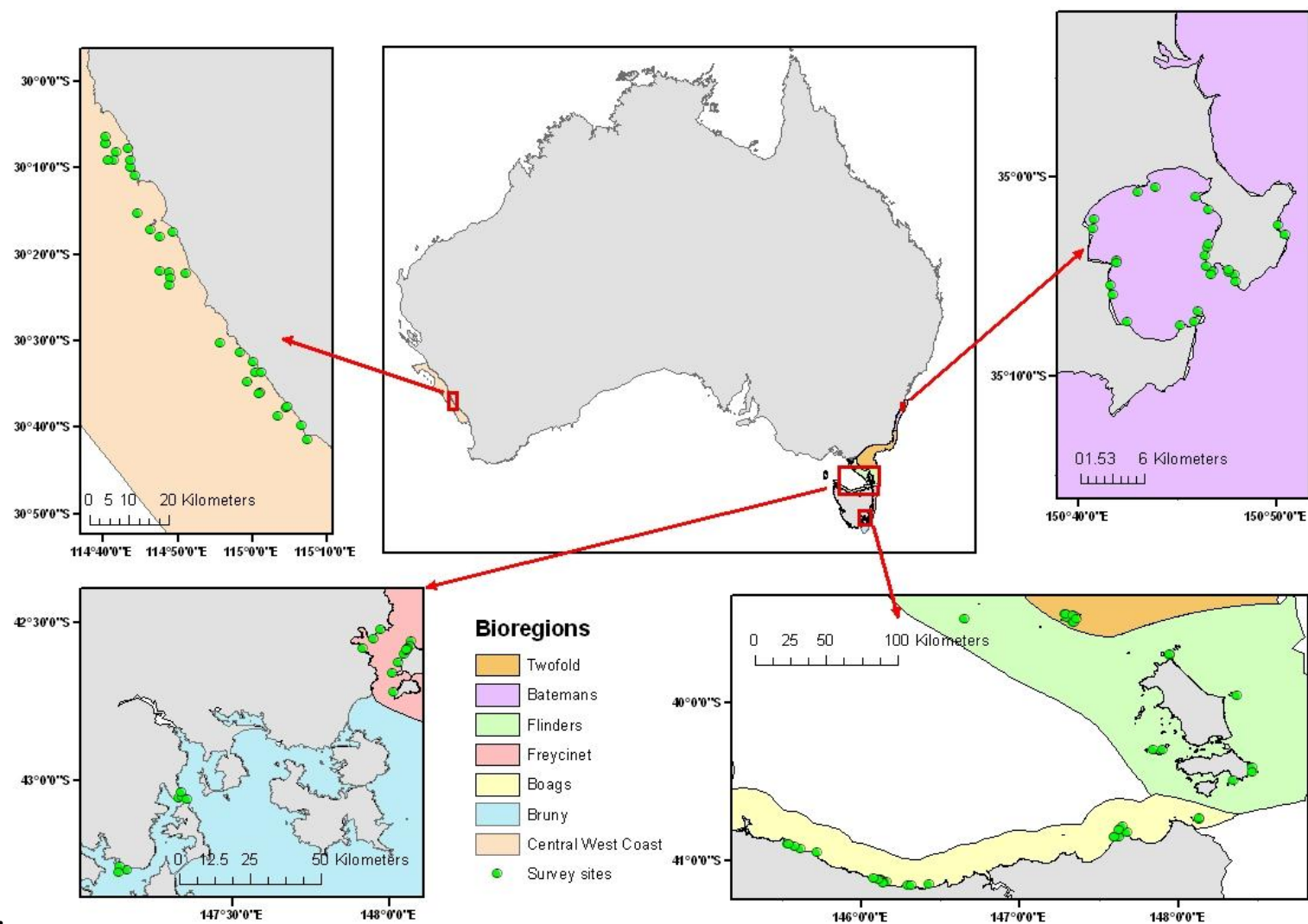


Figure 2.1. Study site locations around Australia.

Table 2.1. Physical habitat variable descriptions.

Variable set	Variable name	Description
Geographic position	Latitude, Longitude	Decimal latitude and longitude of site location.
Habitat substratum	BR, LB, MB, SB, Cobbles, Sand	Percentage of underlying substratum cover of bedrock, large boulders, medium boulders, small boulders, cobbles and sand.
Habitat diversity	Hab_div	Shannon Wiener index of habitat substratum categories
Modal reef height	Mod_ht	Visual estimate of modal height of substratum architecture in metres
Maximum reef height	Max_ht	Visual estimate of maximum height change over 1m in metres
Rugosity	Rugosity	Average of eight measures from randomly distributed 1 x 5 m quadrats. Rugosity was sampled using a 5 m lead core rope as the fixed contour distance in the formula, Rugosity index = 1 - (linear distance / contour distance) (Harman et al., 2003; Risk, 1972).
SD rugosity	SD_rug	Standard deviation of rugosity length measurements for the sample
Refuge space	Sml_ref, Med_ref, Lge_ref, Vlg_ref,	Density of small (1-5cm), medium (6-15cm), large (16-50cm) and very large (> 50cm) refuge spaces.
Refuge diversity	Num_refcat	Number of refuge size categories present in sample
Fractal refuge score	Fract_ref	Absolute value of the slope of the regression line for log ₄ (max extent of refuge size category) vs log ₄ (density of refuges in the size category + 1)
Biogenic cover	Canopy_alg, Sess_inv, Bare_rock	Percentage cover of canopy algae, sessile invertebrates and bare, uncolonised or denuded rock.
Exposure	Exposure	Predominant wave exposure at a site from sheltered to high (1- 4)
Reef gradient	Slight, Moderate, Steep	Categorical label for the slope of the sample: flat - no visible change in depth, 1 = slight (< 1:15), 2 = moderate (1:15 - 1:5), 3 = steep(> 1:5)
Marine reserve status	Reserve, non-reserve	Site within areas of full, no-take marine reserve status or non-reserve, fished areas.

2.3.3 Data analysis

2.3.3.1 Community analyses

For the community analyses the twenty-five physical variables measured at each site were reduced into fourteen variable sets (Table 2.1). This eased analysis by eliminating potential problems of inter-correlations between per cent cover variables. By analysing the physical data in sets it also aided interpretation of analysis by allowing me to explicitly examine the proportion of variation in the fish abundance data explained by habitat heterogeneity and

complexity variables independently from that explained by the spatial variables. This approach is suggested and explained in the PERMANOVA+ for PRIMER manual (“Analysing variables in sets”) and is built in as a function of the PRIMER package (Anderson et al., 2008).

Multivariate analyses of reef fish community abundance data were carried out using routines from the PRIMER PERMANOVA+ software package (Clarke and Gorley, 2006) for the following analyses unless otherwise stated. The ‘PERMANOVA+ for PRIMER’ manual (Anderson et al., 2008) and ‘*Change in marine communities*’ texts (Clarke and Warwick, 2001) provide further, detailed descriptions and explanations of the following statistical approaches and analysis routines applied.

Reef fish abundance data were $\log(x+1)$ transformed for every site to reduce differences in scale among the variables, and to ensure the contribution of rarer species to analytical outcomes. The transformed multispecies data was used to calculate a community resemblance matrices based on Bray-Curtis similarities, which provided the basis for the majority of the following community analyses. Physical data collected from each site were normalised prior to analyses to account for the varying scales of measurement. A draftsman plot of the individual physical habitat variables was consulted prior to analysis in order to identify extreme bi-variate correlations and any need for transformation of the physical habitat data. Any pair of variables with a correlation exceeding $r = 0.95$ were considered as effectively redundant variables and one or other could be freely removed from the analysis without any loss of explanatory power. All variable correlations were judged to be acceptably low and therefore no variables were removed from the analyses.

The reef fish community analyses was carried out across varying spatial scales; variability in reef fish community structure data was investigated at the largest scale across all seven bioregions and at the smallest scale within each bioregion separately. I initially attempted to identify if statistically significant differences in the community similarity data were apparent between bioregions and reserve and non-reserve status sites. This was carried out using PERMANOVA (permutational ANOVA and MANOVA) which is a routine for testing the response of multivariate data to one or more factors, on the basis of a resemblance measure, with the use of permutational methods (Anderson et al., 2008). A nested two factor PERMANOVA analyses was carried out to statistically test the null-hypothesis that there was no difference in the reef fish assemblages (converted to a Bray-Curtis resemblance matrix) associated with the categorical factors of bioregion and reserve status.

Having determined if differences in the community similarity data were apparent between bioregions and reserve and non-reserve status sites, the second step of the analysis applied a canonical analysis of principle coordinates (CAP) to carry out a canonical correlation as a general exploration of the patterns between the multispecies fish and physical data across sites. I was interested to determine if and how the reef fish community structure differed between bioregions in response to variations in the physical habitat. CAP was used to identify the optimum axes through the community similarity data (converted to a Bray-Curtis resemblance measure) and the multivariate physical data that maximised the inter-correlation between the two datasets and perform a permutational test of significance of those canonical relationships. The routine automatically adjusts for the problem of over-parameterisation by selecting an appropriate subset of PCO axes (i.e. $m < (N-1)$) to use in the analysis by minimising the leave-one-out residual sum of squares.

The final stage of the analysis developed parsimonious models that best explained the variability of the reef fish community structure based on multivariate physical variable data. I attempted to identify and model specific patterns of association between the reef fish community (based on Bray-Curtis resemblance measures of $\log(x+1)$ transformed abundance) and the physical structure of the surrounding habitat. The distance-based linear modelling procedure (DISTLM) in PRIMER was used to develop parsimonious multiple regression models which partitioned the maximum variation in measures of the reef fish community structure explained by an optimal number of physical predictor variables. DISTLM is a routine for modelling the relationship between the variation in a multivariate dataset (as described by a resemblance matrix) and one or more predictor variables. The procedure allows the construction of explanatory models using a number of common selection criteria and procedures, and calculates *P*-values of statistical significance using permutational methods for testing null-hypotheses of no relationship between response and predictor variables (Anderson et al., 2008).

DISTLM analyses were carried out using the 'Best' model selection procedure based on the lowest 'Akaike's information criterion' (AIC). The 'Best' model selection procedure aims to maximise parsimony in the final model selections by identifying the simplest models (with as few predictor variables as possible) with the greatest explanatory power through examining all possible combinations of the predictor variables and constructing optimal models based on the lowest AIC values. Initial 'marginal test' analyses were carried out to identify significant relationships between each individual physical variable with the variability in the reef fish community structure. The analysis was then used to identify the 'Best' (i.e. most parsimonious) model for each combination of one to five predictor variables sets, a reasonable number of variables I considered interpretable in a ecological context.

Distance based redundancy analysis (dbRDA) was applied as a constrained ordination technique to visualise the fitted values from the DISTLM modelling. The strength and direction of the strongest correlations between the individual physical and species variables and the dbRDA axes were visually interpreted with simple vector overlays calculated from the multiple partial correlations between each variable and the dbRDA axis scores. Each vector was interpreted as the effect of that particular variable on the construction of the ordination image; the longer the vector, the larger the association of the variable, in the direction of the associated axes.

2.3.3.2 Individual species analyses

Where the previous dbRDA analysis identified a high multiple partial correlation equal to or greater than 0.4 between a species abundance and/or a physical variable and the first or second dbRDA axes (i.e. the overlaid dbRDA ordination vectors), a further univariate linear regression analysis was carried out to identify the statistical significance and specific pattern of association between individual species responses and physical variables.

Regression analysis assumptions of normality and homogeneity of variance were checked by examining plots of normal probability of the residuals and a plot of the residuals against the fitted values of the simple linear regressions. A $\log(x+1)$ transformation was applied to each species abundance response variable investigated to ease interpretation and comparison of the analyses because in general, for most of the species abundance/habitat relationships the assumptions were improved by transformation.

2.4 Results

2.4.1 General findings

A total of two hundred and sixty-one species of fish were identified across reef fish surveys carried out between June 2006 and May 2007, comprising one hundred and fifty genera, seventy-four families, twenty orders and two classes. Plesiopidae (hulafish), Kyphosidae (drummers), Carangidae (trevally), Labridae (wrasses), Pomacentridae (damselfish), Pempheridae (bullseyes), Serranidae (seaperches) and Monodactylidae (batfish) were the eight most numerically abundant families of fishes across the dataset of all seven bioregions. The Central west coast bioregion was numerically dominated by the Labrid, *Coris auricularis*, the Apogonid, *Siphamia cephalotes* and the Kyphosid, *Kyphosus cornelii*. The Bateman's bioregion was numerically dominated by the Plesiopid, *Trachinops taeniatus*, the Pomacentrid, *Chromis hypsilepis* and the Scorpionid, *Atypichthys strigatus*. The Twofold bioregion was numerically dominated by the Serranid, *Caesioperca lepidoptera*. The Boags bioregion was numerically dominated by the Pempherid, *Pempheris multiradiata* and the Plesiopid, *Trachinops caudimaculatus*. The Flinders bioregion was numerically dominated by the Atherinid, *Leptatherina presbyteroides* and the Apogonid, *Siphamia cephalotes*. The Freycinet and Bruny bioregions were numerically dominated by the Plesiopid, *Trachinops caudimaculatus*.

2.4.2 Marine reserve effects

The results of a nested, two-factor PERMANOVA of marine reserve status nested within bioregion, identified significant differences in community similarity between bioregions but failed to identify any significant differences between marine reserve and non-reserve status sites within any of the bioregions (Table 2.2).

2.4.3 Reef-fish community structure

The results of an initial canonical analysis of principle coordinates (CAP) (inclusive of all seven bioregions) identified strong and significant correlations between the reef fish community structure (based on Log (X+1) transformed Bray-Curtis resemblance) and the physical habitat variables (trace statistic = 4.85, $P = 0.0001$). The first two canonical correlations were both high ($\delta_1 = 0.996$, $\delta_2 = 0.991$) and together explained 55.8% of the total variability in the community similarity data. A total of $m = 9$ PCO axes resulted in the smallest leave-one-out residual sum of squares and explained 81.4% of the total variability in the community similarity data.

Figure 2.2 displays the MDS and CAP analysis ordinations inclusive of all seven bioregions with the overlaid eigenvectors for the physical habitat variables and identifies that the greatest variation in the multispecies fish abundance data is correlated (≥ 0.4) with the spatial variables of latitude and longitude and bare rock cover. The MDS plot is included as an unconstrained contrast to show the true depiction of the variability in reef fish community structure independent of the physical variables. The two ordinations show broadly the same patterns suggesting that the variability in the species similarity data would be largely apparent regardless of the physical data. A visual exploration of the CAP ordination identifies that the first canonical axis separates the Central west coast bioregion sites (towards the right of the ordination) from the rest of the bioregions while the second canonical axis separates the Bateman's shelf bioregion sites (towards the bottom of the ordination) from the other remaining bioregions. The Tasmanian bioregion sites group together (towards the top-left of ordination) along with the Twofold shelf bioregion sites.

Further CAP canonical correlation analyses were carried out separately for each individual bioregion but failed to identify any significant correlations between the reef fish community

structure and the physical habitat variables between sites within any bioregion, except for the Central west coast bioregion (trace statistic = 5.14, $P < 0.001$). The first two canonical correlations for the Central west coast CAP analysis were both high ($\delta_1 = 0.976$, $\delta_2 = 0.953$) and together explained 39.5% of the total variability in the multispecies fish abundance data. A total of $m = 6$ PCO axes resulted in the smallest leave-one-out residual sum of squares and explained 68.1% of the total variability in the Central west coast community fish similarity data. Exploration of this ordination (Figure 2.3) identifies a relatively strong correlation (≥ 0.4) between the first and second CAP axis and small refuge density, medium refuge density, habitat diversity and canopy algal cover. The first axis of the CAP ordination is correlated with small refuge density, while the second axis is highly correlated with canopy algae cover. There also appears to be some grouping of reserve and non-reserve sites towards the top and bottom of the ordination respectively

Table 2.2. Two factor nested PERMANOVA analysis of reserve status within bioregion.

Source	df	SS	MS	Pseudo-F	P	Unique permutations
Bioregion	6	2.50E+05	41617	30.504	0.001	999
Reserve(Bioregion)	5	5592.7	1118.5	0.94627	0.599	998
Residual	110	1.30E+05	1182.1			
Total	121	3.97E+05				

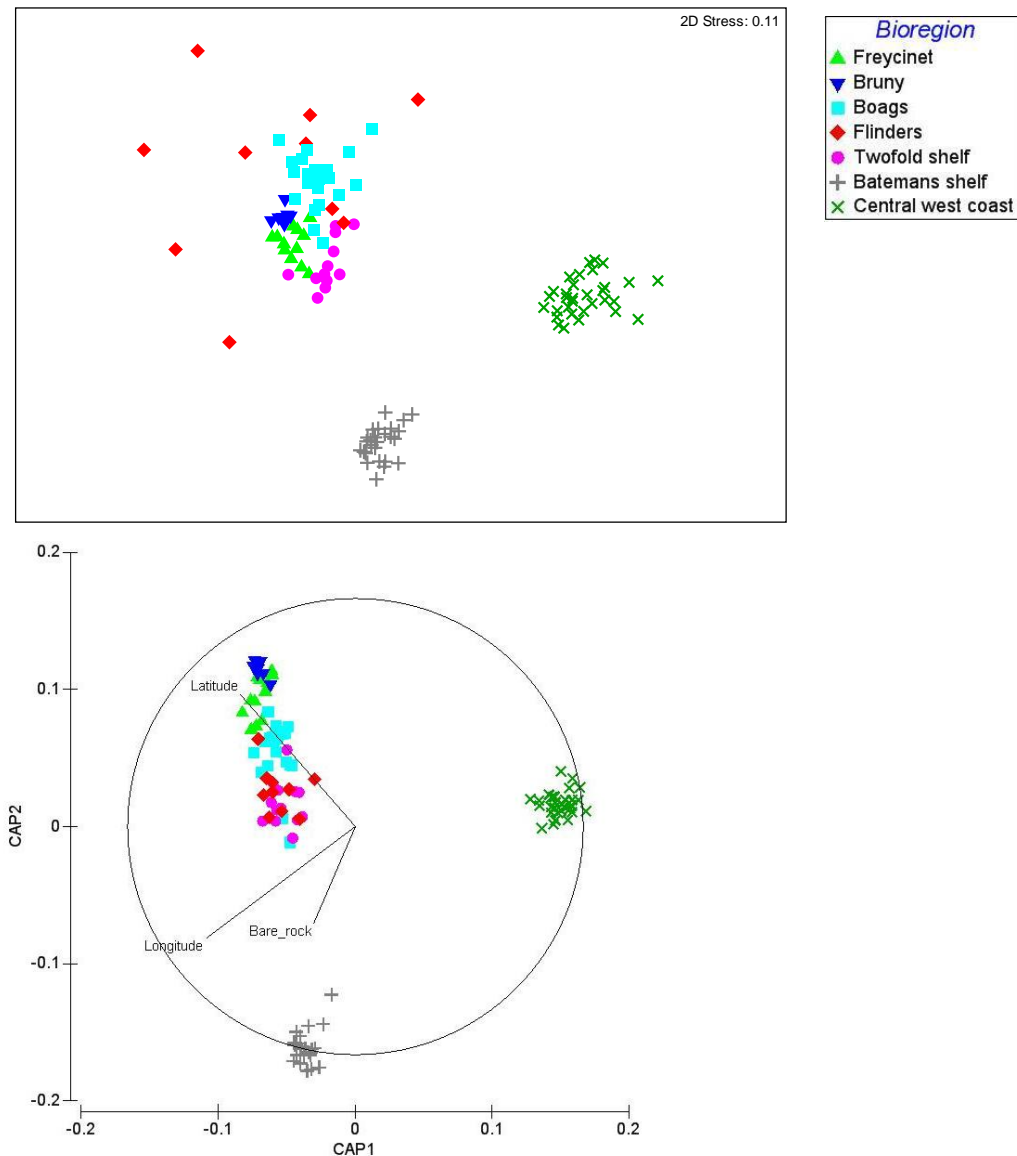


Figure 2.2. MDS (top panel) and CAP (bottom panel) ordinations. CAP identifies the relationships between the multispecies reef fish abundance data and the multivariate physical habitat data for all seven bioregions ($\delta_1 = 0.996$, $\delta_2 = 0.991$). The MDS plot is included as an unconstrained contrast to show the true depiction of the variability in reef fish community structure independent of the physical variables.

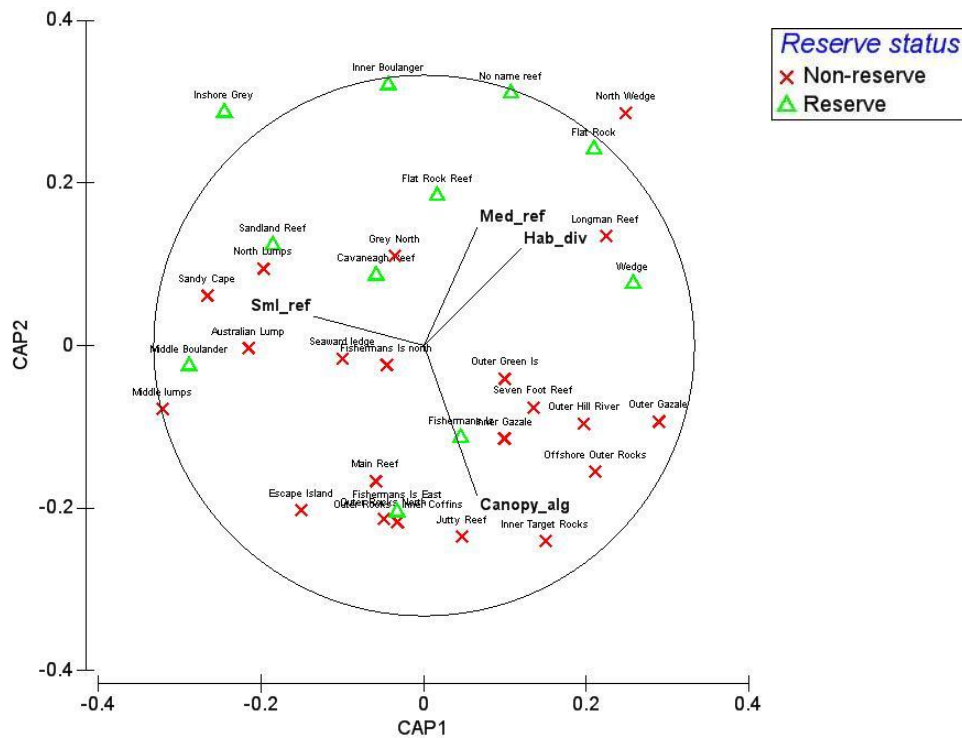


Figure 2.3. CAP ordination identifying the relationships between the multispecies reef fish abundance data and the multivariate physical habitat data within the Central west coast bioregion with symbols denoting sites inside and outside marine reserves (reserve status was not included as a factor in the analysis) ($\delta_1 = 0.976$, $\delta_2 = 0.953$).

2.4.4 Reef fish community modelling

The marginal DISTLM test results of the proportion of variance in community structure explained by each of the predictor variable sets independently are reported in

Table 2.3. Geographic position was the most important variable set explaining the highest, statistically significant proportion of the variance in the reef fish community structure across all bioregions combined.

Table 2.3 also displays the DISTLM test results for the ‘Best’ (i.e. most parsimonious) models identified from one to five variables and the overall ‘Best’ model selection (denoted by *). Geographic position was clearly the most important variable for all of the models identified along with smaller contributions from habitat substratum, biogenic cover and exposure. The ‘Best’ (i.e. the most parsimonious) model identified by the DISTLM procedure for the full scale analysis was a nine variable model which explained a total of 67.2% of the variability in the reef fish community structure.

Figure 2.4 displays the dbRDA ordinations for the full scale model analyses and acts as a visual interpretation of the DISTLM analysis, identifying the greatest variability in the multispecies fish community data and is overlaid with both the correlated physical and individual species variables with the highest multiple correlations with the first and second axes of the ordination ($r \geq 0.4$). For the full scale analyses (all bioregions combined) the dbRDA ordination captured 80.1% of the ‘Best’ fitted model and 53.8% of the total variation in the multispecies reef fish community structure. The ordination clearly identifies the differences in community structure between the Central west coast, Batemans and the remaining Tasmanian and Twofold shelf bioregions and the importance of geographic position and the amount of bare rock cover in explaining this variability. Differences between the Central west coast bioregion communities and the other bioregions are largely due to differences in longitude and latitude. Differences between the Bateman’s bioregion communities and those of the other bioregions are largely due to differences in latitude and urchin barrens cover. A general gradient in differences in community for the four Tasmanian bioregions and the Twofold shelf bioregion appear to generally follow latitude from Twofold shelf in the north to Bruny in the south as would be expected. The distribution of the species

Coris auricularis is highlighted as important in distinguishing between the Central west coast bioregion and the remaining bioregions, since it was only ever observed in this bioregion.

Table 2.3. DISTLM top five and overall ‘Best’ model results for the full bioregion analysis, based on the highest AIC model criteria value. * denotes the most parsimonious model identified.

	<i>Significant Marginal test results</i>	<i>Proportion</i>	<i>‘Best’ 1-5 variable and ‘Best’ overall model results</i>
Full scale (All bioregions)	<i>Geographic position (F= 67.553 p=0.0001)</i>	53%	Geographic position (AIC= 900.05, R ² = 0.53169)
	<i>Habitat substratum (F= 7.4946 p=0.0001)</i>	28%	Geographic position, Habitat substratum (AIC= 894.06, R ² = 0.5959)
	<i>Biogenic cover (F= 10.536 p=0.0001)</i>	21%	Geographic position, Habitat substratum, Biogenic cover (AIC= 890.78, R ² = 0.6255)
	<i>Habitat diversity (F= 20.529 p=0.0001)</i>	15%	Geographic position, Habitat substratum, Biogenic cover, Exposure (AIC= 888.45, R ² = 0.63857)
	<i>Refuge space (F= 3.471 p=0.0001)</i>	11%	Geographic position, Habitat substratum, Maximum reef height, Biogenic cover, Exposure (AIC= 887.61, R ² = 0.64687)
	<i>SD rugosity (F= 8.0683 p=0.0001)</i>	6%	* Geographic position, Habitat substratum, Modal reef height, Maximum reef height, Rugosity, Refuge diversity, Biogenic cover, Exposure, Reserve status (AIC= 886.56, R ² = 0.67212)
	<i>Fractal refuge index (F= 6.427 p=0.0001)</i>	5%	
	<i>Maximum reef height (F= 5.4458 p=0.0002)</i>	4%	
	<i>Refuge diversity (F= 5.3844 p=0.0003)</i>	4%	
	<i>Rugosity (F= 4.2676 p=0.0011)</i>	3%	
	<i>Reserve status (F= 3.6027 p=0.0052)</i>	3%	
	<i>Exposure (F= 2.8716 p=0.0139)</i>	2%	
	<i>Modal reef height (F= 2.1507 p=0.0478)</i>	2%	

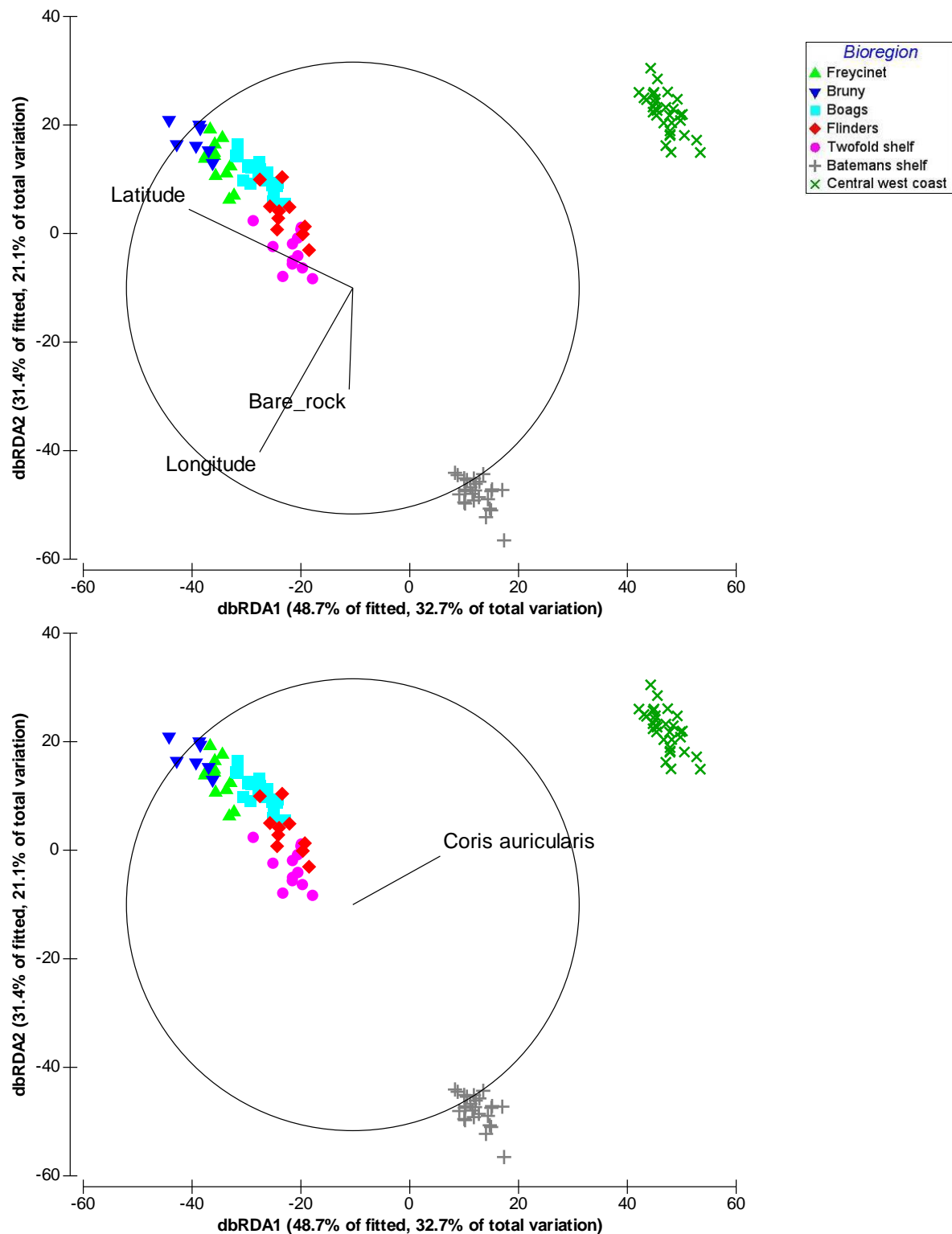


Figure 2.4. dbRDA ordinations identifying the greatest variation through the multispecies reef fish community structure. Ordinations are duplicated with separate vector overlaid of the correlated physical variables ($r \geq 0.4$) (top panel) and the multiple partial correlations with the original species variables ($r \geq 0.4$) ($\log x + 1$ transformed abundances) (bottom panel).

At the intra- bioregional scale, separate DISTLM analyses were carried out considering each bioregion individually to identify the variability in the reef fish community structure that could be explained by the physical variables (Table 2.4). There was insufficient site replication to carry out effective DISTLM analysis for the Freycinet, Bruny, Flinders and Twofold shelf bioregions, so they were combined and analysed in pairs due to their close proximities (i.e. Bruny/Freycinet and Twofold/Flinders). At this scale of investigation, low sample replication led to problems of over-fitting in the model which resulted in uninformative ‘Best’ model results which lacked parsimony.

For the Batemans bioregion, biogenic cover explained the largest, significant proportions of the reef fish community structure. Figure 2.5 displays dbRDA ordinations for the Batemans bioregion, with overlaid bubble plots of the relative proportions of algal canopy cover (ordination a) and bare rock (ordination b), highlighting the general importance of biogenic cover (or the absence of it) in explaining the reef fish community structure across the Batemans bioregion sites. The ordination captured 50.3% of the ‘Best’ fitted model and total variation in the multispecies reef fish community structure. The effect of canopy algal cover, on the reef fish community structure is particularly evident; sites towards the upper right of ordination a) are characterised by relatively high algal canopy cover and there is some suggestion that sites towards the lower left of ordination b) are characterised by higher proportions of bare rock.

For the Central west coast bioregion, biogenic cover explained the largest, significant proportion of the reef fish community structure. Figure 2.6 displays the dbRDA ordination for the Central west coast bioregion, with overlaid bubble plots of the relative proportions of algal canopy (ordination a) and sessile invertebrate cover (ordination b), highlighting the

general importance of biogenic cover in explaining the reef fish community structure across the Central west coast bioregion sites. The ordination captured 45.8% of the 'Best' fitted model and 34.9% of the total variation in the multispecies reef fish community structure. Sites towards the lower left half of the ordination a) are characterised by relatively high algal canopy cover, while sites towards the upper left of ordination b) are characterised by relatively high proportions of sessile invertebrate cover.

For the Boags bioregion, geographic position explained the largest, significant proportion of the reef fish community structure followed closely by refuge space. Figure 2.7 displays the dbRDA ordination for the Boags bioregion, with overlaid bubble plots of the relative density of small refuge spaces, explaining the reef fish community structure across the Boags bioregion sites. The ordination captured 46.5% of the 'Best' fitted model and total variation in the multispecies reef fish community structure. Sites towards the right-hand half of ordination appear to be characterised by marginally higher densities of small refuge spaces.

For the combined Twofold and Flinders bioregions, habitat substratum and geographic position both explained the largest, significant proportions of the reef fish community structure. Figure 2.8 displays the dbRDA ordination for the Twofold and Flinders bioregions, with overlaid bubble plots of the relative density of large boulders (ordination a) and rugosity (ordination b) which appear to differentiate the communities of reef fish between the Twofold and Flinders bioregion sites. The ordination captured 49% of the 'Best' fitted model and total variation in the multispecies reef fish community structure. Sites towards the upper, right-hand half of ordination appear to be characterised by higher densities of large boulders and greater habitat diversity and rugosity.

For the combined Bruny and Freycinet bioregions, refuge space explained the largest, significant proportions of the reef fish community structure, closely followed by biogenic cover. Figure 2.9 displays the dbRDA ordination for the Bruny and Freycinet bioregions, with overlaid bubble plots of the relative proportions of algal canopy (ordination a) and densities of small refuge spaces (ordination b), explaining the reef fish community structure across the Bruny and Freycinet bioregion sites. The ordination captured 40.8% of the fitted model and total variation in the multispecies reef fish community structure. Sites towards the right-hand side of the ordination appear to be characterised by slightly higher canopy algal cover.

Individual bioregion analyses failed to identify clear patterns in the important explanatory variables of reef fish community structure. Overall, biogenic cover (or the lack of it) was the most important variable set explaining the highest, statistically significant proportion of the variance in the reef fish community structure within the Batemans and Central west coast bioregions. For the Boags, Twofold/Flinders and Bruny/Freycinet bioregions varying combinations of geographic position, biogenic cover, habitat substratum and refuge space were important in explaining the reef fish community structure but no single variable stood out as overwhelmingly important in explaining the community structure within any of the seven bioregions investigated.

Table 2.4. Marginal, top five and overall ‘Best’ (denoted by *) DISTLM model results for each individual bioregion.

Bioregion	Significant Marginal test results	Proportion.	‘Best’ (1-5 variable and overall) model results
Batemans	<i>Biogenic cover</i> ($F= 4.8254$, $P= 0.0001$) <i>Habitat substratum</i> ($F= 1.8464$, $P= 0.0042$) <i>Geographic position</i> ($F= 5.939$, $P= 0.0001$) <i>Refuge space</i> ($F= 1.5167$, $P= 0.0453$) <i>Refuge diversity</i> ($F= 5.0288$, $P= 0.0003$) <i>Maximum reef height</i> ($F= 4.7676$, $P= 0.0004$) <i>Exposure</i> ($F= 3.7399$, $P= 0.0009$) <i>Rugosity</i> ($F= 3.3148$, $P= 0.0021$) <i>Modal reef height</i> ($F= 3.2619$, $P= 0.0046$) <i>Reef gradient</i> ($F= 3.2207$, $P= 0.0053$)	40% 37% 34% 22% 17% 17% 13% 12% 12% 12%	<i>Biogenic cover</i> ($AIC= 171.01$, $R^2= 0.39686$) <i>Refuge diversity</i> + <i>Biogenic cover</i> ($AIC= 168.74$, $R^2= 0.4882$) <i>Geographic position</i> + <i>Refuge diversity</i> + <i>Exposure</i> ($AIC= 168.67$, $R^2= 0.48957$) <i>Geographic position</i> + <i>Habitat substratum</i> + <i>Refuge space</i> + <i>Biogenic cover</i> ($AIC= 167.67$, $R^2= 0.78927$) <i>Geographic position</i> + <i>Habitat substratum</i> + <i>Refuge space</i> + <i>Biogenic cover</i> + <i>Reef gradient</i> ($AIC= 165.5$, $R^2= 0.82052$) * <i>All variables</i> ($AIC= \infty$, $R^2= 1$)
Central west coast	<i>Biogenic cover</i> ($F= 3.3174$ $p= 0.0001$) <i>Geographic position</i> ($F= 2.6507$ $p= 0.0004$) <i>SD rugosity</i> ($F= 3.2049$ $p= 0.0022$) <i>Rugosity</i> ($F= 2.8196$ $p= 0.0048$) <i>Exposure</i> ($F= 2.6782$ $p= 0.0067$) <i>Maximum reef height</i> ($F= 2.4166$ $p= 0.0111$) <i>Reserve status</i> ($F= 2.0239$ $p= 0.0293$) <i>Modal reef height</i> ($F= 1.9244$ $p= 0.0395$)	26% 15% 10% 9% 8% 7% 6% 6%	<i>Biogenic cover</i> ($AIC= 222.32$, $R^2= 0.26223$) <i>Rugosity</i> + <i>Biogenic cover</i> ($AIC= 221.51$, $R^2= 0.32429$) <i>Rugosity</i> + <i>Biogenic cover</i> + <i>Exposure</i> ($AIC= 220.64$, $R^2= 0.38219$) <i>Geographic position</i> + <i>Habitat substratum</i> + <i>Rugosity</i> + <i>Biogenic cover</i> ($AIC= 218.65$, $R^2= 0.54779$) <i>Geographic position</i> + <i>Habitat substratum</i> + <i>Rugosity</i> + <i>Biogenic cover</i> + <i>Exposure</i> ($AIC= 218.37$, $R^2= 0.57891$) * <i>Geographic position</i> + <i>Habitat substratum</i> + <i>Habitat diversity</i> + <i>Modal reef height</i> + <i>Rugosity</i> + <i>SD rugosity</i> + <i>Refuge space</i> + <i>Fractal refuge index</i> + <i>Biogenic cover</i> + <i>Exposure</i> + <i>Reef gradient</i> ($AIC= 218.33$, $R^2= 0.76037$)
Boags	<i>Geographic position</i> ($F= 4.7542$, $P= 0.0001$) <i>Refuge space</i> ($F= 1.8506$, $P= 0.0053$) <i>Biogenic cover</i> ($F= 1.5574$, $P= 0.0517$) <i>Exposure</i> ($F= 3.5054$, $P= 0.0014$) <i>Modal reef height</i> ($F= 3.0128$, $P= 0.0039$) <i>Fractal refuge index</i> ($F= 2.9206$, $P= 0.0051$) <i>SD rugosity</i> ($F= 2.377$, $P= 0.0176$) <i>Reef gradient</i> ($F= 2.3329$, $P= 0.0201$)	32% 29% 20% 14% 13% 12% 10% 10%	<i>Geographic position</i> ($AIC= 162.17$, $R^2= 0.32223$) <i>Geographic position</i> + <i>Reef gradient</i> ($AIC= 161.75$, $R^2= 0.38997$) <i>Geographic position</i> + <i>Reef gradient</i> + <i>Reserve status</i> ($AIC= 161.75$, $R^2= 0.38997$) <i>Geographic position</i> + <i>Habitat diversity</i> + <i>Refuge space</i> + <i>Reef gradient</i> ($AIC= 162.17$, $R^2= 0.59773$) <i>Geographic position</i> + <i>Habitat substratum</i> + <i>Max. Reef height</i> + <i>Refuge space</i> + <i>Reef gradient</i> ($AIC= 160.75$, $R^2= 0.75523$) * <i>Geographic position</i> + <i>Habitat substratum</i> + <i>Habitat diversity</i> + <i>Modal reef height</i> + <i>Max. reef height</i> + <i>Rugosity</i> + <i>SD rugosity</i> + <i>Refuge space</i> + <i>Refuge diversity</i> + <i>Fractal refuge index</i> + <i>Biogenic cover</i> + <i>Exposure</i> ($AIC= \infty$, $R^2= 1$)
Twofold/Flinders	<i>Habitat substratum</i> ($F= 2.0632$, $p= 0.0024$) <i>Geographic position</i> ($F= 6.1099$, $p= 0.0001$) <i>Biogenic cover</i> ($F= 1.9205$, $p= 0.0171$) <i>Rugosity</i> ($F= 3.5574$, $p= 0.0033$)	39% 39% 24% 15%	<i>Geographic position</i> ($AIC= 163.81$, $R^2= 0.39141$) <i>Geographic position</i> + <i>Refuge diversity</i> ($AIC= 162.73$, $R^2= 0.47096$) <i>Geographic position</i> + <i>Refuge diversity</i> + <i>Reef gradient</i> ($AIC= 162.64$, $R^2= 0.5189$) <i>Geographic position</i> + <i>Max. Reef height</i> + <i>Refuge diversity</i> + <i>Reef gradient</i> ($AIC= 162.24$, $R^2= 0.56857$) <i>Geographic position</i> + <i>Habitat diversity</i> + <i>Max. Reef height</i> + <i>Refuge diversity</i> + <i>Reef gradient</i> ($AIC= 161.71$, $R^2= 0.61541$) * <i>Geographic position</i> + <i>Habitat substratum</i> + <i>Habitat diversity</i> + <i>Modal reef height</i> + <i>Max reef height</i> + <i>Rugosity</i> + <i>SD rugosity</i> + <i>Refuge space</i> + <i>Refuge diversity</i> + <i>Biogenic cover</i> + <i>Exposure</i> ($AIC= \infty$, $R^2= 1$)
Bruny/Freycinet	<i>Refuge space</i> ($F= 1.821$, $p= 0.0014$) <i>Biogenic cover</i> ($F= 2.3589$, $p= 0.0001$) <i>Geographic position</i> ($F= 2.4668$, $p= 0.0003$) <i>Exposure</i> ($F= 3.2028$, $p= 0.0003$) <i>Rugosity</i> ($F= 2.0923$, $p= 0.0172$) <i>Fractal refuge index</i> ($F= 1.8775$, $p= 0.0338$)	34% 32% 24% 16% 11% 10%	<i>Biogenic cover</i> ($AIC= 128.63$, $R^2= 0.32055$) <i>Geographic position</i> + <i>Biogenic cover</i> ($AIC= 127.56$, $R^2= 0.47954$) <i>Geographic position</i> + <i>Refuge space</i> + <i>Biogenic cover</i> ($AIC= 126.23$, $R^2= 0.68162$) <i>Geographic position</i> + <i>Habitat substratum</i> + <i>Refuge space</i> + <i>Biogenic cover</i> ($AIC= 120.5$, $R^2= 0.86082$) <i>Geographic position</i> + <i>Habitat substratum</i> + <i>Rugosity</i> + <i>Refuge space</i> + <i>Biogenic cover</i> ($AIC= 115.03$, $R^2= 0.90608$) * <i>Geographic position</i> + <i>Habitat substratum</i> + <i>Habitat diversity</i> + <i>Modal Reef height</i> + <i>Max. Reef height</i> + <i>Rugosity</i> + <i>Refuge space</i> + <i>Biogenic cover</i> ($AIC= \infty$, $R^2= 1$)

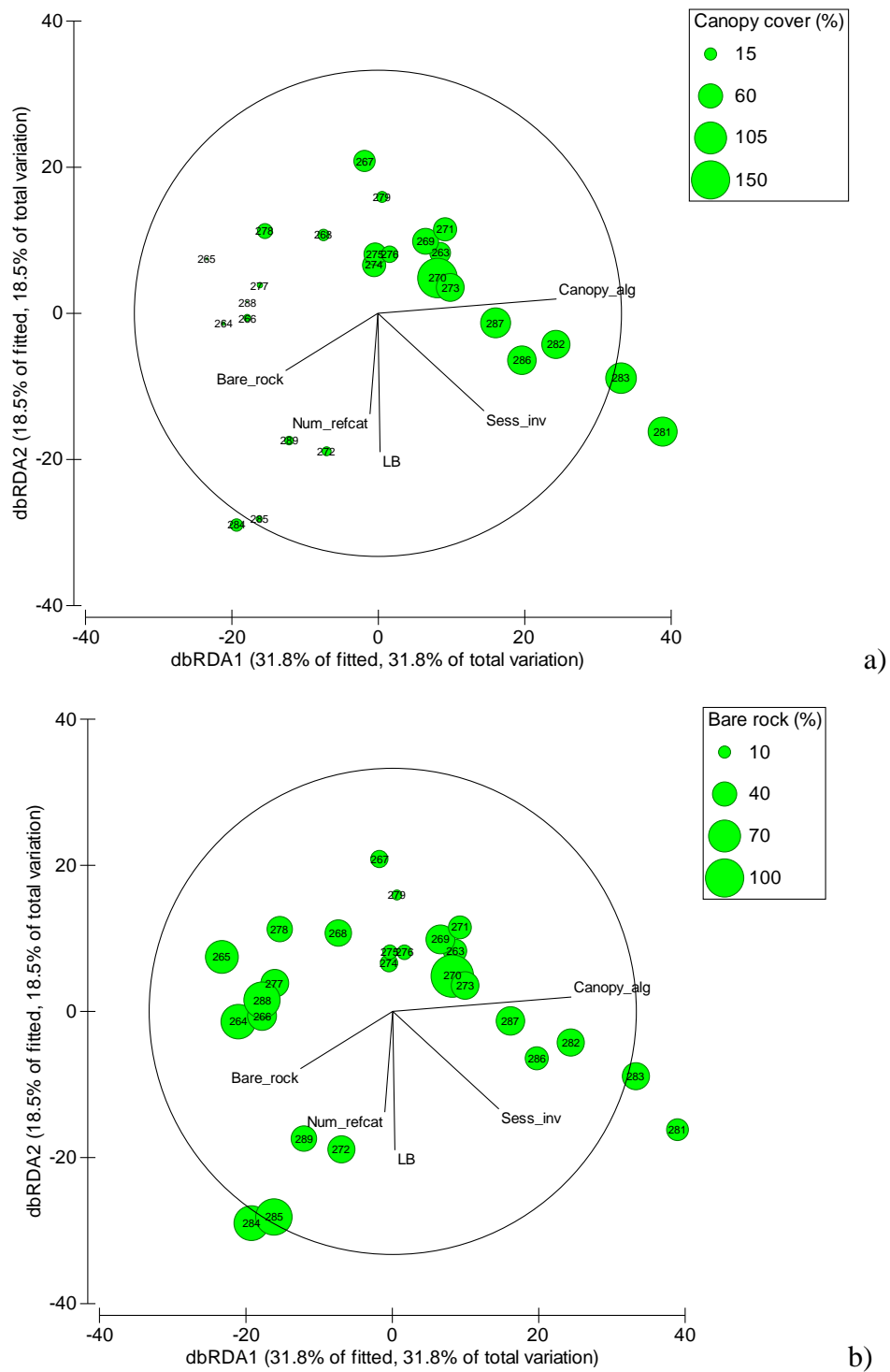


Figure 2.5. dbRDA ordinations showing the variability in reef fish community structure of sites within Batemans bioregion. Bubble overlays indicate the relative proportions of algal canopy cover (upper ordination a) and bare rock (lower ordination b) at each site. Vector overlays display the associated correlated fitted model variables ($r = 0.4$).

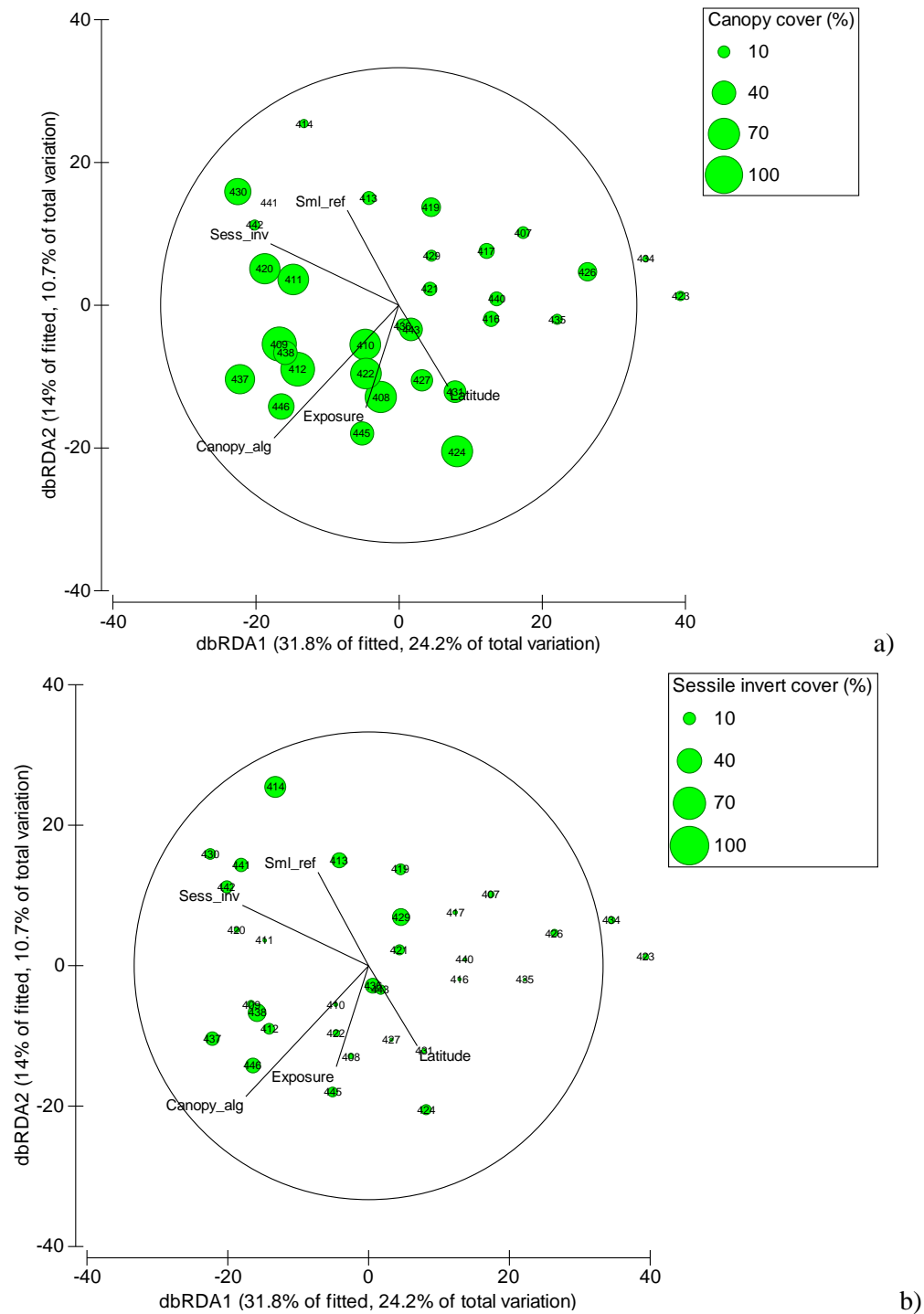


Figure 2.6. dbRDA ordinations showing the variability in reef fish community structure of sites within the Central west coast bioregion. Bubble overlays indicate the relative proportions of algal canopy cover (upper ordination a) and sessile invertebrate cover (lower ordination b) at each site. Vector overlays display the associated correlated fitted model variables ($r = 0.4$).

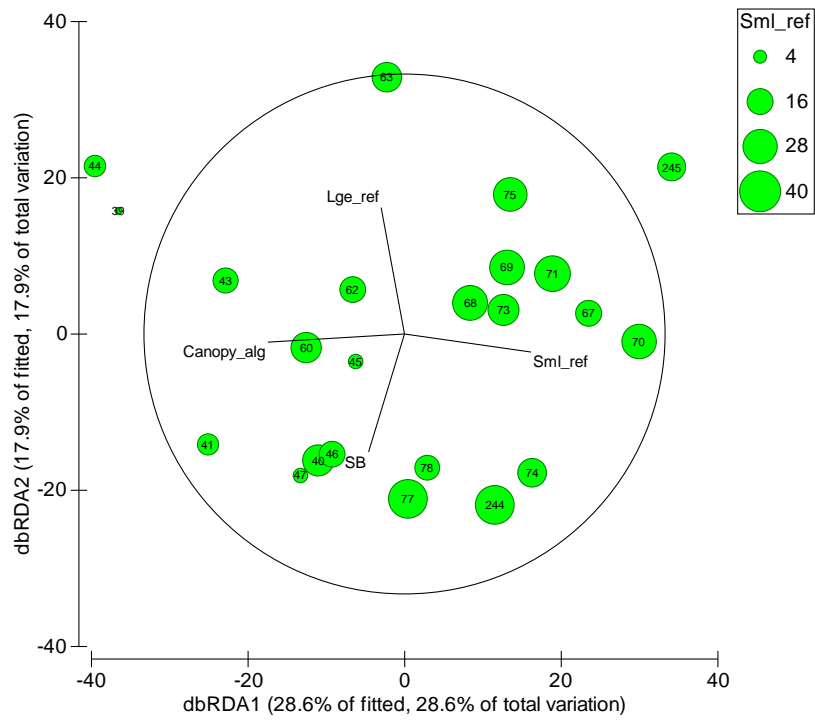


Figure 2.7. dbRDA ordinations showing the variability in reef fish community structure of sites within the Boags bioregion. Bubble overlays indicate the relative densities of small refuge spaces (average number of 1-5 cm refuges per 5 m²) at each site. Vector overlays display the associated correlated fitted model variables ($r = 0.4$).

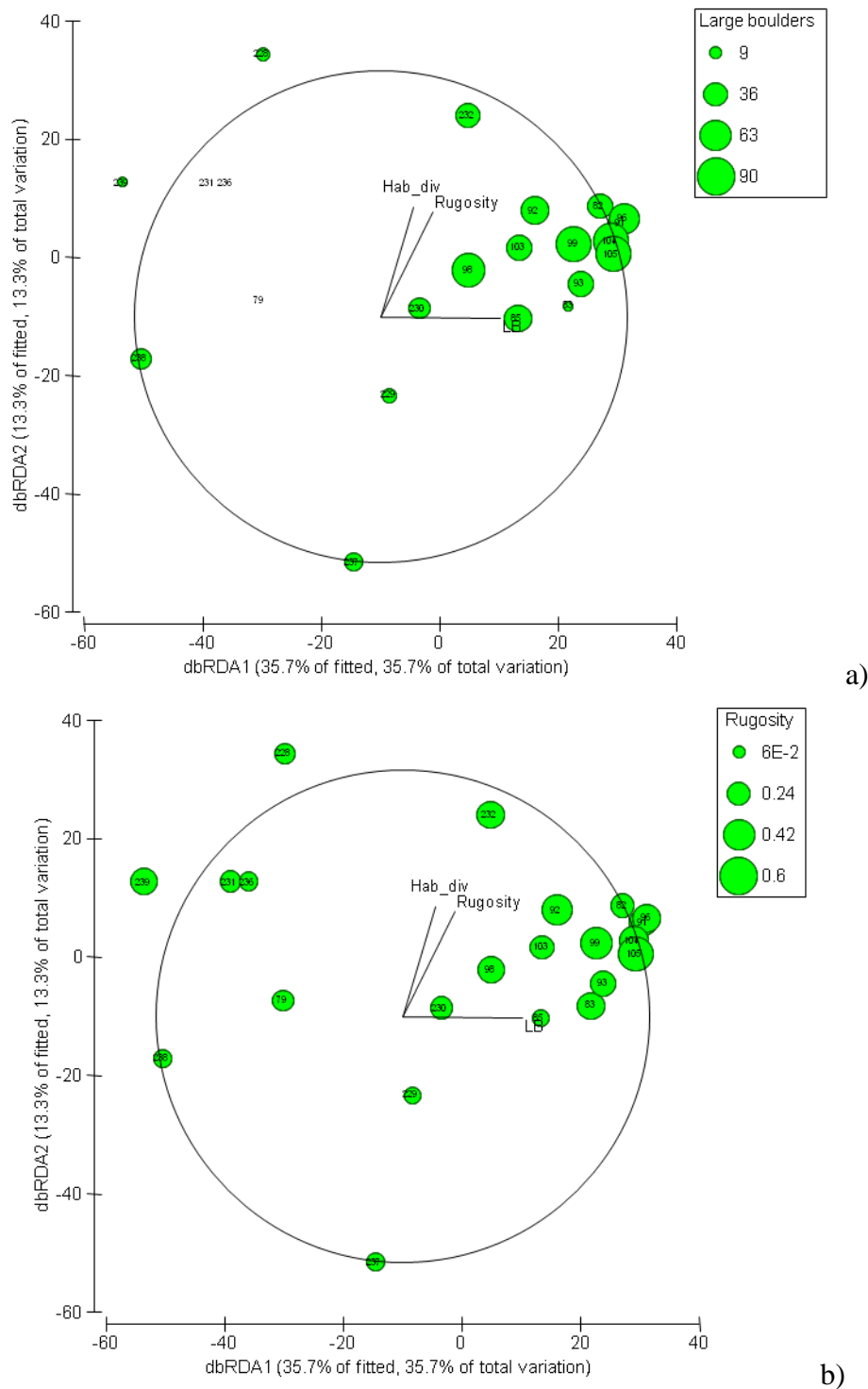


Figure 2.8. dbRDA ordinations showing the variability in reef fish community structure of sites within the Twofold/Flinders bioregions. Bubble overlays indicate the relative proportions of large boulders (upper ordination a) and rugosity (lower ordination b) at each site. Vector overlays display the associated correlated fitted model variables ($r = 0.4$).

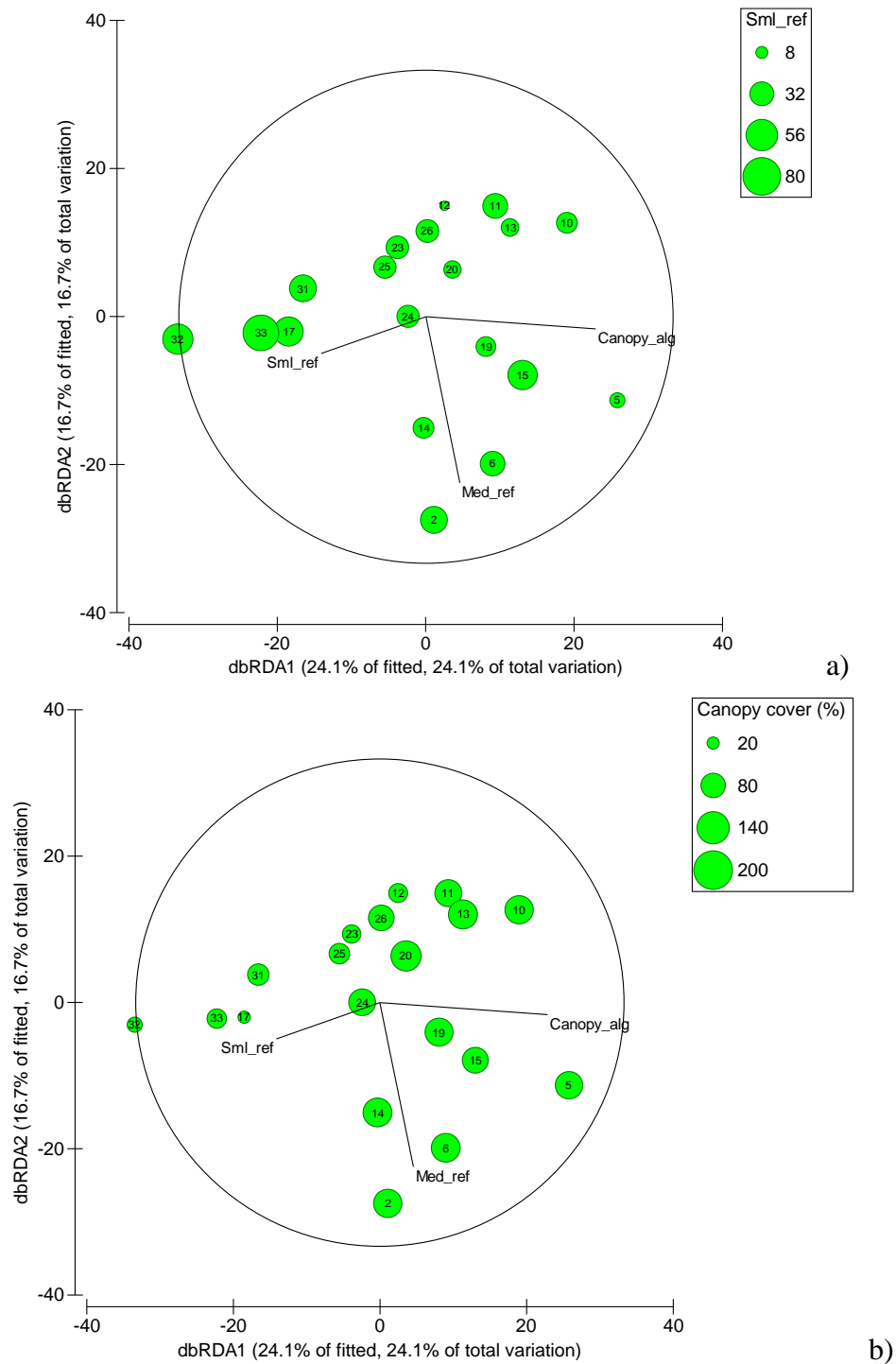


Figure 2.9. dbRDA ordinations showing the variability in reef fish community structure of sites within the Bruny/Freycinet bioregions. Bubble overlays indicate the relative densities of small refuge spaces (average number of 1-5 cm refuges per 5 m²) (upper ordination a) and algal canopy cover (lower ordination b) at each site. Vector overlays display the associated correlated fitted model variables ($r = 0.4$).

2.4.5 Species-habitat relationships

Univariate regression analysis identified the specific relationships between the individual species abundances and the habitat variables identified by the previous multivariate analysis as highly correlated with the overall variability in community structure (Table 2.5).

Relationships between reef fish abundance and physical habitat variables were largely species-specific and differed between bioregions.

Three species were identified as being correlated with variability in the reef fish community structure within the Batemans bioregion. The barber perch, *Caesioperca rasor* showed a positive correlation with the percentage of bedrock, large boulders, number of medium refuge spaces and un-vegetated reef suggesting the importance of relatively structurally complex reef habit and an absence of biogenic cover to the distribution of this species. The purple wrasse, *Notolabrus fucicola* showed a positive relationship with the percentage of canopy cover, again suggesting the importance of biogenic cover to its distribution and the silver sweep, *Scorpiis lineolata*, showed a positive correlation with the percentage cover of small boulders.

Two species were identified as being correlated with variability in the reef fish community structure within the Bruny/Freycinet bioregions. The abundance of the toothbrush leatherjacket, *Acanthaluteres vittiger* was positively correlated with the density of small refuges, percentage of algal canopy cover, sessile invertebrate cover and refuge diversity, suggesting the importance of refuge space, reef complexity and biogenic cover in the distribution of this species. The abundance of the bastard trumpeter, *Latridopsis forsteri* showed a positive relationship with the percentage of bed rock and a negative relationship

with the percentage of un-vegetated reef suggesting the importance of relatively un-complex, vegetated reef to its distribution.

Two species were identified as being correlated with variability in the reef fish community structure within the Batemans bioregion. The abundance of the onespot puller, *Chromis hypsilepsis* was correlated with the percentage of bare (i.e. un-vegetated) rock and refuge diversity and highly negatively correlated with the percentage cover of canopy forming algae suggesting that this species utilises habitats with a high diversity of physical refugia in the absence of biogenic cover. Similarly the abundance of the eastern hulafish, *Trachinops taeniatus* showed a strong negative correlation with the percentage cover of canopy forming algae and positive correlations with small refuge density and refuge diversity suggesting the importance of open, un-vegetated reef environments with suitable available refuge spaces for this small bodied fish.

Two species were identified as being correlated with variability in the reef fish community structure within the central west coast bioregion. The abundance of western buffalo bream, *Kyphosus cornelli* showed a positive relationship to the single habitat variable of per cent cover of sessile invertebrates. The abundance of the Miller's damselfish, *Pomacentrus milleri* across the central west coast bioregion was strongly positively correlated with small and medium refuge space density, suggesting the importance of adequate refuge space to the distribution of this species.

The abundance of the bigscale bullseye, *Pempheris multiradiata* was identified as being correlated with variability in the reef fish community structure within the Boags bioregion

however subsequent univariate analysis failed to identify any significant relationship between the abundance of *P. multiradiata* and any of the physical variables investigated.

Table 2.5. Regression analysis results of Log(x+1) transformed abundances for species identified as highly correlated ($r \geq 4$) with the first and second ordination axes of the within-bioregion dbRDA analyses. Results are displayed for those species-physical variable relationships that were found to be statistically significant.

Bioregion/s	Species	Common name	Correlation 1st dbRDA axes	Correlation 2nd dbRDA axes	Latitude	Longitude	Bed rock	Small boulders	Large boulders	Small refuges	Medium refuges	Canopy cover	Sessile cover	Bare rock	Refuge diversity
Twofold/Flinders	<i>Caesioperca razor</i>	Barber perch	0.545	0.136	-	-	$F=4.96$ $p=0.034$ $R^2=15.5+$	-	$F=6.17$ $p=0.021$ $R^2=21.1+$	-	$F=9.31$ $p=0.004$ $R^2=21.0+$	-	-	$F=8.62$ $p=0.006$ $R^2=19.8+$	-
	<i>Notolabrus fucicola</i>	Purple wrasse	0.165	-0.530	-	-	-	-	-	-	-	$F=6.53$ $p=0.014$ $R^2=11.0+$	-	-	-
	<i>Scorpius lineolata</i>	Silver sweep	0.164	-0.440	-	-	-	$F=6.91$ $p=0.014$ $R^2=19.2+$	-	-	-	-	-	-	-
Bruny/Freycinet	<i>Acanthaluteres vittiger</i>	Toothbrush leatherjacket	0.401	-0.118	$F=12.65$ $p=0.001$ $R^2=19.6+$	-	-	-	-	$F=4.55$ $p=0.038$ $R^2=8.0+$	-	$F=8.03$ $p=0.007$ $R^2=13.4+$	$F=5.78$ $p=0.020$ $R^2=10.0+$	-	$F=6.58$ $p=0.013$ $R^2=11.2+$
	<i>Latridopsis forsteri</i>	Bastard trumpeter	0.111	0.427	-	-	$F=4.24$ $p=0.064$ $R^2=27.8+$	-	-	-	-	-	-	$F=4.71$ $p=0.044$ $R^2=21.7 -$	-
Bateman's	<i>Chromis hypsilepis</i>	Onespot puller	-0.484	-0.271	$F=3.91$ $p=0.066$ $R^2=19.6+$	$F=4.02$ $p=0.062$ $R^2=20.1+$	-	-	-	-	-	$F=6.64$ $p=0.020$ $R^2=29.3 -$	-	$F=15.96$ $p=0.001$ $R^2=49.9+$	$F=8.55$ $p=0.010$ $R^2=34.8+$
	<i>Trachinops taeniatus</i>	Eastern hulafish	-0.483	0.001	-	-	-	-	-	$F=4.16$ $p=0.050$ $R^2=12.6 +$	-	$F=16.00$ $p=0.000$ $R^2=35.6 -$	-	-	$F=4.89$ $p=0.035$ $R^2=14.4+$
Central west coast	<i>Kyphosus cornelii</i>	Western buffalo bream	-0.425	0.040	-	-	-	-	-	-	-	-	$F=6.42$ $p=0.018$ $R^2=19.8+$	-	-
	<i>Pomacentrus milleri</i>	Miller's damselfish	-0.120	0.402	-	-	-	-	-	$F=18.59$ $p=0.001$ $R^2=57.0+$	$F=43.08$ $p=0.000$ $R^2=76.8+$	-	-	-	-
Boags	<i>Pempheris multiradiata</i>	Bigscale bullseye	0.527	0.602	-	-	-	-	-	-	-	-	-	-	-

2.5 Discussion

As would be expected, the results of this study demonstrate that across large inter-bioregional and continental scales, it is principally climatic and biogeographical differences between varying geographic locations which are important in structuring much of the temperate reef fish community, while at smaller, intra-bioregional scales other, more ecologically proximal physical variables, such as biogenic cover, refuge space and habitat substratum begin to come into play. Different habitat variables tended to explain community structure within each bioregion suggesting that habitat surrogates possess limited value in confidently predicting the spatial distribution and abundance of temperate reef fish outside any one particular bioregion, even where communities are comprised of ecologically similar species. The variability of individual species response to their physical habitat structure were largely species-specific in both the extent of responses and the particular types of habitat variables species respond to. Identifying reserve effects across the scales of this investigation was difficult and if effects were present they were probably masked by the overriding influence of other natural sources of environmental variability. A notable outcome of the research was the detection of a clear urchin barrens effect between and within bioregions.

2.5.1 Inter-bioregional patterns

This study considered a range of broad spatial scales; variability in reef fish community structure data was investigated at the largest scale across seven temperate bioregions from Western Australia to South Australia and Tasmania and at the smallest scale within each of seven temperate bioregions individually. Overall variability in the reef fish community structure across the full spatial extent of all seven bioregions investigated appeared to be related largely to the particular geographic position of each site (i.e. the spatial variables of 'latitude' and 'longitude') and the absence of biogenic structure.

The reef fish community structure of the Central west coast and Bateman's shelf bioregion sites differed markedly from the remaining bioregions. For the Central west coast bioregion this difference was largely correlated with the geographical distance in longitude and latitude from the other bioregions in the analysis. The importance of the geographical position of a site in determining its community structure comes as no major surprise as patterns of community at sites would be expected to relate to broad biogeographic and climatic variability between highly distant sites. Spatial location, particularly latitude, is well known to determine large scale patterns of community structure and diversity (Mora et al., 2003, Willig et al., 2003) but what is more informative is understanding at what scales broad latitudinal influences on reef fish community structure begin to be overridden by those of natural physical habitat structure. The study design incorporated high site replication across and within bioregional scales allowing me to identify some idea of the scales at which physical habitat structure becomes important to structuring reef fish communities.

2.5.2 Reserve effects

Significant differences in the reef fish community structure were identified between communities at reserve and non-reserve sites for the Central west coast, but it should be noted that those species identified by the SIMPER analysis between reserve and non-reserve are also characteristic of sheltered inshore and offshore reef species and therefore the apparent reserve effect of the two different assemblages may in fact be due to confounding differences in the distance from shore and apparent exposure between control and reserve sites. To a limited extent, these results agree with those of Claudet et al. (2010) who investigated how habitat characteristics affected abundance and species composition and responses to protection of fishes at transect (250 m²) and seascape (30,000 m²) scales across a Mediterranean marine protected area (Claudet et al., 2010). Their research found that habitat features accounted for a larger proportion of spatial variation in species composition and

abundances than differences in protection status and that this spatial variation was explained best by habitat characteristics at the seascape level than at the transect level. They identified that the response of fish relative abundances to the establishment of an MPA was affected by season, depth range, substratum type and complexity. However their work did not consider the issue of disentangling the effects of marine reserves from those of habitat structure. My analyses has identified significant differences in the communities of reef fish between reserve and non-reserve sites for one of the seven bioregions but the analysis failed to identify reserve status as an important variable explaining the variability in community structure within any bioregion. This is probably because reserve effects are being masked by larger effects of physical habitat variables. Distinguishing the effects of protection on reef fish community structure from those due to the inherent variability in the structure of the habitat is vital in assessing reserve efficacy (Huntington et al., 2010). Chapter four of this thesis attempts to further disentangle the effects of natural physical habitat variability from those of protection from fishing.

2.5.3 Urchins barren effects

The Bateman's shelf reef fish community structure differed markedly from the other bioregions in response to latitude but also notably in response to the proportion of bare rock (i.e. the proportion of reef lacking substantial canopy cover). It is likely that the reef fish community structure in this bioregion is responding to an urchin barren effect particular to the Bateman's shelf coastline. The urchin, *Centrostephanus rodgersii* has been found to be responsible for creating and maintaining urchin barrens habitat across areas of inshore reef along Australia's east coast (Hill et al., 2003). Alexander (2011b) has recorded *C. rodgersii* in high numbers at many of the same study sites surveyed for the study within the Batemans bioregion and urchin barrens habitat may in fact make up more than 50% of the inshore reef environment along the New South Wales coast (Andrew and O'Neill, 2000). Reef habitats

denuded of macroalgae are likely to have reduced levels of food and biogenic refuge structure available to invertebrates and fish resulting in consequences across all trophic levels of the resulting reef community. It is perhaps of little surprise then that the analysis detected a response in the reef fish community structure to urchin barrens but it is noteworthy that trophic effects could be detected at relatively broad scales. The intra-bioregional scale analysis suggests that barrens are affecting the reef fish community structure within the Batemans shelf bioregion. The analysis clearly demonstrates that variability in reef fish community structure is strongly correlated with a gradient in biogenic cover from high algal canopy cover to highly unvegetated bare rock. The trophic cascade effects of urchin barrens have been considered by a number of studies into the response of impacted and recovering algal (Shears and Babcock, 2003, Leleu et al., 2012), invertebrate and reef fish (Anderson and Millar, 2004) communities. The distribution and abundance of herbivorous invertebrates and fish across temperate Mediterranean reefs have been found to be highly associated with algal encrusting communities and it is believed that reef fish have an importance, in addition to invertebrates, in structuring algal communities on sublittoral reefs and that their ecological impact in temperate seas could be greater than is generally thought, particularly in the role of creating algal barrens at depth (Ruitton et al., 2000). Manipulative experiments carried out across temperate rocky reefs along the coast of North Carolina have identified that variability in reef fish abundance and species richness corresponded to that of algal density and proportion of canopy forming algae (Levin and Hay, 1996) while work carried out in New Zealand has identified significant differences in the community structure of reef fish between algal dominated and barrens habitats (Anderson and Millar, 2004). As an aside, the presence of habitat forming invertebrates in themselves (in this case a species of long-spined urchin) have also been shown to be important in increasing observed species richness and abundance of reef fish on Caribbean reefs (Gratwicke and Speight, 2005a). It is clear that these systems

are complex and that further research is needed to fully understand how urchins and their associated barren formations alter the physical biogenic structure of habitats and the causal mechanisms and interactions linking these effects to reef fish community structure.

2.5.4 Intra-bioregional patterns

My study findings have also demonstrated that temperate reef fish community structure responds varyingly to habitat structure at intra-bioregional scales. I have identified some patterns between habitat structure and reef fish community, evident at the scale of individual bioregions but no single, common variable stood out as overwhelmingly important in explaining the community structure of reef fish within or between any of the seven bioregions investigated, suggesting that habitat variables possess limited value in explaining the spatial distribution and abundance of temperate reef fish between bioregions, even where communities are comprised of ecologically or functionally similar species. At this scale the influence of geographic position, although still important in explaining the community structure of temperate reef-fish, became less so and the influences of biogenic cover, habitat substratum and refuge space availability additionally became important as explanatory variables of reef fish community structure. This result agrees to some degree with the conclusions of Alexander (2011b) study of invertebrate associations with physical habitat structure across the same bioregions. His results identified a similar lack of common explanatory variables of invertebrate distribution between bioregions and identified that biogenic cover (in the form of canopy algae cover) was an important predictor of invertebrate distribution across the Bateman's bioregion as it was found for reef fish community structure in my own study, suggesting that similar ecological mechanisms may be influencing both invertebrate and fish community structure on temperate reefs across large scales.

The individual influences of biogenic structure and wave exposure on reef communities are inherently difficult to disentangle. Reef-algae community structure and wave exposure are intricately linked and therefore it is difficult to determine the exact nature of their separate effects on reef fish community structure. A number of studies have considered the effects of exposure (Friedlander et al., 2003, Depczynski and Bellwood, 2005) and algal density on reef fish community structure. Kendrick et al. (1999) investigated the combined effects of swell exposure and canopy dominance on understorey algal community structure in Western Australia and were able to demonstrate that at local scales algal community structure was influenced by the density of kelp canopy just as much as by gradients in exposure to ocean swells, however it should be noted that kelp density itself clearly cannot be considered independently of wave exposure. Similarly the influence of wave exposure on biogenic habitat structure may be mediated by the existing canopy composition and biological situation (Wernberg and Connell, 2008), suggesting a hypothesis that the structuring of canopy and understorey algal assemblages in kelp forests may be influenced by a hierarchy of spatial processes from regional scale influences of exposure to localised disturbance, recruitment, competition and predation, each equally manifested at small spatial scales. Chapter three of this study investigates the finer scale influences of physical habitat structure upon reef fish community structure and in doing so also considers more intricate associations with exposure and the physical characteristics of the biogenic component of reef habitats.

My analyses also considered the individual species responses to their habitats and illustrates the varying species-specific responses and niche utilisation of individual species to elements of their surrounding habitat. These results suggest, that for some species at least, individual species responses are strong enough to allow accurate modelling of their distributions and abundance within bioregions. For example species such as the Miller's damselfish,

Pomacentrus milleri showed very strong positive associations with available refuge space. Significant positive relationships have also been identified between habitat complexity (measured as the number of rocky boulders of varying sizes) and the total abundance of fish across rocky reefs in the south-western Mediterranean (Garcia-Charton and Perez-Ruzafa, 1998) particularly at small spatial scales and these relationships between habitat structure and particular species appear to be largely species-specific (Garcia-Charton and Pérez-Ruzafa, 2001). The availability of variously sized refuge space has been identified as important in determining the abundance and size of coral reef fish in the U.S. Virgin Islands (Hixon and Beets, 1989, Hixon and Beets, 1993) and the percentage of hard substrate and the number of refuge holes were found to be the most important factors in determining fish abundance on Caribbean reefs (Gratwicke and Speight, 2005a). The scales at which measures of habitat structure are investigated may be extremely important in detecting the response of a specific species or assemblage to varying habitat heterogeneity and complexity because the perceived resolution of an animal to its surrounding habitat is likely to depend largely on its body size (Wiens, 1989). Richards et al. (2012) identified relatively low influences of small-scale physical habitat variables (i.e. benthic cover and habitat heterogeneity) on large-bodied reef fish biomass across the Mariana archipelago. Instead they identified that the most important influences on large-bodied reef fish biomass were large-scale variables of human population density, water temperature, depth and distance from deep water. They suggest that small-scale variables are likely to be of prime importance to smaller, lower trophic species that interact directly with the surrounding habitat for food and shelter and less important to wide ranging, large-bodied species. Studies into the important physical habitat variables influencing large-bodied, commercially targeted reef fish in Tasmania would be a valuable future research avenue.

2.5.5 Study limitations

This study has identified a number of physical environmental and habitat variables capable of explaining fish community structure and individual species abundance on temperate rocky reefs across broad, inter and intra-bioregional scales. In the process a number of limitations and improvements to assessing reef fish habitat associations across broad, bioregional scales were encountered and identified.

One major limitation of the data available was that the most important explanatory variables of geographical position, were largely spatially confounded with other large scale biogeographic and climatic variables (which were not considered) and therefore there was no way of determining which aspect of the physical environment the community or a species was responding to. The data utilised in this study was not specifically collected to consider questions of reef fish community responses to habitat structure and the project did not have the means to collect further environmental data across bioregional scales therefore I was forced to work around these limitations.

A similar problem arises with many other large scale environmental variables such as sea surface temperature, nutrient and current variables which tend to vary gradually over large distances. Richards et al. 2012 encountered similar difficulties in drawing causative conclusions from their work because of covariance between many of the larger-scale physical gradients that they measured. Much of the variability explained by physical complexity and heterogeneity could well be concealed by the apparent response of reef fish community structure to broad scale environmental variables. However, since the investigation took a multi-scaled approach to identifying the patterns between habitat and reef fish community structure by considering responses between and within bioregions I was to some extent able

to determine how the hierarchy of ecological responses to spatial gradients of the physical habitat were manifest across bioregional scales.

Models based on ecologically proximal, direct and resource gradients are generally the most robust and widely applicable (Iampietro et al., 2008) although the practical limitations of collecting these data by themselves often limit their use across the extents and resolutions that are required by marine planners. The methods employed to collect the physical habitat data used in this study were extremely time and labour intensive which severely limits the effective application of similar approaches to assessing and predicting reef fish communities. An approach to tackle this problem is further considered in chapter three of this thesis by applying proxy measures of fine resolution physical habitat structure derived from broad scale, remotely sensed data, to model species and communities across relevant management scales.

2.5.6 Conclusions

The work of this chapter lends support to the hypothesis that the structuring of temperate reef fish communities is dictated by a spatially hierarchical series of ecological processes ranging from latitudinal scale climatic and biogeographical responses down to localised disturbance, competition and predation influences of finer scale physical habitat structure. It also suggest the potential for quantitative measures of physical habitat to be applied as predictors of temperate reef fish community structure across temperate regions of Australia. This will require further manipulative investigation to determine the separate ecological roles played by components of the biotic and abiotic components of reef habitats and require further understanding of species-specific responses to these components across their full habitat scales and extents. In addition there is a need for further research into the application of remotely sensed measures of habitat and how habitat structure interacts with the effects of

protection from fishing if the influence of physical habitat structure is to be effectively incorporated into spatial marine planning solutions.

Associations between fish communities and fine-scale, physical habitat structure on temperate inshore rocky reefs.

3.1 Abstract

Understanding the key habitat drivers of spatial variation in the community structure of temperate reef fishes is vital to identifying cost effective surrogate metrics that will improve predictions of biodiversity patterns for marine spatial planning and management. This study investigated the components of physical habitat structure which best explained fish community similarity patterns, diversity and individual species distributions and abundance at scales from metres to kilometres across temperate coastal rocky reefs of southeastern Tasmania. The results identified the importance of exposure and its relationship with biogenic structure, in explaining significant proportions of associated reef fish community similarity and diversity patterns. Towards finer scales of investigation, the addition of other physical variables along with exposure and biogenic cover improved model R^2 results suggesting an increasing importance of physical habitat heterogeneity and complexity towards finer ends of the scales investigated. Reef fish community similarity varied in a spatially hierarchical fashion with greater variability at larger scales, however the greatest variation in the reef fish community similarity for each location was at the level of survey replicates, suggesting high temporal variability in the community assemblages between surveys. No significant effects of protection from fishing could be identified. Reef fish community similarity varied more in response to habitat structure between sites and temporally between replicates than in response to reserve effects, suggesting that any variability in the community similarity resulting from reserve effects across Tasmanian reefs may be difficult to discern from that of pre-existing fine scale spatial and temporal

variability. Individual species occurrence and abundance were found to respond in widely different, species-specific ways to physical environmental and habitat variables. When occurrence was modelled independently for each species, the importance of fetch exposure and biogenic cover were the most important for some species (e.g. *Notolabrus fucicola* and *Neodax balteatus*), while the importance of habitat complexity, refuge space and substratum cover were increasingly evident for others. Models of individual species abundance were able to explain slightly larger proportions of the variability than those of species occurrence but generally the same variable/s were largely responsible for explaining both the occurrence and abundance of an individual species. My findings support a hypothesis that the structuring of reef fish communities is influenced by a compounded hierarchy of spatial processes from regional scale influences of exposure to localised influences of physical habitat complexity and heterogeneity affecting competition, predation, disturbance and recruitment. These results identify patterns and scales of fish-habitat association from which further questions and hypotheses about processes can be generated and highlight the importance of incorporating multiple spatial scales of investigation into future studies of temperate reef fish-habitat relationships.

3.2 Introduction

Habitat heterogeneity and complexity are important factors responsible for structuring the associated faunal and algal compositions of marine communities. They are fundamental components of the physical environment, influencing the availability of food, shelter and refuge from predation for many marine organisms (Hixon and Beets, 1993, Almany, 2004, Caddy, 2007). A number of studies have considered physical and structural features that contribute to the substratum heterogeneity and complexity of sub-tidal reefs and how they influence associated algal (Dahl, 1973, Harlin and Lindbergh, 1977, Ault and Johnson, 1998, Toohey et al., 2007, Toohey and Kendrick, 2008), invertebrate (Lapointe and Bourget, 1999, Beck, 2000, Alexander et al., 2009) and fish community assemblages (Luckhurst and Luckhurst, 1978, Roberts and Ormond, 1987, Garcia-Charton and Pérez-Ruzafa, 2001, Harman et al., 2003, La Mesa et al., 2004, Gratwicke and Speight, 2005a, Gratwicke and Speight, 2005b).

In recent years a growing paradigm shift in conservation management attitudes, away from traditional single species management approaches towards more holistic, ecosystem-based approaches of biodiversity conservation in the marine environment has taken place (Nevill, 2010). The magnitude of sampling effort required to sufficiently quantify marine biodiversity across whole ecosystems is generally prohibitive at broad management scales which has led to the development of more time and cost effective surrogate approaches utilising physical habitat data (Huang et al., 2010, McArthur et al., 2010). The influence of environmental variables on reef fish community structure varies across a hierarchical gradient of scales (Morton and Gladstone, 2011). Consequently, the utility of various environmental variables as surrogates to explain or predict reef fish community structure will also vary depending on the scales at which they are considered (Guisan and Thuiller, 2005). Gradual patterns in

species distributions over large scales and coarse resolutions tend to be correlated with indirect climatic gradients, whereas patchy, small scale distributions at fine resolution are generally the result of direct environmental gradients and patchy resource distributions associated with local topographic variation and habitat fragmentation (Guisan and Thuiller, 2005, Scott, 2002). Developing surrogate approaches to mapping and predicting biodiversity in the marine environment requires an understanding of the specific scales at which species and communities respond to components of their physical habitats. Most attempts to do this have focused on the spatial management of marine resources over relatively large scales, nevertheless marine communities are also exploited at local to regional scales, from metres to kilometres and marine researchers and managers are becoming increasingly aware of the need for effective spatial management of marine resources at much finer scales than traditionally studied (Williams and Bax, 2001).

The findings of other researchers have shown that habitat type and variability are important determinants of marine protected area (MPA) efficacy (Friedlander et al., 2007, Claudet et al., 2010, Hamilton et al., 2010) and are therefore important factors to be considered when determining the effectiveness of marine reserves (García-Charton et al., 2004, Friedlander et al., 2007, Harborne et al., 2008, Huntington et al., 2010). The magnitude of reserve effects will be likely to vary in relation to the spatial variability of the habitat structure that they protect but this variability is rarely accounted for by most attempts to assess reserve efficacy (Huntington et al., 2010). Thus, the reason many prior studies have failed to identify unambiguous differences between protected and fished areas may be linked to problems of distinguishing natural spatial and temporal variability of fish assemblages from the effects of management measures (García-Charton et al., 2004). Disentangling the separate importance of natural spatial and temporal habitat variability effects from those of MPAs is vital for the

effective implementation of future marine spatial planning. To achieve this, scientists need prior understanding of how specific aspects of the physical environment structure temperate reef fish communities and at which scales they become relevant.

Few studies have been carried out which specifically attempt to investigate how assemblage structure and diversity of temperate reef fish communities respond to variations in components of the physical structure and complexity of their associated habitats. Most studies in this field have attempted to identify single species or community-habitat relationships at broad spatial scales across different habitat types (Leathwick et al., 2006, Iampietro et al., 2008, Knudby et al., 2010, Monk et al., 2010) and therefore sample the biota and habitat at appropriately coarse scales to ensure detection of patterns. This was a single habitat study, conceived to investigate the relationships between fine scale physical structure and variability in fish community structure that is often observed across shallow temperate rocky reef habitats at scales of 10's -100's of metres (M.Cameron pers. obs.). Therefore the sampling scale was by necessity particularly fine scale (relative to other similar studies) to ensure quantitative detection of community structure patterns. This fine scale approach risks missing broad ranging and rarer species, therefore a temporal replication component was applied to the sampling strategy to maximise the chances of observing these species.

This study investigates fine-scale community structure, diversity and individual species abundance and occurrence responses of temperate reef fish communities along the eastern coast of Tasmania to aspects of their surrounding habitat structure. A variety of directly measured and indirectly modelled environmental and habitat variables were investigated across a range of ecologically proximal scales (10's – 100's m) in an attempt to elucidate the assemblage structure responses of inshore reef fish communities to their surrounding habitats. Underwater visual censuses were employed to sample reef fish communities across blocks

and sites, inside and outside marine reserves protected from fishing. This approach allowed me to investigate the effects of physical habitat structure and marine reserve effects across a range of spatial scales. This study attempted to test three general hypotheses. Firstly that fish community structure will vary in response to variability in the physical characteristics, heterogeneity and complexity of the reef habitat. Secondly that physical variables important in explaining fish community assemblage structure will vary with the spatial scale at which they are measured and thirdly that the response of fish communities to reserve effects will be smaller relative to the effect of physical habitat variables.

This chapter compliments and advances on the findings of chapter two of this thesis into the assemblage structure responses of temperate reef fish populations to their surrounding physical environments at larger bioregional scales across South and Western Australia and Tasmania. Combined, these multi-scale studies provide marine resource managers and scientists with specific insight into the important physical components of the environment structuring temperate reef fish communities around Australia across a range of ecologically relevant scales and generates further hypotheses regarding the specific ecological mechanisms and physical variables affecting communities and individual species of temperate reef fishes.

3.3 Methods

3.3.1 Study sites

Twelve study sites were positioned on areas of sub-tidal rocky reef inside and around the vicinity of three marine reserves, along the south-eastern and eastern coasts of Tasmania, Australia. The inshore reef across this region is predominantly dominated by high densities of the canopy-forming laminarian algae, *Ecklonia radiata* with a diverse algal understory and communities of sessile invertebrates including hydrozoans, bryozoans, ascidians and sponges (Andrew, 1999). Sites were selected inside and outside marine reserves to allow a control-impact assessment of marine protection. Four sites were located inside and around the vicinity of Ninepin marine reserve at the mouth of the Huon river (Ninepin Point, Huon Island, Garden Island and Charlotte Cove Point), a further four sites were located inside and around the vicinity of Tinderbox marine reserve at the northern end of the D'Entrecasteaux Channel (Tinderbox Point, Pearsons Point, Lucas Point and Dennes Point) and a final four sites were located in and around the vicinity of Maria Island marine reserve at the northern end of the Mercury Passage (Holme Point, Spring Beach, Painted cliffs and Return Point). All three marine reserves were declared and enforced in 1991 under the *National Parks and Wildlife Act 1970*.

The Maria Island MPA (Figure 3.1) covers an area of 15 km², extending up to one kilometre offshore. Fishing or setting of fishing gear is prohibited within a no-take reserve approximately 8 km² along the north-western side of the island. Within the remaining north-eastern portion of the MPA recreational fishing of all types is permitted. The north-western coastline of Maria Island, the majority of which makes up the no-take portion of the MPA, is made up of a mixture of dolerite and sandstone reefs and cliffs interspersed with sandy bays.

Reef extends out to a depth of approximately fifteen metres where it meets sand, grading to silty sand between 20 and 30 m and to fine silt at depths beyond 30 m.

The Tinderbox no-take marine reserve (Figure 3.2) covers an area of 1.4 km², extending 200-300 metres offshore. No fishing or setting of fishing gear of any type is permitted in any part of the reserve. A mix of sandstone outcrops and fractured dolerite reef extends almost continuously around the Tinderbox headland to a depth of approximately ten metres where the substratum then becomes sand and broken shell, interspersed in places with small embayment's and channels. The surrounding seabed is formed of soft sediment shoals out to a depth of approximately fifty metres (Barrett et al., 2001, Nichol et al., 2009).

The Ninepin marine reserve (Figure 3.3) covers an area of approximately 7.3 km², extending approximately a kilometre offshore. No fishing or setting of fishing gear of any type is permitted in any part of the reserve. The coastal geology of this area is dominated by dolerite rock, which forms most of the headlands, islands and rocky offshore reefs out to approximately 15 m depth. Sand intersperses the reef and extends to depths of 20 m, grading to silty sand between 20 and 30 m and to fine silt at depths beyond 30 m (Barrett et al., 2001). The area is heavily influenced by tannin runoff from the Huon River with the depth of the tannin layer varying heavily throughout the year depending on rainfall. This layer can be almost absent during dry periods and extend down to twelve metres or more after heavy rainfall and run off from the catchment resulting in near zero visibility.

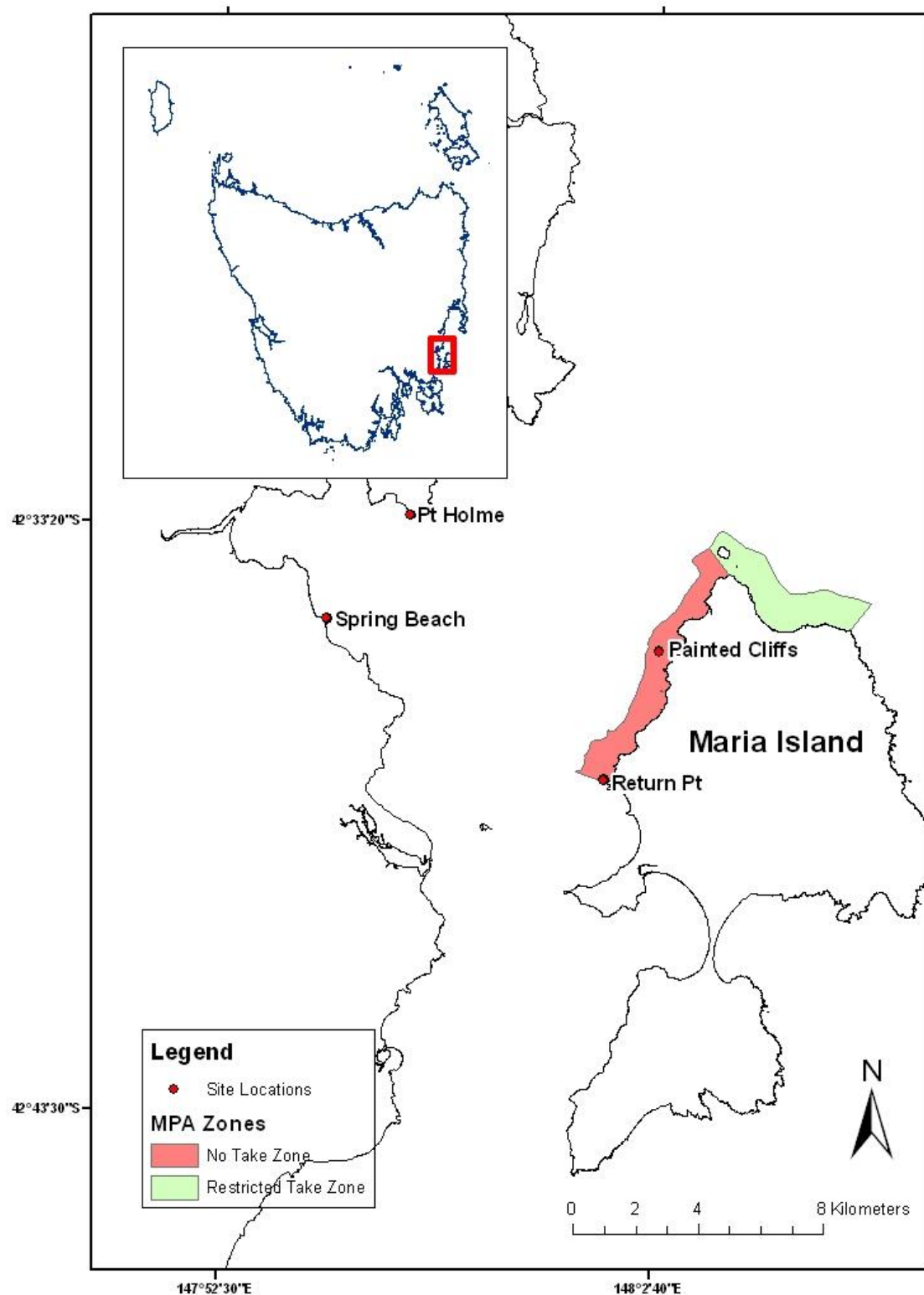


Figure 3.1. Sites across the Maria Island marine reserve study location.

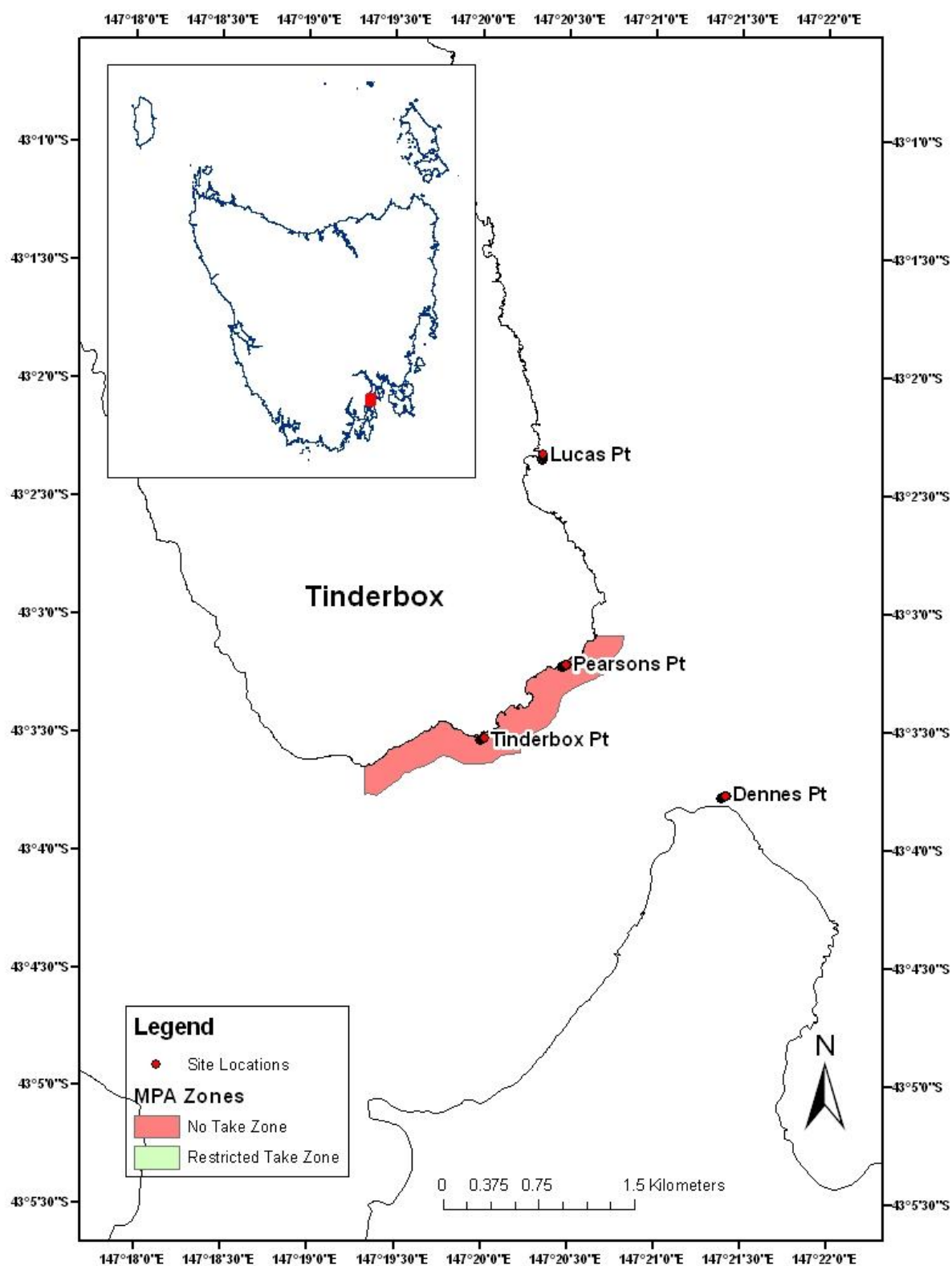


Figure 3.2. Sites across the Tinderbox marine reserve study location.

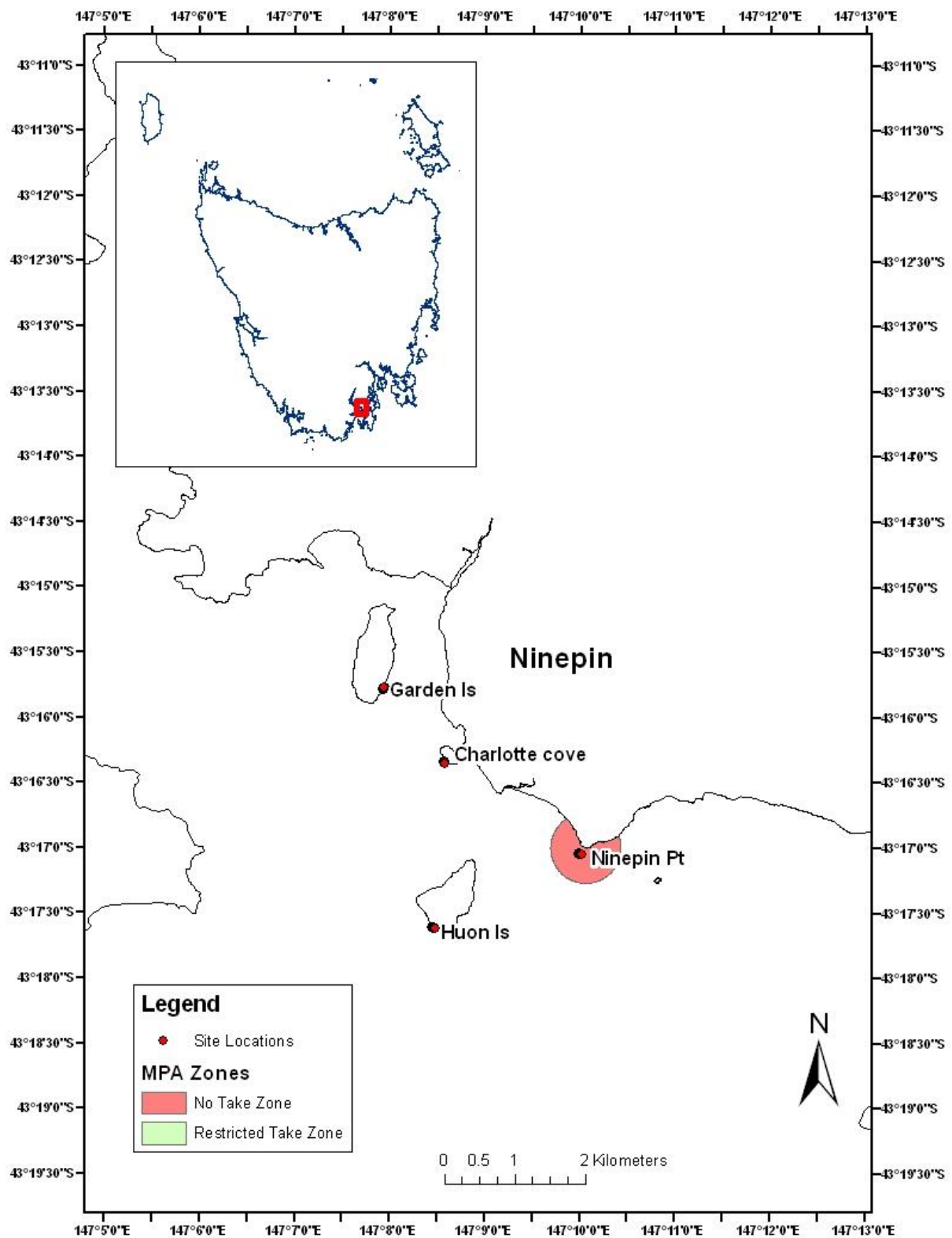


Figure 3.3. Sites across the Ninepin marine reserve study location.

3.3.2 Fish community survey

At each site a single, 10 m x 50 m (500 m²) belt transect was positioned parallel to and within 100 m of the shore inside the 5-10 m depth contour. Each transect was subdivided into twenty 5 x 5 m (25 m²) blocks either side of the transect centreline and marked at the beginning and end with small subsurface buoys (in addition to recording accurate GPS location fixes from a surface vessel) to accurately re-locate the beginning and end of each transect between replicate surveys. Sites were surveyed on open-circuit SCUBA by a two person dive team. Each site was separately surveyed for fish and algal assemblages and physical habitat structure. Fish species and abundance were recorded within each separate 25 m² block, either side of the transect line by a single observer swimming approximately 2.5 m to one side of the transect centreline (

Figure 3.4). Each fish transect was surveyed a total of five times between February 2010 and February 2011 to provide sufficient replication to detect spatial patterns.

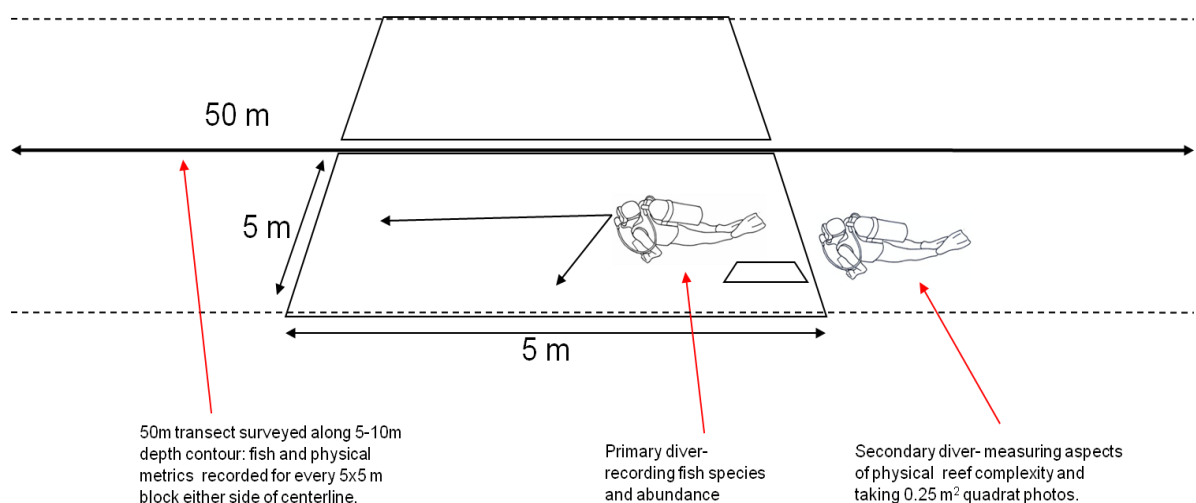


Figure 3.4. Fish transect survey method.

3.3.3 Physical habitat and biogenic cover surveys

A number of physical measures of structure and complexity were recorded separately within each of the 25 m² blocks within each site transect using methods adapted from Alexander *et al* (2009) and Wilding *et al* (2007, 2009) (See Table 3.1 for a complete list and description of variables). Within each 25 m² block separate estimates of rugosity and fractal complexity were recorded along a line 2.5 metres parallel to each side of the transect centreline using a rotating wheel method (Wilding *et al.*, 2007, Wilding *et al.*, 2009). This method uses a distance-wheel tool with four interchangeable wheels of varying circumferences (260 mm, 500 mm, 1000 mm and 2000 mm) to allow scale-dependent measures of distance. It is then possible to calculate a measure analogous to the fractal dimension by log : log plotting the relationship between the wheel circumference and the distance run along the transect over the surface, as one minus the slope of the log transformed contour distances recorded from each wheel run along the transect (Wilding *et al.*, 2007). A rugosity index was calculated as a simple ratio of the linear horizontal distance of the transect across each block (5 m) over the contour distance run by the smallest measuring wheel (260 mm circumference), calculated as $1 - (\text{contour distance (mm)} / 5000)$. This measure of rugosity gives an intuitive relationship between increasing reef structure with increasing rugosity index, differing slightly in its calculation from the original rugosity index developed by Luckhurst and Luckhurst (1978).

Visual estimates of substratum composition as a percentage cover of contiguous consolidated bedrock, sand, cobbles (<0.2 m), small boulders (0.2 - 0.5 m), medium boulders (0.5 - 1.5 m) and large boulders (>1.5 m) were recorded in five randomly selected 1x1 metre quadrats within each 25 m² block. Counts were made of available refuge space of four size categories based on minimum aperture dimensions of 1–5 cm, 6–15 cm, 16–50 cm and >50 cm from a working definition of a predator refuge developed by Alexander *et al.* (2009) whereby at least

one of the meeting angles of three or more planes of the substratum creates an angle of less than 90 degrees or the meeting of two planes of the substratum forms an angle of 45 degrees or less. Measures of reef refugia were categorised by visually estimating a refuge's minimum aperture size and the density of each size category of refuge within five randomly selected 1x1 metre quadrats within each 25 m² block.

Within each block five replicate, randomly positioned 0.25 m² quadrats were photographed and later analysed using the CPCe software (Kohler and Gill, 2006) to determine the structural make-up of biogenic cover within each block. This was recorded as per cent cover of the six categories; upper canopy algae, lower canopy algae, turfing algae, encrusting algae, sessile invertebrates and un-vegetated substratum.

No empirical data for wave exposure across the survey sites was available at the necessary scales, therefore a simple modelled indices of average and maximum fetch distance were calculated as proxies for exposure, for each of the two hundred and forty blocks surveyed using the wave exposure modelling toolbox GREMO for ArcGIS (Pepper, 2009). Fetch distances were calculated at 48 equal intervals through 360° from the centroid of each block and averaged to give a single index of relative wave exposure between sites. The single greatest fetch distance (out to a maximum distance of 650 km) from the same 48 equal intervals through 360° from the centroid of each block was taken as the maximum fetch exposure.

The physical variables measured at each site were reduced into five variable sets (Table 3.1). This eased analysis by eliminating potential problems of inter-correlations between per cent cover variables. By analysing the physical data in sets it also aided interpretation of analysis by allowing explicit examination of the proportion of variation in the fish abundance data

explained by habitat heterogeneity and complexity variables independently from that explained by the spatial variables (Anderson et al., 2008).

Table 3.1. Physical habitat variables and descriptions.

Variable set name	Variables included	Description and method
Habitat substratum	Consolidated bedrock, Large boulders (>1.5 m), Medium boulders (0.5 – 1.5 m), Small boulders (0.2 – 0.5 m), Cobbles (<0.2 m) and Sand.	Average percentage of various dominant substratum types measured visually within five randomly selected 1x1 metre quadrats within each 25 m ² block
Complexity	Rugosity	Rugosity sampled across each block (2.5 m either side of the transect centreline) using a 260 mm circumference rotating wheel measure and calculated as 1-(contour distance measures/5000).
	Fractal dimension	Calculated using a rotating wheel method across each block (2.5 m either side of the transect centreline) adapted from Wilding et al. (2007) and calculated as 1 - the slope of the regression line for log (wheel diameter) vs log(contour distance measures).
Refuge space	Small (1-5cm), medium (6-15cm), large (16-50cm) and very large (> 50cm) refuge spaces.	Average density of 4 size categories of refuge spaces (as defined by Alexander et al. (2009).) within five randomly selected 1x1 metre quadrats within each 25 m ² block.
	Refuge diversity	Number of refuge size categories recorded in each block (i.e 1- 4)
Biogenic cover	Upper canopy algae, Lower canopy algae, Turfing algae, Encrusting algae, Sessile invertebrates and Un-vegetated substrate.	Average percentage cover of six categories of dominant biogenic reef cover analysed from five replicate 0.25 m ² quadrat photographs within each 5 x5 m block.
	<i>Ecklonia</i> density	Average density of <i>Ecklonia radiata</i> stipes within five randomly selected 1x1 metre quadrats within each 25 m ² block
	<i>Macrocystis</i> density	Count of individual <i>Macrocystis pyrifera</i> plants within each 5 x5 m block.
Exposure	Average Fetch Exposure	Average fetch distance calculated from 48 equal intervals through 360° from the centroid of each block out to a maximum distance of 650 km's.
	Maximum fetch exposure	The maximum fetch distance out to a maximum of 650 km's modelled from each block.

3.3.4 Community similarity modelling

Multivariate analyses of reef fish community data were carried out using routines from the *R* and PRIMER 6.1.11 PERMANOVA+ software packages (Clarke and Gorley, 2006). The ‘*PERMANOVA+ for PRIMER*’ manual (Anderson, 2001, Anderson et al., 2008) and ‘*Change in Marine Communities*’ texts (Clarke and Warwick, 2001) provide further, detailed descriptions and explanations of the following statistical approaches and analysis routines applied.

The reef fish abundance data for each survey were, $\log(x+1)$ transformed, converted to Bray-Curtis measures of similarity and used to construct a resemblance matrix between all sample replicates of the 240 sample blocks for all twelve sites across the three locations. The Bray-Curtis coefficient is a commonly applied similarity measure in ecological studies of multispecies communities. It is a robust measure that has the advantage over other forms of similarity measures of being easily interpretable, taking a value of 100 (when two samples are identical) to zero (when two samples have no species in common). Variability in the reef fish community structure was investigated using a nested PERMANOVA (permutational MANOVA) test to identify significant differences between protected and un-protected reef fish assemblages at varying spatial scales. The null-hypothesis that there was no difference in the reef fish community assemblage between locations, sites, blocks and marine reserve status was tested. PERMANOVA is a routine for testing the response of multivariate data to one or more factors, on the basis of a resemblance measure, with the use of permutational methods (Anderson et al., 2008). Community similarity was examined with a nested hierarchical design including reserves and non-reserves (two levels, fixed, within locations), sites (two levels, random, within status) and blocks (twenty levels, random, within sites) (Figure 3.3).

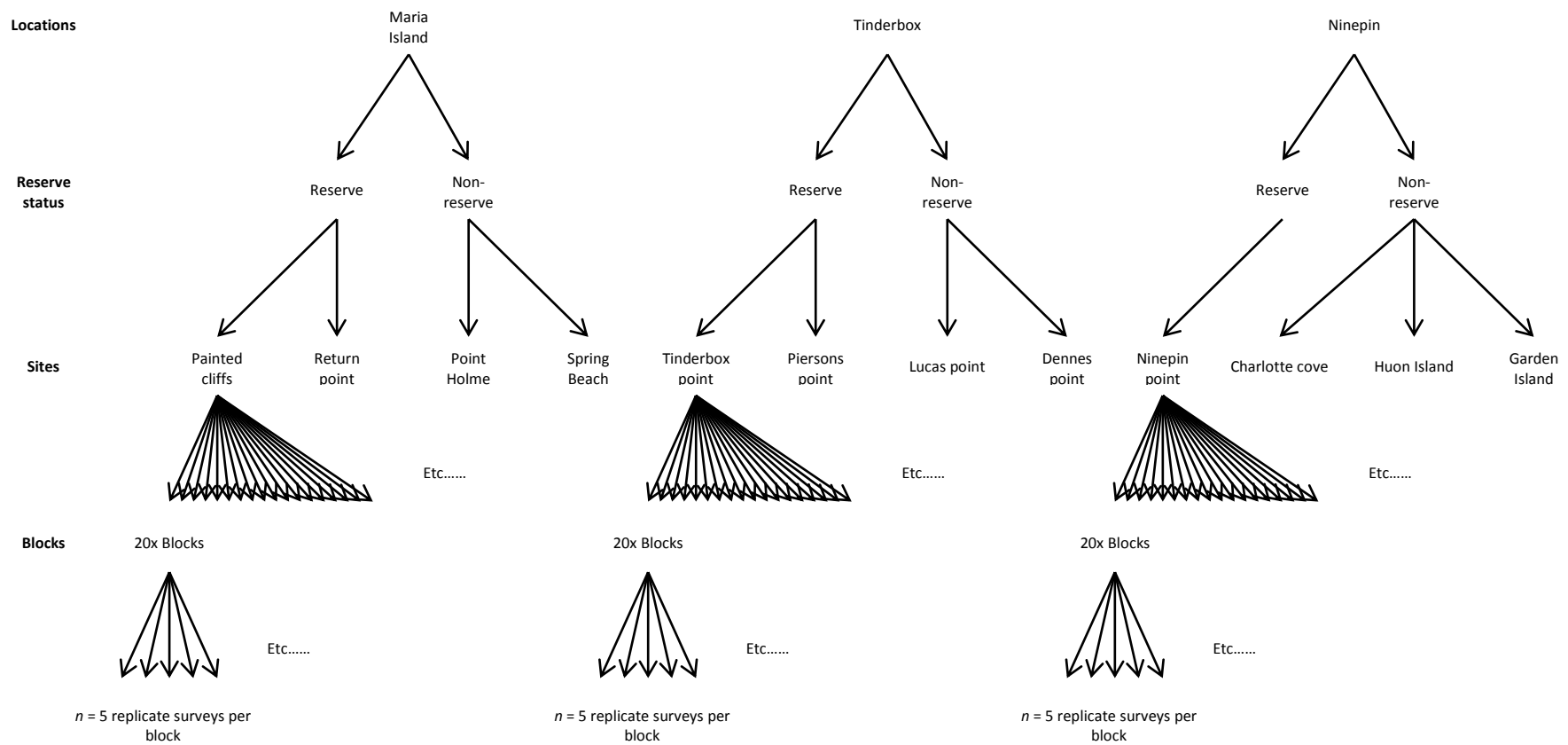


Figure 3.5. Nested PERMANOVA design.

DISTLM (distance-based linear modelling) and dbRDA (distance-based redundancy analysis) were used respectively to model and visualise the variability in reef fish communities between locations and sites in relation to an optimal number of the physical measures of habitat structure. The reef fish abundance data for each survey were averaged for each block, $\log(x+1)$ transformed, converted to Bray-Curtis measures of similarity and used to construct a resemblance matrix between all 240 sample blocks for all twelve sites across the three locations. DISTLM is a routine for modelling the relationship between the variation in a multivariate dataset (as described by a resemblance matrix) and one or more predictor variables. The procedure allows the construction of explanatory models using a number of common selection criteria and procedures, and calculates *P*-values of statistical significance using permutational methods for testing null-hypotheses of no relationship between response and predictor variables (Anderson et al., 2008). dbRDA is a constrained ordination technique to visualise the fitted values from multivariate regression models. The strength and direction of the strongest correlations between the individual physical variables (identified in the proceeding DISTLM) and each of the dbRDA axes were visually interpreted with vector overlays calculated from the multiple partial correlations between each variable and the dbRDA axis scores. Each vector was interpreted as the effect of that particular variable on the construction of the ordination image; the longer the vector, the larger the association of the variable, in the direction of the associated axes.

DISTLM analysis was carried out using the 'Best' model selection procedure and the 'Akaike's information criterion' (AIC) methods. The 'Best' model selection procedure examines all possible combinations of predictor variables and constructs optimal models based on the lowest criterion selection values. The AIC approach aims to maximise parsimony in the final model selection by identifying the simplest model (with as few

predictor variables as possible) with the greatest explanatory power. An initial ‘marginal test’ identified the relationship of each individual physical variable with the community similarity data.

3.3.5 Individual species response and diversity modelling

Occurrence, mean abundance, and three indices of community diversity (calculated from observed abundance and occurrence), averaged across blocks and were used to relate the reef fish community response to physical habitat structure. The abundance for each species surveyed were averaged across replicate surveys for each of the two hundred and forty 25 m² blocks and log(x+1) transformed to reduce differences in scale among the species variables, reduce the contribution of highly abundant species and ensure the contribution of rarer species. Species occurrence (i.e. presence/absence), was determined for each of the two hundred and twenty 25 m² blocks. Three measures of diversity were calculated from the mean species abundance data for each of the two hundred and forty 25 m² blocks to reduce the complexity of the multispecies assemblage data into single, easily interpretable univariate response variables. Species richness (S) was calculated as the total number of different species recorded within each block. Margalef’s species richness (d) is a measure of the number of species present for a given number of individuals and was calculated as:

$$d = (S-1) / \log N$$

where N is the total abundance of individuals. The Shannon-Wiener diversity index (H) is a measure which characterises communities by the total number of species in relation to the proportion each species makes to the overall abundance and quantifies the probability of predicting the species of an individual chosen at random from a dataset. It was calculated as:

$$H = -\sum_i p_i \log(p_i)$$

where p_i is the proportion of the total abundance arising from the i th species.

Individual species abundances and occurrence along with three measures of diversity were modelled in relation to the direct measured reef-habitat metrics using boosted regression trees (BRTs) (Elith et al., 2008). Analyses were carried out using libraries and functions in the R statistics software, version 2.13.1. Only species with greater than 10% occurrence were modelled in order to avoid problems of over-fitting. Of the thirty-five species encountered across all surveys, thirteen species had sufficient numbers of observations to allow individual modelling of their occurrence and abundances. BRT models were fitted using the *gbm* and *gbm.step* packages in R (Elith et al., 2008). Construction of effective BRT models were based on the suitable parameters values of learning rate, tree complexity and bag fraction. The learning rate is a shrinkage parameter which determines the contribution of each tree to the growing model, tree complexity refers to the number of nodes permitted within each tree and controls the level of interactions fitted and the bag fraction is the proportion of the full data selected at each iteration. Together these three parameters determine the number of trees required for optimal prediction (see Elith et al., (2008) for further explanation). Tree complexity, bag fraction and learning rate were initially set at 2, 0.5 and 0.001 respectively following the ‘rule of thumb’ parameter suggestions set out in Elith et al. (2008) to ensure successful model runs with excess of 1000 trees. Abundance of individual species and diversity measures were modelled using a Gaussian error distribution, and species occurrences (i.e. presence or absence) were modelled using a Bernoulli (binomial) error distribution. Measures of relative influence of each predictor term in the BRT models were calculated using script functions included in the *gbm.step* package in R (Elith et al., 2008). For each of the fitted models, D^2 values were calculated as a measure of explained deviance for comparison, where: $D^2 = 1 - (\text{residual deviance}/\text{total deviance})$.

Where possible, analyses were carried out at three separate spatial scales (Region, Location and Site) to identify if reef fish community structure and diversity responded differently to physical habitat variables depending on the scale investigated. At the largest scale community similarity was modelled across the entire region, at an intermediate scale within each of the three locations (Maria Island, Tinderbox and Ninepin) and at the finest scale within each of the twelve sites. Measures of diversity were analysed at the Region and Location scales but due to relatively low numbers of observations and associated limitations in the modelling approaches applied, individual species occurrence and abundances could not be accurately modelled across all three scales and therefore were only analysed at the largest, regional scale.

3.4 Results

3.4.1 General findings

A total of 32,320 individual reef fish observations were recorded across all three survey locations throughout the total survey period, comprising a total of thirty-five species from thirty-one genera, twenty-two families, six orders and two classes (Table 3.2). For the Maria Island sites, the bullseye, *Pempheris multiradiata* was the most numerically abundant species encountered, comprising 70.5% of the total abundance of reef-fishes surveyed, followed by the southern hulafish, *Trachinops caudimaculatus* (11.1%), the bluethroat wrasse, *Notolabrus tetricus* (7.4%), plus all other species combined (11%). For the Maria Island sites, bluethroat wrasse, *Notolabrus tetricus* had the highest proportion of occurrence, occurring in 96.3% of blocks surveyed, followed by the purple wrasse, *Notolabrus fucicola* (50%) and the senator wrasse, *Pictilabrus laticlavius* (48.8 %). The remaining species all occurred in less than 30% of the blocks surveyed (Figure 3.6a). For the Tinderbox sites, the southern hulafish, *Trachinops caudimaculatus* was the most numerically abundant species encountered, comprising 72% of the total abundance of reef-fishes surveyed, followed by the bullseye, *Pempheris multiradiata* (17.9%), the bluethroat wrasse, *Notolabrus tetricus* (6.2%) plus all other species combined (3.9%). For the Tinderbox sites, bluethroat wrasse, *Notolabrus tetricus* had the highest proportion of occurrence, occurring in 87.5% of blocks surveyed, followed by the southern hulafish, *Trachinops caudimaculatus* (41.3%), and the senator wrasse, *Pictilabrus laticlavius* (37.5 %). The remaining species all occurred in less than 35% of the blocks surveyed (Figure 3.6b). For the Ninepin sites, the southern hulafish, *Trachinops caudimaculatus* was the most numerically abundant species encountered, comprising 92.4% of the total abundance of reef-fishes surveyed, followed by the bluethroat wrasse, *Notolabrus tetricus* (3.5%), the barber perch, *Caesioperca rasor* (1.8%), plus all other species combined (2.3%). For the Ninepin sites, bluethroat wrasse, *Notolabrus tetricus* and the southern

hulafish, *Trachinops caudimaculatus* had the highest proportions of occurrence, with both species occurring in 100% of blocks surveyed, followed by the barber perch, *Caesioperca rasor* (73.8%) and the little weed whiting, *Neoodax balteatus* (55%) . The remaining species all occurred in less than 50% of the blocks surveyed (Figure 3.6c).

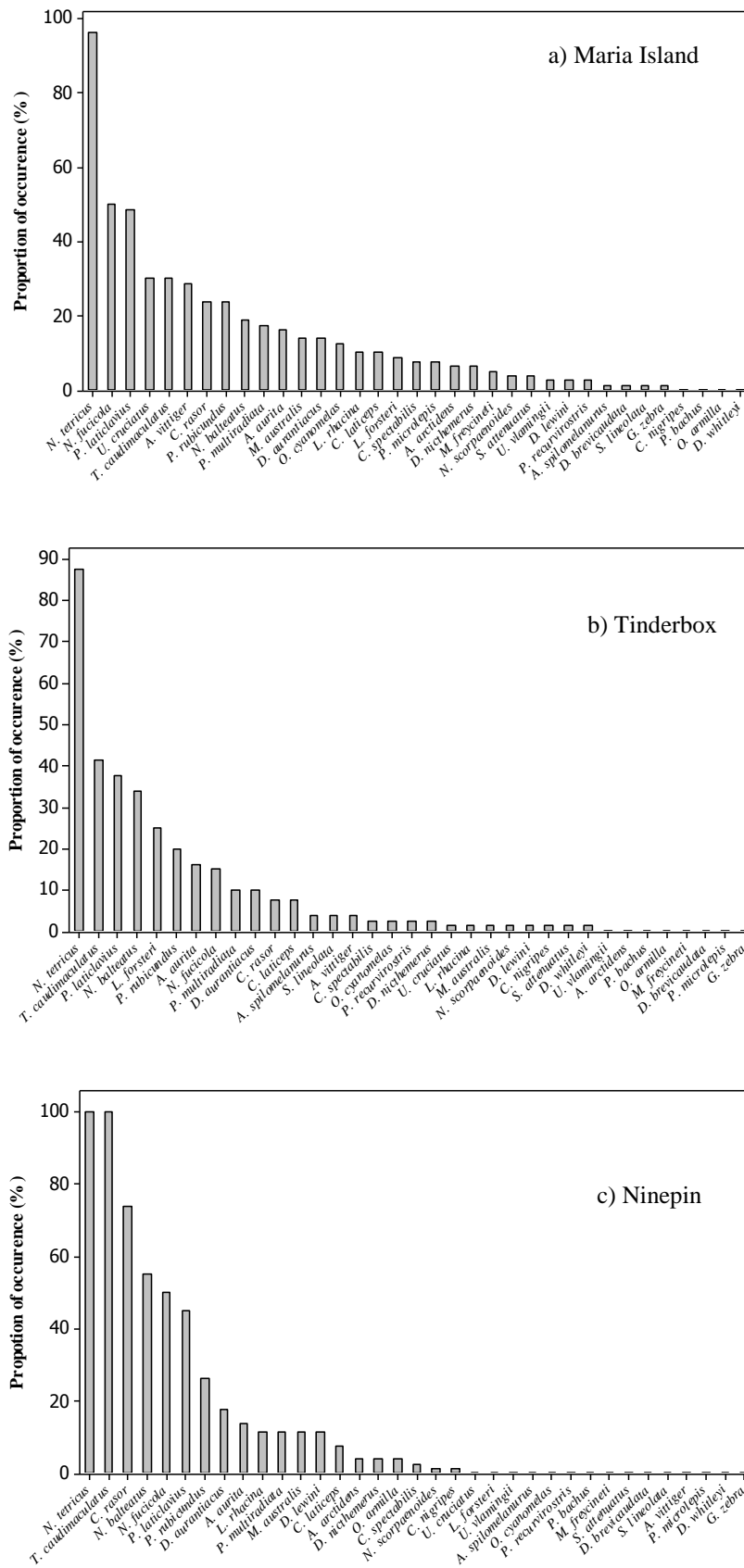


Figure 3.6. Proportion of species occurrence across all blocks surveyed for each of the three study locations.

Table 3.2. Names and taxonomic membership of reef fish species encountered across all surveys.

Species	Common name	Class	Order	Family
<i>Acanthaluteres spilomelanurus</i>	Bridled Leatherjacket	Actinopterygii	Tetraodontiformes	Monacanthidae
<i>Acanthaluteres vittiger</i>	Toothbrush Leatherjacket	Actinopterygii	Tetraodontiformes	Monacanthidae
<i>Aplodactylus arcidens</i>	Marblefish	Actinopterygii	Perciformes	Aplodactylidae
<i>Aracana aurita</i>	Shaw's Cowfish	Actinopterygii	Tetraodontiformes	Aracnidae
<i>Caesioperca rasor</i>	Barber Perch	Actinopterygii	Perciformes	Serranidae
<i>Cephaloscyllium laticeps</i>	Draughtboard Shark	Elasmobranchii	Carcharhiniformes	Scyliorhinidae
<i>Cheilodactylus nigripes</i>	Magpie Perch	Actinopterygii	Perciformes	Cheilodactylidae
<i>Cheilodactylus spectabilis</i>	Banded Morwong	Actinopterygii	Perciformes	Cheilodactylidae
<i>Dasyatis brevicaudata</i>	Smoothback ray	Elasmobranchii	Rajiformes	Dasyatidae
<i>Dinolestes lewini</i>	Longfin Pike	Actinopterygii	Perciformes	Dinolestidae
<i>Diodon nichthemerus</i>	Porcupine fish	Actinopterygii	Tetraodontiformes	Diodontidae
<i>Dipturus whitleyi</i>	Whitley's skate	Elasmobranchii	Rajiformes	Rajidae
<i>Dotalabrus aurantiacus</i>	Pretty Polly	Actinopterygii	Perciformes	Labridae
<i>Girella zebra</i>	Zebrafish	Actinopterygii	Perciformes	Kyphosidae
<i>Latridopsis forsteri</i>	Bastard Trumpeter	Actinopterygii	Perciformes	Latridae
<i>Lotella rhacina</i>	Beardie Cod	Actinopterygii	Gadiformes	Moridae
<i>Meuschenia australis</i>	Brownstriped Leatherjacket	Actinopterygii	Tetraodontiformes	Monacanthidae
<i>Meuschenia freycineti</i>	Six-spined Leatherjacket	Actinopterygii	Tetraodontiformes	Monacanthidae
<i>Neodax balteatus</i>	Little Weed Whiting	Actinopterygii	Perciformes	Odacidae
<i>Neosebastes scorpaenoides</i>	Gurnard Perch	Actinopterygii	Scorpaeniformes	Neosebastidae
<i>Notolabrus fucicola</i>	Purple Wrasse	Actinopterygii	Perciformes	Labridae
<i>Notolabrus tetricus</i>	Bluethroat Wrasse	Actinopterygii	Perciformes	Labridae
<i>Odax cyanomelas</i>	Herring Cale	Actinopterygii	Perciformes	Odacidae
<i>Omegophora armilla</i>	Ringed Toadfish	Actinopterygii	Tetraodontiformes	Tetraodontidae
<i>Parma microlepis</i>	White ear	Actinopterygii	Perciformes	Pomacentridae
<i>Pempheris multiradiata</i>	Bigscale Bullseye	Actinopterygii	Perciformes	Pempheridae
<i>Pentaceropsis recurvirostris</i>	Longsnout boarfish	Actinopterygii	Perciformes	Pentacerotidae
<i>Pictilabrus laticlavus</i>	Senator Wrasse	Actinopterygii	Perciformes	Labridae
<i>Pseudolabrus rubicundus</i>	Rosy Wrasse	Actinopterygii	Perciformes	Labridae
<i>Pseudophycis bachus</i>	Red Cod	Actinopterygii	Gadiformes	Moridae
<i>Scorpi lineolata</i>	Silver Sweep	Actinopterygii	Perciformes	Kyphosidae
<i>Siphonognathus sp.</i>	Slender or Pencil weed whiting	Actinopterygii	Perciformes	Odacidae
<i>Trachinops caudimaculatus</i>	Southern Hulafish	Actinopterygii	Perciformes	Plesiopidae
<i>Upeneichthys vlamingii</i>	Blue-spotted Goatfish	Actinopterygii	Perciformes	Mullidae
<i>Urolophus cruciatus</i>	Banded Stingaree	Elasmobranchii	Rajiformes	Urolophidae

3.4.2 Reef fish community variability in response to marine protection.

The results of a nested PERMANOVA test indicated no significant variability in community structure between reserves and non-reserves could be identified over and above site and block level variability within any of the three study locations (

Table 3.3). Significant variability in community structure was identified among locations (on average 16.8% dissimilar), sites (on average 15% dissimilar) and blocks (on average 8.1% dissimilar). The greatest variation in the reef fish community structure was at the level of survey replicates which were on average 31.3% dissimilar (i.e. the proportion of variability attributed to the residual) suggesting high temporal variability in the community assemblages patterns. These results indicate that reef fish community structure varies more between the spatial scales of locations, sites and blocks and temporally across the three month survey period than it does between reserves and non-reserves themselves. This suggests that variability in the community structure resulting from reserve effects is likely to be very difficult to discern from that of natural fine scale spatial and temporal variability.

Table 3.3. Nested PERMANOVA test results for reef fish community structure between reserve and non-reserve status including estimates of components of variation. Community similarity is based on Bray-Curtis resemblance of $\log(x+1)$ transformed abundance. Significant p -value results are highlighted in bold.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique permutations	Estimate of variance	Proportion
Location	2	254710.00	127360.00	4.76	0.03	9954	282.70	16.81
Status(Loc)	3	80248.00	26749.00	1.14	0.38	9931	18.80	4.34
Site(St(Lo))	6	140440.00	23407.00	17.97	0.00	9907	225.40	15.01
Block(Si(St(Lo)))	228	297110.00	133.10	1.33	0.00	9533	65.85	8.12
Residual	939	919830.00	979.59				979.59	31.30
Total	1178	1785800.00						

3.4.3 Community structure modelling across regions.

DISTLM modelling (based on an AIC criteria and 'Best' selection procedure) across regional scales identified all five of the explanatory variable sets; complexity, biogenic cover, refuge space, substratum cover and exposure combined as the optimum model for the maximum explanation (43.2%) of reef fish community variability between samples (Table 3.4).

Marginal tests showed that all five variable sets explained significant proportions of the reef fish community variability between samples. The single 'Best' variable set was biogenic cover which on its own explained 24.1% of the reef fish community variability between samples. Figure 3.7 displays the dbRDA ordination of the resulting 'Best' DISTLM model. The first and second axes of the plot accurately depict 75.4% of the fitted model and 32.6% of the total variability in the data. In general, samples show fairly distinct groupings by location and site, indicating greater variability in the reef fish community structure between locations than within locations and between sites than within sites. Vector overlays calculated from the multiple partial correlations between the most highly correlated physical variables ($r \geq 0.3$) and the dbRDA axis scores illustrate the importance of each individual physical variable in explaining the variability in reef fish community structure. In agreement with the DISTLM analysis, the dbRDA vector overlays also highlighted aspects of biogenic cover (i.e. the proportional dominance of upper canopy algae and sessile invertebrates) as important in explaining the variability in the reef fish community structure between samples. They also highlighted the correlation of average fetch distance with the dbRDA axes, whilst marginal DISTLM results identified exposure as explaining only 14.1% of the variability in the reef fish community structure. Figure 3.8 a) - d) duplicate the dbRDA ordination from Figure 3.7 with variable bubble plot overlays of upper canopy cover, encrusting algae cover, sessile invertebrate cover and average fetch respectively to highlight the variability of each in relation to the pattern in the reef fish community structure between samples. A slight trend of

increasing per cent cover of upper canopy algae is evident from right to left across the ordination, with lower relative proportions across the Ninepin locations (GI, CP, NP and HI sites) (Figure 3.8a). The inverse of this trend is apparent for encrusting algae and sessile invertebrate cover with higher relative proportions of both at the Ninepin sites (Figure 3.8b and c). The trend in average fetch increasing from right to left across the ordination (Figure 3.8d) appears to mirror that of the upper canopy algae suggesting a possible association between exposure and canopy algae cover and an inverse association with encrusting algal and sessile invertebrate cover.

3.4.4 Community structure modelling across locations.

DISTLM (based on an AIC criteria and the 'Best' selection procedure) across the Maria Island sites identified three of the five explanatory variable sets; complexity, substratum cover and exposure combined as the optimum model for the maximum explanation of reef fish community variability between sites, explaining 45.2% (Table 3.5). Marginal tests showed that all five variable sets explained significant proportions of the reef fish community variability between samples. The single 'Best' variable set was exposure which on its own explained 26.9% of the reef fish community variability between samples. Figure 3.9 displays the dbRDA ordination of the resulting 'Best' DISTLM model. The first and second axes of the plot accurately depict 67.9% of the fitted model and 30.7% of the total variability in the data; samples appear to show groupings by site indicating greater variability in the reef fish community structure between sites than within sites. Vector overlays calculated from the multiple partial correlations between the most highly correlated physical variables ($r \geq 0.3$) and the dbRDA axis scores illustrate the importance of each individual physical variable in explaining the variability in the reef fish community structure. The vector overlays highlight maximum and average fetch distance as important in explaining the variability in the reef fish

community structure between samples, with higher average fetch exposure towards the Spring Beach site and maximum fetch exposure towards the Point Holme sites.

Table 3.4. DISTLM top five and overall ‘Best’ model results across regional scale inclusive of all three study locations. Models based on the highest AIC model criteria value. * denotes the most parsimonious model identified.

Significant marginal test results	Proportion	Best 1-5 variable and ‘Best’ overall model results
Complexity ($F=2.8217$, $p=0.0051$)	0.02	Biogenic cover ($AIC=1789.1$, $R^2=0.24135$)
	4	
Biogenic cover ($F=9.0667$, $p=0.0001$)	0.24	Biogenic cover + Exposure ($AIC=1772.7$, $R^2=0.30389$)
	1	
Refuge space ($F=5.2048$, $p=0.0001$)	0.10	Biogenic cover + Substratum cover + Exposure ($AIC=1758.4$, $R^2=0.37702$)
	1	
Substratum cover ($F=4.3603$, $p=0.0001$)	0.10	Biogenic cover + Refuge space + Substratum cover + Exposure ($AIC=1751.9$, $R^2=0.41888$)
	2	
Exposure ($F=19.136$, $p=0.0001$)	0.14	*Complexity + Biogenic cover + Refuge space + Substratum cover + Exposure ($AIC=1750.6$, $R^2=0.4317$)
	1	

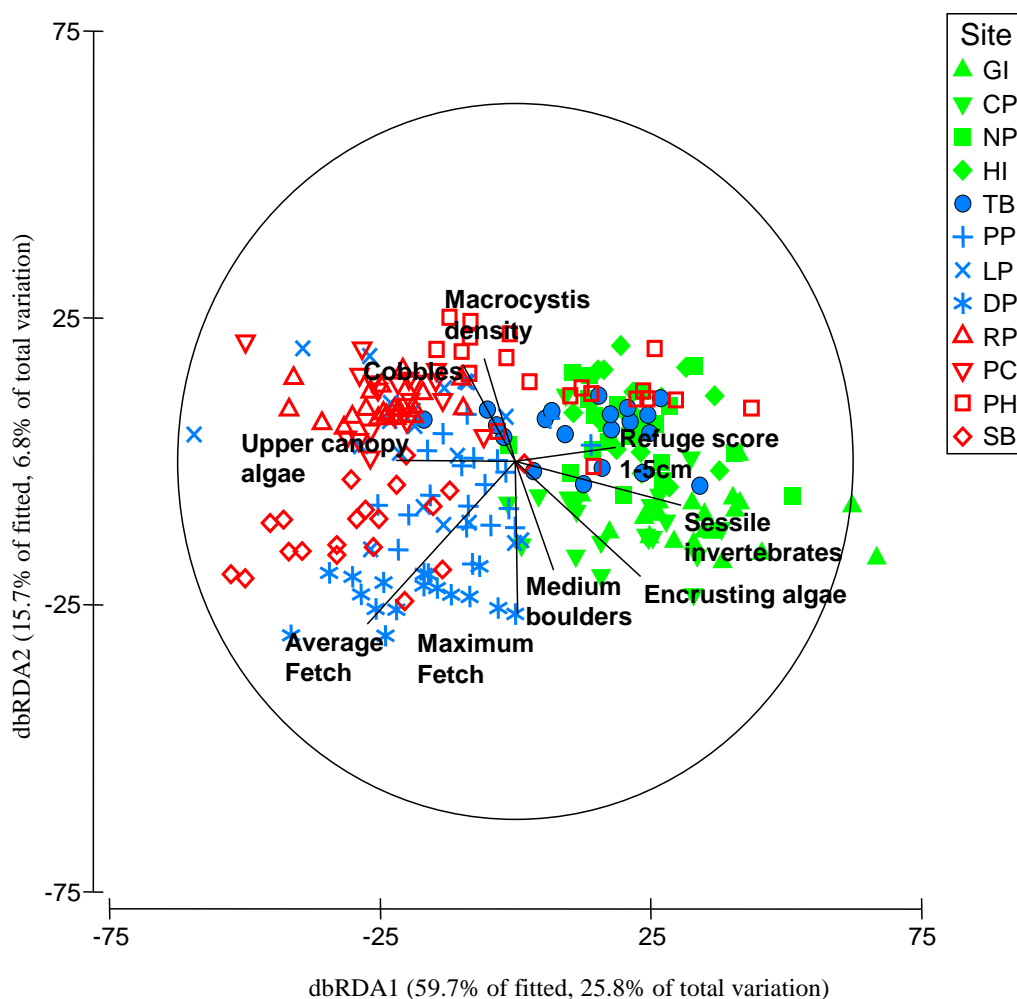


Figure 3.7. dbRDA ordination across all locations and sites identifying the greatest variation through the reef fish community dataset (log(x+1) transformed) for the ‘Best’ fitted DISTLM model, overlaid with the multiple partial correlation vectors ($r \geq 0.3$) of the individual physical variables. Sample blocks are colour coded by location: Green = Ninepin, Blue = Tinderbox and Red = Maria Island. Sites are denoted by symbol: Garden Island (GI), Charlotte cove point (CP), Ninepin point (NP), Huon Island (HI), Tinderbox point (TB), Pearsons point (PP), Lucas point (LP), Dennes point (DP), Return point (RP), Painted cliffs (PC), Point Holme (PH) and Spring beach (SB).

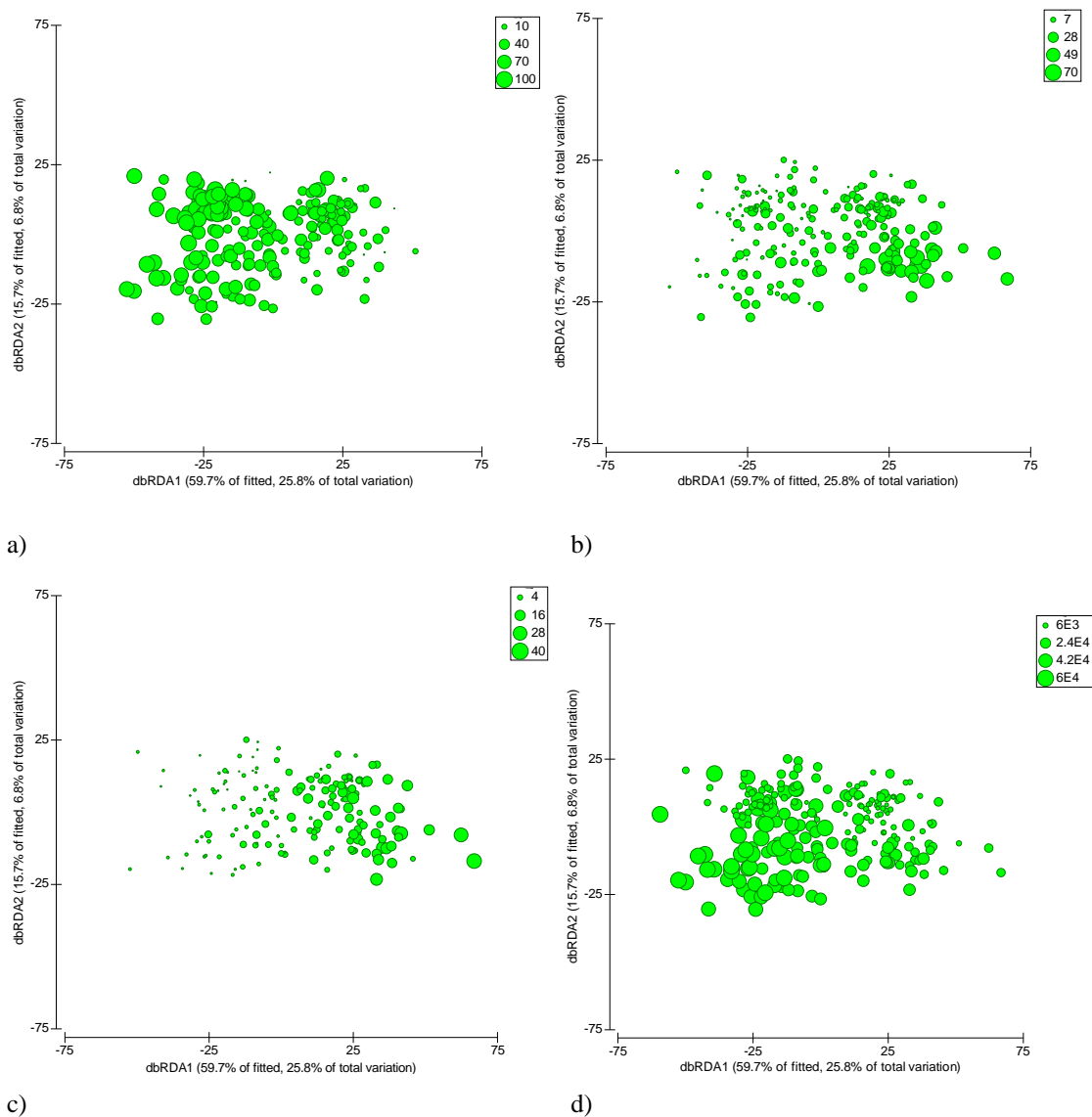


Figure 3.8. dbRDA ordinations (repeated from Figure 3.7) identifying the greatest variation through the reef fish community data ($\log(x+1)$ transformed) for the ‘Best’ fitted DISTLM model and overlaid with bubble plots for a) the proportion of canopy forming algae, b) the proportion of encrusting algae, c) the proportion of sessile invertebrates and d) average fetch exposure.

Table 3.5. DISTLM top five and overall ‘Best’ model results for Maria Island. Models based on the highest AIC model criteria value. * denotes the most parsimonious model identified.

Significant marginal test results	Proportion	Best 1-5 variable and ‘Best’ overall model results
Complexity ($F= 3.0661$, $p= 0.0002$)	0.073764	Exposure ($AIC= 603.95$, $R^2= 0.26859$)
Biogenic cover ($F= 4.1489$, $p= 0.0001$)	0.28743	Substratum cover + Exposure ($AIC= 599.36$, $R^2= 0.40559$)
Refuge space ($F= 3.3159$, $p= 0.0001$)	0.18304	* Complexity + Substratum cover + Exposure ($AIC= 596.87$, $R^2= 0.45194$)
Substratum cover ($F= 2.8466$, $p= 0.0001$)	0.18961	Complexity + Refuge space + Substratum cover + Exposure ($AIC= 598.21$, $R^2= 0.50815$)
Exposure ($F= 14.138$, $p= 0.0001$)	0.26859	Complexity + Biogenic cover + Refuge space + Substratum cover + Exposure ($AIC= 600.78$, $R^2= 0.57365$)

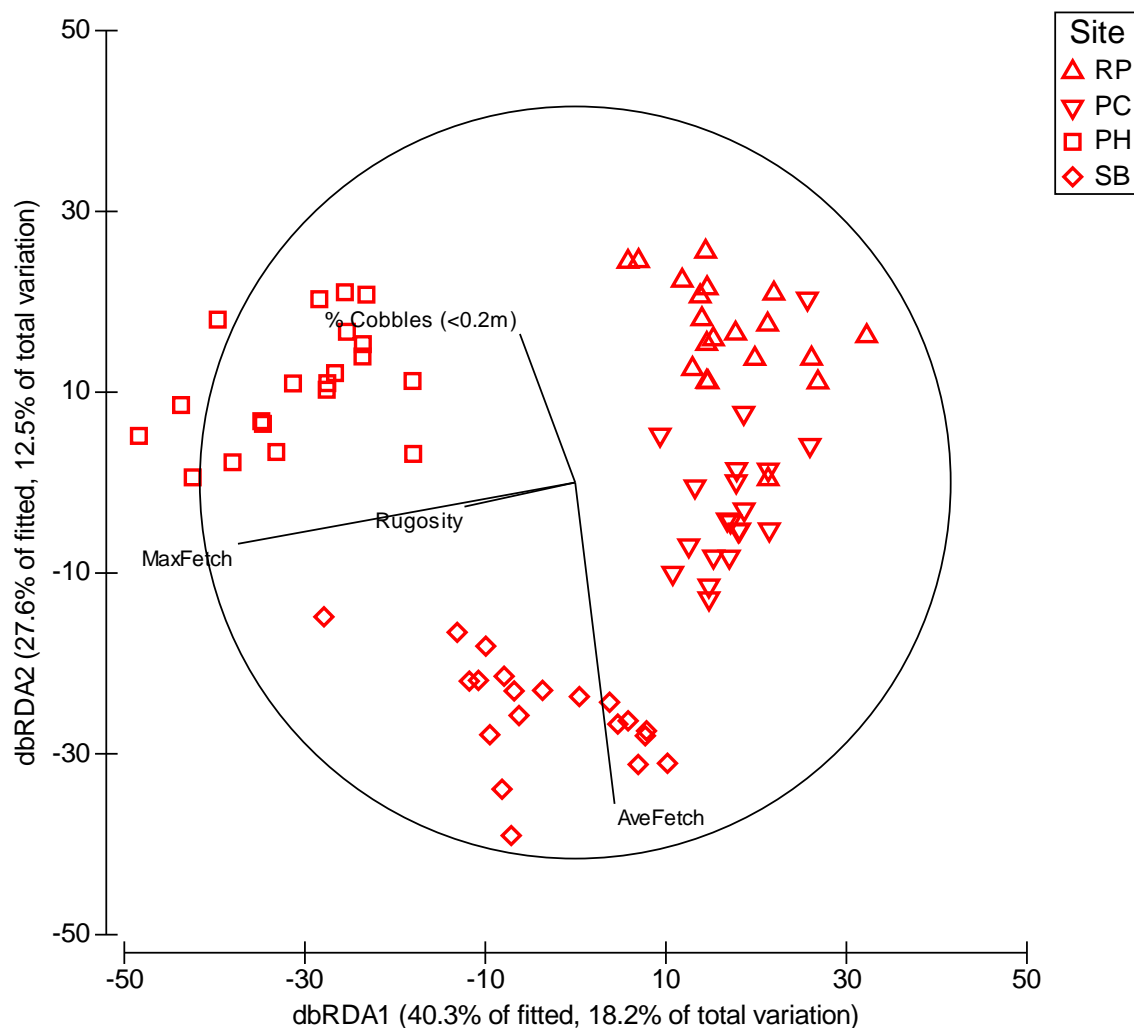


Figure 3.9. dbRDA ordination for Maria Island, identifying the greatest variation through the reef fish community data (log(x+1) transformed) for the ‘Best’ fitted DISTLM model and overlaid with the multiple partial correlation vectors ($r \geq 0.3$) of the individual physical variables. Sites are denoted by symbols and coded as: Return point (RP), Painted cliffs (PC), Point Holme (PH) and Spring beach (SB).

DISTLM (based on an AIC criteria and ‘Best’ selection procedure) across the Tinderbox sites identified three of the five explanatory variable sets; refuge space, substratum cover and exposure combined as the optimum model for the maximum explanation of reef fish community variability between sites, explaining 40.2% (Table 3.6). Marginal tests showed that three of the five variable sets explained significant proportions of the reef fish community variability between samples. The single ‘Best’ variable set was exposure which on its own explained 16.8% of the reef fish community variability between samples. Figure 3.10 displays the dbRDA ordination of the resulting Tinderbox ‘Best’ DISTLM model. The first and second axes of the plot accurately depict 81% of the fitted model and 32.4% of the total variability in the data; samples form a tight group for the Dennes point (DP) site, and looser grouping for the three other sites, indicating greater variability in the reef fish community structure between sites than within sites. Vector overlays calculated from the multiple partial correlations between the most highly correlated physical variables ($r \geq 0.3$) and the dbRDA axis scores illustrate the importance of each individual physical variable in explaining the variability in the reef fish community structure. The vector overlays highlight average and maximum fetch, substratum cover and refuge space variables as important in explaining the variability in the reef fish community structure between samples, with higher average and maximum fetch characterising the Lucas and Dennes point sites and high medium boulder (0.5 – 1.5 m) cover characterising the Dennes point site.

DISTLM (based on an AIC criteria and ‘Best’ selection procedure) across the Ninepin sites identified two of the five explanatory variable sets; complexity and exposure combined as the optimum model for the maximum explanation of reef fish community variability between sites, explaining 33.7% (Table 3.7). Marginal tests showed that all of the five variable sets explained significant proportions of the reef fish community variability between samples. The

single 'Best' variable set was exposure which on its own explained 30.2% of the reef fish community variability between samples. Figure 3.11 displays the dbRDA ordination of the resulting Ninepin 'Best' DISTLM model. The first and second axes of the plot accurately depict 95.6% of the fitted model and 32.2% of the total variability in the data; samples formed general groups for Garden Island (GI) and Charlotte cove point (CP) sites and for the other two sites combined. Vector overlays calculated from the multiple partial correlations between the most highly correlated physical variables ($r \geq 0.3$) and the dbRDA axis scores illustrate the importance of each individual physical variable in explaining the variability in the reef fish community structure. The vector overlays highlight how differences in maximum and average fetch distinguish variability in the reef fish community structure between Garden Island and Charlotte cover point samples from those of the other two.

Table 3.6. DISTLM top five and overall ‘Best’ model results for Tinderbox. Models based on the highest AIC model criteria value. * denotes the most parsimonious model identified.

Significant marginal test results	Proportion	Best 1-5 variable and ‘Best’ overall model results
Complexity ($F= 1.4255$, $p= 0.1581$)	0.037	Exposure ($AIC= 595.87$, $R^2= 0.16816$)
Biogenic cover ($F= 3.4299$, $p= 0.0001$)	0.288	Substratum cover + Exposure ($AIC= 593.67$, $R^2= 0.30823$)
Refuge space ($F= 1.485$, $p= 0.0579$)	0.095	*Refuge space + Substratum cover + Exposure ($AIC= 592.4$, $R^2= 0.40243$)
Substratum cover ($F= 3.0708$, $p= 0.0001$)	0.208	Complexity + Refuge space + Substratum cover + Exposure ($AIC= 594.42$, $R^2= 0.41763$)
Exposure ($F= 7.4795$, $p= 0.0001$)	0.16816	Complexity + Biogenic cover + Refuge space + Substratum cover + Exposure ($AIC= 602.2$, $R^2= 0.47657$)

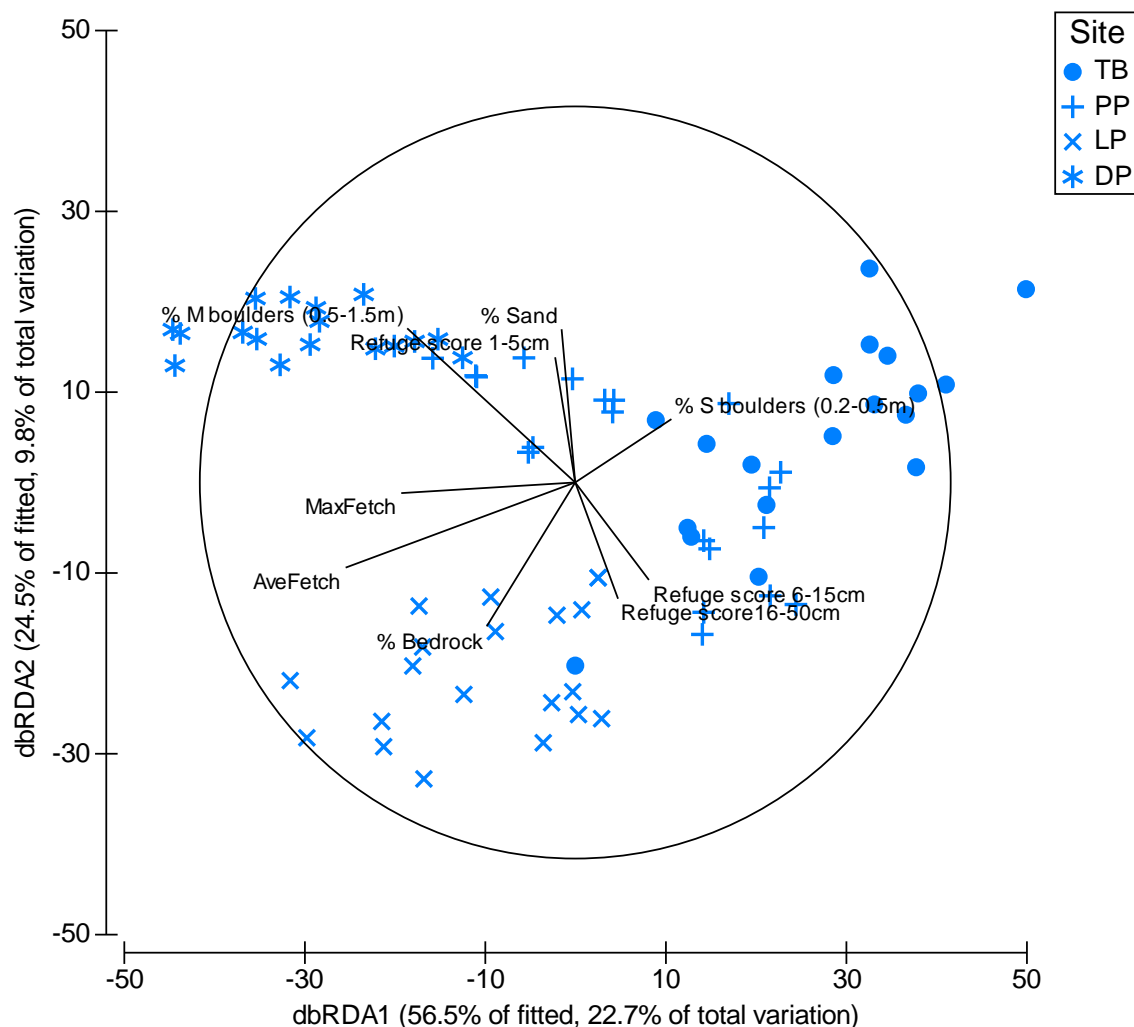


Figure 3.10. dbRDA ordination for Tinderbox, identifying the greatest variation through the reef fish community data ($\log(x+1)$ transformed) for the ‘Best’ fitted DISTLM model and overlaid with the multiple partial correlation vectors ($r \geq 0.3$) of the individual physical variables. Sites are denoted by symbols and coded as: Tinderbox point (TB), Pearsons point (PP), Lucas point (LP), Dennes point (DP).

Table 3.7. DISTLM top five and overall ‘Best’ model results for Ninepin. Models based on the highest AIC model criteria value. * denotes the most parsimonious model identified.

Significant marginal test results	Proportion	Best 1-5 variable and ‘Best’ overall model results
Complexity ($F=10.031$, $p=0.0001$)	0.2067	Exposure ($AIC=453.61$, $R^2=0.30177$)
Biogenic cover ($F=4.148$, $p=0.0001$)	0.31851	*Complexity + Exposure ($AIC=453.46$, $R^2=0.3371$)
Refuge space ($F=3.0056$, $p=0.0001$)	0.1688	Complexity + Biogenic cover + Exposure ($AIC=455.29$, $R^2=0.44467$)
Substratum cover ($F=5.7339$, $p=0.0001$)	0.32032	Complexity + Biogenic cover + Substratum cover + Exposure ($AIC=459.7$, $R^2=0.49494$)
Exposure ($F=16.639$, $p=0.0005$)	0.30177	Complexity + Biogenic cover + Refuge space + Substratum cover + Exposure ($AIC=464.51$, $R^2=0.52666$)

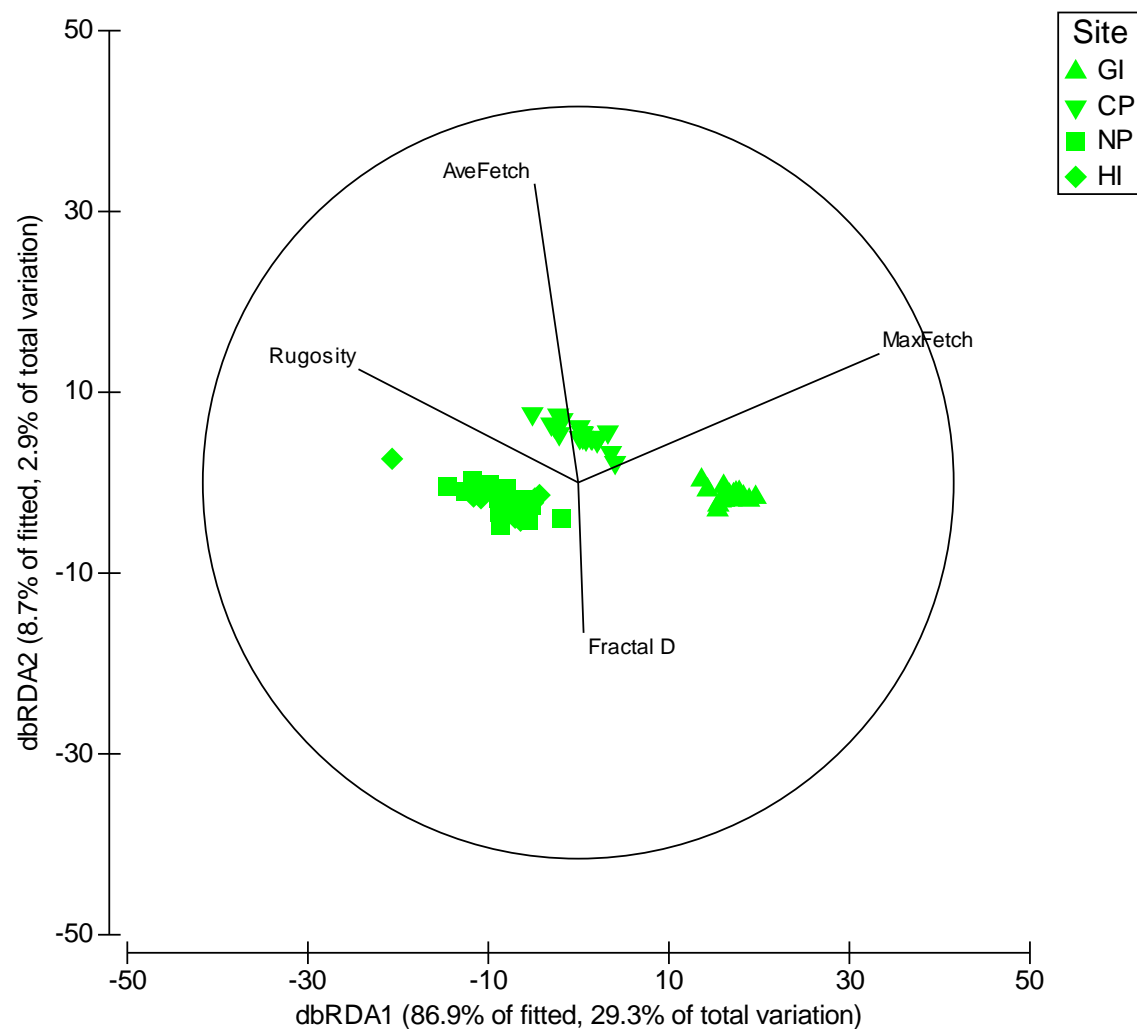


Figure 3.11. dbRDA ordination for Ninepin, identifying the greatest variation through the reef fish community data ($\log(x+1)$ transformed) for the ‘Best’ fitted DISTLM model and overlaid with the multiple partial correlation vectors ($r \geq 0.3$) of the individual physical variables. Sites are denoted by symbols and coded as: Garden Island (GI), Charlotte cove point (CP), Ninepin point (NP), Huon Island (HI).

3.4.5 Community structure modelling across sites.

Marginal DISTLM tests for five of the twelve sites modelled (DP, LP, PP, NP and CP), identified none of the four variable sets as explaining any significant proportions of the reef fish community variability between samples. Table 3.8 displays the DISTLM analysis for the remaining seven sites where marginal tests identified one or more sets explaining significant proportions of the reef fish community variability between samples. Exposure appeared to be the most important physical variable explaining the variability in reef fish community structure at the site scale and was identified as a significant variable for five of the seven sites modelled. Where the analysis identified other significant physical variables by themselves explaining equal or higher proportions of the reef fish community variability than exposure, the analysis often still identified exposure as the ‘Best’ overall explanatory variable. The important physical variables identified by each analysis tended to vary between sites. For instance across the Painted Cliffs site the analyses identified substratum cover as the only variable explaining any significant proportion (33.6%) of the reef fish community variability between samples while for the Garden Island site the analyses identified biogenic cover as the only variable explaining any significant proportion (51.2%) of the reef fish community variability between samples. Within the Painted Cliffs site the analyses identified Substratum cover as the only variable explaining any significant proportion (33.6%) of the reef fish community variability between samples. For the remaining five sites exposure was identified as the single most important variable in explaining reef fish community. In most cases the addition of other physical variables along with exposure improved model R^2 results.

Table 3.8. DISTLM top five and overall ‘Best’ model results for with-site scale analysis. Models based on the highest AIC model criteria value. Significant marginal results are highlighted in bold.

	Significant marginal test results	Proportion	Best 1-4 variable and overall ‘Best’ model results
Return point	Complexity ($F= 1.6785$, $p= 0.0451$)	0.165	Exposure ($AIC= 135.06$, $R^2= 0.2381$)
	Biogenic cover ($F= 1.0415$, $p= 0.4122$)	0.378	Substratum cover + Exposure ($AIC= 136$, $R^2= 0.5157$)
	Refuge space ($F= 1.5772$, $p= 0.0308$)	0.296	Biogenic cover + Substratum cover + Exposure ($AIC= 133.3$, $R^2= 0.7898$)
	Substratum cover ($F= 1.1334$, $p= 0.2874$)	0.288	Biogenic cover + Refuge space + Substratum cover + Exposure ($AIC= 113.35$, $R^2= 0.94805$)
	Exposure ($F= 2.6563$, $p= 0.0003$)	0.238	
Spring beach	Complexity ($F= 2.2735$, $p= 0.0096$)	0.211	Exposure ($AIC= 160.32$, $R^2= 0.14174$)
	Biogenic cover ($F= 1.0288$, $p= 0.4277$)	0.375	Biogenic cover + Substratum cover ($AIC= 157.67$, $R^2= 0.77355$)
	Refuge space ($F= 1.2602$, $p= 0.1667$)	0.31	Biogenic cover + Refuge space + Substratum cover ($AIC= 129.6$, $R^2= 0.96626$)
	Substratum cover ($F= 1.1352$, $p= 0.2801$)	0.344	
	Exposure ($F= 2.9728$, $p= 0.0083$)	0.142	
Point Holme	Complexity ($F= 1.3158$, $p= 0.2642$)	0.134	Exposure ($AIC= 144.94$, $R^2= 0.20764$)
	Biogenic cover ($F= 2.1426$, $p= 0.0164$)	0.556	Biogenic cover + Refuge space ($AIC= 141.79$, $R^2= 0.75096$)
	Refuge space ($F= 2.5033$, $p= 0.0109$)	0.4	Biogenic cover + Substratum cover + Exposure ($AIC= 134.5$, $R^2= 0.84349$)
	Substratum cover ($F= 2.0218$, $p= 0.0437$)	0.35	Complexity + Biogenic cover + Refuge space + Substratum cover ($AIC= 120.22$, $R^2= 0.95351$)
	Exposure ($F= 4.7169$, $p= 0.006$)	0.208	Complexity + Biogenic cover + Refuge space + Substratum cover + Exposure ($AIC= 108.65$, $R^2= 0.97641$)
Painted cliffs	Complexity ($F= 1.0709$, $p= 0.3835$)	0.112	Substratum cover ($AIC= 141.37$, $R^2= 0.33637$)
	Biogenic cover ($F= 0.87589$, $p= 0.6604$)	0.338	Substratum cover + Exposure ($AIC= 139.91$, $R^2= 0.49479$)
	Refuge space ($F= 0.9148$, $p= 0.5649$)	0.196	Biogenic cover + Substratum cover + Exposure ($AIC= 139.03$, $R^2= 0.75992$)
	Substratum cover ($F= 1.9008$, $p= 0.0213$)	0.336	Biogenic cover + Refuge space + Substratum cover + Exposure ($AIC= 129.75$, $R^2= 0.89881$)
	Exposure ($F= 1.7992$, $p= 0.0769$)	0.175	
Tinderbox point	Complexity ($F= 1.4255$, $p= 0.1545$)	0.04	Exposure ($AIC= 595.87$, $R^2= 0.16816$)
	Biogenic cover ($F= 3.4299$, $p= 0.0001$)	0.2875	Substratum cover + Exposure ($AIC= 593.67$, $R^2= 0.30823$)
	Refuge space ($F= 1.485$, $p= 0.0604$)	0.09	Substratum cover + Refuge space + Exposure ($AIC= 592.4$, $R^2= 0.40243$)
	Substratum cover ($F= 3.0708$, $p= 0.0001$)	0.20837	
	Exposure ($F= 7.4795$, $p= 0.0001$)	0.16816	
Huon Island	Complexity ($F= 2.2213$, $p= 0.0297$)	0.207	Exposure ($AIC= 118.44$, $R^2= 0.2398$)
	Biogenic cover ($F= 1.165$, $p= 0.3019$)	0.459	Biogenic cover + Substratum cover ($AIC= 115.85$, $R^2= 0.79884$)
	Refuge space ($F= 1.4666$, $p= 0.1071$)	0.344	
	Substratum cover ($F= 1.0461$, $p= 0.4295$)	0.326	
	Exposure ($F= 2.6812$, $p= 0.0092$)	0.2398	
Garden Island	Complexity ($F= 1.9606$, $p= 0.0656$)	0.187	Biogenic cover ($AIC= 96.69$, $R^2= 0.51297$)
	Biogenic cover ($F= 2.2821$, $p= 0.0061$)	0.513	Complexity + Biogenic cover ($AIC= 95.214$, $R^2= 0.62962$)
	Refuge space ($F= 1.3366$, $p= 0.2183$)	0.263	Complexity + Biogenic cover + Substratum cover ($AIC= 93.108$, $R^2= 0.77654$)
	Substratum cover ($F= 1.1987$, $p= 0.3009$)	0.242	Complexity + Biogenic cover + Refuge space + Substratum cover ($AIC= 89.104$, $R^2= 0.86449$)
	Exposure ($F= 1.2248$, $p= 0.3084$)	0.06	Complexity + Biogenic cover + Refuge space + Substratum cover + Exposure ($AIC= 88.553$, $R^2= 0.88072$)

3.4.6 Individual species occurrence and abundance modelling.

Figure 3.13 displays the fitted functions for the top four terms of the BRT model analysis of species abundance, ordered by relative influence for those species model results which showed explained deviance of greater than 50%.

BRT analysis at the site scale was also explored for diversity, occurrence and abundance measures but due to the low number of observations per site ($n \leq 20$) the results were largely uninformative, showing obvious issues of over fitting.

Table 3.9

Figure 3.13 displays the individual reef fish species occurrence modelled against habitat structure using boosted regression trees (BRTs). The proportions of deviance explained by each of the models ranged from 78.8% for the barber perch, *Caesioperca rasor* to 9.5% for the pretty polly, *Dotalabrus aurantiacus*. Important explanatory variables of individual species occurrence responses appeared to be highly species-specific. A combination of maximum fetch exposure, the 1-5 cm refuge score and the proportion of canopy algal cover exposure was important in explaining the occurrence of the barber perch, *Caesioperca rasor*. Fetch was largely the most important variable explaining species occurrence since it was identified in the top four important terms for eight of the thirteen species modelled. It appears to be particularly important in explaining the occurrence of the wrasse species *Notolabrus tetricus* and *Notolabrus fucicola* and the little weed whiting *Neodax balteatus*. The availability of refuge space was important in explaining the variability in the occurrence of a number of species including *Caesioperca rasor*, *Latridopsis forsteri* and *Pictilabrus laticlavus* while complexity in the form of reef rugosity was highly important in explaining the variability of *Pempheris multiradiata* and *Pseudolabrus rubicundus*. Figure 3.12 displays

the fitted functions for the top four terms of the BRT model analysis of species abundance, ordered by relative influence for those species model results which showed explained deviance of greater than 50%.

Table 3.10 displays the individual reef fish species abundance modelled against habitat structure using BRTs. The proportions of deviance explained by each of the models ranged from 83.1% for the southern hulafish, *Trachinops caudimaculatus* to 14.3% for the pretty polly, *Dotalabrus aurantiacus*. The important explanatory variables of individual species abundance responses appeared to be highly species-specific. The proportion of sessile invertebrates and encrusting algal cover appeared to be the most important variables explaining the abundances of *T. caudimaculatus*. Fetch and the density of 1-5 cm refuge spaces were largely the most important variables explaining species abundances since they were both identified in the top four important terms for seven of the thirteen species modelled. Often the same variable was largely responsible for explaining both the occurrence and abundance of a species. For example, both the occurrence and abundance of *Pempheris multiradiata* was largely explained by rugosity, *Notolabrus tetricus* (and the closely related *Notolabrus fucicola*) by average fetch exposure and *Trachinops caudimaculatus* by the per cent cover of sessile invertebrates. The remaining modelled species results tended to identify similar important explanatory variables of occurrence and abundance in differing orders of relative influence. Figure 3.13 displays the fitted functions for the top four terms of the BRT model analysis of species abundance, ordered by relative influence for those species model results which showed explained deviance of greater than 50%.

BRT analysis at the site scale was also explored for diversity, occurrence and abundance measures but due to the low number of observations per site ($n \leq 20$) the results were largely uninformative, showing obvious issues of over fitting.

Table 3.9. BRT model analysis results of species occurrence including the top four important terms for each model. Models were based on a bag fraction of 0.5, learning rate of 0.001 and a tree complexity of 2.

Species	Number of trees	Important model terms	Per cent relative influence	Residual deviance	Total null deviance	Deviance explained(D ²)
<i>Urolophus cruciatus</i>	4450	Cobbles 0.2m Upper canopy algae Fractal D Encrusting algae	10.22 9.50 9.24 9.05	0.249	0.668	0.627
<i>Caesioperca rasor</i>	8200	Max fetch Refuge score 1.5cm Upper canopy algae Turving algae	16.7 14.97 12.69 12.56	0.274	1.295	0.788
<i>Latridopsis forsteri</i>	1500	Refuge score 1.5cm Bedrock S boulders 0.2-0.5m Average fetch	30.92 12.82 11.66 5.06	0.462	0.703	0.343
<i>Pempheris multiradiata</i>	1600	Rugosity Average fetch Refuge score 16-50cm Bedrock	35.95 10.78 6.02 5.64	0.455	0.703	0.353
<i>Notolabrus tetricus</i>	1800	M boulders 0.5-1.5m Average fetch Refuge score 6- 15cm Unvegetated	29.29 27.84 6.34 5.60	0.193	0.421	0.542
<i>Neodax balteatus</i>	2100	Average fetch Encrusting algae Turving algae Fractal D	19.15 18.66 7.68 5.57	1.046	1.305	0.199
<i>Dotalabrus aurantiacus</i>	2100	Cobbles 0.2m Lower canopy algae Max fetch Fractal D	15.61 11.88 9.27 8.54	0.725	0.801	0.095
<i>Notolabrus fucicola</i>	5400	Average fetch Max fetch Refuge score 6-15cm Rugosity	28.04 7.3 7.22 6.79	0.708	1.331	0.468
<i>Pseudolabrus rubicundus</i>	1800	Rugosity Refuge score 6-15cm Average fetch Bedrock	17.21 10.11 8.26 7.35	0.883	1.087	0.188
<i>Pictilabrus laticlavius</i>	2000	Mean Ecklonia Stipe density 1mx1m Refuge score 6-15cm L boulders >1.5m M boulders 0.5-1.5m	11.65 11.18 11.15 9.65	1.129	1.371	0.177
<i>Arcana aurita</i>	2500	Encrusting algae Average fetch Refuge score 6-15cm Fractal D	19.95 18.30 10.12 7.85	0.565	0.86	0.343
<i>Trachinops caudimaculatus</i>	6550	Sessile inverts Average fetch Rugosity Upper canopy algae	34.08 1.17 9.87 5.70	0.387	1.366	0.717
<i>Acanthaluteres vittiger</i>	4050	Bedrock Upper canopy algae Sand Encrusting algae	29.91 27.47 8.11 5.80	0.278	0.686	0.595

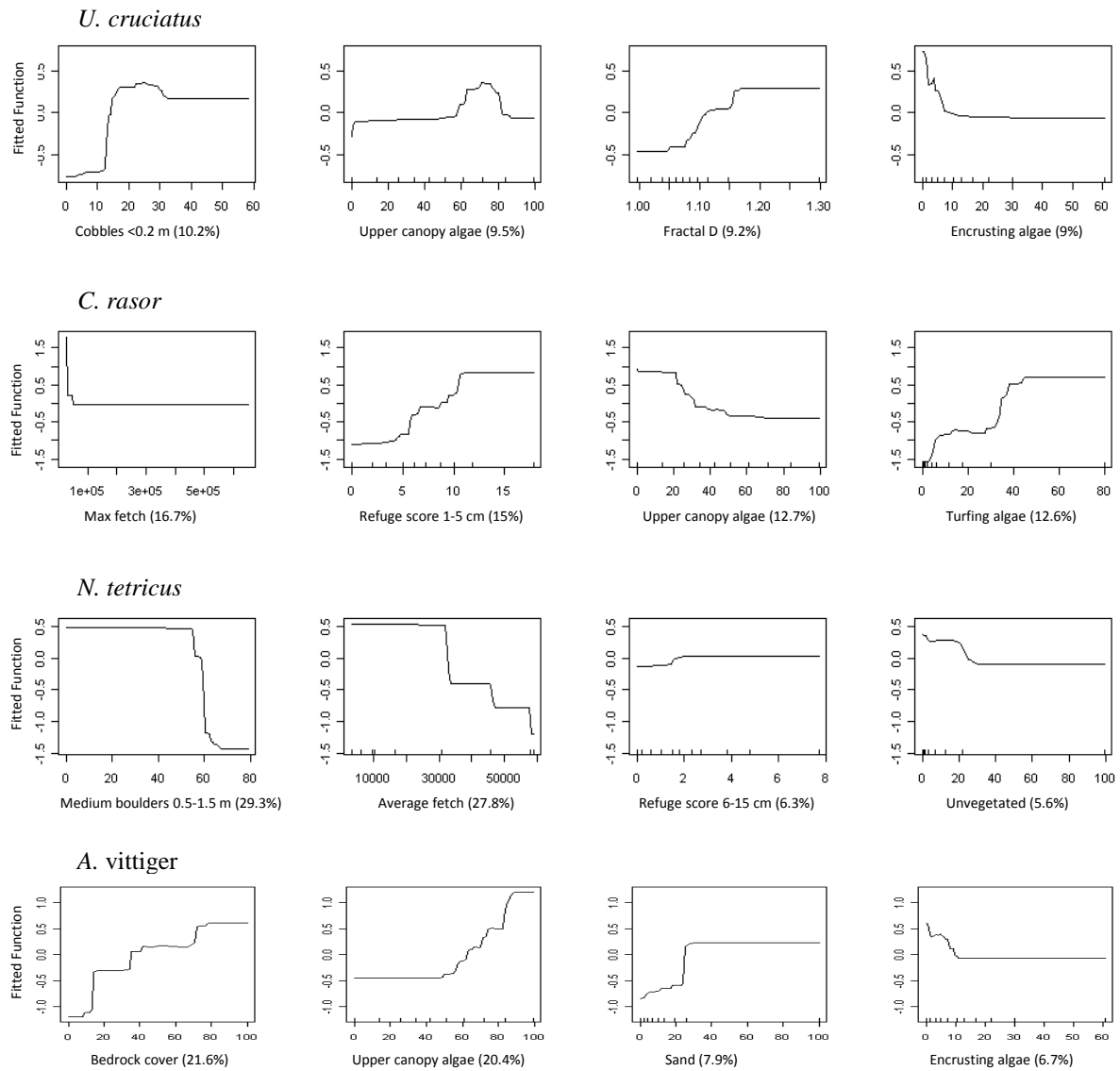


Figure 3.12. Fitted functions versus observed values (indicated by x-axis tabs) for the top four terms of the BRT model analysis of species occurrence, ordered by relative influence (in brackets) for those species with notable proportions of deviance explained ($D^2 \geq 50\%$); *Urolophus cruciatus*, *Caesioperca razor*, *Notolabrus tetricus* and *Acanthaluteres vittiger*.

Table 3.10. BRT model analysis results of species abundance including the top four important terms for each model. Models were based on a bag fraction of 0.5, learning rate of 0.001 and a tree complexity of 2.

Species	Number of trees	Important model terms	Per cent relative influence	Residual deviance	Total null deviance	Deviance explained(D ²)
<i>Urolophus cruciatus</i>	2450	Encrusting.algae % Cobbles (0.2m) % M boulders (0.5-1.5m) Lower.canopy.algae	14.57 13.51 10.08 8.99	0.003	0.005	0.4
<i>Caesioperca razor</i>	10000	Turfing.algae Refuge.score.1.5cm Max.fetch Upper.canopy.algae	25.0 15.07 8.94 5.77	0.036	0.207	0.826
<i>Latridopsis forsteri</i>	1000	% Bedrock Refuge score (1.5cm) % M boulders (0.5-1.5m) Fractal.D	26.88 14.71 7.25 6.57	0.013	0.011	0.154
<i>Pempheris multiradiata</i>	3750	Rugosity Average.fetch Refuge.score.1.5cm Mean...Bedrock	46.84 12.81 5.23 5.12	0.021	0.038	0.447
<i>Notolabrus tetricus</i>	5750	Average.fetch Refuge.score.1.5cm Turfing.algae Refuge.score.6.15cm	37.7 6.55 5.05 4.99	0.056	0.156	0.641
<i>Neodax balteatus</i>	1600	Encrusting algae Average.fetch % M boulders (0.5-1.5m) % Sand	27.61 16.07 6.92 6.90	0.017	0.022	0.227
<i>Dotalabrus aurantiacus</i>	1000	Mean...Sand Fractal.D Max.fetch Turfing.algae	12.41 11.48 10.28 7.71	0.006	0.007	0.143
<i>Notolabrus fucicola</i>	8600	Average.fetch Upper.canopy.algae Max.fetch Mean...Bedrock	32.19 15.2 11.36 7.67	0.02	0.081	0.753
<i>Pseudolabrus rubicundus</i>	1350	Average.fetch Mean...S.boulders..0.2.0.5m. Mean...Bedrock Refuge.score.6.15cm	12.77 11.16 8.62 8.05	0.009	0.011	0.182
<i>Pictilabrus laticlavius</i>	7250	Mean...Sand Mean.Stipe.density..1mx1m. Mean...S.boulders..0.2.0.5m. Refuge.score.6.15cm	11.7 9.26 8.93 8.58	0.013	0.024	0.458
<i>Arcana aurita</i>	1750	Encrusting.algae Refuge.score.1.5cm Average.fetch Mean...Sand	22.46 15.52 9.18 7.96	0.006	0.008	0.25
<i>Trachinops caudimaculatus</i>	7900	Sessile.inverts Encrusting.algae Average.fetch Refuge.score.1.5cm	36.89 11.64 7.56 6.03	0.504	2.987	0.831
<i>Acanthaluteres vittiger</i>	1100	Mean...Bedrock Refuge.score.1.5cm Upper.canopy.algae Average.fetch	56.94 13.28 9.24 7.21	0.018	0.022	0.182

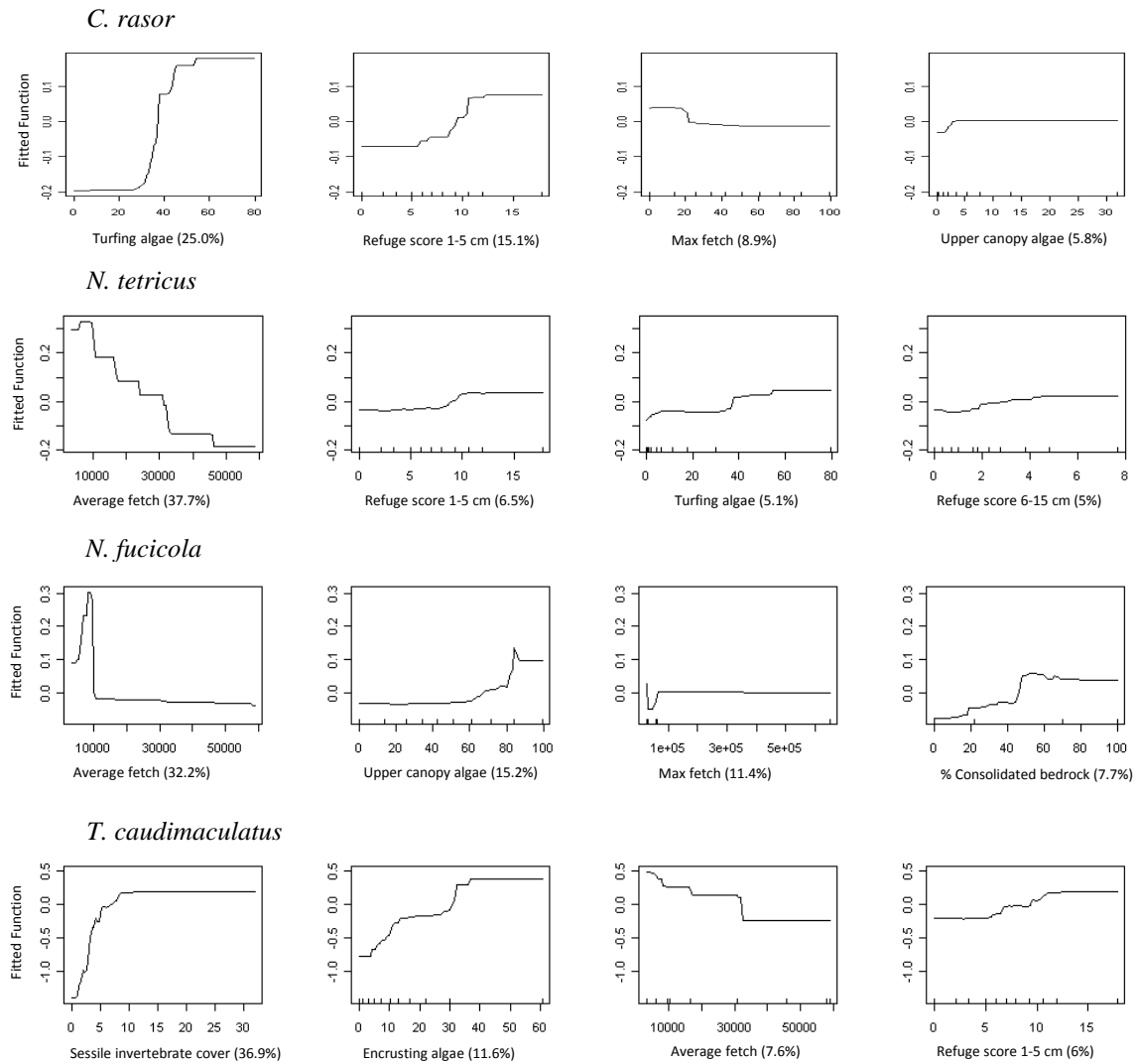


Figure 3.13. Fitted functions versus observed values (indicated by x-axis tabs) for the top four terms of the BRT model analysis of species abundance, ordered by relative influence (in brackets) for those species with notable proportions of deviance explained ($D^2 \geq 50\%$); *Caesioperca razor*, *Notolabrus tetricus*, *Notolabrus fucicola* and *Trachinops caudimaculatus*.

3.4.7 Species diversity modelling.

Table 3.11 displays three species diversity indices modelled against habitat structure using BRTs at the regional scale. Average fetch exposure was clearly the most important variable explaining the variability in each of the individual diversity measures at the overall regional scale. Rugosity and the per cent cover of bedrock also appeared to have some importance in explaining the variability in each of the individual diversity measures. Figure 3.14 displays the fitted functions for the top four terms of the BRT model analysis of regional-scale diversity, ordered by relative influence. Table 3.12 displays the same three species diversity indices modelled against habitat structure using BRTs at the intermediate location scale. Average fetch exposure was again the most important variable explaining the variability in each of the three diversity measures across the Maria Island sites at the intermediate location scale. Maximum fetch exposure and the per cent cover of bedrock also appeared to have some importance in explaining the variability in each of the three diversity measures across Maria island sites. Species richness was well explained across Tinderbox sites largely by a combination of medium boulder cover (0.5 – 1.5 m) and *Ecklonia radiata* stipe density. Margalef's (d) and Shannon-Wiener (H) diversity across the Tinderbox sites was largely explained by refuge space availability and refuge diversity. All three measures of diversity across the Ninepin sites were largely explained by the substratum per cent cover variables of large boulders (>1.5 m), small boulders (0.2 – 0.5 m) and cobbles (<0.2 m). Beyond the site scale there were insufficient numbers of observations to allow reliable BRT analysis of species diversity. Figure 3.15, 3.16 and 3.17 display the fitted functions for the top four terms of the BRT model analyses of location-scale diversity, ordered by relative influence.

Table 3.11. BRT model analysis results of region-scale species diversity including the top four important terms for each model. Models were based on a bag fraction of 0.5, learning rate of 0.001 and a tree complexity of 2.

Diversity indices	Number of trees	Important model terms	Per cent relative influence	Residual deviance	Total null deviance	Deviance explained(D^2)
Species richness (<i>S</i>)	10000	Average fetch Rugosity Max fetch Refuge score 1.5cm	21.36 9.25 8.79 6.72	0.243	0.984	0.753
Margalef's (<i>d</i>)	8650	Average fetch Rugosity Mean Bedrock Upper canopy algae	18.89 9.08 9.07 8.38	0.045	0.13	0.654
Shannon-Wiener (<i>H</i>)	7750	Average fetch Mean Bedrock Rugosity Turving algae	23.26 10.11 8.93 8.72	0.022	0.069	0.681

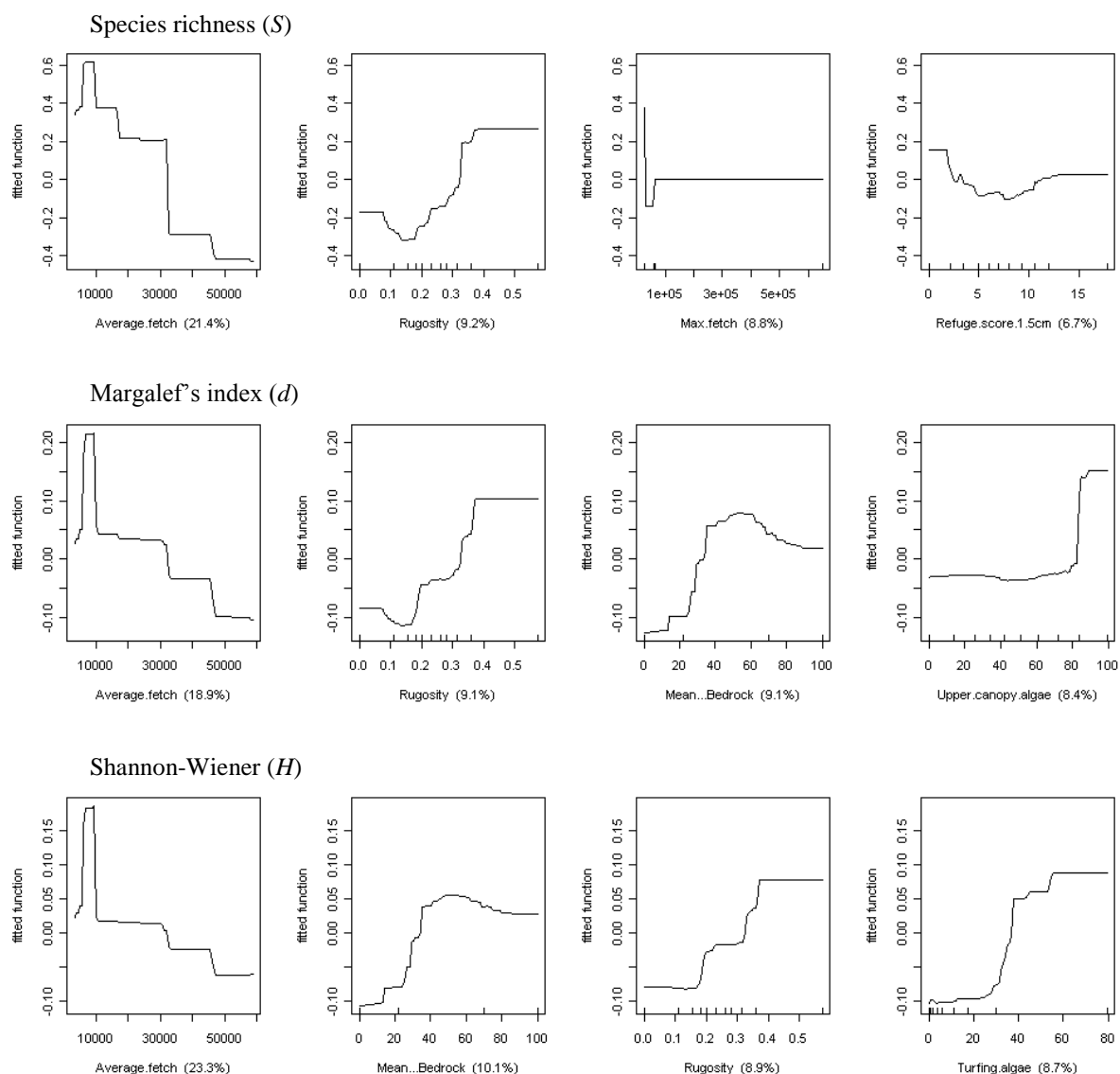


Figure 3.14. Fitted functions versus observed values (indicated by x-axis tabs) for the top four terms of the BRT model analysis of regional-scale species diversity, ordered by relative influence (in brackets).

Table 3.12. BRT model analysis results of location-scale species diversity including the top four important terms for each model. Models were based on a bag fraction of 0.5, learning rate of 0.001 and a tree complexity of 2.

Diversity indices		Number of trees	Important model terms	Per cent relative influence	Residual deviance	Total null deviance	Deviance explained(D ²)
Species richness (<i>S</i>)	Maria	7550	Average fetch	16.81	0.23	1.257	0.817
			Max fetch	10.04			
			Sessile inverts	9.36			
			Turfing algae	8.82			
	Tinderbox	4550	M boulders 0.5-1.5m	29.94	0.104	0.347	0.700
			Stipe density	14.42			
			Sessile inverts	6.90			
			Refuge score 6-15cm	6.74			
	Ninepin	1700	Cobbles 0.2m	21.94	0.27	0.469	0.424
			L boulders 1.5m	15.76			
			Max fetch	10.24			
			Refuge score 6-15cm	9.73			
Margalef's (<i>d</i>)	Maria	8050	Average fetch	12.44	0.036	0.194	0.814
			Bedrock	11.5			
			Max fetch	9.16			
			Fractal D	7.09			
	Tinderbox	1850	Refuge Diversity	14.11	0.034	0.055	0.382
			Refuge score 16-50cm	13.24			
			M boulders 0.5-1.5m	12.37			
			Refuge score 6-15cm	9.54			
	Ninepin	3450	Cobbles 0.2m	16.80	0.028	0.085	0.671
			L boulders >1.5m	13.16			
			S boulders 0.2-0.5m	11.08			
			Max fetch	7.87			
Shannon – Wiener (<i>H</i>)	Maria	9150	Average fetch	13.88	0.015	0.098	0.847
			Bedrock	12.80			
			Cobbles 0.2m	8.66			
			Max fetch	7.9			
	Tinderbox	2000	Refuge Diversity	14.34	0.012	0.022	0.455
			M boulders 0.5-1.5m	14.03			
			Refuge score 16-50cm	13.66			
			Refuge score 6-15cm	12.46			
	Ninepin	7100	Mean L boulders >1.5m	15.72	0.01	0.052	0.808
			Cobbles 0.2m	12.95			
			S boulders 0.2-0.5m	9.84			
			Max fetch	8.55			

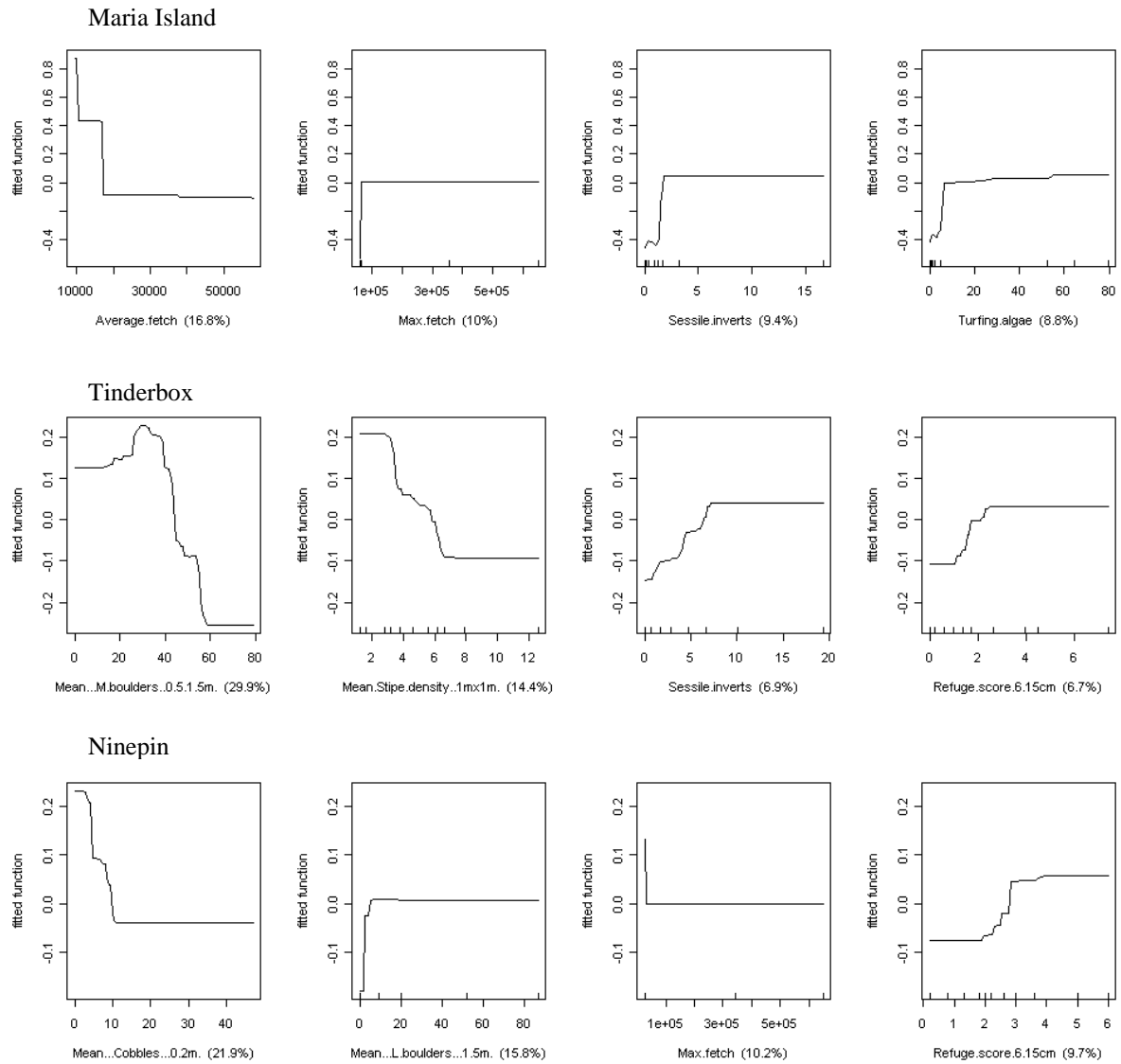


Figure 3.15. Fitted functions versus observed values (indicated by x-axis tabs) for the top four terms of the BRT model analysis of location-scale species richness (S), ordered by relative influence (in brackets).

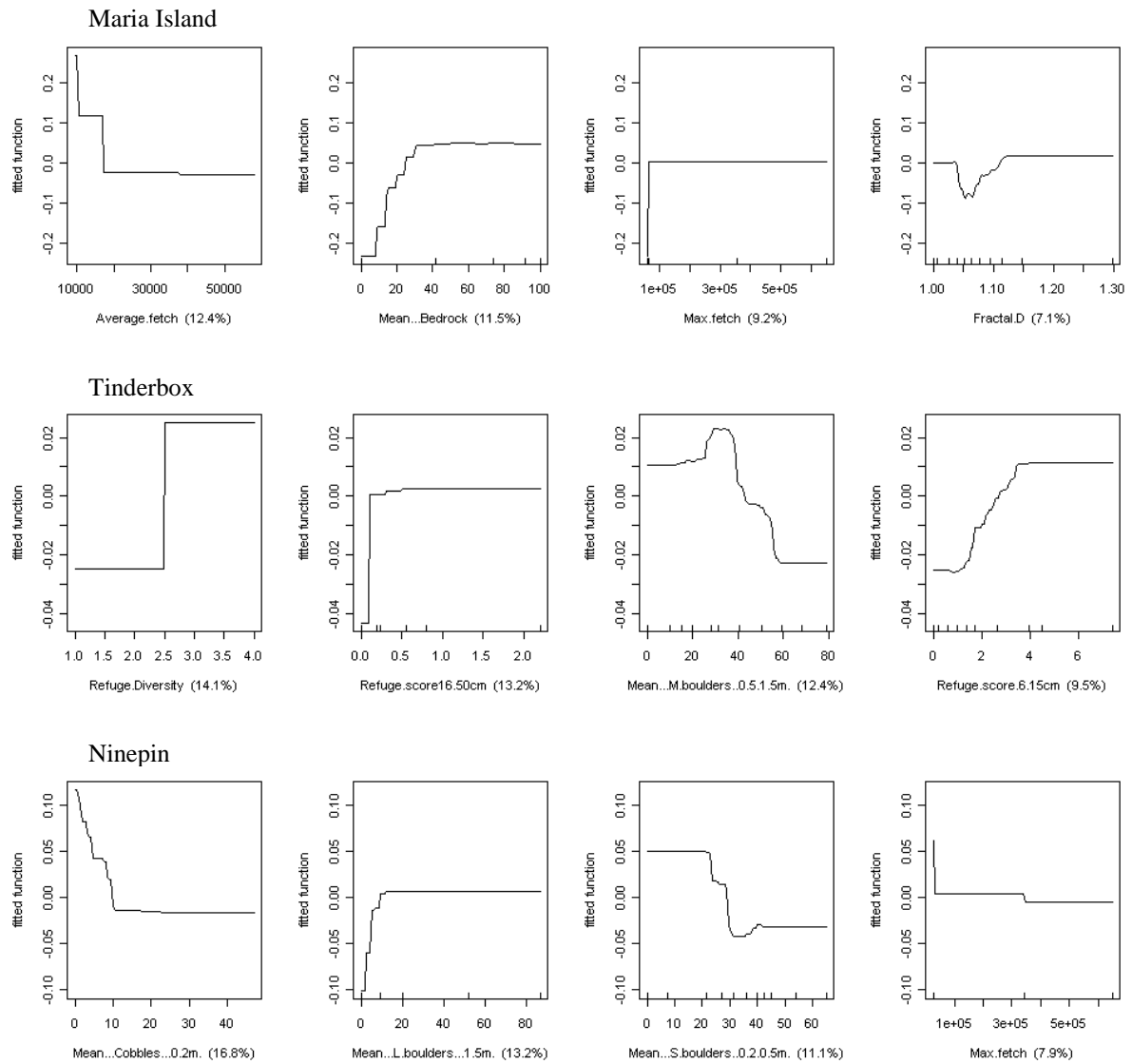


Figure 3.16. Fitted functions versus observed values (indicated by x-axis tabs) for the top four terms of the BRT model analysis of location-scale Margalef's index (D), ordered by relative influence (in brackets).

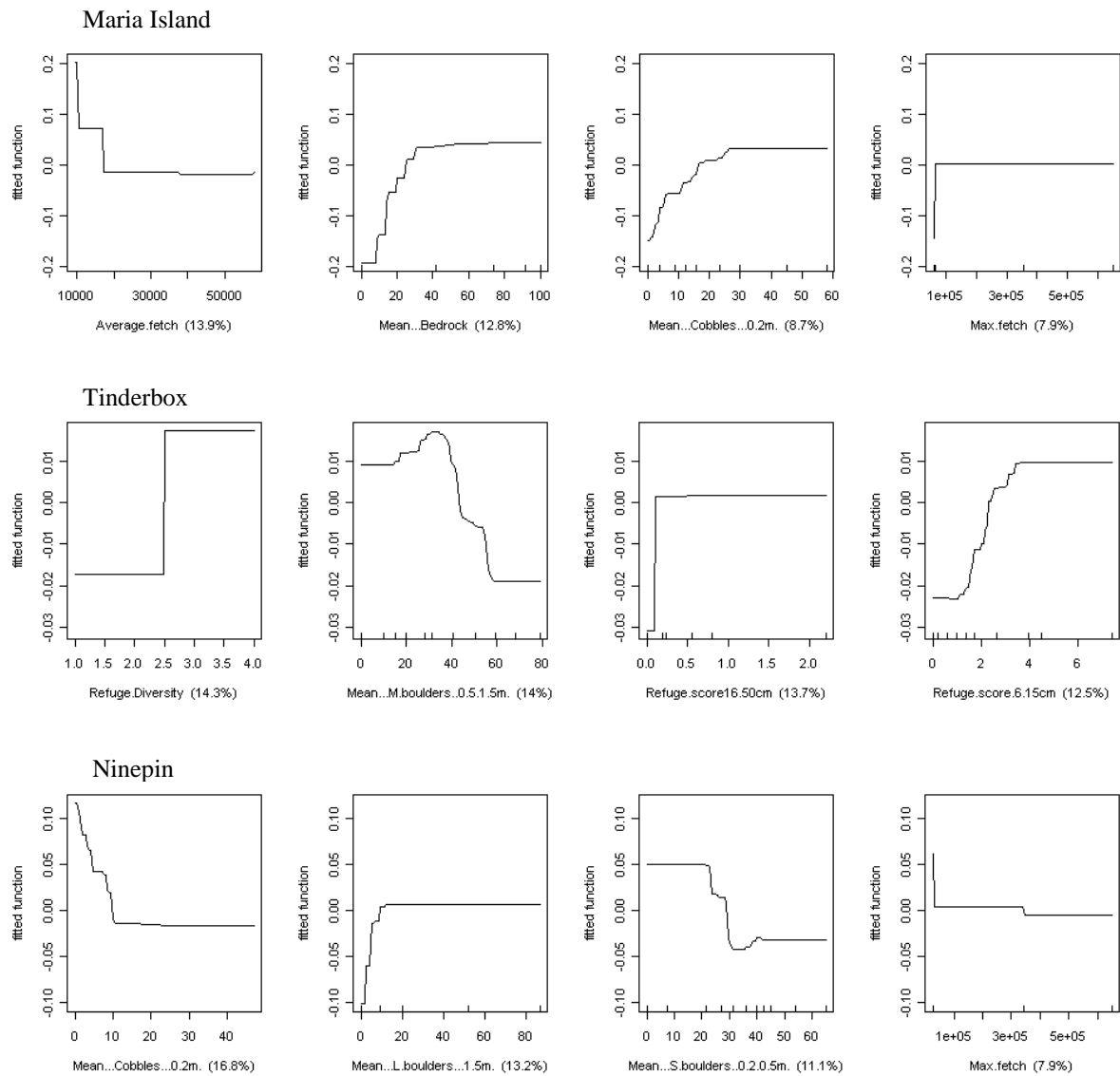


Figure 3.17. Fitted functions versus observed values (indicated by x-axis tabs) for the top four terms of the BRT model analysis of location-scale Shannon-Wiener index (H), ordered by relative influence (in brackets).

3.5 Discussion

Chapter two of this thesis identified how temperate reef fish community structure varied across bioregional and continental wide scales across Australia in response to broad and fine resolution environmental and habitat metrics. The general conclusions of that study were that patterns in reef fish community structure were associated with physical variables along a gradient from geographic position at inter-bioregional scales (acting as a proxy for broad climatic and biogeographic variables) to environmental variables such as exposure which became more important in explaining reef fish assemblage patterns at intra-bioregional scales. The results of chapter two begin to hint at the hypothesis of a hierarchy of spatial processes from bioregional scale influences such as climatic and sea surface temperature variability through to localised physical habitat variables such as biogenic cover and refuge space availability which impart more ecologically proximal influences on disturbance, recruitment, competition and predation at smaller spatial scales. Chapter three investigated this hypothesis further in an attempt to identify the important components of physical habitat structure explaining community assemblage patterns, diversity and individual species distribution and abundance responses to habitat structure at scales from kilometres to metres.

This study has attempted to identify surrogate explanatory measures that possess the potential to be cheaply and easily obtained and utilised by marine spatial planners and applied in the context of biodiversity prediction. Understanding the key habitat related drivers of observed spatial variation in the distribution of temperate reef fishes is vital in developing cost effective surrogate metrics to improve predictions of biodiversity patterns for marine spatial planning and management. In the process of this study I have successfully identified the importance of exposure and its relationship with biogenic structure, in explaining significant proportions of associated reef fish community structure and diversity patterns and the results

suggest an increasing importance of habitat heterogeneity and complexity towards finer ends of the scales investigated. In addition this work investigated the occurrence and abundance responses of a number of common individual species and was able to identify species-specific relationships with various components of physical habitat structure. Importantly, as would be expected, different species were found to respond in different ways to physical environmental variables and an understanding of these individual species relationships will lead to improved fisheries and conservation management.

3.5.1 Reserve effects

This study was unable to identify any significant variability in community structure between long-term protected and fished areas within any of the three study locations of Maria Island, Ninepin or Tinderbox. This was largely expected since the approach applied a one off ‘control-impact’ comparison based on abundances, which would have been largely unable to detect the small response signals to protection. Additionally, marine reserve effects often have the greatest effect on large-bodied, commercially exploited species, which dominate total community biomass but have little significance to total community abundance and therefore significant effects on these types of species may have gone undetected by not considering biomass measures of commercially important species (Edgar et al., 2009). This study was constrained to some extent by its spatial and temporal resolution which limited the ability to detect some larger, wide ranging and commercially exploited species. Edgar et al. (2009) and Barrett et al. (2007) have demonstrated the importance of having extensive temporal datasets of long established reserves in detecting temporally divergent responses to protection of reef fish habitat in Tasmania. Overall, the analysis of reserve effects showed that community structure varied more in response to habitat structure between sites and temporally between replicate surveys within reserves than between reserves and non-reserves status sites. This suggests that any variability in the community structure resulting from

reserve effects across Tasmanian reefs may be difficult to discern from that of pre-existing fine scale spatial and temporal variability. Future studies of a similar nature should ensure that there is sufficient spatial and temporal sampling resolution to identify changes in the biomass resulting from reserve effects and consider the variability due to pre-existing fine scale spatial and temporal variability between study sites.

A well-known issue with ‘control- impact’ assessments is that any restoration effects can be easily confounded by those of other processes within the environment that are highly spatially variable (Underwood, 1994, Osenberg et al., 2006). It is probable that the magnitude of reserve effects will vary in relation to the spatial variability of the habitat structure of the environments that they protect but this variability is rarely accounted for by most attempts to assess reserve efficacy (Huntington et al., 2010). Huntington et al. (2010) identified how the physical structure of reef habitats in Belize masked reserve effects and demonstrated significant effects of fishing protection by grouping sites based on the natural habitat variability between them. Knowledge about the natural variability resulting from the response of fish populations to physical habitat structure will help researchers to separate this influence from that of protection from fishing (Garcia-Charton and Pérez-Ruzafa, 2001). Disentangling the effects of marine protection from those of natural variability in physical habitat structure is the focus of chapter four of this thesis which attempts to address this problem by considering communities in groups based on the natural temporal and habitat variability of their associated habitats prior to analysing for reserve effects.

3.5.2 Varying spatial scale effects

Significant variability in community structure was identified at all three spatial scales investigated, from location to block. On average, reef fish community structure varied in a spatially hierarchical fashion with greater variability across the three locations than between

sites and blocks and more across sites than across blocks. However the greatest variation in the reef fish community structure, for each location was at the level of the survey replicates suggesting high temporal variability in the community assemblages between replicate surveys. Taken together this suggests that variability in the community structure resulting from reserve effects is likely to be very difficult to discern from that of natural fine scale spatial and temporal variability. These results warranted further modelling in an attempt to attribute how the variability in the reef fish community structure related to specific physical habitat structure metrics at each of the three scales.

The most evident patterns in the reef fish community structure across the broadest regional scale appeared, in general, to relate to the proportions of biogenic cover (canopy algae, encrusting algae and sessile invertebrate) which also appeared to be correlated to some degree with fetch exposure. In general a positive relationship was apparent between fetch exposure and the proportion of canopy algae, and an inverse relationship between fetch exposure and encrusting algae and sessile invertebrates. The Tinderbox and Maria Island sites were more exposed than the Ninepin sites and also more highly dominated by canopy forming algae, which in turn appeared to explain the variability in the reef fish community structure. Other components of physical habitat structure also contributed, to a lesser degree, to the variability in the community structure across sites. Modelling identified that habitat complexity, refuge space, substratum cover and exposure each alone explained small but significant proportions of the variability in the reef fish community structure. These variables considered individually did not appear to be important variables in explaining any notable proportion (over approximately 10%) of the reef fish community variability, however when considered in addition to biogenic cover they explained larger proportions suggesting some combined effect of biogenic and topographic reef habitat structure in structuring the

associated reef fish communities. At the intermediate (within-location) scale, similarly to the findings of the previous regional scale analysis, patterns in the reef fish community structure were found to largely relate to the variability of exposure and biogenic cover. However, the structuring importance of substratum cover and complexity also appeared notably larger within locations. A combination of exposure and substratum cover were largely responsible for explaining the variability in the reef fish communities sampled across the Maria Island and Tinderbox locations, while exposure and complexity were largely responsible for explaining the variability in the reef fish communities sampled across the Ninepin location. At the finest (within-site) scale considered, exposure and biogenic cover again appeared to largely explain the variability in reef fish community structure between samples but again, as with the intermediate scales, the structuring importance of substratum cover and complexity, plus also refuge space appeared to be notably more important at the site scale. In most cases the addition of other physical variables along with exposure improved model R^2 results and where individual reef-habitat variables explained significant proportions of the variability in reef fish community structure they were generally larger than at any other scale suggesting the increased importance of physical habitat complexity and heterogeneity at fine spatial resolutions.

For diversity modelled at the regional scale, average fetch distance was clearly the most important variable explaining the variability in each of the individual diversity measures investigated, however rugosity also appeared to have some importance in explaining the variability of each diversity measures. At the intermediate (location) scale, exposure was again important but substratum cover, refuge space and *Ecklonia radiata* stipe density also became important in explaining the variability in each of the individual diversity measures,

again suggesting the increased importance of physical habitat complexity and heterogeneity in determining species diversity at fine spatial resolutions.

Individual species occurrence and abundance responses to habitat structure were found to be largely species-specific. When occurrence was modelled independently for each species the importance of fetch exposure and biogenic cover were the most important for a number of species (e.g. *Notolabrus fucicola* and *Neodax balteatus*), while the importance of habitat complexity, refuge space and substratum cover were increasingly evident for others. Pérez-Matus and Shima (2010) investigated linkages between the abundance of reef fishes and the composition of vegetative structures in a temperate, macroalgal-dominated ecosystem. They identified that macro-algal identities and compositions affected the abundances and structure of the local fish assemblage and that generally, heterogeneity in vegetative structures appeared to increase breadth of habitat use for reef fishes. Many of my own results made sense based on what is already understood of the behaviour of particular species of fish. For instance complexity in the form of reef rugosity was highly important in explaining the variability of occurrence of *Pempheris multiradiata* which is a cryptic species living in or close to caves and overhangs (Edgar, 2000). In this case I was able to demonstrate that rugosity, when surveyed accurately using the rotating wheel method applied, can effectively sample *P. multiradiata* habitat. For other species such as *Trachinops caudimaculatus* the relationships detected are less well understood. It is not initially clear why this species is so strongly determined by sessile invertebrate cover. It may be that it is directly acquiring some form of resource in areas of high invertebrate cover but since it is a planktivorous species it may be utilising open areas dominated by invertebrate cover where currents are uninhibited by dense algal cover or where invertebrate cover is more apparent to surveyors. These relationships require investigation in more detail to better understand them. The availability

of refuge space was important in explaining the variability of occurrence of a number of species including *Latridopsis forsteri* and *Pictilabrus laticlavius* suggesting the need for predator safe refuge spaces for these species. Again these patterns are not entirely clear and require further detailed investigation.

Models of individual species abundance were able to explain slightly larger proportions of the variability than those of species occurrence. Often the same variable was largely responsible for explaining both the occurrence and abundance relationship of a species, which is unsurprising given that absence records comprise one extreme of the abundance continuum. For example, both the occurrence and abundance of *Pempheris multiradiata*, *Notolabrus fucicola* and *Trachinops caudimaculatus* were largely explained by rugosity, the average fetch distance and the per cent cover of sessile invertebrates respectively. The remaining modelled species abundance results tended to identify similar important explanatory variables of occurrence and abundance in differing orders of relative influence.

My findings are comparable to those of a number of other studies. Garcia-Charton and Pérez-Ruzafa (2001) identified similar species-specific responses when they investigated the effects of physical habitat structure on the community structure of Mediterranean reef fish. Their results identified rugosity, medium boulder density, verticality and canopy algae cover, each varying in importance depending on scale, as the major explanatory variables of the reef fish community structure. Syms (1995) observed species-specific relationships and associations of blennioid reef fish assemblages in New Zealand with varying depth and biogenic habitat structure at broad spatial scales (10s km's) while at finer spatial scales (100s m's) habitat specialisation and the importance of topographic reef features became more apparent. Chittaro (2004) also observed species-specific fish-habitat relationships for each of nine reef

fish species surveyed across sites in the US Virgin Islands however they also determined that for most of the species surveyed, these habitat relationships were consistent across spatial scales between 1m^2 and 200m^2 . These slightly conflicting results of scale dependent and independent habitat associations may be the result of a natural difference in the ecology of temperate and tropical reef fish or a result of a difference in the resolution of the two investigations. The increased importance of physical complexity and heterogeneity variables at diminishing scales of investigation suggests a more proximal ecological effect of physical structure on reef fish communities at finer spatial resolutions as might be expected if in fact reef fish communities are influenced by a hierarchy of spatial processes. Hence it becomes clearer that temperate reef fish communities are complex arrangements, defined by their component parts (species) which in turn are influenced in varying degrees by ecological mechanisms responding to different components of their physical habitat at varying spatial scales. These results and the results of other studies indicate patterns and scales of fish-habitat association at which questions and hypotheses about processes can be generated and highlights the importance of incorporating multiple spatial scales of investigation into future studies of temperate reef fish-habitat relationships.

Hill et al. (2010) were able to link algal community structure and the proportion of canopy forming algae, to fetch exposure across Tasmanian coastal inshore reefs. They developed indices of wave exposure which they used to predict algal community structure and general level algal patterns across shallow temperate reef systems. Their work identified average fetch openness (defined as the average fetch distance in 48 directions out to a distance of 650 kms) as important in explaining significant proportions of the variance in the algal community structure and approximately 30% of the variability in the per cent cover of canopy forming algae related to bathymetrically weighted fetch exposure (i.e. exposure

accounting for seafloor slope). These results support the hypothesis that wave exposure has an effect of structuring the dominant biogenic character of temperate reef habitats and my own work further suggests that this effect of structuring of the algal community also indirectly structures the associated reef fish communities on temperate coastal reefs in Tasmania. Exposure and reef-algae community structure are intricately linked and therefore it is difficult to determine the precise nature of their separate effects on reef fish community structure. Friedlander et al. (2003) identified that the direction of wave exposure, the amount of habitat complexity, and the level of protection from fishing all proved to be important determinants of reef fish assemblage structure and standing stock on Hawaiian reefs. Similarly, Kendrick et al. (1999) investigated the combined effects of swell exposure and canopy dominance on understory algal community structure in Western Australia and were able to demonstrate that at local scales algal community structure was influenced by the density of kelp canopy just as much as by gradients in exposure to ocean swells. They concluded by hypothesising that the structuring of canopy and understory algal assemblages in kelp forests are influenced by a hierarchy of spatial processes from regional scale influences of exposure to physical habitat complexity and heterogeneity with increased proximal effects on localised disturbance, recruitment and grazing, each equally manifested at small spatial scales. I believe that similar hypotheses may explain the varying spatial arrangement and structure of reef fish community structure across Tasmanian rocky reef systems either as a direct effect of the variables themselves or as an indirect effect of the resulting biogenic habitat. The exact nature of these relationships warrants further investigation.

3.5.3 Study limitations

This study has identified a number of physical habitat metrics capable of explaining fish community structure, diversity and individual species distributions and abundance on

Tasmanian rocky reefs across varying spatial scales. In the process I have also encountered and identified a number of limitations and improvements to assessing reef fish habitat associations at fine scale resolutions.

Conventional studies investigating fish communities to differing habitat would typically not use such fine scale resolution, however the focus of my study was on relationships between fine scale variability in physical habitat and reef-fish community structure across a single habitat type. This necessitated a particularly fine-scale focus which had distinct disadvantages in detecting large ranging and rarer species of fish. Due to the multi-species nature of this study, there was a necessary trade-off associated with the scale of sampling employed between detecting fine scale patterns of association and detecting adequate numbers of rarer or large ranging species. Only those species which were sufficiently common across the study area could be effectively modelled, which meant that an unknown number of species-habitat associations were possibly overlooked. In this sense the investigation was limited by the project size and the practicality of surveying multispecies communities over sufficiently large extents to encounter rarer species in sufficient numbers to model their distributions and abundance. The temporal replication of the sampling was intended to minimise the chances of missing mobile and rarer species but without an absolute knowledge of the true abundance and ranges of these species it is difficult to be certain if this level of replication was adequate. It should be noted that there will be trade-offs between detection and sampling effort at any sampling scale chosen to investigate whole communities. No single sampling scale will be capable of optimally sampling all species of reef fish you are likely to encounter and therefore investigators should be aware of the sampling scales appropriate to the communities, species and habitats they are targeting. Future studies should consider the

relative abundances of species across habitats when designing surveys in order to make sufficient observations to ensure effective modelling.

Where there were sufficient numbers of observations but patterns of association were still not evident, it may be that a species was too mobile at the resolution investigated to identify clear relationships between distribution and habitat, or that the species may have been responding to its environment at different scales to which were investigated. In all likelihood the extent of this study was not large enough to capture the complete relationship between all reef fish species encountered and habitat structure, and for many species a truncated response was being modelled to a subset of the full gradient of the habitat structure available to the community. Considering environmental predictors at the wrong extent will obviously result in misinterpretation of the true response of an organism or community to its environment. This study has highlighted the necessity of obtaining sufficiently fine resolution data across large, management scale extents to ensure accurate modelling of species responses to their physical environments if a full community understanding is desired.

Environmental gradients that organisms respond to can be categorised into three approximate classes of indirect, direct and resource gradients (Austin, 1980). Organisms and communities often respond to these gradients in a spatially hierarchical fashion resulting in different patterns at different spatial resolutions and extents (Guisan and Thuiller, 2005). Gradual patterns in species distributions over large scales and coarse resolutions tend to be correlated with indirect climatic gradients, whereas patchy, small scale distributions at fine resolution are more likely the result of direct environmental gradients and patchy resource distributions resulting from local topographic variation and habitat fragmentation (Scott, 2002, Guisan and Thuiller, 2005). The type of environmental gradients considered in an investigation can limit

the applicable geographical extent and resolution across which a model can be confidently applied without significant errors. Models based on ecologically proximal, direct and resource gradients are generally the more robust and widely applicable (Iampietro et al., 2008) although the practical limitations of collecting these data by themselves often limit their use across the extents and resolutions that are required by marine planners. This problem is further considered in chapter four of this thesis in an approach which attempts to apply proxy measures of fine resolution physical habitat structure derived from broad scale, remotely sensed data, which would allow modelling of species and communities across broad management scales.

A number of direct factors that influence species and community responses were probably missing from this investigation (i.e. environmental factors such as current that may influence recruitment, competition and predation) and some of those that were included probably lacked direct ecological relevance for many of the modelled species. Including all the possible direct and resource habitat measures that may have been important could have vastly improved the explanatory power of the models however the scale of such an investigation would have been unfeasible within the confines of the project budget, as is often the problem in applied marine management situations. To some extent this was attempted in a surrogate fashion by considering exposure and the dominance of biogenic structure forming components of the habitat which in themselves dictate the presence of more direct, proximal variables. The aim of this study was to identify universal patterns between physical habitat structure and reef fish communities and where able to do so, to understand individual species responses.

Where individual species responses could not be explained, this study has at least been successful in identifying further research avenues by highlighting where possible explanatory physical variables may have been overlooked. For instance future studies may need to focus on other variables such as nutrient availability, water temperature, current flow, recruitment, abundances of known competitors, predators and prey species and other more specific components of the biogenic component of reef habitats to better model specific species responses to reef habitats. Such information can be difficult and time consuming to obtain and was not available in the context of this study but where careful consideration of the ecological requirements and scales of movement of the particular study species is possible, I believe it should be feasible to identify sufficient explanatory variables to effectively model the occurrence and abundance of the majority of Tasmanian reef fish. What is evident from my work is that although surrogates such as exposure and biogenic dominance can adequately explain components of whole community structure, the ability to understand and model specific species responses will, in many cases, require more specific and detailed understanding and measurement of relevant physical variables and the ecological mechanisms behind their effects.

There were some unavoidable limitations of sampling community structure and habitat across contiguous blocks resulting in the non-independence of sampling units. Due to the logistical and physiological time constraints of sampling fish and habitat on SCUBA it would have been very difficult to sample the same number of blocks completely independently. In effect a trade-off made in the sampling strategy between maintaining independence across the sampling units and adequate replication for effective analysis. Future studies should attempt to improve this balance by ensuring some physical separation between sample blocks but it would be difficult to guarantee complete independence without sites being positioned at

relatively large distances apart making survey on SCUBA problematic. These limitations aside, attempts to minimise errors of counting fish multiple times between blocks were made by ensuring divers were swimming at constant rates and directions along the transects making it fairly obvious to see when fish were moving between blocks and therefore avoid recording from one block to the next. Another unknown source of bias potentially exists due to the second pass made by divers along the line. Again this does introduce some non-independence since the same fish may well be sampled twice but it was considered an improvement to make a second pass while dive time permitted in order to increase chances of observing rarer species.

3.5.4 Conclusions

This study has demonstrated that temperate reef fish community structure and diversity can be modelled to some degree in response to the physical characteristics of the surrounding habitat. However modelling these responses can only give an overall insight into those variables that are important in structuring assemblages since they represent the sum of multiple species responses pulling in different ecological directions and will often be inherently biased in their representation of highly common and numerically abundant species. There is no fundamental basis for suspecting that these metrics alone will allow any specific understanding of how individual species may respond to their habitats, therefore there will always be a need to model individual species responses. This creates additional problems for researchers of identifying and modelling relevant environmental and habitat structure variables. A number of researchers have commented on the deficiency of many modelling attempts to adequately consider the ecological response of individual species to environmental gradients (Austin, 2002, Guisan and Thuiller, 2005). The use of ecological theory to underpin species distribution models is often neglected by investigators but it is extremely important for identifying the most appropriate predictors and scales, choosing

ecologically realistic response curves to each predictor and selecting between competing model approaches (Guisan and Thuiller, 2005). This study had little *a priori* knowledge of the possible link between the response of the various species to their physical habitats and it was therefore difficult to confidently apply realistic response curves to any models. Future studies should ideally select predictors based on empirical observations of individual species responses or at the very least sound ecological theory, but as is often the case, where this is not available, flexible modelling approaches such as those applied in this study possess the ability to identify important explanatory variables which can form the basis of more specific modelling of species-habitat relationships.

Understanding community-habitat associations of temperate reef fishes using fine-resolution, bathymetrically derived measures of physical structure.

4.1 Abstract

With modern advancements in remote sensing tools, physical environmental and habitat data are becoming increasingly obtainable from the marine environment. Multibeam hydro-acoustic technology now allows relatively inexpensive, broad scale, fine resolution assessments of marine fish habitats. Parallel advancements in geographic information systems (GIS), coupled with modern analytical techniques are providing researchers with a variety of potentially informative surrogate predictors of biodiversity and species responses. This study aimed to determine whether fine-scale bathymetric derivatives could be feasibly applied as surrogates to explain reef fish diversity and species-habitat associations in the absence of direct metrics of habitat and if successful, identify an effective tool for spatial marine planning. Species-habitat relationships were examined across a marine reserve on the south-eastern coast of Tasmania at ecologically relevant scales at which reef fish interact with their environments. The results of this study suggest that bathymetry derived measures of habitat structure are, by themselves, limited predictors of temperate reef fish community structure at fine resolutions. Overall community similarity patterns were correlated with derivative measures of easterly and southerly reef aspect and plane. These measures are likely acting as proxies of the predominant swell exposure direction across the survey sites. The extent to which derivative based models were able to explain patterns in the reef fish community structure, varied depending on the response variable being modelled and with the modelling approach applied, making it difficult to discern general patterns. Generalised

Additive Model (GAM) and Boosted Regression Tree (BRT) modelling approaches performed comparatively well in explaining community diversity. The most important explanatory variables of community diversity were generally slope, rugosity, bathymetry and reef-plane. There appeared to be little clear agreement between the GAM and BRT approaches in terms of the most important model terms for any of the individual species responses modelled. The responses in species abundance and occurrence to habitat structure appeared to be largely species-specific at the scales investigated here. These results warrant further research into how multibeam derived metrics of reef habitat structure, employed in combination with modern modelling approaches may be applied to explain and predict fine resolution patterns in temperate reef fish community diversity and species distributions and abundances around Tasmania. This knowledge is urgently required to effectively manage marine ecosystems and conserve biodiversity and fisheries resources. This investigation serves as an example of the potential of fine resolution bathymetric and biological data to accurately model marine reef fish communities around Tasmania and also highlights a number of practical considerations for successfully modelling communities of temperate reef fish using bathymetrically derived variables; including issues of scale, selection of appropriate predictors and survey technique.

4.2 Introduction

Apparent failures of traditional single-species fisheries management has led to an increasing impetus towards ecosystem-based approaches (Nevill, 2010), which requires a quantitative understanding of community responses to changing environments at scales relevant to marine management (Garcia et al., 2003). The collection of biological and habitat data across these scales is generally labour intensive, financially expensive, often incomplete and spatially or temporally biased (Post, 2008, Anderson et al., 2009). Understanding community-habitat associations of temperate reef-fishes is vital for effective ecosystem management because of the potential of habitat type and structure to act as surrogates for understanding broad scale patterns of biodiversity (Ward et al., 1999). Targeting suitable habitat structure and types which will maximise conservation value and safeguard over-exploited and threatened species, communities and systems is a major problem faced by policy makers and managers with the task of implementing effective marine protected areas (MPAs) (Babcock et al., 1999). Quantifying fish community responses to habitat structure is crucial for applied aspects of MPA management, particularly if the goals of these particular management approaches are to maximise biodiversity (Garcia-Charton and Perez-Ruzafa, 1998). Cost-effective predictive surrogates of reef fish biodiversity can feasibly be identified to aid ecosystem management and conservation planning where associations between communities, species and habitats can be accurately modelled (Anderson et al., 2009).

A significant number of studies from around the world have identified predictable patterns of association between habitat structure and animal communities of birds, mammals, amphibians, reptiles and insects (Tews et al., 2004). Numerous studies focused on fish have revealed that habitat structure can influence recruitment and post-recruitment survival

(Connell and Jones, 1991, Caley and St John, 1996, Tupper and Boutilier, 1997), prey availability (Warfe and Barmuta, 2004), predation and competition (Hixon and Beets, 1993, Johnson, 2006) home range size, morphology and behaviour (Shumway, 2008). Variability in the structure of marine habitats have been shown to affect the composition of the associated algal (Dahl, 1973, Harlin and Lindbergh, 1977, Ault and Johnson, 1998, Toohey et al., 2007, Toohey and Kendrick, 2008), invertebrate (Lapointe and Bourget, 1999, Beck, 2000, La Mesa et al., 2004, Alexander et al., 2009) and fish communities (Luckhurst and Luckhurst, 1978, Roberts and Ormond, 1987, Garcia-Charton and Pérez-Ruzafa, 2001, La Mesa et al., 2004, Gratwicke and Speight, 2005a, Gratwicke and Speight, 2005b, Anderson et al., 2009). Few studies have considered the community and species-specific relationships of reef fish with habitats at ecologically realistic resolutions at which they are directly interacting with their environments.

With the recent technological advancement of acoustic remote sensing tools, physical habitat data are becoming increasingly obtainable from the marine environment. Technological advances in multibeam hydro-acoustics now allow relatively inexpensive, broad scale, continuous lateral assessment of marine fish habitats at fine resolutions (i.e. across metre scales) (Purkis et al., 2008, Brown et al., 2011). Crucially this information is considerably cheaper and easier to acquire than direct diver assessments of reef habitat structure over equivalent spatial scales. Concurrent advances and developments in geographic information systems (GIS) and other analysis tools have enabled various derivative metrics of habitat structure to be calculated from bathymetric digital elevation models (DEMs) providing researchers with a variety of potentially informative surrogate measures of biodiversity and species-specific environmental responses (Underwood, 1993, Guisan and Zimmermann, 2000).

Recent studies have investigated the effectiveness of using bathymetric DEM-derived metrics of habitat structure to model patterns in the distribution of various benthic biota and habitat types (Holmes et al., 2008, Buhl-Mortensen et al., 2009, Rattray et al., 2009, Ierodiaconou et al., 2010, Hill et al., In Review) but studies utilizing similar metrics to model reef fish distributions are less common and generally focus on broad scale habitat differences. Knudby *et al* (2010) have produced spatially explicit models of species richness, biomass, and diversity of tropical reef fish communities off the coast of east Africa using machine learning models and habitat variables derived from IKONOS satellite imagery data (Knudby et al., 2010). Similarly, Kracker *et al* (2008) have used hydro-acoustic fisheries surveys to estimate fish biomass in the context of underlying features and benthic habitat types. Their research suggested that variables relating benthic habitat structure to estimated fish biomass differed based upon depth and the distance to rock ledges were the best predictors of demersal fish biomass (Kracker et al., 2008). Recently, a number of studies have attempted to apply fine resolution multibeam sonar-derived measures of habitat structure to model reef fish community diversity and species distributions (Monk et al., 2010, Monk et al., 2011). Monk *et al* (2011) successfully modelled blue-throated wrasse habitat suitability using seafloor variables derived from hydro-acoustic survey data at three spatial scales. My study is the first within Tasmanian state waters to investigate reef fish community diversity and multi-species responses in relation to fine resolution bathymetric DEM-derivatives.

The goal of species-habitat modelling is to relate spatio-temporal observations of a species or community to environmental conditions using quantitative techniques to explain and/or predict some measure of that species or community across a region, timeframe and/or range of environmental conditions (Roberts et al., 2010). Species-habitat modelling approaches have been used to explain and predict habitat associations of many different types of

organisms including marine mammals (Roberts et al., 2010), seabirds (Vilchis et al., 2006) and fish (Iampietro et al., 2008). Guisan and Zimmermann (2000) reviewed a wide variety of modelling approaches available for predicting the distribution and abundances of species and communities (Guisan and Zimmermann, 2000).

Generalised additive models (GAMs) are a commonly applied and well established statistical approach for modelling species-habitat associations (Guisan and Zimmermann, 2000). They are a semi-parametric extension of generalised linear models (GLMs) (Hastie and Tibshirani, 1986). GAMs apply a link function to represent the relationship between the mean of a response variable and a 'smoothed' function of the explanatory variable or variables (Guisan et al., 2002). The main advantage of the GAM approach is their ability to deal with highly non-linear and non-monotonic relationships between response and explanatory variables, allowing development of models which realistically represent the underlying data (Guisan et al., 2002). Studies using GAM approaches have been used to predict the distribution and abundance of demersal and pelagic fish (Abeare, 2009, Monk et al., 2012) and marine habitats (Garza-Pérez et al., 2004).

Boosted regression trees (BRTs) are a newly emerging statistical approach to modelling species distributions. The BRT approach is gaining favour with ecologists attempting to model species distribution patterns because of its strong predictive ability to identify ecologically meaningful interactions between species and environments and because model outputs can be summarised intuitively to give clear ecological insight into relationships between response and predictor variables (Elith et al., 2008). Their application in marine ecology to date has been slow but BRTs are being increasingly applied to ecological modelling problems such as the response of fish (Leathwick et al., 2006, Leathwick et al.,

2008, Abeare, 2009, Pittman et al., 2009, Knudby et al., 2010, Richards et al., 2012), benthic communities (Hill et al., In Review) and the distribution of coral diseases (Williams et al., 2010a) to the physical nature of their environments. BRTs have been shown to out-perform and provide superior flexibility over other common methods of modelling, such as GLMs and GAMs (Leathwick et al., 2006, Abeare, 2009, Elith and Leathwick, 2011). They possess many of the advantages of traditional tree based methods in their ability to handle different types of predictor variables, accommodate missing data, fit non-linear relationships, automatically handle interaction effects between predictors and require no dependency on prior data transformation or removal of outliers, while simultaneously they overcome the main problem of poor predictive performance inherent in traditional tree based methods, through fitting multiple tree models (Elith et al., 2008).

The application of BRTs and other machine learning methods to ecological problems have been slow compared to other more strictly statistical approaches, in part because they are considered less interpretable and open to quantitative scrutiny. Statistical modelling approaches start by assuming an appropriate data model based on an empirical understanding of the system and then estimate parameters from the data, focusing on the additive make-up and interactions of the model, how the response is distributed and whether observations are independent. Machine learning differs from traditional statistical approaches by initially assuming that the data generating process is complex and unknown and then developing learning algorithms which explain a particular overall response by observing dominant patterns of varying input and response (Elith et al., 2008). BRTs fall somewhere between these two distinctions. They are fundamentally a machine learning method but recent statistical developments have allowed them to be effectively interpreted as a form of regression, however the approach differs fundamentally from other traditional regression

based approaches by combining large numbers of simple tree models to identify important model terms rather than identifying a single 'Best' model.

This study utilises high resolution, multibeam acoustic data and progressive species-habitat modelling approaches to explain reef fish community responses to their environments at fine spatial scales across coastal Tasmanian reef systems. Multi-species relationships with habitat are examined at the scales relevant to which fish directly interact with their environments. Fine-scale bathymetric derivatives were tested to identify if they could be feasibly applied as surrogates to understanding biodiversity and the specific habitat associations of fish in the absence of direct metrics of habitat and in so doing identify an effective tool for managing the marine environment. This study evaluates if bathymetrically derived measures of habitat structure can be effectively applied as surrogates of direct physical measures to model temperate reef fish community structure, diversity, distributions and abundance and compares two current explanatory modelling approaches; GAMs and BRTs.

4.3 Methods

4.3.1 Study sites

Fish surveys were carried out at eleven sites within the Tinderbox marine reserve (147° 20'E, 43° 2'S) situated at the northern end of the D'Entrecasteaux Channel on the south-eastern coast of Tasmania, Australia (Figure 4.1). The tinderbox reserve covers an area of 1.44km², extending 200-300 metres offshore. A mix of sandstone outcrops and fractured dolerite reef extends almost continuously around the Tinderbox headland to a depth of approximately ten metres where the substratum then becomes sand and broken shell and is interspersed in places with small embayment's and channels. The surrounding seabed is formed of soft sediment shoals out to a depth of approximately fifty metres (Nichol et al., 2009). The reef in this area is predominantly dominated by high densities of the canopy-forming laminarian algae, *Ecklonia radiata* along with a diverse algal understory and communities of sessile invertebrates including hydrozoans, bryozoans, ascidians and sponges, typical of the broader region of eastern Tasmania (Andrew, 1999).

4.3.2 Reef fish Survey

Reef fish species and abundance were recorded at each site by a two person dive team using open-circuit SCUBA. Sites were located on sub-littoral rocky reef at intervals of approximately 300m parallel to the coastline. All sites were positioned less than 100m from shore, within and parallel to the 5-10 metre depth contour. At each site a single, 50 x 10 metre (500 m²) transect was positioned across the reef and the beginning and end marked with fixed subsurface buoys to allow accurate GPS location fixes from a surface vessel. Each transect was divided into twenty, 25 m² blocks either side of the transect centreline, by marking 5 metre intervals along the centre line and visually estimating 5 metre out from

either side. reef fish species identity and abundance were recorded within each 25 m² block by a single observer swimming approximately 2.5 metres to one side of the transect centerline. See methods section of chapter three, Figure 3.4 for a detailed explanation of the survey method employed. Transects were repeatedly surveyed in this fashion across two separate survey periods. Three sites (LP, PP and TB) were each surveyed on five separate occasions between May and July 2010 as part of a previous study and an additional eight sites were each surveyed on three separate occasions, using exactly the same survey method, between October and December 2011. Hence forth these two survey groups are referred to as the winter 2010 and autumn 2011 surveys respectively.

4.3.3 Physical habitat survey

Eleven reef habitat structure metrics were derived from a 2 x 2 m resolution bathymetric digital elevation model (DEM) using a number of toolbox applications in the ArcGIS 9.3 software package. A Kongsberg EM3002(D) 300kHz multibeam sonar was employed to collect the bathymetric data for selected areas of the Tinderbox Marine Reserve courtesy of *Geoscience Australia* (GA). The multibeam bathymetric data was resolved to 2 metre resolution and output as an xyz grid using Caris HIPS/SIPS v. 6.1 software to remove vessel movement and tide related artefacts. Soundings were accurate to within 0.1 of a metre (Barrett and Nichol, 2009). From the DEM, eleven derivative variables used to characterise seafloor structure and topography were generated using toolbox extensions in ArcGIS 9.2 and ArcView 3.2. The eleven bathymetric derivatives are listed in Table 4.1, along with a description of the variable and the software and relevant toolboxes used to generate each.

It does qualify that the accuracy of the soundings should be within 0.1 of a meter. But this all depends on the spatial analysis. The data was resolved to a 2 m grid and given the number of soundings that might be in a 2 m grid I would say the data would be within 0.1 m level of

accuracy. However, we did not model the uncertainty (using the standard deviation of the soundings) so there is no pure reference. I would say though that any of the uncertainty in this particular application is not going to come from the vertical or horizontal uncertainty in the MBES data but more in the relationship between the two scales of data: diver survey and the 2 m grid resolution.

Geo-referenced polygon shapefiles were constructed in ArcGIS 9.3 to delineate the block outlines of each transect at each site and then overlaid onto separate raster layers of the eleven physical derivatives. From these layers average derivative values were calculated for each 25 m² block (using the zonal statistics tool in ArcGIS 9.3). These averaged derivative variables (per block) were considered as the predictor variables in all subsequent model analyses. A draftsman plot of the individual predictor variables was consulted prior to analysis to identify extreme bi-variate correlations and redundant predictors from the models but there were insufficient correlations between any pair of variables to warrant any removals.

4.3.1 Data analysis

Occurrence, mean abundance, and three indices of community diversity (calculated from observed abundance and occurrence) were used to relate the reef fish community response to physical habitat structure. The abundance for each species surveyed were averaged across replicate surveys for each of the two hundred and twenty 25m² blocks and $\log(x+1)$ transformed to reduce differences in scale among the species variables, reduce the contribution of highly abundant species and ensure the contribution of rarer species. Species occurrence (i.e. presence/absence), was determined for each of the two hundred and twenty 25 m² blocks. Three measures of diversity were calculated from the mean species abundance data for each of the two hundred and twenty 25m² blocks to reduce the complexity of the

multispecies assemblage data into single, easily interpretable univariate response variables. Refer to the methods section of chapter three for a complete explanation and description of the diversity indices considered and how they were calculated.

Nested PERMANOVA and ANOVA analyses of site nested within survey season were applied to identify differences in community similarity and the three measures of diversity respectively.

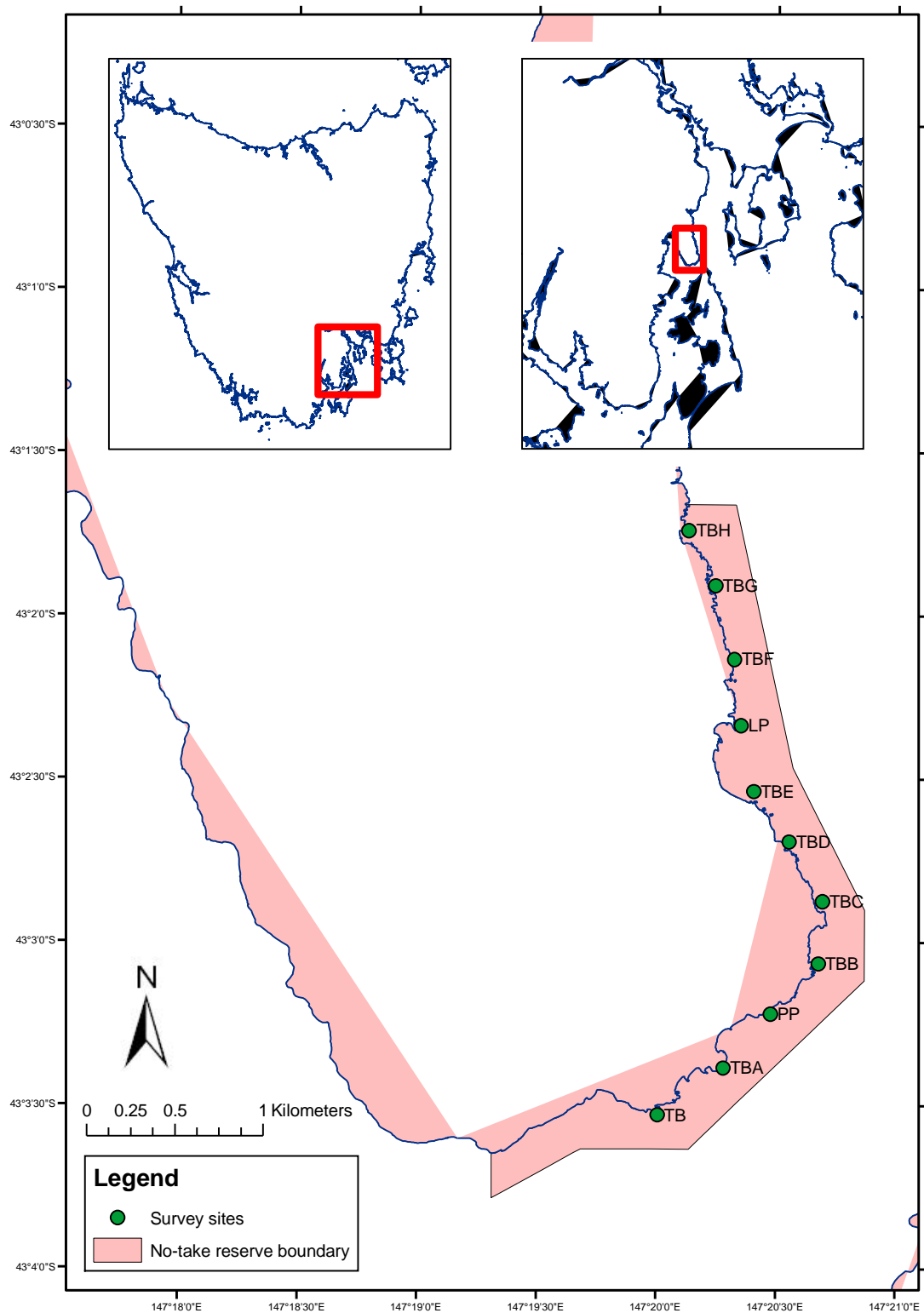


Figure 4.1. Tinderbox marine reserve boundary and study site locations.

Table 4.1. Bathymetric derivative descriptions and software and toolboxes used to generate them.

Derivative	Variable description (3x3 pixel analysis extent unless specified below)	Software/ toolbox
Bathymetry	Depth (negative elevation) of the grid cell. Bathymetric product generated from ascii output file into grid with 2m resolution	Spatial Analyst- ArcGIS 9.3
Slope	Slope denotes the maximum change in depth between each cell and the cells in an analysis neighbourhood. Calculated in degrees from horizontal (Wilson et al., 2007).	Spatial Analyst- ArcGIS 9.3
Curvature	Seabed curvature defined as the derivative of the rate of change of the seabed. It is a quantifiable measure of the shape of the seabed surface.	Spatial Analyst- ArcGIS 9.3
Profile curvature	Profile curvature is a measure of the seabed in the direction of the slope of the seabed	Spatial Analyst- ArcGIS 9.3
Eastness	Deviation from east is a value that reflects how much the aspect value deviates from 90 degrees.	Jenness Grid Tools – ArcView Extension
Southness	Deviation from south is a value that reflects how much the aspect value deviates from 180 degrees.	Jenness Grid Tools – ArcView Extension
Topographic Position Index (TPI)	This is a measure of a location relative to the overall landscape. It is calculated by comparing the elevation of a cell with the mean elevation of surrounding cells by an analysis extent of 10. Locations that are higher than their surroundings will have positive value, whilst areas that are lower will have negative values. Flat areas have values closer to zero (Weiss, 2001).	Benthic Terrain Modeller Tool for ArcGIS
Rugosity	The rugosity measure is a ratio of the surface area to the planar area across the neighbourhood of the central pixel in a 3x3 neighbourhood (Jenness, 2002.). By this method flat areas will have a rugosity value near to 1, whilst high relief areas will exhibit higher values of rugosity. This analysis is limited to a single scale and whether or not it captures rugosity at a level relevant to observed habitat is therefore sensitive to the initial raster resolution.	Jenness Grid Tools – ArcView Extension
Channel morphometric	The proportion of cells within each survey block that lie in a local concavity that is orthogonal to a line with no concavity/convexity (Wood, 1996).	LandSerf 2.3.1
Ridge morphometric	The proportion of cells within each survey block that lie on a local convexity that is orthogonal to a line with no convexity/concavity (Wood, 1996).	LandSerf 2.3.1
Plane morphometric	The proportion of cells within each survey block that do not lie on any surface concavity or convexity (Wood, 1996).	LandSerf 2.3.1

4.3.2 Multivariate community analysis

Multivariate analyses of reef fish community data were carried out using routines from the R and PRIMER 6.1.11 PERMANOVA+ software packages (Clarke and Gorley, 2006). The ‘*PERMANOVA+ for PRIMER*’ manual (Anderson et al., 2008) and ‘*Change in Marine*

Communities' texts (Clarke and Warwick, 2001) provide further, detailed descriptions and explanations of the following statistical approaches and analysis routines applied.

The $\log(x+1)$ transformed reef fish average abundance data for each block were converted to Bray-Curtis measures of similarity and used to construct a resemblance matrix between all 220 pairs of sample blocks for the eleven sites. Community structure was investigated using a PERMANOVA (permutational MANOVA) test to identify significant differences in reef fish community similarity between sites and between the winter 2010 and autumn 2011 survey groups. PERMANOVA is a routine for testing the response of multivariate data to one or more factors, on the basis of a resemblance measure, with the use of permutational methods (Anderson et al., 2008). The similarity percentages routine (SIMPER) was applied to determine the species that characterized and differentiated the community assemblages within and between sites. DISTLM (distance-based linear modelling) and dbRDA (distance-based redundancy analysis) were used respectively to model and visualise the variability in reef fish communities between sites in relation to an optimal number of the physical derivatives. Refer to the methods section of chapter three for a complete description of the DISTLM and dbRDA techniques. The strength and direction of the strongest correlations between the individual physical variables (identified in the proceeding DISTLM) and each of the dbRDA axes were visually interpreted with vector overlays calculated from the multiple partial correlations between each variable and the dbRDA axis scores. Each vector was interpreted as the effect of that particular variable on the construction of the ordination image; the longer the vector, the larger the association of the variable, in the direction of the associated axes.

4.3.3 Univariate response modelling

Individual species abundances and occurrence along with the three measures of diversity were modelled in relation to the eleven bathymetric derived reef-habitat metrics using

generalised additive models (GAMs) and boosted regression trees (BRTs). Both modelling techniques were carried out using libraries and functions in the R statistics software, version 2.13.1.

GAMs were fitted with default parameters and a Gaussian or Bernoulli (binomial) family distribution and identity link using the “gam” function in the “mgcv” library (Wood, 2001) in R. GAMs apply a link function to represent the relationship between the mean of a response variable and a ‘smoothed’ function of the explanatory variable or variables (Guisan et al., 2002). The smooth terms of the models were calculated using penalized regression splines, with selection of smoothing parameters determined by the minimization of an internal generalized cross validation function (Wood, 2004, Wood, 2008). GAMs for each response variable modelled were constructed with the same combination of eleven physical variables for ease of comparison between modelled responses and with BRT modelling approaches. Where a model identified significant terms, the fitted function was plotted against the particular model term to understand the individual relationships between response and predictor variables. For each GAM model run, diagnostic plots and Cook’s leverage plots of the fits were examined to ensure conformity to standard regression assumptions.

BRT models were fitted with cross validation using the *gbm* and *gbm.step* packages in R (Elith et al., 2008). Construction of optimal BRT models for each response variable was achieved through selecting the appropriate values of three parameters; learning rate, tree complexity and bag fraction to minimise residual deviance in the resulting models. The learning rate is a shrinkage parameter which determines the contribution of each tree to the growing model, tree complexity refers to the number of nodes permitted within each tree and controls the level of predictor interactions fitted and the bag fraction is the proportion of the

full data selected at each iteration. Together these three parameters determine the number of trees required for optimal prediction (see Elith et al. (2008) for further explanation). Loop coding was written in R to perform parameter selection and arrive at an ‘optimum’ model with the minimum residual deviance for each response variable investigated. Abundance of individual species and measures of diversity were modelled using a Gaussian error distribution, and species occurrences (i.e. presence or absence) were modelled using a Bernoulli (binomial) error distribution. Measures of relative influence of each predictor term in the regression tree models was calculated using script functions included in the *gbm.step* package in R (Elith et al., 2008). Where a model explained a relatively high proportion of the deviance, partial dependency plots were used to understand the individual relationships between response and predictor variables with the highest relative influence in the model after accounting for the average effects of all other variables in the model. Interactions between predictor variables influencing a particular response variable were identified using the *gbm.interactions* package (Elith and Leathwick, 2011) in R and plotted. For each of the fitted GAM and BRT model, D^2 values were calculated as a measure of explained deviance for comparison, where: $D^2 = 1 - (\text{residual deviance}/\text{total deviance})$.

4.4 Results

4.4.1 General findings

A total of 10,026 individual reef fish observations were recorded throughout the total survey period comprising thirty-three species from twenty-one families. The southern hulafish, *Trachinops caudimaculatus* was the most numerically abundant species encountered, comprising 67.5% of the total abundance of reef fish surveyed, followed by the bluethroat wrasse, *Notolabrus tetricus* (9.3%), the longfin pike, *Dinolestes lewini* (8.7%), the smallscale bullseye, *Pempheris multiradiata* (8.0%) plus all other species combined (6.5%). The bluethroat wrasse, *Notolabrus tetricus* had the highest proportion of occurrence, occurring in 97.7% of blocks surveyed, followed by the southern hulafish, *Trachinops caudimaculatus* (40.0%), the senator wrasse, *Pictilabrus laticlavius* (36.8%), the bastard trumpeter, *Latridopsis forsteri* (26.8%) and the purple wrasse, *Notolabrus fucicola* (26.4%). The remaining twenty nine species all occurred in less than 15% of the blocks surveyed (Figure 4.2).

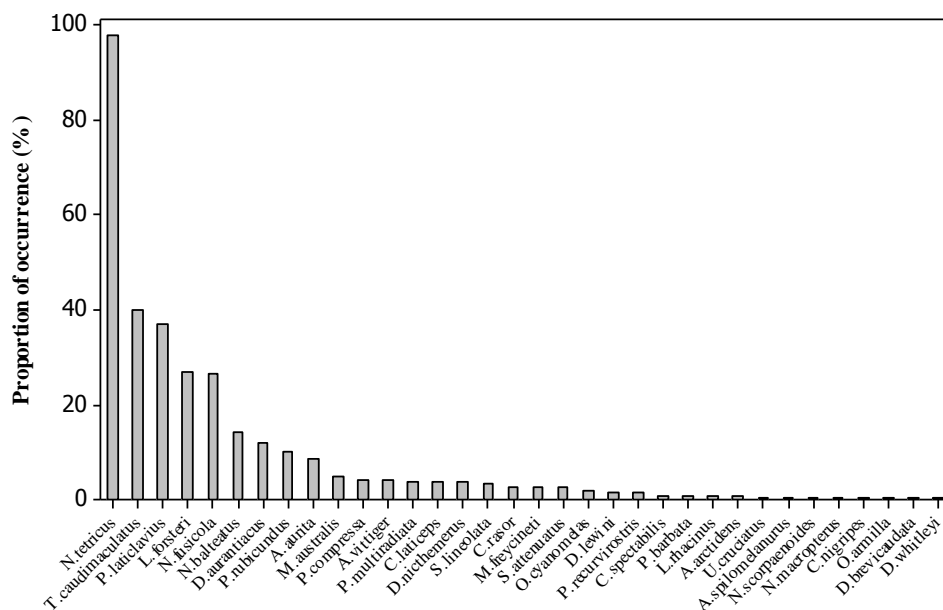


Figure 4.2. Proportion of species occurrence across all 220 blocks surveyed within the Tinderbox marine reserve.

4.4.2 Community assemblage

Significant differences in the reef fish species richness (S) and Margalef's (d) existed between sites and between the winter 2010 and autumn 2011 surveys (Table 4.2). No significant difference in community similarity was detected between the winter and autumn surveys giving me confidence that the differing survey times should not confound any subsequent multivariate community analysis. Differences in the community diversity measures between the winter 2010 and autumn 2011 surveys highlighted potentially confounding issues of seasonal variability with the potential to mask habitat response effects between sites. However, earlier, more extensive work carried out by Edgar and Barrett (1999) found no significant effect of season in the reef fish community assemblages of the Tinderbox marine reserve surveyed between 1992 and 1997 and therefore for the following analyses, the assumption was made that any confounding effect of seasonal variability in the community assemblages would be minimal.

SIMPER analysis identified the individual species which were the most important in characterising and differentiating the community assemblages within and between site (Table 4.4). DISTLM (based on an AIC criteria and 'Best' selection procedure) identified three of the eleven derivatives; *southness*, *eastness* and *plane* as the optimum model for the maximum explanation of reef fish community variability between sites. Figure 4.3 displays the dbRDA ordination of the preceding DISTLM model. The first and second axes of the plot accurately depict 98.7% of the fitted model, however the DISTLM models overall explanation of reef fish community variability was poor with $R^2 = 0.07$ suggesting a lack of general association between individual species and any particular physical variable.

Table 4.2. PERMANOVA and ANOVA results of community similarity and diversity between site and survey group. Community similarity is based Bray-Curtis resemblance of log(x+1) transformed abundance. Significant *p*-value results are highlighted in bold.

Community similarity

Source	Df	SS	Adj MS	Unique permutations	Pseudo- <i>F</i>	P (perm)
Status	1	15459	15459	165	1.9699	0.127
Site (Status)	9	70631	7847.9	994	5.5001	0.001
Residual	209	369.250	369.250			
Total	219	458.595				

Number of species (*S*)

Source	Df	SS	Adj MS	Adj MS	<i>F</i>	P
Status	1	51.212	51.212	51.212	28.99	0.000
Site (Status)	9	38.133	38.133	4.237	2.40	0.013
Residual	209	369.250	369.250	1.767		
Total	219	458.595				

Margalef's index (*d*)

Source	Df	SS	Adj MS	Adj MS	<i>F</i>	P
Status	1	96.965	96.965	96.965	24.06	0.000
Site (Status)	9	211.431	211.431	23.492	5.83	0.000
Residual	209	842.193	842.193	4.030		
Total	219	1150.589				

Shannon-Wiener (*H*)

Source	Df	SS	Adj MS	Adj MS	<i>F</i>	P
Status	1	0.0940	0.0940	0.0940	0.53	0.466
Site (Status)	9	7.4880	7.4880	0.8320	4.71	0.000
Residual	209	36.8899	36.8899	0.1765		
Total	219	44.4718				

4.3. Names and taxonomic membership for reef fish species encountered across all survey within the Tinderbox marine reserve.

Species	Common name	Class	Order	Family
<i>Acanthaluteres spilomelanurus</i>	Bridled Leatherjacket	Actinopterygii	Tetraodontiformes	Monacanthidae
<i>Acanthaluteres vittiger</i>	Toothbrush Leatherjacket	Actinopterygii	Tetraodontiformes	Monacanthidae
<i>Aplodactylus arctidens</i>	Marblefish	Actinopterygii	Perciformes	Aplodactylidae
<i>Aracana aurita</i>	Shaw's Cowfish	Actinopterygii	Tetraodontiformes	Aracanidae
<i>Caesioperca rasor</i>	Barber Perch	Actinopterygii	Perciformes	Serranidae
<i>Cephaloscyllium laticeps</i>	Draughtboard Shark	Elasmobranchii	Carcharhiniformes	Scyliorhinidae
<i>Cheilodactylus nigripes</i>	Magpie Perch	Actinopterygii	Perciformes	Cheilodactylidae
<i>Cheilodactylus spectabilis</i>	Banded Morwong	Actinopterygii	Perciformes	Cheilodactylidae
<i>Dasyatis brevicaudata</i>	Smoothback ray	Elasmobranchii	Rajiformes	Dasyatidae
<i>Dinolestes lewini</i>	Longfin Pike	Actinopterygii	Perciformes	Dinolestidae
<i>Diodon nichthemerus</i>	Porcupine fish	Actinopterygii	Tetraodontiformes	Diodontidae
<i>Dipturus whitleyi</i>	Whitley's skate	Elasmobranchii	Rajiformes	Rajidae
<i>Dotalabrus aurantiacus</i>	Pretty Polly	Actinopterygii	Perciformes	Labridae
<i>Latridopsis forsteri</i>	Bastard Trumpeter	Actinopterygii	Perciformes	Latridae
<i>Lotella rhacina</i>	Beardie Cod	Actinopterygii	Gadiformes	Moridae
<i>Meuschenia australis</i>	Brownstriped Leatherjacket	Actinopterygii	Tetraodontiformes	Monacanthidae
<i>Meuschenia freycineti</i>	Six-spined Leatherjacket	Actinopterygii	Tetraodontiformes	Monacanthidae
<i>Nemadactylus macropterus</i>	Jackass Morwong	Actinopterygii	Perciformes	Cheilodactylidae
<i>Neoodax balteatus</i>	Little Weed Whiting	Actinopterygii	Perciformes	Odacidae
<i>Neosebastes scorpaenoides</i>	Gurnard Perch	Actinopterygii	Scorpaeniformes	Neosebastidae
<i>Notolabrus fuscicola</i>	Purple Wrasse	Actinopterygii	Perciformes	Labridae
<i>Notolabrus tetricus</i>	Bluethroat Wrasse	Actinopterygii	Perciformes	Labridae
<i>Odax cyanomelas</i>	Herring Cale	Actinopterygii	Perciformes	Odacidae
<i>Omegophora armilla</i>	Ringed Toadfish	Actinopterygii	Tetraodontiformes	Tetraodontidae
<i>Pempheris multiradiata</i>	Bigscale Bullseye	Actinopterygii	Perciformes	Pempheridae
<i>Pentaceropsis recurvirostris</i>	Longsnout boarfish	Actinopterygii	Perciformes	Pentacerotidae
<i>Pictilabrus laticlavius</i>	Senator Wrasse	Actinopterygii	Perciformes	Labridae
<i>Pseudolabrus rubicundus</i>	Rosy Wrasse	Actinopterygii	Perciformes	Labridae
<i>Pseudophycis barbata</i>	Red Cod	Actinopterygii	Gadiformes	Moridae
<i>Scorpiis lineolata</i>	Silver Sweep	Actinopterygii	Perciformes	Kyphosidae
<i>Siphonognathus attenuatus</i>	Slender or Pencil weed whiting	Actinopterygii	Perciformes	Odacidae
<i>Trachinops caudimaculatus</i>	Southern Hulafish	Actinopterygii	Perciformes	Plesiopidae
<i>Urolophus cruciatus</i>	Banded Stingaree	Elasmobranchii	Rajiformes	Urolophidae

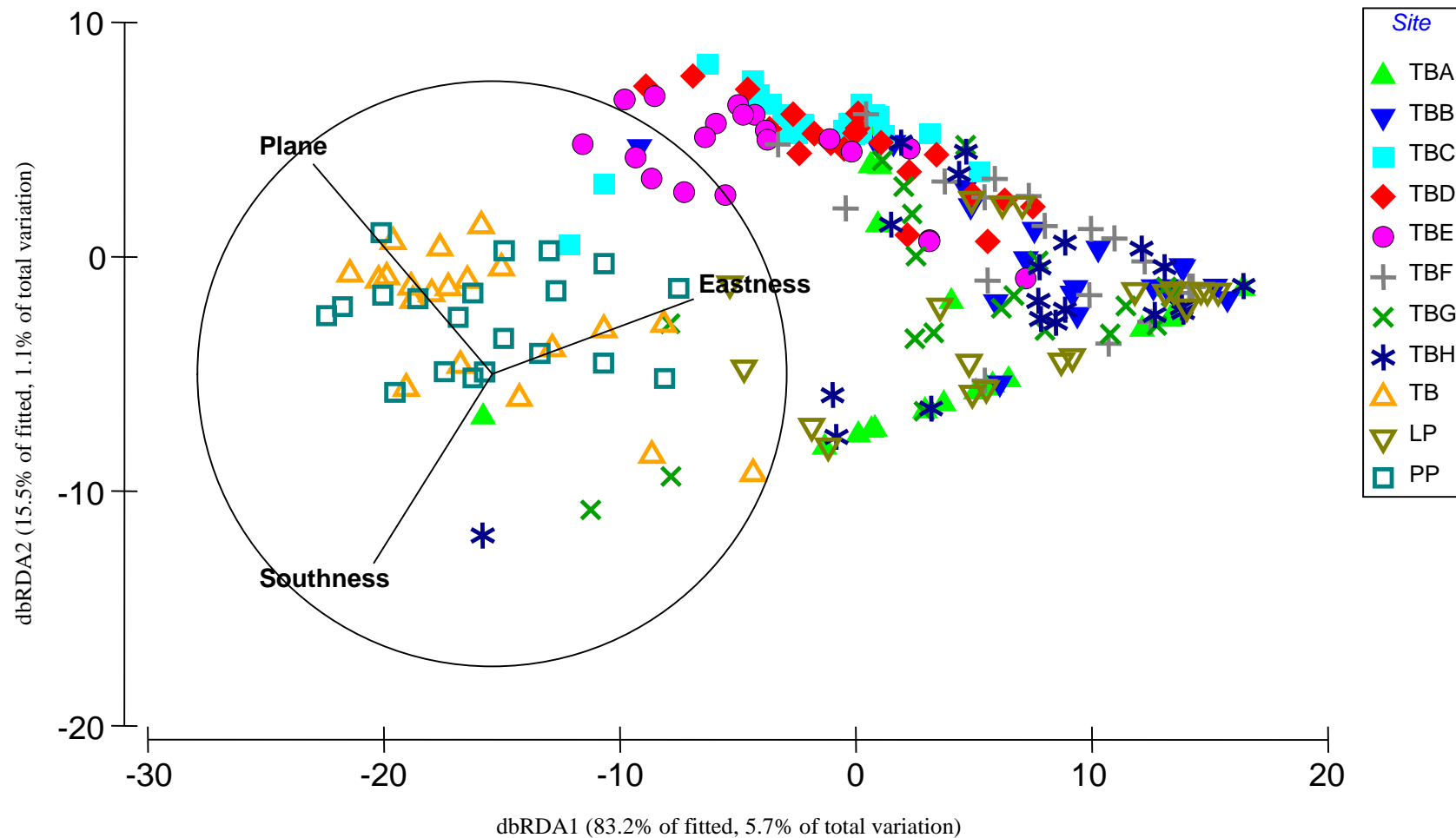


Figure 4.3. dbRDA ordination identifying the greatest variation through the multispecies Tinderbox reef fish abundance data ($\log(x+1)$ transformed) as defined by the ‘Best’ fitted variables identified by the DISTLM model and overlaid with the multiple partial correlations ($r \geq 0.2$) of the derivative variables. See figure 1 for site locations.

Table 4.4. SIMPER results identifying the important individual species responsible for within-site assemblage similarities (shaded grey) and between-site dissimilarities (unshaded). Individual contributions to similarity or dissimilarity are included in brackets.

	TBA	TBB	TBC	TBD	TBE	TBF	TBG	TBH	TB	LP	PP
TBA	<i>N.tetricus</i> (81.42%) <i>T. caudimaculatus</i> (7.46%) <i>N.fucicola</i> (4.42%)										
TB B	<i>T. caudimaculatus</i> (27.32%) <i>P. laticlavus</i> (10.84%) <i>N.fucicola</i> (10.7%)	<i>N.tetricus</i> (78.76%) <i>T. caudimaculatus</i> (16.92%)									
TB C	<i>T. caudimaculatus</i> (39.41%) <i>N.fucicola</i> (10.58%) <i>P. laticlavus</i> (10.56%)	<i>T. caudimaculatus</i> (40.13%) <i>P. laticlavus</i> (11.14%) <i>N.fucicola</i> (9.93%)	<i>T. caudimaculatus</i> (51.6%) <i>N.tetricus</i> (37.84%) <i>P. laticlavus</i> (5.29%)								
TB D	<i>T. caudimaculatus</i> (18.58%) <i>P. laticlavus</i> (12.21%) <i>N.fucicola</i> (11.21%)	<i>T. caudimaculatus</i> (25.22%) <i>P. laticlavus</i> (11.68%) <i>L. forsteri</i> (9.15%)	<i>T. caudimaculatus</i> (39.69%) <i>P. laticlavus</i> (10.08%) <i>N.fucicola</i> (9.04%)	<i>N.tetricus</i> (78.82%) <i>P. laticlavus</i> (6.4%) <i>L. forsteri</i> (6.24%)							
TB E	<i>T. caudimaculatus</i> (20.47%) <i>P. laticlavus</i> (13.09%) <i>N.fucicola</i> (9.7%)	<i>T. caudimaculatus</i> (27.72%) <i>P. laticlavus</i> (13.26%) <i>S. lineolata</i> (8.92%)	<i>T. caudimaculatus</i> (40.24%) <i>P. laticlavus</i> (10.93%) <i>N.fucicola</i> (8.59%)	<i>T. caudimaculatus</i> (17.62%) <i>P. laticlavus</i> (13.52%) <i>L. forsteri</i> (9.2%)	<i>N.tetricus</i> (81.09%) <i>P. laticlavus</i> (9.21%)						
TB F	<i>T. caudimaculatus</i> (16.77%) <i>L. forsteri</i> (16.15%) <i>N.fucicola</i> (15.85%)	<i>T. caudimaculatus</i> (24.87%) <i>L. forsteri</i> (14.7%) <i>N.fucicola</i> (13.17%)	<i>T. caudimaculatus</i> (43.73%) <i>N.fucicola</i> (11%) <i>P. laticlavus</i> (10.34%)	<i>L. forsteri</i> (18.11%) <i>N.fucicola</i> (14.89%) <i>P. laticlavus</i> (14.7%)	<i>L. forsteri</i> (15.23%) <i>T. caudimaculatus</i> (14.82%) <i>P. laticlavus</i> (14.63%)	<i>N.tetricus</i> (74.84%) <i>L. forsteri</i> (11.99%) <i>N.fucicola</i> (8.06%)					
TB G	<i>L. forsteri</i> (17.93%) <i>T. caudimaculatus</i> (14.65%) <i>N.fucicola</i> (13.07%)	<i>T. caudimaculatus</i> (20.09%) <i>L. forsteri</i> (18.42%) <i>N.fucicola</i> (11.47%)	<i>T. caudimaculatus</i> (36.51%) <i>L. forsteri</i> (13.64%) <i>N.fucicola</i> (9.83%)	<i>L. forsteri</i> (17.63%) <i>P. laticlavus</i> (13.21%) <i>N.fucicola</i> (12.74%)	<i>L. forsteri</i> (18.69%) <i>T. caudimaculatus</i> (13.3%) <i>P. laticlavus</i> (12.19%)	<i>L. forsteri</i> (20.98%) <i>N.fucicola</i> (17.23%) <i>P. laticlavus</i> (15.74%)	<i>N.tetricus</i> (56.35%) <i>L. forsteri</i> (24.06%) <i>N.fucicola</i> (9.35%)				
TB H	<i>T. caudimaculatus</i> (16.26%) <i>N.fucicola</i> (12.78%) <i>P. laticlavus</i> (10.77%)	<i>T. caudimaculatus</i> (25.46%) <i>P. laticlavus</i> (9.93%) <i>N.fucicola</i> (9.13%)	<i>T. caudimaculatus</i> (43.3%) <i>P. laticlavus</i> (9.6%) <i>N.fucicola</i> (9.33%)	<i>L. forsteri</i> (13.11%) <i>P. laticlavus</i> (12.74%) <i>N.fucicola</i> (10.7%)	<i>T. caudimaculatus</i> (14.82%) <i>P. laticlavus</i> (13.85%) <i>S. lineolata</i> (9.75%)	<i>L. forsteri</i> (20.54%) <i>N.fucicola</i> (17.38%) <i>P. laticlavus</i> (13.96%)	<i>L. forsteri</i> (21.16%) <i>N.fucicola</i> (13.76%) <i>P. laticlavus</i> (13.04%)	<i>N.tetricus</i> (92.25%)			
TB	<i>T. caudimaculatus</i> (37.92%) <i>P. laticlavus</i> (7.32%) <i>N.fucicola</i> (6.32%)	<i>T. caudimaculatus</i> (40.6%) <i>N. balteatus</i> (8.01%) <i>P. laticlavus</i> (7.44%)	<i>T. caudimaculatus</i> (34.05%) <i>P. laticlavus</i> (9.79%) <i>N.fucicola</i> (7.9%)	<i>T. caudimaculatus</i> (38.67%) <i>P. laticlavus</i> (7.86%) <i>L. forsteri</i> (7.46%)	<i>T. caudimaculatus</i> (39.19%) <i>P. laticlavus</i> (8.97%) <i>N. balteatus</i> (6.76%)	<i>T. caudimaculatus</i> (41.25%) <i>L. forsteri</i> (10%) <i>N.fucicola</i> (7.91%)	<i>T. caudimaculatus</i> (34.56%) <i>L. forsteri</i> (12.56%) <i>P. laticlavus</i> (8.03%)	<i>T. caudimaculatus</i> (41.49%) <i>P. multiradiata</i> (6.1%) <i>P. laticlavus</i> (6.04%)	<i>T. caudimaculatus</i> (46.9%) <i>N.tetricus</i> (45.46%)		
LP	<i>P. laticlavus</i> (13.46%) <i>T. caudimaculatus</i> (12.61%) <i>L. forsteri</i> (11.7%)	<i>T. caudimaculatus</i> (18.53%) <i>P. laticlavus</i> (13.04%) <i>L. forsteri</i> (11.52%)	<i>T. caudimaculatus</i> (34.87%) <i>P. laticlavus</i> (9.53%) <i>L. forsteri</i> (8.66%)	<i>P. laticlavus</i> (13.28%) <i>L. forsteri</i> (12.77%) <i>T. caudimaculatus</i> (9.7%)	<i>P. laticlavus</i> (12.59%) <i>L. forsteri</i> (12.16%) <i>T. caudimaculatus</i> (12.11%)	<i>L. forsteri</i> (15.6%) <i>P. laticlavus</i> (15.34%) <i>N.fucicola</i> (11.95%)	<i>L. forsteri</i> (13.56%) <i>P. laticlavus</i> (12.71%) <i>N.fucicola</i> (11.16%)	<i>P. laticlavus</i> (15.05%) <i>L. forsteri</i> (14.21%) <i>P. rubicundus</i> (7.97%)	<i>T. caudimaculatus</i> (34.32%) <i>P. laticlavus</i> (9.22%) <i>L. forsteri</i> (8.54%)	<i>N.tetricus</i> (55.99%) <i>P. laticlavus</i> (19.73%) <i>L. forsteri</i> (13.13%)	
PP	<i>T. caudimaculatus</i> (25.84%) <i>P. laticlavus</i> (11.64%) <i>N.fucicola</i> (10.02%)	<i>T. caudimaculatus</i> (28.51%) <i>P. laticlavus</i> (12.08%) <i>N. balteatus</i> (10.36%)	<i>T. caudimaculatus</i> (32.01%) <i>P. laticlavus</i> (11.19%) <i>N.fucicola</i> (10.1%)	<i>T. caudimaculatus</i> (27.09%) <i>P. laticlavus</i> (11.26%) <i>N. balteatus</i> (9.55%)	<i>T. caudimaculatus</i> (27.27%) <i>P. laticlavus</i> (11.59%) <i>N. balteatus</i> (9.61%)	<i>T. caudimaculatus</i> (28.57%) <i>L. forsteri</i> (12.31%) <i>P. laticlavus</i> (11.72%)	<i>T. caudimaculatus</i> (23.97%) <i>L. forsteri</i> (14.56%) <i>P. laticlavus</i> (10.55%)	<i>T. caudimaculatus</i> (27.81%) <i>P. laticlavus</i> (11.22%) <i>N. balteatus</i> (9.17%)	<i>T. caudimaculatus</i> (32.83%) <i>P. laticlavus</i> (9.59%) <i>N. balteatus</i> (8.96%)	<i>T. caudimaculatus</i> (23.42%) <i>L. forsteri</i> (10.31%) <i>P. laticlavus</i> (9.07%)	<i>N.tetricus</i> (44.57%) <i>T. caudimaculatus</i> (30.48%) <i>P. laticlavus</i> (10.76%)

4.4.3 Community Diversity

Significant differences in species richness (S) and Margalef's (d) of reef fish diversity existed between sites within seasons (Table 4.2). Significant differences also existed for the number of species (S) and Margalef's index (d) between the two groups of surveys (i.e. the winter 2010 surveyed sites (LP, PP and TB) and the autumn 2011 surveyed sites (TBA-TBH)) (Table 4.2). However, from the evidence of previous, extensive work by Edgar and Barrett (1999), the assumption was made for the following analyses that any confounding effect of seasonal variability in the community assemblages would be minimal. Measures of diversity were generally highest for the LP and TBG sites for the winter 2010 and autumn 2011 surveyed sites respectively (Figure 4.4).

GAMs fitted for all three diversity variables showed statistically significant reductions in model deviance from the null (Table 4.5). BRTs explained notable proportions for each of the diversity response variable modelled (Table 4.6). GAM analysis identified the total species (S) as the best explained diversity response variable modelled, with a D^2 of 30.9%. Significant predictor variables included *rugosity* ($p < 0.001$) and *profile* ($p = 0.045$). The remaining significant models of Margalef's (d) and Shannon-Wiener explained 29.2% and 22% deviance respectively. Figure 4.5 displays the specific relationship between each community diversity measure and the statistically significant predictor variables with GAM partial residual plots. BRT analysis identified Margalef's (d) as the best explained diversity response variable modelled, with a D^2 of 30.1%, largely influenced by a combination of average *bathymetry* (20.9%), *slope* (16.7%) and *rugosity* (16%) (Figure 4.6). The remaining models of number of species (S) and Shannon-Wiener (H) explained between 19.7% and 19.1% deviance respectively. Figure 4.6 displays the specific relationships between each

diversity response variable and the four most influential predictor variables identified by BRT analysis as plots of fitted functions verses the observed values.

Table 4.5. GAM model analysis of community diversity, ANOVA results between null and model deviance and significant model terms.

Indices	<i>F</i>	<i>df</i>	<i>P</i>	Significant model terms	Residual deviance	Total deviance	Deviance explained(D^2)
<i>Total species (S)</i>	3.14	27.0	<0.001	<i>Rugosity</i> ($F=4.69, p=0.001$), <i>Profile</i> ($F=4.08, p=0.045$)	316.11	457.16	30.9%
<i>Margalef's (d)</i>	2.89	27.2	<0.001	<i>Slope</i> ($F=4.05, p=0.002$), <i>Rugosity</i> ($F=3.76, p<0.001$)	812.94	1147.87	29.2%
<i>Shannon-Wiener (H)</i>	3.09	18.22	<0.001	<i>Slope</i> ($F=2.61, p=0.03$) <i>Rugosity</i> ($F=4.08, p=0.004$) <i>Plane</i> ($F=4.3, p=0.04$) <i>Channel</i> ($F=4.66, p=0.03$)	34.7	44.46	22%

Table 4.6. BRT model analysis of community diversity, ‘optimal’ selected model parameters and the top four important terms for each model. Tree complexity (tc), learning rate (lr), bag fraction (bf), number of trees (nt).

Indices	Tree complexity	Learning rate	Bag fraction	Residual deviance	Number of trees	SE	Total deviance	Deviance explained(D^2)
<i>Total species (S)</i>	5	0.0005	0.75	1.676	1350	0.207	2.087	19.7%
<i>Margalef's (d)</i>	5	0.001	0.75	3.664	1100	0.834	5.241	30.1%
<i>Shannon-Wiener (H)</i>	4	0.0005	0.75	0.164	1800	0.013	0.203	19.1%

Notable interactions were identified by the BRT analysis between model terms for two of the three diversity response variables. Interactions were identified for the total number of species (*S*) between average *southness* and *TPI*, with higher species richness expected on more southerly facing, higher *TPI* value reef (Figure 4.7). Interactions were identified for Margalef’s index (*d*) between average *bathymetry* and *profile*, with higher values of *d* expected on shallower, lower profile areas of reef (Figure 4.8).

GAM and BRT models of community diversity explained comparatively similar proportions of model deviance. GAMs achieved D^2 results of between 22% and 30.9% compared to BRT with D^2 results of between 19.1% and 30.1%. BRTs out performed GAMs for Margalef’s (*d*).

The most important explanatory physical variables of community diversity appeared to be *slope*, *rugosity*, *bathymetry* and *plane*. GAMs selected *rugosity* as significant model terms for all of the community diversity response variables and *slope* for Margalef's (*d*) and Shannon-Wiener (*H*) (Figure 4.5). BRTs identified *southness* and *eastness* as the most important model terms explaining the number of species (*S*), *plane* as the most important term explaining Shannon-Wiener (*H*) and *bathymetry*, *rugosity* and *slope* as the most important variables explaining Margalef's (*d*) (Figure 4.6).

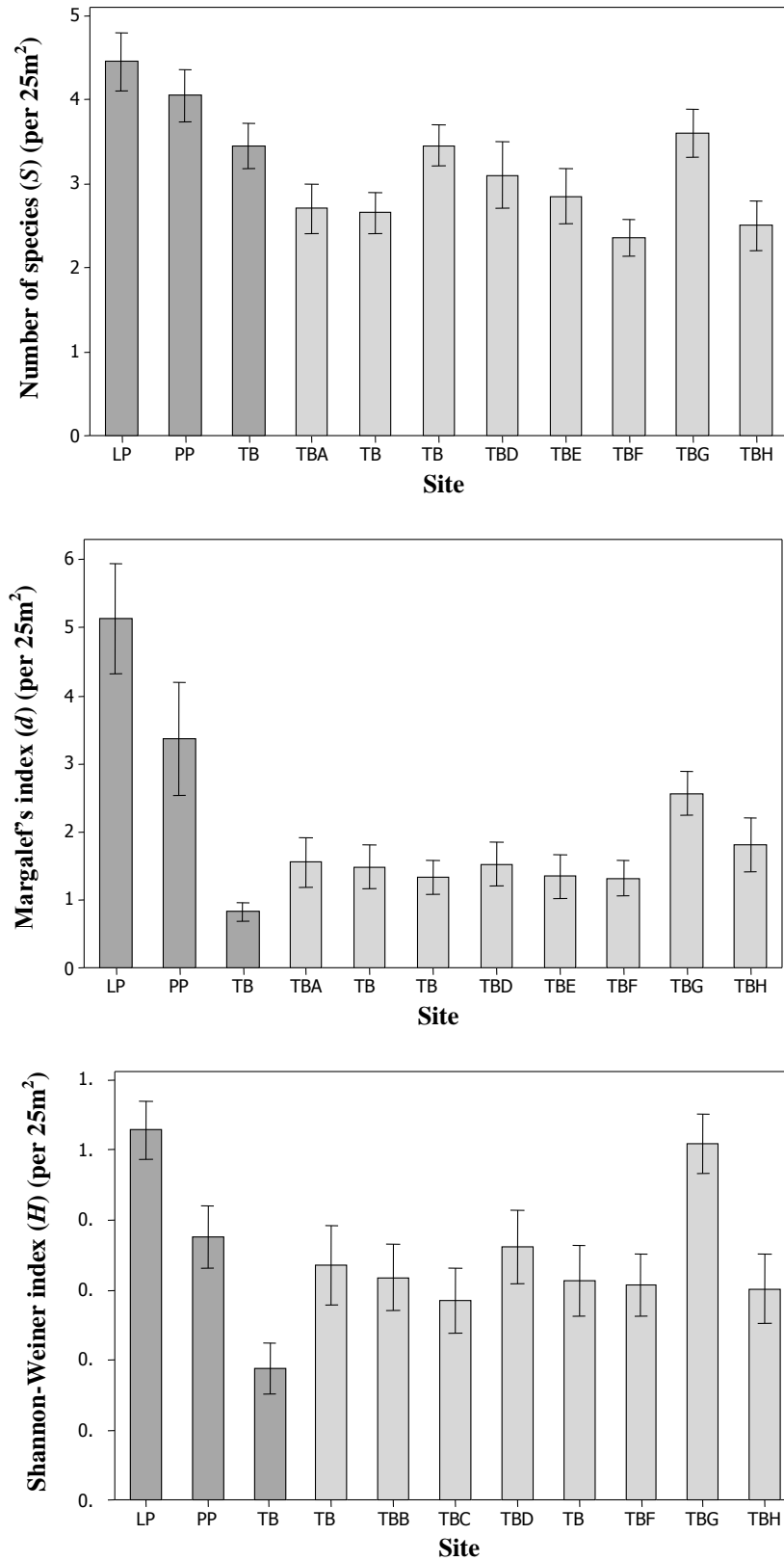


Figure 4.4. Mean Number of species (S), Margalef's index (d) and Shannon-Wiener index (H). Interval bars represent one standard error. Autumn/winter 2010 surveys highlighted by dark grey shading, spring/summer 2011 surveys highlighted by light grey shading.

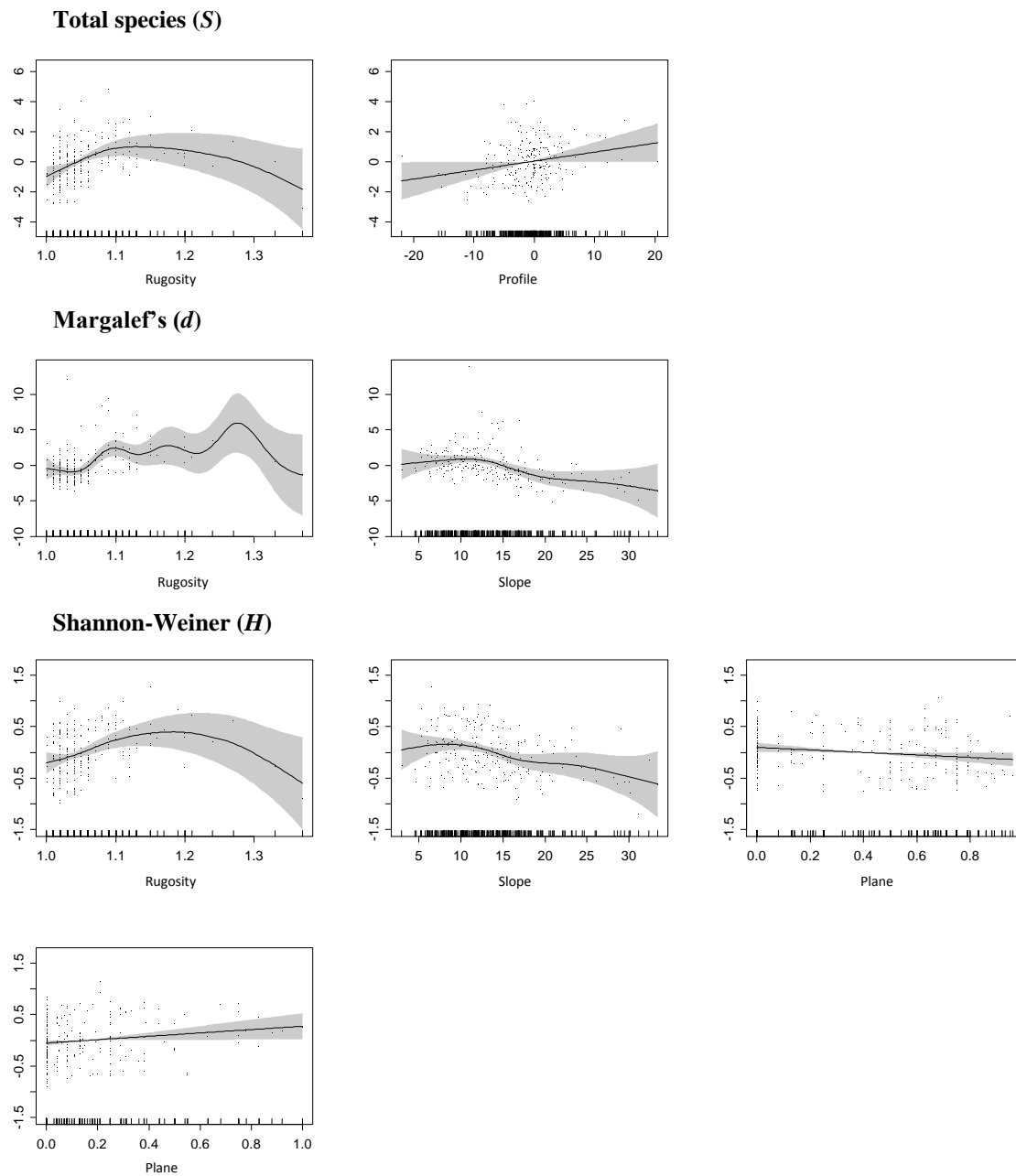
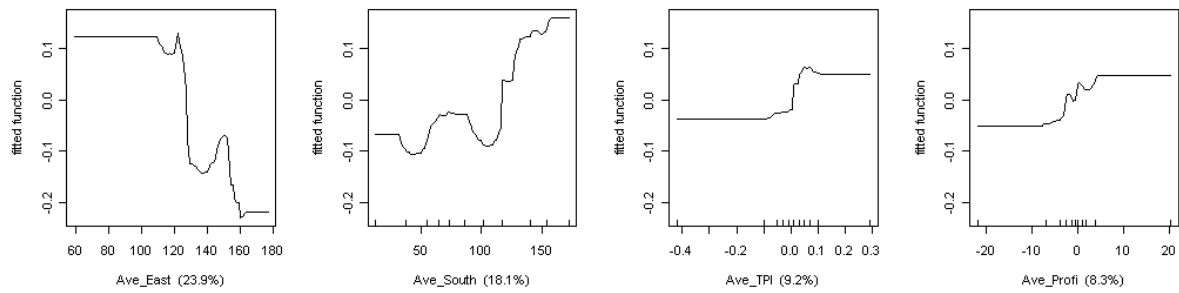
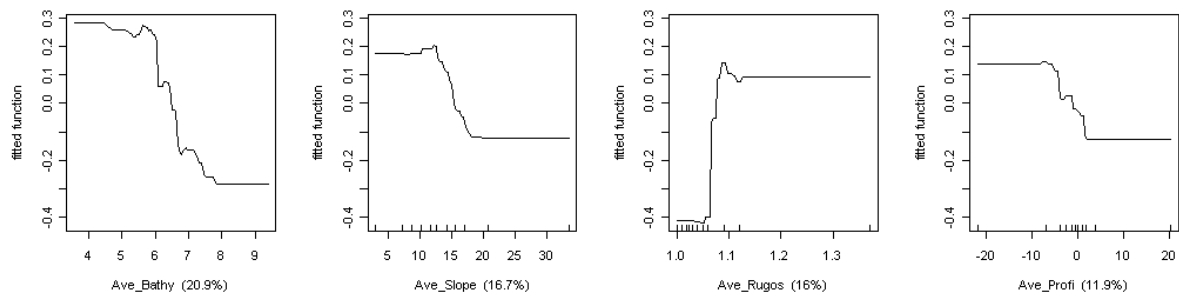


Figure 4.5. GAM partial residual plots of significant model terms identified for each community diversity model response.

Number of species (S)



Margalef's (d)



Shannon-Wiener (H)

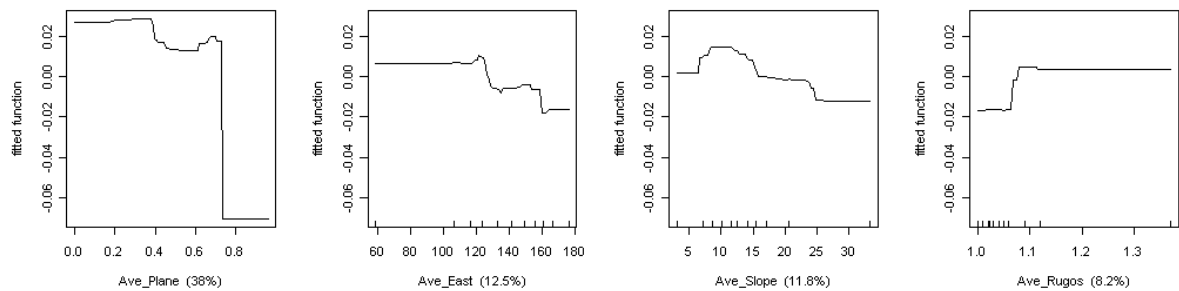


Figure 4.6. Fitted functions versus observed values (indicated by x-axis tabs) for the top four terms of the BRT model analysis for each diversity response variable, ordered by relative influence value (in brackets) for those response variables with notable proportions of deviance explained.

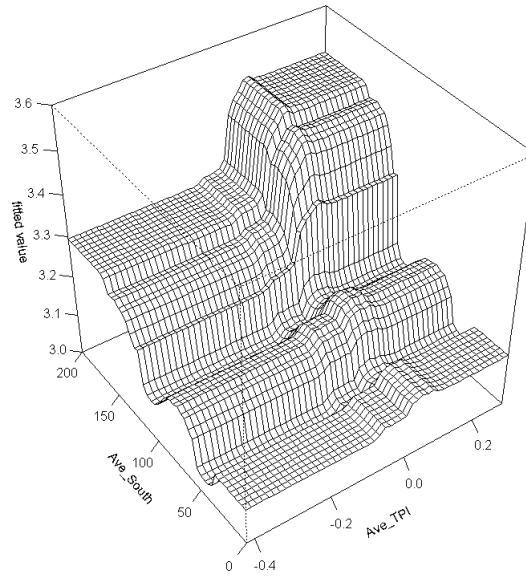


Figure 4.7. Physical variable interaction of Species richness (S) identified between *southness* and *TPI* by BRT analysis.

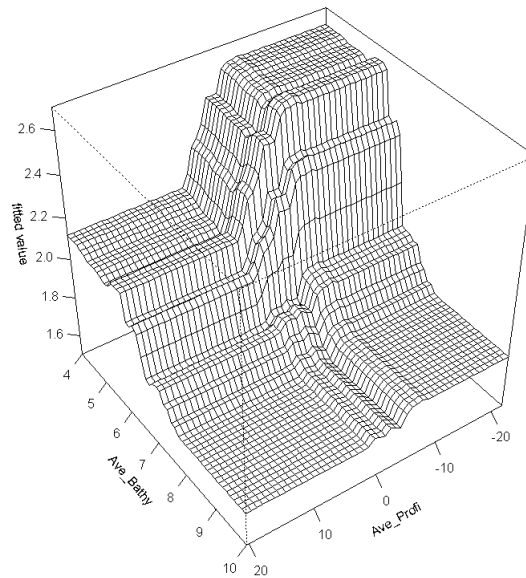


Figure 4.8. Physical variable interactions of Margalef's diversity index (d) identified between *Bathymetry* and *Profile* by BRT analysis.

4.4.4 Species abundance

Ten species of reef fish had sufficient numbers of observations to allow GAM modelling of abundance. GAM models were used to investigate the relative influence of each of the eleven predictor variables on individual reef fish species $\log(x+1)$ transformed abundance.

Statistically significant reductions in model deviance from the null were identified for the fitted abundances of eight of the ten species modelled with GAMs (Table 4.7). No significant reduction in model deviance from the null was identified for the abundances of *D.*

aurantiacus or *P. laticlavus*. *T. caudimaculatus* was the best explained species abundance response variable modelled with GAMs, explaining 43.8% of the model deviance. Significant predictor variables of *T. caudimaculatus* abundance included *bathymetry* and *slope* (Table 4.7). The remaining significant models of abundance for the other species explained between 12% and 35.5% of the deviance. Other notable model results were identified for *N. tetricus* ($D^2 = 35.5\%$), *A. aurita* ($D^2 = 22.1\%$) and *L. forsteri* ($D^2 = 20.7\%$). The specific relationship between each species abundance response and the statistically significant predictor variables were interpreted with GAM partial residual plots (Figure 4.9).

Eight species of reef fish had sufficient numbers of observations to allow BRT modelling of abundance. BRT models were used to investigate the relative influence of each of the eleven predictor variables on individual reef fish species $\log(x+1)$ transformed abundance.

Table 4.8 displays the BRT model results for species abundance. *Trachinops caudimaculatus* was the best explained abundance response variable investigated with an explained deviance of 66.9%, largely influenced by a combination of average bathymetry (19.8%), slope (14.6%), plane (14.6%) and southness (13.6%) (Figure 4.10). The abundance of *T.*

caudimaculatus showed a general positive relationship with depth, slope and plane. Notable interactions existed between average slope and plane with higher abundances of *T.*

caudimaculatus expected on higher plane, steep sloped reef (Figure 4.11). The remaining models of abundance for the other species explained between 4.9% and 48.1% of the deviance. Other notable model results were identified for *N. tetricus* ($D^2 = 48.1\%$), *P. rubicundus* ($D^2 = 34.6\%$) and *N. balteatus* ($D^2 = 26.7\%$). BRTs identified no notable interactions for any of the other species abundances modelled.

GAM and BRT models of species abundance explained comparatively similar proportions of model deviance. GAMs achieved D^2 results of between 8.7% and 43.8% compared to BRT with D^2 results of between 4.9% and 66.9%. BRTs out performed GAMs for five of the ten species abundance variables modelled. There appeared to be little to no agreement in terms of the most important model terms between either the GAM and BRT approaches or obvious patterns between the various species abundance responses. The most important explanatory physical variables of the species abundances, commonly identified by GAMs were slope, ridge and bathymetry. GAMs identified slope and ridge as significant model terms for three of the ten species abundance response variables and bathymetry for two of the ten species abundance response variables (Table 4.7). The most important explanatory physical variables of species abundances, commonly identified by BRTs were bathymetry, south and slope. BRTs identified bathymetry in the top four important model terms for six of the ten species abundance response variables and both *southness* and *slope* for three of the ten response variables (Figure 4.10).

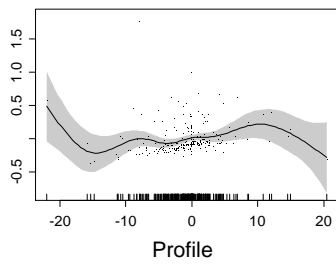
Table 4.7. GAM model analysis results of log (x+1) transformed species abundance including ANOVA results between null and model deviance and significant model terms. Significant *p*-value results are highlighted in bold.

Species	<i>F</i>	<i>df</i>	<i>p</i>	Significant model terms	Residual deviance	Total deviance	Deviance explained (<i>D</i> ²)
<i>L. fosteri</i>	2.29	22.31	0.001	<i>Profile</i> (<i>F</i> =1.95, <i>p</i> =0.05)	11.45	14.44	20.7%
<i>N. tetricus</i>	2.90	34.78	<0.001	<i>Slope</i> (<i>F</i> =5.67, <i>p</i> =0.02), <i>Ridge</i> (<i>F</i> =5.14, <i>p</i> =0.03)	17.97	27.86	35.5%
<i>M. australis</i>	1.78	15.98	0.04	<i>South</i> (<i>F</i> =4.17, <i>p</i> =0.04), <i>Channel</i> (<i>F</i> =5.43, <i>p</i> =0.02)	1.04	1.18	12%
<i>N. balteatus</i>	2.66	16.93	<0.001	<i>East</i> (<i>F</i> =2.34, <i>p</i> =0.03)	2.06	2.53	18.3%
<i>D. aurantiacus</i>	1.52	14.98	0.1	<i>Slope</i> (<i>F</i> =2.27, <i>p</i> =0.04)	2.14	2.38	10.1%
<i>N. fucicola</i>	2.09	13.46	0.015	<i>Ridge</i> (<i>F</i> =5.22, <i>p</i> =0.02)	8.54	9.72	12.1%
<i>P. rubicundus</i>	2.62	17.66	<0.001	<i>Bathymetry</i> (<i>F</i> =2.39, <i>p</i> =0.04), <i>Ridge</i> (<i>F</i> =4.66, <i>p</i> =0.03)	1.41	1.74	18.8%
<i>P. laticlavus</i>	1.35	14.43	0.18	-	7.24	7.93	8.7%
<i>A. aurita</i>	2.94	19.12	<0.001	<i>TPI</i> (<i>F</i> =3.29, <i>p</i> =0.006), <i>Plane</i> (<i>F</i> =5.12, <i>p</i> =0.03)	1.57	2.01	22.1%
<i>T. caudimaculatus</i>	5.79	25.84	<0.001	<i>Bathymetry</i> (<i>F</i> =6.84, <i>p</i> <0.001), <i>Slope</i> (<i>F</i> =3.29, <i>p</i> =0.03)	245.22	436.14	43.8%

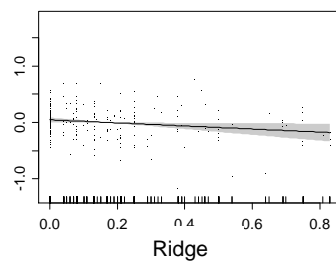
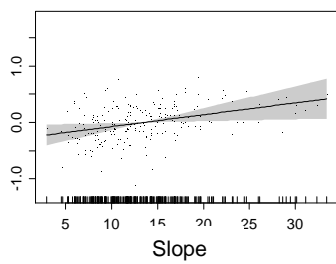
Table 4.8. BRT model analysis results of log(x+1) transformed species abundance with ‘optimal’ selected model parameters and the top four important terms for each model.

Species	Tree complexity	Learning rate	Bag fraction	Residual deviance	Number of trees	SE	Total deviance	Deviance explained(<i>D</i> ²)
<i>L. fosteri</i>	5	0.0005	0.25	0.059	2500	0.025	0.066	11.21%
<i>N. tetricus</i>	3	0.005	0.75	0.066	1000	0.010	0.127	48.09%
<i>M. australis</i>	4	0.0005	0.25	0.005	1400	0.001	0.005	4.85%
<i>N. balteatus</i>	3	0.001	0.75	0.008	1300	0.002	0.012	26.67%
<i>D. aurantiacus</i>	5	0.0001	0.75	0.010	3000	0.002	0.011	8.86%
<i>N. fucicola</i>	4	0.0005	0.25	0.038	2700	0.009	0.044	13.44%
<i>P. rubicundus</i>	5	0.001	0.5	0.005	2200	0.002	0.008	34.58%
<i>T. caudimaculatus</i>	5	0.001	0.75	0.659	3350	0.121	1.991	66.89%

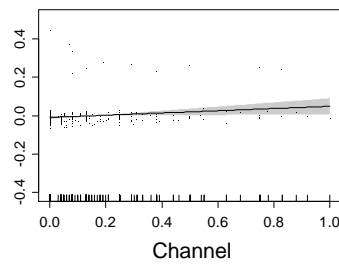
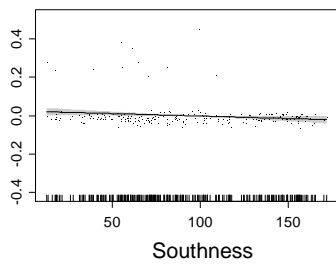
L. forsteri



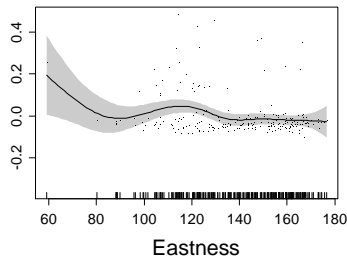
N. tetricus



M. australis



N. balteatus



D. aurantiacus

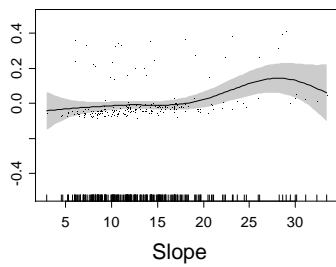
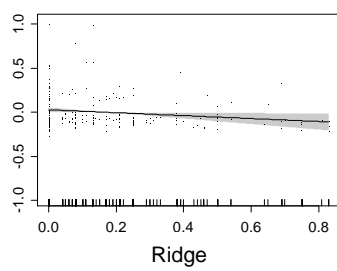
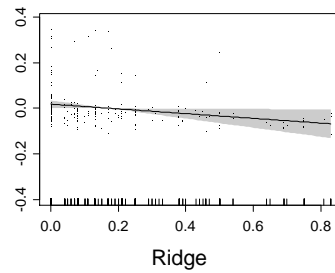
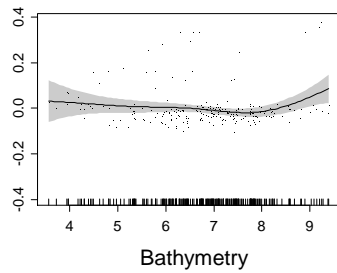


Figure 4.9. GAM partial residual plots of significant model terms identified for each species abundance model response.

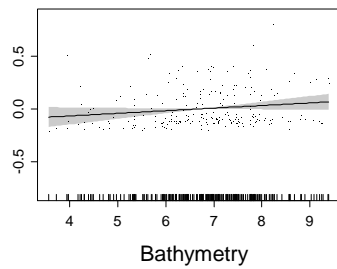
N. fusicola



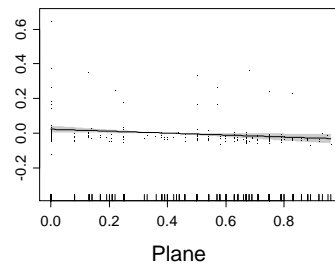
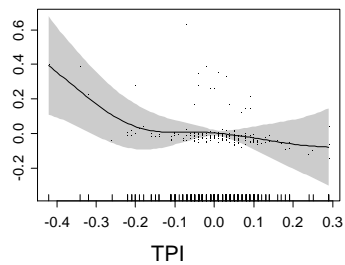
P. rubicundus



P. laticlavus



A. aurita



T. caudimaculatus

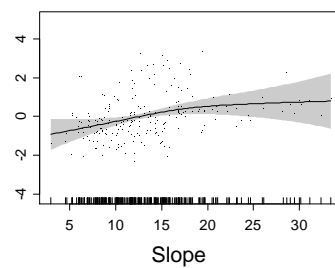
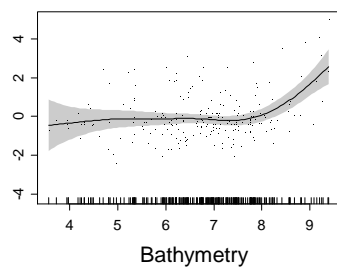


Figure 4.9 continued.

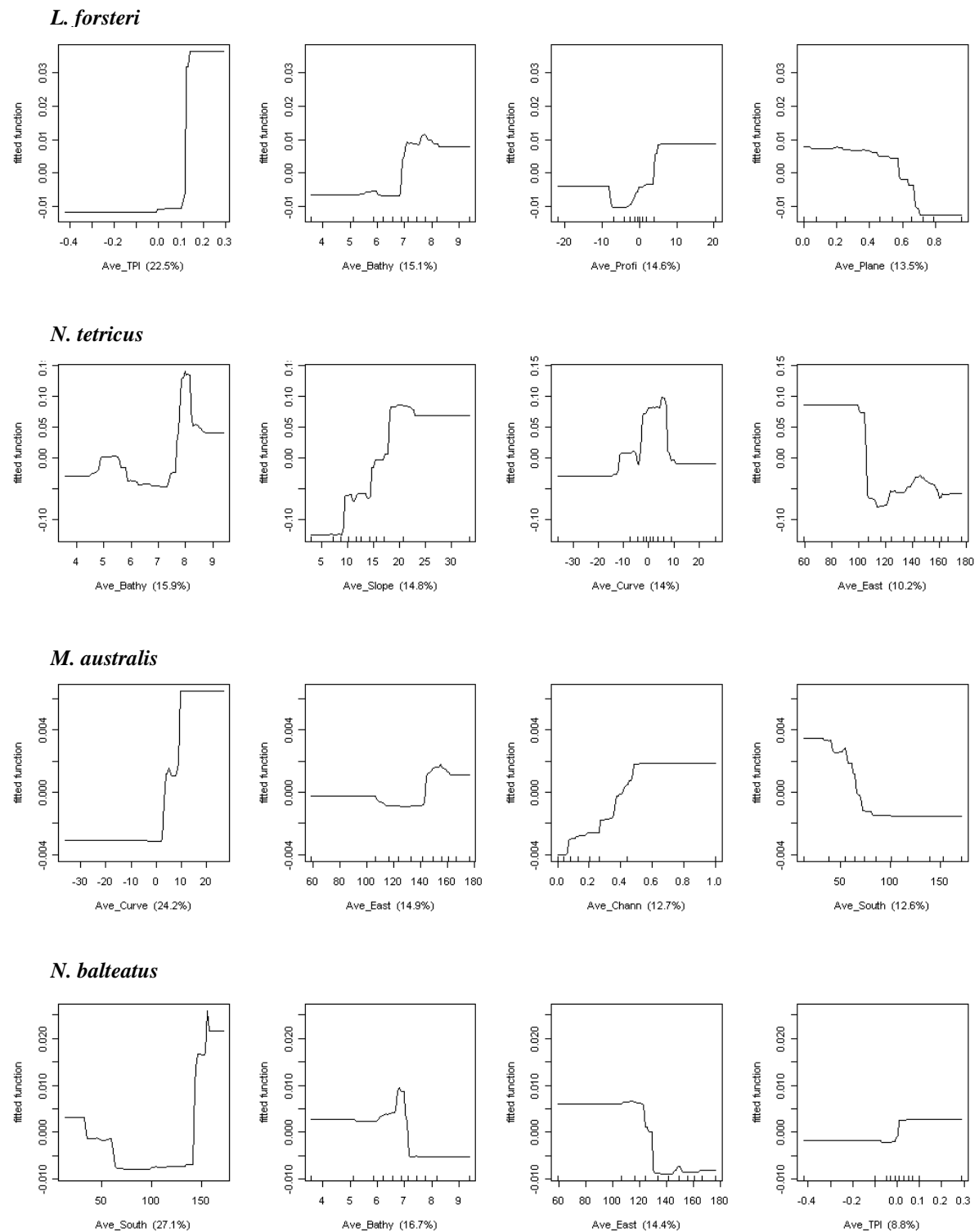
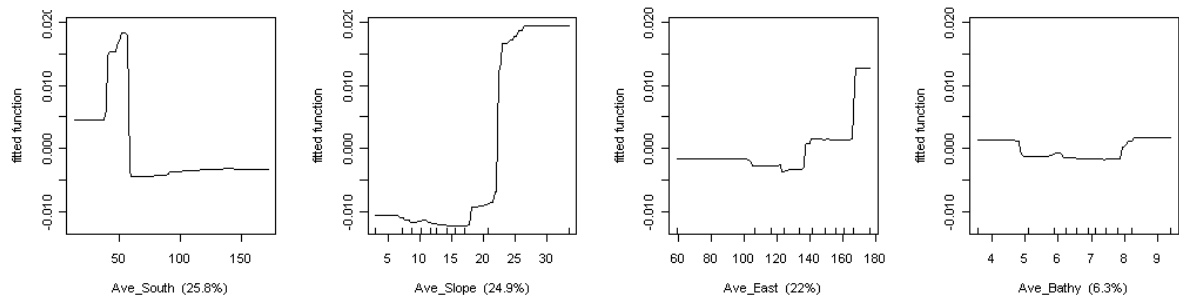
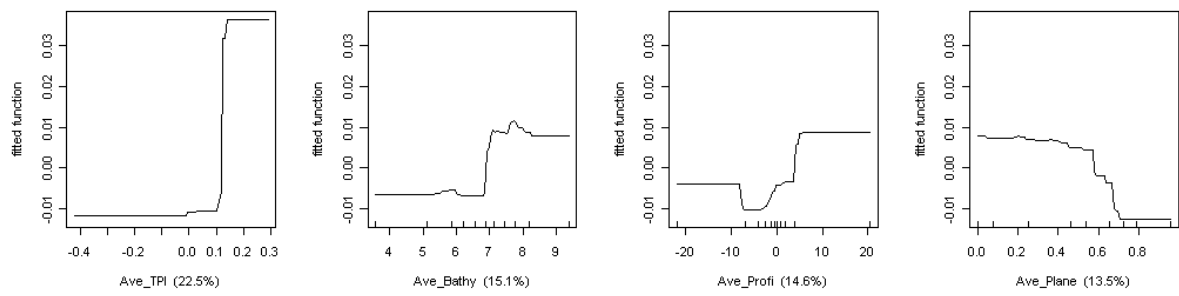


Figure 4.10. Fitted functions versus observed values (indicated by x-axis tabs) for the top four terms of the BRT model analysis of species $\log(x+1)$ transformed abundance, ordered by relative influence (in brackets) for those species with notable proportions of deviance explained.

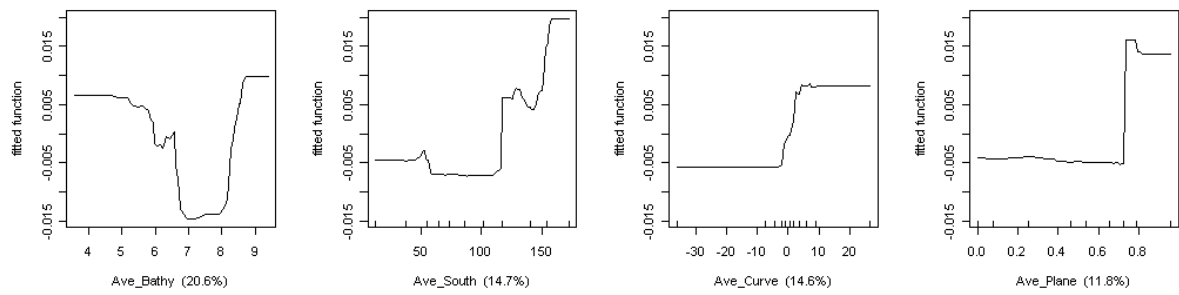
D. aurantiacus



N. fusicola



P. rubicundus



T. caudimaculatus

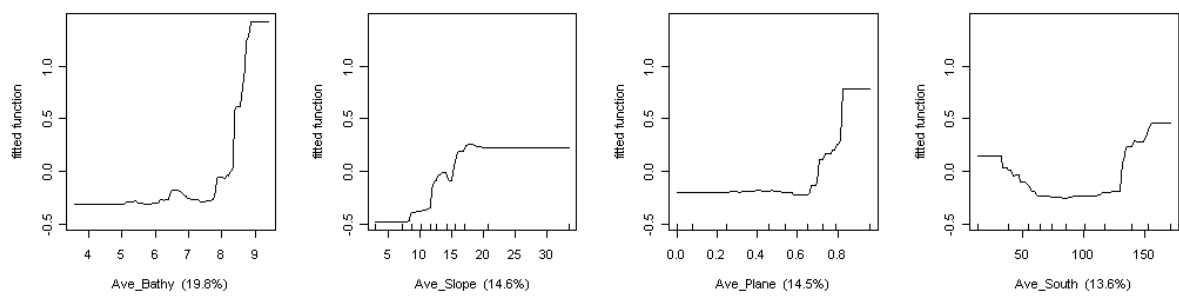


Figure 4.10 continued.

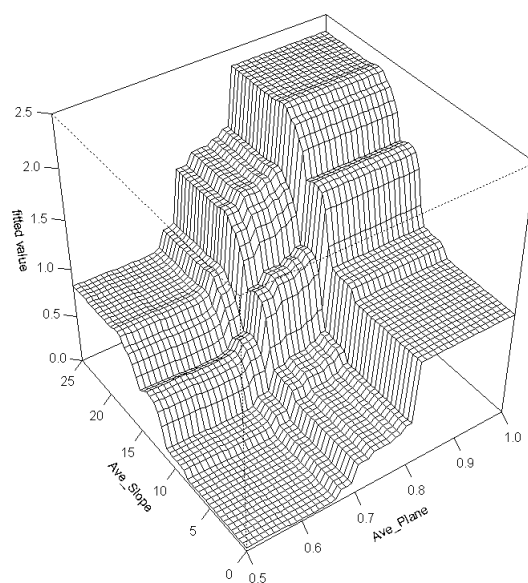
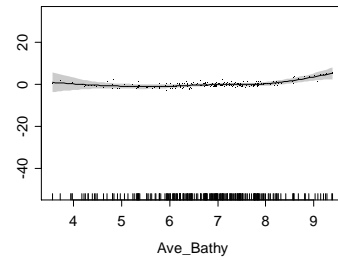


Figure 4.11. Physical variable interaction identified between average *slope* and *plane* from BRT modelling of *T. caudimaculatus* log(x+1) transformed abundance.

4.4.5 Species occurrence

Ten species of reef fish had sufficient numbers of observations to allow GAM modelling of species occurrence. GAM models were used to investigate the relative influence of each of the eleven predictor variables on individual reef fish species occurrence. Statistically significant reductions in model deviance from the null were identified for the fitted occurrences for all ten species modelled with GAMs (Table 4.9). *Trachinops caudimaculatus* was the best explained species occurrence response variable modelled, explaining 43.5% of the model deviance. Significant predictor variables of *T. caudimaculatus* occurrence included *bathymetry*, *slope* and *rugosity* (Table 4.9). There were problems of over-fitting for three of the species modeled; *N. tetricus*, *D. aurantiacus*, and *P. rubicundus* leading to spuriously high explained deviance values. No significant predictor variables were identified for *A. aurita*. The remaining significant models of occurrence for the other species explained between 20.3% and 37.9% of the deviance. Other notable model results were identified for *M. australis* ($D^2 = 37.9\%$) and *N. fucicola* ($D^2 = 30.1\%$). The specific relationship between each

species occurrence response and the statistically significant predictor variables were



interpreted with GAM partial residual plots (Figure 4.12

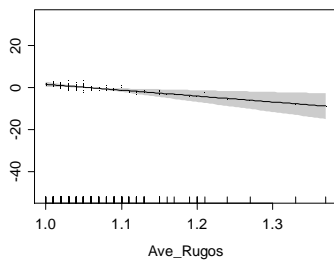
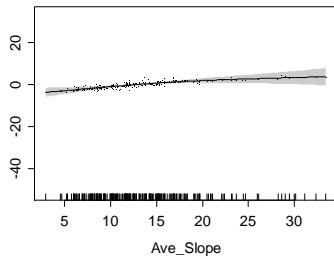


Figure 4.12).

Eight species of reef fish had sufficient numbers of observations to allow BRT modelling of species occurrence. BRT models were used to investigate the relative influence of each of the eleven predictor variables on individual reef fish occurrence.

Table 4.10 displays the BRT model results for species occurrence. As with abundance,

Trachinops caudimaculatus occurrence was again the best explained response variable investigated with an explained deviance of 57.6%, largely influenced by a combination of average *bathymetry* (15.1%), *eastness* (14.5%), *southness* (13.7%) and *slope* (13.1%)

(Figure 4.13). The occurrence of *T. caudimaculatus* showed a general positive relationship with *depth* and *slope*, a weak negative relationship from *eastness* and a somewhat bi-modal

relationship with *southness*. Notable interactions existed between *rugosity* and *slope* with higher occurrences of *T. caudimaculatus* expected on steeper sloped, low rugosity reef (Figure 4.14). The remaining models of occurrence for the other species explained between 2.4% and 57% model deviance. Other notable model results were identified for *P. rubicundus* ($D^2 = 57\%$), *N. tetricus* ($D^2 = 42\%$), *M. australis* ($D^2 = 36.8\%$), *N. balteatus* ($D^2 = 31.1\%$) and *L. forsteri* ($D^2 = 26.7\%$). No notable interactions were identified for any of the other species occurrences modelled.

GAM and BRT models of species occurrence explained comparatively similar proportions of model deviance for some of the species investigated. For a number of species modelled with GAMs there were issues of overfitting leading to dubiously high explained deviances (i.e. *N. tetricus*, *D. aurantiacus* and *P. rubicundus*) which were disregarded. GAMs achieved D^2 results of between 20.3% and 43.5% compared to BRT with D^2 results of between 2.4% and 57.6%. BRTs out performed GAMs for six of the ten species occurrence variables modelled and also avoided problems of over-fitting inherent in GAMs when modelling relatively small or high numbers of occurrence observations. There appeared to be some small agreement of the important model terms between GAMs and BRTs for some of the species investigated. Both approaches identified similar variables as important for occurrence models of *L. forsteri* (*slope*, *rugosity* and *profile*), *M. australis* (*channel* and *curvature*) and *T. caudimaculatus* (*bathymetry* and *slope*) occurrence. The most important explanatory physical variable of species occurrence, commonly identified by GAMs was *slope*, which was identified as a significant model term for three of the ten species (Table 4.7). The most important explanatory physical variables of species occurrence, commonly identified by BRTs were *bathymetry*, *south*, *east* and *slope*. BRTs identified *bathymetry*, *south* and *east* in the top four

important model terms for six of the ten species occurrence response variables and slope for four of the ten response variables (Figure 4.13).

Table 4.9. GAM model analysis results of species occurrence including ANOVA results between null and model deviance and significant model terms.

Species	Dev.	df	p	Significant model terms	Residual deviance	Total deviance	Deviance explained (D^2)
<i>L. fosteri</i>	51.68	17	<0.001	Rugosity ($X^2=18.1$, $p=0.008$) Slope ($X^2=4.8$, $p=0.03$) Profile ($X^2=4.5$, $p=0.03$)	203.53	255.21	20.30%
<i>M. australis</i>	33.03	14.66	0.004	Curve ($X^2=4.3$, $p=0.04$) Channel ($X^2=6.4$, $p=0.01$)	54.21	87.24	37.90%
<i>N. balteatus</i>	47.06	13.45	<0.001	Channel ($X^2=7.5$, $p=0.006$)	131.54	178.6	26.30%
<i>N. fucicola</i>	76.25	35.72	<0.001	Ridge ($X^2=5.02$, $p=0.03$)	176.94	253.19	30.10%
<i>P. laticlavus</i>	77.72	33.65	<0.001	Slope ($X^2=10.27$, $p=0.001$) Curve ($X^2=5.56$, $p=0.02$)	210.88	288.59	26.90%
<i>A. aurita</i>	48.18	24.07	0.002	-	81.02	129.2	37.30%
<i>T. caudimaculatus</i>	128.03	32.77	<0.001	Bathymetry ($X^2=18.61$, $p=0.004$) Slope ($X^2=14.99$, $p=0.001$) Rugosity ($X^2=8.25$, $p=0.004$)	166.26	294.29	43.50%

Table 4.10. BRT model analysis results of species occurrence with ‘optimal’ selected model parameters and the top four important terms for each model.

Species	Tree complexity	Learning rate	Bag fraction	Number of trees	Residual deviance	Total deviance	Deviance explained (D^2)
<i>L. fosteri</i>	2	0.01	0.25	450	0.85	1.17	26.70%
<i>N. tetricus</i>	2	0.005	0.25	600	0.13	0.22	42%
<i>M. australis</i>	5	0.001	0.5	1250	0.25	0.4	36.80%
<i>N. balteatus</i>	5	0.0005	0.5	2300	0.56	0.82	31.10%
<i>D. aurantiacus</i>	3	0.001	0.5	550	0.65	0.73	11.10%
<i>N. fucicola</i>	4	0.0005	0.75	1000	1.05	1.16	9.30%
<i>P. rubicundus</i>	5	0.01	0.5	300	0.28	0.65	57%
<i>T. caudimaculatus</i>	4	0.01	0.75	500	0.57	1.34	57.60%

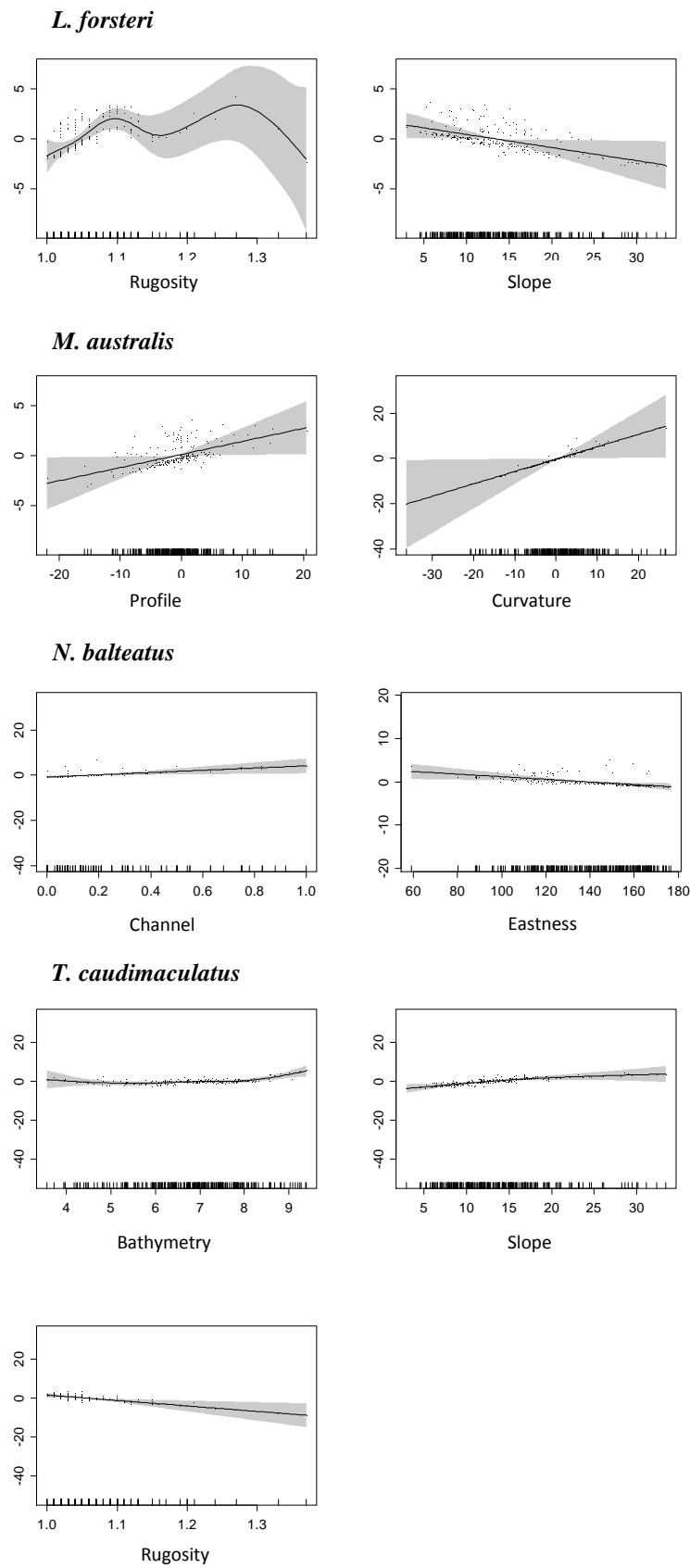


Figure 4.12. GAM partial residual plots of significant model terms identified for each species occurrence model response.

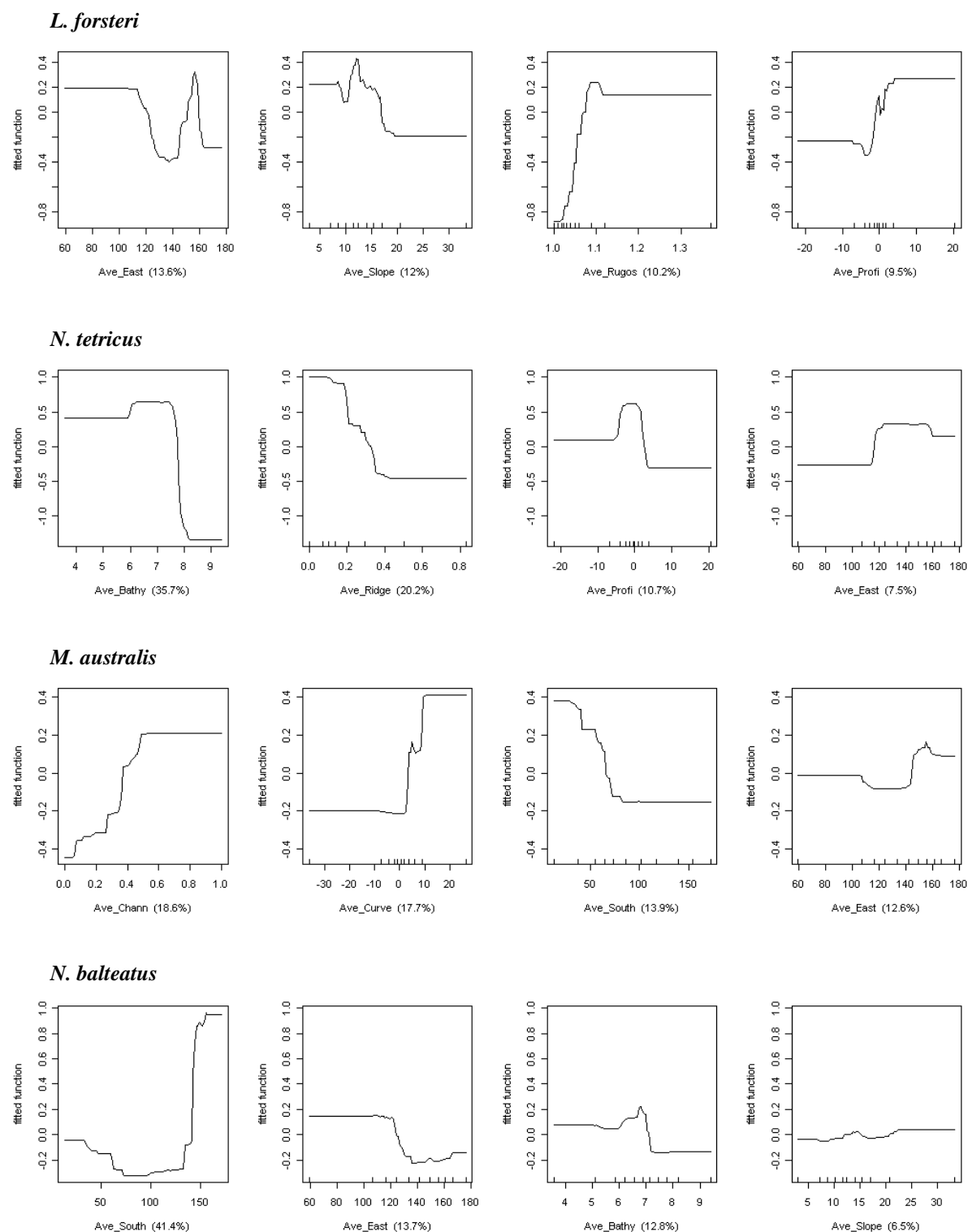
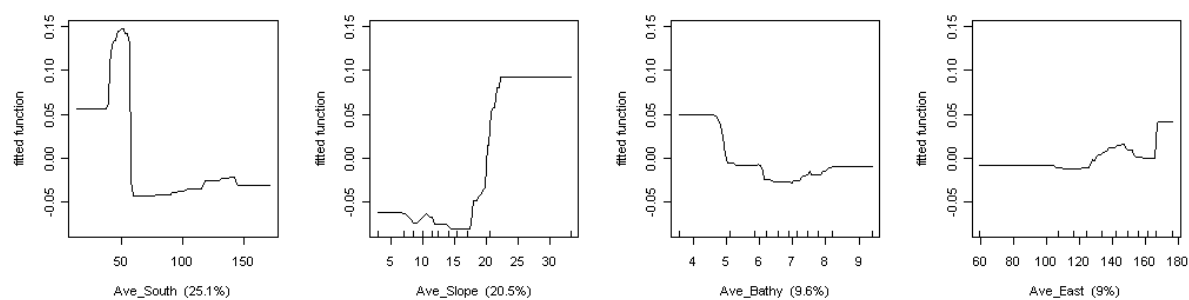
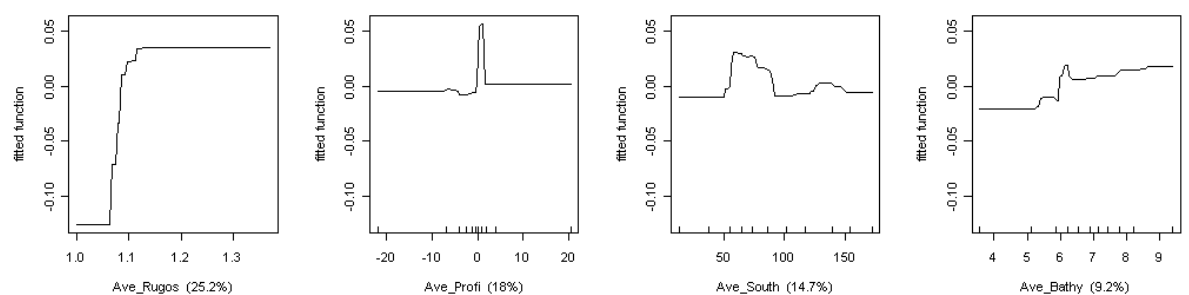


Figure 4.13. Fitted functions versus observed values (indicated by x-axis tabs) for the top four terms of the BRT model analysis of species occurrence ordered by relative influence (in brackets) for those species with notable proportions of deviance explained.

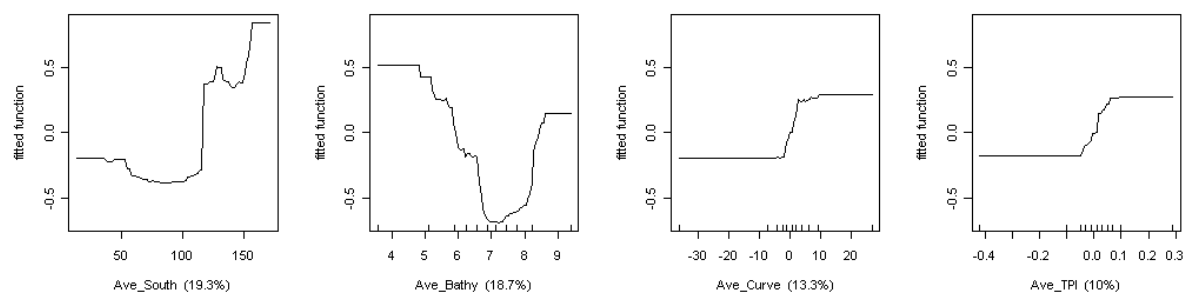
D. aurantiacus



N. fucicola



P. rubicundus



T. caudimaculatus

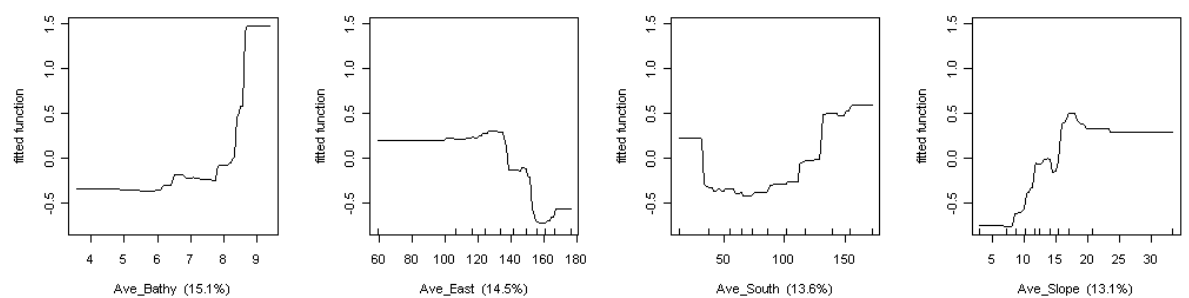


Figure 4.13 continued

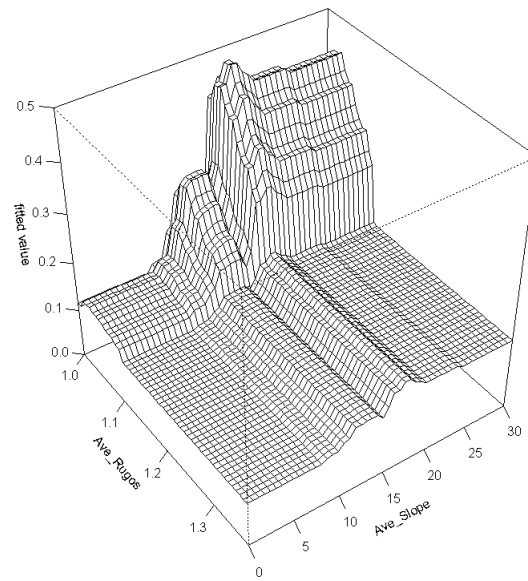


Figure 4.14. Physical variable interaction identified between average rugosity and slope from BRT modelling of *T. caudimaculatus* occurrence.

4.5 Discussion

4.5.1 Overall patterns

The findings of this study suggest that bathymetry derived measures of habitat structure are, by themselves, limited predictors of temperate reef fish community structure at fine resolutions. Community similarity patterns were weakly correlated with derivative measures of *eastness*, *southness* and *plane*. These measures are likely acting as proxies of the predominant swell exposure direction which is from the south and southeast at the majority of the Tinderbox sites. The results suggest precise quantified exposure measures, where available, hold potential as effective surrogates to explain fine resolution patterns in reef fish community similarity.

The extent to which derivative based models were able to explain patterns in the reef fish community structure, varied depending on the response variable being modelled and with the modelling approach applied, making it difficult to discern general patterns. GAM and BRT approaches performed comparatively evenly in explaining community diversity and species abundance and occurrence. The most important explanatory variables of community diversity were generally *slope*, *rugosity*, *bathymetry* and *plane*. *Slope* is an important explanatory variable of community diversity as a probable consequence of its importance to a number of individual species that were identified in the separate species abundance and occurrence analyses. Areas of higher slope appeared important to the associated abundances of *T. caudimaculatus*, *D. Aurantiacus* and *N. tetricus*. The importance of bathymetry to community diversity and particularly the numbers of individuals observed is probably a consequence of its importance to the species *T. caudimaculatus*, which displayed high abundances towards the deeper areas of reef surveyed (8-9m). This species often tends to aggregate in high densities (100's to 1000's) over areas of reef of a few square metres (personal observation),

having the potential to contribute considerably to the total count of individuals across a survey. The relationship between *rugosity*, *plane* and community diversity is less clear in the context of the separate species abundance and occurrence analyses results and appears to be an emergent association specific to measures of community diversity since both variables were rarely identified as important explanatory variables of individual species abundance or occurrence. The specific mechanisms behind these identified patterns between habitat structure and community diversity are not well understood but may be related to swell exposure, refuge space, current flow and associated food availability which require further investigation.

A major benefit of the BRT approach over those of other modelling approaches such as GAMs is their ability to effectively identify interactions between predictor terms. Contrary to what might have been expected, the dominant reef aspect (as a proxy of exposure to the dominant swells) was not identified as an important explanatory variable for most of the response variables investigated. However notable interactions were identified by BRT analysis, between deviation from south and TPI for species richness (S), which would have otherwise been overlooked by GAMs alone. Notable interactions were also identified for Margalef's index (d) between bathymetry and profile. These interactions suggest some form of interplay between variability in depth (i.e. bathymetry) and habitat heterogeneity (i.e. TPI and profile) in structuring reef fish community diversity at fine spatial scales.

GAM and BRT models of abundance performed comparatively evenly for each species modelled. BRTs results were marginally better, with higher explained deviance than GAMs for five of the ten species abundance variables modelled. There appeared to be little clear agreement between the two approaches in terms of the most important model terms for any of

the species modelled. The most important explanatory physical variables of the species abundances, commonly identified by GAMs were *slope*, *ridge* and *bathymetry*. The most important explanatory physical variables of the species abundances, commonly identified by BRTs were *bathymetry*, *south* and *slope*. The responses in species abundance to habitat structure appears to be largely species specific at the scales investigated here. Fine scale variability in bathymetry appears to be important in explaining the abundances of a number of species, particularly that of *T. caudimaculatus*. Slope was also identified as an important explanatory variable of abundance by both model approaches, particularly for *T. caudimaculatus*, *D. aurantiacus* and *N. tetricus*. A notable interaction was identified by BRT analysis for *T. caudimaculatus* between slope and plane, indicating higher abundances on steeper, high plane reef.

For two of the species occurrence variables modelled by GAMs, there were problems of over-fitting due in part to low or extremely high observations. Occurrence for the bluethead wrasse, *N. tetricus* could not be modelled using GAM approaches due to its extremely high rate of detection across all blocks and sites (observed in 215 of the 220 blocks surveyed). There appeared to be some small agreement between GAMs and BRTs as to the important model terms for some of the species investigated. The most important explanatory physical variable of species occurrence, commonly identified by GAMs was *slope*. The most important explanatory physical variables of species occurrence, commonly identified by BRTs were *bathymetry*, *southness*, *eastness* and *slope*. Again, as with the abundance results, the responses in species occurrence to habitat structure appears to be largely species-specific at the scales investigated here. Fine scale variability in slope appears to be important for GAM analysis in explaining in particular the occurrences of *T. caudimaculatus* and *L. forsteri*. Bathymetry appears largely important for BRT analysis in explaining *N. tetricus*

occurrence while reef aspect (*southness* and *eastness*) appears largely important in explaining the occurrence of *N. balteatus* and to a lesser extent the occurrence of *D. aurantiacus*.

Monk *et al* (2011) have applied a similar approach to investigate the habitat preferences of bluethroat wrasse, *N. tetricus*, identifying shallow, high rugosity, high curvature reefs as their preferred habitat. This research did not identify rugosity or curvature as important variables in explaining the distribution of *N. tetricus* but this may have been due to differences in resolution between the two investigations, however fine scale variability in bathymetry was identified as an important explanatory variable with deeper depths associated with higher abundances. *Slope* was also identified as an important variable for abundance suggesting the importance of steep, high profile reef to the fine scale abundance of *N. tetricus*. Other researchers have successfully explained fish species richness and biomass at relatively fine resolutions of 4 to 200m (Wedding and Friedlander, 2008, Pittman *et al.*, 2009, Knudby *et al.*, 2010) suggesting that environmental gradients at these scales are certainly important for predicting local variations in reef fish communities. Coarser scale environmental variables are likely to have a more uniform impact on fish communities at local scales and are therefore less likely to be important in explaining differences in reef fish community structure at local scales (Knudby *et al.*, 2010).

4.5.2 Study limitations

The success of this study in relating community structure and species distributions and abundance to multi-beam derived measures of habitat structure has been limited. However it has been possible to provide some explanations of community and species-habitat associations and in the process identified pitfalls and improvements to assessing reef fish habitat associations at fine scale resolutions.

Many of the species investigated may have been too mobile at fine resolutions to identify clear relationships between distribution and habitat or may simply have been responding to their environments at different spatial scales to which were investigated. There are limitations of fine resolution modelling approaches such as this that rely on direct and resource gradients that are often difficult to remotely sense. Environmental gradients that organisms respond to can be categorised into three approximate classes of indirect, direct and resource gradients (Austin, 1980). Organisms or communities often respond to these gradients in a spatially hierarchical fashion resulting in different patterns at different spatial resolutions and extents (Guisan and Thuiller, 2005). Gradual patterns in species distributions over large scales and coarse resolutions tend to be correlated with indirect climatic gradients, whereas patchy, small scale distributions at fine resolution are more likely the result of direct environmental gradients and patchy resource distributions resulting from local topographic variation and habitat fragmentation (Scott, 2002, Guisan and Thuiller, 2005). The type of environmental gradients considered in an investigation are important because they can limit the applicable geographical extent and resolution across which a model can be confidently applied without significant errors (Iampietro et al., 2008). Models based on ecologically proximal, direct and resource gradients will be the most robust and widely applicable, but caution should be applied when considering similar species and community responses across large regions exposed to differing environmental gradients. Paradoxically, ecologically proximal, direct and resource gradient variables, although the more important in a predictive sense, are often more difficult to understand and measure at the fine resolutions necessary, particularly using remotely sensed methods. At present many ecologically proximal variables can only be measured accurately through direct field observations making their use for predictive modelling of species distributions impractical. This situation is likely to improve in the near future as remote sensing technologies advance, but this will still require comparison with

direct detailed investigation of habitat structure to understand the variability of such surrogates.

Similarly, the extent of the study may not have been large enough to capture the complete relationship between the reef fish community and habitat structure. In effect a truncated response may have been modelled to a subset of the full gradient of the habitat structure available to the community. Considering environmental predictors at the wrong extent can result in misinterpretation of the true response of an organism or community to its environment. This problem of survey extent was largely unavoidable since the location and size of the survey were limited by financial and logistical constraints and the data available at the time. However, this study does highlight the importance of obtaining fine resolution remotely sensed data across large, management scale extents to ensure accurate modelling of species and community responses to their physical environments if such predictive capacity is desired.

This study focused on bathymetrically derived measures in an attempt to test their application as surrogates for modelling community structure responses to physical habitat structure at fine resolutions, and attempted to test if fine-scale bathymetric derivatives could be feasibly applied to understand habitat associations of fish in the absence of direct metrics of habitat. It is doubtful if the derivative measures included in this study were direct factors influencing community responses and may in actual fact have lacked real ecological relevance for many of the modelled species. Including other direct and resource habitat measures such as water temperature, predominant tidal currents and food availability would likely have improved the explanatory power of the models, however these metrics were unavailable at any relevant scale, as is often the problem in real marine management situations. The study also failed to

consider biotic and ecological interactions such as recruitment and the abundances of known competitors and predators in the environment which again, may have improved the explanatory power of the models. Collecting biological and ecological information of this sort with remote sensing methods at the resolutions relevant to this study is particularly difficult at the current time, however advancements in autonomous underwater vehicle and video technology are allowing improved survey capabilities, capable of estimating algal, invertebrate and fish densities at depth and across large spatial extents. AUV mounted video imagery and sonar are now beginning to emerge as a potential tool for measuring physical habitat structure in the marine environment (Shumway et al., 2007) and will likely lead to the development of combined biological and physical survey capabilities in the near future. Future investigations should utilise methods such as AUV or towed underwater video which are capable of sampling the fish, benthic invertebrate and algal communities simultaneously. These sampling technologies in combination with bathymetrically derived metrics of the physical habitat probably represent the best current means of accurately and effectively modelling reef fish community structure of coastal reef habitats across resource management scales.

At broader extents and resolutions it is expected that biotic interactions would have a lesser effect on species distributions than at local, finer resolution scales. Most predictive modelling efforts are based on the broad assumptions of niche theory which describes the response of a species to environmental gradients using a classic unimodal, symmetric bell-shaped curve relationship (Austin, 2002). There is a lack of evidence supporting the classical niche theory assumptions underlying many attempts at species distribution modelling and a general lack of agreement around the specifics of individual species response shapes to environmental gradients (Austin, 2002), an issue which many studies fail to address adequately when

formulating their models. Conflicting theories consider competition and its potential to displace a species from its fundamental niche, altering its realised niche response curve to a variety of shapes from skewed to bimodal (Austin, 1999). The use of ecological theory to underpin species distribution prediction is often neglected by investigators but is extremely important when selecting the most appropriate predictors and scales, choosing ecologically realistic response curves to each predictor and selecting between competing model approaches (Guisan and Thuiller, 2005). This study had no prior knowledge of the possible link between responses of species and the derivative measures and therefore it was difficult to confidently apply realistic *a priori* response curves to our models. Future studies should ideally select predictors based on empirical observations of individual species responses or at the very least sound ecological theory.

The species and communities considered within this study may not have been operating close to or within their fundamental niche. Unobserved influences such as disturbance (e.g. fishing pressure) may have been having an overriding effect on community structure and otherwise masking other natural associations with habitat. There are inherent limitations in the interpretations and application of spatial models across broad scales and locations due to unknown natural differences in the realised niches of separate communities. Ecological modelling implicitly assumes that a pseudo-equilibrium exists between organisms and their environments (Austin, 2002). This assumption risks inherent bias in model interpretations because what is being modelled in nature is the response observed as a result of biotic interactions and stochastic responses of an organism specific to a particular time and region (i.e. the realised niche) rather than the full response of a species occupying all of its suitable habitat (i.e. the fundamental niche) (Guisan and Zimmermann, 2000, Austin, 2002, Guisan et al., 2002, Guisan and Thuiller, 2005). Since it is very difficult to be certain that a statistical

model represents a good approximation of the fundamental niche, models of a particular species or community response across different locations are difficult to compare. The accuracy of a model based on environmental predictors will vary depending on the degree to which the dispersal and disturbance history have defined a particular community assemblage. It is important therefore that investigators are specific about the ecological assumptions underpinning any model and the appropriate extent and accompanying levels of uncertainty with which their predictions can be accurately applied. True models of a species fundamental niche require model development based on a solid theoretical and empirically derived understanding of a species response to its physical environment (Guisan and Thuiller, 2005) and should attempt to include quantitative measures of potential sources of community disturbance such as fishing pressure.

The fish survey approach applied in this study may not have been the most effective sampling strategy for modelling the distribution responses of temperate reef fish species and communities at the resolutions considered. Model accuracy is influenced by the reliability of occurrence data and distribution characteristic of the modelled species (Monk et al., 2012). Monk et al. (2012) demonstrated the importance of the choice of survey technique (i.e. baited verses towed video observations) over the type of modelling approach selected (i.e. GAM, GLM and maximum entropy) in accurately predicting temperate reef fish distributions. They used video and multibeam sonar derived datasets and concluded that towed-video-based occurrence data produced good models of suitable habitat for demersal marine fishes irrespective of the modelling approach applied. Moore et al. (2009) compared the ability of presence/absence methods (GAM and classification and regression trees) to predict fine-scale habitat suitability for demersal fishes based on baited-video and multibeam sonar datasets. They also found that baited-video and multibeam sonar datasets were useful in providing a

detailed understanding of demersal fish-habitat associations, as well as accurately predicting species distributions across unsurveyed locations where continuous spatial seafloor data were available. Reliability of occurrence data to accurately predict a species distribution will depend on the behaviour of a particular species in response to a chosen survey technique and the inherent ability of that technique to detect a species within its environment. Many known and unknown factors will influence a techniques capability to accurately sample a particular species distribution. For instance, species aggregating behaviour, habitat type, behaviour in response to equipment or observer (i.e. avoidance or attraction), feeding behaviour (i.e. carnivorous or herbivorous), diurnal behaviour and body size in relations to refuge availability will all determine how effective a particular sampling technique is. Survey techniques should be selected based on a good prior knowledge of their biases and drawbacks and the spatial extent across which they must be applied to accurately detect a particular species of interest.

4.5.3 Further development

This study has highlighted a number of improvements that should be considered in future studies prior to attempting to model reef fish community diversity in response to habitat structure. Future modelling efforts should focus on the full extent of a species' known range to avoid modelling a truncated response to its habitat. For this reason, in many cases surveying and modelling species separately rather than as communities may be easier and more informative due to the widely varying spatial ranges between different reef fish species. Where feasible, predictive data should be collected at the finest attainable resolution, across the largest scales possible.

The relationships between derivative measures and a species response should be well understood and predictors should be selected based on ecological relevance. Methods such as

BRTs are particularly useful in their ability to identify interactions between predictors which may otherwise not have been obvious. Further research needs to be directed towards identifying how derivative measures relate to underlying ecological mechanisms if they are to be effectively applied as surrogates in predicting reef fish distribution and biodiversity.

Survey techniques should be suited to the species, communities and scale being modelled. Researchers should select the technique with the greatest rate of detection based on the known behaviour and ecology of their focal species (Monk et al., 2012). With limited time and resources, dive surveys may not be the most cost-effective survey approach. Modern underwater photography and video technologies provide effective potential alternatives which can be deployed over large spatial extents and greater depths to sample multiple aspects of reef community.

Future research into remotely sensed derivatives should concentrate on equalling the accuracy and precision of current direct observation techniques. This will depend on the continued improvement in the spatial resolution of bathymetric measurements and the immergence of new imaging technologies. Future research should take advantage of advances in remote sensing of habitat structure such as back-scatter analysis, visual image analysis and fine resolution AUV mounted sonar.

4.5.4 Conclusions

These results demonstrate that multibeam derived metrics of reef habitat structure, employed in combination with modern modelling approaches have the potential to explain and predict fine resolution patterns in temperate reef fish community diversity and species distributions and abundances. This knowledge is urgently required to effectively manage marine

ecosystems and conserve biodiversity and fisheries resources and requires further research focus.

This work also highlights a number of practical considerations for successfully modelling communities of temperate reef fish using bathymetrically derived variables, including issues of scale, selection of appropriate predictors and survey technique. Future work in this field should focus on identifying suitable surrogate predictors and understanding their specific response relationships with communities and individual species. The value of large scale metrics such as the multibeam derivatives I have utilized in this study, are that they are likely to have much greater power than other approaches to predict different processes operating over varying spatial scales. With improved understanding of the ecological relevance of predictors along with the increasing availability of fine resolution bathymetry and biological data across larger extents, this may lead to the future development of robust and accurate models as tools for the prediction of specific species distributions and abundances for marine resource and conservation management. These results should encourage further research into how multibeam derived metrics of reef habitat structure and modern modelling approaches may be applied to explain and predict fine resolution patterns in temperate reef fish community diversity and species distributions and abundances around Tasmania.

Disentangling the effects of protection and spatial habitat variability on temperate marine reef fish communities.

5.1 Abstract

Selecting suitable zones to locate effective marine protected areas (MPAs) is a considerable management challenge. Incorporating sufficient habitat structure and types which maximize conservation value and safeguard over-exploited and threatened species, communities and systems requires knowledge of their specific responses to the physical environment and the effects of protection. Assessment of MPA efficacy is often hindered by a lack of consideration of natural, pre-existing variability in the system being protected and very few assessments adequately distinguish between the effects of protection and intrinsic environmental heterogeneity, leading to the potential for inaccurate estimates of species responses to protection and biased MPA assessments. This study attempted to disentangle the effects of protection on temperate marine reef fish communities from those of natural physical habitat variability. I tested the hypothesis that reef fish community responses to MPAs at a single point in time may be masked by the confounding effects of variability in components of the surrounding physical reef habitat. I assessed reef fish community similarity, species diversity, abundance and biomass of large bodied fish species across three established coastal marine reserves located along the south-eastern coast of Tasmania, Australia. An understanding, obtained from previous work in this thesis, of the important physical environmental variables responsible for structuring temperate reef fish communities, enabled some proportion of the natural variability to be accounted for when testing for the effects of reserve protection using a control-impact approach. The results of this study were largely uninformative, highlighting the need for larger scale studies considering additional factors such as local anthropogenic

pressure and recruitment variability in order to adequately apply this analysis approach across Tasmanian MPAs and maximise the ability to detect reserve effects.

5.2 Introduction

Reef fish community structure is largely influenced by stochastic recruitment events and the prevailing physical and biotic character of the surrounding habitat (Carr, 1994, Guisan and Zimmermann, 2000). Variations in the physical structure of marine habitats has been shown to affect the composition of their associated faunal and algal communities (Choat and Ayling, 1987, Beck, 2000, Toohey and Kendrick, 2008) but the precise ecological mechanisms linking reef fish communities to their habitats are not fully understood. Growing research provides support to the hypothesis that with limited spatial habitat, the effect of increasing structure may lead to amplified space and resource availability and consequently an increase in a given areas carrying capacity or a diversification of resources and niche availability (Garcia-Charton and Perez-Ruzafa, 1998).

The Commonwealth of Australia's Oceans Policy (1998) commits all states and territories to the establishment of a National Representative System of Marine Protected Areas (NRSMPA) to ensure the long term conservation of Australia's marine biodiversity, based on the concept of a comprehensive, representative and adequate network of protection. Marine protected areas (MPAs) have been increasingly promoted as effective ecosystem-based approaches to sustainably managing and conserving the biodiversity and fisheries of the World's oceans (Murray et al., 1999, Halpern and Warner, 2002, Friedlander et al., 2003, Gell and Roberts, 2003, Halpern, 2003, Pauly et al., 2005, Ballantine and Langlois, 2008, Klein et al., 2008, Lester et al., 2009). MPAs aim to achieve long term conservation of marine biodiversity, ecosystem processes and cultural value through a legal framework of sustainable utilisation, management and protection of the marine environment (UQTEC, 2009). In Australia the NRSMPA is managed through a series of zones of increasing protection ranging from strict 'no-take' nature reserves managed for science or wilderness

protection, through national parks, habitat or species management areas, to areas managed for the protection and maintenance of biological diversity while providing a sustainable flow of natural products and services to meet community needs (Commonwealth of Australia's Oceans Policy, 1998). MPAs vary greatly in the type, extent, and range of structure of the habitats that they protect due to the varying management goals underpinning their establishment. Selecting areas for effective MPAs is a difficult management task and targeting suitable habitat structure and types which will maximise conservation value and safeguard over-exploited and threatened species, communities and systems is a major problem faced by policy makers and managers with the task of implementing effective MPAs (Babcock et al., 1999, Ward et al., 1999).

In many parts of the world MPAs are often located arbitrarily with an emphasis on minimising conflicts with existing stakeholders rather than maximising conservation outcomes. MPAs are frequently located in physically complex or heterogeneous coastal areas of high conservation value but in general physical habitat structure is rarely the overriding consideration motivating management decisions (García-Charton et al., 2004). Quantifying fish community responses to habitat structure is crucial for successful MPA design and management, particularly where goals are to maximise biodiversity (Garcia-Charton and Perez-Ruzafa, 1998). Thus, biogeographic information is being increasingly incorporated into current marine conservation planning from global to local scales (Lourie and Vincent, 2004). The relationships between species-habitat responses and species' responses to protection are generally unclear but the objectives of MPAs are most likely to be achieved if these relationships are well understood and considered during the MPA design process (Ward et al., 1999, Friedlander et al., 2003, García-Charton et al., 2004, Claudet et al., 2010). For example it has been shown that the strength of fisheries-induced trophic cascades (FITC) can

be reduced by the presence of available refuge space to reef fish communities (Salomon et al., 2010). Where prey are vulnerable to predation, strong top-down control may result in unstable predator-dependant interactions, whereas where some level of protection to prey is afforded through available refuge space, systems are more likely to maintain a stable equilibrium. In situation such as this, FITC impacts of high fishing pressure could be reduced by complimenting the protection effects of marine reserves with adequate reservation of the full representative range of regional habitat structure. Understanding how physical habitat structure naturally effects the spatial variability in the distribution and abundance of reef fish can help to separate this influence from variation due to the effects of protection from fishing (Garcia-Charton and Pérez-Ruzafa, 2001).

Assessment of MPA efficacy is often hindered by inadequate appreciation of natural, pre-existing temporal and spatial variability in the system being protected (Huntington et al., 2010). Before-after, control-impact (BACI) techniques were developed in part to address and control for the confounding effects of natural temporal variability but in many situations, their application is prevented by a lack of baseline data prior to MPA establishment. Very few assessments of MPA efficacy adequately distinguish between the effects of protection and intrinsic environmental heterogeneity, leading to the potential for inaccurate estimates of species responses to protection and biased MPA assessments (Claudet et al., 2010).

One off, control-impact type comparisons of reef community structure between fished and unfished locations may often contain too much variability to conclusively detect real reserve effects (Barrett et al., 2007). This then begs the question of where the majority of the variability, or ‘noise’, in reef fish communities is coming from. A number of studies have identified reserve effects in reef fish community structure after accounting for how those

communities are responding to variability in the underlying physical structure between habitats (Friedlander et al., 2007, Harborne et al., 2008, Claudet et al., 2010, Hamilton et al., 2010, Huntington et al., 2010). The majority of studies investigating the effects of protection from fishing fail to adequately control for the natural effects of habitat composition and variability (Huntington et al., 2010). Separating the effects of fishing protection from those of natural variability is a difficult task due to the lack of knowledge of the appropriate environmental and habitat variables to control for.

This study tests the hypothesis that reserve effects at a single point in time could be masked by the confounding effects of reef community responses to variability in components of the physical reef habitat. Reef fish community similarity, species diversity, abundance and the biomass of three large bodied fish species targeted by fisher were assessed across three established coastal MPAs located along the south-eastern coast of Tasmania, Australia. Previous work, reported in chapter two of this thesis, has identified the important physical environmental and habitat variables responsible for structuring aspects of the temperate reef fish communities around Tasmania, enabling some proportion of the natural variability to be accounted for when testing for the effects of reserve protection using simple one off, control-impact approaches. Where no effect of reserve on community similarity, species diversity, abundance or biomass could be initially identified I attempted to account for the variability in reef fish community responses due to natural physical reef-habitat structure and classify assemblages into habitat 'groups' based on these responses before again testing for effects of protection.

In order to identify subtle effects of marine reserve protection that may have been missed by the approaches applied in preceding chapters, it was necessary to identify and account for

variability in the reef fish assemblage data relating to habitat variability that might be masking any effects of protection. This was achieved by identifying the physical environmental variables responsible for the largest proportion of the variability in the sample data and using this information to group samples, thereby allowing a modified 'control-impact' approach to detecting reserve effects which may otherwise have been masked by the effects of high spatial variability in habitat structure.

5.3 Methods

5.3.1 Study sites

Twelve study sites were positioned on areas of sub-tidal rocky reef inside and around the vicinity of three marine reserves, along the south-eastern and eastern coasts of Tasmania, Australia (see chapter three, Figure 3.1). Sites were selected inside and outside marine reserves. Four of these sites were located inside and around the vicinity of Ninepin marine reserve at the mouth of the Huon river off Ninepin Point, Huon Island, Garden Island and Charlotte cove Point. A further four sites were located inside and around the vicinity of Tinderbox marine reserve at the northern end of the D'Entrecasteaux Channel off Tinderbox Point, Pearsons Point, Lucas Point and Dennes Point and a final four sites were located in and around the vicinity of Maria Island marine reserve at the northern end of the Mercury Passage off Holme Point, Spring Beach, Painted cliffs and Return Point. See Chapter three of this thesis for further descriptions of the study sites.

5.3.2 Fish community and physical habitat surveys

At each site a single, 10 x 50 metre (500 m²) belt transect was positioned parallel to and within 100m of the shore inside the 5-10 metre depth contour. Each transect was subdivided into twenty 5x5 metre (25 m²) blocks either side of the transect centreline. Each block was surveyed for fish and algal assemblages a total of five separate times and once to survey physical structure. A number of physical measures of structure and complexity were recorded separately within each of the 25 m² blocks within each site transect (see chapter three, Table 3.1 for a complete list and description). See Chapter three of this thesis for detailed descriptions of the fish community and physical habitat survey methodology.

5.3.3 Statistical analyses

Individual species abundances recorded for each of the five replicate surveys were averaged for each survey block. Average block abundances were then $\log(x+1)$ transformed and converted to a matrix of Bray-Curtis similarity. The environmental and habitat variables which explained the greatest variability in the reef fish community similarity, diversity and species abundance within each of the three locations were identified in the previous BRT and DISTLM analyses of chapter three of this thesis. Biomass estimates were made for three large bodied species of fish that were considered the most likely from the surveyed community to show a marked response in biomass to protection from fishing; *L. forsteri*, *N. tetricus* and *N. fucicola*. Biomass was estimated using the relationship $\text{Weight} = a \times \text{Total Length}^b$. The parameters a and b for each species were obtained from the Fishbase website (www.fishbase.org). Abundances for these three species were recorded within fourteen approximate size classes (2.5, 5, 7.5, 10, 12.5, 15, 20, 25, 30, 35, 40, 50, 62.5, 75 cm), averaged across replicates for each block and summed to give a single total biomass estimate for each block. Initially, the community similarity, diversity, species abundance and biomass response variables were tested, where appropriate, using PERMANOVA (i.e. for the multivariate community similarity data) or ANOVA (for univariate responses) to test for significant differences between reserve and non-reserve samples in a simple control-impact approach. Where no reserve effect could be identified for a particular response variable, subsequent hierarchical cluster analyses were applied to identify habitat ‘groupings’ in the data. Hierarchical cluster analyses, using group-average linkage, were applied to the most important habitat variables structuring reef fish communities identified in the preceding chapter two analyses, after being normalised and converted to Euclidean distance matrices. SIMPROF tests were applied to each node of the cluster analysis to identify significant structure (at the 5 % level) in the groupings. In this way the individual sample blocks were

classified into 'groups' based on the important habitat characteristics structuring the associated reef fish community response patterns. Apportioning groups that were too large defeated the object of the investigation since they were too similar to the complete dataset, and therefore unlikely to control for any actual proportion of the physical habitat variability. However, selecting groups that were too small reduced the subsequent power of tests to detect reserve effects. A simple decision rule was applied to identify the best grouping in a cluster, whereby the largest group was selected at each tree split in a step-wise fashion until a point where no further significant structure could be identified between the variables (as identified by SIMPROF). At such point that two similar sized groups were identified at any one split, then subdividing ceased and both groups were selected. Therefore the largest, significantly structured group or groups were selected for each response and tested for reserve effects again, using PERMANOVA and ANOVA procedures, in a standard control-impact approach.

5.4 Results

5.4.1 Community similarity

Initial nested PERMANOVA analyses, including all locations and sites, identified no significant differences in community similarity between reserve and non-reserve status sample blocks (Table 5.1). Significant differences in community similarity were identified between sites within status. Figure 5.1 displays an MDS ordination plot of reef fish community structure between sample blocks for each of the three study locations. There appeared to be a close grouping between the Ninepin samples, irrespective of marine reserve status. For the Tinderbox samples there appeared to be some clustering of reserve status samples suggesting that the reef fish community assemblages were more similar within reserves than they were within non-reserves or between reserves and non-reserves. For the Maria Island samples again there was some suggestion of a pattern of clustering of reserve status samples.

The analysis in chapter three of this thesis identified biogenic cover as the most important physical habitat characteristic explaining reef fish community similarity across the scale of all three study locations (see chapter three, Table 3.4). Hierarchical cluster analyses of the full dataset didn't identify any stand out groupings, based on biogenic cover, so the two largest habitat 'groupings' (based on the smallest grouping distances) were selected (Figure 5.2) and termed as groups I and II. Subsequent PERMANOVA analyses of habitat 'groups' I and II failed to identify any significant effects of reserve status on community similarity within either group (Table 5.2).

Table 5.1. Nested PERMANOVA analyses testing for significant differences in reef fish community similarity between reserve and non-reserve status and sites. Significant results at the 5% level are highlighted in bold.

Source	Df	SS	MS	Pseudo- <i>F</i>	<i>P</i> (perm)	Unique permutations
Status	1	17083	17083	0.66601	0.5463	4653
Site (Status)	10	255990	25599	20.354	0.0001	9865
Residual	226	284240	1257.7			
Total	237	557240				

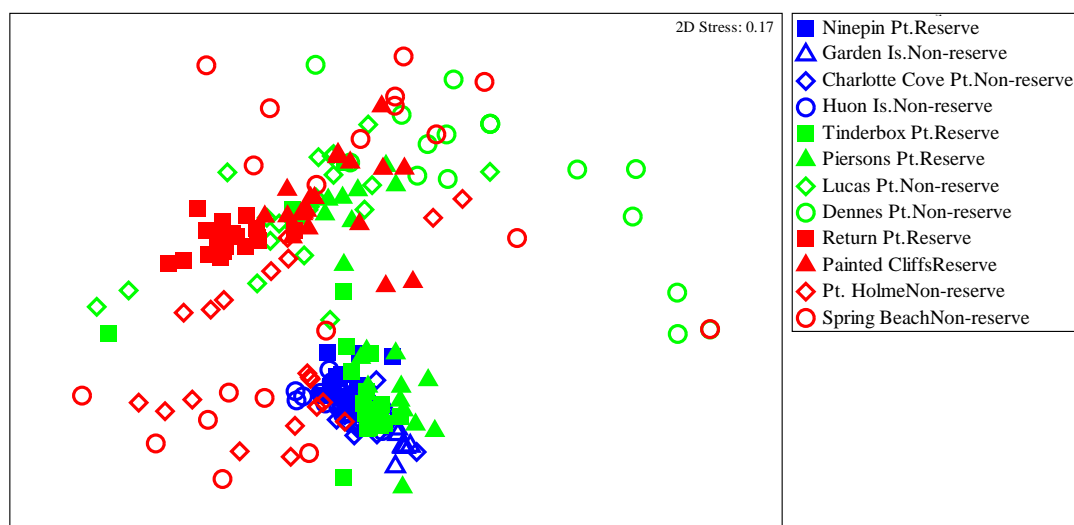


Figure 5.1. MDS plot of reef fish community similarity (based on Bray-Curtis similarity of $\log(x+1)$ transformed averaged abundance between sample blocks for Maria Island, Tinderbox and Ninepin study locations. Blue coloured symbols denote Ninepin sites, green denotes Tinderbox sites and red denotes Maria Island sites. Blocks within reserve boundaries are represented by closed symbols, while blocks within reserve boundaries are represented by open symbols.

Table 5.2. Nested PERMANOVA analyses testing for significant differences in reef fish community similarity between reserve and non-reserve status and sites within identified habitat ‘groups’ based on biogenic cover. Significant results at the 5% level are highlighted in bold.

Group	Source	df	SS	MS	Pseudo- <i>F</i>	<i>P</i> (perm)	Unique permutations
I	Status	1	4811.0	4811	1.1617	0.3185	9683
	Site(Status)	7	65679.0	9382.7	5.3859	0.0001	9849
	Residual	85	148080.0	1742.1			
	Total	93	233660.0				
II	Status	1	5594.50	5594.5	0.94452	0.3684	2462
	Site(Status)	5	80232.0	16046	15.669	0.0001	9919
	Residual	89	91147.0	1024.1			
	Total	95	178590.0				

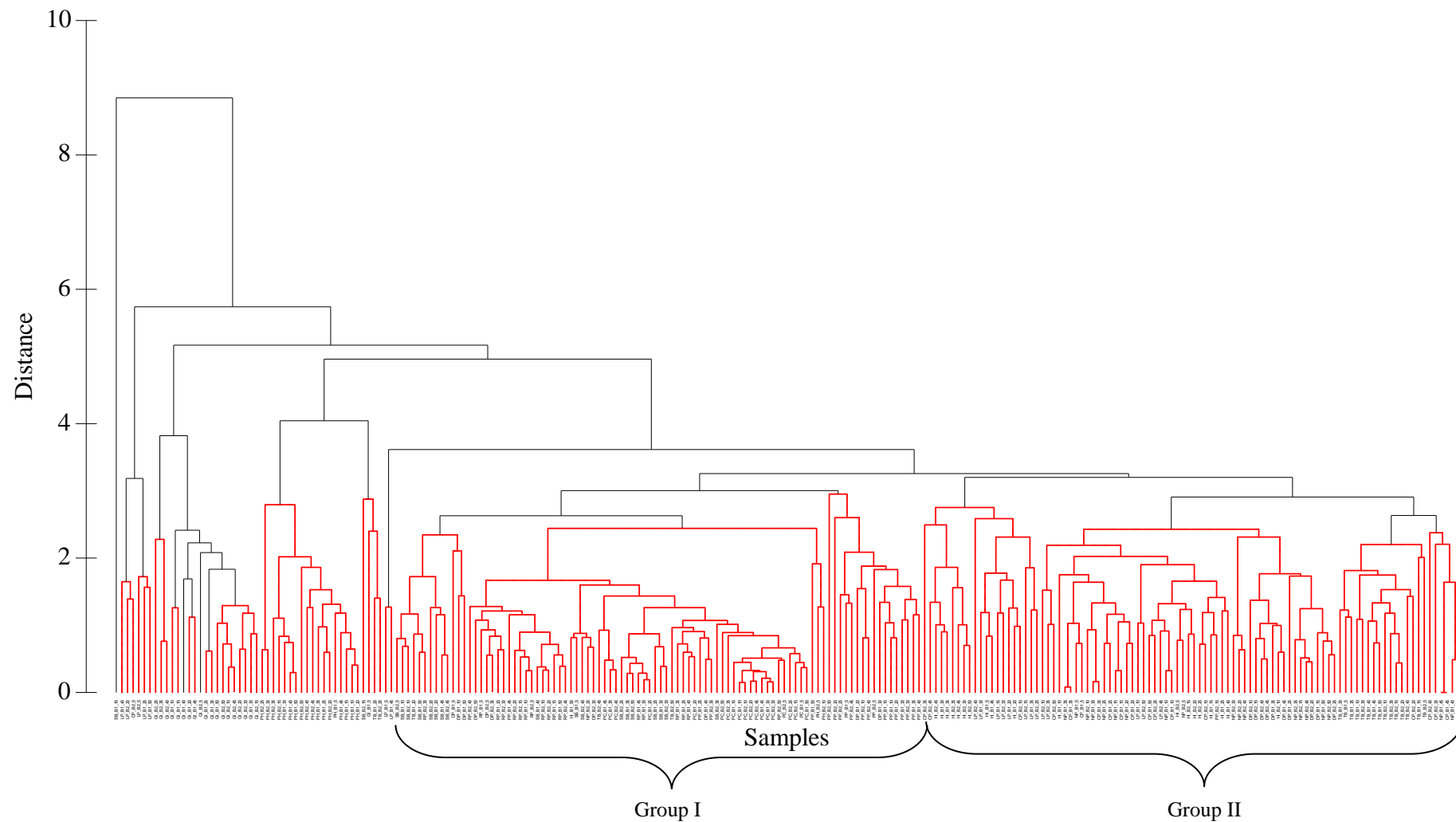


Figure 5.2. Hierarchical cluster analysis for all locations and sites based on biogenic cover habitat variables identified by the preceding chapter two analyses. SIMPROF tests at each node of the cluster analysis identified two groupings of sample blocks; Groups I and II. Branches in red denote no further significant structure in the dendrogram.

5.4.2 Species richness

Initial nested ANOVA analyses, including all locations and sites, identified no significant differences in species richness (*S*) between reserve and non-reserve status sample blocks (Table 5.3). Significant differences in species richness were identified between sites within status. Figure 5.3 displays the mean species richness per site across the three study locations. The analysis in chapter three of this thesis identified average fetch as the most important physical habitat variable explaining species richness across the scale of all three study locations (see chapter three, Table 3.11). Hierarchical cluster analyses of the full dataset, based on average fetch distance, identified no significant grouping structure between sample blocks and therefore no further analysis to test for reserve effects was justified.

Table 5.3. Nested ANOVA analyses testing for significant differences in reef fish species richness (*S*) between reserve and non-reserve status and sites. Significant results at the 5% level are highlighted in bold.

Source	Df	Seq SS	Adj SS	Adj MS	<i>F</i>	<i>p</i>
Status	1	0.034	0.034	0.034	0.00	0.978
Site(Status)	10	413.611	413.611	41.361	11.33	<0.001
Residual	228	832.35	832.35	3.651		
Total	239	1245.996				

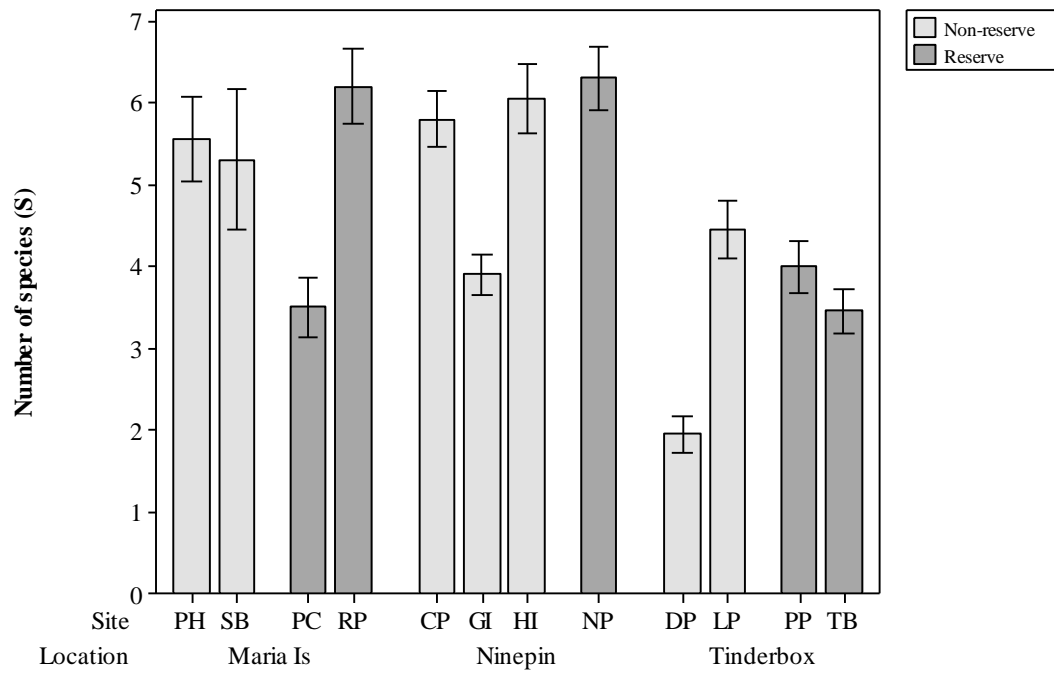


Figure 5.3. Mean species richness (S) per site (inside and outside marine reserves) across the three study locations of Maria Island, Ninepin and Tinderbox. Interval bars indicate one standard error from the mean.

5.4.3 Species abundances

Figure 5.4 displays the average reef fish species abundances across all locations and sites, inside and outside reserves. *T. caudimaculatus* and *P. multiradiata* showed the highest average abundances, both of which were highest outside of reserves. The average abundances of *N. tetricus*, *N. balteatus*, *D. aurantiacus*, *N. fucicola*, *P. rubicundus*, and *P. laticlavus* were all higher inside reserves than outside. Initial nested ANOVA analyses of individual species abundances, identified a close-to-significant difference in the abundance of *D. aurantiacus* between reserve and non-reserve samples but no significant differences in abundances could be identified between reserve and non-reserve samples for any of the other species previously modelled in the chapter three analysis (Table 5.4). For every species, except *D. aurantiacus*, the analyses identified significant differences in individual species abundances between sites within status.

Hierarchical clustering, combined with SIMPROF analyses, identified significant structure and groupings based on the important physical habitat variables for the majority of the reef fish species surveyed. Since there is insufficient space to display each individual cluster analysis here, Table 5.5 has been constructed to give a condensed overview of these results. ANOVA tests for differences in species abundance between reserve and non-reserve, for each of the identified habitat ‘groups’, identified no significant results for any species of the twelve species tested (Table 5.5).

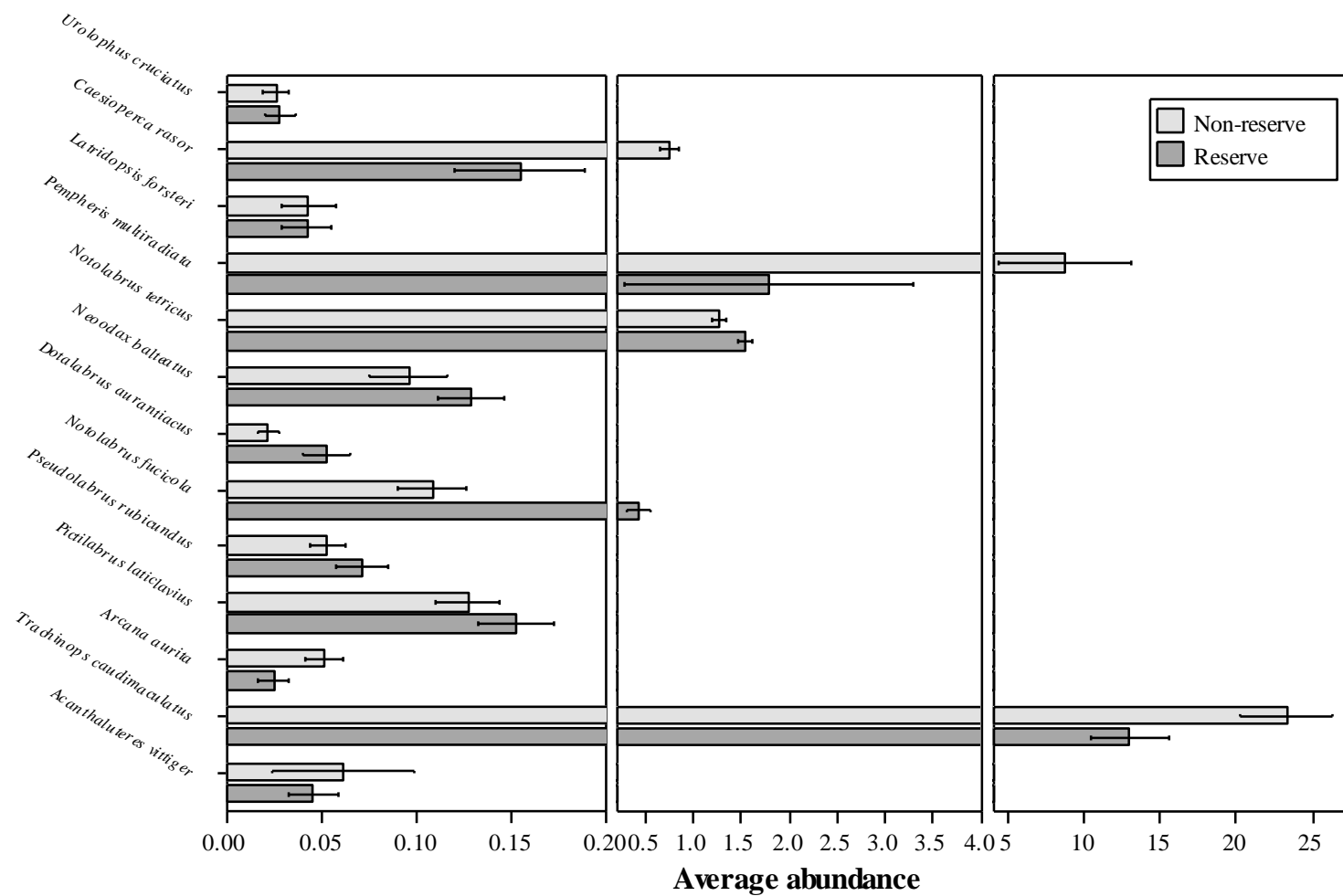


Figure 5.4. Mean species abundances inside and outside marine reserves. Interval bars indicate one standard error from the mean. NB. Change in x axis to accommodate the full range of abundances.

Table 5.4. Nested ANOVA analyses testing for significant differences in reef fish abundance between reserve and non-reserve status and sites. Significant results at the 5% level are highlighted in bold.

Species	Source	df	Seq SS	Adj SS	Adj MS	F	P
<i>Urolophus cruciatus</i>	Status	1	0.000305	0.000305	0.000305	0.01	0.928
	Site(Status)	10	0.353029	0.353029	0.035303	5.77	<0.001
	Error	228	1.396	1.396	0.006123		
	Total	239	1.749333				
<i>Caesioperca rasor</i>	Status	1	20.686	20.686	20.686	1.78	0.212
	Site(Status)	10	116.202	116.202	11.62	26.26	<0.001
	Error	228	100.893	100.893	0.443		
	Total	239	237.782				
<i>Latridopsis forsteri</i>	Status	1	0.00004	0.00004	0.00004	0	0.982
	Site(Status)	10	0.81246	0.81246	0.08125	3.67	<0.001
	Error	228	5.049	5.049	0.02214		
	Total	239	5.8615				
<i>Pempheris multiradiata</i>	Status	1	2793	2793	2793	0.53	0.484
	Site(Status)	10	52920	52920	5292	3.53	<0.001
	Error	228	342173	342173	1501		
	Total	239	397887				
<i>Notolabrus tetricus</i>	Status	1	4.4367	4.4367	4.4367	0.51	0.493
	Site(Status)	10	87.5113	87.5113	8.7511	17.1	<0.001
	Error	228	116.6994	116.6994	0.5118		
	Total	239	208.6474				
<i>Neodax balteatus</i>	Status	1	0.06463	0.06463	0.06463	0.35	0.567
	Site(Status)	10	1.84383	1.84383	0.18438	4.62	<0.001
	Error	228	9.0945	9.0945	0.03989		
	Total	239	11.00296				
<i>Dotalabrus aurantiacus</i>	Status	1	0.056317	0.056317	0.056317	4.72	0.055
	Site(Status)	10	0.119214	0.119214	0.011921	1.36	0.202
	Error	228	2.003375	2.003375	0.008787		
	Total	239	2.178906				
<i>Notolabrus fucicola</i>	Status	1	5.5852	5.5852	5.5852	1.28	0.284
	Site(Status)	10	43.5313	43.5313	4.3531	8.85	<0.001
	Error	228	112.186	112.186	0.492		
	Total	239	161.3025				
<i>Pseudolabrus rubicundus</i>	Status	1	0.02027	0.02027	0.02027	0.61	0.454
	Site(Status)	10	0.33476	0.33476	0.03348	2.38	0.011
	Error	228	3.21037	3.21037	0.01408		
	Total	239	3.56541				
<i>Pictilabrus laticlavius</i>	Status	1	0.03751	0.03751	0.03751	0.3	0.595
	Site(Status)	10	1.24536	1.24536	0.12454	3.33	<0.001
	Error	228	8.51838	8.51838	0.03736		
	Total	239	9.80124				
<i>Arcana aurita</i>	Status	1	0.0423	0.0423	0.0423	1.06	0.327
	Site(Status)	10	0.398814	0.398814	0.039881	4.39	<0.001
	Error	228	2.073375	2.073375	0.009094		
	Total	239	2.51449				
<i>Trachinops caudimaculatus</i>	Status	1	6277	6277	6277	0.43	0.529
	Site(Status)	10	147510	147510	14751	34.46	<0.001
	Error	228	97588	97588	428		
	Total	239	251375				
<i>Acanthaluteres vittiger</i>	Status	1	0.0148	0.0148	0.0148	0.05	0.832
	Site(Status)	10	3.1288	3.1288	0.3129	2.7	0.004
	Error	228	26.4584	26.4584	0.116		
	Total	239	29.602				

Table 5.5. Overview of reserve effect analyses on individual species abundance before and after hierarchical cluster analyses. ‘✓’ denotes a significant test result at the 5% level while ‘✗’ denotes a non-significant test result.

Species	Important model variables	Group structure (SIMPROF)	Group I (ANOVA)	Group II (ANOVA)
<i>Urolophus cruciatus</i>	Encrusting.algae % Cobbles (0.2m) % M boulders (0.5-1.5m) Lower.canopy.algae	✓	✗	
<i>Caesioperca rasor</i>	Turfing.algae Refuge.score.1.5cm Max.fetch Upper.canopy.algae	✓	✗	✗
<i>Latridopsis forsteri</i>	% Bedrock Refuge score (1.5cm) % M boulders (0.5-1.5m) Fractal.D	✓	✗	
<i>Pempheris multiradiata</i>	Rugosity Average.fetch Refuge.score.1.5cm Mean...Bedrock	✓	✗	
<i>Notolabrus tetricus</i>	Average.fetch Refuge.score.1.5cm Turfing.algae Refuge.score.6.15cm	✓	✗	
<i>Neodax balteatus</i>	Encrusting.algae Average.fetch % M boulders (0.5-1.5m) % Sand	✓	✗	✗
<i>Notolabrus fucicola</i>	Average.fetch Upper.canopy.algae Max.fetch Mean...Bedrock	✓	✗	✗
<i>Pseudolabrus rubicundus</i>	Average.fetch Mean...S.boulders..0.2.0.5m. Mean...Bedrock Refuge.score.6.15cm	✓	✗	
<i>Pictilabrus laticlavius</i>	Mean...Sand Mean.Stipe.density..1mx1m. Mean...S.boulders..0.2.0.5m. Refuge.score.6.15cm	✓	✗	✗
<i>Arcana aurita</i>	Encrusting.algae Refuge.score.1.5cm Average.fetch Mean...Sand	✓	✗	
<i>Trachinops caudimaculatus</i>	Sessile.inverts Encrusting.algae Average.fetch Refuge.score.1.5cm	✓	✗	
<i>Acanthaluteres vittiger</i>	Mean...Bedrock Refuge.score.1.5cm Upper.canopy.algae Average.fetch	✗		

5.4.4 Species Biomass

Figure 5.5 displays the average biomass of the three species; *L. forsteri*, *N. tetricus* and *N. fucicola* across all locations and sites, inside and outside reserves. Initial nested ANOVA analyses identified no significant differences in the biomass between reserve and non-reserve for any of the three species (Table 5.6). Hierarchical clustering, combined with SIMPROF analyses, identified significant structure and groupings based on the important physical habitat variables for each of the three species identified previously in the Chapter 3 analysis (Table 5.5). For *N. tetricus* and *L. forsteri* cluster analysis only identified one major habitat grouping for each. For *N. fucicola* cluster analysis identified two major habitat groupings. Subsequent ANOVA tests for differences in species biomass between reserve and non-reserve, for each of the identified habitat groupings, identified no significant results for any species of three species tested (Table 5.7).

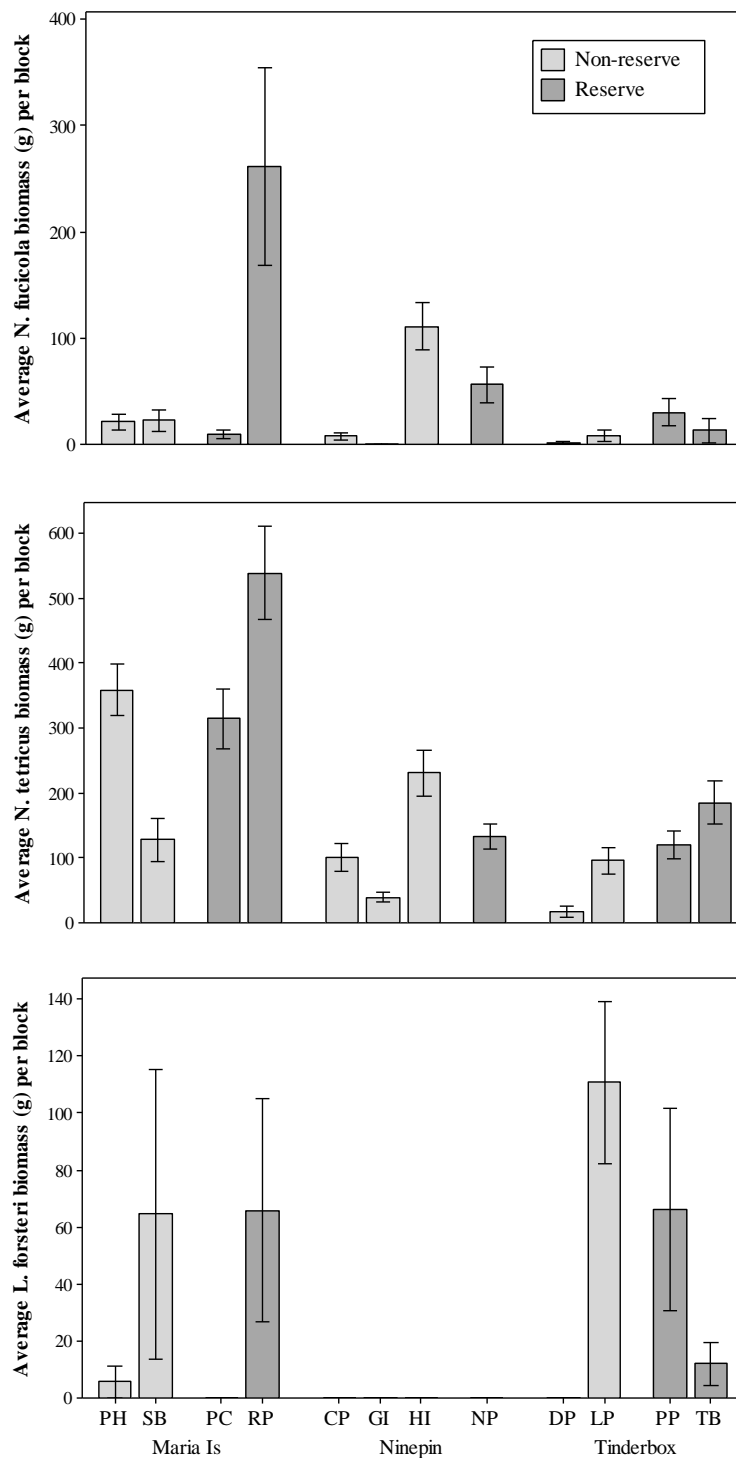


Figure 5.5. Mean species biomass of the species *Notolabrus fucicola*, *Notolabrus tetricus* and *Latridopsis forsteri* inside and outside marine reserves. Interval bars indicate one standard error from the mean.

Table 5.6. Nested ANOVA analyses testing for significant differences in reef fish biomass of three species; *Notolabrus fucicola*, *Notolabrus tetricus* and *Latridopsis forsteri* between reserve and non-reserve status and sites. Significant results at the 5% level are highlighted in bold.

Species	Source	df	Seq SS	Adj SS	Adj MS	F	P
<i>N. fucicola</i>	Status	1	142189	142189	142189	1.30	0.280
	Site(Status)	10	1092141	1092141	109214	6.57	0.000
	Error	228	3792785	3792785	16635		
	Total	239	5027115				
<i>N. tetricus</i>	Status	1	835051	835051	835051	2.02	0.186
	Site(Status)	10	4139993	4139993	413999	17.56	0.000
	Error	228	5374607	5374607	23573		
	Total	239	10349651				
<i>L. forsteri</i>	Status	1	513	513	513	0.02	0.903
	Site(Status)	10	329853	329853	32985	3.16	0.001
	Error	228	2381541	2381541	10445		
	Total	239	2711907				

Table 5.7. Nested ANOVA analyses testing for significant differences in reef fish biomass of three species; *Notolabrus fucicola*, *Notolabrus tetricus* and *Latridopsis forsteri* between reserve and non-reserve status and sites within identified habitat groupings. Significant results at the 5% level are highlighted in bold.

Species	Source	df	Seq SS	Adj SS	Adj MS	F	P
<i>N. fucicola</i> Group I	Status	1	7841.3	7508.9	7508.9	6.20	0.065
	Site(Status)	5	5854.4	5854.4	1170.9	1.34	0.254
	Error	115	100743.7	100743.7	876.0		
	Total	121	114439.4				
<i>N. fucicola</i> GroupII	Status	1	10928	10928	10928	0.04	0.858
	Site(Status)	3	859005	859005	286335	7.44	0.000
	Error	95	3655701	3655701	38481		
	Total	99	4525634				
<i>N. tetricus</i>	Status	1	412739	22371	22371	0.08	0.787
	Site(Status)	5	2040204	2040204	408041	9.65	0.000
	Error	64	2704911	2704911	42264		
	Total	70	5157854				
<i>L. forsteri</i>	Status	1	647	13796	13796	0.38	0.550
	Site(Status)	10	382054	382054	38205	4.26	0.000
	Error	199	1786245	1786245	8976		
	Total	210	2168946				

5.5 Discussion

The majority of studies investigating the effects of protection from fishing fail to adequately control for the natural effects of habitat composition and variability (Huntington et al., 2010). Separating the effects of fishing protection from those of natural variability is a difficult task due to the lack of knowledge of the appropriate environmental and habitat variables to control for. Previous work carried out in this thesis has identified the important physical environmental and habitat variables responsible for structuring aspects of the temperate reef fish communities around Tasmania, enabling some proportion of the natural variability to be controlled for, thus improving the ability to detect effects of reserve protection.

This study tested the hypothesis that the effects of protection from fishing across Tasmanian marine reserves could be masked by the confounding effects of reef community responses to variability in components of the physical reef habitat. To test this, samples surveys of reef fish abundance across a range of habitat variability were classified into habitat ‘groups’ based on the natural variability of important, community determining, sets of variables, and then protection effects were tested within these ‘groups’ following a standard control-impact approach. The analysis was unable to identify any statistically significant effects of marine reserves on community similarity, species richness, abundance or biomass before or after variability in the physical habitat was taken into account. Some limited evidence of a reserve effect for the Pretty Polly, *Dotalabrus aurantiacus*, was identified before natural physical variability in the habitat was taken into account but this species is not subject to direct pressure from fishing suggesting some indirect effect of reserve status. These findings are largely inconclusive and point to the need for larger scale temporal and spatial studies, incorporating the full range of possible physical habitat variables, to adequately apply this

analysis approach across Tasmanian reef habitats and maximise the ability to detect reserve effects.

5.5.1 Identifying reserve effects

The findings of other researchers have shown that habitat type and variability are important determinants of marine reserve efficacy (Friedlander et al., 2007, Harborne et al., 2008, Claudet et al., 2010, Hamilton et al., 2010). This is largely unsurprising given the existing research identifying the importance of habitat variability in structuring marine communities, but few studies assessing the effects of marine reserves have considered this variability within individual habitat types. In a tropical example, Huntington et al. (2010) demonstrated that the application of a habitat classification approach was capable of improving the evaluation of marine reserve efficacy by controlling for the confounding effects of physical habitat structure. They investigated how the physical structure of reef habitats in Belize masked marine reserve effects. When they assessed the efficacy of marine reserves without considering the effects of natural habitat attributes, no reserve effects could be detected in the diversity and abundance of fish and coral communities, despite 10 years of management protection. However, after grouping sites based on the natural variability in the physical habitat attributes of the reef, significant reserve effects between habitat groupings were revealed. They successfully demonstrated that both commercially and non-commercially targeted reef fish displayed higher total biomass inside reserves than outside, supporting the hypothesis that the application of a habitat classification approach can improve the evaluation of marine reserve effects by controlling for confounding effects of natural habitat variability. My own results have been unable to conclusively demonstrate the same outcome in a temperate marine context. The reasons this study may have failed to identify similar reserve effects when variability due to the natural physical habitat was accounted for is unclear. One simple reason may be that large, inherent differences exist between the role played by

physical habitat in structuring different reef fish communities and the varying existence and extent of other confounding effects such as recruitment variability and local fishing pressure. These latter factors may play a more important role across Tasmanian reefs. For instance, where a population is heavily impacted by surrounding fishing activities this may be the principal factor structuring reef fish communities both outside and inside marine reserves, particularly where highly mobile species are considered. Richards et al. (2012) explored the relationships between large-bodied species of reef fish and various quantitative characteristics of their environment. They identified that depth, water temperature and distance to deep water were all important variables but that the principle determining factor of the distribution of large bodied fish was local human population density, presumably acting as a proxy measure of anthropogenic impacts such as over-fishing. Measures of the surrounding local fishing intensity, or proxies of such, should be incorporated into any similar investigations of reserve effects across Tasmanian marine environments.

Detecting differences in individual species abundances and biomass between reserves and non-reserves can be difficult due to the inherent variability of recruitment and the difference in fishing pressure on species at different stages in their life history. Rarer and highly mobile species require extremely high survey replication to detect patterns which is one reason why long time series before-after, control-impact (BACI) approaches are applied by most investigators. Barrett et al. (2007) compared long-term changes within fully protected marine reserves in Tasmania against changes at external reference sites on an annual basis over the first ten years of protection. Their results demonstrate the importance of long-term datasets for detecting reserve effects. Their results identified a tenfold increase in the abundance of large bodied reef fish and a doubling of species richness of large fish within the Tinderbox Marine Reserve relative to controls. Importantly they were also able to demonstrate the high

inter-annual variability in the abundance of some species resulting from episodic recruitment events, suggesting that natural recruitment variability may be an important factor masking reserve effects on temperate reef fish communities beyond the effects of physical habitat structure. Again, as with local anthropogenic pressures, temporal and spatial variability in species recruitment may at times be the principle factor structuring reef fish communities both outside and inside marine reserves and such information, where it is available should be incorporated into any future investigations of reserve effects.

5.5.2 Study limitations

Long-term studies have shown that most species of Tasmanian reef fish display considerable variation in population parameters across reserve and non-reserve areas, much of which cannot be attributed to protection from fishing (Edgar and Barrett, 1999, Barrett et al., 2007). For large-bodied, targeted species such as the bastard trumpeter, *Latridopsis forsteri*, Tasmanian marine reserves appear to afford significant protection from local fishing pressure however, the abundance of this species still appears to be highly temporally variable inside marine reserves due to the variable nature of its recruitment (Barrett et al., 2007). Edgar et al. (2009) identified an order of magnitude increase in the biomass of large bodied fishes (>45 cm TL) across Tasmanian MPAs. Their study was a temporally and spatially large scale investigation surveying fish communities within twenty six sites, inside and outside three MPAs over a sixteen year period. It is probable then, that the temporal and spatial scale of my study may have been insufficient to detect reserve effects, where they clearly exist, particularly for those highly mobile and recruitment variable species. Detecting MPA effects will be limited to a large extent by the size and established age of the reserve. (Edgar et al., 2009) have identified clear positive relationships of reef fish biomass and large bodied fish abundance with the age of reserve. Research carried out across the same reserves considered in this study has previously identified clear reserve effects for fish and invertebrate

communities (Edgar and Barrett, 1997, Edgar and Barrett, 1999, Barrett et al., 2007, Barrett et al., 2009, Edgar et al., 2009, Alexander, Manuscript in review). These findings suggest that MPA length of establishment and size could not have been a major limitation in the detection of reserve effects in this study.

Ultimately the success of this investigation depended on the apparent accuracy of the initial species-habitat model findings from chapter three of this thesis and which also includes an in-depth discussion of some of the limitations of the approach applied so only a brief discussion of these will be included here. The biggest issue was that for many species the extent of the species-habitat modelling study was not sufficient to capture the complete relationships, and for many species a truncated response was likely being modelled on a subset of the full gradient of the habitat structure available to the community. A number of direct factors that influence species and community responses may have been absent from the initial species-habitat investigation and some of those that were included possibly also lacked direct ecological relevance for many of the modelled species. As already mentioned, quantitative measures of fishing pressure and temporal recruitment variability would likely have improved explanatory model outcomes, and therefore produced more realistic habitat 'groupings' from which to test the effects of protection from fishing. Including all the possible direct and resource habitat measures that may have been important could have vastly improved the explanatory power of the models, however doing so was unfeasible within the resource and logistical limitations of the project.

5.5.3 Conclusions

This study has explored a method that can be used to partition habitat effects from effects of protection from fishing that could be improved upon in future broader-scale studies. Where I

failed to identify reef fish community responses to protection from fishing I have been able to identify future research considerations by highlighting where possible explanatory physical variables may have been overlooked. The importance of habitat in structuring reef fish communities is undoubtedly apparent but understanding the extent to which these variables interact with reserve effects requires the consideration of additional factors such as local anthropogenic pressure, recruitment variability and other species-specific influences of reef habitats. The approaches applied in this study have the potential to identify reserve effects which would otherwise be overlooked by less detailed methods. Community responses to protection will rarely be uniform across the marine environment and by identifying the principle sources of natural variability affecting community and species responses to their environments, and factoring this into the design of marine reserve evaluations, investigators afford themselves the greatest chance of revealing subtle effects of protection. Ideal reserve assessments should apply BACI approaches to control for the confounding effects of natural temporal variability but in many situations, their application often suffers from a lack of baseline data prior to MPA establishment. In such cases where prior information is absent, approaches which attempt to account for variability resulting from natural habitat structure offer the best available solution to the perennial problem of confounding effects of habitat differences between MPA and control sites.

Chapter 6. Final Discussion

The distributions of marine species and communities are determined by the spatial and temporal variability of complex interactions between the physical, chemical and biological characteristics of their environments (Menge and Sutherland, 1987, Underwood, 2000, Valesini et al., 2004a). Physical habitat structure is responsible for influencing a large proportion of the associated faunal and algal composition of marine communities by determining the availability of food, shelter and refuge from predation for many marine organisms (Hixon and Beets, 1993, Almany, 2004, Caddy, 2007). Patterns in community structure and species distributions over large scales and coarse resolutions tend to be correlated with indirect climatic gradients, while patchy, small scale distributions are generally the result of highly variable, direct resource gradients associated with local topographic variation and habitat fragmentation (Guisan and Thuiller, 2005, Scott, 2002). A shift in marine management attitudes, away from single species management approaches towards, ecosystem-based approaches (Nevill, 2010) has necessitated the development of time and cost effective surrogate approaches capable of quantifying biodiversity at fine resolutions, across ecosystem scales (Huang et al., 2010, McArthur et al., 2010). Developing surrogate approaches to mapping and predicting biodiversity in the marine environment requires an understanding of the specific scales at which species and communities respond to components of their physical habitats (Wiens, 1989). Most attempts to do this have focused on the spatial management of marine resources over relatively large spatial scales, but marine communities are also exploited at local to regional scales, necessitating effective spatial management of marine resources across a wide range of spatial scales (Williams and Bax, 2001). Habitat type and structural variability are important determinants of marine spatial planning outcomes (Friedlander et al., 2007, Claudet et al., 2010, Hamilton et al., 2010) and

are important factors to be considered when estimating their effectiveness (García-Charton et al., 2004, Harborne et al., 2008). Disentangling the separate importance of natural spatial and temporal habitat variability affects from those of marine protected area is vital for the effective implementation of future marine spatial planning and sustainable resource management (Huntington et al., 2010).

6.1 Research findings and implications

Habitats are not perceived uniformly by organisms, the responses of species and communities to physical habitat structure varies with the spatial resolution of the area considered (Anderson and Yoklavich, 2007, Claudet et al., 2010). Identifying the appropriate scale at which to investigate the associations of species and communities with their habitats is one of the principal problems of species-habitat studies (Wiens, 1989, Guisan and Thuiller, 2005). The distributions and abundance of species vary markedly over large latitudinal and longitudinal extents in response to large scale climatic and biogeographic gradients (Mora et al., 2003, Willig et al., 2003). The underlying mechanisms controlling these patterns are poorly understood as are the scales at which components of physical habitat structure begin to affect a greater influence on community structure than geographic position or how fish communities from different geographical localities, respond to similar habitat structure. This study addressed these questions by investigating patterns in fish community structure in response to physical metrics characterising the environment and habitat of temperate rocky reefs. The study considered multiple spatial scales, ranging from bioregions separated by 1000's of kilometres to scales of 10's of metres across individual reefs, to determine how the effect of environmental and habitat characteristics dictate resulting fish community structure. The results of chapters two and three identified some key environmental and habitat variables and the scales at which they best explained responses in the associated reef fish community

structure and highlighted the potential extent for quantitative measures of physical environment and habitat to be applied as predictors of reef fish community structure across temperate regions of Australia at multiple management scales. Detecting patterns of association at the finest spatial scales is challenging and requires physical data at sufficiently detailed resolutions and extents to allow accurate modelling of species and communities. The responses of individual species to habitat structure were largely found to be species-specific and highly variable. Few studies prior to this have investigated how community structure and diversity of temperate reef fish communities respond to variations in components of the physical structure of their associated habitats across such a broad range of spatial scales. The findings of this study provide marine resource managers and scientists with specific insight into the important physical components of the environment structuring temperate reef fish communities around Australia across a range of ecologically relevant scales and generate further hypotheses regarding the specific ecological mechanisms affecting communities and distributions of reef fishes.

Modern advances in remote sensing tools now allow various physical habitat data to be sampled from the marine environment across broad spatial extents at increasingly detailed resolutions (Knudby et al., 2007). This information is generally cheaper and easier to acquire than direct diver assessments of reef habitat structure over equivalent spatial scales. Chapter four assessed remotely sensed derivative measures to determine their potential as surrogates of direct measures of habitat structure for explaining reef fish community structure at fine, ecologically proximal resolutions. These results demonstrate that remotely sensed metrics of reef habitat structure, employed in combination with modern modelling approaches, have the potential to explain and predict fine resolution patterns in temperate reef fish community structure around Tasmania. Remotely sensed environmental data are routinely utilised in

spatial marine planning over large scales but the practicality of applying them over small scales has rarely been tested. These findings suggest the potential of remotely sensed models of reef fish community as valuable marine spatial planning tools for explaining and predicting community structure and distributions between ecologically proximal scales of 10's to 100's of metres.

Physical habitat structure is rarely a principle consideration in designing effective marine protected areas (MPAs), instead most management decisions largely focus on minimising conflicts with existing stakeholders rather than maximising conservation outcomes (García-Charton et al., 2004). Understanding how physical habitat structure effects the spatial variability in the distribution and abundance of reef fish can help to separate this influence from variation due to the effects of protection from fishing (Garcia-Charton and Pérez-Ruzafa, 2001). The majority of studies investigating the effects of protection from fishing fail to adequately control for the natural, pre-existing temporal and spatial variability effects of habitat composition and structure (Claudet et al., 2010, Huntington et al., 2010). The final study, chapter five of this thesis, applied control-impact assessments of reserve efficacy across three coastal marine reserves in Tasmania in an attempt to disentangle natural variability in community structure from that due to reserve effects. Attempts to identify clear reef fish community responses to marine reserves were limited even where the principle sources of natural variability affecting community and species responses to their environments could be identified and accounted for before testing for reserve effects. Despite the largely null results, in future studies this approach has the potential to maximise the chances of identifying subtle effects of protection which would otherwise be overlooked by traditional control-impact investigations. This approach would be particularly valuable in monitoring the early stage effects of new reserves where there is an absence of long-term,

‘Before-After, Control-Impact’ (BACI) datasets of community structure (Huntington et al., 2010).

With respect to chapters three, four and five which applied analysis on relatively fine scale sampling units of 5 x 5 m blocks there were potential issues of adequate sampling detection, replication and sampling independence which should be highlighted. Conventional studies investigating fish across entire communities and multiple habitat types would typically not use such fine scale resolution. These chapters focused on how fine scale variability in physical habitat structure might influence the particular associations of different species within temperate reef habitat which necessitated a particularly fine scale approach. Therefore this approach was limited by the probability of encountering rarer and larger ranging species in sufficient numbers to model their distributions and abundance. The temporal replication of the sampling was intended to minimise the chances of missing mobile and rarer species but without an absolute knowledge of the true abundance and ranges of these species it is difficult to be certain if this level of replication was adequate. Additionally the lack of transect replication at the site scale resulted in limitations on some of the analysis approaches at this scale. Future studies should consider the sampling scales and levels of replication (both spatial and temporal) appropriate to the communities, species and habitats they are targeting and the relative abundances of species across habitats when designing surveys in order to make sufficient observations to ensure effective modelling. Sampling fish and physical habitat with the use of SCUBA imposed specific limitations on the level of independence between samples. Due to the logistical and time constraints of sampling fish and habitat underwater it was necessary to sample blocks in a continuous grid arrangement to maximise the survey work in the time available. There was a necessary trade-off balance between maintaining independence across the sampling units and adequate replication for

effective analysis. Future studies, if constrained by similar limitations, should make attempts to adequately balance the need for independence of the sampling data with adequate replication. Obviously much of this relies on the scale and resources of the individual project.

6.2 Linking chapter findings

Chapter two results identified broad, bioregional scale variability in reef fish community structure largely relating to latitudinal differences, acting as a proxy for large scale climatic and biogeographic variability between sites. At regional scales, the importance of ecologically proximal physical variables, such as biogenic cover (probably closely related to exposure), refuge space and habitat substratum begin to come into effect. Chapter three then considered finer scales of investigation from regional to local scales, identifying the importance of exposure and its relationship with biogenic structure, in explaining significant proportions of associated reef fish community similarity and diversity patterns across regional scales and the increasing importance of physical habitat heterogeneity and complexity variables towards finer ends of the scales investigated. Taken together the findings of chapters two and three lend support to the hypothesis that the structuring of temperate reef fish communities are dictated by a spatially hierarchical gradient of ecological processes ranging from distal influences of climate and biogeography at latitudinal scales to proximal influences of fine scale physical habitat structure. Other researchers have supported similar hypotheses with their findings of algal (Kendrick et al., 1999) and fish (Syms, 1995) community responses. How individual fish respond to their environments and habitats appear to be largely species-specific and vary in complexity between species. For some species, a simple association with a particular habitat feature, at a particular scale will likely be sufficient to explain its distribution and abundance, but for other species, more complicated combination of variables across a range of scales must be considered (Anderson et al., 2009).

This study identified the general importance of wave exposure and resulting biogenic structure in explaining the maximum variability in reef fish community similarity and diversity across intermediate and regional to local spatial scales. Remotely sensed measures of exposure were unavailable to us at the fine scales investigated in chapter four but measures of the proportion of reef structure deviating from south and east facing aspects were interpreted as proxies of wave exposure since the predominant swell exposure across the Tinderbox sites was from the southeast. The findings of chapter four, when metrics of south and east reef aspect are considered as proxies for exposure, agree well with those of the Tinderbox sites from the preceding chapter three in identifying the likely importance of wave fetch exposure. The similarity in findings between the direct and remotely sensed approaches demonstrates that simple, remotely sensed metrics can be effectively applied as surrogates to explain some degree of reef fish community structure. This is particularly useful in situations where the availability of fine scale direct measures of exposure are unavailable. Advances in GIS and other analysis tools have enabled various fine-scale derivative metrics of habitat structure to be calculated from bathymetric digital elevation models (DEMs) providing researchers with a variety of potentially informative surrogate measures of fish community structure (Guisan and Zimmermann, 2000) in the absence of direct metrics of habitat and providing an effective tool for spatial marine planning.

Variability in habitat type and structure can be important determiners of the effectiveness of marine reserves across reef environments (Friedlander et al., 2007, Harborne et al., 2008) and have been shown to conceal underlying reserve effect responses of reef fish (Hamilton et al., 2010, Huntington et al., 2010). The finding of chapter three, which identified the important habitat variables explaining associated reef fish community structure across regional to local

scales, were applied in chapter five in an attempt to disentangle the separate effects of habitat structure and reserves across Tasmanian reefs. Where baseline data is lacking for the assessment of spatial marine planning outcomes, supplementing traditional control-impact assessments with a knowledge of existing spatial habitat variability can improve evaluations by controlling for habitat influences that affect communities and species. This method can be applied to existing community monitoring data to ensure that appropriate control sites are compared to impacted sites or applied to specific target species for accurate single species assessments.

6.3 Future research directions

Species-habitat associations detected in this work do not necessarily imply direct causal relationships, nor do they implicitly suggest a behavioural choice of an organism, but simply identify significant non-random relationships between a species or community and aspects of their environment or habitat. The exact ecological and behavioural processes behind apparent associations need to be tested through well designed manipulative field and laboratory experiments. Syms and Jones (2000) investigated the direct relationships between different agents of disturbance and tested their effects on reef fish communities through manipulative field experiments. Reef fish assemblage structure was found to be resilient to pulsed fish removal events across areas of reef but differed significantly from control plots following physical habitat degradation, suggesting that the effects of physical habitat disturbance on fish community structure may be more important than those due to depletions from fishing. Future work should focus on the design of similar factorial experiments to extract how proximal ecological processes such as recruitment, competition, foraging ability and predator interactions are individually influenced by aspects of physical reef habitat.

Future approaches wishing to successfully apply remotely sensed surrogate metrics to model reef fish community structure should ‘calibrate’ model finding against those based on similar direct measures and be aware of how the community or species of interest will vary across spatial scales and between different locations. As our understanding expands of how communities and species vary in relation to their physical habitats, the development of ecologically relevant surrogates of habitat structure should become possible. Remote sensing technologies have for some time allowed scientists to measure physical variables from coastal marine environments across large spatial scales. Many fine-scale habitat variables can currently only be measured accurately through direct field observations. Measures of habitat structure have been correlated with remote methods of data collection with varying degrees of success (Kuffner et al., 2007) so researchers should be aware of the relative weakness of a particular approach when trying to identify ecological associations between organisms and aspects of their environments. Modern developments in multi-beam hydro-acoustics and other technologies such as optical satellite and aerial imagery (e.g. IKONOS and LIDAR) (Stumpf et al., 2003) are beginning to allow relatively inexpensive, broad scale, continuous lateral assessment of marine fish habitats at equivalent resolutions to traditional direct measures (Purkis et al., 2008, Brown and Blondel, 2009, Brown et al., 2011). Future research should focus on identifying derivatives from increasingly detailed bathymetric data as it becomes available, which directly relate to ‘real’ measures of physical habitat structure known to effect the community structure of organisms. Lucieer and Pederson (2008) employed surface analysis theory to generate derivative measures of surface features from a seabed digital terrain model (DTM) at biologically relevant scales and applied them to model the movement and habitat utilisation of the commercially important southern rock lobster, *Jasus edwardsii* in Tasmania. Similarly useful derivatives could be developed and tested for individual species of commercially important fin-fish that utilise reef environments given

enough prior knowledge of their relationships with habitat structure in determining their distributions and extents. As habitat mapping becomes more detailed and able to resolve biologically relevant features, an increasing unification of large scale environmental and fine-scale seascape metrics will allow highly predictive models of species-habitat association (Anderson et al., 2009).

Study areas must be large enough to capture the complete relationship between reef fish communities or species and habitat structure in order to avoid inadvertently modelling a truncated response to a subset of the full gradient of a particular habitat variable. This requires prior knowledge of the full extent and habitat range of a given species and how they interact with their environments at varying spatial scales. Collecting biological and ecological information of this sort over the full range of many species is a big challenge, however modern advancements in autonomous underwater vehicle (AUV) and video technology are allowing improved survey capabilities, capable of estimating algal, invertebrate and fish densities at depth and across large spatial extents (Desa et al., 2006). AUV mounted video imagery and sonar are now beginning to emerge as a potential tool for measuring physical habitat structure in the marine environment (Shumway et al., 2007) and are already leading to the development of combined biological and physical survey capabilities (Williams et al., 2010b). Future investigations should test the applicability of fine-scale patterns of association over broad, management scales, utilising methods such as underwater video and AUV which are capable of broad-scale sampling of fish, benthic invertebrate and algal communities simultaneously. These sampling techniques in combination with bathymetrically derived metrics of physical marine habitats probably represent the best current means of accurately and effectively modelling reef fish community structure across coastal reef habitats over large resource management scales.

Modelling species or community-habitat associations effectively requires an accurate assumption that they are operating close to or within their fundamental niche. Ecological modelling implicitly assumes that a pseudo-equilibrium exists between organisms and their environments (Austin, 2002), an assumption which risks inherent bias in model interpretations because in general what is being realistically modelled in nature is a response to biotic interactions and stochastic responses of an organism specific to a particular time and region (i.e. the realised niche) rather than the full response of a species occupying all of its suitable habitat (i.e. the fundamental niche) (Guisan and Zimmermann, 2000, Austin, 2002, Guisan et al., 2002, Guisan and Thuiller, 2005). Unaccounted for influences such as disturbance (e.g. fishing pressure) can have overriding effects on community structure and otherwise mask other natural associations with habitat. Difficulty lies in the certainty that a statistical model represents a good approximation of the fundamental niche and therefore comparisons between different locations. The accuracy of a model based on environmental predictors will vary depending on the degree to which the dispersal and disturbance history have defined a particular community assemblage, therefore it is important that researchers are specific about the ecological assumptions underpinning any model and the appropriate extent and accompanying levels of uncertainty with which their predictions can be accurately applied. Future model development should be based on a solid theoretical and empirically derived understanding of a species response to its physical environment (Guisan and Thuiller, 2005), potential sources of community disturbance such as fishing pressure and an awareness of the spatial applicability of resulting models.

Reliability of occurrence and abundance data to accurately predict a species distribution will depend on the behaviour of species in response to the applied survey technique and the

inherent ability of that technique to detect a species within its environment. Many known and unknown factors will influence the capability of a particular method to accurately sample a particular species response. For example, species aggregating behaviour, behaviour in response to equipment or observer (i.e. avoidance or attraction), feeding behaviour, diurnal behaviour and body size in relations to refuge availability will all determine how effective a particular sampling technique is. Survey techniques applied to future investigations should be selected based on a good prior knowledge of their biases and drawbacks and the spatial extent across which they must be applied to accurately detect a particular species of interest.

This study has attempted to determine the separate effects of physical habitat structure and marine protection, however it is not sufficient to only test for the existence of differences between control and reserve sites. With sufficiently large sample sizes, statistically significant difference between sites can almost always be obtained due simply to true natural biological variability between the sites. Determining the important effects of protection relies on identifying the magnitude of an effect and the uncertainty that surrounds estimates of it (Willis et al., 2003). To be confident that detected reserve effects are real and not simply the result of natural site variability, future studies need to be based on well designed studies of long-term, before-after, control-impact datasets with sufficient site replication and controls for spatial confounding.

6.4 Final Conclusions

The findings of this work have identified direct and surrogate variables of physical habitat structure that effectively explain the community structure, diversity and individual species responses of temperate Australian reef fish across scales from 10's of metres to 1000's of kilometres. In addition this study attempted to disentangle the separate effect of natural

habitat related variability in reef fish community structure from that of MPA effects. This information affords marine resource managers and scientists specific insights into important physical components of the environment that may be used as surrogates to map and predict reef fish communities and distributions across a range of ecologically relevant scales and generates further hypotheses regarding the specific ecological mechanisms affecting communities and distributions of reef fishes. The application of ecosystem-based management and associated marine spatial planning approaches is rapidly increasing around the world and managers and scientists face the considerable challenge of identifying, quantifying and monitoring the effects of MPAs. Understanding how communities and species respond to MPAs and the varying physical structure of their environments is vital to the effective planning, application, management and monitoring of MPAs. A biased assessment that overlooks apparent effects of MPAs can generate false conclusions and retard future management efforts to develop their use as a conservation tool. We need further objective assessments of the conservation, fisheries and human benefits of MPAs based on robust assessment approaches and clear ecological understanding of their effects on marine communities.

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Appendix 1. Mean and standard errors for of each of the physical variables plotted across the seven bioregions.

