Responses of temperate mobile macroinvertebrates to reef habitat structure and protection from fishing

Timothy John Alexander, B.Sc. (Hons)

Submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy,

University of Tasmania, January 2011

Frontispiece: *Heliocidaris erythrogramma* in reef refuge

Declaration of originality

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Statement of co-authorship

As primary supervisor, Dr. Graham J. Edgar contributed general advice and editing to all chapters.

Chapter 3: Dr. Neville S. Barrett and G.J. Edgar contributed transect scale invertebrate data. Dr. Malcolm Haddon assisted with statistical analyses. This chapter has been published as: Alexander, T.J., Barrett, N., Haddon, M., Edgar, G., 2009. Relationships between macroinvertebrates and reef structure in a temperate marine reserve. *Marine Ecology Progress Series* 389: 31-44 (see appendix)

Chapter 4: N.S. Barrett and G.J. Edgar provided invertebrate, fish and macroalgae data.

Chapter 5: G.J. Edgar and N.S. Barrett contributed the long-term marine reserve monitoring data. G.J. Edgar, Prof. Craig R. Johnson and M. Haddon assisted with the development of the statistical analysis techniques

Chapter 6: General advice and editing by G.J. Edgar

Abstract

This study assesses the importance of crevices and other physical aspects of reef structure to macroinvertebrates associated with rocky reefs. No-take marine reserves have the potential to interact with reef structure to influence the organisation of the benthic community. Despite wide recognition that such relationships influence ecosystem structure, very few quantitative field studies have reported previously on relationships between reef structure and macroinvertebrates at the assemblage level, and none on interactions additionally involving protection from fishing.

The relative importance of protection from fishing and reef habitat structure were determined by surveying reef structure and invertebrates at three spatial scales at protected and fished sites around the ‘no-take’ Maria Island marine reserve. Small reef features and protection from fishing both affected abundances of the majority of taxa, while rugosity – the most commonly employed metric of reef structure – proved to be a poor predictor of invertebrate abundance and richness. Models developed on the basis of Tasmanian data that use habitat surrogates to describe the spatial distribution of invertebrate assemblages and populations were found to have limited predictive ability when applied in New South Wales and Western Australian bioregions. Single habitat predictors tended to dominate species models for each bioregion suggesting that surrogates identified in one region should not be extrapolated outside that region without local validation. Analysis of a long-term (16 years) ecological dataset from eastern Tasmania indicated that the strength of relationships between reef structure and exploited rock lobsters (*Jasus edwardsii*) decreased within newly-declared MPAs. Cascading trophic effects also apparently affected habitat links for prey sea urchins (*Heliocidaris erythrogramma*) and abalone

(*Haliotis rubra*). Given the changing nature of relationships through time and space, caution is clearly required when generalising from results of studies undertaken in a single time period or single region.

Cryptic invertebrates sampled below flat sandstone blocks were significantly influenced by the surface structure of the underlying reef. These cryptofaunal assemblages were similar between sites inside and outside the Maria Island marine reserve; however juvenile abalone, one of the most abundant species in this habitat, were recorded in much lower numbers at protected sites. Combined with evidence of declining adult populations, this finding suggests the possibility that recruitment failure may occur for abalone populations in Tasmanian marine reserves with abundant rock lobsters.

Through analysis of relationships between mobile invertebrates and reef structure at protected and fished sites, and at multiple spatial- and temporal-scales, this project has provided valuable insight into temporal stability and instability, and spatial specificity of linkages between temperate reef-associated invertebrates and their environment.

Acknowledgements

Firstly, I would like to thank to all the people who dedicated themselves to the massive field effort required for this project. Particularly, Jan Seiler, Ryan Downie, Arianna Polacheck, Dave Stephenson, Jacqui Shelton, Pickles, Chris Brown, Stephen Leporati, Mani Thom and Paul Burch.

Thank you to my primary supervisor Graham Edgar for endless patience and advice, Malcolm Haddon for statistical advice, Neville Barrett for access to broad scale and long-term monitoring data and Craig Johnson for directional advice for chapter 5.

Thank you to Australian Research Council for providing financial support for field operations.

Thank you to the Quantitative Marine Science program for the top-up scholarship and providing a foundation in multiple marine science fields through postgraduate coursework.

Finally, thank you to my friends, fellow students, housemates and family for the inexhaustible supply of inspiration, distraction and motivation. I could not have completed this thesis without your love and support.

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Chapter 1:

General introduction

"All exploited marine taxa depend on invertebrates either directly or indirectly and marine ecosystems would collapse without their services."

"There is little or no information on the ecology and basic biology of most marine invertebrates, even for many abundant, ecologically or commercially important taxa."

Ponder W., Hutchings P. and Chapman R. 2002. Overview of the Conservation of Australian Marine Invertebrates. Australian Museum, Sydney and Environment Australia, Canberra

Invertebrates comprise 95-99% of animal life on earth today (Ponder and Hutchings, 2000), with many species playing ecologically important roles such as controlling primary production (Silliman and Bertness, 2002), assisting decomposition and nutrient cycling (Manuel, 2001), and providing a source of food for many terrestrial (Dickman, 1988), aquatic (Crowder and Cooper, 1982) and marine animals (Metcalf et al., 2008). Benthic invertebrates are those that live in close association with the ocean floor and the benthic environment can be broadly divided into soft (sand and silt) habitats and hard substratum; generally constituting coral reefs in tropical waters and rocky reefs in cooler temperate regions. Perhaps as a function of the transition in habitat structure from coral to rocky reefs (Ohman and Rajasuriya, 1998), the number of decapod and echinoderm species in Australia display a latitudinal gradient, decreasing towards the southern regions (O'Hara and Poore, 2000), however biogeographic patterns for other marine invertebrate taxa are less clear (Ponder and Hutchings, 2000).

The ecological influence of benthic marine invertebrates can extend throughout the subtidal rocky reef community. Sea urchins contribute to the creation of ‘barrens’ habitat where overgrazing of the macroalgae assemblage results in a bare or coralline algae encrusted rock surface (Andrew, 1991). Macroalgae provide food and shelter for many species of fish and invertebrates and the reduced physical complexity of the barrens habitat (Andrew, 1991) results in dramatically lower species diversity (Ling, 2008) and increased susceptibility to invasive species (Edgar et al., 2004). Urchin populations are often controlled by fish and invertebrate predators (Babcock et al., 1999; Clemente et al., 2009; Guidetti, 2004; Pederson and Johnson, 2006; Shears and Babcock, 2003) and overfishing of these predators contributes to the creation and persistence of barrens habitat (Shears and Babcock, 2003). The creation of barrens habitat is also influenced by the proximity of shelter for urchins as provided by physical reef structure (Andrew, 1993).

The habitat structure formed by the arrangement of physical objects in the environment has important influences on the community dynamics of marine benthic systems (Sale, 1991; Sebens, 1991). Habitat structure within the context of rocky reefs is generated by both biogenic features in the form of macroalgae or large sessile (permanently attached) invertebrates such as the red-throat ascidian *Herdmania momus*, and geologic or rock-based structure created by features of the reef surface. A great variety of terms have been used to describe the habitat structure formed by the surface of the reef, including reef structure (Moura et al., 2007), reef habitat structure (Dumas et al., 2007), reef heterogeneity (Molles, 1978), vertical relief (Luckhurst and Luckhurst, 1978), reef architecture (Holbrook et al., 1992), habitat architecture (Gratwicke and Speight, 2005a), substratum typography (Camus et al., 1999), surface roughness (Sanson et al., 1995), verticality (Garcia-Charton and

Perez-Ruzafa, 2001), fractal structure and complexity (Taniguchi and Tokeshi, 2004) and rugosity (Risk, 1972). This diversity of terminologies makes it difficult to locate relevant literature and may impede advancement of the field as the use of different descriptors can obscure the identification of patterns consistent across habitats and disciplines. McCoy and Bell (1991) suggested a solution to this problem through the use of a simple graphical model representing the components of habitat structure as habitat heterogeneity (number of different kinds of structure), complexity (amounts of structure) and the scale at which these characteristics are measured. Terms subsequently derived from this model include topographic heterogeneity (Guichard and Bourget, 1998), topographic complexity (Zawada and Brock, 2009), substratum complexity (Drolet et al., 2004a), substratum heterogeneity (Bourget et al., 1994) and structural complexity (Hereu et al., 2005). The use of the umbrella terms of complexity and heterogeneity to describe components of habitat structure achieves the important goal of allowing the comparison of results across studies but has not been widely implemented in studies of reef habitat structure. The reasons for this are explored further in the next chapter and for now the terms 'reef structure' and 'reef habitat structure' will be used to refer to all forms of habitat structure formed by the reef surface, and thus encompasses the concepts of both habitat heterogeneity and complexity. The exception to this is in reference to literature where the authors themselves have used a different term; in which case the author's terminology is maintained.

The interaction between benthic invertebrates and reef habitat structure influences animal growth (Beck, 1995), survival (Diaz et al., 2005; Hereu et al., 2005), fecundity (Beck, 1995), movement (Shepherd, 1986; Underwood and Chapman, 1989) and behaviour (Drew, 1990). Habitat complexity is even correlated with brain size in some animals (Shumway, 2008). Despite the overwhelming evidence for relationships between reef structure and benthic invertebrates, assemblage level tests are rare for subtidal rocky reefs. In the only known peer-reviewed study on temperate reefs, Ruitton et al. (2000) identified that boulder size and refuge apertures displayed no correlation with invertebrate populations on artificial reefs and natural surfaces in the Mediterranean Sea. Numerically dominant invertebrate species appear to be more closely associated with encrusting algal communities than with reef structure (Ruitton et al., 2000). Similarly in the eastern Atlantic, Entrambasaguas et al. (2008) identified that spatial variation in the total abundance of echinoderms was better explained by depth and sand cover than habitat structure metrics. The first two axes of a canonical correspondence analysis between the multivariate environmental data and the echinoderm assemblage cumulatively accounted for only 17.6% of total variance (Entrambasaguas et al., 2008). On the other hand, indications from grey literature suggest that benthic macroinvertebrates in southern Australia appear to be more closely related to reef structure with, in one study, a concordance of 0.65 determined by the BIOENV routine between the invertebrate assemblage and interstitial space, complexity index, depth, slope and longitude (Edmunds et al., 1999).

Assemblage-level studies of habitat association are more common in fish communities and provide comparable models in the absence of more comprehensive invertebrate tests. As with invertebrates, benthic dwelling cryptic fishes share a close association with the reef surface and are potentially influenced by similar aspects of reef habitat structure. Willis and Anderson (2003) investigated the relationship between cryptic reef fish assemblages with respect to habitat characteristics in New Zealand and found that there was a strong positive correlation between rugosity (or the level of folding or topographic variability in the substrate) and the number and diversity of cryptic fishes. Cryptic fish species richness, diversity, assemblage abundance and composition also exhibited the strongest relationships to substratum composition (boulders or solid rock) on rocky reefs in two separately studied Mediterranean island groups (La Mesa et al., 2006; La Mesa et al., 2004).

Non-cryptic fish communities also show links to habitat structure on rocky reefs, although the most important descriptive factors appear to vary with the species and region that is being studied. Garcia-Charton and Perez-Ruzafa (1998) found that the numbers of different size classes of boulders on Mediterranean rocky reefs was significantly correlated with the number of fish species and the mean total abundance. Substratum rugosity was positively related to fish abundance, species richness and diversity off San Jose Island, Mexico (Villegas-Sanchez et al., 2009), while the size and numbers of holes influenced fish abundance on artificial reefs in the U.S. Virgin Islands (Hixon and Beets, 1989). The diversity of results suggests that no one measure of habitat structure can explain the variation of all functional groups in all habitats and multiple measures that include rugosity, boulder sizes, refuge size and density are more likely to be generally applicable. Gratwicke and Speight (2005a) have made steps to accommodate this by developing a Habitat Assessment Score (HAS) that incorporates estimates of rugosity, height variability, habitat complexity and refuge sizes. They found that the combination of HAS variables accounted for 71% of variation in fish species richness but only 22% of variation in total fish abundance. Appropriate statistical analyses also allow the consideration of the additive or multiplicative effects of multiple habitat variables. Multiple linear regression or generalised linear models test the relationship between multiple predictors on univariate responses such as species richness, the abundance or presence-absence of a species. The combined influence of multiple measures of reef habitat structure on the arrangement of an invertebrate assemblage (a matrix of the abundance or presence-absence of multiple species across samples) can be determined using canonical correspondence analysis (CCA; ter Braak, 1986), RELATE (Clarke and Gorley, 2006), BIOENV (Clarke and Ainsworth, 1993) or distance based linear modelling (DistLM; Anderson et al., 2008).

The declaration of marine reserves represents a manipulative experiment at ecologically meaningful scales and provides the opportunity to investigate the effects of fishing on ecosystem organisation and functioning. Most fisheries target high order predators (Pauly et al., 1998) and the removal of these players from a complex ecosystem can have indirect and far reaching implications. Trophic cascades are an example of such an indirect effect and have been identified in marine ecosystems around the world (see review by Pinnegar et al., 2000). These occur as a cascade of predatory effects between trophic levels and are often reported as beginning with the return of top-level predators to an area protected from fishing (eg. ↑ large fish → ↓ sea urchins → ↑ macroalgae; Shears and Babcock, 2003).

Reef structure has the potential to dampen cascading effects resulting from the return of predatory populations in reserves through its influence on the availability of physical refuges from predation. Sea urchins, abalone, small fishes and small crustaceans such as crabs and shrimp can make use of the physical refuges of crevices, holes or overhangs to reduce the predatory efficiency of lobsters and large fish species that have been shown to increase in temperate marine reserves in Tasmania (Barrett et al., 2009; Edgar and Barrett, 1997; 1999; Edgar et al., 2009) and New Zealand (Babcock et al., 1999; Davidson et al., 2002; Shears and Babcock, 2002; Shears and Babcock, 2003). For example, predation on post-settlement juveniles of the sea urchin *Paracentrotus lividus* increased with greater abundance of predatory fishes, and decreased with greater structural complexity (Hereu et al., 2005). Smaller urchins also experience reduced predation by lobsters when allowed access to cryptic microhabitats in Tasmania (Pederson and Johnson, 2006) and New Zealand (Shears and Babcock, 2002).

Effective protection from predation usually requires that shelter is scaled to match the body size of prey animals (Hixon and Beets, 1993) and the interaction between animal body size and shelter dimensions can have population limiting effects, possibly as predators eliminate members of the population unable to find suitable refuges. This pattern has been studied in detail for lobsters (Arce et al., 1997; Briones-Fourzán and Lozano-Álvarez, 2001; Briones-Fourzán et al., 2007; Eggleston and Lipcius, 1992; Eggleston et al., 1992; Mintz et al., 1994; Parrish and Polovina, 1994; Sosa-Cordero et al., 1998; Wahle and Steneck, 1991; 1992) and stone crabs (Beck, 1995; 1997). The provision of artificial shelter at the limiting size class results in higher juvenile abundance (Arce et al., 1997), larger size classes or biomass of target animals (Briones-Fourzán and Lozano-Álvarez, 2001), depending on which lifestage is shelter-limited. Artificial addition of shelter can also influence the fecundity and growth of target animals (Beck, 1995) and allow them to inhabit areas where they have previously not been observed (Briones-Fourzán and Lozano-Álvarez, 2001). Despite the reported importance of shelter for benthic invertebrates, I am not aware of any studies that have investigated the long-term effects of reef structure on the response of communities to marine reserves.

The island state of Tasmania provides an ideal location for a study of reef structure and invertebrates because of the commercial and recreational importance of two of the most abundant invertebrate species. The southern rock lobster *Jasus edwardsii* and blacklip abalone *Haliotis rubra* contribute 94% of the value of the Tasmania's wild-caught fishery income. The state has the largest gross value of fisheries production of all Australian states, valued at $475 million, which constitutes 22% of Australia's total production (ABARE, 2009). The value of the rock lobster and abalone fisheries has consistently decreased in Australia over the past decade, largely as a result of decreasing catch volume (ABARE, 2009). Marine reserves have been suggested as complementary fisheries management tools (Roberts et al., 2001) and to provide insurance against recruitment failure (Jennings, 2001). The two key commercial species have shown differing population trends in Tasmanian marine reserves, however, with increasing numbers and biomass of rock lobster corresponding with declining abalone numbers (Barrett et al., 2009; Pederson et al., 2008).

This project aims to determine the relationships between reef habitat structure and the benthic invertebrate assemblage of temperate rocky reefs and will include simultaneous analysis at multiple taxonomic levels including for selected species, classes and at the community level. Sampling invertebrates and reef structure at multiple spatial scales will shed light on the spatial consistency and scaling of these relationships (chapter 3) while the models developed on sites distributed over 100's of kilometres will be applied to interstate regional snapshots to determine the spatial transferability and predictive power of the models (chapter 4). This has important implications for the use of reef structure metrics as habitat surrogates to predict the presence or abundance of invertebrates in data-poor regions. Spatially consistent relationships also provide the potential to account for extraneous variance in impact assessments where insufficient pre-impact biological data are available. Measuring habitat variables known to correlate with species abundance or a community type can provide a clearer indication of the initial state of an impacted ecosystem (Parker and Wiens, 2005).

The project also has considerable practical relevance for fisheries management. Habitat structure presumably has a strong influence on the recovery of invertebrate species within marine reserves following cessation of fishing. Examining the temporal trajectory of species-habitat relationships during the recovery of fished species will enable us to better understand biotic responses following the establishment of marine reserves and assist in site selection of future protected areas for fisheries enhancement and protection of fishery insurance populations (chapter 5). Following these relationships for the prey of fished species will improve our understanding of the dynamics of temperate rocky reef ecosystems and inform future conservation strategies. This is especially relevant for abalone, where declining densities in some marine reserves (Barrett et al., 2009), probably as a result of increased predation (Pederson et al., 2008), could potentially lead to localised recruitment failure.

The decline of abalone in the Tasmanian marine reserves also provides motivation for the exploration of a technique for sampling cryptic invertebrates, including juvenile abalone (described in Chapter 6). Sandstone blocks have been successfully used on intertidal rocky shores to sample invertebrates living under boulders (Chapman, 2003) and provide a non-destructive, standardised-area method for sampling this often-overlooked portion of the subtidal biodiversity. Deploying the blocks at sites in and around the marine reserve provides a test of the influence of increased predator biomass on the cryptic invertebrate assemblage, further contributing to knowledge of the ecosystem effects of fishing. A two-dimensional profile gauge deployed in the footprint of the sampled block allows characterisation of the shape and volume of the sub-block refuge. These data were used to determine the microhabitat associations of macroinvertebrates, and test the potentially confounding effects of differences in the refuge volume between units on the abundance of invertebrates sampled by this technique.

A note on word usage…

The majority of the data chapters presented in this thesis describe the association between mobile macroinvertebrates and their habitat using statistical modelling techniques. Ultimately, these analyses provide the ability to say that variability in the abundance or presence-absence of species among samples is non-random (or not) and a certain proportion of this variance is explained by measures of reef habitat structure. At no point are causal mechanisms behind these patterns assumed, however, the section on future research outlines further work and experiments that work towards this goal. Despite this clarification, continuously describing the outcomes of these analyses using phrases such as ‘variance explained’ or ‘significant relationship’ creates a thesis that is laborious to read. Certain words are therefore used that can have implications beyond those intended in the context of this thesis. The intended meanings in this thesis and wider applications of these words are clarified here.

The word ‘preference’ in this thesis does not imply a behavioural choice (Singer, 2000), but a non-random association where a significant portion of the variance in the data can be explained by one of the independent metrics tested in the analysis. Similarly, the word ‘influence’ in the context of ‘…rugosity influenced the abundance of sea urchins…’ does not imply that rugosity directly effects the growth or survivorship of sea urchins, but that rugosity has a detectable ability to describe spatial variability in the abundance of sea urchins at the sampling scale tested.

‘Refuge’ is a term used here to describe a reef feature that may provide some protection to a resting invertebrate. An alternative is the word ‘microhabitat’, however, the measurement and criteria for inclusion in this metric were created to describe a reef feature that was likely to provide protection from predation. The term refuge was therefore used to reflect this although, in the absence of manipulative experiments, it is not assumed that the feature actually achieves this end.

Plate 1: *Octopus tetricus*, Jervis Bay, NSW

Chapter 2:

Quantifying reef structure

Habitat structure is an extremely broad concept, with a vast array of applied terminologies. In an attempt to focus research effort, McCoy and Bell (1991) introduce a graphical model which they suggest encompasses “the breadth of ecological relationships implied by habitat structure” on three perpendicular axes represented as heterogeneity, complexity and the scale of measurement. The heterogeneity axis encompasses variation attributable to the relative abundance of different structural components, while the complexity axis encompasses variation attributable to the absolute abundance of individual structural components. In an example given to illustrate the model, they also describe complexity as amounts of structure and heterogeneity as kinds of structure. The model provides an elegant conceptual framework with which to compare studies of habitat structure between ecosystems and study species (eg. Jones and Syms, 1998). The framework is also useful when designing experimental manipulations to consider the potentially confounding effects of the type and amounts of structure, and independently control their contributions to the response. For example Beck (2000) presented a manipulative experiment which showed that species richness and the total density of gastropods in mangrove habitat were greater in high complexity treatments when the amount of only one type of structure was varied (ie. the number of pits in the substratum). When complexity was held constant, species richness and the density of most gastropods was found to vary with the type of structure (ie. pits versus pneumatophores). Thus, by application of McCoy and Bell (1991)’s model, Beck (2000) was able to show that both the amount (complexity) and identity (heterogeneity) of structural components of the habitat influenced the gastropod assemblage.

The habitat structure model and its terminological conventions have not been widely adopted in observational studies of reef habitat structure aimed at identifying one or a combination of independent factors that account for significant amounts of variance in a biotic response variable (but see Entrambasaguas et al., 2008; Friedlander and Parrish, 1998; Garcia-Charton and Perez-Ruzafa, 1998; Garcia-Charton and Perez-Ruzafa, 2001; Garcia-Charton et al., 2004). A contributing reason for this is that McCoy and Bell (1991) based their model on a review of habitat structure literature bounded by the criterion that "a functional interaction between habitat structure and the organism must be demonstrated" (page 6; Bell et al., 1991). This criterion was created to exclude studies such as those that concerned 'habitat selection'. Nonetheless, McCoy and Bell (1991) make a salient point that the use of diverse and inconsistent terminology to describe aspects of habitat structure can impede the recognition of general patterns across studies, regions and habitats. My study introduces three broad categories for grouping measures of the physical structure of subtidal rocky reefs: substratum composition, topographic variability, and reef architecture. The identification of these categories will hopefully assist researchers in recognizing consistently important reef characteristics, and ultimately to identify the pathways through which these habitat features influence the biological community on subtidal rocky and coral reefs.

Substratum composition

The composition of reef substrata in temperate and tropical reef systems creates dramatically different benthic habitat structure. Different hard coral species form the majority of hard substratum on tropical reefs and present a vast diversity of growth forms that make specific contributions to benthic habitat structure through their shape and form (Fig. 2.1a). Most studies of habitat structure in coral reef environments acknowledge the potential influence of the variability in these forms on the associated biological communities (Bergman et al., 2000; Friedlander & Parrish, 1998; Friedlander et al., 2003; Garpe & Ohman, 2003; McClanahan & Shafir, 1990; Sale & Douglas, 1984). Other studies measure the proportion of substratum contributed by living or dead coral (Garpe and Ohman, 2003; Risk, 1972) or exposed rock (Brokovich et al., 2006; Sale and Douglas, 1984) and correlate these against species abundance or community metrics.

Different substratum categories can be also defined and quantified within rocky reef habitat, including percent cover of consolidated (unbroken) bedrock, sand or gravel patches and counts or percent cover of a variety of boulder size classes (Fig. 2.1b; Entrambasaguas et al., 2008; Garcia-Charton and Perez-Ruzafa, 2001; La Mesa et al., 2004; Ordines et al., 2005). Loose reef objects (ie. boulders, cobbles, fractured bedrock sections) create interstitial space that can act as refuges for juvenile and cryptic species that are vulnerable to predation (Chapman, 2002a; Menge et al., 1983). The size and shape of the boulder interacts with the substratum on which it lies to determine the shape and volume of the resultant interstitial space (Chapman, 2002b). Characterising the cover or numbers of boulder size classes therefore provides a rough proxy for the volume of refuge space available on a reef (Barry and Wickins, 1992).

Substratum categories may be included in analyses as separate variables or combined in a habitat diversity index. Garcia-Charton and Perez-Ruzafa (2001) applied the

Shannon-Weiner diversity index to counts of different boulder size classes and the percentage cover of rock, sand and seagrass within each quadrat to create indices of boulder diversity and heterogeneity respectively. Species diversity was significantly related to the heterogeneity index (Garcia-Charton and Perez-Ruzafa, 2001) reflecting that each substratum type provides specific resources (eg. shelter, food) for different fish species and the proportional representation of these habitats influences the structure of the benthic assemblage.

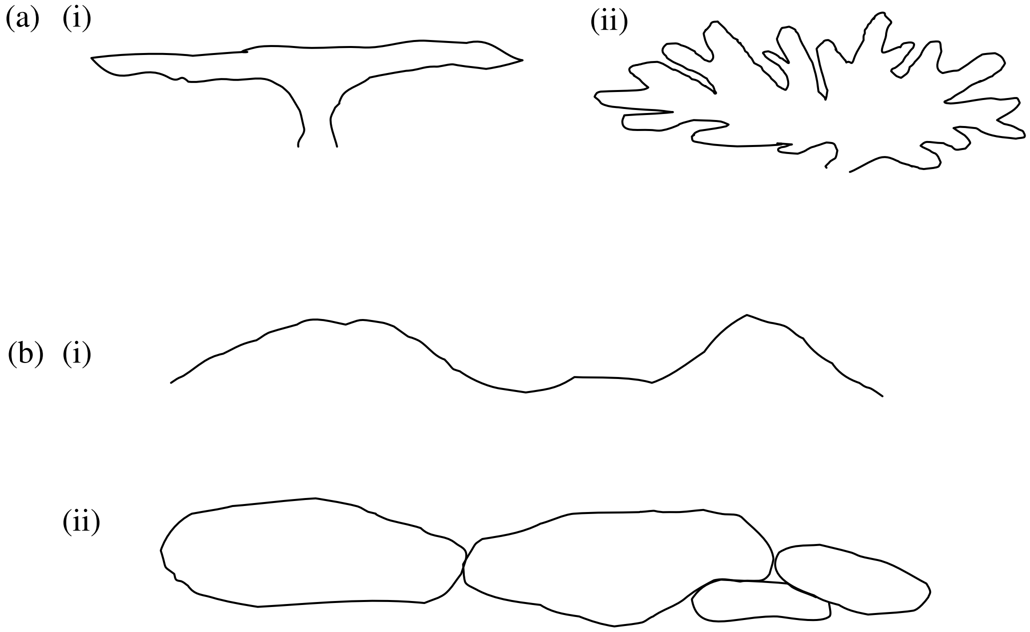

Fig. 2.1: Representation of reef surface profiles for (a) coral reefs (i) plate coral and (ii) branching coral, (b) rocky reefs (i) consolidated bedrock and (ii) boulder habitat

Topographic variability

Measures of topographic variability quantify the relative changes in vertical height of the substratum over a specified horizontal distance. Topographic complexity or variability of the substratum profile influences the organization of the species assemblage through broadly-acting processes such as shading (Adams, 2001;

Bernaford and Vasquez, 2008; Drolet et al., 2004a), hydrodynamic effects (Koehl, 2007; McShane et al., 1988) or through provision of transient refuges where the complexity of the reef surface can limit the visual range of hunting predators (Caley and St John, 1996). At its most basic level, areas with high topographic variability have a higher colonisable reef surface area for species associated with the benthos. The conceptual simplicity and ease of measurement by divers and remote-sensing methods makes measures of topographic variability, such as rugosity, attractive representatives of reef habitat structure, yet their ability to describe the spatial distribution of fishes and benthos-associated invertebrates shows little consistency across regions and taxa. Luckhurst and Luckhurst (1978), and Friedlander et al. (2003) identified strong correlations between fish species richness on coral reefs, and Gratwicke and Speight (2005a) found the same pattern on rocky reefs; however rugosity estimates were highly inter-correlated with the percent cover of hard substratum in the latter study. Most studies that measure rugosity find that the metric has little correlation with characteristics of the reef community (Bergman et al., 2000; Ferreira et al., 2001; Sale and Douglas, 1984; Shepherd and Partington, 1995; Walker et al., 2009), or is of secondary importance to other habitat measures (Friedlander and Parrish, 1998; La Mesa et al., 2004; McCormick, 1994).

Rugosity, within the context of reef characterisation, is the ratio between the contoured length of a substratum profile to the linear distance over which the contour length is measured. A flat surface therefore will have a rugosity value close to 1 where there is very little difference between the length of the contoured surface profile and the horizontal distance over which it is measured. A measure of rugosity for a site will be influenced by the vertical variability of the reef profile, the size and density of specific reef features such as cracks and crevices, and the horizontal spacing of these features. It will also be influenced by the scale of measurement which is characterised by the grain (the finest level of detectable spatial resolution) and extent (the size of the study area under consideration) of the technique (Turner et al., 1989).

Subtle differences in the way that rugosity is measured between studies may be contributing to the variability in the reported strength of its relationship to biota. The two main techniques are to contour a chain along the substratum (Friedlander and Parrish, 1998; Friedlander et al., 2003; Garcia-Charton and Perez-Ruzafa, 1998; Gratwicke and Speight, 2005b; La Mesa et al., 2004; Luckhurst and Luckhurst, 1978; McClanahan and Shafir, 1990; Risk, 1972; Sale and Douglas, 1984) or to measure the variability of the height of the substratum at regularly spaced intervals to create a representation of the reef profile (Beck, 1998; Frost et al., 2005; McCormick, 1994). The contoured distance for a measure of rugosity based on a regularly measured profile can be estimated using Pythagoras' theorem: $\sum\sqrt{}((y_2 - y_1)^2 + x_2)$ where y_1 and y_2 are consecutive height measurements and x is the horizontal distance between adjacent height measurements. The x distance and the length over which measurements are made define the grain and extent respectively for this metric.

A similar measurement can be calculated using a two dimensional array of height measurements (length and breadth; Underwood and Chapman, 1989). The ratio of the contoured surface area to the planar area over which it is measured is referred to as planar rugosity. The main difference between the chain and profile methods for quantifying rugosity is that profile-based measurements reflect only the structure visible from plan-view. That is, they are not influenced by any overhanging features such as ledges or horizontally oriented crevices. This is a subtle but ecologically important differentiation as horizontally oriented reef features provide important habitat for a number of key benthic species (Love et al., 2006), including juveniles of the southern rock lobster *Jasus edwardsii* (Booth, 2001).

Applications of the chain method also vary. The most common approach is to measure the length of the contoured reef profile using a chain or lead-core rope over a fixed linear horizontal distance (Friedlander and Parrish, 1998; Friedlander et al., 2003; Garcia-Charton and Perez-Ruzafa, 1998; Gratwicke and Speight, 2005b; La Mesa et al., 2004; Luckhurst and Luckhurst, 1978; McClanahan and Shafir, 1990; Risk, 1972; Sale and Douglas, 1984). In this method, the size of the links in the chain or diameter and flexibility of rope define the grain of the measurement. The extent is provided by the linear distance over which the rugosity measurement is made. An alternative to the most common approach is to quantify the linear horizontal distance spanned by a fixed length of chain when contoured to the reef surface along a transect (Dulvy et al., 2002; Harman et al., 2003). The disadvantage of the standard formula is that divers may need to carry a length of chain up to three times the linear distance to make the measurement at sites with high topographic variability (rugosity ≈ 3). Fixing the contoured distance minimizes the amount of rope or chain that divers are required to carry; however, the formula must be modified to recover a linear relationship between the rugosity index and the measured distance by calculating the inverse of the standard rugosity formula (Fig. 2.2). The measurement should also be subtracted from 1 to return it to the more intuitive positive relationship of an increase in the structure of the reef corresponding to an increase in the rugosity index.

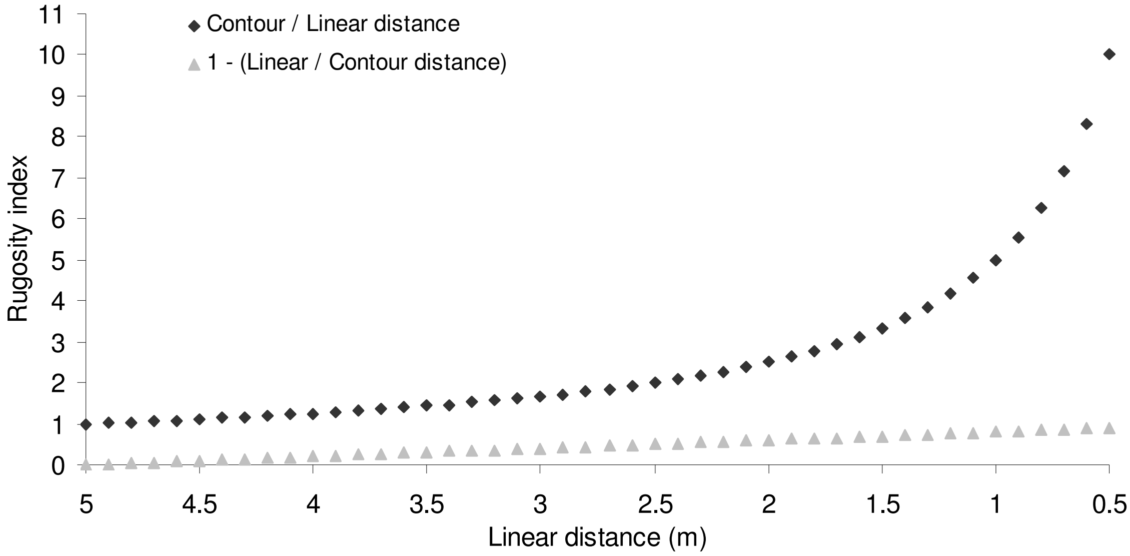

Fig. 2.2: Relationship between the linear distance measurement and the rugosity index using the traditional and modified formulas with a fixed contour distance of 5 metres.

McCormick (1994) reviews a variety of other calculations of topographic variability based on linear reef profiles measured at regular intervals. He identified that metrics that incorporate information on the spatial arrangement of substratum heights best differentiate between schematic profiles, and these displayed the higher numbers of significant correlations with fish species. For example, the sum of the squared distance between consecutive heights was among the best performers in differentiating theoretical profiles and exhibited the strongest correlations with fish community metrics. On the other hand, the standard deviation of heights is not influenced by the horizontal arrangement of heights (Fig. 2.3) and performed poorly in profile differentiation and fish correlation tests. Uniquely, McCormick (1994) calculated the rugosity index as linear distance / contour distance; the inverse of the traditional formula. Comparing calculations on simulated profiles with consistent horizontal spacing between heights shows that the traditional rugosity formula relates very closely to the sum of consecutive height difference (Fig. 2.4). Thus the correlation of -0.878 between rugosity and consecutive height differences (reported in Table 2 of McCormick, 1994) would be much closer to 1 if curvilinear relationships were considered or if the traditional rugosity formula (contour/linear) had been used in this paper.

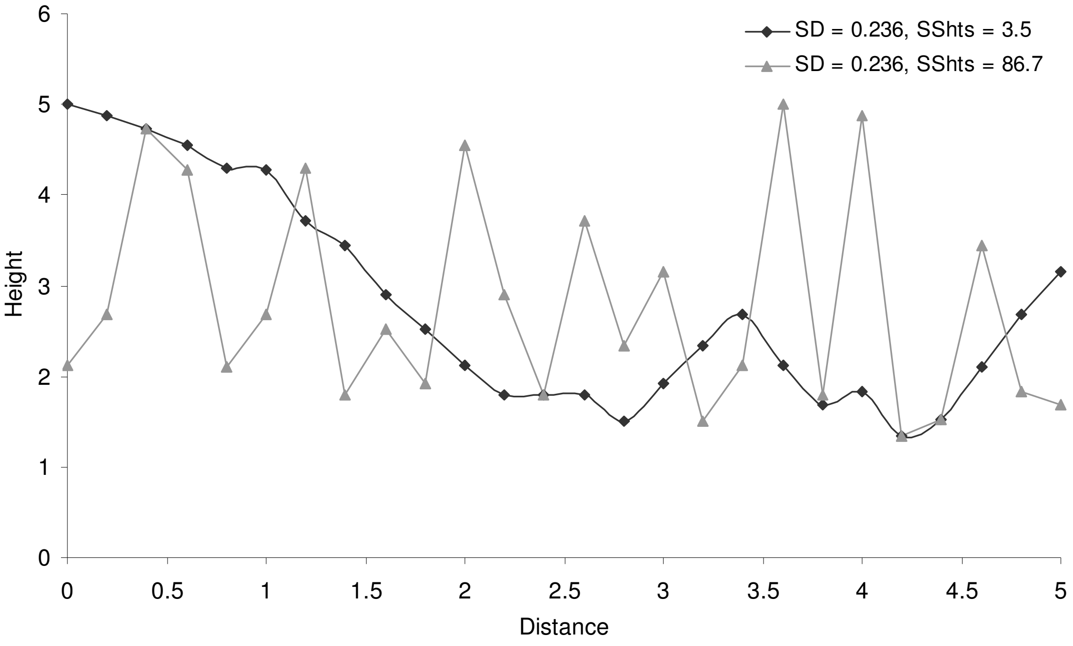

Fig. 2.3: Two simulated profiles with the same standard deviation of heights (SD) but vastly different sum of squared difference between consecutive heights (SShts).

The fractal dimension offers another method for characterising the topographic variability of a reef profile that is more closely aligned with human perception of reef structural complexity (Knudby and LeDrew, 2007) and is theoretically independent of the scale of measurement (Halley et al., 2004). In Euclidean geometry, a straight line has 1 dimension (length) and a surface has the 2 dimensions of length and breadth, however as a line becomes increasingly convoluted it begins to fill space, taking on characteristics approaching those of breadth. Fractal geometry allows measurement of the non-integer dimensionality of a line or surface, which in this example is between 1 and 2. Quantification of the fractal dimension of an object, such as the surface profile of a reef, is based on the rate of increase of the length of the profile when measured with increasingly finer resolution or grain. Frontier (1987), Klinkenberg (1994) and Schmid (2000) provide excellent reviews of techniques available to estimate the fractal dimension of natural objects. Specific examples for rocky reefs include estimating the length of the contoured reef surface using different length links of chain (Knudby and LeDrew, 2007) or trundle wheels of different diameters (Robson et al., 2002; Wilding et al., 2007). Finer measurement scales (smaller chain link length or wheel diameter) capture more structural detail and therefore produce a greater reef surface contour length.

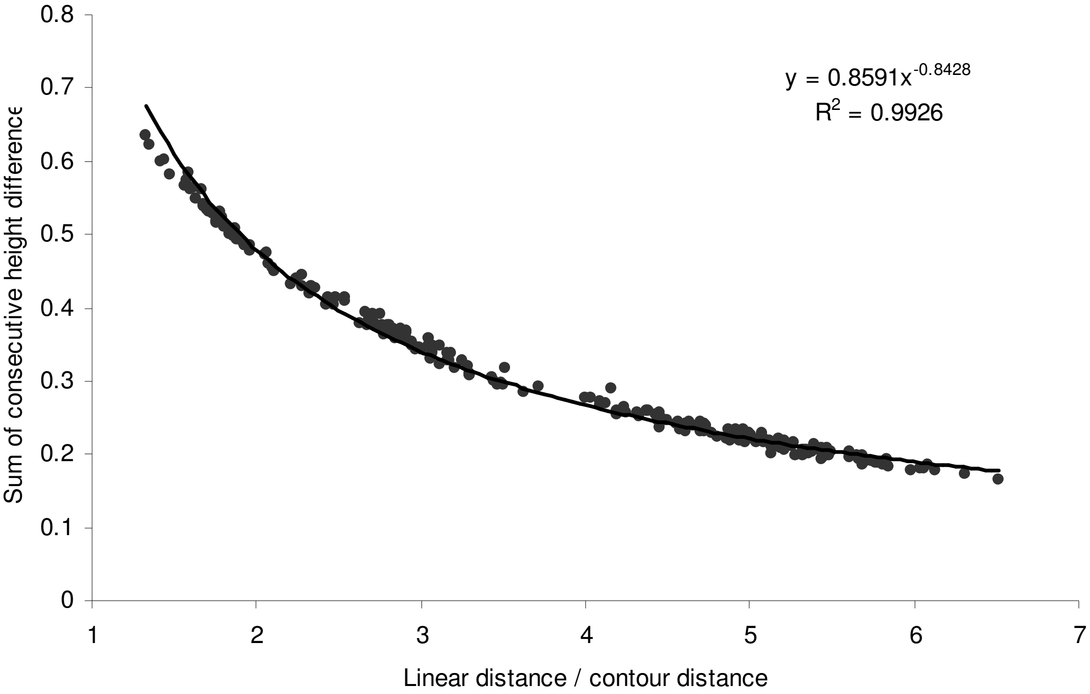

Fig. 2.4: Relationship between McCormick's (1994) formula for calculating rugosity and the sum of the squared difference between consecutive heights (square root transformed)

Reef architecture

Architecture can be defined as the orderly arrangement of parts; and similarly reef architecture concerns the arrangement of elements of the reef surface in a manner that forms a consistently recognisable reef feature. The application of this concept in studies of reef habitat structure recognises that many invertebrate species are closely associated with specific structural formations such as holes (Beck, 1995; 1997), ledges (Jernakoff, 1990) and crevices (Drolet et al., 2004a; Shepherd, 1986). The links to these features under natural conditions may be driven by a behavioural preference (ie. active selection) towards the features or the removal of animals in unfavourable positions by predation or adverse environmental conditions (Crowe and Underwood, 1998). Studies investigating links between reef architecture and biota can be divided into those quantifying the direct association between individuals and architectural features and those exploring spatial associations between the presence or density of reef features and the organisation of the benthic community within an area.

The association between individual animals and reef architectural features (which may also be generically referred to as microhabitats) are most commonly determined using laboratory experiments. Studies in aquaria have, for example, identified the preference of juvenile slipper lobsters for horizontally oriented shelters with more than one opening (Spanier and Almogshtayer, 1992). Juvenile rock lobster also prefer shelters with horizontally-facing apertures (Booth, 2001), and exhibit an ontogenetic shift in preference in the number of shelter openings with small lobsters preferring two openings over one, and those >30 mm carapace length preferring one over two (Booth and Ayers, 2005). Field studies of association between individuals and reef architectural features are rarer as they require the difficult task of quantifying the abundance of animals occupying specific microhabitats relative to the amount (volume or area) of each microhabitat available for colonisation in the area. Jernakoff (1990) determined the association between juvenile western rock lobster *Panulirus cygnus* and 11 different microhabitats formed by combinations of substratum type (rock rubble, solid reef), biogenic habitat structure (seagrass) and reef architecture (reef plateau, reef face, ledges, caves) on the limestone reefs of western Australia. Greater numbers of lobsters were found in ledges than caves and flat reef after the abundance of lobsters occupying each microhabitat type had been standardised by the area of each habitat that had been searched.

Observational studies testing for links between habitat metrics and the benthic community have also quantified the characteristics of reef architectural features. Ruitton et al. (2000) measured the size of cavity apertures in the reef surface and found that it held little relationship to the abundance of benthic herbivorous invertebrates and fishes in the Mediterranean. On the other hand, Tuya (2004) found that the number of large and medium crevices in quadrats was very strongly correlated with the abundance of the sea urchin *Diadema antillarum* for some sites in the Canary Islands. The density of specific reef features, such as holes, are also important for describing variation in the abundance of reef fishes in Hawaii (Friedlander and Parrish, 1998) and the Red Sea (Roberts and Ormond, 1987). Manipulation of the number of holes on experimental artificial reefs positively influences the total abundance of fishes (Caley and St John, 1996), although the scaling of the refuge relative to the body size of the fish species is important for prey species (Hixon and Beets, 1993).

The concept of the fractal dimension can also be applied to describe the size frequency distribution of specific reef features such as holes within a patch of reef (Caddy and Stamatopoulos, 1990). An inherent property of a true or mathematical fractal is that it is self-similar; in other words, it will have the same characteristics regardless of the scale of measurement (Mark, 1984). While the surface of a natural rocky or coral reef is rarely self-similar across all realistically measurable scales (Bradbury et al., 1984), the premise that the density of reef features decreases with the scale of the feature generally still applies (Caddy and Stamatopoulos, 1990). Under these circumstances, cohorts of species reliant on shelter scaled to their body size will reach a bottleneck in shelter availability, limiting the population of larger individuals. This concept is thoroughly discussed with examples in Caddy (2007). The rate of decrease in the density of reef features with increasing scale can therefore provide information on the potential for a population-limiting influence of reef architecture for benthic animals.

Despite the many observational studies measuring reef architecture, detailed quantitative descriptions of the architectural features in question are often overlooked. Many authors give no further information beyond that they are counting ‘holes’ (Friedlander and Parrish, 1998; Roberts and Ormond, 1987) or ‘crevices’ (Nemeth, 1998; Tuya et al., 2004). In these cases the authors assume that readers share their interpretation of the term and can consistently recognise these features amongst the background complexity of a natural reef surface. The decision as to when a feature qualifies for inclusion in a category such as a ‘reef hole’ is rarely clear-cut, however, even when a reef surface profile is simplified and reduced to one dimension (representing a linear profile; Fig. 2.5). Quantitative descriptions, based on geometric shapes, surface planes and angles, provide the objective, repeatable criteria required to identify reef architectural features. Suggested criteria are developed in the following chapter and applied in a study of the benthic macroinvertebrate assemblage.

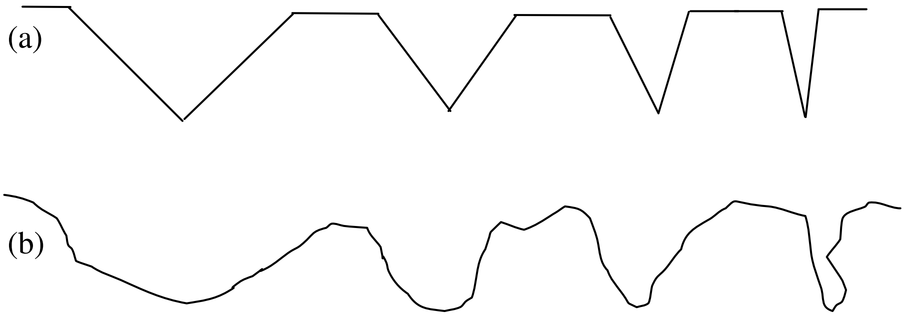

Fig. 2.5: A depiction of the arbitrariness of hole identification on (a) stylised and (b) simulated natural reef surface profiles

Plate 2: Maria Island, Tasmania

Chapter 3:

Relationships between mobile macroinvertebrates and reef structure in a temperate marine reserve

This chapter has been published as:

Alexander, T.J., Barrett, N., Haddon, M., Edgar, G.,(2009). Relationships between macroinvertebrates and reef structure in a temperate marine reserve. *Marine Ecology Progress Series* 389: 31-44

http://dx.doi.org/10.3354/meps08210

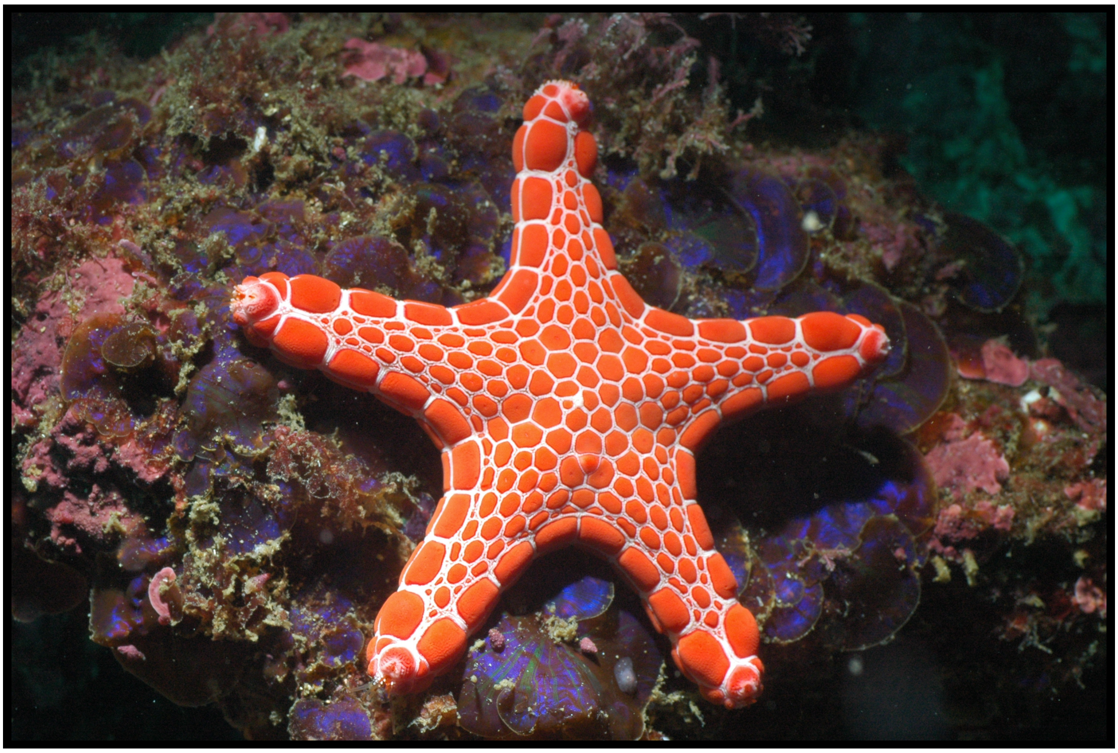

Plate 3: *Pentagonaster dubeni*, Jervis Bay

Chapter 4:

Influences of reef habitat structure, fish predators and macroalgae on the distribution of mobile macroinvertebrates on temperate Australian reefs

ABSTRACT

The ability of predictive habitat models to explain spatial variance of mobile invertebrates is tested for rocky reefs outside a model training area. Models applied are based on data from sites distributed around the island state of Tasmania (69 sites) to bioregional data surveyed in southeastern Australia (Batemans Shelf, New South Wales; 29 sites) and Western Australia (Central West Coast, 32 sites). Explanatory variables investigated were depth, duration of protection from fishing within marine protected area, rugosity, boulder substratum at a site, the average number of refuge size categories, and a fractal refuge index that reflected the frequency distribution of different sized physical refuges. Also considered were biogenic habitat structure in the form of the percent cover of canopy algae and the biomass of predatory fishes. The predictive power of the optimal Tasmanian model to the testing regions was determined by its performance against the observed response. Total combined abundance of invertebrates was the only response where the Tasmanian model predicted a significant portion of observed variance, through a relationship with the fractal refuge index in both of the test regions. Tasmanian models also predicted almost 25% and 50% of variance in the Central West Coast bioregion for the abundance of crustaceans and echinoids, respectively. Further explanatory analyses were carried out to determine important habitat descriptors within each bioregion. A

single habitat predictor tended to dominate the species models for each bioregion (canopy algae in Batemans Shelf, fractal refuge index in Central West Coast, and boulder substratum in northern Tasmania). These results suggest that, without validation, habitat surrogates possess limited value to predict the spatial distribution of invertebrate assemblages and populations outside the region of model development, even where benthic communities are dominated by functionally similar species.

INTRODUCTION

Improved understanding of habitat relationships for species and assemblages is increasingly recognised as an important goal for both marine conservation, impact assessments and fisheries management (Gislason et al., 2000; Pauly et al., 2005). Knowledge of these relationships allows the prediction of biota for the purposes of conservation planning in the absence of comprehensive species data, allows the partitioning of variance in biota attributed to habitat quality when determining the extent of environment impacts in the absence of pre-impact data and assists in understanding fishery patterns to inform management including the use of spatial fishery closures for the creation of enhancement or insurance populations. While considerable research effort has been directed at identifying the habitat characteristics that most affect the distribution of commercially-harvested invertebrate species, such as abalone (Roberts et al., 1999; Schiel et al., 1995; Shepherd and Partington, 1995), rock lobster (Booth, 2001; Booth and Ayers, 2005), and ecologically-important barren-forming sea urchins (Andrew, 1993), assemblage-level tests of association with habitat are less common (but see Edmunds et al., 1999; O'Hara, 2001; Ruitton et al., 2000).

Models that describe the spatial distribution of inshore marine assemblages using measurements of their habitat have been created for tropical (eg. Ault and Johnson, 1998; Brokovich et al., 2006; Friedlander and Parrish, 1998; Garpe and Ohman, 2003; McCormick, 1994) and temperate reefs (eg. Garcia-Charton and Perez-Ruzafa, 1998; Harman et al., 2003; Jennings et al., 1996; Willis and Anderson, 2003). Most are concerned with fish assemblages (eg. Ault and Johnson, 1998; Friedlander and Parrish, 1998; Garcia-Charton and Perez-Ruzafa, 1998; Garpe and Ohman, 2003; Harman et al., 2003; Mellin et al., 2009; Willis and Anderson, 2003), although a few models involving invertebrates have been described (Edmunds et al., 1999; O'Hara, 2001; Pante et al., 2006; Robinson and Tully, 2000; Ruitton et al., 2000). Generally these models are developed over a limited spatial range with no testing to determine whether the models are applicable elsewhere. Little consensus exists between studies as to the most important habitat metrics for taxonomic or functional groups within a region, let alone to another region outside the span of tested sites.

Many taxa exhibit a higher abundance or species richness at sites with greater vertical complexity of the reef surface. The most commonly suggested mechanism driving this positive association is the provision of shelter from predation for juvenile and cryptic animals (Caley and St John, 1996; Hixon and Beets, 1993; Nelson and Bonsdorff, 1990). The presence of reef architectural features such as holes can allow species vulnerable to predatory attack to persist despite high predator densities (Caley and St John, 1996; Hixon and Beets, 1989). The presence of persistent prey populations can result in further increases in community diversity and abundance as other species that benefit from relationships with the prey are encouraged to settle (Rodríguez et al., 1993).

Reefs with greater structural complexity also have a higher surface area relative to reefs of similar planar dimension with low structural complexity, and hence have a greater area of substratum for benthic species to colonise. Measures of rugosity are commonly used to reflect this difference; however, rugosity is not always positively related to invertebrate density, showing negative (McClanahan and Shafir, 1990) and no association (Chapter 3; Dulvy et al., 2002) in some cases. A causal effect of rugosity on interactions between members of the reef community is difficult to elucidate as it influences, and is influenced by, most other measures of structure (eg. topographic variability, reef architecture, substratum composition). This intercorrelation between reef structure metrics nevertheless makes rugosity an attractive choice amongst structural metrics as it is easily defined and measured.

The subtidal rocky reef environment can be divided into sub-habitat categories including solid bedrock, boulders and sand patches (Chapter 3; Garcia-Charton and Perez-Ruzafa, 2001; La Mesa et al., 2004; Ordines et al., 2005). For the development of descriptive models using multiple habitat characteristics, the use of several sub-habitat categories as independent predictors within a sampling unit can cause problems with multicollinearity (Friedlander and Parrish, 1998). The juxtaposition of loose reef objects (ie. boulders, cobbles, fractured bedrock sections) and the bedrock creates interstitial space that can act as refuges for juvenile and cryptic species that are vulnerable to predation (Chapman, 2002a; Menge et al., 1983). The shape of the boulder and the substratum on which it lies play major role in determining the resultant interstitial space, influencing the shape of the refuge as well as the volume (Chapman, 2002b). Characterising this interstitial space based on boulders and their substratum rather than directly quantifying refuge density and volume has practical benefits as it avoids operator bias when deciding which refuges meet the definition for inclusion, a difficult task in highly complex environments, particularly when surveyed with limited dive time.

The focus of this study is to identify empirical relationships between reef habitat structure and the spatial distribution of mobile macroinvertebrate taxa on subtidal rocky reefs. The relevance of commonly employed measures of reef structure (eg. rugosity) is tested for different target groups and new ways of characterising the structure of the reef (eg. boulder substratum and the fractal refuge index) are introduced. The predictive value of two other key biological factors is also assessed: (i) the density of predatory benthic-feeding fishes, and (ii) the biogenic habitat structure afforded by canopy algae. These two factors could potentially influence the structure and composition of the invertebrate assemblage through predation pressure by fishes, and hydrodynamic flow moderation and provision of physical refuges and food by canopy algae. In our study, invertebrate-habitat models were developed for sites distributed over 100’s of kilometres, then the trans-continental predictive capability of these models tested for sites in two separate regions outside the model development area. The best combination of habitat characteristics that describe the abundance and presence-absence of species, the abundance of major taxa, and the similarity of invertebrate assemblages among sites, were also identified for each region.

Although the model training and testing regions are separated by 1000’s of kilometres, ecological niches across the regions are occupied by taxonomically and morphologically similar species. For example, the dominant invertebrate predators for the three regions are lobsters in the family Palinuridae; *Jasus edwardsii* in

Tasmania, *Panulirus cygnus* in Western Australia and *Jasus verreauxi* in New South Wales. Sea urchins of the genera *Heliocidaris* and *Centrostephanus*, and gastropod species of the genera *Haliotis* and *Turbo*, are among the numerically dominant grazers and are represented by different species across the regions. These functionally similar species provide an interesting platform over which to test the broad spatial consistency of habitat models

METHODS

Study sites

Aspects of physical reef structure were measured in conjunction with surveys of mobile macroinvertebrates, fishes and macroalgae at 69 sites around Tasmania (June 2006 – March 2007), 32 sites in the Central West Coast bioregion in Western Australia (surveyed in October 2006) and 29 sites in the Batemans Shelf bioregion in New South Wales (May 2007; Fig. 4.1). Bioregions were defined by the Integrated Marine and Coastal Regionalisation of Australia (Commonwealth of Australia, 2006).

Sites around Tasmania were distributed across five bioregions and over four degrees of latitude, with annual sea surface temperatures (SST) ranging from 10 to 19 ^{o}C (Bottomley et al., 1990). Reefs surveyed in this region were predominantly composed of dolerite and granite, with some sandstone, quartzite and basalt. Sites in Batemans Shelf were located around Jervis Bay, with SST ranging from of 16 to 23 ^{o}C, and predominantly sandstone and siltstone bedrock geology. Central West Coast sites were clustered around Jurien Bay and were at a slightly higher latitude, with SST ranging from 18 to 23 ^{o}C, and an exclusively limestone geology. Sites in this region were distributed both on the limestone barrier reef (5-7 km offshore) and on rocky outcrops in the relatively sheltered waters on the leeward side of the barrier.

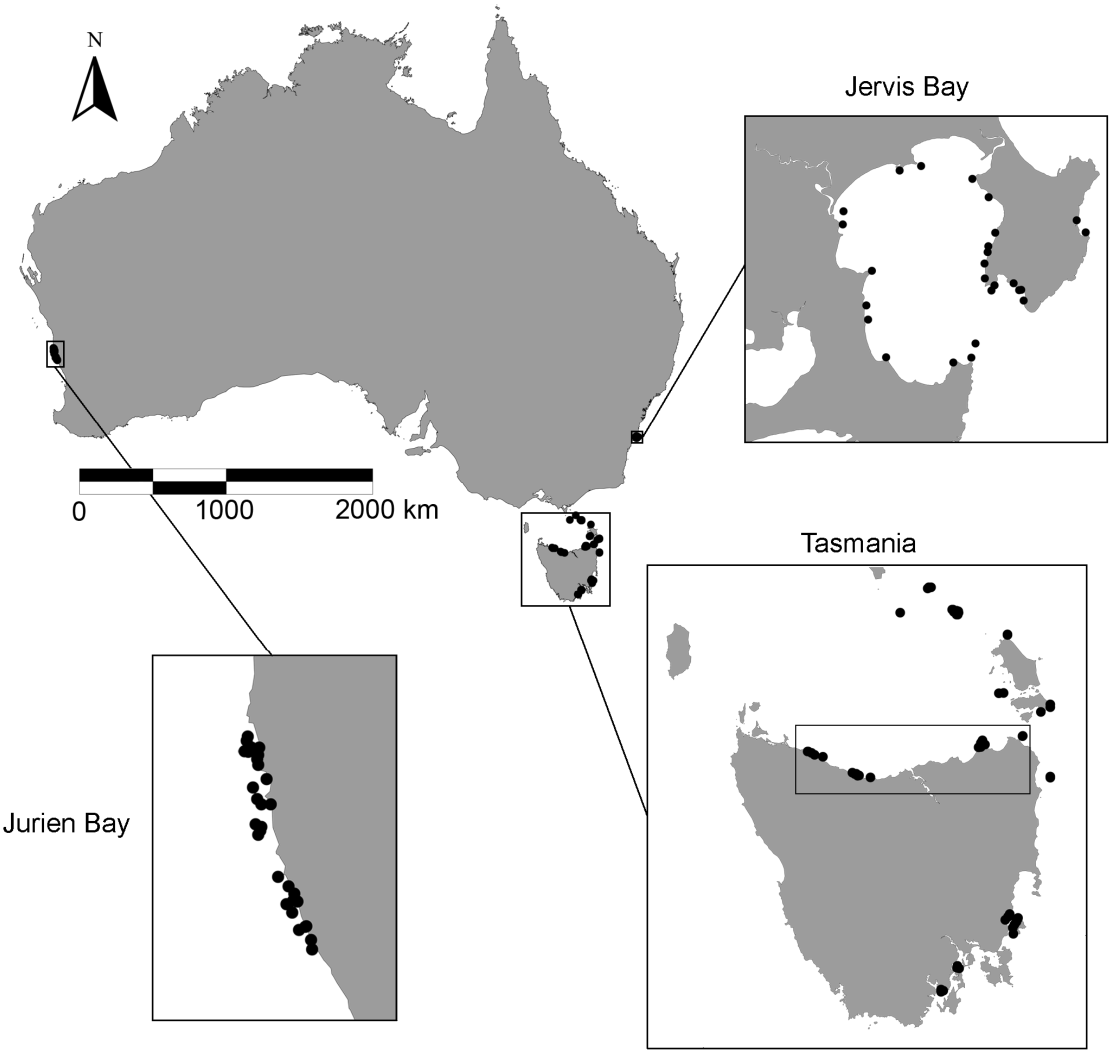

Fig. 4.1: Maps showing the sampling locations and regions around Australia. The boxed region on the left shows locations around Jurien Bay in the Central West Coast bioregion. Bottom right is the state of Tasmania with the Boags bioregion locations contained within the box on the north coast. The box on the top right shows locations around Jervis Bay in the Batemans Shelf bioregion.

Habitat characteristics

Each site was surveyed using a 200 m transect line set on either the 5 or 10 m depth contour, with divers using quantitative underwater visual census procedures to quantify densities of macroalgae, invertebrates and fishes, as described by (as described by Edgar and Barrett, 1997; 1999). All mobile invertebrate species larger than 2 cm, observable without overturning boulders or otherwise disturbing the substratum, were counted along a 1 x 200 m swath on one side of the transect line. The length and density of reef associated fishes were visually estimated in a 5 m swath along both sides of transect line (i.e. 10 x 200 m of reef surveyed for each site).

Fish abundance and size estimates were converted to biomass using length-weight relationships provided by Fishbase (http://fishbase.org/) for each species or its closest studied taxonomic relative. Explanatory variables considered in the analysis included bioregion, depth, protection from fishing, biomass of benthic carnivorous fishes (feeding preferences identified using dietary information provided by Fishbase), percent cover of canopy forming algae (measured as the aggregation of twenty 0.25 m^2 quadrats surveyed along the 200 m transect at each site), and physical habitat structure measurements (Table 4.1).

Intra-reef habitat structure measurements consisted of three substratum classes (see chapter 3): composition (dominant substratum of boulders on the reef), topographic variability (rugosity index) and architecture (number of refuge size categories and fractal refuge index). Le Hir and Hily (2005) previously identified that boulders resting on different substratum types supported distinct assemblages. Substratum composition was considered here as a categorical variable reflecting if boulders at a site were generally resting on other boulders, consolidated bedrock or sand. An additional level of this categorical variable recognized if there were no boulders on the transect.

Table 4.1: Description of the explanatory variables considered in multiple regression analyses.

Variable name	Description
Bioregion	IMCRA bioregion (Commonwealth of Australia, 2006)
Depth	Depth of transect; either 5 m or 10 m
Boulder substratum	Most common substratum that boulders in the sample rest on: boulders, bedrock, sand, no boulders present
Rugosity	Rugosity index = 1 - (linear distance / contour distance)
Number refuge size categories	Mean number of refuge size categories represented in each of the 1 x 5 m blocks surveyed for the site (1 - 5 cm, 6 - 15 cm, 16 - 50 cm, > 50 cm)
Fractal refuge index	Absolute value of the slope of the regression line for $\log_4$(upper size limits of refuge size category) vs $\log_4$(density of refuges in the size category + 1)
Benthic fishes	Biomass of predatory benthic fishes that feed on crustaceans, echinoids, gastropods
Canopy algae	% cover of canopy brown algal species: Alariaceae, Cystoseiraceae, Durvilleaceae, Fucaceae, Lessoniaceae, Sargassaceae, Seirococcaceae. Cover may exceed 100% due to multiple layers of canopy structure
Protection	Years elapsed for sites in no-take marine reserves between marine reserve gazettal and survey dates: 0 (no protection from fishing), <10 years, >10 years

Rugosity and the density of refuges (contributing to the fractal refuge index and number of refuge size categories) were impractical to measure across the full 200 metres of reef so were sub-sampled in eight randomly distributed 1 x 5 m blocks, with site averages used in analyses. Rugosity was sampled using a 5 m lead core rope as the fixed contour distance in the formula, Rugosity index = contour distance / linear distance (Harman et al., 2003; Risk, 1972). The formula was inverted and the result subtracted from 1 to return the calculation to a linear, positive relationship between the rugosity index and reef structure.

A refuge was defined as an individual crevice, hole or other feature of the substratum that had the potential to provide a mobile macroinvertebrate some measure of protection from predation (see Chapter 3 for more details). The number of refuges were counted in a 5 m^2 area using 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 more readily recognised by a diver.

The number of refuges in each of four size categories were counted in each block and used in the calculation of two prediction metrics. The number of refuge size categories at a site (Gratwicke and Speight, 2005a) was calculated as the mean of the number of size categories represented in each of the eight 5 m^2 blocks (0 – 4). The fractal refuge index was calculated using the concepts of Caddy and Stamatopoulos (1990) as the absolute value of 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). The fractal refuge index describes the relative frequency of different sized refuges in a sample and is different from the classic fractal dimension which describes the convolution of the profile or surface (Sugihara and May, 1990). A fractal index of around 0.5

indicated that the size frequency distribution of refuges approximately followed fractal expectations (ie. that the number of refuges declined with refuge size based on a log-log scale). An index close to 1 suggested that refuges in the block were numerically dominated by the smaller size category and a value close to 0 that approximately equal numbers of refuges were present in each of the four size categories. The index provides a compromise between the close scaling of each size category to individual species and the use of a single metric that should be more relevant to describing multi-species or assemblage level variability. Details of the explanatory variables are summarised in Table 4.1.

Model training and testing

The ability of habitat models to explain the spatial variance of mobile invertebrates in regions outside a model training area was tested by constructing models on sites distributed around Tasmania and applying them to regional data obtained in New South Wales and Western Australia. Analyses tested two aspects of predictive capability: 1) the ability of Tasmanian models to predict the value of an invertebrate response at a site based on the observed habitat metrics and 2) the ability to predict the coefficients for the parameters of the same invertebrate-habitat model for a group of sites in a new region. The former concerns the prediction of individual data points and is based on the calculation of expected values for each site in the testing regions using coefficients from the Tasmanian model. The proportion of variability in the observed response described by the model-predicted values was quantified by the significance level and r^2 value from linear regression analysis. The second aspect of the training and testing analyses determines if characteristics of the relationship between the habitat metrics and the response are consistent across the regions. The model coefficients were estimated in the test regions for the same combination of habitat metrics that optimally described the response in Tasmania and compared to the 95% confidence intervals of coefficients for the Tasmanian model.

Optimal generalized linear models developed using the Tasmanian data are defined as the smallest set of explanatory variables that explain the greatest proportion of the deviance in the response. These models were identified using forward stepwise fitting procedures with the selection of a new variable for addition to the model based on the greatest improvement to Akaike's Information Criterion (AIC - Burnham and Anderson, 2002) as long as it made a significant contribution to the explained deviance ($p > 0.01$ based on a Chi-squared distribution). The fit of the model to the selected error distribution was checked using quantile-quantile plots and influential outliers were removed based on Cook's distance. An indication of model fit to the Tasmanian data was given by the calculation of a pseudo-r^2 value (hereafter referred to as simply r^2) using the formula 1 – (residual deviance / null deviance).

The Tasmanian generalised linear models were constructed using a variety of error distributions and link functions to correspond to the statistical characteristics of the responses, including Gaussian for continuous data such as the inverse of the Simpson's Dominance Index and transformed abundance data, and Poisson for untransformed abundance data. Negative binomial distributions were employed for over-dispersed abundance data (where the residual deviance is over twice the residual degrees of freedom) and binomial models on presence-absence data were used to handle response variables that had high proportions of zero counts (e.g. crinoid abundance).

Response variables tested included the community summary metrics species richness, total combined abundance, and the inverse of the Simpson's Dominance Index (Hill, 1973; Simpson, 1949). The inverse of the Simpson's Index (hereafter referred to simply as the Simpson's Index) was used as it is correlated with most other measures of diversity or evenness and is relatively unaffected by animal abundance in the sample (Edgar, 1983).

Models were also developed for the abundance of numerically dominant taxonomic classes Asteroidea, Crinoidea, Echinoidea, Crustacea and Gastropoda. This level of taxonomic resolution was selected because representatives of most groups were recorded in a sufficient number of samples to allow analysis across regions. Also analysed were the abundance of the two commercially important families Haliotidae (abalone) and Palinuridae (rock lobster).

Bioregion-specific model development

Further analyses were carried out to identify habitat metrics that were consistently important for taxa across bioregions or across species within a bioregion. A subset of the Tasmanian data set was used in this analysis to allow comparability between similar sample sizes and spatial coverage across different regions. The Boags bioregion (Commonwealth of Australia, 2006), situated along the north coast of Tasmania, represented the Tasmanian bioregion with the largest number of surveyed sites (23), so was used for this analysis.

Multiple regression analyses were conducted on the data for this bioregion and the two previously described interstate bioregions (Central West Coast and Batemans Shelf) separately using a reduced set of habitat variables (owing to the reduced number of sites at this scale). Explanatory variables selected from the larger set to represent the three different types of reef habitat structure measurement were (i) dominant substratum of boulders on the reef (substratum composition), (ii) rugosity index (substratum topographic variability), and (iii) fractal refuge index (substratum architecture). Biological habitat structure (percent cover of canopy algae) was also included. Predatory fishes were not included in this analysis as the primary focus of the study was on habitat structure and also this variable produced only one weakly significant relationship in the model training and testing analysis.

Optimal models were constructed for the community summary metrics and combined class abundances for each bioregion using the model building techniques described in the previous section. Optimal logistic models were also developed using the same techniques to describe relationships between species presence-absence and habitat structure for all species surveyed in >30% of locations in any of the three regions. A negative binomial distribution was used with abundance data for species that occurred in more than 75% of sites in the region—*Phyllacanthus irregularis*, *Heliocidaris erythrogramma* (except for the low numbers in Batemans Shelf where the logistic model was applied), *Centrostephanus rodgersii*, *Campanile symbolicum*, *Haliotis rubra*, *Astralium tentoriformis*. Taxonomic authorities for species discussed in this article are provided in Edgar (2008).

Multivariate analyses

Relationships between habitat metrics and the composition of the invertebrate assemblage were tested using a similar approach to the univariate data analyses. Optimal descriptive models were identified for the Tasmanian data using distance based linear modeling (DistLM) in Primer 6 (Anderson et al., 2008) and then applied to the interstate test regions to determine spatial generality. The most parsimonious models were also identified for each of the three bioregions (Boags, Central West Coast and Batemans Shelf) separately using the same reduced set of explanatory variables as the bioregional univariate tests. The model building followed similar procedures to the univariate analysis with the inclusion of new variables based on the greatest reduction in Akaike's Information Criterion (AIC), providing it made a significant different to the explained variance. Values of r^2 were again used as indicators of model fit and, for this analysis, described as the proportion of the variation in the multivariate data cloud that is explained by the explanatory variables (Anderson et al., 2008).

RESULTS

Seventy-nine species of large mobile invertebrates were recorded across the 130 sites surveyed in this study, comprising 35 echinoderms, 33 molluscs and 11 crustaceans. Species richness was much lower in Batemans Shelf than elsewhere (Wilcoxon's rank-sum test with Tasmania $p < 0.001$ and Central West Coast $p < 0.001$), with an average of 3.6 species per site compared to an average of 11.5 for both of the other two regions (Wilcoxon's rank-sum test, $p = 0.886$; Table 4.2). Sites in Tasmania and Central West Coast generally supported representatives of the five major classes (crinoids, asteroids, echinoids, gastropods and crustaceans) while Batemans Shelf was heavily dominated by echinoids and gastropods, but with very few asteroids and no crustaceans recorded that matched the survey criteria. A summary of the explanatory data is provided in Table 4.3.

Table 4.2: Summary of assemblage and class level response data for Tasmania (Tas), and the Boags (BGS), Batemans Shelf (BAT) and Central West Coast (CWC) bioregions. Value for mean (± standard error) is calculated across sites where animals present.

Response	Data region	Mean ± SE	Minimum	Maximum	Number of sites where taxa were recorded
Species richness	Tas	11.5 ± 0.4	5	22	69
	BGS	10.9 ± 0.7	6	17	23
	BAT	3.6 ± 0.3	2	7	29
	CWC	11.5 ± 0.6	3	19	32
Total abundance	Tas	403.0 ± 31.2	51	1124	69
	BGS	331.7 ± 47.4	51	883	23
	BAT	287.5 ± 43.9	35	968	29
	CWC	103.9 ± 16.9	7	406	32
Simpsons Index	Tas	2.9 ± 0.1	1.07	4.72	69
	BGS	1.8 ± 0.2	1.07	4.00	23
	BAT	1.8 ± 0.1	1.08	2.34	29
	CWC	4.4 ± 0.3	1.43	8.83	32
Asteroid abundance	Tas	31.3 ± 13.9	0	834	65
	BGS	7.7 ± 1.3	0	23	22
	BAT	1.0 ± 0	0	1	3
	CWC	7.2 ± 1.5	0	28	24
Crinoid abundance	Tas	136.4 ± 29.4	0	864	53
	BGS	14.5 ± 5.3	0	75	14
	BAT	3.9 ± 1.3	0	11	8
	CWC	15.1 ± 5.5	0	70	15
Crustacean abundance	Tas	6.2 ± 1	0	46	57
	BGS	3.4 ± 0.6	0	9	16
	BAT	0	0	0	0
	CWC	13.0 ± 2.9	0	63	26
Echinoid abundance	Tas	213.9 ± 21.7	0	734	68
	BGS	249.4 ± 44.3	7	734	23
	BAT	213.1 ± 38.3	18	854	29
	CWC	55.7 ± 12.2	0	241	31
Gastropod abundance	Tas	50.4 ± 9.3	0	429	67
	BGS	61.9 ± 18.2	3	429	23
	BAT	73.2 ± 13.2	12	345	29
	CWC	25.0 ± 4.5	1	117	32

Table 4.3: Summary showing number of sites classed in each habitat category and mean (± SE) for continuous habitat data for Tasmania (Tas), and the Boags (BGS), Batemans Shelf (BAT) and Central West Coast (CWC) bioregions.

Categorical data					
		5 metres	10 metres		
Depth	Tas	56	13		
	BAT	26	3		
	CWC	26	6		
		None	<10yrs	>10yrs	
Protection	Tas	55	5	9	
	BAT	13	16	0	
	CWC	21	11	0	
		Bedrock	Boulders	Sand	No boulders
Boulder substratum	Tas	30	21	18	0
	BGS	12	1	10	0
	BAT	7	11	6	5
	CWC	0	0	0	32

Continuous data				
		Mean	Min	Max
Rugosity	Tas	0.23 ± 0.01	0.09	0.52
	BGS	0.18 ± 0.01	0.09	0.36
	BAT	0.18 ± 0.02	0.06	0.35
	CWC	0.21 ± 0.01	0.05	0.39
Number refuge size categories	Tas	1.66 ± 0.07	0.50	3.13
	BAT	1.81 ± 0.10	1.00	3.00
	CWC	2.23 ± 0.13	0.25	3.25
Fractal refuge index	Tas	0.68 ± 0.02	0	1.02
	BGS	0.70 ± 0.04	0	0.89
	BAT	0.64 ± 0.03	0.27	0.88
	CWC	0.54 ± 0.04	0	0.98
Benthic fishes (kilograms)	Tas	15.4 ± 1.6	0.7	101.9
	BAT	70.0 ± 14.1	5.7	344
	CWC	25.9 ± 3.3	1.9	72.1
Canopy algae (% cover)	Tas	74.0 ± 3.9	0	122.1
	BGS	55.0 ± 6.2	1.1	101.1
	BAT	39.6 ± 7.5	0.2	161.2
	CWC	34.1 ± 4.7	0	83.4

Model training and testing

The only component of the invertebrate assemblage where the Tasmanian model explained a significant proportion of variance in the observed data for the two test regions was for the combined abundance of all invertebrates (hereafter referred to as total abundance; Table 4.4). Variability in total abundance and echinoid abundance followed similar trends and were both optimally described by the fractal refuge index in Tasmania. Models predicted almost 50% of variability in observed data for both of these responses when applied to the Central West Coast bioregion. The model for total abundance also described a significant proportion of the observed data in the Batemans Shelf bioregion and although the model between echinoids and the fractal refuge index for Batemans Shelf sites shared similar coefficients with the Tasmanian model (Table 4.5), high variability of observed data around the fitline meant that the model did not have significant predictive power in this region (Fig. 4.2). The similarities between the models for total and echinoid abundance are not surprising given that echinoids were the numerically dominant class in all regions, dominating the invertebrate counts at 68%, 90% and 63% of sites in Tasmania, Batemans Shelf and Central West Coast, respectively.

Variability in species richness was significantly described by a positive relationship with the percent cover of canopy algae in Tasmania. Applying this model to Batemans Shelf explained a significant proportion of variability in the observed data; however observed values were negatively related to expected levels (slope = - 0.392, $p < 0.05$, $r^2 = 0.174$). Contrary to Tasmania, species richness is therefore higher at sites with lower cover of canopy algae in the Batemans Shelf region (Table 4.5).

Table 4.4: Tasmanian models used to predict invertebrate responses in test regions and compared to observed response values using linear regression. Optimal Tasmanian model presented in the form $Y = \beta_1 + \beta_2 (X_1) + \beta_3 (X_2) + \ldots$ where Y = response variable, X = explanatory variables and β_1 β_2 etc. are the coefficients to be estimated. Superscript letters indicate the error distribution and link used for the model: ^{a} Poisson (link = log), ^{b} Negative binomial (link = log), ^{c} Gaussian (link = identity), ^{d} Binomial (link = logit).

Optimal Tasmanian model	**Pseudo-r^2 for Tasmanian model**	**% variance explained by Tas. model in test regions**	
		CWC	**BAT**
Species richness ~ 2.19 + 0.003 (Canopy algae)^a	0.145**	0.7	17.4* †
Total abundance ~ 4.40 + 2.16 (Fractal refuge index)^b	0.160***	49.1***	18.5*
Simpson's Index ~ 3.17 - 1.6 (Fractal refuge index)^c	0.127**	3.7	3.8
Asteroid abundance ~ 1 ^{c}	-	-	-
Crinoid presence ~ (Boulder substratum) + 13.42 (Rugosity)^d	0.485***	10.2	7.56
Crustacean abundance ~ 0.19 + 0.786 (Number refuge size categories)^b	0.192***	24.3**	-
Echinoid abundance ~ 3.50 + 2.58 (Fract_ref)^b	0.151***	47.2***	8.0
Gastropod abundance ~ (Boulder substratum) + 0.014 (Canopy algae)^b	0.268***	0.3	32.1** †
Abalone presence ~ 6.82 - 12.44 (Rugosity) + 0.02 (Canopy algae)^d	0.206*	8.7	2.2
Rock lobster presence ~ (Protection) + 13.06 (Rugosity)^d	0.389***	16.2*	-

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

† Observed responses are negatively related to expected values according to the model

Y- intercepts of the models for crinoids, gastropods and rock lobster models vary across levels of the categorical factor as follows:

Crinoids: - 5.75 [Bedrock] + 13.07 [Boulders] + 14.90 [Sand]

Gastropods: 3.12 [Bedrock] + 1.56 [Boulders] + 3.08 [Sand]

Rock lobster: - 7.55 [No protection] - 6.83 [<10yrs] + 12.77 [>10yrs]

Table 4.5: Model coefficients for test regions compared to ± 95% confidence intervals of optimal Tasmanian models. Test region coefficients falling between Tasmanian confidence intervals are shown in bold. See Table 4.4 for error distributions and link functions.

Model		**Tasmanian model coefficients ± 95% CI**	**Test region model coefficients**	
			CWC	**BAT**
Species richness				
Canopy algae		0.003 ± 0.002	-0.001	-0.004
Intercept		2.2 ± 0.19	2.48	1.45
Total abundance				
Fractal refuge index		2.16 ± 0.67	2.83	**2.65**
Intercept		4.40 ± 0.43	2.93	3.89
Crustacean abundance				
Number refuge categories		0.786 ± 0.37	**1.06**	-
Intercept		0.190 ± 0.68	**-0.25**	-
Echinoid abundance				
Fractal refuge index		2.58 ± 1.25	**3.61**	**2.29**
Intercept		3.50 ± 0.89	1.71	**3.84**
Gastropod abundance				
Canopy algae		0.014 ± 0.01	NS	-0.013
Boulder substratum	Bedrock	3.12 ± 0.68		4.04
	Boulders	1.55 ± 0.62		1.02
	Sand	3.08 ± 0.63		0.289
Rock lobster presence				
Rugosity		13.06 ± 8.74	**9.81**	-
Protection	No protection	-7.55 ± 4.48	**-4.5**	
	< 10 yrs	-6.83 ± 2.11	-3.64	
	> 10 yrs	12.78 ± 9.72		

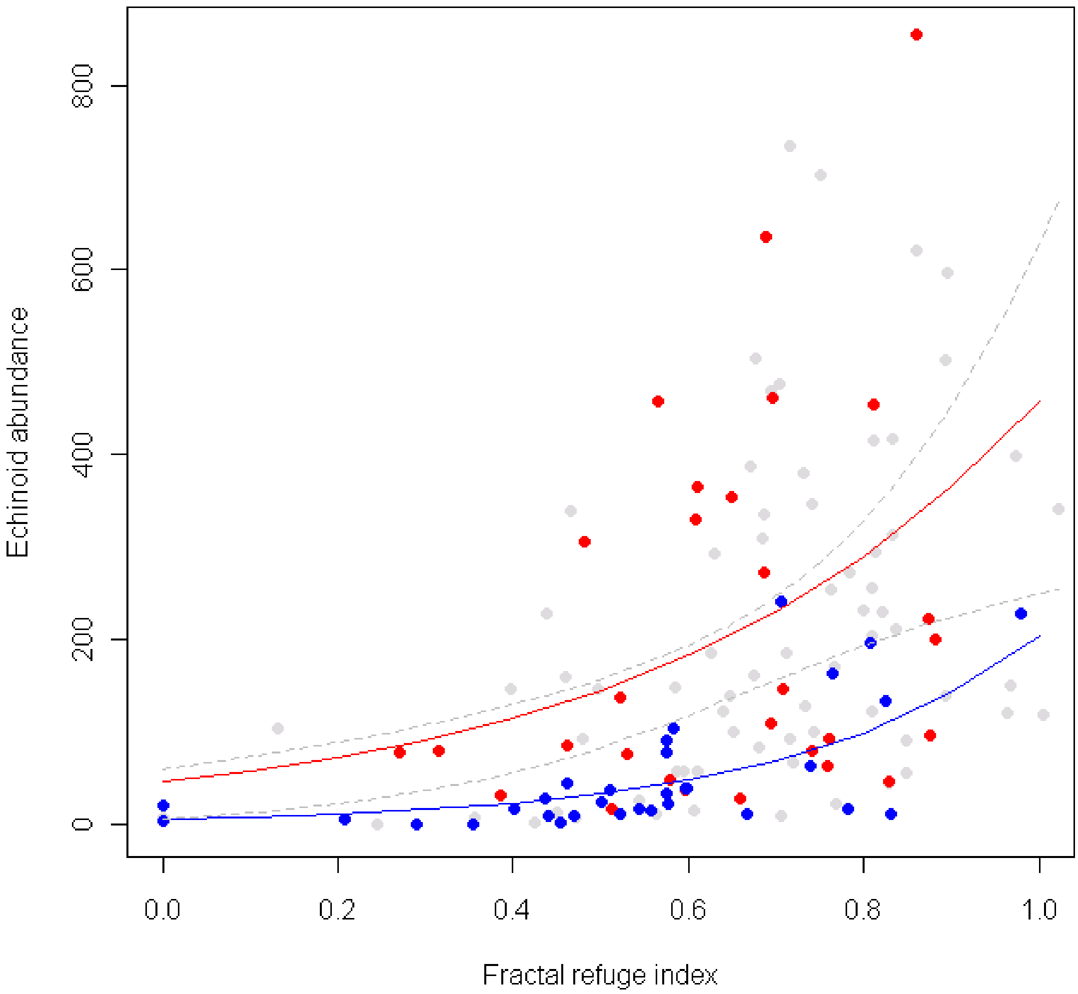

Fig. 4.2: Relationship between the abundance of echinoids and the fractal refuge index in Tasmania (grey symbols), Batemans Shelf (red) and Central West Coast (blue). Solid lines indicate best fit lines for models in test regions. Dashed lines represent upper and lower 95% confidence intervals for the Tasmanian model.

The crustacean-habitat relationship also exhibited consistency across the tested regions. The average number of refuge size categories was the strongest habitat descriptor of crustacean abundance in Tasmania and predictions based on this model explained approximately a quarter of the variation of observed data in the Central West Coast. Coefficients for the Central West Coast model were within confidence intervals for the Tasmanian model confirming the consistency of this relationship between these regions. Negligible numbers of survey-size crustaceans were recorded on transects in Batemans Shelf.

Gastropods were numerically dominant in 13, 10 and 20 percent of samples in Tasmania, Batemans Shelf and Central West Coast, respectively. These taxa showed a strong positive relationship with the percentage cover of canopy algae and boulder substratum for Tasmanian data (Table 4.4). The absence of any boulders prevented the full Tasmanian model from being applied in the Central West Coast and canopy algae alone had no predictive power in this region. Gastropod abundances predicted using the Tasmanian model in Batemans Shelf were strongly negatively related to observed values (slope = -2.29, $p < 0.01$, $r^2 = 0.341$). The inconsistency in model coefficients between the regions is reflected in Table 4.5.

Protection from fishing was significantly associated only with the presence of rock lobsters (plus rugosity, $p < 0.001$, $r^2 = 0.389$). This model had significant but weak explanatory power in Central West Coast. Very large errors around the coefficient estimates for Tasmania (Table 4.5) suggest that the model is unreliable as a predictive tool. No lobsters were surveyed on transects in Batemans Shelf, preventing testing of the model in this region. The abundance of asteroids was the only response that was not significantly influenced by any of the habitat variables tested in the Tasmanian dataset. All other tested components of the invertebrate assemblage showed significant relationships with one or more habitat metrics in Tasmania, although the models were often non-significant when applied to the test regions.

Bioregion-specific model development

The exploratory analysis revealed some consistencies in the habitat factors that were important across bioregions and within taxa. The combined abundance of invertebrates was the only community summary metric to show strong links to measured habitat (the fractal refuge index) across all three bioregions (Table 4.6). No habitat metrics significantly explained spatial variability in species richness in the Boags and Batemans Shelf bioregions while the fractal refuge index was positively related to species richness in Central West Coast ($r^2 = 0.464$). Boulder substratum and canopy algae were also important in describing variability in the Simpson's Index for Boags and Batemans Shelf bioregions but no models were significant for this response in the Central West Coast (Table 4.6).

Invertebrate-habitat models were consistently strong for echinoids, with the fractal refuge index appearing in the optimal model for almost all species and combined abundances for this taxa across the bioregions (Table 4.7). Asteroids on the other hand showed consistently weak relationships with the habitat metrics, with only two significant (but low r^2) species models in Western Australia. Crinoids exhibited a strong preference for sites where boulders rested mostly on sandy substratum in Boags bioregion ($p < 0.001$, $r^2 = 0.504$). This relationship was not echoed in the other regions. Few clear patterns emerged from analysis of the crustacean data across the bioregions. Canopy algae was positively linked to the presence of the red bait crab *Plagusia chabrus* ($p < 0.01$, $r^2 = 0.362$) in Boags bioregion while the fractal refuge index had a positive influence on the combined abundance of all crustaceans in Central West Coast ($p < 0.01$, $r^2 = 0.200$).

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Table 4.6: Optimal models for community summary metrics developed independently for each bioregion using forward stepwise multiple regression procedures. Superscript letters indicate the error distribution used for the test: ^{a} Poisson, ^{b} Negative binomial, ^{c} Gaussian.

Response variable	**Boags bioregion, Tasmania**	**Pseudo-r^2**	**Central West Coast, WA**	**Pseudo-r^2**	**Batemans Shelf, NSW**	**Pseudo-r^2**
Species richness ^{a}	*Null model*		Fractal refuge index	0.464***	*Null model*	
Total abundance ^{b}	Fractal refuge index + Boulder substratum + Rugosity	0.600***	Fractal refuge index	0.494***	Fractal refuge index - Canopy algae	0.671***
1/ Simpsons Index ^{c}	- Fractal refuge index + Boulder substratum + Canopy algae	0.700***	*Null model*		Boulder substratum + Canopy algae	0.442***

Table 4.7: Optimal models for higher taxa and single species responses developed independently for each bioregion using forward stepwise multiple regression procedures. Single species data were analysed as presence-absence using a logistic distribution unless otherwise indicated. – indicates that the data were not analysed as the species was recorded in less than 30% of sites for the bioregion. Superscript letters indicate the error distribution used for the test: ^{a} Poisson, ^{b} Negative binomial, ^{c} Gaussian, ^{d} Logistic (presence-absence)

Response variable	**Boags bioregion, TAS**	**Pseudo-r^2**	**Central West Coast, WA**	**Pseudo-r^2**	**Batemans Shelf, NSW**	**Pseudo-r^2**
Asteroid abundance ^{c}	*Null model*		*Null model*		*Null model*	
Petricia vernicina	-		Rugosity	0.186**	-	
Plectaster decanus	*Null model*		-		-	
Pentagonaster dubeni	*Null model*		Fractal refuge index	0.186**	-	
Tosia australis	*Null model*		-		-	
Uniophora granifera	*Null model*		-		-	
Fromia polypora	-		*Null model*		-	
Nectria ocellata	*Null model*		-		-	
Crinoid presence ^{d}	Boulder substratum	0.504***	*Null model*		*Null model*	
Cenolia trichoptera	Boulder substratum	0.571***	*Null model*		*Null model*	
Crustacean abundance ^{b}	*Null model*		Fractal refuge index	0.200**	-	
Plagusia chabrus	Canopy algae	0.362**	-		-	
Pagurid spp	-		*Null model*		-	

Panulirus cygnus	-		*Null model*		-	
Echinoid abundance [b]	Fractal refuge index + Boulder substratum	0.462**	Fractal refuge index	0.397***	Fractal refuge index - Canopy algae	0.544***
Phyllacanthus irregularis [b]	-		Fractal refuge index	0.445***	-	
Centrostephanus rodgersii [b]	-		-		- Canopy algae	0.359***
Heliocidaris erythrogramma [b]	Fractal refuge index + Boulder substratum	0.462**	Fractal refuge index	0.298***	*Null model*	
Holopneustes porossimus	-		Rugosity + Canopy algae	0.331***	-	
Gastropod abundance [b]	Rugosity + Canopy algae	0.557***	*Null model*		Fractal refuge index - Canopy algae	0.646***
Campanile symbolicum [b]	-		*Null model*		-	
Haliotis laevigata	Boulder substratum	0.575***	-		-	
Haliotis rubra [b]	*Null model*		-		-	
Dicathais orbita	Boulder substratum + Canopy algae	0.580***	*Null model*		*Null model*	
Astralium tentoriformis [b]	-		-		Fractal refuge index - Canopy algae	0.562***
Phasianella spp	*Null model*		-		-	
Turbo pulchra	-		*Null model*		-	
Turbo torquatus	-		*Null model*		-	

** $p < 0.01$, *** $p < 0.001$.

Gastropods also showed mixed relationships with their habitat across the bioregions. Despite four gastropod species occurring in a sufficient number of sites to warrant testing, no models were significant for the Central West Coast data. In the Batemans Shelf bioregion, gastropod abundance was higher on reefs dominated by smaller refuges (high fractal refuge index) and showed a negative relationship with canopy algae ($p < 0.001$, $r^2 = 0.646$). In the Boags bioregion the commercially fished greenlip abalone *Haliotis laevigata* was recorded almost exclusively at sites where boulders rested on a sandy substratum ($p < 0.001$, $r^2 = 0.575$), while total gastropod abundance was driven by a strong positive relationship with rugosity and canopy algae ($p < 0.001$, $r^2 = 0.557$).

Some elements of the habitat appeared to be consistently more important than others within each of the bioregions. The fractal refuge index was included in three out of the five significant species models in the Central West Coast and was also the best explanatory variable to describe the abundance of crustaceans and echinoids in this bioregion. Boulder substratum was consistently important for species in the Boags bioregion. It was present in four of the six significant species models, and also comprised a component of the optimal models for crinoid and echinoid abundance. Finally, sites with lower cover of canopy algae supported higher numbers of invertebrates in Batemans Shelf bioregion with this habitat variable present in the only two significant species models (*Centrostephanus rodgersii* and *Astralium tentoriformis*), as well as combining with the fractal refuge index to create the optimal model to describe patterns of echinoid and gastropod abundance

Multivariate analyses

The combination of habitat metrics that best describe the community structure of mobile invertebrates in Tasmania were the factor bioregion, the fractal refuge index, and the most common substratum of boulders at the site. The r^2 value attained through the DistLM procedure using community data was 0.436. The Tasmanian model was significantly different from the null model when applied to the Batemans Shelf bioregion data with both terms (fractal refuge index and boulder substratum) making significant contributions to the explained variance, producing an r^2 of 0.409. The absence of boulders on the transects in the Central West Coast meant that there was only one level of the categorical variable ‘boulder substratum’ recorded for the entire bioregion. The fractal index alone explained a significant but weak proportion of the variance ($p < 0.01$, $r^2 = 0.117$) in this bioregion.

Further exploratory analysis identified that the strongest explanatory variable in the Boags bioregion was the percent cover of canopy algae ($p < 0.01$, $r^2 = 0.139$; Table 4.8). The addition of further independent variables to the model only increased the AIC. The optimal model to describe the separation of sites for Batemans Shelf bioregion was a combination of canopy algae, boulder substratum and the fractal refuge index ($r^2 = 0.574$). All habitat metrics exhibited poor explanatory power in the Central West Coast bioregion with the optimal model of fractal refuge index and canopy algae explaining just less than 19% of variability in the similarity of the invertebrate assemblages between sites.

Table 4.8: Proportion of variance in macroinvertebrate assemblage structure explained by single habitat metrics across bioregions. Results shown are the r^2 values from the marginal tests in the DistLM procedure. Optimal models for each region are described in the text.

Habitat metric	Boags bioregion, TAS	Central West Coast, WA	Batemans Shelf, NSW
Boulder substratum	0.170*	NA	0.345***
Fractal refuge index	0.104*	0.117**	0.099*
Rugosity	0.077	0.056	0.147**
Canopy algae	0.139**	0.074*	0.331***

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

DISCUSSION

Habitat surrogates have been suggested as tools for biodiversity prediction in the absence of more comprehensive data (eg. Banks et al., 2005; Gladstone, 2002; O'Hara, 2001) and the linkages between broad definitions of marine habitats (such as seagrass, rocky reef, coral reef and unvegetated soft substratum), fishes and invertebrates are consistently strong (Abele, 1974; Friedlander et al., 2007; Grantham et al., 2003; Harborne et al., 2008; Kohn, 1967; Williams and Bax, 2001). Within a habitat (such as subtidal rocky reefs) the relationship between animals and habitat-quality metrics such as habitat structure can be used to account for part of the spatial variability in tests of impacts such as the effect of marine protected area on target taxa (Garcia-Charton et al., 2000). However, current research has found little broad-scale spatial consistency in the habitat structure metrics (such as rugosity) that display strong relationships with marine taxa. In this study, the poor performance of the Tasmanian models in the other states for most components of the invertebrate assemblage, as indicated by their weak predictive power, strengthens this need for caution when extrapolating intra-habitat surrogate models to new sites outside the region of model development. I propose that a more conservative and ecologically meaningful approach is to base the model development on a relatively uniform distribution of sites across a biogeographic range (eg. bioregion or province, IMCRA; Commonwealth of Australia, 2006) and then only make predictions for new sites within the spatial extent of those used to train the models. This approach provides the highest likelihood that the range of physical and ecological conditions for this region is encompassed in the model training data and the prediction of biological communities for new sites within the region are unlikely to encounter new conditions that may alter the nature of these relationships.

The relationship between the total abundance of invertebrates, the abundance of echinoids and the fractal refuge index were the only models that were spatially transferable across the regions tested here. The fractal refuge index was also correlated with variation of invertebrate assemblages across the three regions studied. This echoes the results of Edmunds et al (1999) who found that interstitial space (the number of holes) was the strongest single habitat variable to describe invertebrate assemblage patterns at five sites in central Victoria, Australia. In the U.S. Virgin Islands, increasing the number of small holes in artificial reefs increased the abundance of small fish species (Hixon and Beets, 1993), with an analogous increase in the number of large fishes with large holes (Hixon and Beets, 1989). By contrast, holes in the reef were not related to the distribution of herbivorous invertebrates and fishes in the Mediterranean (Ruitton et al., 2000), or to fishes in the British Virgin Islands (Gratwicke and Speight, 2005a).

The parallel relationship to the fractal refuge index for total abundance and echinoids is unsurprising given the echinoids were the most numerically dominant taxa across the study area (contributing almost 57% of the total number of animals). Characteristics of reef architecture such as crevices can moderate the effects of fish predation on sea urchins (Hereu et al., 2004), and animals occupying open microhabitats exhibit a greater alarm flight response than animals sheltering in refuges (Parker and Shulman, 1986). The spine characteristics of the sea urchin species in this study and personal observation suggest that the strength of their grip on the substratum, largely driven by wedging the spines into the structure of the reef, increases with a greater level of enclosure of the animal by the reef profile. The definition of a refuge used in this study reflects this sheltering behaviour and a high fractal refuge index indicates a reef dominated by small refuges, which provides refuge for smaller animals such as urchins without offering appropriate shelter for larger invertebrate predators that also utilise reef structure as shelter (Booth and Ayers, 2005; Mislan and Babcock, 2008).

The recurrence of single and different measures of habitat complexity within each of the bioregions suggests a dominant influence of one particular element of the structure at this scale. In the Boags bioregion, four of the five significant models describing species distributions included boulder substratum. The three species *Cenolia trichoptera*, *Heliocidaris erythrogramma* and *Haliotis laevigata* preferred sites with boulders resting on a sandy substratum, while *Dicathais orbita* preferred a solid bedrock base. Chapman (2002b) and Le Hir and Hily (2005) have identified that the substratum beneath boulders on an intertidal shore significantly affected the composition of the invertebrate assemblage that colonised it. The preference of *C. trichoptera* for sandy reefs is intriguing given that this feather star filter feeds, hence suspended sand particles would be expected to interfere with its filtering mechanism. Although there is no replication to support the theory, it is noteworthy that models tested at the larger Tasmania scale did not have any particular habitat metric predominating in optimal models. This suggests that the taxonomic generality of the one dominant aspect of the habitat having a greater influence on the biota is restricted to the scale of bioregion or less than hundreds of kilometres.

Species richness showed only very weak associations to the habitat metrics considered in this study. This assemblage metric appears to vary on a scale much larger than reef, such as that of provincial bioregion (Commonwealth of Australia, 2006), possibly due to the influence of broad-scale forcing factors such as oceanographic currents or continental history (O'Hara and Poore, 2000; O'Hara, 2001). The presence of habitat altering species such as *Centrostephanus rodgersii* which influence canopy algae through the creation of urchin barrens can also dramatically influence the number of species on a reef (Ling, 2008). Spatial patterns of species richness in this study differ from the negative latitudinal gradient reported by other authors (eg. Hillebrand, 2004) including O'Hara and Poore (2000). By contrast, the Tasmanian sites studied here supported similar mean numbers of invertebrate species as sites from Western Australia, and far greater numbers than that further north in New South Wales. The discrepancy between this and O'Hara and Poore's study probably relates to differences in the spatial scale of the sampling unit (single reef versus 1 degree of latitude and longitude – potentially reflecting species area considerations), taxa assessed, and the range of habitats covered. O'Hara and Poore (2000) considered echinoderms and decapods in all shallow marine habitats whereas this study examined all mobile macroinvertebrates with focus on shallow rocky reefs.

The species richness of mobile macroinvertebrates recorded in the Batemans Shelf bioregion was much lower than that of the two other locations. One potential explanation is that the sea urchin species *Centrostephanus rodgersii* was recorded in high numbers at the majority of sites surveyed in Batemans Shelf bioregion. This urchin creates and maintains barrens habitat that is impoverished in numbers of other invertebrate species (Hill et al., 2003; Ling, 2008). The weak negative relationship between species richness and canopy algae in Batemans Shelf was surprising and is unlikely to represent patterns for other components of biodiversity. Clearance of foliose macroalgae directly reduces the food resources available to herbivorous invertebrates and indirectly limits biogenic habitat structure available for small invertebrate species to colonise, with cascading implications for other trophic levels.

Centrostephanus rodgersii and the turbinid gastropod *Astralium tentoriformis* were the only two species to display any significant linkages to habitat in the Batemans Shelf bioregion, both possessing negative associations with canopy algae. *Australium tentoriformis* was also found in higher numbers on reefs dominated by small refuges (high fractal refuge index; Table 4.6). This gastropod is commonly associated with *C. rodgersii* on the barren reefs of New South Wales but does not make a significant contribution to the exclusion of non-crustose algae in the urchin barrens (Fletcher, 1987).

Centrostephanus rodgersii also associates closely with reef structural features (Andrew, 1993) but was not linked to the fractal refuge index in this study. The fractal refuge index is highly correlated with the density of small refuges (defined here as crevices with aperture between 1 cm and 5 cm; Pearsons correlation for all data $r^2 = 0.851$). The adult test diameter of *C. rodgersii* is > 40 mm (Andrew, 1991), with spines at least as long again; consequently, adult urchins are unlikely to directly benefit from refuges in this size class. The medium refuge size class (6 – 15 cm) would be more likely to provide shelter for the body size of this species and indeed further exploratory analysis showed a significant positive relationship between this habitat metric and the abundance of *C. rodgersii* in the Batemans Shelf bioregion (negative binomial distribution, $p > 0.01$, $r^2 = 0.201$). This model was made even stronger by the inclusion of a negative association with canopy algae ($p > 0.001$, $r^2 = 0.487$). Other invertebrate (Beck, 1995; Casariego et al., 2004) and fish (Hixon and Beets, 1989; 1993) species associate with shelters that most appropriately match their body size. Such associations can also be influenced by an animal's life stage (Wahle and Steneck, 1992), the level of predation (Eggleston and Lipcius, 1992) and the density of conspecifics (Eggleston and Lipcius, 1992; Mintz et al., 1994).

No clear difference was found in the proportion of significant descriptive models for the combined class level abundance and the models for its component species. The difference in the statistical distributions used for presence-absence (logistic – the majority of species) and abundance data (negative binomial – most class level tests) need to be considered when making this comparison; however, models for fish taxa in the Mediterranean were stronger for the class level tests (Jennings and Polunin, 1997; Jennings et al., 1996). This is expected as species within a class are likely to be functionally similar in terms of morphology, mobility and trophic status and therefore relate to habitat in a similar way, with idiosyncratic species-habitat relationships overwhelmed. Thus, the more general influences on each functional group may become pronounced at the higher taxonomic levels (Garcia-Charton et al., 2000). An alternative process is that if the different habitat metrics influence different species in the class in slightly different ways, then combining abundances at the class level could obscure these relationships.

Asteroids lacked strong relationships with any habitat metrics, both for the abundance of individual species and for the class as a whole. At the scale of microhabitat, some asteroid species are also known to seek shelter in the form of shade, as might be provided by biogenic or reef habitat structure (Bernaford and Vasquez, 2008). A potential reason why no asteroids were strongly related to habitat structure metrics in this study may be that their spatial distributions are influenced by characteristics of the habitat other than those considered here. Another explanation may be high spatial variability in settlement can produce a distribution closer to random, dampening any significant effects of habitat (Balch and Scheibling, 2000). Ontogenetic shifts in habitat preference (Verling et al., 2003) may also obscure the search for invertebrate-habitat linkages, as the life stage or size of the individual animals were not considered here.

This study identified strong associations between measured elements of the habitat and components of the mobile macroinvertebrates on Australian temperate rocky reefs. Despite morphologically and functionally similar species occupying corresponding ecological niches across the regions tested here, the most important measures of habitat to describe the presence-absence of similar species or abundance of higher taxa (such as class) varies across southern Australia. Further studies are required to investigate the causal mechanisms and conditions driving the context dependency of these relationships. The spatial transferability of models using reef architecture to describe the combined abundance of all macroinvertebrates, and particularly the echinoids, can be applied to partially account for habitat-driven variance in impact assessments, such as during assessments of the influence of marine reserves on benthic communities.

Plate 4: *Jasus edwardsii*, Maria Island, Tasmania

Chapter 5:

Exploited invertebrate species in Tasmanian marine reserves show declining links with habitat structure through time

ABSTRACT

Interactions between predators, prey and habitat are well established for many marine ecosystems yet few studies examine the long-term effects of interactions between these factors, including effects of differing levels of predation on habitat preferences of subtidal rocky reef invertebrates. I here assess changing patterns of association between benthic habitat structure (reef architecture and topographic variability), the invertebrate assemblage and key component species over 16 years at fished and protected sites around two southern Australian marine reserves. The relationship between reef profile variability and the invertebrate assemblage grew weaker inside marine reserves over the duration of study. The southern rock lobster *Jasus edwardsii* was most influenced by reef profile variability, initially displaying an r^2 of up to 0.9 during the first years of protection, as calculated using linear regression modelling, but the strength of this relationship consistently decreased to $r^2 < 0.15$ after 12 years of protection. Increasing rock lobster size within reserves has apparently reduced their dependency on reef shelters as refuges from predation or, alternatively, increasing abundance has caused lobsters to increasingly forage on suboptimal reefs. Increasing predation pressure in the marine reserves also corresponded with diminishing invertebrate-habitat relationships for herbivorous sea urchins (*Heliocidaris erythrogramma*) and abalone (*Haliotis rubra*). This unexpected

outcome possibly resulted from increased numbers of larger predators overcoming the benefits of reef refuges.

INTRODUCTION

Ecological theory suggests that, all other factors remaining equal, an increase in predation pressure will strengthen the association between habitat structure and prey for species that utilize physical refuges to avoid predators (see references in Anderson, 2001; Sih et al., 1985). This pattern may be caused by a behavioural response whereby prey species seek or remain in refuges in the presence of elevated predation risk (Parker and Shulman, 1986; Pederson et al., 2008; Shears and Babcock, 2002) or by differential predation success where prey animals are more readily removed from areas that lack complexity (Connell and Jones, 1991). With strong predation pressure, individuals that persist are typically associated with structural features or refuges that are either inaccessible, or the time and energy required to remove them is not worthwhile from the predator's perspective. The expression of this pattern depends on whether the prey species can rely on anti-predation mechanisms additional to the use of spatial refuges (eg. spines in sea urchins), and also the availability of appropriately scaled reef features in the local region (Eggleston et al., 1997).

In areas of high predation pressure, scaling between animal body size and available reef shelter can influence the abundance and size structure of prey species (Beck, 1995; Wahle and Steneck, 1992). Sala and Zabala (1996) identified that the sea urchin *Paracentrotus lividus* exhibited crevice dwelling behaviour in response to intense fish predation in a Mediterranean marine reserve. Smaller urchins were able to benefit most from the refuge provided by available reef features, resulting in a shift in the size structure of the species towards smaller animals at marine reserve sites (Sala and Zabala, 1996). Predation by rock lobsters was most intense on the smallest size class of urchin in New Zealand during tethering experiments conducted by Shears and Babcock (2002), yet there was no difference in the density of cryptic juvenile urchins between reserve and fished sites, suggesting that predation on this size of urchin is reduced when they are permitted to seek shelter. Hereu et al. (2005) also identified that predation on sea urchins increased at greater abundance of predatory fishes, and decreased with greater structural complexity, although the benefit provided by structure decreased with increasing size of sea urchin recruits.

Characterizing the structure of a reef surface is a difficult task given the highly complex three-dimensional nature of the benthic environment. The most common approach used by researchers in this field is to measure general characteristics of the reef surface such as topographic variability (e.g. rugosity) or substratum composition. Variability in the height of the reef surface is likely to influence organization of the species assemblage through processes such as shading (Adams, 2001; Bernaford and Vasquez, 2008; Drolet et al., 2004b), hydrodynamics (Koehl, 2007; McShane et al., 1988) or through provision of transient refuges where the complexity of the reef surface can limit the visual range of hunting predators (Caley and St John, 1996). Quantifying substratum composition consists of measuring the cover of different categories of coral growth forms (Bergman et al., 2000; Friedlander and Parrish, 1998; Gratwicke and Speight, 2005a; Sale and Douglas, 1984) or boulder sizes (Garcia-Charton et al., 2004; Ordines et al., 2005), each of which have consistent physical characteristics that produce similar reef surface profiles. Areas of reef within each category should also support similar sizes and numbers of reef architectural features (Barry and Wickins, 1992).

The third main approach is to create an explicit definition of a reef feature (e.g. hole, crevice, overhang) that hypothetically reduces the probability of success for a predatory attack (permanent refuges; *sensu* Caley and St John, 1996). Owing to the diversity of predatory attack strategies and prey defence mechanisms, it is probably impossible to create a definition that applies to all predator-prey interactions in an ecosystem, let alone between systems, however some consistencies are evident. For example a reef feature such as a thin crevice can shelter juvenile abalone (Shepherd, 1986), shrimp (Caillaux and Stotz, 2003) or the soft body of an ophiuroid (Drolet et al., 2004a). Identification and enumeration of these features can help to describe and predict spatial variation in the abundance of some benthos-associated marine species (Friedlander and Parrish, 1998; chapter 3, 4; Roberts and Ormond, 1987)

Marine reserves can act as large scale manipulative experiments, particularly for site attached species, to investigate the impacts of human and natural predation on community organization and species' relationships to their habitat. Commercial fisheries usually target top level carnivores (Pauly et al., 1998) and consequently these species most commonly exhibit the greatest benefit from protection within no-take marine reserves (Babcock et al., 1999; Edgar and Barrett, 1999; Guidetti, 2006). Indirect effects of fishing/protection can cause trophic cascades as a result of increased predation in marine reserves (Pinnegar et al., 2000), although the expression of these effects vary with local physical conditions such as exposure (Micheli et al., 2005) and habitat (Garcia-Charton et al., 2000). The presence of reef shelter can moderate the effects of fish predation (Caillaux and Stotz, 2003;

Eggleston et al., 1997; Hereu et al., 2005), and an influence of marine reserves on non-target invertebrate species is now widely accepted (Guidetti, 2006; McClanahan and Shafir, 1990; Sala and Zabala, 1996; Shears and Babcock, 2002), however the interacting expression of these patterns for invertebrates across multiple trophic levels and over long time periods remains to be adequately documented.

This study utilizes data from a long-term (16 years) ecological monitoring program at two marine reserves in southeastern Tasmania, Australia, to identify shifts attributable to increasing predation pressure in habitat preference by the macro-invertebrate assemblage and its key component species. Data collected at adjacent areas exposed to fishing pressure allow the separation of the effects of the marine reserve from regional fluctuations such as strong recruitment years (Booth et al., 2001) or regional ocean temperature change (Ling et al., 2009).

Maria Island and Tinderbox marine reserves were declared in September 1991 but were not signposted or policed for the first twelve months and some fishing occurred during this period (Edgar and Barrett, 1997). Since establishment, biomass of large fishes has increased by an order of magnitude in these reserve sites (Edgar et al., 2009), including a hundred-fold increase in abundance of the carnivorous fish species bastard trumpeter *Latridopsis forsteri* during the first six years, and an increase in mean size of blue throated wrasse *Notolabrus tetricus* (Edgar and Barrett, 1999). *Notolabrus tetricus* along with the purple wrasse *N. fucicola* feed on juveniles of the commercially important southern rock lobster *Jasus edwardsii* (Mills et al., 2008) and abalone (Shepherd and Clarkson, 2001), amongst other invertebrates (Metcalf et al., 2008).

Jasus edwardsii, the dominant benthic predator on Tasmanian rocky reefs (Ling et al., 2009; Pederson and Johnson, 2006), has also greatly increased in number and size in Tasmanian marine reserves (Barrett et al., 2009; Edgar et al., 2009). Increased predation, particularly by lobsters, has apparently affected herbivorous invertebrates, altering the behaviour, abundance and size structure of the blacklip abalone *Haliotis rubra* and purple sea urchin *Heliocidaris erythrogramma* (Barrett et al., 2009; Pederson and Johnson, 2006; Pederson et al., 2008). The general aim of this study is to examine relationships between reef habitat structure, macroinvertebrate communities, and their key component species through time at protected and fished sites to determine if fishing prohibitions generally alter habitat preferences of abundant invertebrate taxa.

METHODS

Mobile invertebrates

Populations of mobile invertebrates were censused annually in autumn between 1992 and 2008 at 16 sites in and around two marine reserves on the east and south east coast of Tasmania, Australia (Fig. 5.1), as described by Edgar and Barrett (1997, 1999). Six sites were located within the no-take Maria Island marine reserve and two sites in the Tinderbox marine reserve. Data from the two reserves were considered together with sites haphazardly distributed ca. 1 km apart across both reserves. An equivalent number of control sites in close proximity to the protected areas were also monitored for each marine reserve. The abundance of all observed mobile invertebrates with a maximum dimension >2 cm were counted in a 1 x 200 m transect along the 5 metre depth contour at each site. All animals observed within cracks and crevices on the transect were counted; however, no destructive sampling, such as overturning boulders, was carried out.

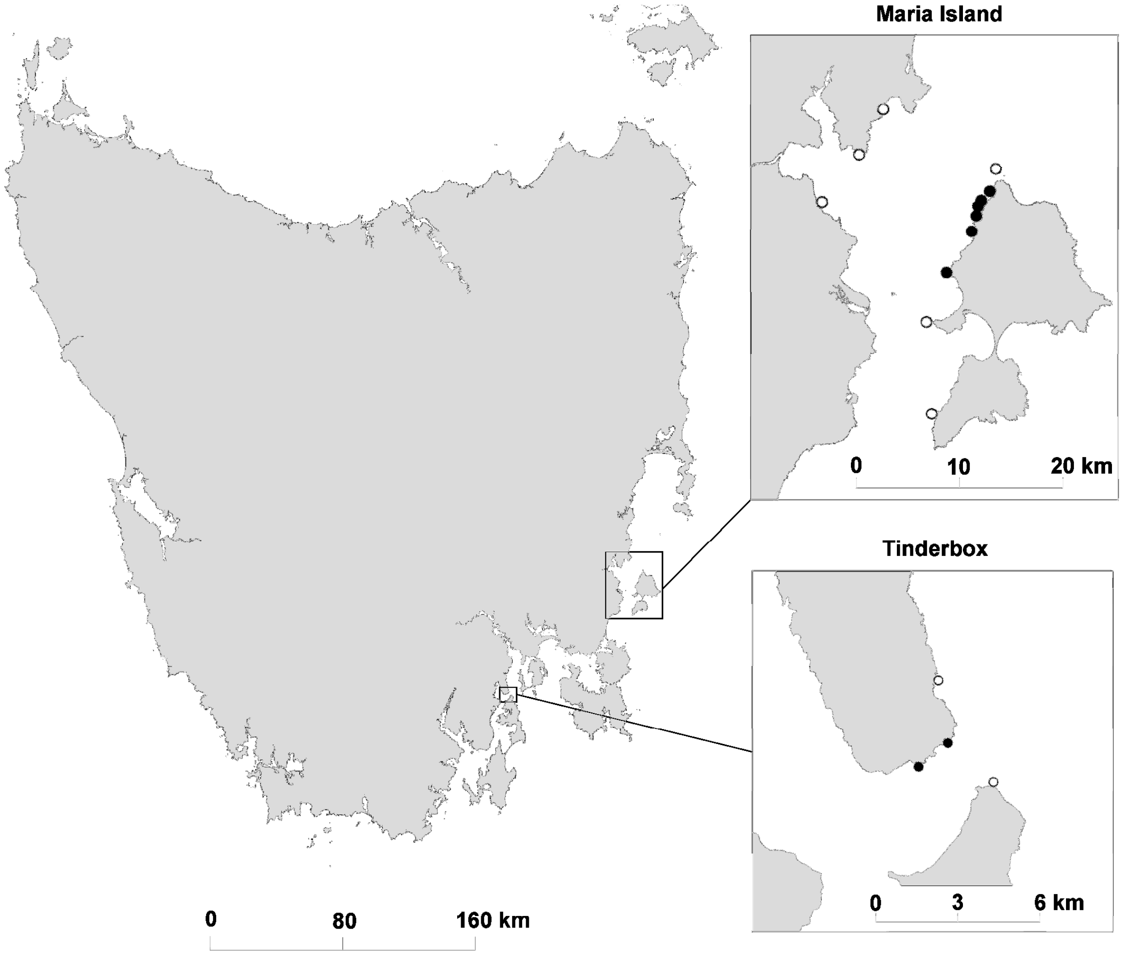

Fig. 5.1: Map showing the distribution of study sites. Site markers with solid circles were located within reserves, open circles indicate fished sites.

Preliminary inspection of the data indicated ten taxa were present in >50% of transects surveyed; these taxa consequently formed the basis for multivariate data analyses. Listed in order of frequency of occurrence, these taxa were *Heliocidaris erythrogramma* (purple sea urchin), *Cenolia* spp. (feather star), *Haliotis rubra* (blacklip abalone), *Jasus edwardsii* (southern rock lobster), *Plagusia chabrus* (red bait crab), *Strigopagurus strigmanus* (red hermit crab), *Goniocidaris tubaria* (pencil urchin), *Petricia vernicina* (velvet seastar), *Nectria ocellata* (spotted seastar) and *Tosia australis* (southern biscuit star). The feather stars *Cenolia trichoptera* and *Cenolia tasmaniae* were grouped together as *Cenolia* spp. due to the difficulty of distinguishing these species in the field.

The four species recorded on >50% of occasions at all 16 sites were selected for univariate analyses. *Cenolia* spp. numerically dominates the subtidal rocky reefs in most regions of Tasmania (see, e.g., chapter 4). *Heliocidaris erythrogramma* is a sea urchin of functional importance as the dominant herbivore on the east coast of Tasmanian (Sanderson et al., 1996) with the ability to create small urchin barrens (Pederson and Johnson, 2008), and is the basis of a small fishery in the region (DEH, 2005). The southern rock lobster *Jasus edwardsii* and blacklip abalone *Haliotis rubra* are the two most valuable wild-caught species in Tasmania, generating fisheries valued in 2006-07 at $59 and $111 million Australian dollars, respectively (ABARE, 2008).

Reef structure measurements

The limited number of sites for which biological data were available meant that few of the diverse range of predictor variables available for characterizing reef habitat structure (eg. McCormick, 1994) could be tested before a significant result would be discovered by chance alone. Representatives of the three major categories of rocky reef metrics (substratum composition, topographic variability and substratum architecture) were measured at all 16 sites. A principal component analysis (PCA) was then used to select two metrics that characterized different but important aspects of the habitat.

The level of folding or rugosity of the reef surface is one of the most frequently considered measures of topographic variability in the literature. A rugosity index was calculated in this study as: 1 – (L / C) where L = the linear horizontal distance spanned by a 5 m length of lead-core rope when contoured to the reef surface along the transect, and C = the contoured distance, which in this case was fixed at the length of the rope (5 m; see chapter 3). The rugosity value applied was calculated as the average of twelve measurements over the 200 m transect distance.

A second quantification of reef profile variability was calculated based on depth measurements to 0.1 m accuracy recorded using a dive computer under calm sea-state conditions at 1 m intervals along the 200 m of reef investigated at each site. Reef profile variability was calculated as the sum of the squared difference between consecutive depths for a transect, so this metric is sensitive to sudden rather than gradual vertical changes in the profile of the reef. The square root of the sum total was taken to linearise this metric (McCormick, 1994).

The contribution of the substratum composition in explaining variability of invertebrate abundance was considered by estimating the percent cover of consolidated bedrock, small (maximum diameter 0.2 - 0.5 m), medium (maximum diameter 0.5-1.5 m) and large (maximum diameter > 1.5 m) boulders within the transect area at each site.

Substratum architecture was represented by counts of different size classes of reef features that have the potential to form refuges from predation for prey species (see chapter 3). Briefly, reef features were considered to comprise a refuge where 1) three planes of the substratum meet with at least one of these planes forming an angle of less than 90°, 2) two planes of the substratum meet at an angle of 45° or less and 3) the refuge is deeper than the minimum dimension of its entrance. Counts of refuges with the minimum dimension of their aperture falling between the ranges 1 – 5 cm, 6 - 15 cm, 16- 50 cm and > 50 cm were carried out in eight 1 x 5 m blocks randomly distributed within the 200 m site. These measures were repeated on two occasions with the transect reset within sites for each occasion, thereby reflecting the slight variability in habitat surveyed between years for the invertebrate time series data.

Statistical analysis

Changing strength of invertebrate-habitat relationships through time was assessed using a two stage analysis. Initially, the association between the assemblage of commonly occurring invertebrates and reef structure was determined for each temporal survey using distance-based linear modelling (DistLM) constructed in the PERMANOVA+ add-on to PRIMER 6. DistLM identifies the relationship between the multivariate data cloud and one or more predictor variables, and determines if the amount of variation explained by the model is different from a distribution of outcomes generated by random permutation of samples (Anderson et al., 2008). All abundance data were square-root transformed and multivariate analyses carried out based on Bray-Curtis resemblance matrices for biological data and Euclidean distance resemblance for physical metrics, as recommended by Anderson et al. (2008). The proportion of variance explained by the model provides an indicator of the descriptive power of reef structure metrics for each test.

Univariate models were also investigated, where the association between the abundance of the four key species and reef structure metrics at each time step was determined using linear regression models in R version 2.9.2 (R Development Core

Team, 2009). The size of the r^2-value from each regression was used to represent the relative strength of reef structure metrics in describing variation in the abundance of species among sites. Separate DistLM and linear regression models were created for sites inside and adjacent to the marine reserve in each year.

The second stage in the analysis involved the construction of the linear regression model: r^2 = constant + time + marine reserve + time * marine reserve, where r^2 is the proportion of variance explained (i.e. the r^2-value derived from the multivariate or bivariate models between the response variable and reef habitat structure metric) for each year, 'time' is the number of years since the declaration of the reserve, and 'marine reserve' is a categorical factor reflecting whether the test was carried out on data from inside or external to the marine reserve.

The null hypothesis that protection from fishing has not affected relationships between invertebrates and reef structure was tested by quantifying the significance of the marine reserve * time interaction term in the above model. Invertebrate populations at Tinderbox and Maria Island marine reserves are changing in response to protection from fishing while populations at fished control sites are relatively stable (Barrett et al., 2009; Edgar and Barrett, 1999; Edgar et al., 2009). This situation increases the likelihood of identifying a falsely significant interaction term. Assuming that the reef structure at sites is static through time, relationships to reef structure will not change if the invertebrate abundance at these sites remains constant. On the other hand, habitat relationships for dynamic populations, such as across marine reserve sites, will almost certainly change through time. This creates a situation where testing the biological data against any independent data will potentially produce significantly different slopes inside (positive or negative) and external to the reserve (relatively flat) on a plot representing the change in strength of the invertebrate-habitat association through time. To accommodate this increased likelihood of Type I error, the values for each reef structure metric were randomized 1000 times and the full two-stage analysis carried out on each randomization using the true abundances of each of the four key species. The F-statistic for the interaction model based on the true data was compared to the distribution of F-statistics from the randomisation tests. The interaction term was deemed significant if less than 5% of randomised tests produced an F-statistic less than that the value for the real data.

RESULTS

Principal component analysis indicated that reef profile variability and density of small refuges (representing substratum architecture) were strongly correlated with the first and second principal components (Fig. 5.2). These metrics had no zero values for any sites (unlike some substratum types and the larger refuge size classes) and were approximately orthogonal to each other (i.e. represented groups of metrics that discriminated different aspects of reef structure). They also had similar means and ranges across fished and protected sites (reef profile variability: fished sites 3.39 – 6.60, protected sites 2.84 – 5.62; $t = 0.544$, $p = 0.595$ for Welch two sample t-test; small refuges: fished sites 20.0 - 54.8; protected sites 10.1 – 47.63; $t = 1.31$, $p = 0.211$ for Welch two sample t-test). By contrast, the variable rugosity was represented by an uneven range of values for fished (0.225-0.352) and protected (0.063-0.416) sites, consequently reef profile variability was selected in preference to rugosity for further analysis in this study (also rugosity was identified as of low importance for structuring invertebrate populations in this region; chapter 3).

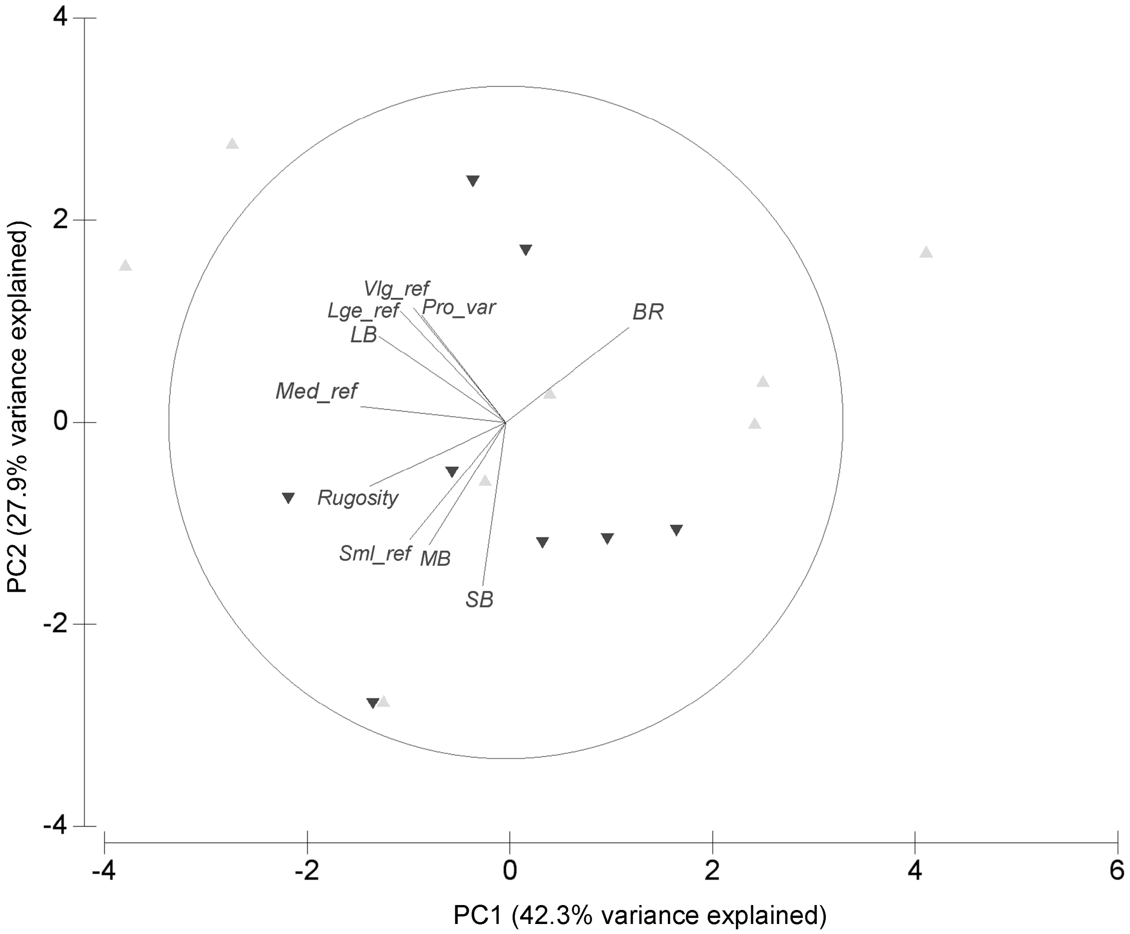

Fig. 5.2: Principal component analysis of normalized reef habitat structure metrics. Dark grey triangles represent sites within a marine reserve while light grey triangles are sites exposed to fishing. SB: small boulders, MB: medium boulders, LB: large boulders, BR: bedrock, Pro_var: reef profile variability, Sml_ref: density of refuges 1 – 5 cm, Med_ref: 6 – 15cm, Lge_ref: 16 – 50 cm, Vlg_ref: >50 cm.

The strength of the relationship between the assemblage of common invertebrates and reef profile variability decreased through time (Table 5.1, Fig. 5.3a). Data for 1992 appear anomalous; with a very weak relationship for protected sites (see also relationships between reef profile variability and the abundance of *Jasus edwardsii* and *Haliotis rubra* abundance). When the 1992 survey is excluded from the analysis the significance of the interaction term increases substantially to F-statistic = 44.32, p < 0.01. The invertebrate assemblage showed no clear changes in its relationship to small refuges through time (Table 5.1, Fig. 5.3b).

Table 5.1: F-values and significance levels for the interaction term in the model: r^2 ~ constant + time + marine reserve + time * marine reserve, where the r^2 is derived from the relationship between reef structure and biological response at each time using a) DistLM and b) linear regression. Significance levels for single species are based on the proportion of tests on randomised data with F-values smaller than that for the true data ($^{\#}$ $p < 0.1$, * $p < 0.05$)

Response	**Profile variability**	**Small refuges**
a) Invertebrate assemblage	26.5*	4.5*
b) *Jasus edwardsii*	8.29*	1.35
Haliotis rubra	$3.82^{\#}$	0.44
Heliocidaris erythrogramma	0.57	17.4*
Cenolia spp.	8.13	$31.6^{\#}$

Jasus edwardsii (southern rock lobster) exhibited a strong positive association with reef profile variability at protected sites at the start of the time series; however, an increase in density at sites with low and some medium values of this habitat metric caused this relationship to decrease until it was no longer significant past 1999 surveys (Fig. 5.4). Overall, the strength of the association between *J. edwardsii* and reef profile variability declined significantly through time at protected sites, whereas the relationship at fished sites was highly variable with a slight increase through time (Fig. 5.5). A significant interaction term (Table 5.1) reflects the difference in the strength of this relationship through time at fished and protected sites.

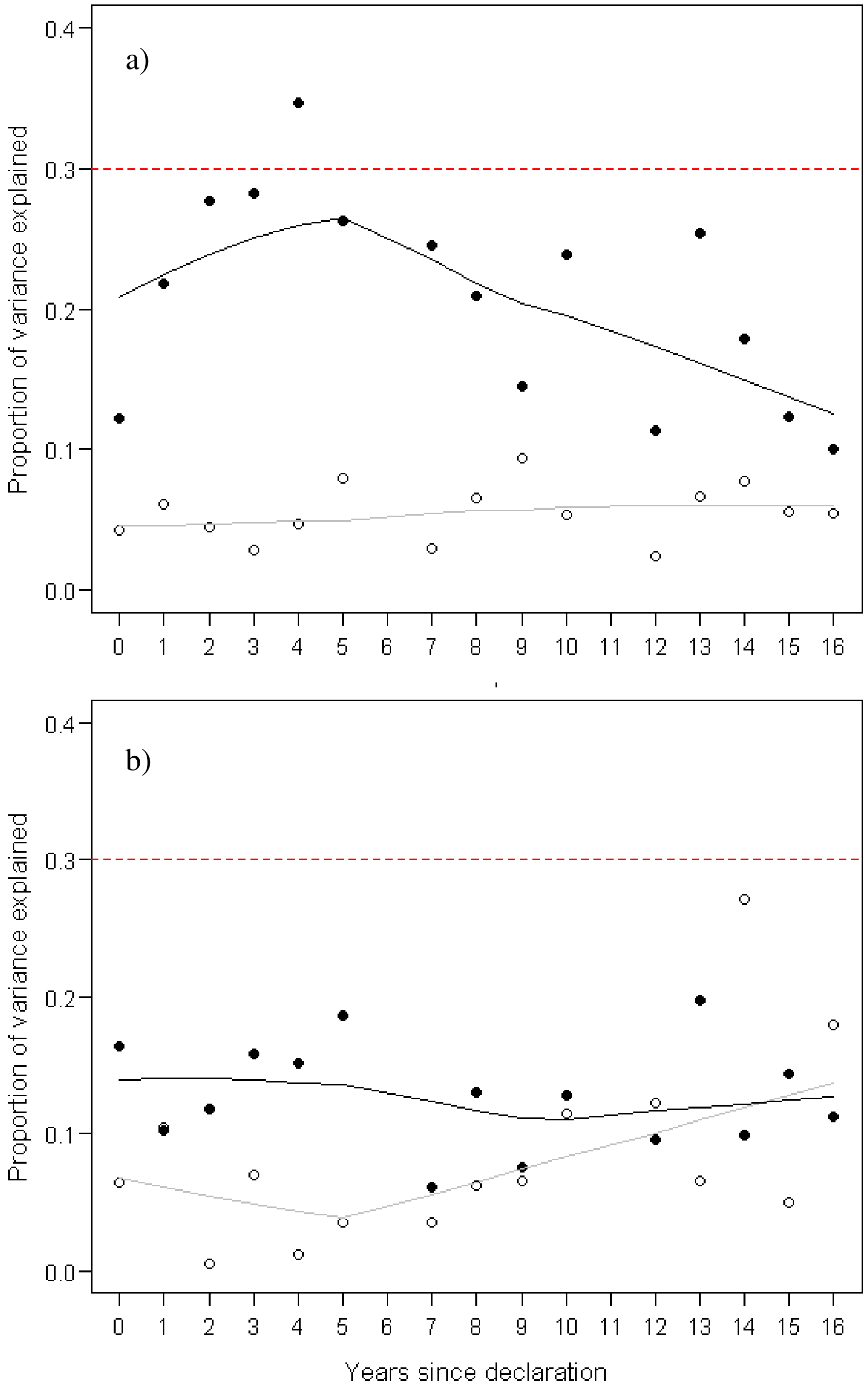

Fig. 5.3: r^2 values for linear regression models through time that describe the relationship between the species assemblage and a) reef profile variability and b) the density of small refuges at protected (●) and fished (○) sites using DistLM. The dashed red line shows the approximate $p = 0.05$ significance level for an individual year. Solid lines are LOWESS trend lines.

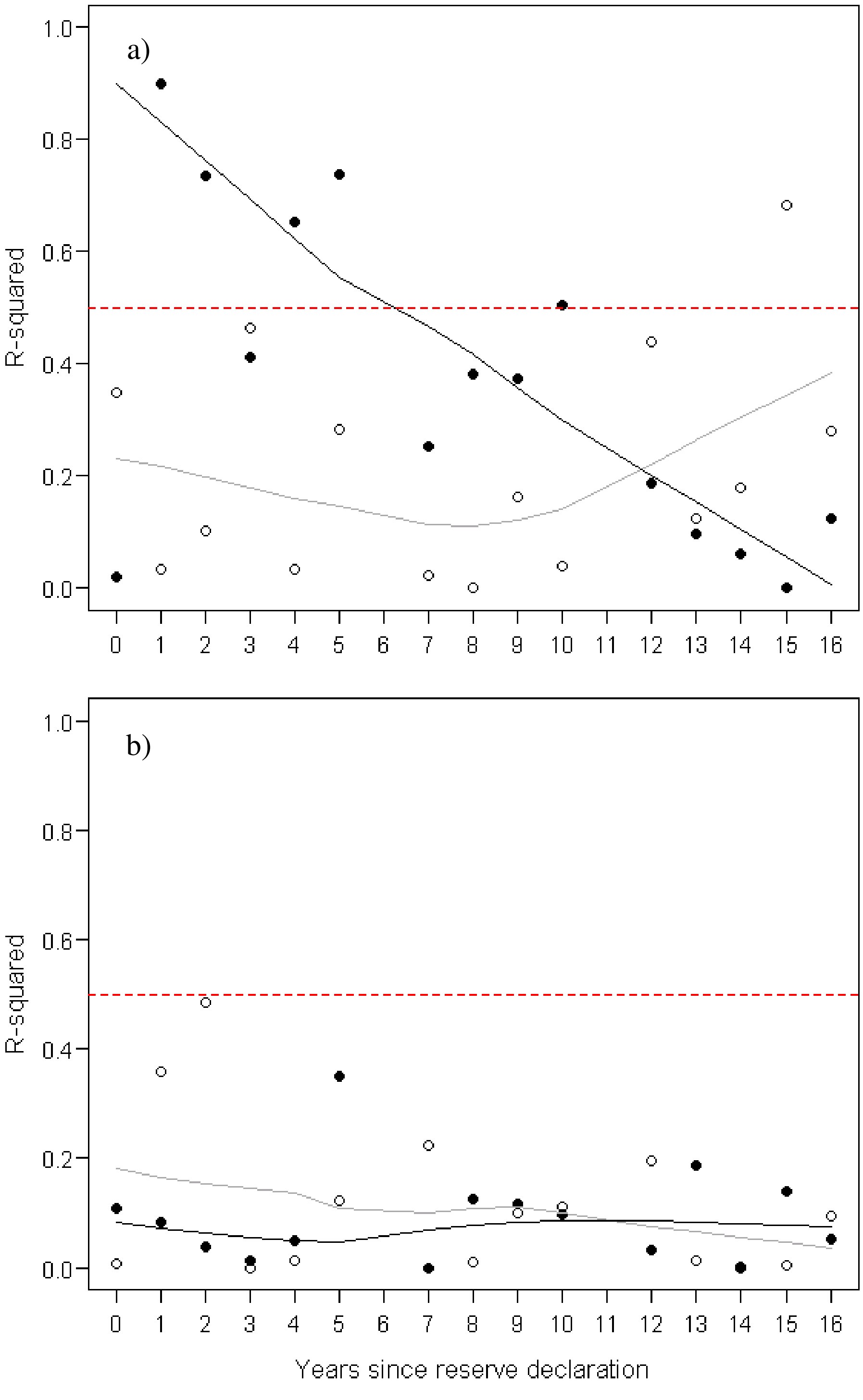

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Fig. 5.4: r^2 values for linear regression models through time that describe the relationship between the abundance of *Jasus edwardsii* and a) reef profile variability and b) the density of small refuges at protected (●) and fished (○) sites. The dashed red line shows the p = 0.05 significance level. Solid lines are LOWESS trend lines.

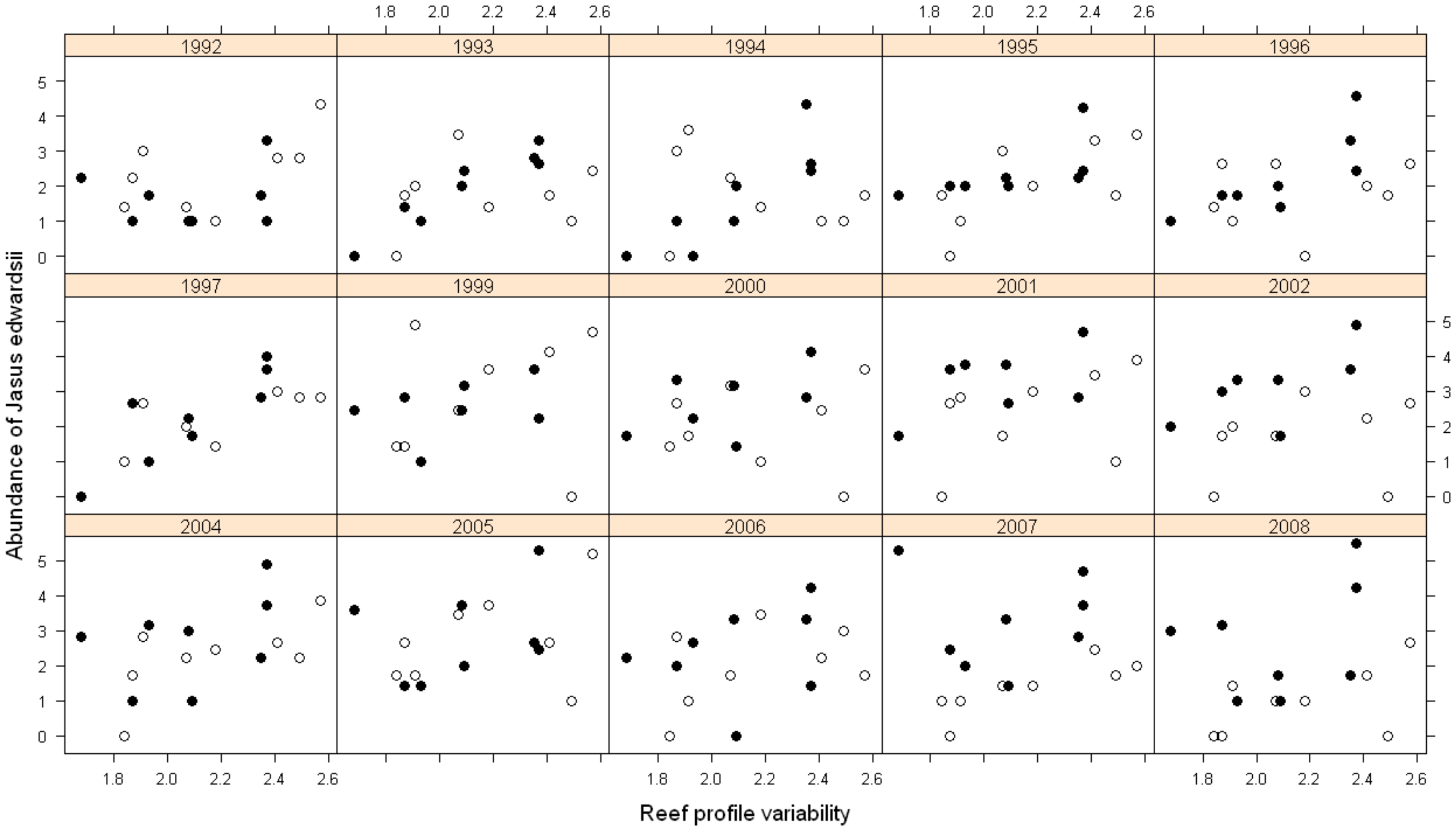

Fig. 5.5: Relationship between the abundance of *Jasus edwardsii* (square root transformed) and reef profile variability at protected (●) and fished (○) sites for each temporal survey. Data are truncated to facilitate visualisation of trends. Excluded data at protected site: profile variability = 2.37, abundance = 9.43 (1999), 6.86 (2000), 7.75 (2001), 6.93 (2002).

Heliocidaris erythrogramma and *Haliotis rubra* both showed reductions in the strength of their relationship with reef structure at protected sites (Table 5.1). *Heliocidaris erythrogramma* decreased in abundance at protected sites following the declaration of the marine reserves (Barrett et al., 2009), with sites supporting high numbers of small refuges experiencing the greatest loss of animals through time, weakening the invertebrate-habitat linkage for this metric (Table 5.1). The decline in the strength of this relationship was strongest for the first 7 years of protection when the r^2-value decreased steadily from 0.42 in 1992 to 0.01 in 1999, after which it varied but remained less than 0.2 (Fig. 5.6). The abundance of *H. rubra* also decreased in Maria Island and Tinderbox marine reserves (Barrett et al., 2009). A proportionally greater loss of individuals from sites with low reef profile variability has caused a decrease through time in the strength of the negative, but non-significant relationship, between this species and reef profile variability (maximum $r^2 = 0.341$, $F = 3.10$, $p = 0.129$ for protected sites in 1996; Fig. 5.7). Associations between reef habitat structure and *H. erythrogramma* and *H. rubra* have generally remained stable at fished sites throughout the survey period.

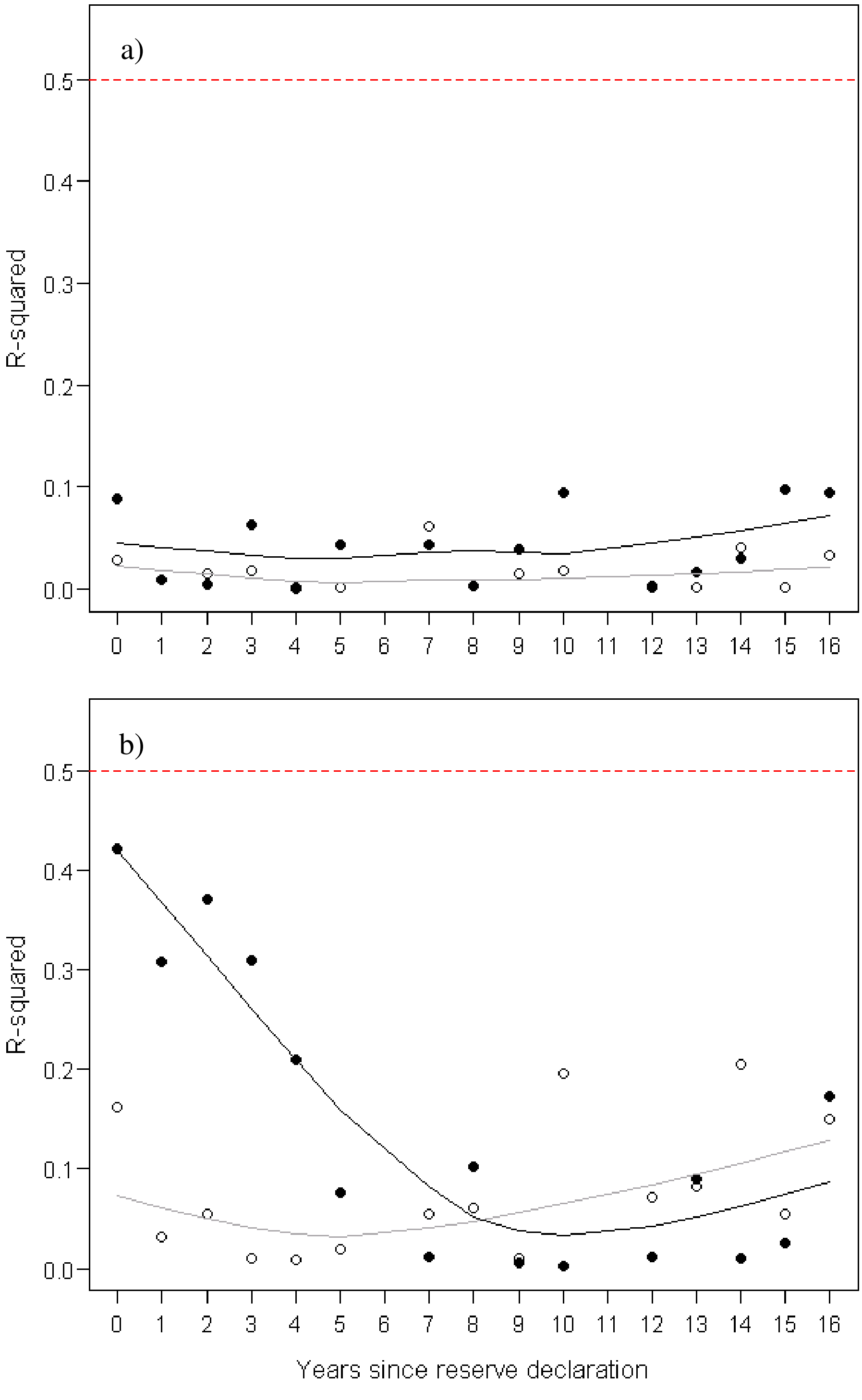

Fig. 5.6: r^2 values for linear regression models through time that describe the relationship between the abundance of *Heliocidaris erythrogramma* and a) reef profile variability and b) the density of small refuges at protected (●) and fished (○) sites. The dashed red line shows the $p = 0.05$ significance level. Solid lines are LOWESS trend lines.

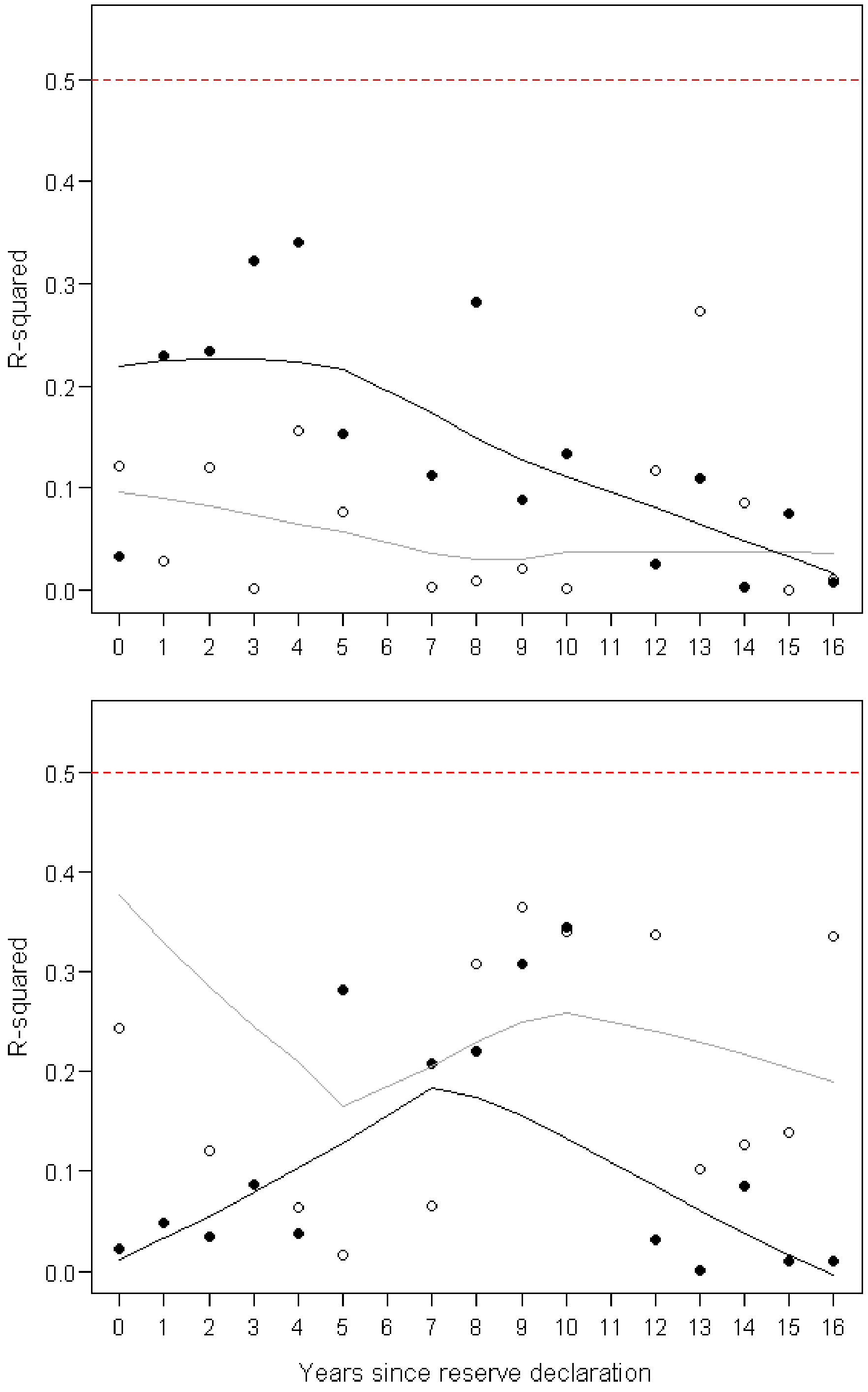

Fig. 5.7: r^2 values for linear regression models through time that describe the relationship between the abundance of *Haliotis rubra* and a) reef profile variability and b) the density of small refuges at protected (●) and fished (○) sites. Plot b) is truncated to improve data visualisation and exclude points for fished sites at 2, 0.634 and 4, 0.779. The dashed red line shows the p = 0.05 significance level. Solid lines represent the LOWESS trend lines.

Cenolia spp. exhibited markedly different temporal patterns to the other focal species with an increase in the strength of the association between this species and reef habitat structure at protected sites through time. The strength of the model relating abundance of *Cenolia* spp. to reef profile variability linearly increased at protected sites over the first six years of protection from $r^2 = 0.148$ ($F = 1.04$, $p = 0.346$) in 1992, to $r^2 = 0.509$ in 1997 ($F = 6.22$, $p < 0.05$) before reaching a plateau around $r^2 = 0.400$ for the remainder of the time series (with the exception of 2002 where $r^2 = 0.605$, $F = 9.19$, $p < 0.05$; Fig. 5.8). This pattern corresponded with a stable but weak relationship through time at fished sites ($r^2 < 0.1$ for all temporal surveys). Despite this great disparity in the relationships through time at sites inside and outside the marine reserve, the F-statistic for this test was not significantly different from a distribution of F-statistics where the values of profile variability were repeatedly randomly re-assigned for each site. A near significant interaction ($p < 0.1$) between time and marine reserve for the relationship of this species to small refuges reflects a faster rate of increase in the strength of the relationship at fished sites; however, even in the final few years of the time series when the relationship was at its strongest, the regression was still non-significant ($r^2 = 0.381$, $F = 3.69$, $p = 0.102$).

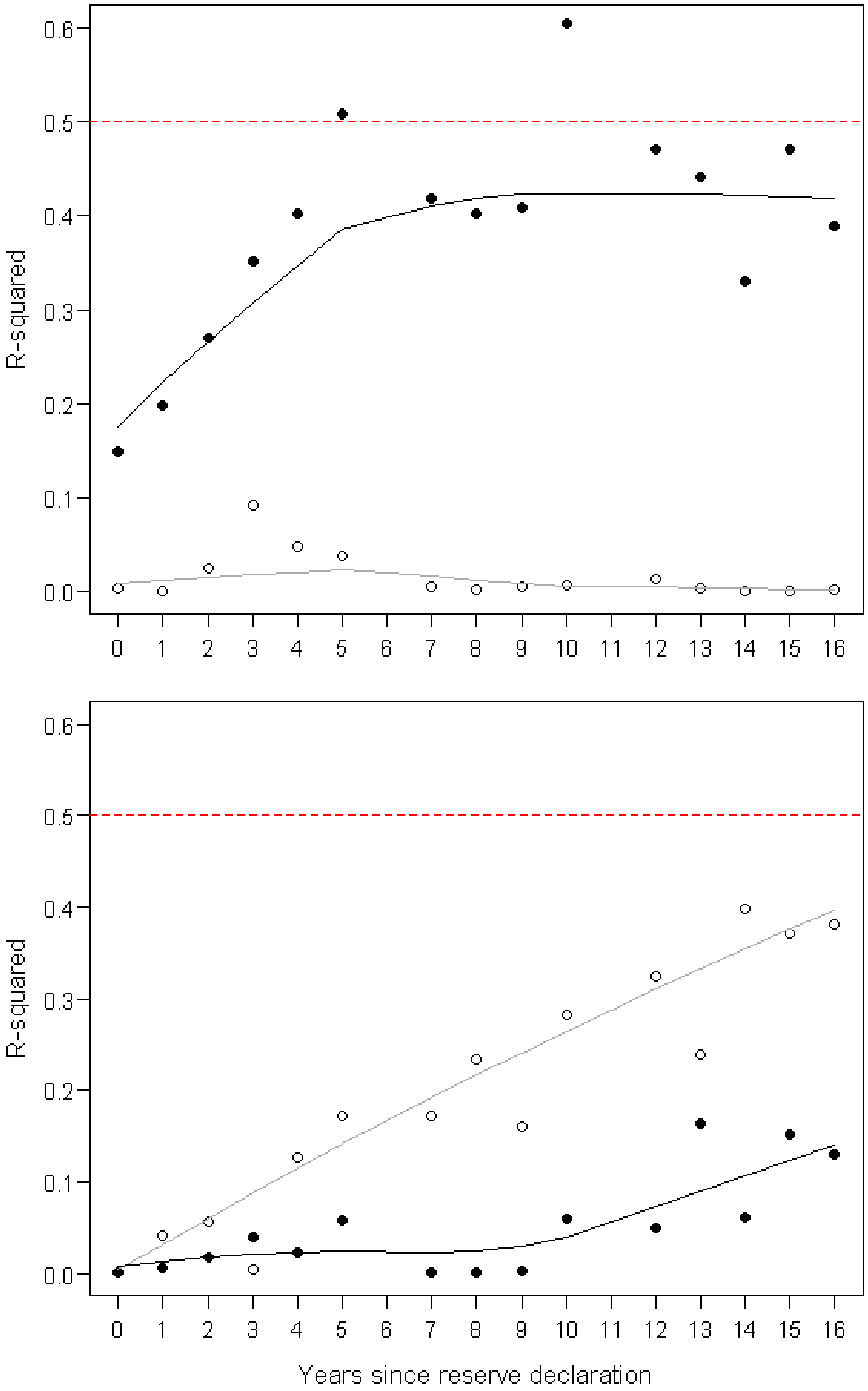

Fig. 5.8: r^2 values for linear regression models through time that describe the relationship between the abundance of *Cenolia* spp. and a) reef profile variability and b) the density of small refuges at protected (●) and fished (○) sites. The dashed red line shows the p = 0.05 significance level. Solid lines represent the LOWESS trend lines.

DISCUSSION

Marked temporal variability in relationships between mobile macroinvertebrates and their habitat were found. The dynamic state of these relationships suggests that models describing habitat associations of marine species should not be assumed to persist through time without validation. This is particularly applicable for communities subject to a disturbance such as the declaration of a marine reserve where species, and most likely their relationship to the environment, can continue to change after more than a decade of protection (Edgar et al., 2009; Russ and Alcala, 2004; Shears and Babcock, 2003). Several studies of relationships between reef habitat structure and fishes and invertebrates have been undertaken in marine reserves (chapter 3; Friedlander et al., 2003; Garcia-Charton et al., 2004; Hereu et al., 2005; La Mesa et al., 2004; Lecchini et al., 2002; Willis and Anderson, 2003). The temporal stability of the relationships reported in these studies depends on whether the community has reached equilibrium after the return of fished species. Results presented here also suggest that future studies of relationships between species and their habitat should consider predation pressure, especially by humans on exploited species, as a co-variate.

The strong relationship evident between the southern rock lobster *Jasus edwardsii* and reef profile variability at marine reserve sites prior to effective protection perhaps reflects a strong interaction between the efficiency of human predatory ability and reef structure. Scuba divers are responsible for approximately one third of the recreational catch of rock lobster from shallow inshore reefs in southeastern Tasmania (Lyle and Tracey, 2010) and high variability in the reef profile can inhibit the hunting efficiency of divers. A lobster occupying a particularly deep refuge or one with close match between refuge size and body size has a high probability of avoiding a capture attempt by a diver (pers. obs.). This can contribute to the observed spatial relationship where lobster densities are low on reefs with low reef structure while greater numbers of animals elude capture and persist on reefs with high reef profile variability.

Increasing abundance and size of rock lobster populations at Maria Island and Tinderbox marine reserves corresponded with a marked decrease in the association of this species with reef profile variability. Studies have shown that juvenile *J. edwardsii* prefer horizontally oriented, hard-walled reef features with two entrances (Booth, 2001; Booth and Ayers, 2005), and that the specificity of these preferences reduces with increasing carapace length (Edmunds, 1995). The physical size of larger animals may prevent successful attacks from many predators (Guidetti and Mori, 2005), relaxing the dependency of *Jasus edwardsii* on reef features. Many species of marine invertebrates also exhibit an ontogenetic shift in their relationship to habitat structure, increasing the scale of their preferred refuge to match their body size (eg. Beck, 1995) or the type of structure (Childress and Herrnkind, 2001; Jernakoff, 1990). Other species that exhibit a strong association with reef holes and crevices as juveniles move onto exposed surfaces as adults, presumably relying on body-size and / or alternative defenses such as spines or hard shells to provide security against predatory attack (Andrew and Macdiarmid, 1991; Pederson et al., 2008; Wahle and Steneck, 1991).

The changing association with habitat observed here may also have resulted from reduced intraspecific cohabitation with increasing body size (Macdiarmid, 1994). Larger juvenile *J. edwardsii* are highly gregarious, with less than 16% of animals surveyed in north-east New Zealand displaying solitary behaviour for size classes smaller than the legal size of 110 mm carapace length (Macdiarmid, 1994). This figure increased to 36% in lobsters 175 mm CL. Thus, increasing lobster size in Tasmanian marine reserves may have contributed to a decreased tendency to share shelter, causing some lobsters to seek sub-optimal refuges.

For full confidence that the diminishing relationships between reef structure and invertebrates can be attributed to protection from fishing, invertebrate-habitat relationships at continuously fished sites should be of a similar strength as marine reserve sites before protection and should remain at this level throughout the duration of the time series. The strength of the relationship between reef profile variability and the abundance of *J. edwardsii* at fished sites was highly variable between consecutive years and was only significant in 2007 after a trend of vaguely strengthening relationships since 2000. A potential explanation for this is that the minimum profile variability for protected sites was lower than that of any fished sites (3.39 - 6.60 and 2.84 – 5.62 for protected and fished sites respectively). Experimental studies have shown that the relationship between habitat structure and invertebrate prey survivorship is asymptotic, where adding structure to a habitat with no cover will increase prey survivorship rapidly but only up to a certain point, above which it makes little difference (Bartholomew, 2002). Hixon and Beets (1993) also identified that the number of holes in an artificial reef limited prey populations between 0 and 12 holes per reef; but between 12 and 24 holes per reef, the number of holes was not limiting. The greater minimum topographic variability for sites external to the marine reserve suggests that these sites may be above the threshold where increasing habitat structure no longer benefits prey survivorship.

The decreasing association between rock lobster abundance and reef profile variability suggests that vertical reef profile variability is not a critical consideration for lobsters when selecting reefs as insurance or fishery enhancement populations. In fact, the magnitude of the response to protection from fishing was greater at locations with lowest reef profile variability because, at the time of protection, these sites had initially very low numbers of lobsters. On the other end of the spectrum, high profile variability reefs appear to allow the persistence of lobsters under fishing pressure and although populations show some increases with protection, the largest relative increases occur on low profile sites. This does not imply that reef structure is unimportant for rock lobsters and it is unlikely that protecting featureless bedrock reefs will result in the same biomass of lobsters as more complex reefs. Small crevices are critically important as refuges from predation for juvenile lobsters (Booth, 2001) and sites without reef structure are likely to experience a population bottleneck (Casariego et al., 2004). Protection from fishing allows the lobsters to grow to a larger size however where their vulnerability to predation decreases, and they become less dependent on reef refuges.

In this study, the herbivorous species *Heliocidaris erythrogramma* and *Haliotis rubra* were associated with elements of reef structure before the marine reserves came into effect, and these associations decreased with time following protection from fishing. Initial relationships with reef structure suggest that under low levels of predation, reef structure provided some benefit for grazing species. This benefit may be in the form of higher food availability (Shepherd, 1973), higher settlement rates with topographic variability restricting hydrodynamic flows causing greater retention of larvae (McShane et al., 1988), or the structural characteristics of the reef provided protection against predation (Eggleston et al., 1997; Grabowski, 2004; Weiss et al., 2008). The relationship of sea urchins to reef architecture in areas subject to fishing is supported by analyses in chapter 4 where the total echinoid abundance (of which *H. erythrogramma* constituted 90%) was significantly related to the fractal refuge index (reflecting the size distribution of reef features in a sample) around Tasmania, and the abundance of *H. erythrogramma* was strongly related to this metric off the north coast of Tasmania.

An explanation for the unexpected weakening of prey-habitat linkages through time is that the structural features of the reef were sufficient to provide a buffer against the predator guild present before the reserve came into place (ie. small lobsters, fishes), but as rock lobsters and demersal fishes increased in size and number, the predatory ability of these animals also increased until they were able to overcome the benefits offered by the refuges. For *Jasus edwardsii*, the dominant benthic predator on rocky reefs in Tasmania (Pederson and Johnson, 2006), larger individuals are able to attack and consume larger sea urchins, and become more effective at consuming juvenile urchins with increasing lobster carapace length (Andrew and Macdiarmid, 1991; Guidetti, 2004; Pederson and Johnson, 2006). It is also likely that large animals possess greater strength in the fore-legs, which allows these individuals to remove urchins or abalone from some reef structural features that provide refuge against smaller lobsters.

Andrew and Macdiarmid (1991) identified that the provision of shelter increased the survivorship of small sea urchins (*Evechinus chloroticus*) under predation by *Jasus edwardsii* (110-140 mm carapace length) in laboratory studies. Pederson & Johnson (2006) reported a higher mortality of adult compared to juvenile urchins using tagging studies while there was no significant relationship between urchin size and mortality for animals tethered to prevent them from seeking shelter. The experiments of Andrew & Macdiarmid (1991) could be extended to test the ability of a range of different sized lobsters to remove and consume small urchins (and abalone) from within different shapes and sizes of reef architectural features. Explicit, quantitative criteria could be derived to identify specific reef features that provide spatial refuge for these species and determine if not only the ability to handle and consume urchins and abalone increases with increasing lobster size, but also its ability to overcome the protection offered by different reef features. This information would be useful in selecting areas of reef for protection in Tasmania that offer reef refuges that could potentially allow the persistence of healthy abalone populations in the presence of elevated rock lobster predation.

Decreasing numbers of *Haliotis rubra* at protected sites with low and medium reef profile variability has contributed to a reduction in the strength of the invertebrate-habitat association through time. Large abalone rely on their hard shell and strong muscular attachment to the reef surface as a mechanism against predation. Mature individuals are often observed on exposed sections of reef while juvenile abalone display cryptic behaviour, sheltering in crevices and under boulders (chapter 6). The density of small to medium abalone (30-130 mm) has decreased at the Maria Island marine reserve (Barrett et al., 2009), hence increasing lobster predation at sites with low profile variability may have contributed to more abalone being lost from smaller size classes at these sites. An alternative explanation is that abalone remain within cryptic habitat until they reach a larger size in the presence of elevated predation risk (Pederson et al., 2008), and are thus overlooked by non-destructive visual census techniques. However, the number of juvenile abalone recruiting to microhabitats created by experimentally placed garden pavers was significantly lower inside the

Maria Island marine reserve (chapter 6), suggesting that the pattern observed by Barrett et al. (2009) is at least partly the result of increased adult or post-settlement mortality at these sites.

The invertebrate assemblage, and abundances of both rock lobster and abalone, exhibited altered associations with reef profile variability during the course of long-term monitoring. This reef structure metric was calculated as the sum of the squared difference in height between consecutive regularly spaced measurements. It was introduced by McCormick (1994) in a study where it differentiated between schematic profiles and displayed the highest number of significant correlations with fish species amongst nine metrics tested. The advantage of this metric over the conceptually similar and more commonly used chain-and-tape rugosity measure is that it incorporates information on the spatial arrangement of substratum heights (McCormick, 1994), with the squared operator particularly giving emphasis to large height changes over a short horizontal distance. This has ecological relevance as many reef species tend to aggregate around large ledges and drop-offs (Leum and Choat, 1980), features that are also often associated with deeply undercut horizontal crevices on granite and sandstone reefs around Tasmania (pers. obs.). This is confirmed by the strong positive correlation relating profile variability to the density of large refuges in the data collected here (see Fig. 5.2).

Reef profile variability characterizes topographic changes along the reef surface but provides no direct information on the availability of specific reef features for use as refuges from predators. This metric can be more relevant for community level studies, however, where each component species can exhibit an association with different reef features, the frequency of which are all usually positively related to vertical changes in the reef profile. Indeed, the invertebrate assemblage showed a stronger relationship to this profile variability than the number of specific reef features.

Small reef features, such as holes and crevices, exhibited linkages to the abundance of sea urchins in this study, and have also been identified as associated with spatial variability in fish abundance (Roberts and Ormond, 1987) and fish community metrics (Friedlander and Parrish, 1998). Holes in artificial reefs matching the body size of prey fish species can maintain abundance in the face of increased numbers of predators (Hixon and Beets, 1993). Reef architecture, particularly smaller features, explains a significant portion of variability in the abundance of echinoids and all invertebrates in the region of this study (chapter 3) and across southern Australia (chapter 4). However, in one of the few other assemblage level studies of invertebrates on temperate reefs, Ruitton et al. (2000) found that reef shelter had little effect on invertebrate populations, although they suggested that the scale of reef shelter in their Mediterranean study area (mean size of cavity aperture = 63 cm) may have been too large to provide any benefit to invertebrates such as sea urchins.

The results presented in this study suggest that size selective extraction of rock lobsters by humans can increase their association with reef habitat structure. An increase in predation pressure also appears to have cascading effects on the links to habitat for prey species, sea urchin (*Heliocidaris erythrogramma*) and abalone (*Haliotis rubra*), potentially through the diminished benefit of reef shelters with increasing predator size and foraging ability. The changing nature of these relationships through time suggests that caution is required when generalizing from results of studies of habitat association undertaken in a single period. Further manipulative studies are required to confirm the causative mechanisms behind the patterns presented here, however this will be difficult given that reserve effects have increasingly manifest over many years. Experimental closure to fishing for rock lobster and abalone individually, and both species together, of areas selected for high and low reef profile variability after background monitoring for several years should shed further light on the dynamics of the relationship between these species and their habitat.

Plate 5: *Haliotis rubra*, Maria Island, Tasmania

Chapter 6:

Variation in subtidal rocky reef assemblages of cryptic invertebrates with location, microhabitat structure and protection from fishing

ABSTRACT

The deployment of sandstone blocks on subtidal reefs can replicate the microhabitats associated with natural boulders and thus allows standardized sampling of benthic cryptofauna without permanent disturbance to the substratum. The shape of the space beneath the block is related to reef topography and has the potential to bias sampling through its influence on the physical availability of space for animals to colonise or its contribution to predator defence strategies. Temporal and spatial variation in the influence of sub-block reef structure, and protection from fishing, on benthic cryptofauna were explored by deploying blocks at locations inside and external to the Maria Island marine reserve in eastern Tasmania. Unconstrained ordination techniques indicated that cryptofaunal assemblages exhibited little change between seasons relative to variation between locations. Invertebrate assemblages exhibited no apparent association with protection from fishing. Greatest variation was evident at the scale of metres, with only a small but significant proportion of this variation explained by the surface area of the reef surface beneath the block. Total abundance of cryptic invertebrates and presence of feather stars (*Cenolia* spp.) were positively associated with reef surface area, while the presence of the sea urchin *Heliocidaris erythrogramma* was linked to sub-block volume. Juvenile abalone *Haliotis rubra* were not linked to any reef structure metrics but were significantly lower in

abundance at fished locations, the only species to exhibit such a response. Elevated predation associated with the marine reserve possibly contributed to these patterns and could lead to recruitment failure of abalone at some fully protected locations in Tasmania.

INTRODUCTION

Benthic cryptofauna represent a poorly-sampled but trophically important functional group of animals that live on subtidal rocky reefs in microhabitats difficult for both predators and researchers to access. These small (< 100 mm) animals live amongst the cracks, crevices and ledges of bedrock as well as between and beneath loose reef objects such as boulders, cobbles, and fractured bedrock sections. Benthic cryptofauna are rarely considered in biodiversity surveys, presumably because they are, by definition, hidden from view and difficult to locate without damaging the substratum. Regardless, this component of the benthic invertebrate assemblage contains both ecologically and commercially valuable species. Important elements of the cryptic benthic fauna include juvenile sea urchins (Hereu et al., 2005), abalone (Shepherd, 1986), brittle stars (Drolet et al., 2004a) and shrimp (Caillaux and Stotz, 2003). The juveniles of some species of lobster also frequent holes or shelters that closely match their body size (Edmunds, 1995). A prevailing paradigm suggests that animals are offered a degree of protection from predation and adverse environmental conditions by associating with cryptic reef features (eg. Drolet et al., 2004a).

Boulder fields, through their fragmented nature, contain more space for cryptic fauna to colonize than consolidated bedrock, both on the exposed surface layer of boulders (Barry and Wickins, 1992) and in the layers beneath (Le Hir and Hily, 2005). Boulders in the subtidal environment can be resting on sediment, bedrock or on other boulders, and the juxtaposition between these different reef elements affects the number and type of microhabitats (Le Hir and Hily, 2005), which in turn influences faunal assemblages that colonise and persist on the reef (Chapman, 2002a; Le Hir and Hily, 2005). Intertidal boulder shores have received considerable research attention through the exploration of hypotheses relating to disturbance regimes (McGuinness, 1987a; b; Smith and Otway, 1997; Sousa, 1979), species-area relationships (Londoño-Cruz and Tokeshi, 2007; McGuinness, 1984; Smith and Otway, 1997), and factors affecting temporal and spatial variability in invertebrate taxa (Chapman, 2002a; b; 2005; Grayson and Chapman, 2004; Smoothey and Chapman, 2007). This research has identified intermediate-sized boulders as harbouring the highest levels of biodiversity because this size-class of boulder is disturbed by waves at a frequency appropriate for overcoming the space-covering dominance of opportunistic species while disrupting the competitive dominance of late successional-stage species (Sousa, 1979).

The total number of invertebrate species present in samples has also been found to increase with the planar area of boulder surface surveyed (McGuinness, 1984). By contrast, abundances of individual species exhibit little or mixed species-specific relationships with the under-boulder surface area (Grayson and Chapman, 2004; Smith and Otway, 1997). Species abundance and invertebrate assemblages generally tend to exhibit greatest variability at the scale of metres (Chapman, 2002a), with the magnitude of this variability influenced by the type of substratum beneath the boulders (Chapman, 2002b).

The benthic cryptofauna of subtidal reefs has received much less attention than the cryptic fauna of the intertidal environment. While destructive sampling appears to be the best option for studying benthic cryptofauna in deeper waters (Barnes, 2008; Griffiths et al., 2008), the flexibility of SCUBA allows more creative approaches, such the use of mesh trays of coral rubble to create a standardized habitat area (Takada et al., 2007). Baronio and Bucher (2008) applied a multi-plate sampler, previously used in freshwater (Hester and Dendy, 1962), for the first time in the marine environment when studying spatial patterns in cryptic crevice-dwelling fauna. This study identified substantial differences in the faunal assemblages between three reefs studied, between seasons, and between three crevice sizes sampled. The size of the experimental crevices used in this study (0.5 - 2 cm), and elevation of sampling units above the seabed, likely restricted entrance by many of the larger and more strongly benthic-associated species, including echinoderms and larger fleshy-footed molluscs. Assemblages that colonised the multi-plate sampler were dominated by crustaceans, bivalves, polychaetes, and to a lesser extent, small gastropods (Baronio and Bucher, 2008), making it similar to the assemblages sampled by artificial kelp holdfasts (eg. Smith et al., 2006), rope fibre sampling units (eg. Edgar, 1991) and nylon pan scourers (eg. Rule and Smith, 2005).

Chapman (2003) found invertebrate assemblages that developed under artificially-placed, uniformly-sized sandstone blocks were similar to those under naturally occurring boulders on the same shore. This finding suggests that experimentally-placed blocks with standardized area can provide a useful tool when sampling cryptic invertebrates, including in studies that test hypotheses relating to causative mechanisms behind spatial patterns. Confounding effects are not, however, completely eliminated when sampling blocks are used on topographically-complex substrata. In these environments, the space available for animals to colonize under the block will vary with the rugosity of the reef surface, a potential source of error that may contribute to faunal patterns more than variation associated with the hypothesis under test.

The aim of this study is to use artificial boulders in the form of sandstone blocks to investigate the benthic cryptofaunal communities of subtidal rocky reefs; specifically to quantify temporal and spatial patterns, the influence of the sub-block reef profile, and protection from fishing on these animals. My study was conducted off eastern Tasmania, Australia, where benthic habitats support a diverse macroinvertebrate assemblage, including the state's most valuable fishery species, the blacklip abalone (*Haliotis rubra*). Research was undertaken in and around the long-standing 'no-take' Maria Island marine reserve, where the numbers of carnivorous fish species bastard trumpeter *Latridopsis forsteri*, blue throat wrasse *Notolabrus tetricus*, and the biomass of the dominant benthic predator, the southern rock lobster *Jasus edwardsii*, have greatly increased in response to protection from fishing (Barrett et al., 2009; Edgar and Barrett, 1999). Barrett et al. (2009) documented a decline in the numbers of mid-sized abalone (30-130 mm) at locations inside the marine reserve between 1992 and 2002. Babcock et al. (2010) reported that abalone numbers in the reserve have decreased further between 2002 and the most recently published survey data in 2008. Increased predation by rock lobsters is generally cited as the reason for this decline. The work of Pederson et al (2008) offers an alternative hypothesis: that abalone emerge from cryptic habitats for their adult existence at a larger body size at locations with high abundance and mean size of rock lobsters, and hence have been overlooked by standard underwater visual census techniques. The free-spawning strategy of *Haliotis rubra* (release of sperm and eggs into the water) means that the probability of successful fertilisation depends on the local density of mature adults (Babcock and Keesing, 2000). When this is combined with localised dispersal of larvae (McShane et al., 1988), it creates the potential for recruitment failure in the marine reserve should adult densities continue to decline. By undertaking this study at locations evenly distributed inside and outside the Maria Island marine reserve, I test the effects of increased predation on common cryptofaunal species, establish the occurrence of recently recruited abalone in the reserve and determine whether the density of cryptic abalone are lower at protected locations in correspondence with adult populations.

METHODS

Survey methods

Five large sandstone garden pavers (300 x 300 x 50 mm – hereafter referred to as blocks) were haphazardly deployed with 1-3 m separation at two sites separated by 50 m, at each of twelve locations distributed throughout Mercury Passage inside Maria Island on the east coast of Tasmania (Fig. 6.1). Six of the surveyed locations were within the Maria Island Marine Reserve while the remaining six locations were distributed adjacent to the marine reserve and on the Tasmanian coast. Blocks were deployed for three intervals of three months and retrieved in January, April and July 2007 (Fig. 6.2a,b). The abundances of mollusc and echinoderm species were surveyed on the undersurface of the block (Fig. 6.2c) and on the reef in the footprint of the block. The length of any abalone (*Haliotis rubra*) was measured to the nearest millimetre using veinier calipers. Fishes (mainly Scorpaenidae, Clinidae) and crustaceans (primarily Paguridae, Alphaeidae, Rynchocinetidae) were excluded from the study because they are fast-moving and difficult to observe long enough to identify and enumerate. After numbers had been counted, the upper surface of the block was scraped free of foliose algae and the block replaced in a new position on the reef to provide habitat for the subsequent survey period.

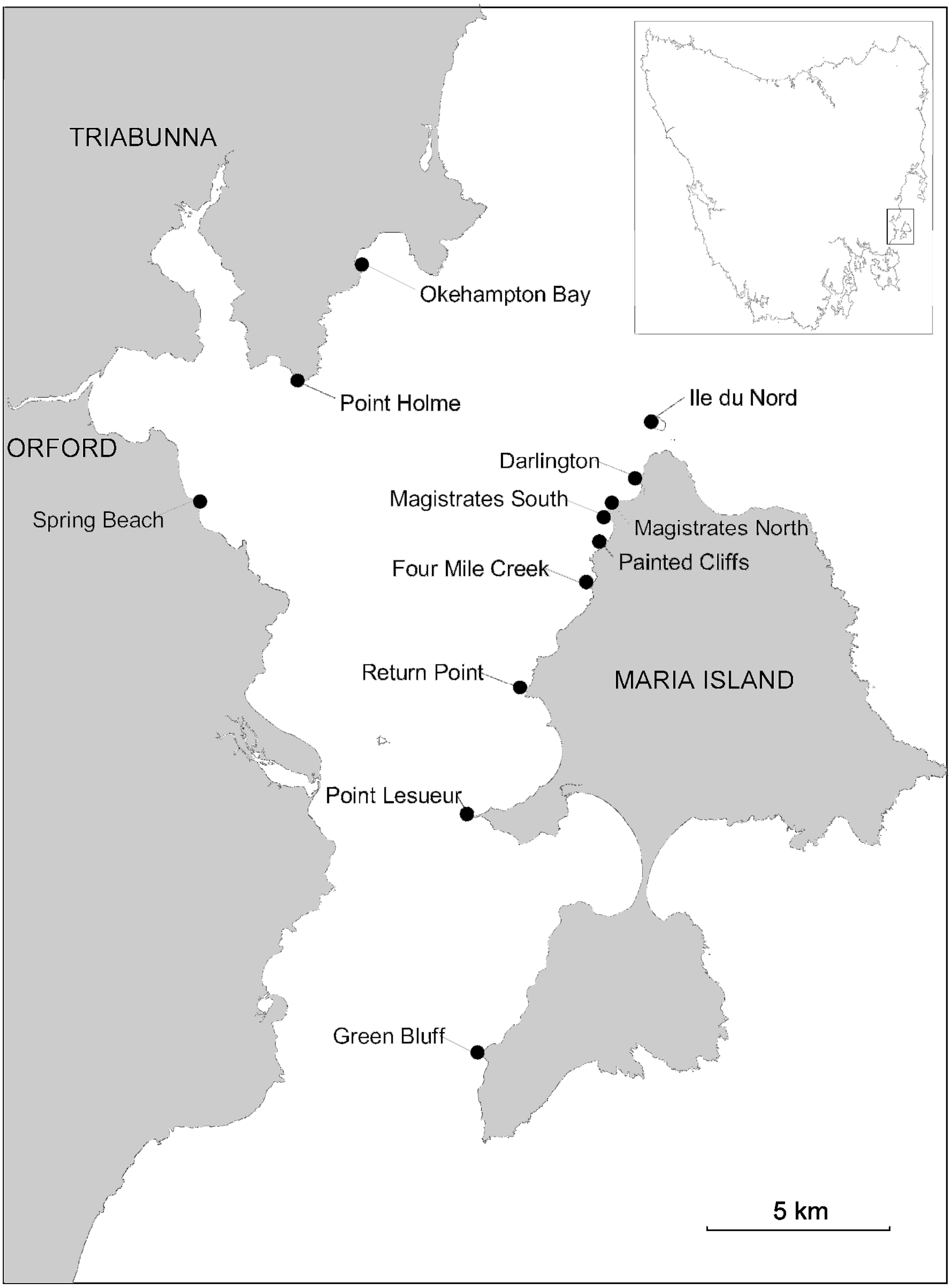

Fig. 6.1: Map of locations where blocks were deployed. Darlington, Magistrates North, Magistrates South, Painted Cliffs, Four Mile Creek and Return Point were located inside the Maria Island Marine Reserve. Inset shows the island state of Tasmania.

The shape and volume of the sub-block refuge was quantified for all blocks in the July survey using a profile gauge consisting of a clear 12 x 300 x 300 mm acrylic plate with 49 sliding stainless steel pins, each 20 cm length, arranged in a 7 x 7 grid (50 mm between adjacent pins). This gauge is a two-dimensional extension of the linear profiling gauge introduced by McCormick (1994). The gauge was deployed in the removed block's position on the reef after animals had been identified and counted (Fig. 6.2d). The profile gauge was photographed using a housed Olympus 3.2 megapixel compact camera at approximately 12 positions around the gauge at an angle of elevation of approximately 45° from horizontal. Photogrammetry was used to identify the position of each pin-head on the Z axis where X and Y are horizontal axes aligned with two sides of the profile gauge plate (Photomodeler Pro 4.0). The X, Y and Z positions of each of the pin-heads (hereafter points) were exported from the software along with precision, tightness and residual diagnostics. Positional accuracy on the Z axis was calculated as <0.5 cm.

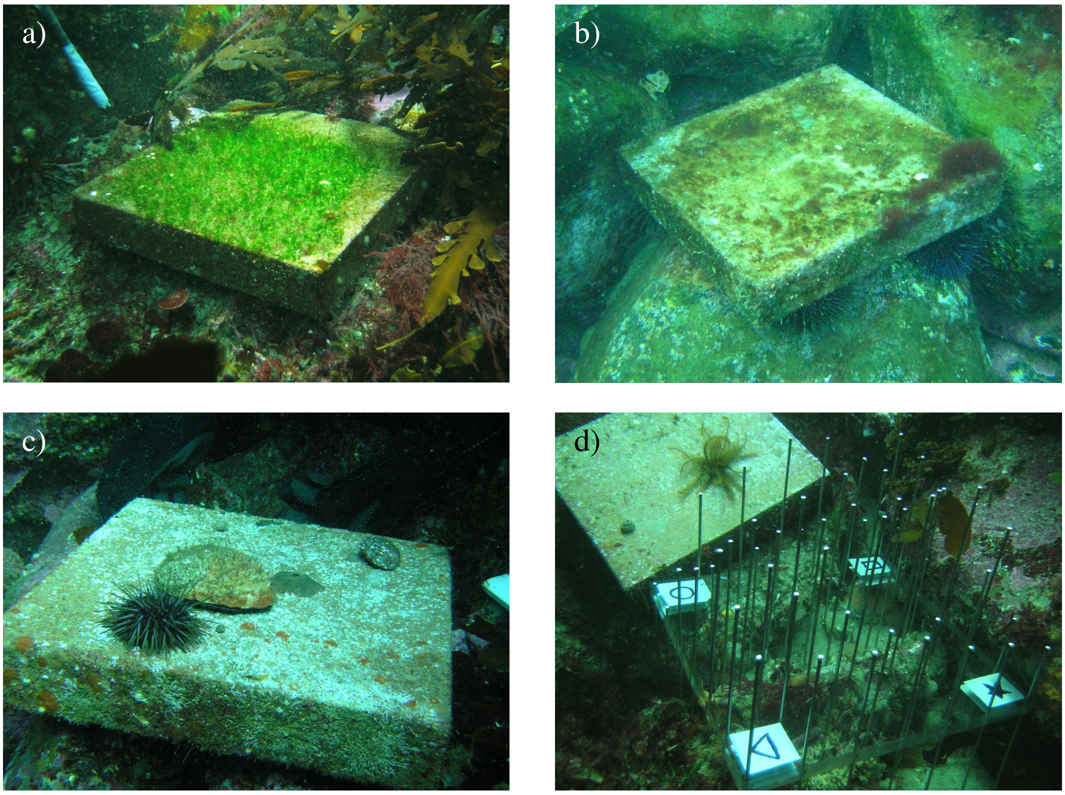

Fig. 6.2: Photographs of blocks in situ on the reef surface at a) Darlington and b) Pt Holme; c) molluscs and echinoderms attached to the undersurface of a block; d) profile gauge deployed at Darlington (north, block 2)

Reef profile calculations

The exported points were used to calculate the surface area of the sub-block profile, the volume of the refuge space beneath the block and the perimeter cross-sectional access area. The surface area of the profile represents the topographic complexity or the level of "folding" or convolutions of the reef surface beneath the block (which influences both the volume and the perimeter access area). This metric was calculated using a regular triangular network (Li et al., 2005) by dividing the profile into thirty-six cells, each delineated by four corner points (each cell is 5 cm x 5 cm on the horizontal plane; Fig. 6.3). A fifth pseudo-point was created in the horizontal centre of the cell with a Z value (height) of the average of the four corner points. The surface within each cell was then calculated as the area of four triangles with each triangle formed by lines joining two adjacent corner points and the fifth pseudo point. The 36 cell surface areas were summed to give the surface area of the sub-block profile. The surface area of a perfectly flat profile (900 cm2) was subtracted from the surface area value for each profile to allow meaningful interpretation of intercept in regression analyses. The surface area was also calculated using two triangles within each cell formed by the maximum or minimum length diagonal. The surface area resulting from these different profile calculations were very highly correlated with each other (Pearson's correlation coefficient, r = 0.999) and the four triangle technique described above (r = 0.998), hence were not considered further. The four triangle surface was selected over the other two as it created a more smooth representation of the surface.

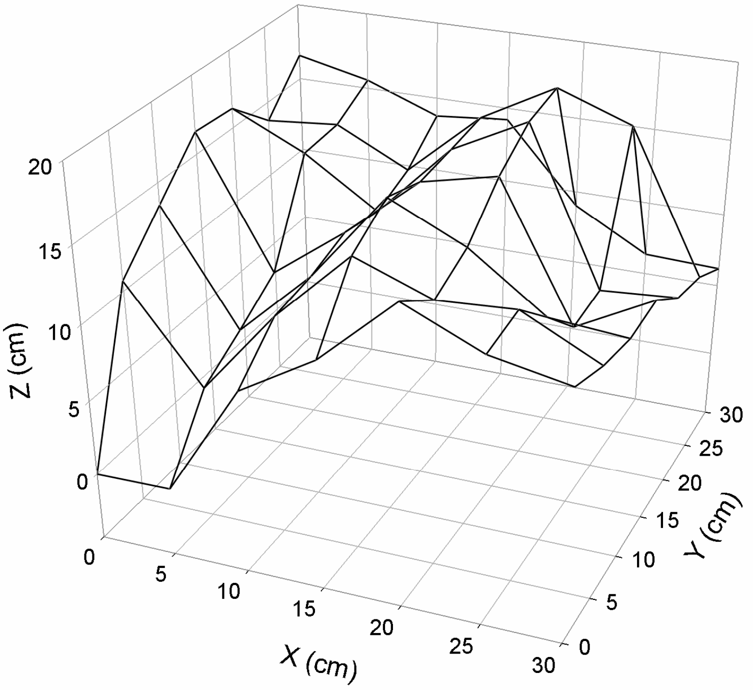

Fig. 6.3: Wireframe representation of profile data for block 2 at Darlington north.

The volume of space between the block and the reef reflects the potential refuge space available for animals to colonize. In raw form, the X, Y, Z positions of the points recreate the shape of the reef surface at a distance above the actual reef surface corresponding to the length of the pins. The Z height of each pin was subtracted from the Z height of the longest pin in the profile (which should be very close to 18.5 cm - the actual length of the pins above the Perspex plate) to give a positive inverse of the surface profile for the calculation of sub-block volume and perimeter access area. The refuge volume was then calculated by approximating the volume beneath each cell as an upright square prism with a width of 5 x 5 cm and height consisting of the mean of the four corner points. The volume for each cell was summed to give a total for the profile.

Perimeter access cross-sectional area was calculated by breaking the perimeter profile for each side of the plate into a series of shapes formed by two adjacent points and the base plate (X or Y axis). The area of the shape beneath the line joining two adjacent points was calculated by breaking it into a rectangle and a triangle. The area of the rectangle was calculated as based on a height of the lower of the two points and width of the horizontal distance between the two points (5 cm). The area of the triangle is calculated as half the horizontal distance between two points multiplied by the absolute value of the difference in vertical height for the two points. This is repeated for each of the six two-point spaces on each side, summed to get the perimeter access area for each perimeter side and summed again to give a total perimeter access area for the four sides of the profile.

A fourth reef profile metric was calculated as the volume of the sub-block space / the total perimeter access area to represent accessibility of the sub-block space relative to the space available.

Statistical analyses

Multivariate response data were square-root transformed and assemblages compared based on Bray-Curtis measures of similarity (Bray and Curtis, 1957). In order to reduce the influence of outlier samples with one or few species present, only species that occurred under more than 5% of all blocks were considered. Unconstrained ordinations in the form of non-metric multidimensional scaling (hereafter MDS) were used to visualize the similarity of assemblages under blocks for each sampling occasion and for location-aggregated data through time.

Differences in the cryptofaunal assemblages beneath blocks for locations inside and external to the marine reserve were tested using PERMANOVA (carried out in the PERMANOVA+ add-on to PRIMER 6; Anderson et al., 2008), an analysis analogous to multivariate analysis of variance with permutations to develop an appropriate distribution for the calculation of a pseudo-F statistic, as based on a Bray-Curtis resemblance matrix. Tests were carried out on the data for each season separately using a three factor analysis of reserve (fixed), locations and sites (both random and nested in the factor above). Estimates of the components of variation for each spatial scale of the hierarchical sampling design were also calculated for each season. The effects of the marine reserve on community summary metrics, the abundance of key species, and shell length of *Haliotis rubra*, were also tested by performing a PERMANOVA on the Euclidean distance resemblance matrix for the location averaged data, with season and reserve as two fixed factors.

Distance based linear modeling (DistLM) was carried out to assess the influence of sub-block reef profile characteristics and spatial variation on the invertebrate assemblage. Models were developed based on AICc which is a modification of 'An Information Criterion' (Akaike, 1973) for situations where the number of samples is small relative to the number of predictor variables (Anderson et al., 2008). A significance level of $p < 0.01$ (in combination with the AICc) was used to accommodate the increased probability of a significant test arising by chance alone with multiple tests. Blocks within locations were expected to be more similar to one another than those from other locations, and this spatial autocorrelation can cause inflated r^2 values if blocks were used as independent samples (Legendre, 1993). Multivariate analyses were therefore undertaken in two ways. The initial approach was to treat all replicate blocks as if they were independent while acknowledging that the reef profiles within a location are more likely to be similar to each other, while other environmental factors may also be acting to create similarity at this scale, thus contributing to the elevated r^2 values. The second approach reflects the strength of the reef profile metric for explaining variability of cryptofaunal assemblages within each location, with analyses focused on the contribution of sub-block profile metrics to explaining variance in the response data in addition to that of the prior-fitted factor of location.

Relationships between sub-block profile characteristics and (i) the spatial distribution of community summary metrics, and (ii) the abundance or presence of common and scientifically important species, were analysed using generalized linear mixed-effects models (GLMMs - Bolker et al., 2009). The GLMMs were used to analyse the contribution of fixed (reef profile metrics) and random (Location, Site) factors while acknowledging the non-normality of integer count data and spatial autocorrelation of blocks within locations. Poisson distributions were used for total invertebrate abundance and species richness and a binomial distribution for the presence-absence of single species data. This technique allows inferences to be made about the fixed effects (profile metrics) which represent the average characteristics of the population represented by these samples, and the variability of this relationship amongst locations (Pinheiro and Bates, 2000). GLMMs were fitted using an AIC to select the reef profile metric that made the greatest contribution to explaining deviance in each response variable and then testing the significance of the explanatory power of this model against the null model based on Chi-squared expectations (Buckley et al., (2003). The assumption of a common slope for each location was also tested by fitting a model with random effects for both the intercept and the slope. In this case, a Chi-squared distribution was again used to test the change in deviance to the simpler model with a common slope and random variability of the intercept among locations. The relative importance of reef structure metrics were assessed by calculating the change in the deviance explained when the reef structure metrics were added to a model containing only the random factor of location (Δ deviance).

RESULTS

Biological data

Eighty one species of benthic cryptofauna were recorded under 345 blocks sampled over the three seasonal deployments. The fauna was numerically dominated by gastropods and crinoids (Table 6.1), with the majority of individuals of each species recorded in higher numbers on the under-surface of the block compared with the reef beneath the unit (1602 and 586 animals recorded on block and reef surfaces, respectively). The sea cucumber *Australostichopus mollis* was the only species to show a strong preference for the reef underneath the block over the block base (28 individuals on the blocks and 59 on the reef; $p < 0.01$, Wilcoxon signed rank test with paired samples). No animals were recorded beneath 43 blocks (12.5%), while the mean number of species under a block was 3.28 (SE = 0.12) and the mean number of individuals was 6.32 (SE = 0.35). Over the course of the study, fifteen blocks were damaged or moved by large swell to a position on the substratum where they were unsuitable to survey as very little habitat remained for cryptic invertebrates to colonise.

Table 6.1: Total number of taxa recorded under blocks at locations around Mercury Passage for the three surveys.

Phylum		**Number of species**	**Total number of individuals**
Echinodermata	Asteroidea	8	191
	Crinoidea	2	580
	Echinoidea	2	46
	Holothouroidea	1	87
	Ophiuroidea	7	73
Mollusca	Gastropoda		
	Orthogastropoda	42	1095
	Opisthobranchia	8	12
	Pulmonata	1	1
	Bivalvia	1	4
	Polyplacophora	8	99

The commercially-important black-lip abalone (*Haliotis rubra*) was the third most commonly recorded species, occurring under 25.5% of blocks (Table 6.2). The shell lengths of abalone sampled ranged from 11 mm to 140 mm, with an overall mean length of 51.8 mm (SE = 1.9). Abalone, like most other species, preferred the underside of the block over the reef surface beneath the block; a total of 23 individual abalone were found on the reef and 145 individuals on the block surface across all surveys ($p < 0.001$, Wilcoxon signed rank test with paired samples). A slight but non-significant difference was evident in the mean length of abalone on each surface at 47.0 ± 4.6 and 53.5 ± 2.1 mm on reef and block respectively ($p = 0.073$, Welch two sample t-test).

Table 6.2: Abundance and spatial distribution of the six most abundant species across all three surveys

Species	Number of individuals	Percentage of blocks occupied by species
Cenolia trichoptera	525	65.2
Clanculus plebejus	512	33.3
Haliotis rubra	168	25.5
Clanculus limbatus	119	11.6
Allostichaster polyplax	100	19.1
Australostichopus mollis	87	9.9

Results of the variance components analysis were consistent between seasons. The greatest variation in the cryptofaunal assemblage composition occurred at the level of block (Table 6.3). Assemblages among various locations differed significantly from each other in all seasons ($p < 0.01$), while sites within each location were not significantly different ($p = 0.251, 0.051, 0.143$ for summer, autumn and winter surveys respectively). Although there was considerable variation of benthic cryptofaunal assemblages under blocks within a location (Fig. 6.4 a-c), assemblages at locations were generally more similar to assemblages at the same location for other seasons than other locations (for the same or other seasons; Fig. 6.5).

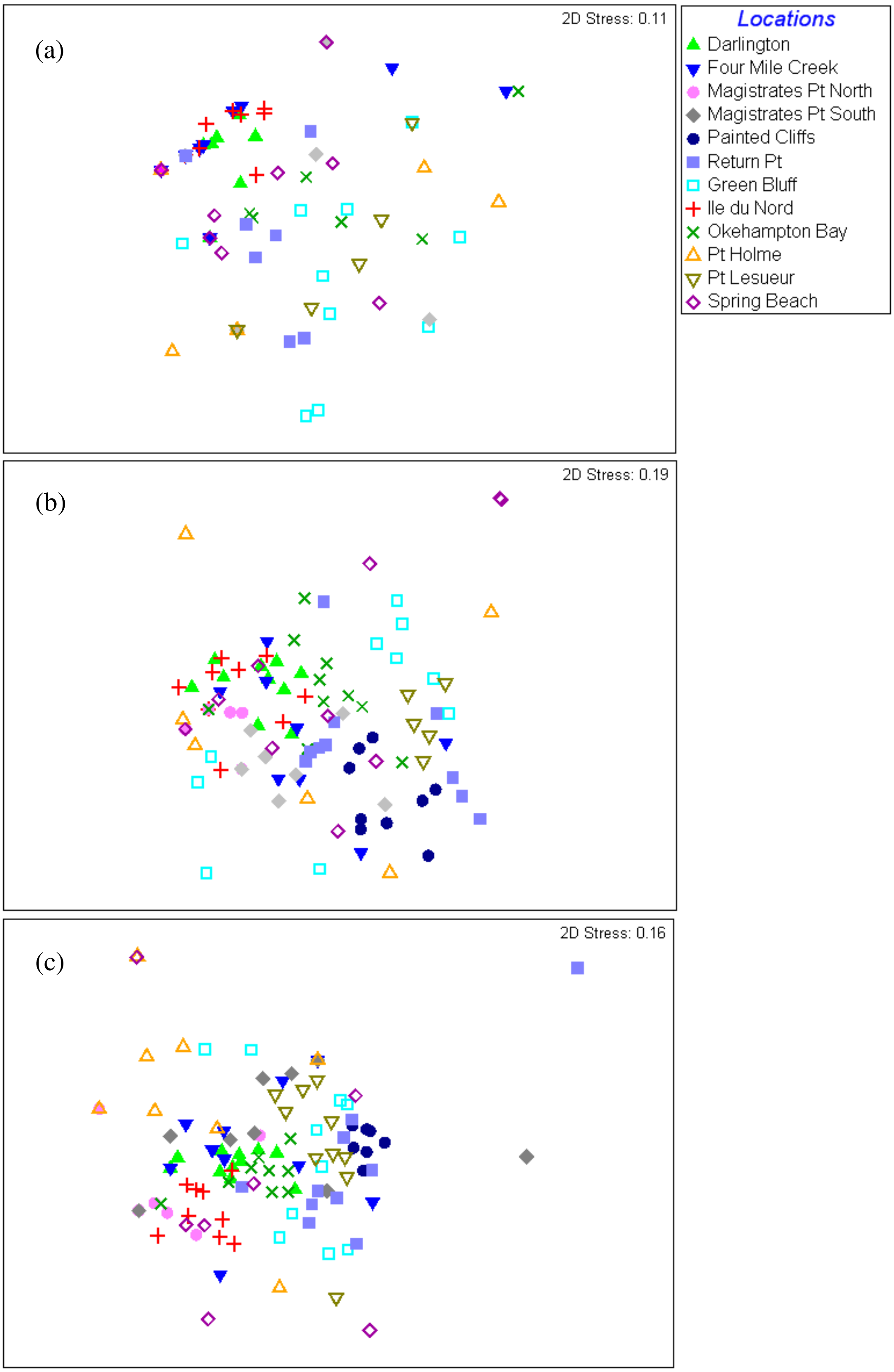

Fig. 6.4: MDS plots for similarity of cryptofaunal assemblages beneath blocks among locations for a) summer (no data for Painted Cliffs), b) autumn and c) winter. Data were square root transformed and calculated using a Bray-Curtis similarity matrix for species occurring in more than 5% of all samples. Filled symbols indicate locations inside the marine reserve.

Table 6.3: PERMANOVA summary table for analysis of the spatial variance in cryptofaunal assemblages between locations, sites and blocks. Summer data comprises 11 locations and 22 sites; autumn and winter data comprises 12 locations and 24 sites.

Season	Source	Variance	Proportion
Summer	Locations	666.11	21.18
	Site	96.30	3.06
	Block	2382.10	75.75
Autumn	Location	796.55	27.82
	Site	156.11	5.45
	Block	1910.40	66.73
Winter	Location	915.13	29.65
	Site	93.95	3.04
	Block	2077.60	67.31

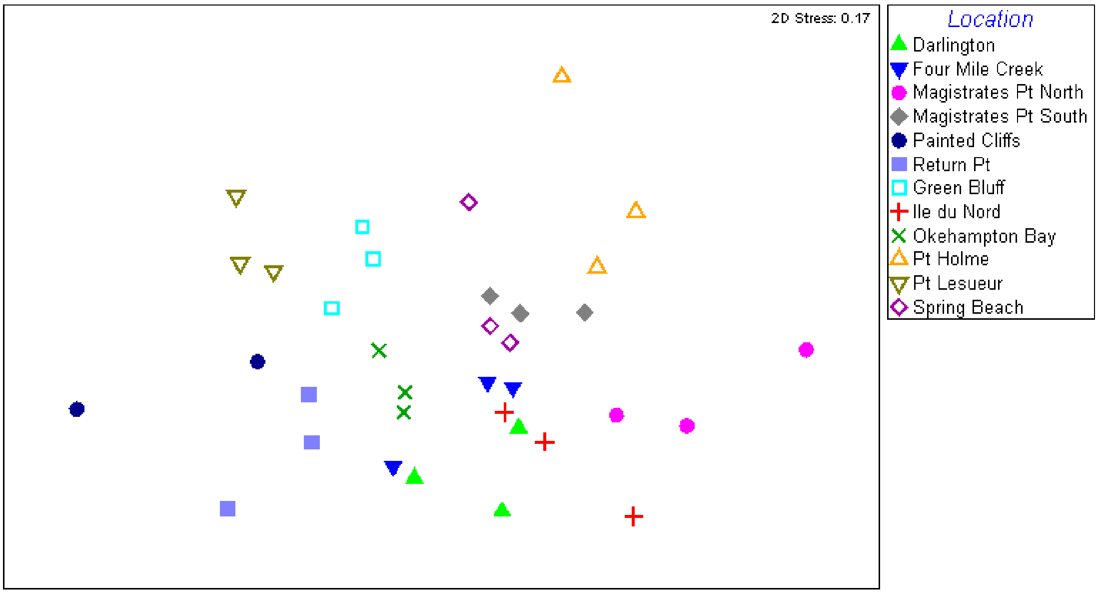

Fig. 6.5: Results of MDS for six locations in marine reserve (filled symbols) and six adjacent fished locations, each surveyed on three seasonal occasions.

Effect of the marine reserve

Cryptofaunal assemblages were not significantly different between locations inside and external to the marine reserve at any time (Table 6.4). Species richness, the combined abundance of all invertebrates, and the location-averaged abundance of most common species, were also not significantly affected by the marine reserve (Table 6.5). The only response that exhibited a significant relationship with the reserve was the abundance of *Haliotis rubra*, which was higher at locations external to the reserve ($p < 0.05$; Table 6.5). The mean abundance of this species at protected locations was 50%, 29% and 41% that of fished locations in summer, autumn and winter surveys (Fig. 6.6). The mean length of abalone was slightly higher at locations surveyed within the marine reserve relative to external locations (57.1 mm and 52.3 mm respectively; Pseudo-F = 4.46, $p = 0.053$). Additionally, abalone larger than 100 mm constituted 1.6% of individuals for locations external to the marine reserve (one individual of 103 mm) while this size class contributed 12.2% of individuals for locations within the reserve.

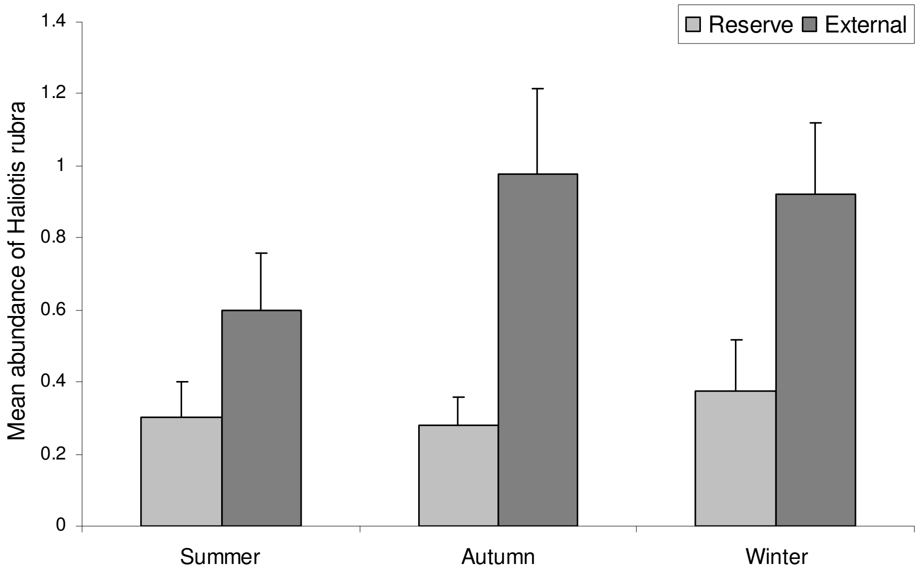

Fig. 6.6: The mean abundance (+SE) of *Haliotis rubra* under blocks inside and outside the Maria Island marine reserve in three seasons.

Table 6.4: PERMANOVA output tables testing the effect of the marine reserve on benthic cryptofauna for each survey. Type III (partial) sums of squares were used with permutation of the residuals carried out under a reduced model. Species occurring in less than 5% of samples were removed from the analyses.

Summer

Source	***df***	**SS**	**MS**	**Pseudo-*F***	**p**
Reserve	1	11904	11904	1.9481	0.1289
Location(Reserve)	9	62686	6965.1	2.5782	0.0034
Site(Location(Reserve))	11	29830	2711.9	1.1384	0.251
Residuals	61	145310	2382.1		
Total	82	253540			

Autumn

Source	***df***	**SS**	**MS**	**Pseudo-*F***	**p**
Reserve	1	8284.9	8284.9	0.9559	0.3802
Location (Reserve)	10	93768	9376.8	3.6643	0.0001
Site(Location(Reserve))	12	30803	2567	1.3437	0.0467
Residuals	80	152830	1910.4		
Total	103	290460			

Winter

Source	***df***	**SS**	**MS**	**Pseudo-*F***	**p**
Reserve	1	9567.8	9567.8	0.92204	0.4431
Location(Reserve)	10	106000	10600	4.2615	0.0001
Site(Location(Reserve))	12	29878	2489.8	1.1984	0.1398
Residuals	83	172440	2077.6		
Total	106	319810			

Table 6.5: Results of PERMANOVA based on the Euclidean distance resemblance matrix calculated for each univariate response to determine the difference in the cryptofaunal community summary metrics and species abundances for locations inside and external to the Maria Island marine reserve. * p < 0.05; ** p < 0.01; no asterisk indicates p > 0.05

		Species richness		**Total abundance**	
Source	*df*	MS	Pseudo-*F*	MS	Pseudo-*F*
Survey	2	78.9	2.07	4860.8	2.43
Reserve	1	0.1	0	2156	1.08
Survey x Reserve	2	47.9	1.26	1011.6	0.51
Res	29	38.1		1999.1	
Total	34				

		Haliotis rubra		***Allostichaster polyplax***		***Cenolia sp.***		***Clanculus plebejus***		***Clanculus limbatus***		***Australostichopus mollis***	
Source	*df*	MS	Pseudo-*F*	MS	Pseudo-*F*	MS	Pseudo-*F*	MS	Pseudo-*F*	MS	Pseudo-*F*	MS	Pseudo-*F*
Survey	2	6.4	0.24	31	6.37**	65	0.23	1100.8	1.55	71.1	0.88	7.3	1.37
Reserve	1	187.9	6.90*	0.4	0.09	291.9	1.05	1092.5	1.54	25.8	0.32	0.8	0.16
Survey x Reserve	2	6.5	0.24	3	0.62	2.5	0.01	310.5	0.44	24	0.3	3	0.57
Res	29	27.2		4.9		278.9		708.7		80.9		5.3	
Total	34												

* p < 0.05; ** p < 0.01; no asterisk indicates p > 0.05

Effect of microhabitat characteristics

The three reef profile metrics (surface area, sub-block volume and perimeter access area) were all strongly inter-correlated. Pearson's correlation coefficients for surface area and volume, surface area and perimeter access area, and volume and perimeter access area, are 0.81, 0.80 and 0.80, respectively. Distance based linear modelling for the winter survey data identified that although surface area, volume and perimeter access area all had significant explanatory power when blocks were treated as independent replicates (Table 6.6a), only surface area explained a significant (but small) proportion of the variation of invertebrate assemblages within locations ($p < 0.001$, r^2 increased by 0.032 to 0.424; Table 6.6b).

Reef profile metrics showed no influence on the number of species recorded beneath blocks but exhibited a significant relationship with the total abundance of invertebrates and the presence of four of the seven most common species (Table 6.7). The surface area of the reef was the most commonly significant reef structure metric while perimeter access cross sectional area was the only metric to not have an influence on any component of the invertebrate assemblage. Most responses tested exhibited a positive relationship with sub-block structure; however, the small trochid *Clanculus plebejus* showed a significant negative relationship with the surface area of the profile.

Table 6.6: a) DistLM results relating contribution of sub-block reef profile metrics to spatial variability in cryptofaunal assemblages and b) shows the contribution of reef profile metrics in explaining variance of assemblages after variation between locations has been taken into account. * Increase in the proportion of variance explained relative to a model including only location.

a)

Model	**AICc**	**SS (trace)**	**Pseudo-*F***	**p**	**Proportion variance explained**
Location	773.37	119220	5.10	0.001	0.392
Surface area	786.48	36461	13.21	0.001	0.120
Total perimeter access area	791.1	23684	8.19	0.001	0.078
Volume	791.8	21696	7.45	0.001	0.071
Volume : perimeter access area	797.84	3904.6	1.26	0.256	0.013

b)

Model: Location +	**AICc**	**SS (trace)**	**Pseudo-*F***	**p**	**Cumul. variance explained**	**Increase in variance explained ***
Surface area	770.66	9762.6	4.79	0.001	0.424	0.032
Volume	773.43	4789.9	2.29	0.036	0.408	0.016
Volume : perimeter access area	773.86	4002.7	1.90	0.074	0.405	0.013
Total perimeter access area	774.67	2514.7	1.19	0.325	0.400	0.008

Table 6.7: Results of the GLMMs using a Poisson error distribution to model species richness and total abundance against the sub-block reef structure metrics: surface area, volume, perimeter access area and the ratio between volume and perimeter access area. A binomial (logistic) error distribution was used for the presence-absence of individual species. The p-value indicates if the deviance explained by the model is significantly different from the null model based on Chi-squared expectations. Δ deviance provides an indication of the relative contribution of reef structure and represents the change in deviance when the reef structure metric is added to a model containing only the random factor of location.

Response	**AIC selected optimal model**	**p-value**	**Δ deviance**	**Slope**	**SE**
Species richness	Null	-	-	-	-
Total abundance	Surface area	< 0.001	0.070	0.188	0.041
Allostichaster polyplax	Surface area	0.132	-	-	-
Australostichopus mollis	Volume : perimeter access area	< 0.001	0.150	0.279	0.122
Cenolia spp.	Surface area	< 0.001	0.138	1.402	0.408
Clanculus plebejus	Surface area*	< 0.01	0.032	- 0.856**	0.390
Clanculus limbatus	Null	-	-	-	-
Haliotis rubra	Null	-	-	-	-
Heliocidaris erythrogramma	Volume	< 0.05	0.087	0.069	0.031

* *Optimal model included random effects for both the slope and the intercept (p<0.05 when compared against the reduced model)*
** Mean value around which the slopes for each location randomly varied

DISCUSSION

Effects of the marine reserve

Commercially-valuable abalone *Haliotis rubra* comprised the only taxon to exhibit a significant marine reserve effect, with this species recorded at significantly lower mean densities at protected locations. These results correspond with the observations of Barrett et al. (2009) of a divergence in the numbers of juvenile abalone (30 – 130 mm) between protected and fished locations over time. Prior to protection at Maria Island, more abalone and more juvenile abalone were present at locations to be included within reserve boundaries. Over the first 10 years of protection, numbers declined within the reserve to approximately equal numbers of abalone inside and outside the reserve, with the proportion of juveniles declining dramatically (Barrett et al., 2009). Continued decline in abalone numbers since 2002 (Babcock et al., 2010), coupled with data presented here for juvenile abalone, suggest the possibility of a predator-driven Allee effect (Allee et al., 1949) at locations within the reserve. This theory suggests that fewer adult abalone and the broadcast spawning strategy of this species can result in reduced fertilisation success through a decreased likelihood of the meeting of viable sperm and eggs (Babcock and Keesing, 2000).

Allee effects are implicated in the stock collapse of the white abalone *Haliotis sorenseni* and contributed to that species becoming the first marine invertebrate proposed as an endangered species in the United States (Hobday et al., 2001). Populations of *Haliotis laevigata* in southern Australia have apparently suffered a similar fate (Shepherd and Partington, 1995). The short pelagic larval phase for *Haliotis rubra*, and resulting localised dispersal of propagules (McShane et al., 1988), create the potential for recruitment failure (Tegner et al., 1989) at the protected locations considered in this study. The lower abundance of cryptic juvenile abalone at protected locations confirms that the recruitment is declining with the abundance of mature abalone (Prince et al., 1988) and that, like other gastropod species (Stoner and Ray-Culp, 2000), decreased population density is not compensated by increased reproductive output. While the abundance juvenile abalone was significantly lower inside the marine reserve, their presence at these sites indicates that recruitment is still taking place suggesting that adult densities have not yet passed the critical threshold below which the population cannot sustain itself (Courchamp et al., 1999).

An alternative explanation for reduced recruitment at locations within the marine reserve is that fertilised propagules are settling but massive post-settlement mortality caused by the elevated predation pressure is inhibiting recruits from moving under blocks. Wrasse prey only on abalone >5 mm length (Shepherd and Turner, 1985), which is the same length at which individuals move to more cryptic positions from the exposed crustose coralline algae on which they settle from the water column (Shepherd and Turner, 1985). Diet analysis of *Jasus edwardsii* has also confirmed the presence of abalone in the foregut of individuals ranging from < 30 mm to > 60 mm carapace length (Edmunds, 1995). The numbers of wrasse and *J. edwardsii* have increased in the marine reserve and the resulting increased predation on juvenile abalone may be contributing to their lower abundances at protected locations. The strength of this explanation therefore hinges on the degree of effective protection from predation that occupying cryptic habitat offers. Preliminary studies by Shepherd and Turner (1985) excluding fish predators from cryptic boulder habitat showed no influence of predation on juvenile abalone numbers, although the authors recognise that cage artefacts may have affected results. Further experimental work is required to determine the extent of protection from predation afforded by occupying different forms of cryptic habitat.

The hypothesis that juvenile abalone delay emergence from crypsis in the presence of elevated predation pressure is supported by data collected in this study. The higher proportion of individuals greater than 100 mm occupying the cryptic habitat presented by the blocks inside the reserve supports the findings of Pederson et al. (2008) that interactions with predators, particularly rock lobster influence the microhabitat preferences of abalone. Pederson et al. (2008) reported size at emergence estimates of 117.8 and 87.6 mm for protected and fished locations respectively, which represents the shell length when there is a probability of 0.5 that an individual will emerge from cover. Similar proportions of individuals were observed at lengths greater than these estimates in the cryptic habitat surveyed inside and external to the marine reserve in this study (7.3 and 10.2 % respectively) supporting the validity and temporal consistency of this pattern.

In contrast to the situation with rock lobster, reduced recruitment of juvenile abalone at protected locations indicates that no-take marine reserves may not be an appropriate tool for the optimal management of populations of this particular species in Tasmania. Thus, because of the complexity of trophic interactions, populations of some species may decline in marine reserves. Species-specific fishery closures on selected reefs may be more suitable to create insurance populations for species such as abalone that appear to benefit from fishing pressure on their predatory species. This phenomenon does not detract from the net value of marine reserve networks for conservation of ecosystem diversity (Edgar et al., 2009), and as scientific reference areas for investigation of ecosystem-level effects of fishing, including interactions involving habitat structure, invasive species and climate change (see Chapter 5; Edgar and Barrett, 1999; Edgar et al., 2005; Micheli et al., 2005; Salm and Coles, 2001; Shears et al., 2008).

Effects of microhabitat characteristics

The taxonomic composition of species sampled by deploying sandstone blocks on subtidal reefs was comparable to those surveyed under natural boulders (Chapman, 2002b; 2005) and artificially placed blocks (Chapman, 2003; 2007) in the intertidal rocky shore. The biota collected by more complex artificial substratum such as nylon pan scourers, rope-fibre and artificial crevice habitats deployed in the subtidal environment tend to be numerically dominated by amphipods, bivalves or polychaetes (Baronio and Bucher, 2008; Edgar, 1991; Rule and Smith, 2005; Smith and Rule, 2002; Smith et al., 2006). This is most likely a result of the arrangement of intricate microhabitats in these units replicating the structure of complex natural habitats such as foliose macroalgae or kelp holdfasts (Hacker and Steneck, 1990). Although the methods of the present study were focused on sampling molluscs and echinoderms, observations of the units as they were being collected suggested that polychaetes, bivalves and crustaceans were not frequently encountered or observed in high numbers. This technique therefore offers a method of surveying cryptic fauna on subtidal reefs complementary to other artificial substrata collector methods. The structural simplicity of the technique is also less likely to bias the species composition of sampled biota (Smith and Rule, 2002) as the material composition of the paver is similar to adjacent boulders, the structural complexity of the adjacent natural cryptic microhabitats are similar, and the unit is resting on a natural reef allowing the easiest and most natural migration route into the unit. The development of apparatus to contain more mobile species underneath the blocks while sampling, or the use of a venturi suction sampler (Kennelly and Underwood, 1985), would allow a more quantitative comparison of the fauna sampled by the respective techniques and could shed further light on the relationship between cryptic invertebrates and their microhabitat refuge requirements.

Significant associations between reef structure and some components of the invertebrate assemblage suggest a degree of caution when using sandstone blocks to monitor cryptic invertebrates among sites displaying a variety of reef topographies. All calculations of reef structure were based on the same XYZ coordinates for each profile and it was therefore no surprise that reef measurements were highly correlated. The relative importance of different structure metrics for each component of the invertebrate assemblage appears to match the body shape and suggests the refuge requirements of the taxa under consideration. As the volume of space beneath the block increases, it increases the three dimensional area for animals to colonise but consequently decreases the usefulness of the space as a refuge for prey species that rely on their small size to allow them to wedge themselves into small cryptic habitats as a defence against predation.

A small refuge space beneath the block does not appear to benefit the sea urchin *Heliocidaris erythrogramma*, which exhibited a significant positive association with sub-block volume, as it possesses spines as an additional predatory defence and uses cracks and crevices, such as those created between the block and the reef, as a means of enclosing its vulnerable oral surface. This species has also previously been found to exhibit a significant relationship with features of the reef architecture in this region (see Chapter 3). By contrast, *Australostichopus mollis* is an example of a large-bodied cryptic species (a sea cucumber) that has no supplementary defence against predation. This species displayed a highly significant relationship to the ratio of the volume to perimeter access cross-section, suggesting that it selects or benefits from sub-block refuges that have a large internal volume with limited access for predators from the perimeter.

In my study, surface area had a significant influence on the spatial variability of the invertebrate assemblage, the total combined abundance of invertebrates, and the presence of *Cenolia* spp. One explanation for the benefit to *Cenolia* spp. from high topographic complexity is that a complex surface allows the animals to conceal their vulnerable disc while still offering pathways for the extension of their arms for feeding in the water column. The negative relationship found between the trochid *Clanculus plebejus* and surface area reflects the small size of this species (maximum width 10 mm - Gowlett-Holmes, 2008) and its tendency to occur in high abundances under blocks on near-flat surfaces (pers. obs.), minimising the potential for predator access and attack.

The lack of association between the reef structure and the presence of the abalone *Haliotis rubra* suggests that sandstone blocks can be used to survey and monitor abalone without significant bias from reef structure. Data obtained using blocks have the potential to provide more reliable density estimates to form the basis of investigation of recruitment for commercially important species. Corrugated polycarbonate sheets (Nash et al., 1995), venturi suction samplers (McShane and Smith, 1988) and boulders contained in crates (Shepherd and Turner, 1985) have been used for monitoring the density of newly settled abalone, however mortality is between 90 and 100 % for the first 5 months after settlement (McShane, 1991). An ability to attain an accurate estimate of cryptic juveniles should be more reliable than estimates of settlement for making decisions concerning stock management.

The spatial distribution of cryptic invertebrate assemblages was consistent among seasons, with by far the greatest the variation occurring between individual blocks (66 - 75%). A similarly high level of variability exists for both natural and artificial boulders on the rocky intertidal shore (Chapman, 2002b; 2003). The shape of the reef beneath the block was expected to be a major contributor to small-scale patchiness, yet, while crevice architecture explained a significant component of the spatial variation for some species, very little of the total variation was explained. Moreover, a significant relationship was not found between species richness and sub-boulder structure. Other factors that possibly contributed to small-scale patchiness in the assemblages included the aggregation of certain invertebrate species under particular blocks (eg. chiton - Grayson and Chapman, 2004), water flow, the proximity of individual blocks to extrinsic resources such as patches of sessile invertebrate prey, or the presence of a source of disturbance such as sand or macroalgae (Duggins et al., 1990).

Important research areas for further development of the use of sandstone blocks in the subtidal environment include assessment of rates and timing of colonisation of the blocks by different species, including temporal changes in benthic cryptofaunal assemblages over longer time periods than studied here. Blocks could also be placed in a more targeted manner to deliberately create particular structural features between the block and the reef. This approach would be particularly useful to attempt to isolate and manipulate variability of the different structural metrics investigated here while holding the other metrics as constant as possible. For example it would be possible to select a position on the reef to create a large enclosed space with a low perimeter access surface area but high internal volume by placing a block at the junction of three or four boulders with appropriate spacing and of similar heights. For comparison, blocks could be placed on top of a gently rounded boulder so that the perimeters are open and there is little contained volume within. Such a manipulative approach also offers the potential to identify the association between slow-moving cryptic species and specific microhabitats within the sub-block space.

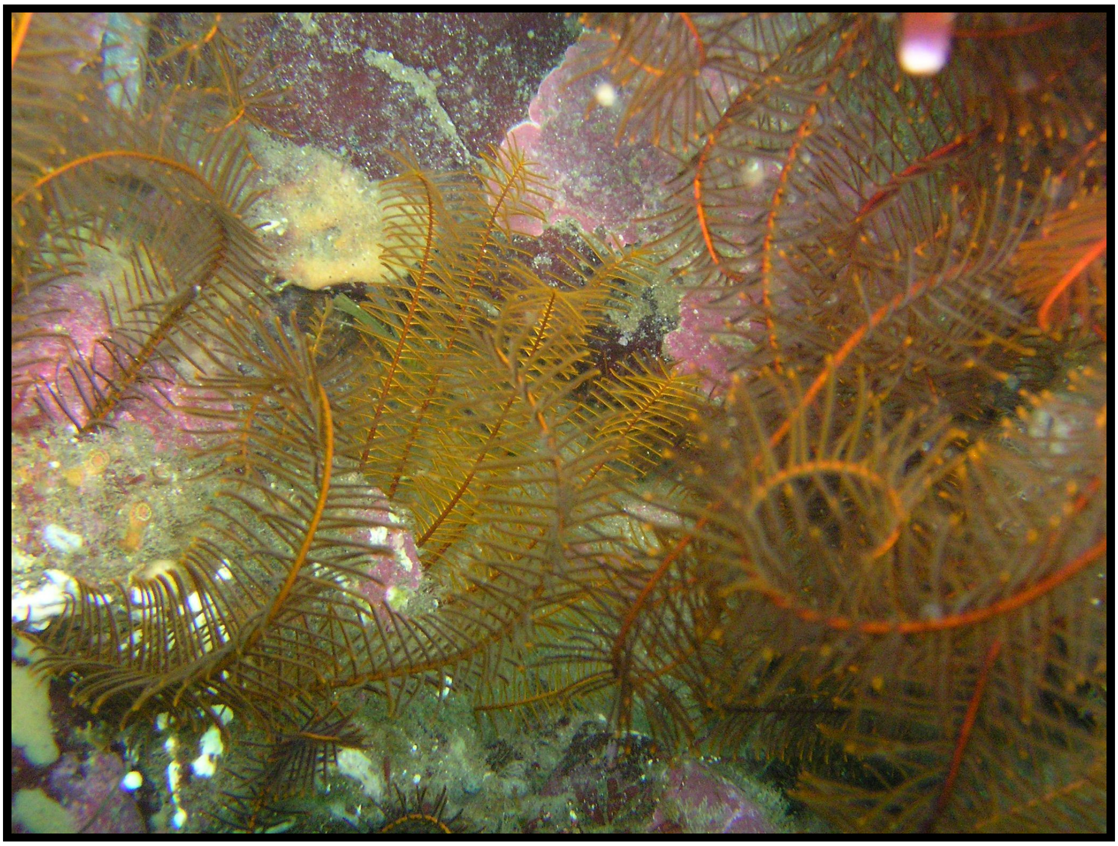

Plate 6: *Cenolia trichoptera*, Maria Island, Tasmania

Chapter 7:

General discussion

Reef habitat structure has a detectable influence on the organisation of mobile macroinvertebrate communities on subtidal rocky reefs in temperate Australia. Most species and taxonomic groups are more abundant at sites with greater reef structure and consequently the combined abundance of invertebrates exhibited one of the strongest positive associations with reef structure around Maria Island, Tasmania and for bioregional snapshots in Western Australia and New South Wales. Among the summary metrics available to describe an assemblage, the total number of individuals is most commonly influenced by reef structure for rocky reef fishes (Garcia-Charton and Perez-Ruzafa, 2001; Harman et al., 2003; La Mesa et al., 2004; Ohman and Rajasuriya, 1998; Willis and Anderson, 2003), coral reef fishes (Ault and Johnson, 1998; Friedlander and Parrish, 1998; Garpe and Ohman, 2003; McClanahan, 1994; McCormick, 1994; Roberts and Ormond, 1987; Sale and Douglas, 1984) and fishes in other shallow tropical marine habitats (Gratwicke and Speight, 2005a). Assemblage-level studies on benthic invertebrates show a weaker relationship between total abundance and habitat structure. Entrambasaguas et al. (2008) reported that variability in the abundance of echinoderms was better described by water depth and the cover of sand than reef structure, and Ruitton et al. (2000) also found relatively few associations between the invertebrate assemblage and physical habitat metrics on Mediterranean rocky reefs. A potential explanation for this stems from the diversity of morphological forms within the invertebrate assemblage. Whilst body shape is relatively consistent for inshore reef fishes, benthic invertebrate morphology ranges from sea urchins to abalone to rock lobster and reflects their varying dependence on the utilisation of reef habitat structure as an anti-predation mechanism.

Macroinvertebrate abundance was consistently related to measures of reef architecture in the data presented here. Although other studies have quantified the size or density of cracks, crevices and holes (Ault and Johnson, 1998; Friedlander and Parrish, 1998; Gratwicke and Speight, 2005a; Roberts and Ormond, 1987), this is the first study I am aware of to explicitly describe criteria for identification and enumeration of these and other features on a complex reef surface. The density of small reef features considered to be refuges from predation significantly described spatial variability of total invertebrate abundance at Maria Island for regression models based on samples taken at block (5 x 1 m), transect (50 x 1 m) and site (200 x 1 m) scales respectively. Another measure of reef architecture, the fractal refuge index, which reflected the frequency distribution of different sized reef features in a sample, was identified as the best descriptor of the abundance of invertebrates for sites around Tasmania. This model proved to be spatially consistent when tested on samples from bioregions on the mainland of Australia, significantly describing invertebrate abundance in the Central West Coast (Western Australia) and Batemans Shelf (New South Wales). The addition of canopy algal cover to the latter model brought the explained deviance to 67% (an increase of 18%). This reflects the importance of urchin barrens, which dominate many of the more exposed sites in samples from this bioregion, in structuring local invertebrate communities (Ling, 2008).

The strength of invertebrate-habitat models for echinoid abundance followed similar inter-regional patterns to total invertebrate abundance with consistently strong associations to reef architecture. These similarities are not surprising given that echinoids contributed more individuals than other invertebrate classes in Batemans

Shelf (74% of animals were echinoids, 96% of which were *Centrostephanus rodgersii*), Central West Coast (52% echinoids, 71% of these were *Heliocidaris erythrogramma*) and Tasmania (52% echinoids, 90% of these were *H. erythrogramma*). Samples at Maria Island were numerically dominated by crinoids (contributing 52% of individuals) and secondly by echinoids (38% of individuals, 96% of which were *H. erythrogramma*). Although sea urchins are protected by spines, the evolution of negative phototaxis, resulting in shelter seeking or covering behaviour in some species (Adams, 2001; Sharp and Gray, 1962), suggests that additional benefit to growth or survival are derived from association with reef features. Observations suggest that sheltering within refuges can enhance the effectiveness of the spines as a predatory defence. Reef features can enclose the vulnerable oral surface of the urchin and improve their grip on the substratum by allowing them to wedge spines into the structure of the rock surface.

Analysis of *H. erythrogramma* under increasing predation pressure showed that the number of sea urchins decreased at sites with greater numbers of small reef features. Although the strength of this relationship at fished control sites was weak and variable, data from around Tasmania confirmed the importance of reef architecture for this species at sites where large numbers of fish and invertebrate predators are reduced by fishing. These results suggest that adult *H. erythrogramma* and other sea urchins associate with reef refuges that should theoretically provide protection from predation, and may do so under low levels of predation, but when predators are large and abundant the benefits of the refuges decline. Further experimental work should be undertaken to assess the validity of this explanation.

Models using reef habitat structure to describe variability of invertebrate species richness were generally weak. The two exceptions both involve measures of substratum architecture: a significant link to the number of refuge size categories in blocks (1 x 5 m) around Maria Island ($r^2 = 0.304$) and a significant association to the fractal refuge index for sites in the Central West Coast bioregion ($r^2 = 0.464$). The findings at Maria Island follow the commonly reported importance of close scaling between animal body size and physical refuges to obtain effective protection from predation (Beck, 1995; Eggleston and Lipcius, 1992; Hixon and Beets, 1989; 1993). A greater variety of sizes and types of reef architectural features can theoretically allow the persistence of species with a wide variety of body shapes and sizes. Very few empirical studies have directly tested this hypothesis, however, with most reporting on the number of holes in each size category (Roberts and Ormond, 1987), aggregating data for hole sizes and shapes into one metric such as the total number of holes (Friedlander and Parrish, 1998; Talbot and Goldman, 1972), mean hole diameter (Almany, 2004) or mean hole volume (Friedlander and Parrish, 1998). In a study using artificial reefs, Gratwicke and Speight (2005b) manipulated the presence-absence of two size categories of holes and reported inconclusive effects on fish species richness; while observations across a variety of shallow tropical marine habitats also showed that the number of refuge size categories was not a strong predictor of fish species richness (Gratwicke and Speight, 2005a).

The second significant model to describe spatial variability of species richness was for sites in Western Australia where samples with a higher fractal refuge index supported greater numbers of species. The limestone reefs of the Central West Coast bioregion are highly complex surfaces, reflected by a fractal refuge index of 0.541 ± 0.04 (mean ± SE), indicating that the frequency distribution of refuges on the average reef approximately follows fractal expectations (ie. that the number of refuges declines with increasing size-class of refuges based on a log-log scale). Fractal refuge index values for Boags (Tasmania) and Batemans Shelf (New South Wales) bioregions were 0.699 ± 0.04 and 0.642 ± 0.03 (bioregion mean ± standard error), respectively, indicating that the size frequency distribution of refuges in these regions are dominated by the smaller refuge size classes. A reef surface dominated by small reef features limits the available spatial refuges to small species or individuals due to the importance between scaling of physical refuge to animal body size. Sites with a more even size frequency distribution of refuge can therefore support a greater number of invertebrate with a wide range of body shapes and sizes. These results and those of previous studies suggest that although reef structure frequently has an influence on the abundance of fish and invertebrates on a reef, its effects on the number of species in an assemblage are less consistent but seem to be stronger for benthic invertebrates than fishes. This could be a consequence of the physical association between marine macroinvertebrates and the substratum being more direct than for fish. Benthic macroinvertebrates also tend to rely on mechanisms other than speed or manoeuvrability (such as a hard shell, spines or retreating into a hole) to avoid predation.

The abundance of abalone surveyed by visual census was one of the few components of the invertebrate assemblage to display a negative relationship with measures of reef habitat structure. Abalone are more likely to be surveyed at sites with low rugosity around Tasmania (and high canopy algae); with a similar relationship evident in the spatially focused study of sites around Maria Island (*H. rubra* abundance ~ –protection status – rugosity + status*rugosity). Analysis of an ecological time series for protected sites at Maria Island suggests that this negative relationship with reef structure has been weakened with increasing predation pressure, presumably as fish and invertebrate predators remove the more vulnerable younger animals from the system. This negative relationship to reef structure applies to the emergent portion of the abalone population only, with surveys using sandstone blocks to replicate subtidal boulders confirming the well established paradigm that juvenile abalone require cryptic reef habitat. Within the cryptic habitat the shape of the reef surface has no detectable effect on the probability of encountering abalone.

Asteroids comprise one of the few components of the macroinvertebrate assemblage to show no strong relationship with any habitat structure metric investigated. Although optimal models for this class at Maria Island included some habitat descriptors, these only became significant after the factor marine reserve was included in the model. The presence of *Pentagonaster dubeni* and *Plectaster decanus* were significantly influenced by the fractal refuge index and rugosity, respectively, in Western Australia; however, r^2 values were still less than 0.2. This is unsurprising given that the large asteroid species recorded in visual census surveys were rarely observed to associate with any shelter. Entrambasaguas et al. (2008) reported that of the three asteroids for which models were generated to describe the spatial distribution in an island group in the eastern Atlantic, only one species was influenced by a reef structure metric – number of medium boulders for *Ophidiaster ophidianus*, and when combined with depth and its quadratic the full model still only accounted for 12.4% of the variance. Several smaller asteroid species were observed exclusively in the cryptic microhabitat created by experimentally placed sandstone blocks. *Allostichaster polyplax* and *Meridiastra atyphoida* are commonly found under rocks (Edgar, 2008), presumably as a result of a negative response to solar radiation (Bernaford and Vasquez, 2008).

Cryptic invertebrates of subtidal rocky reefs are often overlooked in studies of biodiversity, including investigations of effects of marine reserves. Sandstone blocks have been previously employed on rocky intertidal shores to sample cryptic mobile invertebrate species (Chapman, 2003). This study presents the first application of this technique in the subtidal environment, and is the first to test the potentially confounding influence of the shape of the reef beneath the block, which influences the habitat structure and amount of space for animals to colonise. Three deployments of 120 blocks identified a diverse array of 81 species of echinoderms and molluscs. This is compared to a total of 46 species of macroinvertebrates (including crustaceans) observed over 10 years of visual census techniques of emergent animals at the same sites (Barrett et al., 2009). These results show that sandstone blocks can be successfully used to sample the diverse assemblages of slow-moving cryptic invertebrates on subtidal rocky reefs.

The reef structure beneath sandstone sampling units had a small but significant positive effect on many components of the cryptic invertebrate assemblage. Juveniles of the sea urchin *Heliocidaris erythrogramma* were more likely to be found under units with a high volume of refuge space, thus reflecting their larger relative size and the benefit of spines as an additional predatory defence. The surface area of the sub-block reef profile had a positive influence on total abundance of invertebrates and on the probability of recording the common feather star *Cenolia trichoptera*. Only the presence of the gastropod *Clanculus plebejus* was negatively related to reef structure metrics, presumably as a function of its small size and the reduced spatial refuge that comes with increased space beneath the block. The number of species present beneath a block was not influenced by the reef surface profile, echoing the results for emergent species richness. The confirmation of a significant relationship between the reef profile and the invertebrate assemblage needs to be taken into consideration when employing this technique for sampling the cryptic invertebrate community.

Species richness, total abundance and the composition of the cryptic invertebrate assemblage were similar for protected and fished sites; however, the abundance of commercially fished blacklip abalone *Haliotis rubra* was significantly lower for sites inside the marine reserve. This finding contributes to research investigating the decline of juvenile abalone with increasing size and abundance of predators inside the reserve (Barrett et al., 2009). Pederson et al. (2008) identified that the size at which abalone shift from a cryptic to emergent lifestyle is related to predation pressure, which would reduce the proportion of the population that can be observed using visual census techniques. Data collected in this study suggests that the observed trend is more than an artefact of the visual census survey technique and the abundance of juvenile abalone, including the fully cryptic component, is indeed lower than fished control sites. This important finding provides further evidence of the likely development of a predator driven Allee effect for abalone populations in Tasmanian marine reserves, with implications for multi-species fisheries management and the design of marine reserves for enhancement of fisheries production.

This research highlights the importance of considering variability within a habitat type when planning for conservation or impact assessments. Broad associations of species with different substratum types (ie. rocky reefs, sand, silt, seagrass) are well established for many marine ecosystems (eg. Chatfield et al., 2010; Moore et al., 2009) and form the basis of conservation planning in some areas (RPDC, 2006). This research contributes to the next level of information in recognising that intra-habitat variability can influence the persistence of species. The effect of reef structure on the abundance or presence-absence of a species can be factored into studies where the priority is to determine the influence of a particular impact on rocky reef species or community (for example a sewerage outfall or marine protected area). Variability of continuous extraneous factors can be incorporated into the analysis as covariates, providing that the slope of the regression between the covariate and dependent variable is homogeneous across treatments and other assumptions are met (see Underwood, 1997).

Garicia-Charton et al., (2004) included the residuals of fish-habitat regressions as dependent variables in analyses of variance and found that corrected responses were generally more similar between levels of fishing protection than analyses on raw values. They attributed this to a bias in the selection of Mediterranean marine reserves in favour of areas that contribute structurally complex habitats which favour the development of rich and abundant fish fauna. However, the same data were used to generate the fish-habitat regression as for the reserve effect tests in this study, making it difficult to separate the effects of habitat from those of the marine reserve. Ideally, the regression model between habitat and biota should be trained on data from surrounding areas subject to a consistent level of fishing pressure, this model applied to the marine reserve and adjacent study area, and the ANOVA carried out on the deviations of the study data from the trained model (Fig. 7.1). In the present study, the relationship between reef architecture and the abundance of echinoids, particularly the abundance of *Heliocidaris erythrogramma,* is sufficiently strong and spatially consistent to be applied in this manner around Tasmania. These results indicate that this pattern is also likely to extend to the mainland of Australia, however the model test data had limited spatial extent and further local verification is recommended for applications on mainland Australia.

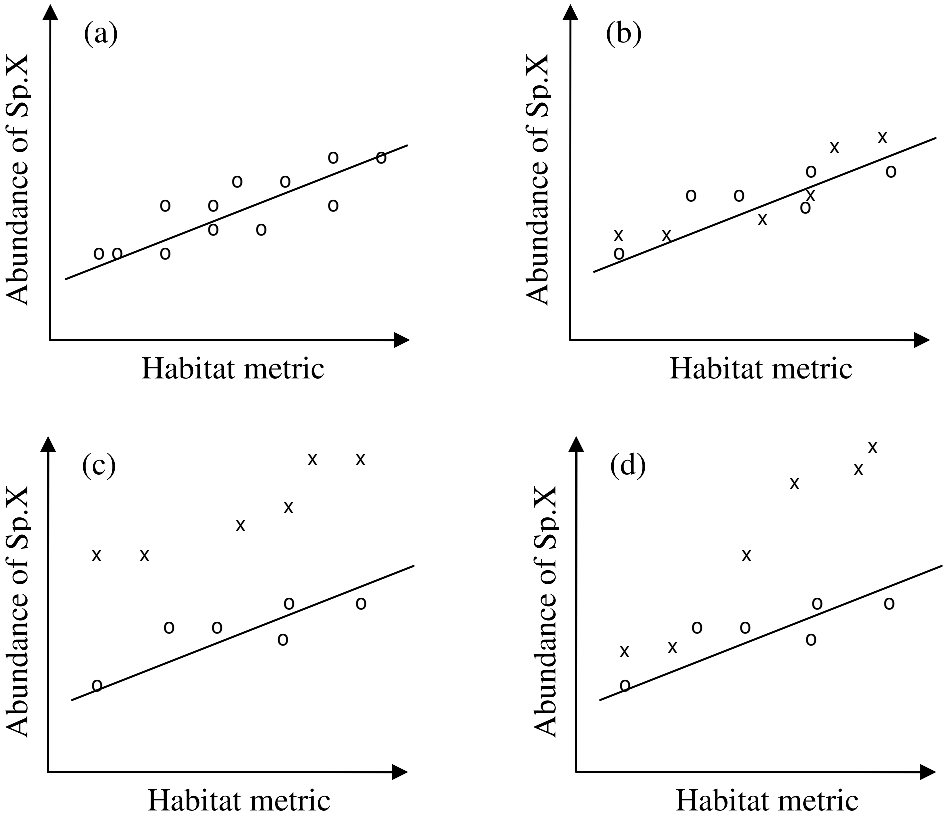

Fig. 7.1: Hypothetical example showing protected (x) and fished site (o) data for (a) a model training area, (b) no effect of the marine reserve, (c) increases in fish abundance across all sites with no influence of habitat on the proportional response and (d) an interaction between protection and habitat shows a greater increase in fish abundance at sites with higher values of the habitat metric

My study shows that relationships between macroinvertebrates and reef structure vary through space, time and with protection from fishing. Studies have reported on links between reef structure and biota based on samples collected over scales of kilometres (chapter 3; Brokovich et al., 2006; Friedlander and Parrish, 1998; Garcia-Charton and Perez-Ruzafa, 2001; Gratwicke and Speight, 2005a; b; Harman et al., 2003; La Mesa et al., 2004; Ohman and Rajasuriya, 1998; Willis and Anderson, 2003), 10’s of kilometres (Ault and Johnson, 1998; Garpe and Ohman, 2003; Jennings et al., 1996; Ordines et al., 2005) or 100’s of kilometres (Friedlander et al., 2007; Friedlander et al., 2003) and see Garcia-Charton et al. (2004) for an excellent multi-scale test of habitat structure on fish communities. None of these studies quantitatively tested the predictive ability of the models for data outside the area where the model was developed. Most models developed on the basis of Tasmanian data that use habitat surrogates to describe the spatial distribution of invertebrate assemblages and populations were found to have limited predictive ability when applied in New South Wales and Western Australian bioregions. Single habitat predictors tend to dominate species models for each bioregion, suggesting that surrogates identified in one region should not be extrapolated outside that region without local validation.

Invertebrate-habitat relationships also vary through time, particularly for communities subject to environmental or management-induced change, such as the declaration of a marine reserve where species, and most likely their relationship to the environment, can continue to change after more than a decade of protection (Edgar et al., 2009; Russ and Alcala, 2004; Shears and Babcock, 2003). Ecological theories describing the dynamics of exploited ecosystems may not necessarily apply to areas protected from exploitation, and vice versa. The results presented here suggest that future studies of relationships between species and their habitat should consider predation pressure, especially by humans on exploited species, as a co-variable.

Ecosystem-based fisheries management requires knowledge of the interactions between fishers, fished and non-target species, and the influence of habitat on these relationships. This study has contributed to knowledge of the influence of intra-habitat variability on the spatial distribution and on interactions between mobile macroinvertebrate species in southern Australia. It highlights the risk of assuming that invertebrate-habitat relationships are stable through space and time, and therefore emphasises the financial and ecological value of long-term, broad scale monitoring projects.

My study confirms that the physical structure of temperate rocky reefs has an important structuring influence on the associated benthic invertebrate assemblage. Of the components of the invertebrate assemblage tested here, the abundance of animals in an assemblage most consistently related to habitat; however different measures of structure are of greater importance for different taxa within the assemblage. The density of specific elements of reef architecture appears more important in explaining the spatial variability of many components of the rocky reef invertebrate assemblage than measures of topographic variability or substratum composition. Small scale experiments have previously highlighted the importance of reef structure to interactions between prey and one or more predator species, yet manipulating multiple prey and / or multiple predators for lengths of time sufficient to allow the full expression of effects is logistically difficult. Broad temporal and spatial scale observational studies such as this that encompass a wide range of predator densities and reef structure help to shed light on the dynamics of these relationships. This information is useful for interpreting community changes resulting from protection from fishing, and ultimately improved understanding of the influence of human activity on the marine ecosystem.

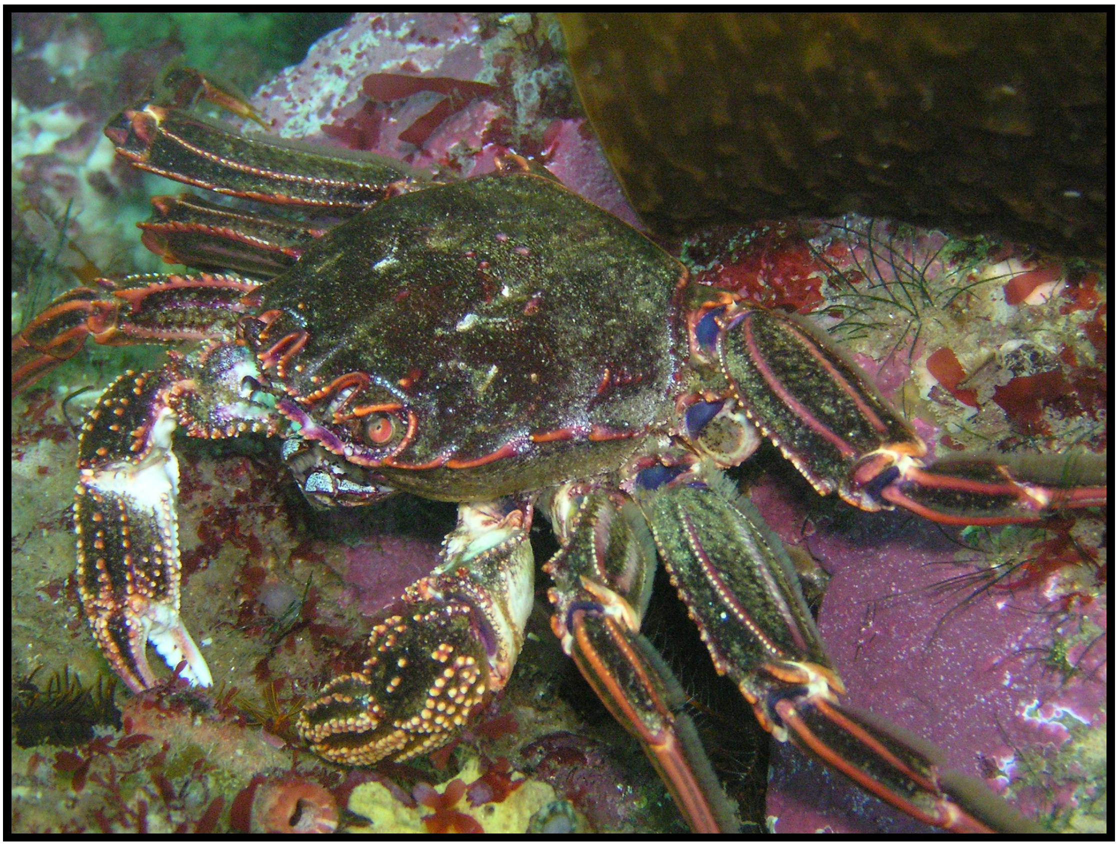

Plate 7: *Plagusia charbus*, Maria Island, Tasmania

Chapter 8:

Future studies

This study presents an initial investigation into the relationship between reef habitat structure and the mobile macroinvertebrates of temperate reefs. Prior to this research, very little information was available on assemblage or class level associations between these two sets of variables in the Southern Hemisphere (but see Edmunds et al., 1999). Research was therefore carried out from ecological first principles: identifying measures of reef structure to describing spatial variation of these animals and determining the variability in these relationships through space and time. Although key species were given specific attention, the focus was on identifying habitat associations for higher taxonomic groups. As a result, it was necessary to carry out sampling at spatial scales large enough to encompass a large proportion of possible interactions occurring within an assemblage. Although most of the mobile invertebrates surveyed here move at the scale of metres, the average home range area of rock lobsters in the Maria Island marine reserve is up to 15 000 m^2, depending on season (Frusher et al., 2009), much greater than the sampling scales used in this study (5 – 200 m^2). A future direction for this research is to test the extension of these relationships upwards to the scale of entire reefs, and also to smaller scales such as for individual reef features.

Remote sensing tools provide a cost-effective method for characterizing reef habitat structure across large spatial scales. Optical sensors such as satellite imagery (eg. IKONOS; Stumpf et al., 2003) or airborne Light Detection and Ranging (LIDAR; Brock et al., 2004) can determine variability of water depth in shallow (< 50 metres), clear water making them particularly suited for use in coral reef ecosystems. Shipmounted or towed acoustic mapping equipment can also be deployed for the same purpose in most water deeper than 5 metres (Jordan et al., 2005), although LIDAR is the more cost effective alternative (Costa et al., 2009). The direct scaling up from diver-collected to remotely sensed measurements requires a degree of caution however with conflicting results between studies that have directly compared the two approaches. LIDAR was highly correlated to in-situ rugosity in a Hawaiian study while rugosity measurements derived from Experimental Advanced Airborne Research Lidar (EAARL) were poorly correlated with chain-transect rugosity in work done in Florida, USA (Kuffner et al., 2007). The complementary use of diver-collected and remotely-sensed data allows the characterisation of reef habitat structure across spatial scales from centimetres to kilometres.

The intricacies of the relationship between reef profile variability and the abundance of rock lobster in fished waters deserve further investigation, particularly given the commercial value of this species and its ability to influence the abundance and behaviour of other invertebrates including commercially important species of sea urchin and abalone (Pederson and Johnson, 2006; Pederson et al., 2008). Future research needs to focus on whether this relationship extends from the direct association within transects to a reef-wide linkage. Surveys for both the habitat metric and the abundance of lobsters can be carried out without the need for labour intensive diving operations. Multi-beam sonar provides 3-dimensional bathymetric mapping of the seafloor from which complexity measures can be derived (Costa et al., 2009), however this methodology is prohibitively expensive for many research budgets. Variability in the surface of inshore reefs can be cheaply quantified using single-beam acoustics operated from a relatively small vessel equipped with a colour echosounder and a differential global positioning system. Although single beam sonar is limited to linear sampling, multiple randomly oriented tracks or a regular grid of tracks allow useful estimates of profile variability of the reef (eg. Lucieer and Pederson, 2008). The density of rock lobsters on a reef patch can be sampled using commercial potting techniques. If the strong relationship identified on transects extends to reef-wide data, large areas could be mapped relatively easily and knowledge of the habitat suitability used to inform fisheries management, including the selection of areas as potential marine reserves for fisheries enhancement or insurance populations.

Reef architecture is identified in this study as influencing multiple components of the mobile invertebrate assemblage. Representatives of this type of reef structure have previously been employed in many correlative and manipulative studies, however very few researchers devote attention to the issue of discriminating these features amongst the natural complexity of subtidal reefs. On a highly complex surface, the decision as to which features fall within the definition becomes somewhat arbitrary, particularly if the only criteria is that you are counting “holes” (Friedlander and Parrish, 1998; Roberts and Ormond, 1987) or “crevices” (Nemeth, 1998). Some authors use the criteria that the feature must have a maximum depth greater than the minimum diameter of the hole entrance (Ault and Johnson, 1998), however it is sometimes difficult to even identify where the “entrance” to the hole lies. Manipulative experiments are able to control the size and shape of holes, however these have currently been limited to controlling availability of shelter (Andrew and Macdiarmid, 1991) or altering the presence and density of two different sized holes (Caley and St John, 1996; Gratwicke and Speight, 2005; Hixon and Beets, 1989; 1993).

This study introduced quantitative criteria based on simple geometry for identification of reef features that may be important for benthic invertebrates. The refuge criteria were generated on the basis of providing protection from predation; however these features are also likely to provide shelter from adverse environmental conditions. Surveys of the specific microhabitat preferences of key Tasmanian species under field conditions would allow confirmation and refinement of refuge criteria developed in this study. Laboratory experiments could then be used to confirm the preference for microhabitats and determine the influence of these reef features on predation success.

Developments in the field of underwater photogrammetry from single and stereo images have created opportunities for quantitative characterisation of reef structure at fine scales. The combination of stereo imagery with advanced image processing software such as Photomodeler Scanner (www.photomodeler.com) allows the creation of 3-dimensional digital representations of the reef formed by a dense cloud of points, each with a specified x, y, z position within the context of the image. Mathematical or architectural descriptions of a microhabitat can be created using a selection of stylised geometric shapes such as a hemisphere, open cylinder or an angular arrangement of two or more planes. Rotating shapes of different sizes through a subset of the dense point cloud of the digital reconstruction of the surface allows us to solve for the particular shape, size and orientation that best describes the feature (minimises the volume between the reef surface model to the stylised shape; Fig. 8.1). The microhabitats of randomly located individuals of different size classes at multiple sites can be described in situ using this technique and correlated against the factors listed in table 8.1. Laboratory or manipulative experiments then provide the opportunity to confirm the most important biological and physical influences on these preferences (Underwood et al., 2004).

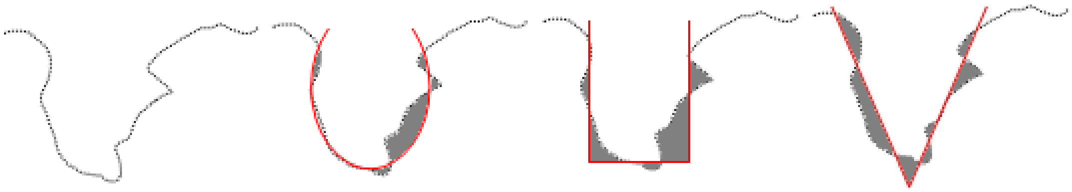

Fig. 8.1: A selection of stylised shapes that could be used to represent a reef feature

The ability of invertebrate and fish predators to remove and consume different sizes of urchins, abalone or other species of interest from favoured microhabitats could be tested using a modified version of the laboratory experiments of Andrew & Macdiarmid (1991). These experiments will confirm if particular features act as a buffer from predation, or whether other factors such as environmental conditions are driving the preference of species for particular microhabitats. Aside from contributing to understanding the dynamics of rocky reef ecosystems, this information would be useful in selecting areas of reef for protection in Tasmania that offer reef refuges that could potentially allow the persistence of healthy abalone populations in the presence of elevated rock lobster predation.

Table 8.1: Factors influencing the refuge preferences of a species at a site

Factor	Pathway of influence	
Intra-specific interaction	Safety in numbers	
	Crowding -> displacement	
Inter-specific interaction	Predation	Behavioural response in prey species
		Elimination of animals not in appropriate refuges
	Competition	Displaced from optimum refuges by individuals of other competitively dominant species
	Facilitation	Attracted to refuges occupied by individuals of another species
Exposure	Physical refuge from wave force	
	UV sensitivity	
Macroalgal canopy	Biological refuge -> visual or physical obstruction from predator	
	Predator ambush	
	Food resource	
Time of day	May leave refuge to feed	
Season	Mating activity	
Types of refuges available	May not have access to optimal refuge -> suboptimal	

Plate 8: *Chromodoris westraliensis*, Jurien Bay, WA