



<http://researchspace.auckland.ac.nz>

ResearchSpace@Auckland

Copyright Statement

The digital copy of this thesis is protected by the Copyright Act 1994 (New Zealand).

This thesis may be consulted by you, provided you comply with the provisions of the Act and the following conditions of use:

- Any use you make of these documents or images must be for research or private study purposes only, and you may not make them available to any other person.
- Authors control the copyright of their thesis. You will recognise the author's right to be identified as the author of this thesis, and due acknowledgement will be made to the author where appropriate.
- You will obtain the author's permission before publishing any material from their thesis.

To request permissions please use the Feedback form on our webpage.

<http://researchspace.auckland.ac.nz/feedback>

General copyright and disclaimer

In addition to the above conditions, authors give their consent for the digital copy of their work to be used subject to the conditions specified on the Library Thesis Consent Form.

**Influence of Reef-Associated Predators on
Adjacent Soft-Sediment Communities**

Timothy John Langlois

A thesis submitted in partial fulfilment of the requirements for the
degree of Doctor of Philosophy, The University of Auckland,
2005.

Frontispiece



A large *Dosinia subrosea* shell with distinct markings of predation by a large *Jasus edwardsii* (see Chapter 4).

This thesis is dedicated to Ruth and Leslie (Brockie) Brocklehurst,
Mary and Fred (Pépère) Langlois,
and Jack Taylor.

Abstract

'Infaunal haloes' of either decreasing or increasing abundances of individual soft-sediment species with distance from reefs have been suggested to be caused by reef-associated predators. A large-scale mensurative experiment was used to investigate the distribution of two size classes of macrofauna with distance from the reef edge across three locations in northeastern New Zealand. The role of reef-associated predators, the snapper (*Pagrus auratus* Sparidae) and rock lobster (*Jasus edwardsii* Palinuridae), was investigated using established marine reserves at each location. Consistent patterns were found in a few large-bodied fauna. The hermit crab *Pagurus novizelandiae* occurred more frequently near the reef edge, whilst the heart urchin *Echinocardium cordatum* and bivalve *Dosinia subrosea* were more abundant further away from the reef. *Dosinia subrosea* and another bivalve, *Myadora striata*, exhibited lower biomass at sites with higher densities of snapper and rock lobster. In contrast, small-bodied macrofauna showed no consistent patterns with distance from the reef or among sites with different predator populations.

It was hypothesised that predation was driving the distribution of large bivalves. An experiment was done to investigate this model using *D. subrosea*. Equal densities of this bivalve were established in plots either with or without cages at sites either inside or outside of reserves. Significant predation was detected, but only inside reserves. Much of this mortality could be specifically attributed to predation by large rock lobsters, given the distinctive marks on the valves of dead *D. subrosea*.

Inside reserves, predators are not only more abundant but also larger. It was hypothesised that different size classes of predators would result in different levels of predation. Laboratory feeding experiments were used to investigate this model. Lobsters of all sizes chose *D. subrosea* over the heavier shelled *D. anus*. Small lobsters chose to prey on small *D. subrosea* and large lobsters more frequently chose larger prey. The distributions of these two bivalve species at protected (large predators) and fished sites (small predators) reflected the feeding choices observed in the laboratory.

Results suggested that rock lobster populations are capable, where their size structure is not truncated by fishing pressure, of controlling population-level dynamics of bivalve communities adjacent to reefs.

Acknowledgements

This study would not have been possible without a scholarship from the Education Committee, States of Jersey, Channel Islands.

First and foremost I want to thank my supervisor Marti Anderson. I'm honoured you asked me to count your fish! I may not have always been the model student but you've always been an awesome advisor. Under your tutelage I've developed a love of ecology that I want to pass on. However, if I ever take on students I think they should come to you for advice on grammar. I enjoyed talking the talk so now let's walk the walk.

Bill, not only have you helped me clarify my thinking and originate new thoughts but you've housed me and fed me whenever it was needed (often!). You've taught me the ways of Mother Carey and I'm looking forward to putting it into practice.

Russ, you encouraged me from the start. I turned up at the lab after missing out on the first PhD I applied for. When I realised what great potential there was for original work (and learning to surf) I was even more determined to stay. I hope we get the chance to work together again.

The following thanks are to people who have helped me in life and in thesis for the past five years, the two things have been inextricably linked and so the acknowledgments cannot be separated. Geordie and Rosemary for advice and tales of fish, Laurie for charcoal, Nick T for pizza, Katie for a home from home, Ian for teaching me how to duck-dive, Tom for the sewing circle and help beyond measure, Monica for mini-me, Jo-anne for lending me Graeme and JP for adventures at T-point, Andy for cheese, Nick for perspective, Peggy and Gordon for watching over us, Carl and Monique for making me a Kiwi, Jo for juice, Neil for inspirational play, Sarah for enthusiasm, Trevor for the idea, Viv for putting Ian through many times, Guy for water control, Sarah and Duncan for glorious food, Jake for not dropping in on me, Christina for worms, Megan for not complaining about the smell, Maren and Damian for quick visits, Pam for the fishes, Chris for his photography, Daniel for talk about MR's, Michelle for Harry and glow worms, Craig for answering my rhetorical questions, Varenka for the pump, Agnes for

dancing, Alan for buffing, Lee for ‘Hello’, Kara for your family, Kat for the ice, Emma for the poetry, Carlos for the pisco, Sandra for composure, Shin for cage fighting, Brian for the nuts, Tony for horns, Sharon for the tea-towels, Saskia for solid shoulders, Margot for the mojo, Natalie for your dedication, Kent and Perrin for the kites, Lisa for taming the muss, Camilo for music, Jimmy for going to Hawaii by himself (must have been hard), Phil the trousers, Jo for di papa, Saporio for taking Charlie for a walk, Dan for the Buddha, Aletha for not telling me off, Bruce for the left hook, Adam for the grunt, Dave for the drums, Justine for the beach, Gilles for my head, Steff for not minding, Marta for the encouragement, Anne and Tim for telemark and the fins, Murray for practicality, Richard for ecology, Chris and Andrea for discussions on fences and life, Eliza for dolphins, Hernando for the security, Brady for patience, Sophie for art, Arthur for looking after us, Caroline for da family, Olivia for early ups, Monty for the race, Janne for tea, Elke for the brownies, Schannel for pool, Ivan and Christina for their views on marine life, Alwyn for being a good neighbour, Mark for 100%, Bruce for the funk, Dave for sincerity, Javier for orthogonal designs, Ben for Taranaki, Daz for Barry, Adrian for the waves, Tracy for “big lobster”, Matt for the glorious cumber, Francesca for tarts, Claire for the smiles, Rich for the swims and T for giving me the motivation.

In Jersey I would like to thank Gerard Le Claire for having faith in me and being so supportive in my application for a scholarship. Mike Taylor for giving me the accolade of ‘best new deckhand’ on his lobster boat – although I think he’s forgotten. Chris Le Masurier for hurling the lobster pots, Chris also taught me many other things including windsurfing. Bobby and Emma for taking me fishin’. Simon for keeping Paula under control. Amanda for making me happy. Sue and Paulo for wine with dinner. Maurice for encouragement. Sacha for cups of tea. Jerome for the great tarts and Sarah for being so bloody enthusiastic.

Without the following people I would have been homeless on my multiple trips to Auckland: Mike and Rae, Carl and Monique, Gilles and Maurine, Emma and Carlos, Gautier and Khadija, Chris and Tracey.

This thesis would not have been possible without the love and encouragement of John, Jenny and Shirley.

Table of Contents

Frontispiece	ii
Abstract.....	iv
Acknowledgements	v
Table of Contents	vii
CHAPTER ONE.....	1
General Introduction	1
Introduction and Rationale.....	1
Marine Soft-sediment Communities.....	3
Top-down Control of Community Structure	5
Cross-habitat Processes.....	8
Halo patterns in soft-sediment systems	9
Scope of Thesis.....	11
Thesis outline.....	12
References.....	13
CHAPTER TWO	24
Inconsistent Effects of Reefs on Different Size Classes of Macrofauna in Adjacent Sand Habitats.....	24
Abstract.....	24
Introduction.....	25
Methods	34
Results.....	39
Discussion.....	47
Acknowledgements.....	51
References.....	51
CHAPTER THREE	60
Reef-Associated Predators Influence Adjacent Soft-Sediment Communities	60
Abstract.....	60
Introduction.....	61
Methods	62
Results.....	67
Discussion.....	76

Conclusions.....	78
Acknowledgements.....	79
References.....	79
Appendices.....	86
CHAPTER FOUR.....	97
Marine Reserves Demonstrate Trophic Interactions across Habitats.....	97
Abstract.....	97
Introduction.....	98
Materials and methods	100
Results.....	103
Discussion.....	105
Acknowledgements.....	108
References.....	109
Appendices.....	115
CHAPTER FIVE	116
Importance of Rock Lobster Size-Structure for Trophic Interactions: Choice of Soft-Sediment Bivalve Prey	116
Abstract.....	116
Introduction.....	117
Methods	120
Results.....	123
Discussion.....	127
Acknowledgements.....	130
References.....	130
CHAPTER SIX	136
General Discussion.....	136
Influence of Reefs on Nearby Soft-Sediment Systems.....	136
Spatial Patterns of Infauna near Reefs.....	142
Placing this Study in Perspective.....	145
New Tools for Soft-Sediment Ecology.....	147
References.....	151

CHAPTER ONE

General Introduction

Introduction and Rationale

The population and community structure of living organisms varies in space and time in response to many physical and biotic factors. Ecology is the integrated study of the relation of living organisms, including human beings, to their environment. Investigators have long recognised how human actions have altered terrestrial environments (Leopold 1933). It is now being acknowledged that anthropogenic activities have drastically altered marine ecosystems (Jackson et al. 2001). As stated in the UN Millennium Declaration (2005b), we must “spare no effort to free all of humanity, and above all our children and grandchildren, from the threat of living on a planet irredeemably spoilt by human activities, and whose resources would no longer be sufficient for their needs”. The Millennium Project (2005a) laid down a challenge to world governments to maintain the life support systems of the planet by achieving a healthy and sustainable environment. Ecology as a science has been criticised for not making a satisfactory contribution to achieving this sustainability (Peters 1991, Underwood 1995). Ecologists can help by understanding, valuing and educating society of the state of the environment and predicting or forecasting environmental change. Ecological research can provide useful predictions regarding the drivers of environmental change and the sustainability of human activities, by testing theories regarding the causes of the distribution and abundance of organisms. Using such predictive models, ecologists can inform the public and global leaders about the implications of policies and identify obstacles to halting environmental degradation.

Peters (1991) discussed how the development of ecological theory has been limited by ‘insoluble questions’ that do not form testable hypotheses. Underwood (1995) commented that decision-makers frequently ask ecologists these types of questions, often concerning the ‘causes’ and ‘mechanisms’ responsible for the spatial and temporal variation in the distribution and abundance of organisms. Underwood

(1995) suggested that instead, probable outcomes of management plans should be explicitly stated, allowing the hypotheses and predictions behind managerial decisions to be tested. Such an approach would enable ecological research to become an increasingly informative component of environmental decision-making.

In comparison to terrestrial systems, ecologists studying assemblages of benthic marine organisms are faced with a paucity of data (Carr et al. 2003). Any comparison of these two systems is limited by the relative “openness” of marine communities (Piepenburg et al. 1997). However, despite the lack of knowledge a variety of observational tools are available for ecologists to investigate and test predictions regarding changes in the distribution and abundance of organisms. These can be grouped into 1) mensurative studies, 2) field manipulations and 3) manipulative laboratory experiments. A mensurative study (*sensu* Hurlbert 1984) investigates the relationships between the organisms of interest and biotic or abiotic variables, and can suggest predictive models regarding causal mechanisms underlying such relationships. These models can then be investigated in the field by manipulative experiments, which involve the manipulation of predictor variables. Laboratory experiments can provide better control of extraneous unexplained variation, allowing better quantification of the variables of interest than field experiments. However, results obtained in laboratory conditions may be irrelevant to make predictions in inherently complex ecological systems in the field (e.g. Dayton and Oliver 1980, Hilborn and Stearns 1982). All these experimental tools are flawed to a lesser or greater extent (Diamond 1986) and thus resultant predictive models are likely to be biased. Peters (1991) suggested that ecologists should test models using a combination of these techniques and treat hypotheses that have not stood the test of manipulative experiments with caution.

In ecology we seek not only to develop predictive theories and hypotheses but also to define broader generalities. Mixed-model designs, with random factors, provide a strong experimental framework and address many of the problems with other methods for addressing the generality of ecological theories (e.g. correlative studies, *sensu* Shrader-Frechette and McCoy 1993). For example, in mensurative and manipulative field studies comparable locations can provide a random factor to explicitly test the generality of other manipulated factors of interest (Beck 1997).

Marine Soft-sediment Communities

Subtidal marine soft sediments are the largest yet least-known habitats on the globe. The majority of these sediments are in the deep sea, where their communities rely on the transport of productivity from surface waters or chemotrophic pathways (Van Dover 2000). In the photic zone sediments have been found to have very high levels of production by micro and macro-benthic algae (Thomas and Cahoon 1993, Heil et al. 2004). The primary production in these sediments is commonly found to be greater than that in overlying waters (Cahoon 1999) and may be regulated by activities of infauna (Snelgrove et al. 1997). The rapid cycling of nutrients observed in these shallow systems also implies that they are important in global elemental budgets (Lohrer et al. 2004).

These productive shallow-water systems are where most of the world's fisheries were historically based (Myers and Worm 2005). In many parts of the world, commercially important benthic (e.g. the oyster *Ostrea edulis* from the Wadden Sea, Riesen and Reise 1982) and pelago-benthic (e.g. the cod *Gadus morhua* from the Grand Banks, Blake 1945) populations have been depleted by harvesting pressure. As overexploitation has occurred, fishing has moved 'down the food web' (Pauly et al. 1998) or turned to less productive habitats (e.g. deep sea, Haddon and Willis 1995). The effective fisheries management of these potentially productive shallow-water habitats would benefit from comprehensive ecological investigations (Lipcius and Cobb 1994).

The worldwide recognition of the significant direct and indirect impacts of fishing (Botsford et al. 1997) has lead scientists to suggest that fisheries management should be approached with an ecosystem perspective (Murawski 2000). However, fisheries scientists often conflict on the interpretation of this approach (Browman and Stergiou 2004). A basic requirement of ecosystem-based fisheries management is an understanding of the top-down control of community structure, in particular food-web interactions and the compensatory effects which occur when certain species are removed by harvesting (Pauly et al. 2000, Jennings 2001). However, this approach is limited by a lack of knowledge of food-webs and requires the strength of trophic interactions to be estimated (Christensen and Walters 2004). This thesis has been designed to contribute towards the understanding of trophic interactions in near-shore soft-sediment systems

and in particular the role of higher-order predators, which are commonly exploited by fishing (Pauly et al. 1998), in controlling community structure.

Ecologists have studied shallow-water soft-sediment habitats for more than a century (e.g. reviews for the North Sea, Pettersson 1896, Ducruet et al. 2000). Various studies have demonstrated how community structure in these habitats can be predicted to some extent by abiotic variables (e.g., Gray 1974, Probert and Grove 1998), competitive interactions (e.g., Peterson 1979a, Hewitt et al. 1997), the supply of recruits (e.g., Watzin 1986, Olafsson et al. 1994) and predation (e.g., Limburg 1972, Thrush et al. 1994).

Thrush (1999) discussed the apparently complex role of predation in structuring soft-sediment communities. His review described how investigations of predation at different spatial scales have often resulted in contrasting measures of community effects. The most frequently used experimental tool to investigate predation in soft-sediment communities is the manipulative field experiment (e.g., Peterson 1982, Jones et al. 1992). Mensurative investigations of predation are less common and have been conducted using either large-scale gradients in predator density (e.g. over 10's-100's km's, Arnold 1984, Eggleston et al. 1992, Kvitek et al. 1992, Seitz et al. 2001) or smaller-scale gradients (from m's - 10's m's) at the edges of adjacent habitats from which predators are presumed to forage (e.g., Ogden et al. 1973, Posey and Ambrose 1994). For example, Kvitek (1992) correlated the density of several soft-sediment bivalves with a gradient in the density of the sea otter *Enhydra lutris* around the Kodiak archipelago. However, this mensurative design could have been confounded by other processes operating at intermediate scales that might influence the distribution of clams in the sediment. Large-scale gradients do not lend themselves to mensurative experiments (*sensu* Hurlbert 1984) as they tend not to allow for the interspersion and randomisation of treatments. Posey and Ambrose (1994) investigated the effect of proximity to a hard-bottom reef on infaunal abundances and suggested that mobile reef-associated predators reduced densities of soft-sediment fauna near the reef edge. Their mensurative and manipulative experiments, due to the spatial extent of the sampling and with some loss of cage treatments during storms, were pseudoreplicated (Barros 2005). Dahlgren et al. (1999) have also suggested that pre-existing gradients in bioturbating fauna and sediment grain-size may have confounded their results.

Laboratory studies of predation in soft sediments have frequently been used to develop models and hypotheses to be tested in the field (Peterson 1979b). However,

there are various examples of such investigations finding no corroborative evidence when hypotheses are tested in manipulative and mensurative field experiments (e.g., Thrush 1986, Kneib 1988, Legendre et al. 1997). Investigations of soft-sediment systems are complicated by a variety of factors and there are few examples of models of predation being supported by all experimental tools (*sensu* Peters 1991, Thrush 1999). It has been suggested that the lack of consistency in results is due to the intrinsic heterogeneous nature of soft-sediment systems (Thrush et al. 1997, Ugland et al. 2003). High levels of spatial and temporal variability in biotic and abiotic factors leads to a highly variable and unpredictable community structure (Thrush et al. 2000). This can result in the inability of various experimental tools to detect the influence of predation from natural variation, particularly at larger scales (Thrush et al. 1997).

This thesis investigates the influence of reef-associated predators on nearby soft-sediment communities. Two models were initially considered, regarding how the influence of predators might change 1) with distance from the reef and 2) with different predator populations. These hypotheses were tested over a variety of scales from small-scale manipulations to large-scale mensurative experiments. A novel observational and experimental approach combining mensurative and manipulative field experiments was also used. This involved a large-scale mensurative experiment, using random locations, to test predator effects with distance from the reef. At each of the locations used there was a pre-existing manipulation of predator populations caused by the establishment of several marine reserves.

Top-down Control of Community Structure

May and Seger (1986) defined predation as mortality of living organisms resulting from consumption by animals. In this thesis such trophic relationships will be termed “predation” for animal prey and “grazing” for plants. Predation can take many forms and is not always comparable between habitat types. For example, in terrestrial environments omnivory has been found to be relatively rare (Yodzis 1984), whilst in aquatic habitats the majority of fauna can be considered omnivorous during at least one stage in their life cycle (Larkin 1978). Predation or grazing may not only affect the abundance of prey but also their population structure (e.g., Holt 1977, Cappuccino 1995). For example, the blue tit (*Parus caeruleus*) can alter the size-structure, sex ratio and microhabitat use of the codling moth (*Cydia pomonella*) in beech forests in the

northeastern USA by preying disproportionately on large (i.e. male) unconcealed larvae (Glen et al. 1981). In central America size-selective grazing by insects on seeds of the sunflower (*Helianthus annuus*) was observed to limit the predispersal fecundity and subsequent recruitment of its progeny in the lower part of their altitudinal range (Louda 1982). In the planktonic freshwater ecosystems of the Great Lakes the removal of large, active predators has been shown to affect the relative abundance and mean size in prey assemblages (Brooks and Dodson 1965, Macan 1965). In marine systems harvesting (i.e. predation by humans) has been shown to alter the density and size-structure of populations of crustacea (Acosta and Robertson 2003) and fish (Jennings et al. 1999).

Predation has been observed to not only directly control the structure of prey populations but also result in the top-down control of communities as a whole. For example, the reintroduction of grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) into parts of the Adirondack National Park, where previously they had been exterminated by humans, caused a cascade of ecological events (Berger et al. 2001). The increase in predation pressure from these reintroduced carnivores led to changes in ungulate foraging behaviour that allowed the reestablishment of rare fruiting plants, which in turn provide an important food source for migrating birds. The impact of artisanal harvesting of a predatory whelk (*Concholepas concholepas*) has been demonstrated by comparison with 'human exclusion zones' on intertidal rocky shores along the coast of Chile (Castilla and Duran 1985). Protection from human exploitation resulted in substantial increases in the density and size-structure of *Concholepas*, and predation by these whelks led to a dramatic decline in the cover of mussels (*Perumytilus purpuratus*), which previously formed dense beds. The mussel beds supported much richer infaunal and epiphytic assemblages than the barnacle-dominated communities that replaced them (Alvarado and Castilla 1996).

The above investigations of the top-down control of community structure are all examples of the results of larger-scale mensurative experiments being corroborated by smaller-scale manipulative experiments inside protected areas (Castilla and Duran 1985, Berger et al. 2001). However, such controls of the processes under investigation are not always available at appropriate spatial scales. For example, in subtidal communities in rocky coastal habitats along the coast of Maine and Nova Scotia, a trophic cascade was predicted to occur between the American lobster (*Homarus americanus*), a sea urchin (*Strongylocentrotus droebachiensis*), and macroalgal populations (Wharton and Mann 1981). The American lobster is extensively fished along the length of this coastline,

resulting in a limited size-distribution (Moody and Steneck 1993). Manipulative experiments have shown that lobster predation can control urchin populations, but mass mortalities in urchins have also been attributed to outbreaks of disease (Scheibling 1996). Models predicting trophic cascades in this system have not been tested in a mensurative design due to the lack of contrast in lobster abundance and size between any comparable sites. Such a design might allow the effects of mortality in urchins by disease to be separated from effects of predation, thus testing the relative importance of the trophic cascade model.

Tegner and Dayton (2000) suggested that no-take marine reserves could provide a large-scale contrast in the density of predators to investigate top-down processes in subtidal rocky reef systems. In several comparable locations in northeastern New Zealand, reserves have been used to investigate the top-down control of community structure. Strong contrasts inside versus outside reserves have been observed in the density and size structure of exploited predators, in particular the snapper *Pagrus auratus* (Willis et al. 2003) and rock lobster *Jasus edwardsii* (Kelly et al. 2000). Unlike a before / after control / impact (BACI) designed study (Underwood et al. 2000), a potential problem with the investigation of established marine reserves is that evidence of higher densities of previously exploited predators does not eliminate other potential models to explain their current patterns of distribution. Therefore, the studies by Willis et al. (2003) and Kelly et al. (2000) were conducted at several ecologically comparable locations, which were treated as a random factor in order to examine the generality of patterns (*sensu* Beck 1997) of recovery of previously exploited fauna within no-take reserves. At each location, sampling sites were interspersed inside and outside the reserves to mitigate the potential confounding influence of other environmental variables. Subsequent investigations have used the existing contrasts in predator density (inside versus outside these marine reserves) to study the existence of a predator-urchin-macroalgal trophic cascade (Shears and Babcock 2002), comparable to that suggested for the northeastern coast of the US (Wharton and Mann 1981). Shears and Babcock (2002) demonstrated that the density of large predators, in particular large rock lobster, could be used to predict the survivorship, density, and population structure of the urchin *Evechinus chloroticus*. Manipulative experiments and mensurative correlations, inside and outside reserves, were also used to demonstrate that grazing by *E. chloroticus* could control macroalgal populations (Shears 2003).

No-take areas offer unique opportunities to investigate how the recovery of large predators affects communities, including the extent, if any, of interactions at different trophic levels (Berger et al. 2001). This thesis investigates the top-down control of communities in coastal shallow-water sediments. A combination of experimental techniques was used to contrast characteristics of the soft-sediment communities between areas with different predator size-structure and density (inside versus outside marine reserves). Field studies used comparable locations, containing reserve and nonreserve areas. Interspersion of sampling sites inside and outside reserves attempted to prevent spatial confounding with continuous environmental gradients (see Kelly et al. 2000, Shears and Babcock 2002, Willis et al. 2003).

Cross-habitat Processes

In ecology, changes in populations of organisms have frequently been observed to coincide with changes in habitat type. ‘Edge effects’ have been suggested to indicate how processes originating from adjacent habitats can influence community structure and the extent of these patterns have often been termed ‘haloes’ (*sensu* Fairweather 1988). There are several studies that have suggested ‘halo’ patterns result from a predator or herbivore foraging given distances from a ‘shelter habitat’ out into a ‘food habitat’. For example, ‘halo’ patterns of bare substrate on rocky shores were described by Lewis (1954) on the west coast of Scotland and by Suchanek (1978) on the east coast of the US. These authors suggested that foraging by limpets, sheltering within the interstices of seaweed and mussel patches respectively, was responsible for the zones of bare substrate. In terrestrial grasslands, Bartholomew (1970) observed comparable ‘grazed’ zones adjacent to patches of shrub in southern California. His study suggested nocturnal foraging by rabbits created this ‘floral halo’. Gradients in abiotic variables have also been observed to result in ‘halo’ patterns in the abundances of certain organisms. For example, labile expression in the orchid *Catasetum viridiflavum* in the tropical rain forests of Panama was found to vary with the intensity of light (Zimmerman 1991). Increased expression of female sexual characteristics correlated with increased light penetration at the edge of old-growth forests, resulting in a ‘halo’ of sexual dimorphism. ‘Halo’ patterns have also been observed in the biomass of phytoplankton in the oligotrophic waters of the equatorial Pacific. Increased biomass of phytoplankton was observed in a down-stream plume from the Galapagos Islands (Martin et al. 1994). This

plume has been correlated with increased concentrations of iron thought to be derived from the volcanic rocks of the islands.

Halo patterns in soft-sediment systems

A variety of studies in temperate and tropical marine ecosystems have described ‘haloes’ in the abundances of organisms in coastal and off-shore sandy habitats near hard-bottom reefs. Some have shown decreases (Ogden et al. 1973, Davis et al. 1982, Riddle et al. 1990, Posey and Ambrose 1994, Barros et al. 2001), whilst others have shown increased density (Davis et al. 1982, Ambrose and Anderson 1990, Dahlgren et al. 1999) or increased variability (Barros et al. 2001) near the reef. Various models have been suggested to predict the patterns observed. These include various processes, such as grazing, predation, biotic disturbance and gradients in abiotic variables.

Ogden (1973) described ‘haloes’ of reduced seagrass cover (0 - 5 m) around patch reefs (~5 m deep) in the Caribbean, that were correlated with nocturnal grazing by a sea urchin (*Antillarum philippi*). Evidence of sub-lethal predation by reef-associated fishes was found by Davis et al. (1982), who suggested that foraging by these fishes could predict the decreased density of an epifaunal sea pen (*Stylatula elongata*) which extended 200 m from the edge of a 13 m deep reef in southern California. In North Carolina Posey and Ambrose (1994) described a pattern of decreasing infaunal abundance from the edge of an offshore reef in 30 m of water. Although there was also a gradient in the distribution of sediment grain sizes with distance from the reef, this ‘infaunal halo’ was suggested to be the result of foraging by reef-associated predators. This theory was supported by observations of fish feeding and results of a gut contents analysis conducted at the same location (Lindquist et al. 1994). However, subsequent investigation of bioturbation at this location found the distribution of infauna with distance from the reef edge to be inversely correlated with the abundance of the burrowing holothurian *Holothuria princeps* (Dahlgren et al. 1999). Laboratory experiments also suggested this large bioturbator could directly reduce the abundance of certain infauna.

Barros et al. (2001) used four comparable sites in Botany Bay southeastern Australia, to investigate the distribution of soft-sediment fauna near a rocky reef. The level of replication used in this study was greater than any previously published investigation. Barros et al. (2001) did not find any consistent trends, however, in the

density of infauna with distance from the reef edge. A subsequent manipulative study at this location using predator exclusion cages found no evidence to support the model that predation controlled community structure in this habitat (Barros 2005). This author also mentioned the “remarkable logistical difficulties” faced by ecologists investigating the role of predation in structuring soft-sediment communities near reefs and highlighted the “poor spatial replication” of previous studies.

Patterns of increasing density or variability of infauna with proximity to hard substrate reefs have also been suggested to result from reef-derived particulate organic matter (Dahlgren et al. 1999). Comparative studies have found reef-derived organic matter to contribute towards the nutrition of suspension and deposit feeding infauna in offshore (Duggins et al. 1989) and beach communities (Soares et al. 1997). For example, the increased densities of the deposit feeding *Holothuria princeps* near the reef edge at two sites in North Carolina may have been the result of reef-derived organic matter (Dahlgren et al. 1999).

The influence of reefs on the hydrodynamic regime influencing nearby sediments has been discussed by various studies (e.g. Alongi 1990, Ambrose and Anderson 1990, Clavier and Garrigue 1999). DeFelice and Parrish (2001) described how onshore wave energy on an exposed Hawaiian coast is reflected by reefs, resulting in increased mean grain size of sediments near the reef edge. The increased variability in community structure near a reef edge observed by Barros et al.(2001), has been suggested by subsequent studies to be related to gradients in sediment characteristics (Barros et al. 2004). Laboratory based hydrodynamic studies have demonstrated how an increase in the mean grain size results in greater ripple height and wavelength (Reineck and Singh 1973). Previous investigations of community composition within these microtopographic features found differences in faunal abundance and diversity between ripple crests and troughs (Hogue and Miller 1981). Barros et al. (2004) found the increased variance and diversity of the infaunal community near the reef to be linked with gradients in the height of ripple formations.

It is apparent that predation is one of several theories predicting gradients in the abundances of infauna in sediments adjacent to reefs. This thesis attempts to investigate these models of biotic and abiotic control by initially observing patterns over a much larger spatial scale than that attempted by previous studies of such communities. The large-scale mensurative study investigating the effect of distance from the reef on community structure and the existing manipulation of predator density allowed the

influence of reef-associated predators to be investigated. The use of random factors and a mixed model design (*sensu* Beck 1997) provided a strong experimental framework from which to suggest predictive models. These were then tested with further manipulative and laboratory experiments.

Scope of Thesis

This thesis aims to describe how the density and size-structure of reef-associated predators, in particular snapper and rock lobster, influences the population and community structure of adjacent soft-sediment infauna in coastal habitats of northeastern New Zealand. The studies that make up this thesis also examine the distribution of other biotic and abiotic variables that may vary with distance from the reef. These variables were also tested for their ability to predict the structure of soft-sediment communities adjacent to reefs.

Previous investigations of infaunal communities adjacent to reefs have mainly focused on smaller-bodied macro-invertebrate fauna (> 0.5 mm) by using 10 cm or 13 cm diameter cores to collect samples (Davis et al. 1982, Posey and Ambrose 1994, Barros et al. 2001). One exception is Dahlgren et al. (1999) who used larger samples (1 m²) to collect large-bodied fauna (> 4 mm). Observations of feeding and gut contents in rock lobster (MacDiarmid 1991) and snapper (Colman 1972) around northeastern New Zealand suggest that they feed on both small and large-bodied infauna. The initial experiments in this thesis therefore considered both small (0.5 - 4 mm) and large-bodied (> 4 mm) infauna.

Previous investigations of predation in soft-sediment communities are likely to have been limited by unknown spatial and temporal variation in predator density (e.g. Hall et al. 1990, Barros 2005). This thesis is the first study to use a contrast in predator density, found inside and outside comparable marine reserves, to investigate processes influencing soft-sediment community structure. An investigation of the role of predator size in structuring prey populations in soft-sediments was also examined by laboratory experiments.

Predictive models exist regarding the recovery of snapper and rock lobster within marine reserves in coastal habitats around northeastern New Zealand (Babcock 2003). This thesis aims to further predict how the recovery of snapper and rock lobster indirectly changes the soft-sediment community adjacent to these coastal reefs. The

development of such predictive tools may assist the management of these ecologically important shallow-water systems by providing information on the effects of fishing for higher-order predators.

Thesis outline

This thesis combines novel field (Chapters 2, 3 & 4) and laboratory experiments (Chapter 5) to test models and hypotheses regarding the distribution of fauna in near-reef sediments. Each chapter contains its own introduction (with rationale, explicit models and hypotheses), methods, results, and discussion. Two mensurative studies combine mensurative observations and existing manipulations of predator density (Chapters 2 & 3) to investigate the distribution of soft-sediment fauna with distance from the reef edge inside and outside marine reserves. Various ecological variables were also measured that have been shown to influence community structure. Chapter 2, which has been submitted to the *Journal of Experimental Marine Biology and Ecology*, focuses on the distribution of small-bodied infauna (0.5 - 4 mm), whilst Chapter 3 is published in *Ecology* and describes the distribution of large-bodied fauna (> 4 mm). Predation is suggested as a model to explain the distribution of the most abundant bivalve observed in Chapter 3. Chapter 4 (*Oecologia in press*) tests this prediction using density and caging manipulations conducted at two locations. Survivorship is compared between caging treatments and open plots both inside and outside marine reserves. The feeding mechanisms inherent in the predation by lobsters of different size classes and species of bivalves were investigated in laboratory choice experiments (Chapter 5, submitted to *Marine Biology*). A range of sizes of lobster was used to test the hypothesis that the size-structure of a predator population can control the relative abundances and population structures of two prey species (Chapter 5). Finally, the findings of the various components of this study are synthesised and discussed in the General Discussion (Chapter 6). The role of predators and other physical factors in structuring subtidal soft-sediment communities is reviewed in light of the findings of this thesis. The value of no-take areas in studying these systems is also discussed along with the ecosystem-level effects resulting from fishing pressure.

References

- Acosta, C. A., and D. N. Robertson. 2003. Comparative spatial ecology of fished spiny lobsters *Panulirus argus* and an unfished congener *P. guttatus* in an isolated marine reserve at Glover's Reef atoll, Belize. *Coral Reefs* **22**:1-9.
- Alongi, D. M. 1990. The ecology of tropical soft-bottom benthic ecosystems. *Oceanography and Marine Biology. An Annual Review* **28**:381-496.
- Alvarado, J. L., and J. C. Castilla. 1996. Tridimensional matrices of mussels *Perumytilus purpuratus* on intertidal platforms with varying wave forces in central Chile. *Marine Ecology Progress Series* **133**:135-141.
- Ambrose, R. F., and T. W. Anderson. 1990. Influence of an artificial reef on the surrounding infaunal community. *Marine Biology* **107**:41-52.
- Arnold, W. S. 1984. The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus* (Rathbun), on the hard clam, *Mercenaria mercenaria* (Linne). *Journal of Experimental Marine Biology and Ecology* **80**:207-219.
- Babcock, R. C. 2003. The New Zealand marine reserve experience: the science behind the politics. Pages 108-119 in P. Hutchings and D. Lunney, editors. *Conserving marine environments. Out of sight out of mind?* Royal Zoological Society of New South Wales, Mosman, New South Wales.
- Barros, F. 2005. Evaluating the importance of predation on subtidal benthic assemblages in sandy habitats around rocky reefs. *Acta Oecologia* **27**:211-223.
- Barros, F., A. J. Underwood, and P. Archambault. 2004. The influence of troughs and crests of ripple marks on the structure of subtidal benthic assemblages around rocky reefs. *Estuarine, Coastal and Shelf Science* **60**:781-790.
- Barros, F., A. J. Underwood, and M. Lindegarth. 2001. The influence of rocky reefs on structure of benthic macrofauna in nearby soft-sediments. *Estuarine, Coastal and Shelf Science* **52**:191-199.

- Bartholomew, B. 1970. Bare zone between California shrub and grassland communities: the role of animals. *Science* **170**:1210-1212.
- Beck, M. W. 1997. Inference and generality in ecology: current problems and an experimental solution. *Oikos* **78**:265-273.
- Berger, J., P. B. Stacey, L. Bellis, and M. P. Johnson. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. *Ecological Applications* **11**:947-960.
- Blake, J. 1945. The Cod. *Nature* **156**:213-213.
- Botsford, L. W., J. C. Castilla, and C. H. Peterson. 1997. The management of fisheries and marine ecosystems. *Science* **277**:509-515.
- Brooks, J. L., and S. I. Dodson. 1965. Predation body size and composition of plankton. *Science* **150**:28-&.
- Browman, H. I., and K. I. Stergiou. 2004. Perspectives on ecosystem-based approaches to the management of marine resources. *Marine Ecology Progress Series* **274**:269-270.
- Cahoon, L. B. 1999. The role of benthic microalgae in neritic ecosystems. Pages 47-86 *in* *Oceanography and Marine Biology*, Vol 37.
- Cappuccino, N. 1995. Novel approaches to the study of population dynamics. *in* N. Cappuccino and P. W. Price, editors. *Population dynamics: new approaches and synthesis*. Academic Press, London, UK.
- Carr, M. H., J. E. Neigel, J. A. Estes, S. Andelman, R. R. Warner, and J. L. Largier. 2003. Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecological Applications* **13**:S90-S107.
- Castilla, J. C., and L. R. Duran. 1985. Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). *Oikos* **45**:391-399.

- Christensen, V., and C. J. Walters. 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* **172**:109-139.
- Clavier, J., and C. Garrigue. 1999. Annual sediment primary production and respiration in a large coral reef lagoon (SW New Caledonia). *Marine Ecology Progress Series* **191**:79-89.
- Colman, J. A. 1972. Food of snapper, *Chrysophrys auratus* (Forster), in the Hauraki Gulf, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **6**:221-239.
- Dahlgren, C. P., M. H. Posey, and A. W. Hulbert. 1999. The effects of bioturbation on the infaunal community adjacent to an offshore hardbottom reef. *Bulletin of Marine Science* **64**:21-34.
- Davis, N., G. R. VanBlaricom, and P. K. Dayton. 1982. Man-made structures on marine sediments: effects on adjacent benthic communities. *Marine Biology* **70**:295-304.
- Dayton, P. K., and J. S. Oliver. 1980. An evaluation of experimental analyses of population and community patterns in benthic marine communities. *in* K. R. Tenore and B. C. Coull, editors. *Marine Benthic Diversity*. University of South Carolina Press, Georgetown, US.
- DeFelice, R. C., and J. D. Parrish. 2001. Physical processes dominate in shaping invertebrate assemblages in reef-associated sediments of an exposed Hawaiian coast. *Marine Ecology Progress Series* **215**:121-131.
- Diamond, J. M. 1986. Overview: laboratory experiments, field experiments, and natural experiments. Pages 3-22 *in* M. L. Cody and J. M. Diamond, editors. *Community Ecology*. Harper & Roe, New York.
- Ducrutoy, J.-P., M. Elliott, and V. N. de Jonge. 2000. The North Sea. Pages 43-63 *in* C. Sheppard, editor. *Seas at the millenium: an environmental evaluation*. Pergamon, Amsterdam, the Netherlands.

- Duggins, D. O., C. A. Simenstad, and J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* **245**:170-173.
- Eggleston, D. B., R. N. Lipcius, and A. H. Hines. 1992. Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. *Marine Ecology Progress Series* **85**:55-68.
- Fairweather, P. G. 1988. Predation creates haloes of bare space among prey on rocky seashores in New South Wales. *Journal of Experimental Marine Biology and Ecology* **114**:261-273.
- Glen, D. M., N. F. Milsom, and C. W. Wiltshire. 1981. The effect of predation by blue tits (*Parus caeruleus*) on the sex ratio of codling moth (*Cydia pomonella*). *Journal of Applied Ecology* **18**:133-140.
- Gray, J. S. 1974. Animal-sediment relationships. *Oceanography and Marine Biology. An Annual Review* **12**:707-722.
- Haddon, M., and T. J. Willis. 1995. Morphometric and meristic comparison of orange roughy (*Hoplostethus atlanticus*: Trachichthyidae) from the Puysegur Bank and Lord Howe Rise, New Zealand, and its implications for stock structure. *Marine Biology* **123**:19-27.
- Hall, S. J., D. Raffaelli, and W. R. Turrell. 1990. Predator-caging experiments in marine systems: a re-examination of their value. *American Naturalist* **136**:657-672.
- Heil, C. A., K. Chaston, A. Jones, P. Bird, B. Longstaff, S. Costanzo, and W. C. Dennison. 2004. Benthic microalgae in coral reef sediments of the southern Great Barrier Reef, Australia. *Coral Reefs* **23**:336-343.
- Hewitt, J. E., P. Legendre, B. H. McArdle, S. F. Thrush, C. Bellehumeur, and S. M. Lawrie. 1997. Identifying relationships between adult and juvenile bivalves at different spatial scales. *Journal of Experimental Marine Biology and Ecology* **216**:77-98.
- Hilborn, R., and S. C. Stearns. 1982. On inference in ecology and evolutionary biology: the problem of multiple causes. *Acta Biotheoretica* **31**:145-164.

- Hogue, E. W., and C. B. Miller. 1981. Effects of sediment micro-topography on small-scale spatial distributions of meiobenthic nematodes. *Journal of Experimental Marine Biology and Ecology* **53**:181-191.
- Holt, R. D. 1977. Predation, apparent competition and the structure of prey communities. *Journal of Experimental Marine Biology and Ecology* **216**:191-210.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**:187-212.
- Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**:629-638.
- Jennings, S. 2001. The effects of fishing on marine ecosystems. *Marine Ecology Progress Series* **213**:127-142.
- Jennings, S., S. P. R. Greenstreet, and J. D. Reynolds. 1999. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology* **68**:617-627.
- Jones, G. P., D. J. Ferrell, and P. F. Sale. 1992. Fish feeding and dynamics of soft-sediment mollusc populations in a coral reef lagoon. *Marine Ecology Progress Series* **80**:175-190.
- Kelly, S., D. Scott, A. B. MacDiarmid, and R. C. Babcock. 2000. Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. *Biological Conservation* **92**:359-369.
- Kneib, R. T. 1988. Testing for indirect effects of predation in an intertidal soft-bottom community. *Ecology* **69**:1795-1805.
- Kvitek, R. G., J. S. Oliver, A. R. Degange, and B. S. Anderson. 1992. Changes in Alaskan soft-bottom prey communities along a gradient in sea otter predation. *Ecology* **73**:413-428.

- Larkin, P. 1978. Fisheries management: an essay for ecologists. *Annual Review of Ecology and Systematics* **9**:57-74.
- Legendre, P., S. F. Thrush, V. J. Cummings, P. K. Dayton, J. Grant, J. E. Hewitt, A. H. Hines, B. H. McArdle, R. D. Pridmore, D. C. Schneider, S. J. Turner, R. B. Whitlatch, and M. R. Wilkinson. 1997. Spatial structure of bivalves in a sandflat: scale and generating processes. *Journal of Experimental Marine Biology and Ecology* **216**:99-128.
- Leopold, A. S. 1933. The conservation ethic. *Journal of Forestry* **31**:634-643.
- Lewis, J. R. 1954. Observations on a high-level population of limpets. *Journal of Animal Ecology* **23**:85-100.
- Limburg, K. E. 1972. Fish predation. *Environmental Biology of Fishes* **51**:141-159.
- Lindquist, D. G., L. B. Cahoon, I. E. Clavijo, M. H. Posey, S. K. Bolden, L. A. Pike, S. W. Burk, and P. A. Cardullo. 1994. Reef fish stomach contents and prey abundance on reef and sand substrata associated with adjacent artificial and natural reefs in Onslow Bay, North Carolina. *Bulletin of Marine Science* **55**:1994.
- Lipcius, R. N., and J. S. Cobb. 1994. Ecology and fishery biology of spiny lobster. Pages 5-15 in P. B. F, C. J. S, and K. J, editors. *Spiny lobster management*. Blackwell Scientific, Victoria, Australia.
- Lohrer, A. M., S. F. Thrush, and M. M. Gibbs. 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* **431**:1092-1095.
- Louda, S. M. 1982. Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. *Ecological Monographs* **52**:25-41.
- Macan, T. T. 1965. Predation as a factor in the ecology of water bugs. *Journal of Animal Ecology* **34**:691-698.
- MacDiarmid, A. B. 1991. Seasonal changes in depth distribution, sex ratio and size frequency of spiny lobster (*Jasus edwardsii*) on a coastal reef in northern New Zealand. *Marine Ecology Progress Series* **70**:129-141.

- Martin, J. H., K. H. Coale, K. S. Johnson, S. E. Fitzwater, R. M. Gordon, S. J. Tanner, C. N. Hunter, V. A. Elrod, J. L. Nowicki, T. L. Coley, R. T. Barber, S. Lindley, A. J. Watson, K. Vanscoy, C. S. Law, M. I. Liddicoat, R. Ling, T. Stanton, J. Stockel, C. Collins, A. Anderson, R. Bidigare, M. Ondrusek, M. Latasa, F. J. Millero, K. Lee, W. Yao, J. Z. Zhang, G. Friederich, C. Sakamoto, F. Chavez, K. Buck, Z. Kolber, R. Greene, P. Falkowski, S. W. Chisholm, F. Hoge, R. Swift, J. Yungel, S. Turner, P. Nightingale, A. Hatton, P. Liss, and N. W. Tindale. 1994. Testing the iron hypothesis in ecosystems of the equatorial Pacific ocean. *Nature* **371**:123-129.
- May, R. M., and J. Seger. 1986. Ideas in ecology. *American Scientist* **74**:256-267.
- Moody, K. E., and R. S. Steneck. 1993. Mechanisms of predation among large decapod crustaceans of the Gulf of Maine coast: functional vs phylogenetic patterns. *Journal of Experimental Marine Biology and Ecology* **168**:111-124.
- Murawski, S. A. 2000. Definitions of overfishing from an ecosystem perspective. *International Council for the Exploration of the Sea Journal of Marine Science* **57**:649-658.
- Myers, R. A., and B. Worm. 2005. Extinction, survival or recovery of large predatory fishes. *Philosophical Transactions of the Royal Society B-Biological Sciences* **360**:13-20.
- Ogden, J. C., R. A. Brown, and N. Salesky. 1973. Grazing by echinoid diadema *Antillarum philippi*: formation of halos around West Indian patch reefs. *Science* **182**:715-717.
- Olafsson, E. B., C. H. Peterson, and W. G. Ambrose, Jr. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanography and Marine Biology. An Annual Review* **32**:19-32.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres. 1998. Fishing down marine food webs. *Science* **279**:860-863.

- Pauly, D., V. Christensen, and C. Walters. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *International Council for the Exploration of the Sea Journal of Marine Science* **57**:697-706.
- Peters, R. H. 1991. *A critique for ecology*. Cambridge University Press, Cambridge, United Kingdom.
- Peterson, C. H. 1979a. Approaches to the study of competition in benthic communities in soft sediments. *Proceedings of the Fifth Biennial International Estuarine Research Conference*; Jekyll Island.
- Peterson, C. H. 1979b. Importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey. *Oecologia* **39**:1-24.
- Peterson, C. H. 1982. Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. *Marine Biology* **66**:159-170.
- Pettersson, O. 1896. Über die Beziehungen zwischen hydrographischen und meteorologischen Phänomenen. *Meteorology and Zoology* **13**:285–321.
- Piepenburg, D., W. G. Ambrose, A. Brandt, P. E. Renaud, M. J. Ahrens, and P. Jensen. 1997. Benthic community patterns reflect water column processes in the northeast water polynya (Greenland). *Journal of Marine Systems* **10**:467-482.
- Posey, M. H., and W. G. Ambrose. 1994. Effects of proximity to an offshore hard-bottom reef on infaunal abundances. *Marine Biology* **118**:745-753.
- Probert, P. K., and S. L. Grove. 1998. Macrobenthic assemblages of the continental shelf and upper slope off the west coast of South Island, New Zealand. *Journal of the Royal Society of New Zealand* **28**:259-280.
- Reineck, H. E., and I. B. Singh. 1973. *Depositional sedimentary environments*. Springer-Verlag, New York.
- Riddle, M. J., D. M. Alongi, P. K. Dayton, J. A. Hansen, and D. W. Klumpp. 1990. Detrital pathways in a coral-reef lagoon. 1. macrofaunal biomass and estimates of production. *Marine Biology* **104**:109-118.

- Riesen, W., and K. Reise. 1982. Macrobenthos of the subtidal Wadden Sea: revisited after 55 years. *Helgolander Meeresuntersuchungen* **35**:409-423.
- Scheibling, R. E. 1996. The role of predation in regulating sea urchin populations in eastern Canada. *Oceanologica Acta* **19**:421-430.
- Seitz, R. D., R. N. Lipcius, A. H. Hines, and D. B. Eggleston. 2001. Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. *Ecology* **82**:2435-2451.
- Shears, N. T. 2003. Response of shallow subtidal reef communities to marine reserve protection in northeastern New Zealand. PhD thesis, University of Auckland, Auckland, New Zealand.
- Shears, N. T., and R. C. Babcock. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* **132**:131-142.
- Shrader-Frechette, K. S., and E. D. McCoy. 1993. *Method in ecology: strategies for conservation*. Cambridge University Press, Cambridge.
- Snelgrove, P., T. H. Blackburn, P. A. Hutchings, D. M. Alongi, J. F. Grassle, H. Hummel, G. King, I. Koike, P. J. D. Lamshead, N. B. Ramsing, and V. Solis-Weiss. 1997. The importance of marine sediment biodiversity in ecosystem processes. *Ambio* **26**:578-583.
- Soares, A. G., T. A. Schlacher, and A. McLachlan. 1997. Carbon and nitrogen exchange between sandy beach clams (*Donax serra*) and kelp beds in the Benguela coastal upwelling region. *Marine Biology* **127**:657-664.
- Suchanek, T. H. 1978. The ecology of *Mytilus edulis* in exposed rocky inter tidal communities. *Journal of Experimental Marine Biology and Ecology* **31**:105-120.
- Tegner, M. J., and P. K. Dayton. 2000. Ecosystem effects of fishing in kelp forest communities. *International Council for the Exploration of the Sea Journal of Marine Science* **57**:579-589.

- Thomas, C. J., and L. B. Cahoon. 1993. Stable isotope analyses differentiate between different trophic pathways supporting rocky-reef fishes. *Marine Ecology Progress Series* **95**:19-24.
- Thrush, S. F. 1986. Community structure on the floor of a sea-lough: are large epibenthic predators important? *Journal of Experimental Marine Biology and Ecology* **104**:171-183.
- Thrush, S. F. 1999. Complex role of predators in structuring soft-sediment macrobenthic communities: implications of changes in spatial scale for experimental studies. *Australian Journal of Ecology* **24**:344-354.
- Thrush, S. F., J. E. Hewitt, V. J. Cummings, M. O. Green, G. A. Funnell, and M. R. Wilkinson. 2000. The generality of field experiments: interactions between local and broad-scale processes. *Ecology* **81**:399-415.
- Thrush, S. F., R. D. Pridmore, J. E. Hewitt, and V. J. Cummings. 1994. The importance of predators on a sandflat: interplay between seasonal changes in prey densities and predator effects. *Marine Ecology-Progress Series* **107**:211-222.
- Thrush, S. F., D. C. Schneider, P. Legendre, R. B. Whitlatch, P. K. Dayton, J. E. Hewitt, A. H. Hines, V. J. Cummings, S. M. Lawrie, J. Grant, R. D. Pridmore, S. J. Turner, and B. H. McArdle. 1997. Scaling-up from experiments to complex ecological systems: where to next? *Journal of Experimental Marine Biology and Ecology* **216**:243-254.
- Ugland, K. I., J. S. Gray, and K. E. Ellingsen. 2003. The species-accumulation curve and estimation of species richness. *Journal of Animal Ecology* **72**:888-897.
- UN Millennium Project. 2005a. Environment and human well-being: a practical strategy.
- UN Millennium Project. 2005b. Investing in development: a practical plan to achieve the millennium development goals.
- Underwood, A. J. 1995. Ecological research and (and research into) environmental management. *Ecological Applications* **5**:232-247.

- Underwood, A. J., M. G. Chapman, and S. D. Connell. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology & Ecology* **250**:97-115.
- Van Dover, C. 2000. The ecology of deep-sea hydrothermal vents. Princeton University Press, Princeton.
- Watzin, M. C. 1986. Larval settlement into marine soft-sediment systems: interactions with the meiofauna. *Journal of Experimental Marine Biology and Ecology* **98**:65-113.
- Wharton, W. G., and K. H. Mann. 1981. Relationship between destructive grazing by the sea urchin, *Strongylocentrotus droebachiensis*, and the abundance of American Lobster, *Homarus americanus*, on the Atlantic Coast of Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences* **38**:1339–1349.
- Willis, T. J., R. B. Millar, and R. C. Babcock. 2003. Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *Journal of Applied Ecology* **40**:214-227.
- Yodzis, P. 1984. How rare is omnivory? *Ecology* **65**:321-323.
- Zimmerman, J. K. 1991. Ecological correlates of labile sex expression in the orchid *Catasetum viridiflavum*. *Ecology* **72**:597-608.

CHAPTER TWO

Inconsistent Effects of Reefs on Different Size Classes of Macrofauna in Adjacent Sand Habitats

Timothy J. Langlois, Marti J. Anderson and Russell C. Babcock

This chapter is in review in the *Journal of Experimental Ecology and Marine Biology*

Abstract

In soft-sediment communities near to reefs a variety of patterns have been described with distance from the reef edge. Various studies have observed contrasting patterns and one study has reported different patterns for different size classes of macrofauna. This study in northeastern New Zealand obtained samples from 24 randomly allocated sites across three locations in a large-scale mensurative sampling design. At each location there was a manipulation of reef-associated predator populations provided by established marine reserves. A concurrent study using the same sites found large macrofauna (> 4 mm) to vary with distance from the reef and relative to predator density. The present study sampled small-bodied infauna (< 4 mm and > 0.5 mm), which was also predicted to change with distance from the reef and predator density. In contrast to patterns found for larger fauna and to previous studies of small macrofauna, no consistent patterns were found for small-bodied infauna. These results suggest that models of community structure need to consider different size classes of macrofauna separately and that multiple sampling methods will assist their investigation. The ‘haloes’ in small-bodied macrofauna around reefs may not be as widespread or consistent as previous studies have suggested. This may be because the spatial extent of previous studies has been limited.

Introduction

Investigations of community structure along discontinuities in marine habitat types have often revealed patterns suggesting interactions between the adjacent biomes (Suchanek 1978, Paine 1980). The term ‘halo’ has been used to describe these ‘edge effects’, which have often been attributed to foraging by mobile fauna from a ‘shelter habitat’ out into a ‘food habitat’ (Ogden et al. 1973, Fairweather 1988). Such ‘haloes’ have been observed in soft-sediment communities adjacent to subtidal temperate reefs (Table 2.1), both natural (Posey and Ambrose 1994, Dahlgren et al. 1999, Barros et al. 2001, Langlois et al. 2005) and artificial (Davis et al. 1982, Ambrose and Anderson 1990), but there is disagreement on the mechanisms behind these patterns (Barros 2005).

‘Haloes’ of decreasing abundance with increasing distance from the reef edge have been described for some organisms (Ambrose and Anderson 1990, Dahlgren et al. 1999, Langlois et al. 2005), but more frequently ‘haloes’ of increasing infaunal abundance with increasing distance have been documented (Davis et al. 1982, Ambrose and Anderson 1990, Posey and Ambrose 1994, Barros et al. 2001, Langlois et al. 2005). Various processes have been proposed which could explain these ‘infaunal haloes’, including enrichment by reef productivity (Dahlgren et al. 1999), bioturbation (Suchanek 1983, Dahlgren et al. 1999), physical disturbance (Barros et al. 2001, DeFelice and Parrish 2001), gradients in physical properties (Ambrose and Anderson 1990, Barros et al. 2004), infaunal predation (Ambrose 1991), predation by reef-associated fauna (Posey and Ambrose 1994, Langlois et al. 2005), or a combination of several factors acting together. The investigation of ‘infaunal haloes’ provides a way of gauging the relative importance of physical (e.g. Gray 1974, Snelgrove and Butman 1994) and biological (e.g. Commito and Ambrose 1985, Thrush et al. 1991, Ambrose 1993) models of community structure at the edge of soft-sediment habitats. A recent study by Barros et al. (2004) has linked an increase in the variance of the infaunal community with gradients in height of ripple formations with distance from the reef edge. Field studies have found infaunal composition to vary between the crests and troughs of sediment ripples (Hogue and Miller 1981, Barros et al. 2004). These observations explained the greater infaunal variance adjacent to the reef reported in an earlier study by Barros et al. (2001).

Table 2.1. Comparison of this study and previous investigations that describe ‘haloes’ in macrofauna near rocky reefs. Small-bodied fauna are larger than 0.5 mm and large-bodied fauna are larger than 4 mm. The biological and physical patterns found are compared, ‘–’ indicates insufficient information was provided in the publication.

Study	Location	Spatial extent and scales of sampling	Significant effect of distance from reef on:			Other features:	
			Small-bodied fauna	Large-bodied fauna	Grain size	Correlation of fauna and grain size	Depth / Aspect
This study	NE New Zealand	3 Locations ~ 100’s km’s 8 Sites ~ km’s (24 sites)	No	–	No	Weak	Shallow ~10 m / Open coast
Langlois et al. 2005	NE New Zealand	3 Locations ~ 100 km’s 8 Sites ~ km’s (24 sites)	–	Yes	No	Yes	Shallow ~10 m / Open coast
Davis et al. 1982	SW USA	2 Sites ~ 10’s m’s	No	Yes	Yes	Yes	Shallow ~13 m / Open coast
Ambrose and Anderson 1990	SW USA	4 Sites ~ 100’s m’s	Yes	–	Yes	Yes	Shallow ~13 m / Open coast
Barros et al. 2004	SE Australia	4 Sites ~ km’S 2 Transects ~ m’s (8 sites)	Yes	–	Yes	Yes	Shallow ~8 m / Embayment
Barros et al. 2001	SE Australia	4 Sites ~ km’s	Yes	–	Yes	Weak	Shallow ~5 m / Embayment
Dahlgren et al. 1999	E USA	1 Site	–	Yes	–	–	Deep ~32 m / Offshore
Posey and Ambrose 1994	E USA	2 Sites ~ 10’s m’s	Yes	–	Yes	–	Deep ~32 m / Offshore

Given the limited spatial extent and sometimes-conflicting observations of haloes in these communities (Barros 2005), it is appropriate for this study to attempt to develop a generalised conceptual model. Mixed model designs provide ecologists with a useful tool to test the generality of patterns by increasing the scope of any statistical tests (Beck 1997). However, given the limited resources of ecologists it is often difficult to conduct experiments with a high level of taxonomic resolution when research effort has been allocated towards testing the generality of models by including replicated random factors (Beck 1997). There is also solid evidence for soft-sediment systems that higher levels of taxonomic resolution (e.g. families or even phyla) reflect patterns shown at the species level quite well (Warwick 1988, Osgard et al. 1998).

Biomass-size spectra have been used to describe communities in marine sediments (e.g. Warwick 1984, Warwick and Clarke 1996). In most communities, the body-size spectrum for species is bimodal (Parry et al. 1999). The central and minimum value of this distribution is approximately equivalent to 0.5 mm spherical diameter, a value used traditionally to separate macrofauna and meiofauna (Warwick 1984). It has been recommended that different core sizes and sieve sizes be used to sample these two different size classes of organisms, in order to improve the efficiency of sample processing (Rumohr 1990).

Given the strong relationship between body size and density in soft-sediment communities (Blackburn et al. 1993), it is necessary to increase sample area and sieve size for larger macrofauna (after Weinberg 1978). Therefore, to investigate the entire macrofaunal community (> 0.5 mm) it is necessary to use more than one sampling method. Only one study of soft-sediment communities near reefs has considered different size classes of macrofauna using more than one method (Dahlgren et al. 1999).

In Dahlgren et al.'s (1999) study, contrasting 'halo' patterns were described for two size classes of infauna sampled at the same sites. Larger-bodied infauna (> 15 mm) were found to be more abundant near the reef edge, whilst smaller fauna (> 0.5 mm) were found to be less abundant near the reef edge. Dahlgren et al. (1999) suggested that these patterns may be due to different processes working on the different size classes of fauna, but also hypothesised that the small fauna may be affected by the actions of some of the larger fauna (e.g. the large bioturbating holothurian *Holothuria princeps*). The most conspicuous predators associated with reefs in northeastern New Zealand are the sparid fish *Pagrus auratus* (snapper) and the rock lobster *Jasus edwardsii*. Observations of feeding and gut contents in rock lobster (MacDiarmid 1991) and snapper (Colman

1972, Berquist 1994) around northeastern New Zealand suggest that they feed on both small and large-bodied soft-sediment macrofauna. In the habitats considered by this study there are a variety of small epibenthic reef-associated predators, including trevally (*Pseudocaranx dentex*), goat fish (*Upeneichthys lineatus*) and smaller-than-legal-size snapper and rock lobster (Cole 1999). Bi-annual monitoring of the study locations, over four years, did not find any consistent spatial or temporal patterns in these small predators (Willis and Babcock 2000). Therefore, this study only attempted to quantify the distribution of greater-than-legal-size snapper and rock lobster. The established marine reserve at each of the study locations provides an existing manipulation of the populations of these large predators (Kelly et al. 2000, Willis et al. 2003).

Various studies have found evidence of interactions with epibenthic predators (Commito and Ambrose 1985, Thrush 1986, Kneib 1988) particularly at larger scales (Kvitek et al. 1988). However, the reduced densities of large infaunal bivalves near reefs found by Langlois et al. (2005) can be attributed largely to rock lobster predation as determined by a subsequent manipulative caging experiment using multiple sites inside and outside two reserves (Langlois et al. in press).

The biomass of small-bodied infauna (greater than 0.5 mm and less than 4 mm) adjacent to coastal subtidal reefs was investigated at three locations having similar subtidal reef / soft-sediment interfaces in northeastern New Zealand. The existence of underlying environmental gradients with distance from the reef, as reported by studies at other locations (Table 2.1), was also investigated. We tested the hypotheses that (1) there will be an effect of distance from the reef on assemblage structure (relative biomass or variability). With the contrast in predator density provided by reserve status at each location, we also tested the hypothesis that (2) any effects (hypothesis 1) will be more marked inside of marine reserves, where large reef-associated predators are abundant and haloes have already been documented for large bivalves (Langlois et al. 2005).

We also tested the hypothesis that (3) patterns occurring in the community will have a strong relationship with environmental variables that may also occur as gradients with distance from the reef edge (e.g. sediment grain size and microtopography, Barros et al. 2001, Barros et al. 2004).

Methods

Study sites and sampling methods

Samples were obtained from eight comparable sites at each of three locations in northeastern New Zealand between January and March of 2002. These twenty-four sites were chosen from areas of similar wave exposure and reef / soft-sediment interfaces within the three locations of Leigh (36° 16' S, 174° 48' E), Tawharanui (36° 22' S, 174° 50' E) and Hahei (36° 50' S, 175° 49' E) (Fig. 2.1). At each location four of the sites lay within a marine reserve and four lay outside. Within each site, sampling was done at each of four distances from the reef edge: 2, 5, 15 and 30 m. These distance strata were comparable to those used in previous studies (e.g. Posey and Ambrose 1994, Barros et al. 2001). Four replicate samples were obtained at each distance using cylindrical cores measuring 13 cm in diameter (132.7 cm²) and 15 cm deep (1991 cm³).

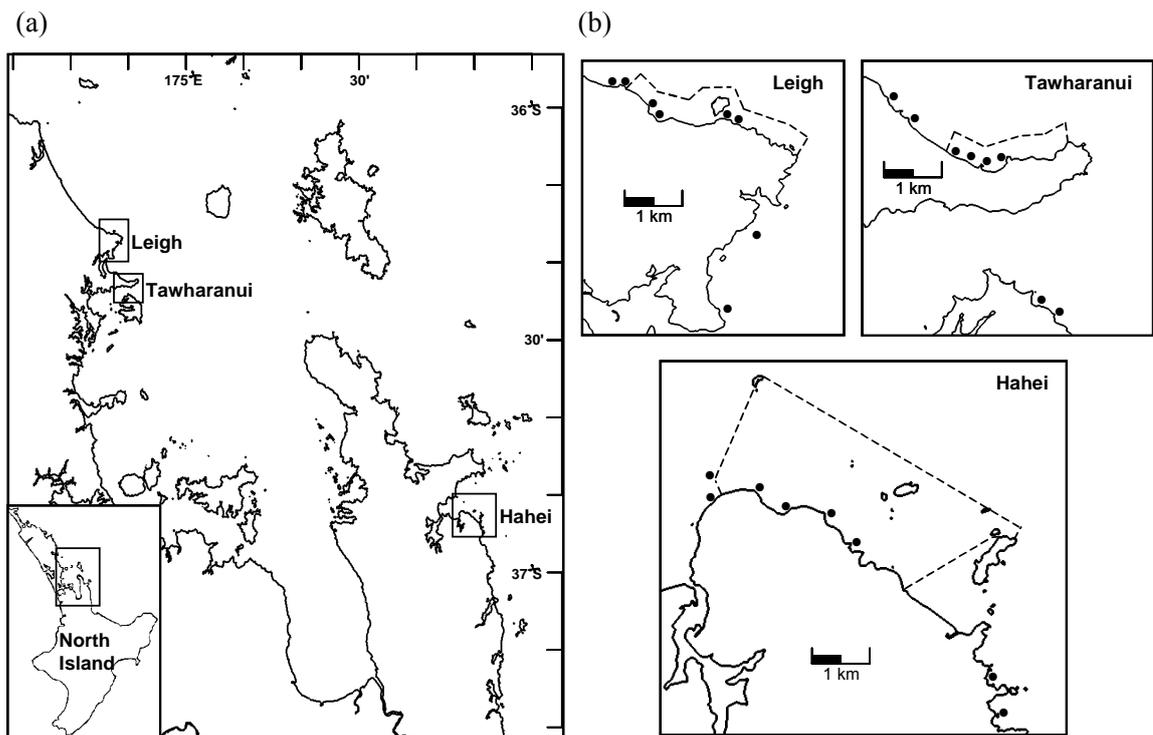


Fig. 2.1. (a) Map of Hauraki Gulf and environs showing the location of the three reserves surveyed in this study. (b) The insets show the reserve boundaries (dashed lines) and survey sites (solid circles) at the three locations.

Pilot studies found that samples from large box-cores (0.5 m² and 15 cm deep), used to sample large macro-invertebrate fauna at these locations (see Langlois et al. 2005), when sieved over 0.5 mm mesh obtained a prohibitively large abundance of small-bodied fauna. The small cores described above were used to obtain more manageable samples and efficiently sample small-bodied fauna over the large spatial extent of this study. In the pilot study, these small cores obtained good precision for the majority of small-bodied infauna. For example, amphipoda had a level of precision of 0.11 at 2 m (with 95% confidence bounds of 0.09 to 0.12) and 0.18 at 30 m (with 95% confidence bounds of 0.14 to 0.22) from the reef edge. However, larger fauna (> 4 mm) were not sampled representatively by the small cores and so were excluded from analyses. For example, the mean density estimate for *Dosinia subrosea* (> 4 mm) at all sites was 0.18 m⁻² using the small cores but 1.25 m⁻² using the larger box cores.

Samples were preserved in 5% formalin before being elutriated (10 times per sample) onto a 0.5 mm sieve. Only small infauna (0.5 – 4.0 mm in size) were examined here. Larger organisms were analysed using other methods (see Langlois et al. 2005). Organisms retained on the sieve were transferred to 70% ethanol and identified to broad taxonomic groups (after Posey and Ambrose 1994, Barros et al. 2001). Biomass was estimated by obtaining ash-free dry weights for each individual taxon (see Table 2.2). Comparative studies for macrofauna have suggested that using a taxonomic resolution based on coarse morphological features would cause little information to be lost whilst allowing greater replication at both large and small scales (e.g. James et al. 1995, Somerfield and Clarke 1995, Chapman 1998).

Environmental variables

The abundance of large predatory and bioturbating infauna was obtained from sampling described by Langlois et al. (2005). Replicate measurements were made of grain size ($n = 3$) by dry sieving and of organic content ($n = 3$) by loss on ignition at 550°C. Bed-form measurements were made ($n = 4$) and an additional measure of bed stress was calculated using a depth-integrated formula developed by Dingler (1974). Wave exposure was estimated using an index of potential fetch (Thomas 1986). The index was calculated by summing the potential fetch for each 10 degree sector of the compass rose. For open sectors of water the maximum fetch was arbitrarily set at 300 km. A list and brief description of the environmental variables measured and subsequently included in analyses is given in Table 2.3. Details of preliminary analyses

Table 2.2. List of 26 taxa from 10 phyla of small-bodied macrofauna (0.5 mm – 4 mm) from 384 sediment cores and used in multivariate analyses.

Phylum	Order / Class	Species
Annelida	Oligochaeta	
	Polychaeta (Sedentaria)	
	Polychaeta (Errantia)	
Arthropoda	Amphipoda	
	Cumacea	
	Decapoda	<i>Callinassa filholi</i> (Milne-Edwards)
	Paguroidea	
	Isopoda	
	Ostracoda	
	Pycnogonida	
	Stomatopoda	
	Tanaidacea	
	Chordates	Cephalochordata
Echinoderms	Ophiuroidea	
	Echinoidea	<i>Echinocardium cordatum</i> (Pennant) <i>Fellaster zelandiae</i> (Gray)
	Holothuroidea	
Echiura		
Mollusca	Bivalvia	<i>Dosinia</i> spp. (juveniles)
		<i>Gari</i> spp.
	Gastropoda	<i>Amalda</i> spp. <i>Cominella</i> spp.
Nematoda		
Nemertea		
Platyhelminthes	Turbellaria	<i>Stylochoplana</i> sp.
Sipuncula	Sipunculidea	<i>Sipunculus</i> sp.

of the individual physical and biological factors, to test for obvious confounding of the sampling design, is described in Langlois et al. (2005). Estimates of the density of snapper at the reef edge were obtained using baited underwater video (BUV) ($n = 4$) during April and May 2002 as part of an ongoing monitoring program. BUV is a relatively new method, which has been shown to provide better measures of relative abundances of snapper than underwater visual censuses by divers in these systems (Willis et al. 2000). Estimates of the density of lobster at the reef edge were obtained by underwater visual census (UVC) of 25 m² quadrats ($n = 10$) during February and March

2002, and the sizes of lobster were estimated using a visual method as described by MacDiarmid (1991). The time discrepancy between the estimates of snapper and rock lobster are not likely to confound any comparison given the relative stability in the temporal variation of these species over summer (Kelly 2001, Willis et al. 2003).

Table 2.3. List of environmental variables used in exploratory analysis.

Variable	Abbreviation	Description
Predatory Infauna	PIn	Infauna considered to be predators (Langlois et al. 2005)
Bioturbating Infauna	BIn	Infauna considered to be bioturbators (Langlois et al. 2005)
Grain Size (GS)	GS1 – GS7	Seven variables expressing percentage of grain sizes of ambient sediments (by weight) falling into particular grain-size classes: (GS1 < 0.125 mm and GS7 > 4mm)
Organics	Org	Sediment organic matter (%)
Bed Stress	Bed	Estimated using bed form ripple measurements and depth.
Exposure	Exp	Estimation of fetch (km)
Depth	Dep	Water depth (m)

Statistical analyses

The overall experimental design consisted of four factors: location (random with three levels: Leigh, Tawharanui and Hahei), status (fixed with two levels: inside versus outside a marine reserve), site (random with four levels, nested within location x status) and distance (fixed with four levels: 2, 5, 15 or 30 m from the reef edge). Although location was treated as a random factor in order to examine the hypothesis of generality (*sensu* Beck 1997), we were also interested in examining the sources of any inconsistencies detected when effects of distance varied among locations. Comparisons within each separate location were sometimes warranted.

Multivariate statistical methods

In order to investigate patterns in the infaunal assemblage as a whole, the entire experimental design was analysed using permutational multivariate analysis of variance (PERMANOVA, Anderson 2001a, McArdle and Anderson 2001). This method is an improvement on previous non-parametric methods because it allows a direct additive partitioning of multivariate variation for more complex models. All tests used 4999 permutations of the raw biomass data or appropriate units as required by the design (see Anderson 2001b). Significant terms and interactions were investigated using *a*

posteriori pair-wise comparisons with the PERMANOVA *t*-statistic and 999 permutations. The variability of the community with distance from the reef was investigated using the index of multivariate dispersion (IMD, Warwick and Clarke 1993). Metric multi-dimensional scaling (mMDS, principal coordinate analysis) was used as an unconstrained ordination method to visualize multivariate patterns with distance from the reef. All multivariate analyses were done on the untransformed biomass data of soft-sediment taxa using Gower's dissimilarity measure, excluding double zeros, calculated between every pair of cores.

Univariate analyses

To estimate effects on individual taxa, the biomass data for each of the most conspicuous and abundant fauna were analysed with separate univariate analyses. These data contained a great many zeros and were too overdispersed to consider using either a GLM or a traditional ANOVA on either raw or transformed values. Therefore, we used an ANOVA to partition the variability and obtain *F*-statistics on the original raw data, with all *P*-values obtained using 4999 permutations of the appropriate exchangeable units (Anderson and ter Braak 2003). This avoided making any particular distributional assumptions, apart from additivity of effects and exchangeability of errors, for these analyses.

Testing for habitat gradients and correlation of fauna with environmental variables

The distribution of coarse sediments and height of ripple formations (microtopography) were analysed using the same ANOVA procedure as for univariate taxa. The distribution of each of these variables with distance from the reef edge at each location was summarised in terms of their range and coefficient of variation. The relationship between the entire set of measured environmental variables (all of those listed in Table 2.3) and the community assemblage was investigated using distance-based multivariate analysis for a linear model (DISTLM, Anderson 2005) and distance-based redundancy analysis (dbRDA, Legendre and Anderson 1999, McArdle and Anderson 2001). The density of large snapper and rock lobster were analysed using a log-linear generalised linear model (GLM) with overdispersed Poisson errors.

Results

Environmental variables

If any of the measured environmental variables displayed a similar or inverse pattern to the density of large predators, such variables would confound the interpretation of results. To test for obvious confounding in the sampling design an analysis of individual physical and biological factors has already been described by Langlois et al. (2005). Also, if higher densities of large predators were not found inside reserves, there would be no basis for subsequent comparisons.

Large rock lobster were found to be consistently and significantly more abundant at reserve sites of all locations ($\chi^2_1 = 54.47, P < 0.001$). The estimated effect was a 3.8-fold higher density in greater-than-legal-size rock lobster at reserve sites compared to nonreserve sites (with 95% confidence bounds of 2.4 to 5.9). Large snapper were also more abundant at the reserve sites of all locations ($\chi^2_1 = 15.07, P < 0.001$). The estimated effect was a 12-fold higher density in greater-than-legal-size snapper at reserve sites compared to nonreserve sites (with 95% confidence bounds of 2.7 to 53.2).

Multivariate analyses

There were 26 taxonomic groups from 10 phyla obtained from 384 sediment cores in this study (Table 2.2). The effect of distance from the reef edge on community structure (in terms of biomass) was found to depend on location and on status (Table 2.4, significant location by status by distance interaction, $F_{6, 54} = 1.42, P < 0.05$). However, out of 36 uncorrected pair-wise comparisons among distance strata within each combination of location x status, only two statistically significant differences were found. Using a significance level (α) of 0.05, this is no more than would be expected by chance alone. Contrary to hypothesis (1), no consistent effect of distance was found. Instead, effects of distance from the reef edge on assemblages were found to vary significantly from site to site (Table 2.4, $F_{54, 288} = 1.9, P < 0.001$), indicating a large amount of small-scale variability. Pair-wise comparisons among distance strata within each site did not show any clear or consistent trends.

Table 2.4. Results of four-factor permutational multivariate analysis of variance (PERMANOVA) on biomass of soft-sediment fauna (26 variables).

Source	df	MS	<i>F</i>	<i>P</i>	Permutable units of Denom MS
Location (Lo)	2	0.258	3.975	< 0.001	24 Si (Lo x St)
Status (St)	1	0.047	0.307	0.863	6 Lo x St
Site (Lo x St)	18	0.065	10.551	< 0.001	384 Res
Distance (Di)	3	0.024	1.502	0.217	12 Lo x Di
Lo x St	2	0.154	2.369	0.005	24 Si (Lo x St)
Lo x Di	6	0.016	1.385	0.056	96 Di x Si (Lo x St)
St x Di	3	0.014	0.814	0.643	24 Lo x St x Di
Di x Si(Lo x St)	54	0.012	1.898	< 0.001	384 Res
Lo x St x Di	6	0.017	1.423	0.05	96 Di x Si (Lo x St)
Residual	288	0.006			
Total	383				

The inconsistent nature of distance effects was also illustrated by the mMDS plot of these assemblages at each location (Fig. 2.2). At several individual sites, there appeared to be a directional change in the community from 2 m through to 30 m distance from the reef edge, but these patterns were not consistent in either their size or direction for different sites. In addition, assemblages at Leigh and Tawharanui were more variable among sites close to the reef than they were at greater distances (i.e., the points representing assemblages at 2 m are more dispersed on the plot than the points corresponding to assemblages at 30 m, Fig. 2.2). The opposite pattern is displayed in the mMDS plot for Hahei, with the near-reef distance strata points being more tightly clustered than those further away. These patterns were confirmed by the values obtained for indices of multivariate dispersion (Table 2.5).

In the analysis of community structure there was also a clear interaction of location and status ($F_{2, 18} = 2.37, P < 0.01$); pair-wise comparisons at each location found a significant effect of status only at Leigh ($t_{24} = 2.05, P < 0.05$) with some slight evidence of an effect at Tawharanui ($t_{24} = 1.89, P = 0.066$) but not at Hahei ($t_{24} = 0.82, P = 0.581$). The mMDS plots (Fig. 2.2) for Leigh and Tawharanui suggested the differences in communities with status were partly due to differences in mean assemblage structure, but may also be due to differences in variability, although the nature of these patterns were not consistent across these two locations.

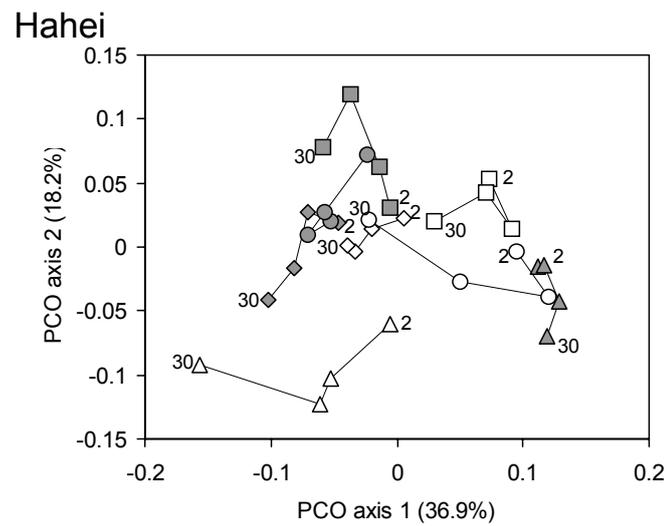
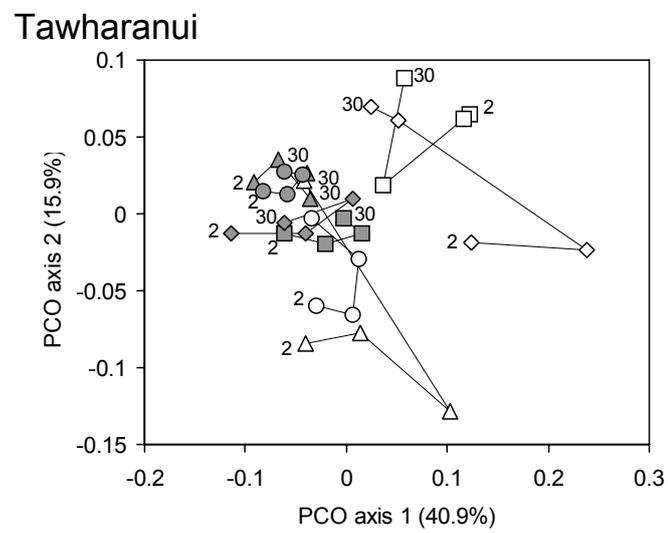
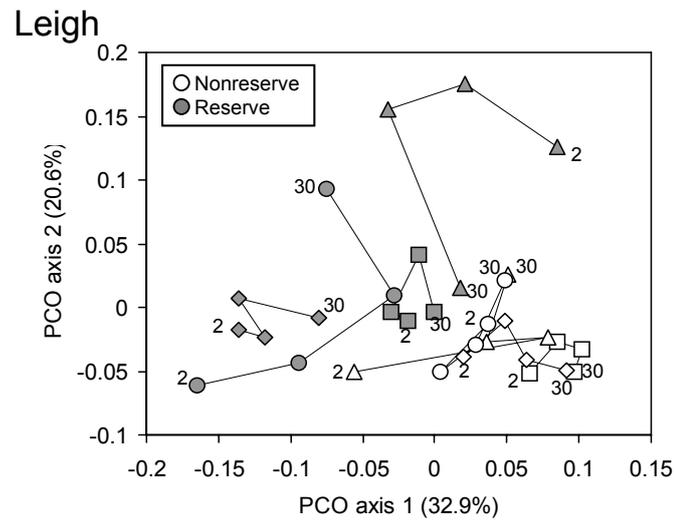


Fig. 2.2. Metric MDS ordination of Leigh (20 taxa), Tawharanui (22 taxa) and Hahei (25 taxa) (with $n = 4$ replicates pooled). On the ordinations, 2 m and 30 m distance strata are indicated and a line connects distance strata within a given site. These analyses were done using Gower's distance measure on untransformed data.

Table 2.5. Indices of multivariate dispersion (IMD) for biomass of soft-sediment fauna (26 variables) at each of the four distances from the reef edge and at each location. Samples ($n = 4$) taken at each distance stratum were pooled and variability was analysed using sites as replicates (no. of sites = 8).

Leigh		Tawharanui		Hahei	
Distance (m)	Dispersion	Distance (m)	Dispersion	Distance (m)	Dispersion
2	1.197	2	1.142	2	0.869
5	0.965	5	1.1	5	0.949
15	0.974	15	0.887	15	1.104
30	0.863	30	0.871	30	1.077

Univariate analyses of prominent taxa

Analyses of individual taxonomic groups showed similar patterns to those found in community analyses. Analyses of the four most conspicuous taxa along with the total biomass of all fauna are presented here. The effect of distance on total biomass of all fauna and the biomass of Errantia, Amphipoda, Sedentaria and Ostracoda varied significantly among sites (Fig. 2.3, Tables 2.6) across the large spatial extent covered by the locations sampled (Fig. 2.1, Table 2.1). Pair-wise comparisons between each distance stratum at each site found a variety of significant differences but none that were consistent across sites. The effects of status on the biomass of Errantia, Sedentaria and the total biomass of all infauna were found to vary significantly among locations, with no consistent patterns uncovered for any of these variables. For the total biomass (Table 2.6, $F_{2, 18} = 9$, $P < 0.01$) and Errantia (Table 2.6, $F_{2, 18} = 5.95$, $P < 0.01$), the interaction was caused by significantly greater biomass inside compared to outside the reserve at Leigh (Total: $t_{24} = 4.45$, $P < 0.01$, Errantia: $t_{24} = 3.26$, $P < 0.05$, Fig. 2.3b, 3e). For Sedentaria, this interaction (Table 2.6, $F_{2, 18} = 6.74$, $P < 0.01$) was due to significantly greater biomass being found inside versus outside the reserve at Hahei ($t_{24} = 2.32$, $P < 0.05$, Fig. 2.3d). Within particular sites, significant trends of increasing or decreasing biomass with distance from the reef edge were not found to be consistent for different taxa or within either level of status. The effect of distance on the biomass of Ostracoda was also found to vary significantly among the three locations (Table 2.6, $F_{6, 54} = 2.96$,

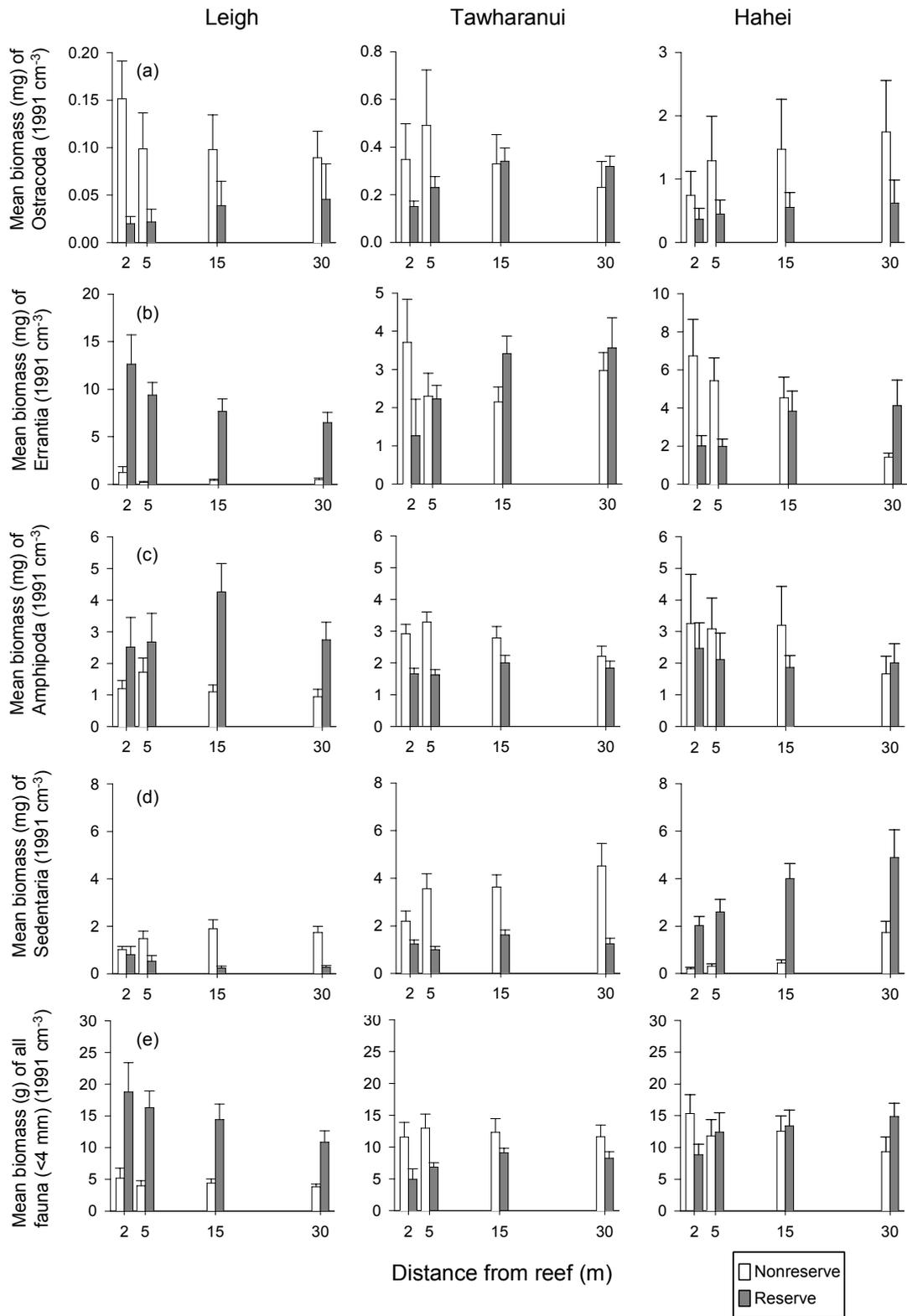


Fig. 2.3. Average (+ 1SE) biomass of (a) Ostracoda, (b) Errantia, (c) Amphipoda, (d) Sedentaria and (e) total of all fauna at each distance stratum, reserve status and location (sites and replicates pooled, $n = 16$).

Table 2.6. Results of four-factor analyses of variance examining effects of site, distance, status and location on the biomass of Ostracoda, Errantia, Amphipoda, Sedentaria and total biomass of all infauna. The denominator mean square for each term is the same as in the PERMANOVA in Table 2.4.

Source	df	Ostracoda		Errantia		Amphipoda		Sedentaria		Total biomass	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Location	2	2.45	0.106	0.91	0.425	0.14	0.873	2.09	0.144	1.30	0.306
Status	1	1.70	0.333	0.52	0.553	0.01	0.945	0.02	0.913	0.19	0.687
Site (Lo x St)	18	61.61	< 0.001	21.24	< 0.001	36.20	< 0.001	24.91	< 0.001	9.62	< 0.001
Distance	3	1.31	0.357	1.13	0.415	2.28	0.181	3.17	0.112	0.43	0.734
Lo x St	2	0.60	0.565	5.95	0.012	1.74	0.210	6.74	0.006	9.01	0.003
Lo x Di	6	2.96	0.014	0.91	0.477	1.41	0.203	1.72	0.124	1.23	0.279
St x Di	3	0.25	0.858	0.2	0.888	1.19	0.376	0.42	0.747	0.31	0.814
Di x Si(Lo x St)	54	2.30	< 0.001	4.51	< 0.001	2.58	< 0.001	3.45	< 0.001	2.26	< 0.001
Lo x St x Di	6	2.21	0.058	2.08	0.071	1.83	0.110	1.52	0.196	2.36	0.051
Residual	288										
Total	383										

$P < 0.05$). However, pair-wise comparisons revealed no significant differences between any pair of distance strata at any location.

Habitat gradients and correlation of fauna with environmental variables

No gradient was seen in the percentage of coarse sediments (sum of all sediment > 0.5 mm) or height of ripple structures (microtopography) with distance from the reef edge (Table 2.7). However, at Leigh there was a pattern of decreasing variation (COV) for the % coarse sediments and for ripple height with increasing distance from the reef edge. This corresponds to decreasing variability in the assemblages for Leigh from 2 m to 30 m as shown in Table 2.5. Unlike the assemblage data, these environmental variables did not show location-specific patterns of either increasing or decreasing variability with distance from the reef edge.

Altogether the 14 environmental variables measured (Table 2.3) explained 30.8% (DISTLM) of the variability in the biomass of the assemblage. However, the dbRDA ordination (Fig. 2.4) showed no clear separation of the distance strata and thus the environmental variables could not explain any distance-from-reef effects, however variable, on community structure. The first two dbRDA axes explained 31.2% of the relationship between the community and the measured environmental variables, but only 6.3% of the total variability in the community data. The analysis did show, however, a gradient from coarse (GS4, 0.5 – 1 mm) to fine (GS2, 0.125 – 0.25 mm) sediments in the assemblage structure and suggested that bed-form characteristics ('Bed') and fetch ('Exp') were also weakly related to community structure (Fig. 2.4).

Table 2.7. Mean, range and coefficient of variation (COV = $100 \times$ standard deviation / mean) for percentage of coarse sediments (> 0.5 mm) and ripple height (cm) sampled at each combination of location and distance.

Location	Distance	% Coarse sediments			Ripple height		
		Mean	Range	COV	Mean	Range	COV
Leigh	2	17.72	1.20-57.94	103.1	5.17	1-14	78.0
	5	18.65	1.18-53.37	98.7	4.58	1-11	72.5
	15	18.75	1.29-47.64	79.8	5.10	1-12	58.0
	30	17.02	1.24-44.41	81.5	4.19	1-8	47.2
Tawharanui	2	11.79	0.33-57.94	149.6	2.81	0.5-5.5	60.3
	5	10.74	0.48-53.37	164.7	2.98	0.5-6	45.3
	15	11.41	1.09-47.64	120.4	2.88	0.5-7	62.9
	30	8.57	0.85-44.41	128.7	2.75	1-6.5	56.3
Hahei	2	11.57	0.78-44.69	138.8	3.29	1-6	43.8
	5	11.17	0.65-42.25	132.7	2.94	1.5-6	44.0
	15	16.55	1.22-47.64	109.1	2.41	1-6	44.8
	30	10.91	0.85-44.41	129.3	2.33	1-5	43.6

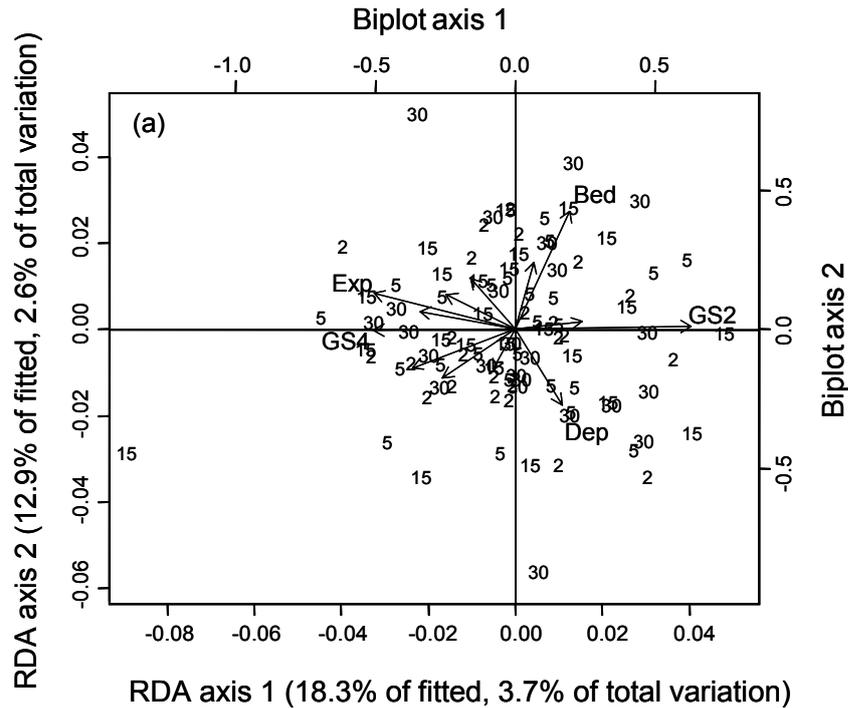


Fig. 2.4. Distance-based RDA ordination of first and second fitted axes relating the environmental variables to the faunal data. Biplot projections are given for the environmental variables listed in Table 2. Arrows are plotted showing the correlations of environmental variables with RDA axis 1 (r_1) and RDA axis 2 (r_2), with the length and direction of the arrow representing the strength and direction of the relationship. Symbols for arrows having length $\sqrt{r_1^2 + r_2^2}$ less than 0.4 were not included.

Discussion

In this study of small-bodied macrofauna, no consistent patterns in the distribution of biomass or variability in the community were observed with increasing distance from the reef edge or at sites with different predator density. Trends of increasing or decreasing biomass with increasing distance from the reef edge were observed at certain sites for certain taxonomic groups. However, there was significant among-site variation in these distance effects for the multivariate community as a whole, for each of the individual taxa analysed and for the total biomass of all infauna. These results contrast with the consistent patterns in several abundant large-bodied taxa sampled in a concurrent study at the same sites (Langlois et al. 2005). However, most other studies that focused on small-bodied macrofauna have consistently found ‘halo’ patterns (Table 2.1). This study has achieved an unprecedented spatial extent of

sampling for soft-sediment fauna near reefs. The use of a mixed-model design has meant greater replication and sampling effort to allow more rigorous testing of the generality of patterns.

The inconsistency of effects could be due to various factors. Three possibilities are (1) lack of sufficient statistical power, (2) inadequacy taxonomic resolution or (3) that small macrofauna respond to various smaller-scale processes in these habitats more dramatically than do larger fauna. Lack of power was unlikely, given the four samples per distance stratum at each site and the use of twenty-four comparable sites in the sampling design. If there were general differences in the community structure it is likely that this design would have detected them. A pilot study found the 32.7 cm² core samples to be inadequate for estimating the density of large-bodied fauna but to achieve good precision for small-bodied infauna. The use of such coarse levels of taxonomic resolution may have led to patterns at the species level being masked by opposing patterns among various species being pooled together (Olsgard et al. 1998). It is also possible that processes in this near-reef sediment environment influence small and large-bodied macrofauna differently.

In the present study, measured environmental variables correlated with little of the biological variability in the assemblages. This suggests that, despite the large-scale replication and high information content of the data obtained, this study was unable to determine which biological or physical processes might be most important in regulating community structure for small infauna (from 0.5 to 4 mm) in this system. The biological and physical patterns found by previous studies of 'infaunal haloes' along reef / soft-sediment interfaces are summarised in Table 2.1. This summary places the results of our study in context by providing a comparison of the spatial extent and range of near-reef sediment environments investigated. Barros (2005) emphasised that most previous studies were done at only one site or at a limited number of sites at relatively small scales (Ambrose and Anderson 1990, Posey and Ambrose 1994, Dahlgren et al. 1999). The most striking difference is the multiple levels of replication and greater spatial extent of sampling undertaken by our study and Langlois et al. (2005). The 'halo' patterns documented by other studies, using similar taxonomic resolution to our study (Table 2-1, Posey and Ambrose 1994, Dahlgren et al. 1999, Barros et al. 2001), and the distribution of large-bodied fauna observed by Langlois et al. (2005), using identical sites, make the lack of consistent patterns in this study particularly interesting. The distinct patterns observed by Langlois et al. (2005) were only observed in the four most-

abundant large-bodied macrofauna. The small-bodied macrofauna in the current study were generally at least 10 times more abundant than the most abundant fauna sampled by Langlois et al. (2005).

Of the previous studies that found evidence of ‘infaunal haloes’ in small-bodied infauna, the majority were conducted in relatively sheltered locations. In particular, the sites used in the two studies off the east coast of North Carolina rarely experience physical disturbance by virtue of their depth (Renaud et al. 1996, Posey and Alphin 2002). The sites sampled by Barros et al. (2001), whilst being of shallow depth, are also relatively sheltered within Botany Bay, SE Australia. These studies, conducted within relatively sheltered locations, found correlations between distance from the reef edge and infauna with various sediment characteristics. However, our study found no gradients in sediment characteristics with distance from the reef and only a weak link between the assemblages of small-bodied infauna and measured environmental variables.

Previous studies of soft-sediment communities have suggested differences between sites could be driven by environmental heterogeneity over study locations (Legendre et al. 1997, Hewitt et al. 1998, Schlacher et al. 1998). This has been attributed to the mobile nature of soft sediments (Hume et al. 2000), which allows physical characteristics of sediments to vary over small spatial scales (Hogue 1982, Gimenez and Yannicelli 2000, Paiva 2001) and small time periods of days to weeks (Grant et al. 1997). It has been suggested that such factors lead to spatial variability at the scale of tens of metres, resulting in the need for sampling at various spatial scales (Morrisey et al. 1992, Cummings et al. 2001), which our study did achieve (Table 2.1).

The lack of consistent patterns in any physical or biological variables could be due to the coastal system sampled here being more disturbed by wave action than those sampled by the majority of the previous studies. Within our region of sampling, the sediments have been described as mobile and observed to be frequently turned over by storm events, down to a depth of 25 m (Hilton and Hesp 1996). Studies of sediments frequently disturbed by wave action and current flow have found associated communities to be relatively impoverished (DeFelice and Parrish 2001). Mobile and well sorted sediments are generally coarser (Buchan 1984) and the mean body-size of infauna has been reported to increase with increasing grain size (Parry et al. 1999). It has also been observed that communities inhabiting mobile sediment in high-energy environments recover quickly from mechanical disturbance such as trawling

(MacDonald et al. 1996, Kaiser et al. 1998). However, these habitats can also support high densities of large and long-lived biogenic reef forming organisms that do not recover quickly from trawl disturbance (Lenihan and Peterson 1998, Fossa et al. 2002). The resilient nature of communities without biogenic reefs (Dernie 2002) could be the result of the sediments being continually turned over and the relatively impoverished infauna redistributed by ambient hydrodynamic forces (Cummings et al. 1995). However, larger-bodied fauna in these communities (Langlois et al. 2005) have been found to be more resilient than smaller-bodied infauna to such disturbance regimes (Haddon et al. 1996). In an environment having relatively high ambient levels of hydrodynamic disturbance, larger-bodied fauna may be more likely to exhibit patterns in response to biological processes such as predation, whilst smaller infauna may be continually redistributed by physical processes (see Table 2-1, Davis et al. 1982, Langlois et al. 2005).

These observations suggest a model for the control of community structure in these infaunal communities. Such a model might be based on the model of Menge and Sutherland (1987) where evidence of biotic processes are only detectable below certain thresholds of physical disturbance. Our investigations would suggest that such a model should be dependent on the body size of the organisms considered.

To further investigate the influence of disturbance on physical and biological regimes in near-reef soft-sediment communities, the existence of 'haloes' in different size classes of infauna should be investigated in a range of disturbance regimes. The 24 sites used in this study were chosen to be of similar aspect and wave exposure, which may have been above the threshold of disturbance that could allow 'infaunal haloes' to be established for small-bodied but not for larger-bodied infauna. The detection of 'haloes' in various size classes of infauna from a range of locations along a disturbance gradient would provide a basis for investigating the above model.

Clearly, more work is warranted regarding the interaction of biological and physical processes on soft-sediment fauna in variable disturbance regimes. Our study indicates that patterns of 'infaunal haloes' around reefs may not be as widespread or consistent as previous small-scale studies would suggest. More complex models that include a combination of the variable effect of biotic and physical factors on different size classes of fauna are likely needed to explain the small-scale natural variation in these communities.

Acknowledgements

Thanks to the following for assistance with field work: Christina Armstrong, Sarah Croft, Laurie Kraaijeveld, Varkenka Lorenzi, Darren Parsons, Tracy Smith, Alison Smith and Andrew Wilson. This research was supported by a scholarship to T.J. Langlois from the Education Committee, States of Jersey, Channel Islands. Thanks also to Bill Ballantine, Richard Ford and Claire Honeywill for ideas and suggestions. This manuscript was greatly improved by comments from *P. Herman* and two anonymous reviewers.

References

- Ambrose, R. F., and T. W. Anderson. 1990. Influence of an artificial reef on the surrounding infaunal community. *Marine Biology* **107**:41-52.
- Ambrose, W. G. 1993. Effects of predation and disturbance by ophiuroids on soft-bottom community structure in Oslofjord: results of a mesocosm study. *Marine Ecology Progress Series* **97**:225-236.
- Ambrose, W. G., Jr. 1991. Are infaunal predators important in structuring marine soft-bottom communities. *American Zoologist* **31**:849-860.
- Anderson, M. J. 2001a. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26**:32-46.
- Anderson, M. J. 2001b. Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:626-639.
- Anderson, M. J. 2005. DistLM v.5: a FORTRAN computer program to calculate a distance-based multivariate analysis for a linear model. Department of Statistics, University of Auckland, New Zealand.

- Anderson, M. J., and C. J. F. ter Braak. 2003. Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* **73**:85-113.
- Barros, F. 2005. Evaluating the importance of predation on subtidal benthic assemblages in sandy habitats around rocky reefs. *Acta Oecologia* **27**:211-223.
- Barros, F., A. J. Underwood, and P. Archambault. 2004. The influence of troughs and crests of ripple marks on the structure of subtidal benthic assemblages around rocky reefs. *Estuarine, Coastal and Shelf Science* **60**:781-790.
- Barros, F., A. J. Underwood, and M. Lindegarth. 2001. The influence of rocky reefs on structure of benthic macrofauna in nearby soft-sediments. *Estuarine, Coastal and Shelf Science* **52**:191-199.
- Beck, M. W. 1997. Inference and generality in ecology: current problems and an experimental solution. *Oikos* **78**:265-273.
- Berquist, R. M. 1994. Patterns of activity and movement in New Zealand snapper, *Pagrus auratus*. MSc Thesis, University of Auckland, Auckland.
- Blackburn, T. M., V. K. Brown, B. M. Doube, J. J. D. Greenwood, J. H. Lawton, and N. E. Stork. 1993. The relationship between abundance and body-size in natural animal assemblages. *Journal of Animal Ecology* **62**:519-528.
- Buchan, J. B. 1984. Sediment analyses. Pages 41-65 in N. A. Holme and A. D. McIntyre, editors. *Methods for the studies of marine benthos*. Blackwell Scientific Publications, London.
- Chapman, M. G. 1998. Relationships between spatial patterns of benthic assemblages in a mangrove forest using different levels of taxonomic resolution. *Marine Ecology Progress Series* **162**:71-78.
- Cole, R. G. 1999. Trophic relationships between fishes and benthic organisms on northeastern New Zealand reefs. *Life & Environment* **49**:201-212.

- Colman, J. A. 1972. Food of snapper, *Chrysophrys auratus* (Forster), in the Hauraki Gulf, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **6**:221-239.
- Commuto, J. A., and W. G. Ambrose. 1985. Multiple trophic levels in soft-bottom communities. *Marine Ecology Progress Series* **26**:289-293.
- Cummings, V. J., R. D. Pridmore, S. F. Thrush, and J. E. Hewitt. 1995. Post-settlement movement by intertidal benthic macroinvertebrates: do common new zealand species drift in the water column? *New Zealand Journal of Marine and Freshwater Research* **29**:59-67.
- Cummings, V. J., S. F. Thrush, J. E. Hewitt, and G. A. Funnell. 2001. Variable effect of a large suspension-feeding bivalve on infauna: experimenting in a complex system. *Marine Ecology Progress Series* **209**:159-175.
- Dahlgren, C. P., M. H. Posey, and A. W. Hulbert. 1999. The effects of bioturbation on the infaunal community adjacent to an offshore hardbottom reef. *Bulletin of Marine Science* **64**:21-34.
- Davis, N., G. R. VanBlaricom, and P. K. Dayton. 1982. Man-made structures on marine sediments: effects on adjacent benthic communities. *Marine Biology* **70**:295-304.
- DeFelice, R. C., and J. D. Parrish. 2001. Physical processes dominate in shaping invertebrate assemblages in reef-associated sediments of an exposed Hawaiian coast. *Marine Ecology Progress Series* **215**:121-131.
- Dernie, K. M. 2002. Predicting post-disturbance recovery of soft-sediment communities. *Marine Ecology Progress Series* **215**:121-131.
- Dingler, J. R. 1974. Wave-formed ripples in nearshore sands. PhD. PhD Thesis, University of California, San Diego.
- Fairweather, P. G. 1988. Predation creates haloes of bare space among prey on rocky seashores in New South Wales. *Journal of Experimental Marine Biology and Ecology* **114**:261-273.

- Fossa, J. H., P. B. Mortensen, and D. M. Furevik. 2002. The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. *Hydrobiologia* **471**:1-12.
- Gimenez, L., and B. Yannicelli. 2000. Longshore patterns of distribution of macroinfauna on a Uruguayan sandy beach: an analysis at different spatial scales and of their potential causes. *Marine Ecology Progress Series* **199**:111-125.
- Grant, J., S. J. Turner, P. Legendre, T. M. Hume, and R. G. Bell. 1997. Patterns of sediment reworking and transport over small spatial scales on an intertidal sandflat, Manukau Harbour, New Zealand. *Journal of Experimental Marine Biology and Ecology* **216**:33-50.
- Gray, J. S. 1974. Animal-sediment relationships. *Oceanography and Marine Biology. An Annual Review* **12**:707-722.
- Haddon, M., T. J. Willis, R. G. Wear, and V. C. Anderlini. 1996. Biomass and distribution of five species of surf clam off and exposed west coast North Island beach, New Zealand. *Journal of Shellfish Research* **15**:331-339.
- Hewitt, J. E., S. F. Thrush, V. J. Cummings, and S. J. Turner. 1998. The effect of changing sampling scales on our ability to detect effects of large-scale processes on communities. *Journal of Experimental Marine Biology and Ecology* **227**:251-264.
- Hilton, M. J., and P. Hesp. 1996. Determining the limits of beach-nearshore sand systems and the impact of offshore coastal sand mining. *Journal of Coastal Research* **12**:496-519.
- Hogue, E. W. 1982. Sediment disturbance and the spatial distributions of shallow-water meiobenthic nematodes on the open Oregon coast. *Journal of Marine Research* **40**:551-573.
- Hogue, E. W., and C. B. Miller. 1981. Effects of sediment micro-topography on small-scale spatial distributions of meiobenthic nematodes. *Journal of Experimental Marine Biology and Ecology* **53**:181-191.

- Hume, T. M., J. W. Oldman, and K. P. Black. 2000. Sediment facies and pathways of sand transport about a large deep water headland, Cape Rodney, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **34**:695-717.
- James, R. J., M. P. L. Smith, and P. G. Fairweather. 1995. Sieve mesh-size and taxonomic resolution needed to describe natural spatial variation of marine macrofauna. *Marine Ecology Progress Series* **118**:187-198.
- Kaiser, M. J., D. B. Edwards, P. J. Armstrong, K. Radford, N. E. L. Lough, R. P. Flatt, and H. D. Jones. 1998. Changes in megafaunal benthic communities in different habitats after trawling disturbance. *International Council for the Exploration of the Sea Journal of Marine Science* **55**:353-361.
- Kelly, S. 2001. Temporal variation in the movement of the spiny lobster *Jasus edwardsii*. *Marine and Freshwater Research* **52**:323-331.
- Kelly, S., D. Scott, A. B. MacDiarmid, and R. C. Babcock. 2000. Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. *Biological Conservation* **92**:359-369.
- Kneib, R. T. 1988. Testing for indirect effects of predation in an intertidal soft-bottom community. *Ecology* **69**:1795-1805.
- Kvitek, R. G., A. K. Fukayama, B. S. Anderson, and B. K. Grimm. 1988. Sea otter foraging on deep-burrowing bivalves in a California coastal lagoon. *Marine Biology* **98**:157-167.
- Langlois, T. J., M. J. Anderson, and R. C. Babcock. 2005. Reef associated predators influence adjacent soft-sediment communities. *Ecology* **86**:1508-1519.
- Langlois, T. J., M. J. Anderson, R. C. Babcock, and S. Kato. in press. Marine reserves demonstrate trophic interactions across habitats. *Oecologia*.
- Legendre, P., and M. J. Anderson. 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* **69**:512.

- Legendre, P., S. F. Thrush, V. J. Cummings, P. K. Dayton, J. Grant, J. E. Hewitt, A. H. Hines, B. H. McArdle, R. D. Pridmore, D. C. Schneider, S. J. Turner, R. B. Whitlatch, and M. R. Wilkinson. 1997. Spatial structure of bivalves in a sandflat: scale and generating processes. *Journal of Experimental Marine Biology and Ecology* **216**:99-128.
- Lenihan, H. S., and C. H. Peterson. 1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecological Applications* **8**:128-140.
- MacDiarmid, A. B. 1991. Seasonal changes in depth distribution, sex ratio and size frequency of spiny lobster (*Jasus edwardsii*) on a coastal reef in northern New Zealand. *Marine Ecology Progress Series* **70**:129-141.
- MacDonald, D. S., M. Little, N. C. Eno, and K. Hiscock. 1996. Disturbance of benthic species by fishing activities: a sensitivity index. *Aquatic Conservation* **6**:257-268.
- McArdle, B. H., and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* **82**:290-297.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental-stress and recruitment. *American Naturalist* **130**:730-757.
- Morrisey, D. J., L. Howitt, A. J. Underwood, and J. S. Stark. 1992. Spatial variation in soft-sediment benthos. *Marine Ecology Progress Series* **81**:197-204.
- Ogden, J. C., R. A. Brown, and N. Salesky. 1973. Grazing by echinoid diadema *Antillarum philippi*: formation of halos around West Indian patch reefs. *Science* **182**:715-717.
- Olsgard, F., P. J. Somerfield, and M. R. Carr. 1998. Relationships between taxonomic resolution, macrobenthic community patterns and disturbance. *Marine Ecology Progress Series* **172**:25-36.

- Osgard, F., P. J. Somerfield, and M. R. Carr. 1998. Relationships between taxonomic resolution, macrobenthic community patterns and disturbance. *Marine Ecology Progress Series* **172**:25-36.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. The Third Transley Lecture. *Journal of Animal Ecology* **49**:667-685.
- Paiva, P. C. 2001. Spatial and temporal variation of a nearshore benthic community in southern Brazil: implications for the design of monitoring programs. *Estuarine, Coastal and Shelf Science* **52**:423-433.
- Parry, D. M., M. A. Kendall, A. A. Rowden, and S. Widdicombe. 1999. Species body size distribution patterns of marine benthic macrofauna assemblages from contrasting sediment types. *Journal of the Marine Biological Association of the United Kingdom* **79**:793-801.
- Posey, M., and T. Alphin. 2002. Resilience and stability in an offshore benthic community: responses to sediment borrow activities and hurricane disturbance. *Journal of Coastal Research* **18**:685-697.
- Posey, M. H., and W. G. Ambrose. 1994. Effects of proximity to an offshore hard-bottom reef on infaunal abundances. *Marine Biology* **118**:745-753.
- Renaud, P. E., W. G. Ambrose, S. R. Riggs, and D. A. Syster. 1996. Multi-level effects of severe storms on an offshore temperate reef system: benthic sediments, macroalgae, and implications for fisheries. *Marine Ecology* **17**:383-398.
- Rumohr, H. 1990. Soft bottom macrofauna: collection and treatment of samples. International council for the exploration of the sea, Copenhagen.
- Schlacher, T. A., P. Newell, J. Clavier, M. A. Schlacher-Hoenlinger, C. Chevillon, and J. Britton. 1998. Soft-sediment benthic community structure in a coral reef lagoon: the prominence of spatial heterogeneity and 'spot endemism'. *Marine Ecology Progress Series* **174**:159-174.

- Snelgrove, P. V. R., and C. A. Butman. 1994. Animal-sediment relationships revisited: cause versus effect. *Oceanography and Marine Biology. An Annual Review* **32**:111-177.
- Somerfield, P. J., and K. R. Clarke. 1995. Taxonomic levels, in marine community studies, revisited. *Marine Ecology Progress Series* **127**:113-119.
- Suchanek, T. H. 1978. The ecology of *Mytilus edulis* in exposed rocky inter tidal communities. *Journal of Experimental Marine Biology and Ecology* **31**:105-120.
- Suchanek, T. H. 1983. Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea Thalassinidae) bioturbation. *Journal of Marine Research* **41**:281-298.
- Thomas, M. L. H. 1986. A physically derived exposure index for marine shorelines. *Ophelia* **25**:1-13.
- Thrush, S. F. 1986. Community structure on the floor of a sea-lough: are large epibenthic predators important? *Journal of Experimental Marine Biology and Ecology* **104**:171-183.
- Thrush, S. F., R. D. Pridmore, J. E. Hewitt, and V. J. Cummings. 1991. Impact of ray feeding disturbances on sandflat macrobenthos: do communities dominated by polychaetes or shellfish respond differently? *Marine Ecology Progress Series* **69**:245-252.
- Warwick, R. M. 1984. Species size distributions in marine benthic communities. *Oecologia* **61**:32-40.
- Warwick, R. M. 1988. The level of taxonomic resolution required to detect pollution effects on marine benthic communities. *Marine Pollution Bulletin* **19**:259-268.
- Warwick, R. M., and K. R. Clarke. 1993. Increased variability as a symptom of stress in marine communities. *Journal of Experimental Marine Biology and Ecology* **172**:215-226.

- Warwick, R. M., and K. R. Clarke. 1996. Relationships between body-size, species abundance and diversity in marine benthic assemblages: facts or artefacts. *Journal of Experimental Marine Biology and Ecology* **202**:63-71.
- Weinberg, S. 1978. The minimal area problem in invertebrate communities of Mediterranean rocky substrata. *Marine Biology* **49**:33-40.
- Willis, T. J., and R. C. Babcock. 2000. Cape Rodney to Okakari Point Marine Reserve fish monitoring programme, 2000. Department of Conservation, Wellington, New Zealand.
- Willis, T. J., R. B. Millar, and R. C. Babcock. 2000. Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. *Marine Ecology Progress Series* **198**:249-260.
- Willis, T. J., R. B. Millar, and R. C. Babcock. 2003. Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *Journal of Applied Ecology* **40**:214-227.

CHAPTER THREE

Reef-Associated Predators Influence Adjacent Soft-Sediment Communities

Timothy J. Langlois, Marti J. Anderson and Russell C. Babcock

This chapter has been published in *Ecology* July (2005)

Abstract

Marine reserves provide a large-scale manipulation of predator densities, which provides a means to investigate the potential effects of predation. The effects of reef-associated predators were examined in northeastern New Zealand by comparing soft-sediment assemblages at sites having different densities of large predators. Large rock lobsters (*Jasus edwardsii*) were 3.8 times more abundant and large snapper (*Pagrus auratus*) 12 times more abundant, on average, at reserve sites compared with nonreserve sites. The overall structure of infaunal communities differed between areas with high predator densities (reserve) and those with lower densities (fished). Sites with consistently higher densities of snapper and lobster were found to have lower biomass of two bivalve species and the greatest decreases were found near the reef edge (2 - 5 m). For several fauna a strong gradient in their density with distance from the reef was observed at both reserve and nonreserve sites. The hermit crab *Pagurus novizelandiae* occurred more frequently near the reef edge, whilst the heart urchin *Echinocardium cordatum* and bivalve *Dosinia subrosea* occurred more frequently further away from the reef. The results suggest that certain species in this assemblage are affected differently by a combination of physical and biological forces. We concluded that, where reef predators are removed by fishing pressure, a resultant indirect effect is an increase in prey species in adjacent soft-sediment assemblages.

Introduction

In ecology, 'haloes' have been described in many contexts (Suchanek 1978, Fairweather 1988) and generally are thought to result from a predator or herbivore foraging given distances from a 'shelter habitat' out into a 'food habitat'. Studies in temperate marine ecosystems have found 'infaunal haloes', areas of decreased density of soft-sediment fauna adjacent to reefs, at a variety of scales (0 - 30 m Davis et al. 1982, 0 - 70 m Posey and Ambrose 1994). Various models have been proposed to explain these patterns, including bioturbation (Suchanek 1983, Dahlgren et al. 1999), physical disturbance (DeFelice and Parrish 2001, Barros et al. 2004), recruitment (Watzin 1986), infaunal predation (Ambrose 1991), and predation by reef fauna (Posey and Ambrose 1994, Barros et al. 2001). The model suggesting reef-associated predators are responsible for haloes is supported by studies of gut contents of fish on temperate reefs (Lindquist et al. 1994). However, convincing demonstrations of predators causing haloes of prey in these systems have been hampered due to limited replication and problems involved with caging studies (Posey and Ambrose 1994, Barros 2005) and the lack of large-scale manipulations (Thrush et al. 2000).

The most conspicuous predators associated with reefs in northeastern New Zealand are the sparid fish *Pagrus auratus* (snapper) and the rock lobster *Jasus edwardsii*. Snapper occur across the continental shelf from estuarine habitats to depths > 100 m (Paul 1976) and are generalist predators that take primarily large (> 4 mm) invertebrate prey from both soft-sediment and rocky reefs (Babcock et al. 1999). Studies have shown that rock lobster, although commonly assumed to spend the majority of their time on rocky reefs, do forage up to one kilometre over adjacent sandy areas (Kelly et al. 1999).

Snapper and rock lobster are both heavily fished in northeastern New Zealand's coastal areas. They occur at higher densities inside no-take marine reserves: greater than legal-sized snapper (> 270 mm fork length) and rock lobster (> 100 mm carapace length) are 14 times and 3.7 times respectively more abundant inside compared to outside no-take reserves (Babcock et al. 1999). In this region the influence of predators on rocky reefs has been examined using the existing large-scale experimental framework provided by marine reserves (Babcock et al. 1999, Shears and Babcock 2002). Using this approach, it is possible to examine the potential role of large reef-

associated predators in structuring adjacent soft-sediment communities, by contrasting the densities of predators and prey found inside versus outside several no-take areas. At these locations several other large macro-invertebrate predators, including rays (*Dasyatis brevicaudata* and *Myliobatis tenuicaudatus*) and octopus (*Octopus maorum*), associate with the reef / soft-sediment interface but have not been observed to occur at higher densities within reserves.

Unlike a BACI designed study, a potential problem with studies of established marine reserves is that evidence of a negative relationship between predator densities and densities of prey does not eliminate other potential models (Hurlbert 1984, Underwood et al. 2000). Results might be confounded by other factors that may structure the soft-sediment community (e.g. wave action, sediment grain-size distributions, organic matter, infaunal interactions). Due to the complex nature of soft-sediment marine communities, it has been recognized that to investigate patterns and processes, large-scale and long-term studies are needed to avoid problems associated with making erroneous inferences from short-term manipulations (Thrush et al. 2000). In addition, the inclusion of several scales of sampling and replication at larger scales can be used to unravel these issues and to test hypotheses concerning the generality of patterns and processes (Underwood 1997).

In this study we used three marine reserves as part of a large-scale experiment with replication at various scales. The hypothesis was that predation by large reef-associated predators would result in lower densities of large (> 4 mm) soft-sediment macrofauna inside reserves compared to outside reserves (*Predator model*). A further hypothesis was that predation would decrease with increasing distances from the reef, resulting in a 'halo' pattern in the community (Posey and Ambrose 1994), i.e., an increase in prey densities with increasing distances from the reef edge (*Distance model*).

Methods

Study sites and sampling methods

New Zealand's northeastern bioregion contains eight reserves, three of which are considered broadly comparable biotype replicates (Shears 2003, Willis et al. 2003a). This study was carried out between January and March of 2002, using these three locations as a random factor to explicitly test the generality of any potential differences in the effects of marine reserve status (as in Beck 1997). The Cape Rodney to Okakari

Point (Leigh) Marine Reserve (36° 16'S, 174° 48'E) was gazetted in 1975, the Tawharanui Marine Park (36° 22'S, 174° 50'E) was declared a no-take area in 1981 and the Te Whanganui a Hei (Hahei) Marine Reserve (36° 50'S, 175° 49'E) was gazetted in 1993 (Fig. 3.1). At each location eight sites of similar wave exposure and reef / soft-sediment interfaces were chosen, four inside and four outside each marine reserve. To ensure interspersed, in each case, two of the nonreserve sites were located north and the other two located south of the reserve (see Fig. 3.1). The use of three locations and the interspersed of sites on either side of each reserve area was also to mitigate the potential confounding influence of other environmental variables (such as recruitment or food supply). Within each site, sampling was done at each of four distances from the reef edge: 2, 5, 15 and 30 m. These distance strata were comparable to previous studies of infaunal haloes (Posey and Ambrose 1994) and within the likely foraging ranges of snapper (Parsons et al. 2003) and rock lobster (MacDiarmid et al. 1991). At each distance, six replicate samples were obtained using box quadrats measuring 0.5 m² (1 m x 0.5 m) x 13 cm deep (0.065 m³). Sediment was excavated by hand with a metal scoop and sieved in the field using a sieve with a 4 mm mesh. Other studies from different systems (Ambrose 1991, Lindquist et al. 1994, Posey and Ambrose 1994, Dahlgren et al. 1999) have focused on smaller infauna (> 0.5 mm) where the corresponding reef-associated predators were also smaller. In the present study, we focused on larger infauna (> 4 mm), corresponding to the larger reef-associated predators found within reserves (snapper are ~316 mm mean total length and rock lobster are ~109.9 mm mean carapace length inside reserves, Babcock et al. 1999). Pilot studies showed that large (> 4 mm) fauna in the soft sediment around the chosen locations were relatively patchy in their spatial distribution, thus requiring a sampling unit area of 0.5 m². Organisms retained on the sieve were preserved in 5% formalin and later transferred to 70% ethanol. All organisms were identified to the lowest taxonomic resolution possible. Dry weight biomass estimates were made for all infauna, with the shells of bivalves being excluded from such measurements.

Environmental variables

Physical environmental variables measured at each distance stratum at each site included replicate measurements of grain size ($n = 3$) by dry sieving (with a focus on the proportion of coarse sediments), organic content ($n = 3$) by ignition at 550°C, bed form

measurements ($n = 4$). Wave exposure was estimated using an index of potential fetch (Thomas 1986). The index was calculated by summing the potential fetch for each 10

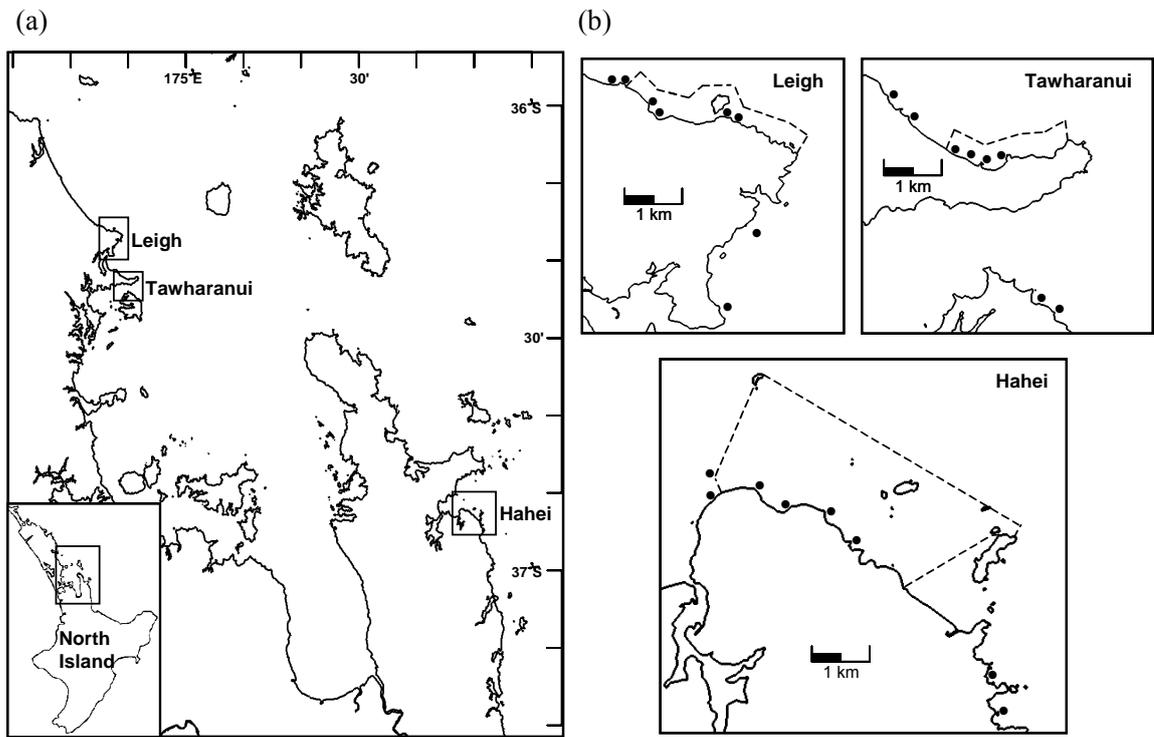


Fig. 3.1. (a) Map of Hauraki Gulf and environs showing the location of the three reserves surveyed in this study. (b) The insets show the reserve boundaries (dashed lines) and survey sites (solid circles) at the three locations.

degree sector of the compass rose. For open sectors of water the radial distance was arbitrarily set to be 300 km. Estimates of the density of snapper at the reef edge were obtained using baited underwater video (BUV) ($n = 4$) during April and May 2002 as part of an ongoing monitoring program. BUV is a relatively new method, which has been shown to provide better measures of relative abundances of snapper than underwater visual censuses by divers in these systems (Willis et al. 2000). Estimates of the density of lobster at the reef edge were obtained by underwater visual census (UVC) of 25 m² quadrats ($n = 10$) during February and March 2002, and the sizes of lobster were estimated using a visual method as described by MacDiarmid (1991). The time discrepancy between the estimates of snapper and rock lobster are not likely to confound any comparison given the relative stability in the temporal variation of these species over summer (Kelly 2001, Willis et al. 2003a). Densities of octopus and other species known to be predators of soft-sediment fauna were also looked for during rock lobster census dives. From the samples of the infaunal assemblages, the densities of infaunal bioturbators and infaunal predators were also recorded. A list and brief description of the environmental variables measured and subsequently included in analyses are given in Appendix 3.A.

Statistical analyses

The overall experimental design consisted of four factors: location (random with three levels: Leigh, Tawharanui and Hahei), status (fixed with two levels: inside versus outside a marine reserve), site (random with four levels, nested within location x status) and distance (fixed with four levels: 2, 5, 15 or 30 m from the reef edge). Although location was treated as a random factor in order to examine the hypothesis of generality, we were also interested in examining the sources of any inconsistencies detected when effects of either status or distance varied among locations. Thus, separate individual comparisons at each location were sometimes warranted.

To test for any obvious confounding in the study design preliminary analyses of several individual physical and biological predictor variables (see Appendix 3.A) were done using univariate analysis of variance (ANOVA). These variables were abundant enough to be analysed using univariate ANOVA on either raw or transformed values, except for the density of large snapper and rock lobster, which were analysed using a log-linear GLM model with overdispersed Poisson errors. All ANOVA analyses were preceded by Cochran's test for homogeneity of variance (see Underwood 1981, Winer 1991). Where the test showed significant heterogeneity, variables were transformed to $x' = \ln(x + 1)$. Analyses of variance were followed by *a posteriori* Student-Newman-Keuls tests (SNK tests) on appropriate terms of the model found to be significant with $P < 0.05$.

In order to investigate effects on the infaunal assemblage as a whole, the entire experimental design was analysed using permutational multivariate analysis of variance (PERMANOVA, Anderson 2001a, McArdle and Anderson 2001). All tests used 4999 permutations of the raw data or appropriate units as required by the design (see Anderson 2001b). Significant terms and interactions were investigated using *a posteriori* pair-wise comparisons with the PERMANOVA *t*-statistic and 999 permutations. All multivariate analyses were done on the untransformed abundance data of soft-sediment taxa using Gower's dissimilarity measure, including double zeros, calculated between every pair of cores. Double zeros were not excluded because in this study of potential predatory effects joint absences were considered to increase similarity among cores.

Overall patterns of variation in the community were visualized with metric multi-dimensional scaling (MDS) plots. To examine the nature of significant community effects, canonical analysis of principal coordinates (CAP, Anderson and

Robinson 2003) was used. In addition, the particular taxa that might be responsible for any group differences seen in the CAP plots were investigated by calculating correlations with canonical ordination axes (Anderson and Willis 2003). The relationship between the entire set of measured environmental variables (all of those listed in Appendix 3.A) and the community assemblage was investigated using distance-based redundancy analysis (dbRDA, Legendre and Anderson 1999, McArdle and Anderson 2001).

To estimate effects on individual taxa, the biomass data for each of the most conspicuous and abundant fauna were analysed with separate univariate analyses. These data contained a great many zeros and were too overdispersed to consider using either a GLM or a traditional ANOVA on either raw or transformed values. Therefore, we assumed only additivity of effects and exchangeability of errors and used an ANOVA to partition the variability and obtain *F*-statistics on the original raw data, but all *P*-values were obtained using 4999 permutations of the appropriate exchangeable units (Anderson and ter Braak 2003). This avoided making any particular distributional assumptions, apart from exchangeability, for these analyses.

Results

Examination of potential confounding factors

The following results are from the preliminary analyses of individual physical and biological factors to test for obvious confounding in the design with the factors of either distance or reserve status. If higher densities of large predators were not found inside reserves, there would be no basis for subsequent comparisons. Also, if any of the other measured environmental variables displayed a similar or inverse pattern to the density of large predators, such variables would confound the interpretation of results.

Large rock lobster were found to be consistently and significantly more abundant at reserve sites of all locations (Fig. 3.2a, $\chi^2_{1,2} = 54.47$, $P < 0.001$). The estimated effect was a 3.8-fold higher density in greater-than-legal-size rock lobster at reserve sites compared to nonreserve sites (with 95% confidence bounds of 2.4 to 5.9). No octopuses or rays were seen during the censuses of rock lobster. Large snapper were also more abundant at the reserve sites of all locations (Fig. 3.2b, $\chi^2_{1,2} = 15.07$, $P < 0.001$). The estimated effect was a 12-fold higher density in greater-than-legal-size

snapper at reserve sites compared to nonreserve sites (with 95% confidence bounds of 2.7 to 53.2).

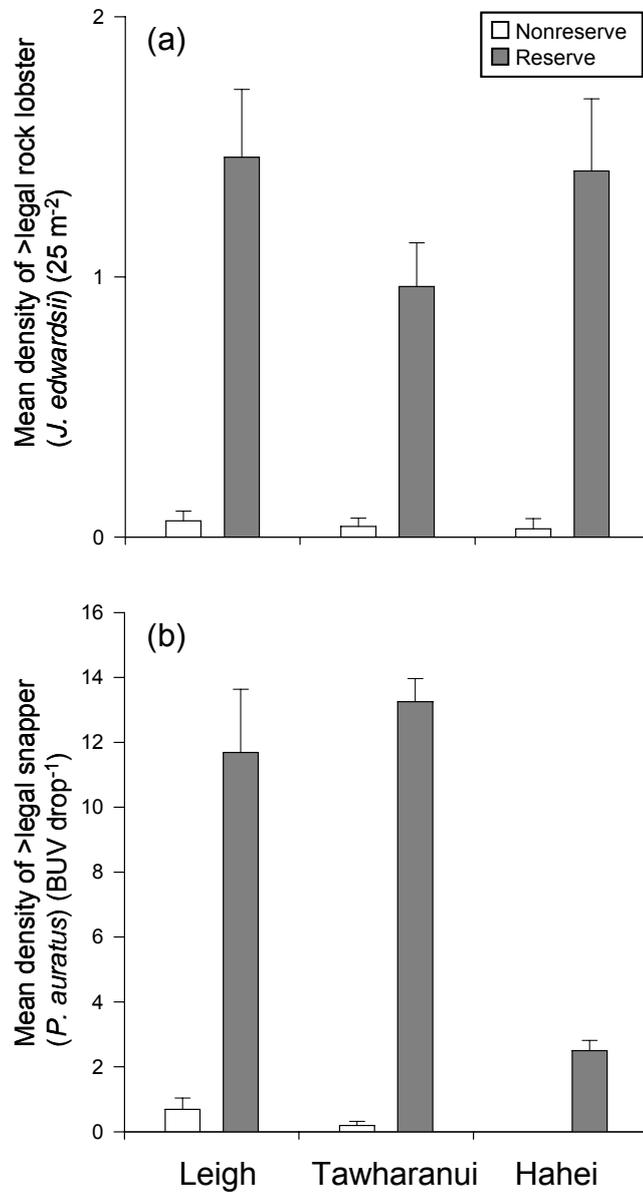


Fig. 3.2. Average (+ 1SE) density of legal-sized (a) rock lobster (*Jasus edwardsii*) per 25 m² and (b) snapper (*Pagrus auratus*) per baited underwater video (BUV) deployment at reserve and nonreserve sites of each location.

There was an apparent negative relationship between the average abundance of all predatory infauna (Appendix 3.B) and the percentage of coarse sediments (Appendix 3.C). However, there were no consistent patterns in the proportions of coarse sediments or in the distribution of potential infaunal predators (Morton and Miller 1968), with a significant interaction between location and status in each case (Appendices C and D, $F_{2,18} = 6.52, P < 0.01$ and $F_{2,18} = 5.9, P < 0.05$, respectively). The most abundant bioturbator was the heart urchin *Echinocardium cordatum*. This species is an important prey item for snapper associating with soft-sediments (Colman 1972) and so could potentially confound any comparison of the effects of bioturbation and predation. The abundance of all infaunal bioturbators was significantly different among locations (Appendices C and D, $F_{2,18} = 5.34, P < 0.05$), with lower average abundances at Leigh. The lack of any consistent patterns in these variables indicated that comparisons of soft-sediment assemblages inside versus outside these reserves would not be confounded in any systematic way with these physical and biological factors.

Multivariate analyses

Distance-based redundancy analysis

The first three axes from the dbRDA explained 30.1% of the variability in the fitted relationship between the ecological and environmental variables and 10.5% of the overall variability in the ecological data. In the biplot of the first two dbRDA axes (Appendix 3.E), lobster density was positively correlated with the first axis. Variation in sediment characteristics, from fine to coarse grain sizes (see Appendix 3.A), correlated strongly with the second axis. However, there was no distinct separation of reserve and nonreserve observations along this axis. A biplot of the first and third dbRDA axes (Appendix 3.E) showed a fairly clear separation between the reserve and nonreserve observations, mainly on the third axis, which correlated strongly with lobster density and, to a lesser extent, snapper density. There was no strong correlation between predatory or bioturbating infauna and any of the first three dbRDA axes. These results indicated that although variation in sediment texture explained a large portion of the variability in the biota, any effects of status on the community would likely be due to densities of large predators.

Predator model

In total there were 61 taxa from 7 phyla obtained from 576 box quadrats in this study (Appendix 3.F). The interaction found in the multivariate analysis between location and status (Appendix 3.G, $F_{2, 18} = 2.44$, $P < 0.001$) indicated that analyses of status should be done separately for each location. There were significant differences between assemblages at sites inside the reserves versus those at nonreserve sites for each location: Leigh ($t_{24} = 2.88$, $P < 0.001$), Tawharanui ($t_{24} = 1.95$, $P < 0.001$) and Hahei ($t_{24} = 2.37$, $P < 0.001$). There was a significant multivariate interaction between distance and site ($F_{54, 480} = 1.37$, $P < 0.01$), indicating small-scale variability in the structure of the assemblages from site to site at different distances from the reef.

Patterns in the assemblage shown in the mMDS ordinations for each location (Fig. 3.3a) indicated that communities at Leigh and Hahei differed between reserve and nonreserve sites but no clear effect was evident at Tawharanui. The effect at Leigh largely appeared to be caused by greater variability (dispersion) of the assemblages within the reserve. Canonical analyses for Tawharanui and Hahei (Fig. 3.3b) showed a strong separation between reserve and nonreserve assemblages with an allocation success of 75% for Tawharanui and 93.8% for Hahei. The canonical plot for status effects at Leigh also appeared to show a strong effect (good separation) but the allocation success was only 59.4% suggesting reserve effects were not as clear for Leigh as for the other two locations. (Note that with two groups, an allocation success of 50% or less would suggest that any separation of groups seen in the CAP plot was purely arbitrary). Correlations of individual species with the canonical axis for status indicated that only a few individual taxa were responsible for the separation between reserve and nonreserve sites (Table 3.1).

Distance model

There were significant differences among assemblages located different distances from the reef (Appendix 3.G, $F_{3, 6} = 2.25$, $P < 0.05$). The lack of any significant interaction between distance and either location or status suggested that the effect of distance from the reef edge on the soft-sediment fauna was consistent at larger scales, although variable at individual sites. Results of pairwise *a posteriori* comparisons found communities that were 2 m and 5 m from the reef edge did not differ

significantly from each other, but were significantly different from communities either 15 m or 30 m away from the reef edge (Appendix 3.H).

The multivariate distance by site interaction (Appendix 3.G) was also illustrated in the mMDS ordination of distance strata where no consistent pattern could be discerned (Appendix 3.I). However, the canonical correlation of the assemblage data with distance from the reef edge showed some slight evidence of a gradient in community structure ($\delta^2 = 0.27$) from 2 m to 30 m (Appendix 3.I). The correlations of the individual species with the canonical axis for distance from the reef showed this gradient to be due to variation in both relative abundances and species composition (Table 3.2).

Univariate analyses of prominent taxa

Correlation of species with the canonical axis for reserve status suggested that the bivalves *Dosinia subrosea* and *Myadora striata*, the 3rd and 5th most abundant taxa, consistently occurred with greater abundance at sites outside reserves (Table 3.1). These bivalves showed the strongest influence of status with a consistent pattern of greater average biomass outside reserves (Appendix 3.D, Fig. 3.4a, *D. subrosea* $F_{1,2} = 21.09$, $P < 0.05$, Fig. 3.4b, *M. striata* $F_{1,2} = 8.84$, $P < 0.05$). *D. subrosea* had a mean density of 0.56 m⁻² inside reserves and 1.3 m⁻² outside reserves. Correlation of species with the canonical axis for distance from the reef also suggested that *D. subrosea* occurred in greater average abundance away from the reef edge (Table 3.2). However, there was a pattern of increasing biomass of *D. subrosea* with distance from the reef at Tawharanui but not at Hahei or Leigh, resulting in a significant interaction between location and distance ($F_{6,54} = 2.64$, $P < 0.05$). *M. striata* exhibited a pattern of low biomass within the reserves and a pattern of increasing biomass with distance from the reef outside the reserves but not inside, producing a significant interaction of St x Di ($F_{3,6} = 2.64$, $P < 0.05$), with a mean density of 0.16 m⁻² inside reserves and 7.2 m⁻² outside reserves. In addition, the gastropod *Philine angasi* occurred more frequently at sites inside reserves but at a lower abundance compared to other taxa (Table 3.1).

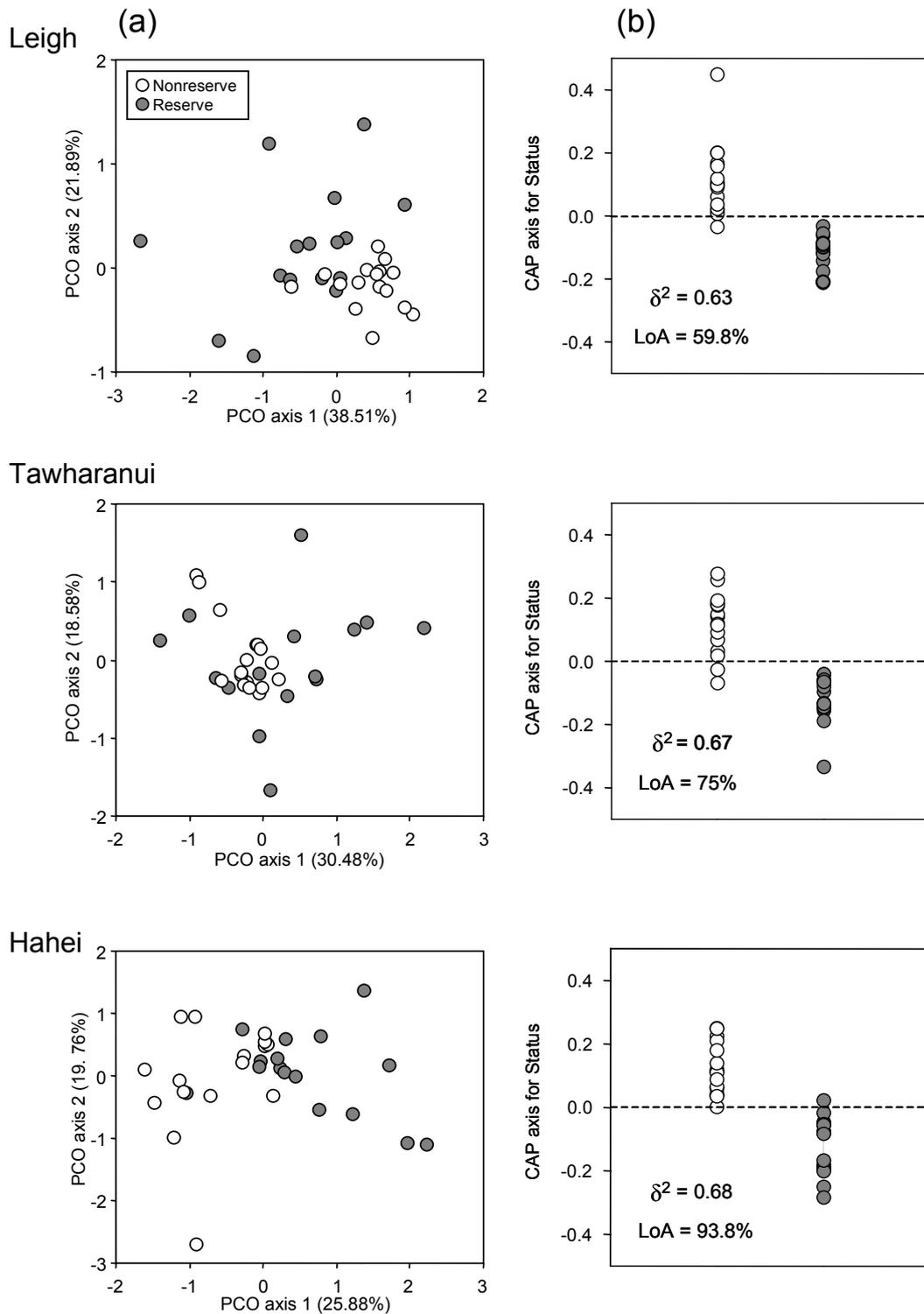


Fig. 3.3. (a) Unconstrained metric MDS plots and (b) constrained CAP plots of the effect of reserve status at each of Leigh (37 taxa), Tawharanui (41 taxa) and Hahei (49 taxa) (with $n = 6$ replicates pooled). The percentage of total variation explained by each axis of the metric MDS plot is given. Additional text on the CAP figure indicates squared correlation coefficients (δ^2) and results of Leave-one-out Allocation (LoA) success.

Table 3.1. Correlations of individual species (r) with canonical axis for reserve status for each of the three locations, as shown in Fig. 3.3 (right-hand side). For each location the mean (SE) abundance of species from nonreserve (fished) and reserve sites is shown.

Name	Class / Order	Leigh			Tawharanui			Hahei		
		r	Fished	Reserve	r	Fished	Reserve	r	Fished	Reserve
a) Positive correlation (Nonreserves)										
<i>Myadora striata</i>	Bivalvia	0.71	0.37(0.07)	0	0.29	0.34(0.07)	0.22(0.06)	0.58	0.38(0.07)	0.02(0.02)
<i>Dosinia subrosea</i>	Bivalvia	0.61	0.95(0.12)	0.04(0.02)	0.04	0.77(0.13)	0.72(0.16)	0.25	0.24(0.07)	0.08(0.04)
b) Negative correlation (Reserves)										
<i>Philine angasi</i>	Gastropoda	-0.44	0.01(0.01)	0.06(0.03)	-0.22	0.01(0.01)	0.06(0.04)	-0.26	0.04(0.02)	0.14(0.04)
Contrasting patterns										
c) - Leigh, + Tawharanui and + Hahei										
<i>Scalpomactra scalpellum</i>	Bivalvia	-0.18	0	0.01(0.01)	0.59	0.37(0.07)	0	0.46	0.19(0.05)	0.03(0.02)
d) + Leigh, - Tawharanui and - Hahei										
<i>Amalda novaezelandiae</i>	Gastropoda	0.61	1.9(0.19)	0.4(0.08)	-0.24	0.99(0.12)	1.19(0.14)	-0.58	0.15(0.04)	1.81(0.03)
<i>Marginella pygmaea</i>	Gastropoda	0.23	0.21(0.06)	0.03(0.02)	-0.56	0.13(0.03)	1.44(0.22)	-0.2	0	0.03(0.02)
<i>Pagurus novizelandiae</i>	Decapoda	0.47	1.49(0.04)	0.4(0.08)	-0.07	0.45(0.11)	0.43(0.1)	-0.23	0.5(0.09)	0.88(0.14)
e) - Leigh, - Tawharanui and + Hahei										
<i>Sigalion capense</i>	Polychaeta	-0.56	0	0.12(0.04)	-0.1	0.05(0.02)	0.07(0.04)	0.29	0.09(0.03)	0.02(0.02)
<i>Ovalipes catharus</i>	Decapoda	-0.42	0.01(0.01)	0.06(0.03)	-0.17	0	0.01(0.01)	0.23	0.02(0.02)	0

A positive correlation (a) indicates species associated with nonreserve sites, while a negative correlation (b) indicates species associated with reserve sites. Several species (c-e) displayed strong patterns of contrasting positive (+) and negative (-) correlations at different locations. Species are given in decreasing order of the absolute value of their average for the correlation across the three locations. Species that occurred at fewer than 6 sites (out of a total of 24) and with an average absolute value of the correlation among locations less than 0.25 were not included.

For the other most abundant species, the opisthobranch *Amalda novaezelandiae*, the hermit crab *Pagurus novizelandiae* and the heart urchin *Echinocardium cordatum*, there were no consistent effects of reserve status but some evidence of effects of distance from the reef. *A. novaezelandiae* occurred with greater abundance within reserve sites at Tawharanui and Hahei but at nonreserve sites at Leigh (Table 3.1), *P. novizelandiae* occurred with greater frequency near the reef edge (Table 3.2) and *E. cordatum* occurred with greater frequency further away from the reef edge. The most abundant species, *A. novaezelandiae*, was primarily responsible for the strong negative relationship between the mean density of predatory infauna and the percentage of coarse sediments (Appendix 3.C). That is, the biomass of *A. novaezelandiae* (Fig. 3.4c, Appendix 3.D) had a positive relationship with the percentage of fine sediments. The biomass of *P. novizelandiae* and *E. cordatum* were not found to have any consistent effects due to significant small-scale variability at the site level (Fig. 3.4d & 3.4e, Appendix 3.D).

Table 3.2. Correlations of individual species (r) with the canonical axis for distance from the reef, as shown in Appendix 3.I. The mean abundance (SE) of species from each distance stratum is shown.

Name	Distance from the reef edge	Mean (SE)			
		r	2 m	5 m	15 m
Positive correlation (near)					
<i>Pagurus novizelandiae</i>	0.34	0.83(0.11)	0.86(0.1)	0.48(0.08)	0.59(0.1)
<i>Lophopagurus cristatus</i>	0.24	0.06(0.04)	0.06(0.03)	0.02(0.02)	0.01(0.01)
<i>Philine angasi</i>	0.22	0.01(0.01)	0.14(0.04)	0.03(0.02)	0.03(0.01)
<i>Marginella pygmaea</i>	0.22	0.58(0.13)	0.36(0.09)	0.2(0.08)	0.08(0.03)
<i>Nemertea</i> spp.	0.20	0.07(0.02)	0.08(0.02)	0.06(0.02)	0.06(0.02)
Negative correlation (far)					
<i>Echinocardium cordatum</i>	-0.49	0.10(0.03)	0.03(0.02)	0.34(0.07)	0.49(0.09)
<i>Dosinia subrosea</i>	-0.46	0.27(0.05)	0.34(0.06)	0.45(0.09)	0.81(0.12)
<i>Dosinia anus</i>	-0.40	0.01(0.01)	0.01(0.01)	0.1(0.03)	0.22(0.06)
<i>Amalda depressa</i>	-0.30	0.01(0.01)	0	0.01(0.01)	0.04(0.02)
<i>Paguristes setosus</i>	-0.26	0.13(0.05)	0.09(0.03)	0.24(0.07)	0.41(0.13)
<i>Amalda australis</i>	-0.24	0.03(0.01)	0	0.06(0.02)	0.03(0.02)

Species are grouped by positive correlation (near to the reef) and negative correlation (far from the reef), and are given in decreasing order of the absolute value of their correlation. Species that occurred at fewer than 6 sites (out of a total of 24) and with an average absolute value of the correlation among locations less than 0.2 were not included.

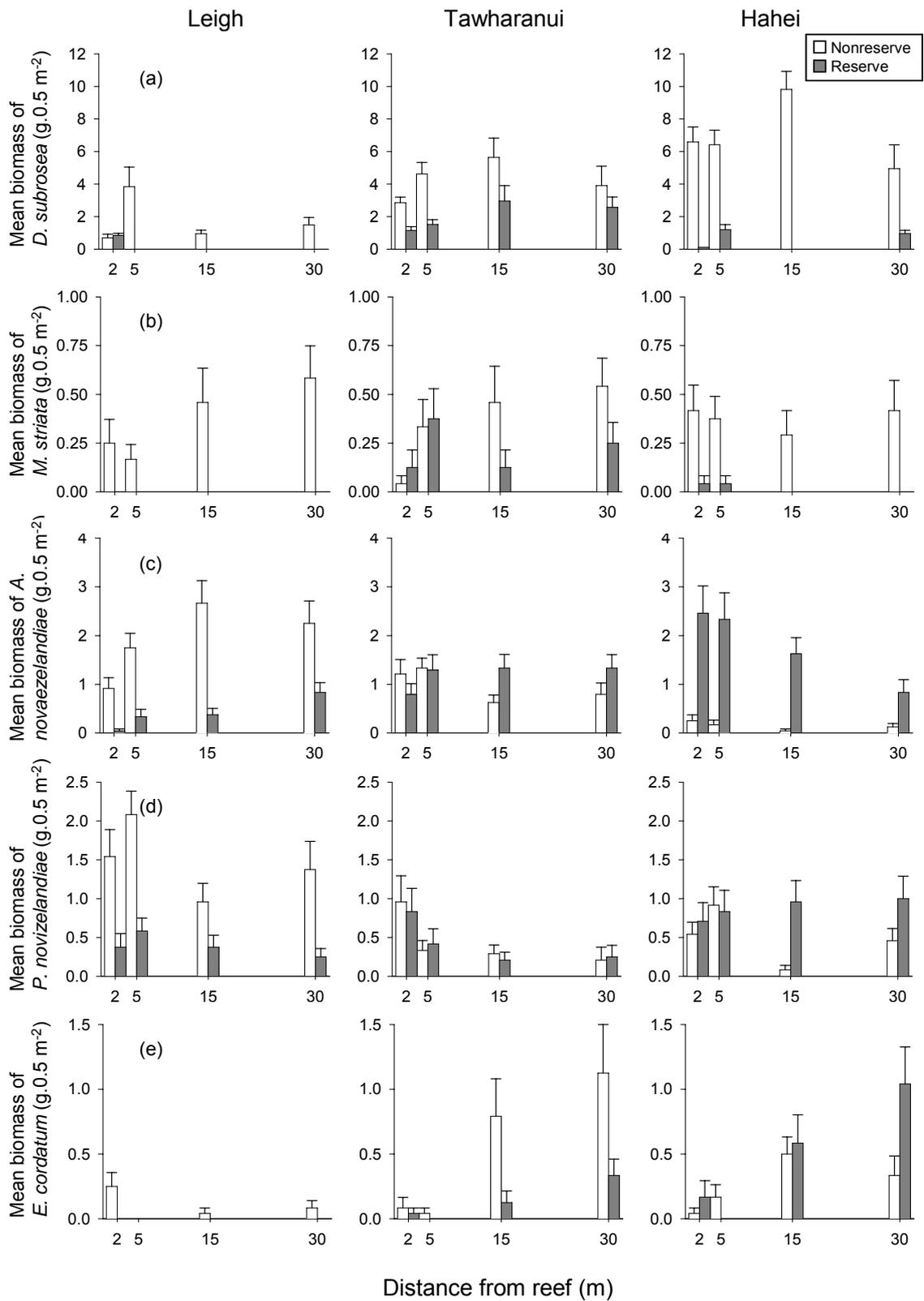


Fig. 3.4. Average (+ 1SE) biomass of (a) *Dosinia subrosea*, (b) *Myadora striata*, (c) *Amalda novaezelandiae* (d) *Pagurus novizealandiae* and (e) *Echinocardium cordatum* at each distance stratum, reserve status and location (sites and replicates pooled, $n = 24$).

Discussion

Sites with consistently higher densities of snapper and lobster were found to have lower biomass of several bivalve species, including the third and fifth most abundant taxa: *Dosinia subrosea* and *Myadora striata*. This result was consistent across several locations separated by 100's of kilometres. In contrast, the biomass of the three other most abundant species, the heart urchin *Echinocardium cordatum*, the hermit crab *Pagurus novizelandiae* and the opisthobranch *Amalda novaezelandiae*, did not show any consistent pattern with predator density.

Comparison of sites with different densities of predators was not confounded in any systematic way with other measured environmental variables, including sediment characteristics, bioturbating or predatory infauna. There was a consistent pattern of decreased biomass of bivalves with increased lobster and snapper density inside reserves, in contrast with the inconsistent distribution of grain size and other variables. This suggests that large predators have an important ecological influence on the distributions of these bivalves. The difference in the community inside and outside the reserves was also driven by the gastropod *Philine angasi* that was found to be more abundant inside reserves.

The distribution of certain components of the community are apparently driven more by sediment texture, regardless of reserve status (Appendix 3.E). For example, the most abundant species, the opisthobranch *A. novaezelandiae*, appeared to have a positive relationship with the percentage of fine sediments. In contrast, the abundances of other prominent taxa in the assemblage (i.e. the bivalves *D. subrosea* and *M. striata*) were driven by predator density and were primarily responsible for the detected effects of reserve status.

There were also some differences in the magnitude of the effects detected at each location, with the greatest response being shown by *D. subrosea* at Hahei, having a mean density of 0.08 m⁻² inside reserves and 1.88 m⁻² outside reserves. High small-scale variability detected in all locations could have been due to patchiness in foraging (Connell and Kingsford 1998). However, there was a consistent overall pattern in the community response to the large-scale manipulative experiment provided by marine reserve status. The greater community variability in the reserve sites at Leigh could be

due to greater levels of disturbance, as the highest densities of predators were observed there.

Several other studies have found bivalve populations to be susceptible to predation. For example, sea otters have been found to dramatically reduce some bivalve species through predation and disturbance (Kvitek et al. 1992) and spiny lobster (*Panulirus interruptus*) have been shown to control intertidal mussel populations (Robles et al. 1990).

A pattern of increasing abundance with increasing distance from reefs ('haloes') was observed in several species, in particular *D. subrosea* and *E. cordatum*, but the reverse pattern was also observed, particularly for the hermit crab *P. novizelandiae*. The pattern of increasing abundance with increasing distance from reefs occurred at sites both inside reserves, with high relative densities of predators, and at nonreserve sites, with relatively low densities of predators.

Posey and Ambrose (1994) found significantly decreased abundances of polychaetes, bivalves, isopods and scaphopods up to 75 m away from the edge of an offshore reef near Wrightsville Beach, North Carolina (depth ca. 30 m). In that study, no levelling off in the increase of infaunal abundance with increasing distance from the reef edge was observed. In our study, at nonreserve sites (areas with low densities of reef-associated predators), several bivalve taxa exhibited a trend of increasing abundance with increasing distance from the reef edge. This suggests that subtle predation effects or other, perhaps physical (DeFelice and Parrish 2001), factors are important in influencing the distribution of infauna in relation to distance from the reef edge. A study of the stomach contents of reef-associated fishes in North Carolina's Onslow Bay by Lindquist et al. (1994) indicated that feeding by these fish might play a major role in creating infaunal haloes. However, a study by Dahlgren et al. (1999) at the same location suggested that in this system bioturbation is of sufficient magnitude to influence infaunal abundances close to the reef, and may work concurrently with predation to produce observed infaunal abundance patterns. The dominant bioturbator found in our study has been shown to be an important component of the diet of snapper in offshore soft-sediment areas (Godfriaux 1970). However, their abundance was not found to correlate with snapper and lobster density in this study, suggesting that the influence of bioturbators is not confounded by the abundance of large predators. Dahlgren et al. (1999) found a very different distribution of their dominant infaunal bioturbator, the holothurian *Holothuria princeps*, compared with the present study.

Dahlgren et al. (1999) found significantly higher densities close to the reef edge (1 m) compared to further away (10 - 25 m), whereas in the present study we found the distribution of infaunal bioturbators increased with increasing distance from the reef edge, in particular for *E. cordatum*. Our study dealt with the responses of animals greater than four millimetres and these larger organisms may, by virtue of their size, be less affected by bioturbation than small infauna.

No-take marine reserves provide a strong and consistent large-scale contrast in the density of previously exploited predators and this has enabled us to investigate the potential role of reef-associated predators in soft-sediment communities. Another approach to demonstrating such roles is to conduct smaller-scale caging experiments. Such experiments are useful in that they can reduce or remove concerns relating to confounding environmental effects at larger scales. However, these will only be successful if there are significant levels of predation in the 'uncaged' treatment (Connell 1997).

Conclusions

Long-term and large-scale manipulations, such as the establishment of marine reserves, are necessary to appreciate fully the impacts of fishing (Dayton et al. 1998). They can also allow us to investigate how the removal of top-level predators from the ecosystem affects other trophic levels. Direct effects of fishing on soft-sediment communities due to the impacts of trawling and dredging have been described in several studies (Watling 1991, Jennings and Kaiser 1998, Thrush et al. 2001). Secondary effects have also been documented where, in the wake of bottom trawling activities, the diet of benthivorous fishes has changed to reflect changes in the soft-sediment community (Frid and Hall 1999). Our study suggests that the exploitation of predatory fauna can have important indirect effects on soft-sediment communities, where the fishing pressure on snapper and rock lobster results in positive effects on their prey species. No-take marine reserves provide a release from fishing pressure allowing the investigation of indirect harvesting effects. Caging manipulations (with controls and replication inside and outside reserves) are needed to establish that large snapper and rock lobster are indeed causing observed effects. There have not been, to our knowledge, any previous studies of the effects of predatory fauna on soft-sediment systems using marine reserves.

Marine reserves have provided us with new insights into ecosystem function and the pervasiveness of the indirect effects of fishing (Shears and Babcock 2003, Willis et al. 2003b). Marine reserves are ecosystems that are generally less disturbed by humans, but this study shows that they do not necessarily result in increases in the abundance, biomass and diversity of all communities as suggested in recent meta analyses by Halpern and Warner (2002, 2003). The indirect effects of fishing uncovered by this study emphasise the importance of a “system-level” approach to the modelling and investigation of marine reserves (Agardy 2000).

Acknowledgements

Thanks to the following for assistance with field work: S. Croft, L. Kraaijeveld, D. Parsons, A. Smith, T. Smith, and A. Wilson. This research was supported by a scholarship to T.J. Langlois from the Education Committee, States of Jersey, Channel Islands. Thanks to W. Ballantine, T. Willis and the Leigh Lab discussion group for ideas and suggestions. This manuscript was greatly improved by comments from S. Thrush, P. Raimondi and one anonymous reviewer.

References

- Agardy, T. 2000. Effects of fisheries on marine ecosystems: a conservationist's perspective. *International Council for the Exploration of the Sea Journal of Marine Science* **57**:761-765.
- Ambrose, W. G., Jr. 1991. Are infaunal predators important in structuring marine soft-bottom communities. *American Zoologist* **31**:849-860.
- Anderson, M. J. 2001a. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26**:32-46.
- Anderson, M. J. 2001b. Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries & Aquatic Sciences* **58**:626-639.
- Anderson, M. J., and J. Robinson. 2003. Generalised discriminant analysis based on distances. *Australian & New Zealand Journal of Statistics* **45**:301-318.

- Anderson, M. J., and C. J. F. ter Braak. 2003. Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* **73**:85-113.
- Anderson, M. J., and T. J. Willis. 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* **84**:511-525.
- Babcock, R. C., S. Kelly, N. T. Shears, J. W. Walker, and T. J. Willis. 1999. Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series* **189**:125-134.
- Barros, F. 2005. Evaluating the importance of predation on subtidal benthic assemblages in sandy habitats around rocky reefs. *Acta Oecologia* **27**:211-223.
- Barros, F., A. J. Underwood, and P. Archambault. 2004. The influence of troughs and crests of ripple marks on the structure of subtidal benthic assemblages around rocky reefs. *Estuarine, Coastal and Shelf Science* **60**:781-790.
- Barros, F., A. J. Underwood, and M. Lindegarth. 2001. The influence of rocky reefs on structure of benthic macrofauna in nearby soft-sediments. *Estuarine, Coastal and Shelf Science* **52**:191-199.
- Beck, M. W. 1997. Inference and generality in ecology: current problems and an experimental solution. *Oikos* **78**:265-273.
- Colman, J. A. 1972. Food of snapper, *Chrysophrys auratus* (Forster), in the Hauraki Gulf, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **6**:221-239.
- Connell, S. D. 1997. Exclusion of predatory fish on a coral reef: the anticipation, pre-emption and evaluation of some caging artefacts. *Journal of Experimental Marine Biology and Ecology* **213**:181-198.
- Connell, S. D., and M. J. Kingsford. 1998. Spatial, temporal and habitat related variation in the abundance of large predatory fish at one tree reef, australia. *Coral Reefs* **17**:49-57.

- Dahlgren, C. P., M. H. Posey, and A. W. Hulbert. 1999. The effects of bioturbation on the infaunal community adjacent to an offshore hardbottom reef. *Bulletin of Marine Science* **64**:21-34.
- Davis, N., G. R. VanBlaricom, and P. K. Dayton. 1982. Man-made structures on marine sediments: effects on adjacent benthic communities. *Marine Biology* **70**:295-304.
- Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecological Applications* **8**:309-322.
- DeFelice, R. C., and J. D. Parrish. 2001. Physical processes dominate in shaping invertebrate assemblages in reef-associated sediments of an exposed Hawaiian coast. *Marine Ecology Progress Series* **215**:121-131.
- Fairweather, P. G. 1988. Predation creates haloes of bare space among prey on rocky seashores in New South Wales. *Journal of Experimental Marine Biology & Ecology* **114**:261-273.
- Frid, C. L. J., and S. J. Hall. 1999. Inferring changes in North Sea benthos from fish stomach analysis. *Mar. Ecol. Prog. Ser.* **184**:183-188.
- Godfriaux, B. L. 1970. Food of predatory demersal fish in hauraki gulf: part 1 food and feeding habits of snapper. *New Zealand Journal of Marine and Freshwater Research* **3**:518-544.
- Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. *Ecology Letters* **5**:361-366.
- Halpern, B. S., and R. R. Warner. 2003. Matching marine reserve design to reserve objectives. *Proceedings of the Royal Society of London - Series B: Biological Sciences* **270**:1871-1878.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**:187-212.

- Jennings, S., and M. J. Kaiser. 1998. The effects of fishing on marine ecosystems. Pages 201-515 in *Advances in Marine Biology*, Vol 34. Academic Press Ltd, London.
- Kelly, S. 2001. Temporal variation in the movement of the spiny lobster *Jasus edwardsii*. *Marine and Freshwater Research* **52**:323-331.
- Kelly, S., A. B. MacDiarmid, and R. C. Babcock. 1999. Characteristics of spiny lobster, *Jasus edwardsii*, aggregations in exposed reef and sandy areas. *Marine & Freshwater Research* **50**:409-416.
- Kvitek, R. G., J. S. Oliver, A. R. Degange, and B. S. Anderson. 1992. Changes in Alaskan soft-bottom prey communities along a gradient in sea otter predation. *Ecology* **73**:413-428.
- Legendre, P., and M. J. Anderson. 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs* **69**:512.
- Lindquist, D. G., L. B. Cahoon, I. E. Clavijo, M. H. Posey, S. K. Bolden, L. A. Pike, S. W. Burk, and P. A. Cardullo. 1994. Reef fish stomach contents and prey abundance on reef and sand substrata associated with adjacent artificial and natural reefs in Onslow Bay, North Carolina. *Bulletin of Marine Science* **55**:1994.
- MacDiarmid, A. B. 1991. Seasonal changes in depth distribution, sex ratio and size frequency of spiny lobster (*Jasus edwardsii*) on a coastal reef in northern New Zealand. *Marine Ecology Progress Series* **70**:129-141.
- MacDiarmid, A. B., B. Hickey, and R. A. Maller. 1991. Daily movement patterns of the spiny lobster *Jasus edwardsii* (Hutton) on a shallow reef in northern New Zealand. *Journal of Experimental Marine Biology and Ecology* **147**:185-205.
- McArdle, B. H., and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* **82**:290-297.
- Morton, J., and M. Miller. 1968. *The New Zealand Sea Shore*, 2nd edition. Collins, Auckland.

- Parsons, D. M., R. C. Babcock, R. K. S. Hankin, T. J. Willis, J. P. Aitken, R. K. O'Dor, and G. D. Jackson. 2003. Snapper *Pagrus auratus* (Sparidae) home range dynamics: acoustic tagging studies in a marine reserve. *Marine Ecology Progress Series* **262**:253-265.
- Paul, L. J. 1976. A study on age, growth, and population structure of the snapper, *Chrysophrys auratus* (Foster), in the Hauraki Gulf, New Zealand. New Zealand Ministry of Agriculture and Fisheries, Wellington, New Zealand.
- Posey, M. H., and W. G. Ambrose. 1994. Effects of proximity to an offshore hard-bottom reef on infaunal abundances. *Marine Biology* **118**:745-753.
- Robles, C., D. Sweetnam, and J. Eminike. 1990. Lobster predation on mussels: shore-level differences in prey vulnerability and predator preference. *Ecology* **71**:1564-1577.
- Shears, N. T. 2003. Response of shallow subtidal reef communities to marine reserve protection in northeastern New Zealand. PhD thesis, University of Auckland, Auckland, New Zealand.
- Shears, N. T., and R. C. Babcock. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* **132**:131-142.
- Shears, N. T., and R. C. Babcock. 2003. Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Marine Ecology Progress Series* **246**:1-16.
- Suchanek, T. H. 1978. The ecology of *Mytilus edulis* in exposed rocky inter tidal communities. *Journal of Experimental Marine Biology & Ecology* **31**:105-120.
- Suchanek, T. H. 1983. Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea Thalassinidae) bioturbation. *Journal of Marine Research* **41**:281-298.
- Thomas, M. L. H. 1986. A physically derived exposure index for marine shorelines. *Ophelia* **25**:1-13.

- Thrush, S. F., J. E. Hewitt, V. J. Cummings, M. O. Green, G. A. Funnell, and M. R. Wilkinson. 2000. The generality of field experiments: interactions between local and broad-scale processes. *Ecology* **81**:399-415.
- Thrush, S. F., J. E. Hewitt, G. A. Funnell, V. J. Cummings, J. Ellis, D. Schultz, D. Talley, and A. Norkko. 2001. Fishing disturbance and marine biodiversity: role of habitat structure in simple soft-sediment systems. *Marine Ecology Progress Series* **221**:255-264.
- Underwood, A. J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Oceanography and Marine Biological Annual Review* **19**:513-605.
- Underwood, A. J. 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge, UK.
- Underwood, A. J., M. G. Chapman, and S. D. Connell. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology* **250**:97-115.
- Watling, L. 1991. The sedimentary milieu and its consequences for resident organisms. *American Zoologist* **31**:789-796.
- Watzin, M. C. 1986. Larval settlement into marine soft-sediment systems: interactions with the meiofauna. *Journal of Experimental Marine Biology and Ecology* **98**:65-113.
- Willis, T. J., R. B. Millar, and R. C. Babcock. 2000. Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. *Marine Ecology Progress Series* **198**:249-260.
- Willis, T. J., R. B. Millar, and R. C. Babcock. 2003a. Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *Journal of Applied Ecology* **40**:214-227.

Willis, T. J., R. B. Millar, R. C. Babcock, and N. Tolimieri. 2003b. Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? *Environmental Conservation* **30**:97-103.

Winer, B. J. 1991. *Statistical principles in experimental design*, 3rd edition. McGraw-Hill, Sydney, Australia.

Appendices

Appendix 3.A

List of environmental variables used in multivariate models.

Variable	Abbreviation	Description
Snapper	Sna	Density of legal-sized snapper estimated by BUV
Rock Lobster	Lob	Density of legal-sized rock lobster estimated by UVC
Predatory Infauna	PIn	Infauna considered to be predators (Appendix B)
Bioturbating Infauna	BIn	Infauna considered to be bioturbators (Appendix B)
Grain Size (GS)	GS1 – GS7	Seven variables expressing percentage of grain sizes of ambient sediments (by weight) falling into particular grain-size classes:
	GS1	< 0.125 mm
	GS2	0.125 – 0.25 mm
	GS3	0.25 – 0.5 mm
	GS4	0.5 mm – 1 mm
	GS5	1 mm – 2mm
	GS6	2 mm – 4 mm
	GS7	> 4mm
Organics	Org	Sediment organic matter (%)
Bed Stress	Bed	Estimated using bed form ripple measurements and depth
Exposure	Exp	Estimation of fetch (km)
Depth	Dep	Water depth (m)

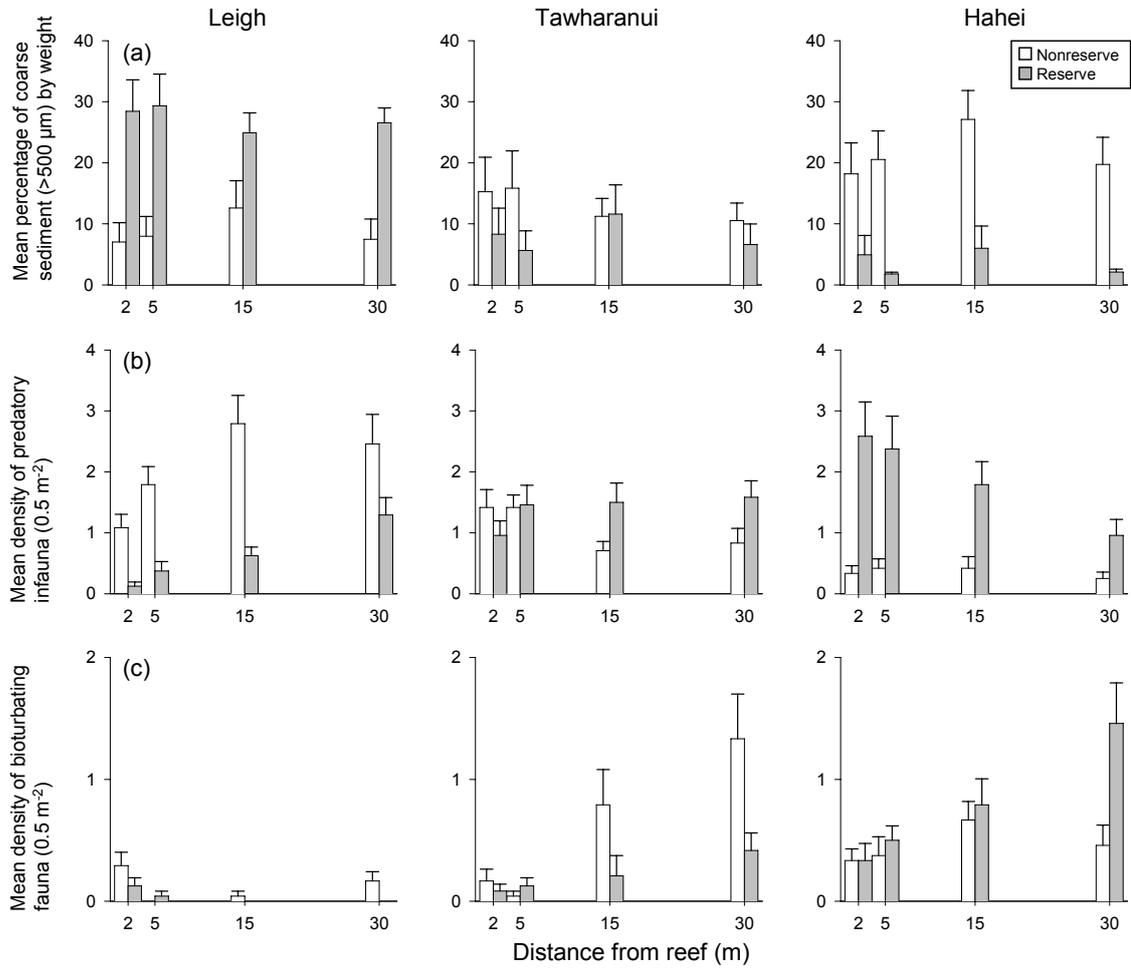
Appendix 3.B

Predatory and bioturbating infauna found in the study that were used as environmental variables in multivariate models.

Type	Class / Order	Taxon
Predatory Infauna	Decapoda	<i>Ovalipes catharus</i>
	Asteroidea	<i>Asterina regularis</i>
		<i>Astropecten polyacanthus</i>
		<i>Amalda australis</i>
	Opisthobranchs	<i>Amalda depressa</i>
		<i>Amalda novaezelandiae</i>
		<i>Cominella adspersa</i>
	Archeogastropoda	<i>Cominella maculosa</i>
		<i>Cominella quoyana quoyana</i>
Bioturbating Infauna	Echinoidea	<i>Echinocardium cordatum</i>
	Holothuroidea	<i>Trochodota dendyi</i>

Appendix 3.C

Mean +1SE of (a) percentage of coarse sediments ($> 500 \mu\text{m}$), (b) abundance of infaunal predators and (c) abundance of infaunal bioturbators at each distance stratum, reserve status and location (sites and replicates pooled, $n =$ (a) 12 and (b & c) 24).



Appendix 3.D

Results of four-factor analyses of variance examining: (a) percentage of coarse (> 500 μm) sediment by weight, abundance of infaunal predators and bioturbators; (b) biomass of *Dosinia subrosea*, *Myadora striata*; (c) biomass of *Amalda novaezelandiae*, *Pagurus novizelandiae* and *Echinocardium cordatum* at each distance stratum, reserve status and location (sites and replicates pooled).

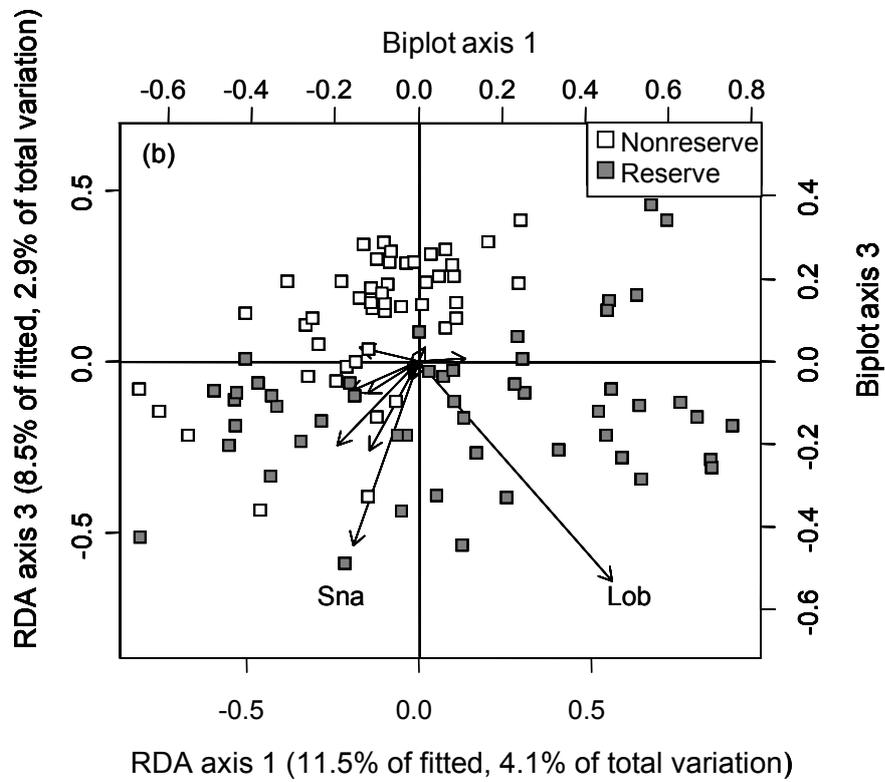
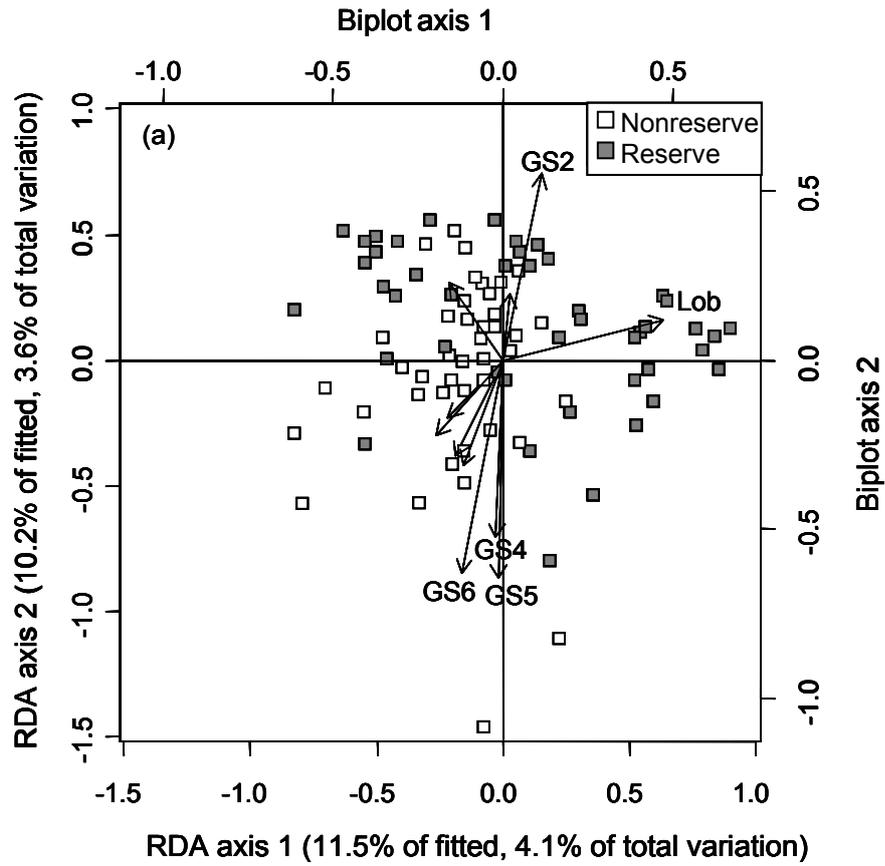
(a)	Source	% sediment >500 μm			Infaunal predators			Infaunal bioturbators			Denom MS		
		df	MS	F	P	df	MS	F	P	MS		F	P
	Location	2	1419.21	1.138	0.342	2	1.07	0.409	0.670	4.14	5.339	0.015	Si(Lo x St)
	Status	1	149.24	1.835	0.905	1	0.23	0.015	0.915	0.10	0.121	0.732	Lo x St
	Site (Lo x St)	18	1247.15	9.295	<0.001	18	0.36	0.257	0.854	1.23	2.230	0.185	Res
	Distance	3	141.22	2.897	0.124	3	2.63	11.652	<0.001	0.77	8.167	<0.001	Lo x Di
	Lo x St	2	8133.87	6.522	0.007	2	15.51	5.902	0.011	1.06	1.371	0.279	Si(Lo x St)
	Lo x Di	6	48.75	0.371	0.895	6	1.39	2.688	0.023	0.55	1.974	0.086	Di x Si(Lo x St)
	St x Di	3	40.81	0.319	0.821	3	0.12	0.156	0.922	0.17	0.420	0.746	Lo x St x Di
	Di x Si(Lo x St)	54	131.83	0.982	0.484	54	0.52	2.302	<0.001	0.28	2.947	<0.001	Res
	Lo x St x Di	6	127.71	0.969	0.455	6	0.76	1.456	0.211	0.41	1.473	0.205	Di x Si(Lo x St)
	Residual	192	134.16			480	0.23			0.09			
	Total	287				575							

(b) Source	df	<i>Dosinia subrosea</i>			<i>Myadora striata</i>			Denom MS
		MS	F	<i>P</i>	MS	F	<i>P</i>	
Location	2	6.10	3.011	0.074	0.00	0.016	0.984	Si (Lo x St)
Status	1	22.50	21.088	<0.05	0.67	8.842	<0.05	Lo x St
Site (Lo x St)	18	2.02	4.860	<0.001	0.12	4.590	<0.001	Res
Distance	3	2.15	1.578	0.290	0.12	6.846	<0.05	Lo x Di
Lo x St	2	1.07	0.527	0.599	0.01	0.636	0.541	Si (Lo x St)
Lo x Di	6	1.36	2.637	<0.05	0.02	1.017	0.424	Di x Si (Lo x St)
St x Di	3	0.07	0.068	0.975	0.06	4.877	<0.05	Lo x St x Di
Di x Si(Lo x St)	54	0.52	1.239	0.127	0.02	0.646	<0.05	Res
Lo x St x Di	6	1.00	1.931	0.092	0.01	0.767	0.599	Di x Si (Lo x St)
Residual	480	0.42			0.03			
Total	575							

(c) Source	df	<i>Amalda novaezelandiae</i>			<i>Pagurus novizelandiae</i>			<i>Echinocardium cordatum</i>			Denom MS
		MS	F	<i>P</i>	MS	F	<i>P</i>	MS	F	<i>P</i>	
Location	2	0.65	2.090	0.153	12.25	2.063	0.167	3.05	3.072	0.105	Si (Lo x St)
Status	1	0.07	0.037	0.866	8.75	0.316	0.669	0.03	0.077	0.828	Lo x St
Site (Lo x St)	18	0.31	6.795	<0.001	5.94	6.379	<0.001	0.99	9.395	<0.001	Res
Distance	3	0.10	0.741	0.565	4.91	2.044	0.234	0.91	1.164	0.452	Lo x Di
Lo x St	2	1.84	5.966	<0.01	27.72	4.668	<0.05	0.35	0.349	0.566	Si (Lo x St)
Lo x Di	6	0.14	2.012	0.080	2.40	0.877	0.524	0.78	3.059	<0.05	Di x Si (Lo x St)
St x Di	3	0.04	0.656	0.608	2.22	2.535	0.140	0.27	0.602	0.657	Lo x St x Di
Di x Si(Lo x St)	54	0.07	1.545	<0.01	2.74	2.942	<0.001	0.25	2.408	<0.001	Res
Lo x St x Di	6	0.06	0.791	0.581	0.88	0.320	0.922	0.44	1.739	0.176	Di x Si (Lo x St)
Residual	480	0.05			0.93			0.11			
Total	575										

Appendix 3.E

(a) Distance-based RDA ordination of first and second fitted axes relating the environmental variables to the faunal data. Biplot projections are given for the environmental variables listed in Appendix 3.A. Arrows are plotted showing the correlations of environmental variables with RDA axis 1 (r_1^2) and RDA axis 2 (r_2^2), with the length and direction of the arrow representing the strength and direction of the relationship. Symbols for arrows having length $\sqrt{r_1^2 + r_2^2}$ less than 0.5 were not included. The first three dbRDA axes explained 11.5%, 10.2% and 8.5% of the fitted relationship, respectively. (b) Distance-based RDA as in (a), but showing the first and third axes.



Appendix 3.F

List of 61 taxa from 7 phyla obtained from 576 box quadrats in this study.

Class / Order	Taxon	Class / Order	Taxon	
Bivalvia	<i>Atrina zelandica</i>	Gastropoda	<i>Amalda australis</i>	
	<i>Borniola decapitata</i>		<i>Amalda depressa</i>	
	<i>Corbula zelandica</i>		<i>Amalda novaezelandiae</i>	
	<i>Diplondonta globus</i>		<i>Cominella adspersa</i>	
	<i>Divaricella huttoniana</i>		<i>Cominella maculosa</i>	
	<i>Dosinia anus</i>		<i>Cominella quoyana quoyana</i>	
	<i>Dosinia maoriana</i>		<i>Cookia sulcata</i>	
	<i>Dosinia subrosea</i>		<i>Marginella pygmaea</i>	
	<i>Gari lineolata</i>		<i>Philine angasi</i>	
	<i>Gari strangeri</i>			
	<i>Glycymeris modesta</i>		Echiura	<i>Urechis novaezelandiae</i>
	<i>Myadora striata</i>		Nemertea	<i>Nemertea</i> spp.
	<i>Nucula hartvigiana</i>			
	<i>Paphies subtriangulata</i>		Platyhelminthes	<i>Stylochoplana</i> spp.
	<i>Pecten novaezelandiae</i>			
	<i>Protothaca crassicosta</i>		Polychaeta	<i>Glycera americana</i>
	<i>Scalpomactra scalpellum</i>			<i>Iosphilus</i> spp.
	<i>Tawera spissa</i>			<i>Macroclymenella stewartensis</i>
<i>Telina gaimardi</i>	<i>Magelona capensis</i>			
<i>Tucetona laticostata</i>	<i>Magelona papillicornis</i>			
<i>Zenatia acinaces</i>	<i>Notomastus zeylandicus</i>			
Crustacea	<i>Ampelisca chiltoni</i>	<i>Orbina papillosa</i>		
	<i>Callianassa filholi</i>	<i>Owenia fusiformis</i>		
	<i>Lophopagurus cristatus</i>	<i>Perineris australis</i>		
	<i>Ovalipes catharus</i>	<i>Sigalion capense</i>		
	<i>Paguristes setosus</i>	<i>Spionid</i> spp.		
	<i>Pagurus novizelandiae</i>			
	<i>Pagurus spinulimanus</i>	Pycnogonidae	<i>Pallene novaezelandiae</i>	
	<i>Squilla armarta</i>	Sipunculids	<i>Sipunculus mundanus</i>	
<i>Upogebia hirtifons</i>				
Echinodermata	<i>Asterina regularis</i>			
	<i>Astropecten polyacanthus</i>			
	<i>Fellaster zelandiae</i>			
	<i>Kolostoneura novaezealandiae</i>			
	<i>Trochodota dendyi</i>			

Appendix 3.G

Results of four-factor permutational multivariate analysis of variance (PERMANOVA) of soft-sediment fauna. The untransformed abundance data of 61 taxa was analysed using Gower's dissimilarity measure, including double zeros.

Source	df	MS	<i>F</i>	<i>P</i>	Permutable units of Denom MS
Location (Lo)	2	30.09	1.711	0.070	24 Si (Lo x St)
Status (St)	1	43.33	1.012	0.466	6 Lo x St
Site (Lo x St)	18	17.58	5.813	0.002	576 Res
Distance (Di)	3	14.95	2.252	0.018	95 Lo x Di
Lo x St	2	42.82	2.436	0.008	24 Si (Lo x St)
Lo x Di	6	6.64	1.445	0.064	95 Di x Si (Lo x St)
St x Di	3	5.68	1.004	0.480	95 Lo x St x Di
Di x Si(Lo x St)	54	4.59	1.365	0.002	576 Res
Lo x St x Di	6	5.66	1.232	0.130	95 Di x Si (Lo x St)
Residual	480	2.32			
Total	575				

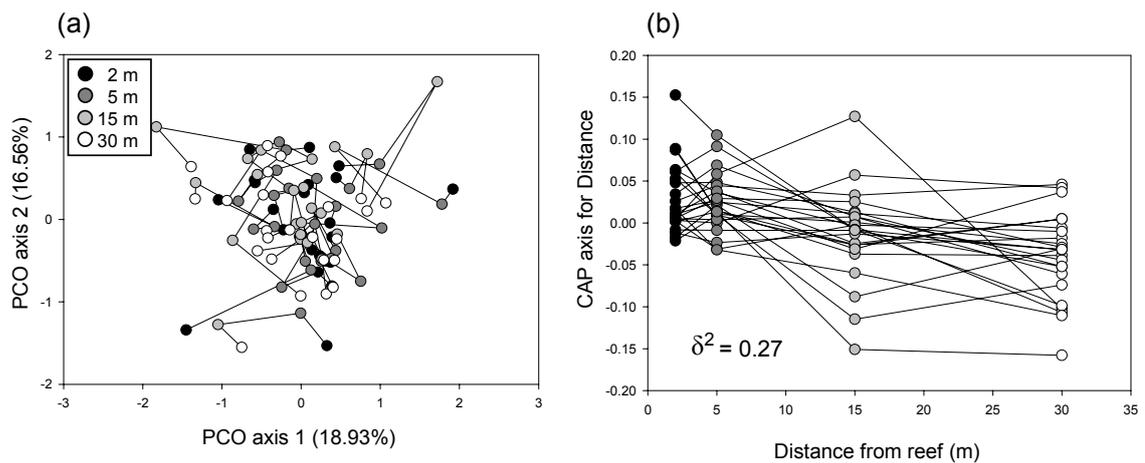
Appendix 3.H

Results of pair-wise *a posteriori* comparisons of soft-sediment communities among the four distance strata.

Comparison	<i>t</i>	<i>P</i>
2m vs. 5m	0.729	0.827
2m vs. 15m	1.284	0.016
2m vs. 30m	1.539	0.011
5m vs. 15m	1.474	0.039
5m vs. 30m	1.518	0.014
15m vs. 30m	0.907	0.585

Appendix 3.I

(a) Metric MDS ordination and (b) Canonical (CAP) analysis of the correlation of soft-sediment fauna with distance from the reef edge. Replicates were pooled and lines connected 2 m, 5 m, 15 m and 30 m samples from individual sites. Additional text on the CAP figure indicates the squared correlation coefficient (δ^2).



CHAPTER FOUR

Marine Reserves Demonstrate Trophic Interactions across Habitats

Timothy J. Langlois, Marti J. Anderson, Russell C. Babcock and Shin Kato

This chapter is currently in press in *Oecologia*.

Abstract

Several infaunal bivalve taxa show patterns of decreased biomass in areas with higher densities of adjacent reef-associated predators (the snapper, *Pagrus auratus* and rock lobster, *Jasus edwardsii*). A caging experiment was used to test the hypothesis that patterns observed were caused by predation, using plots seeded with a known initial density of the bivalve *Dosinia subrosea* to estimate survivorship. The caging experiment was replicated at several sites inside and outside two fully protected marine reserves: predators are significantly more abundant inside these reserves. Survivorship in fully caged, partially caged and open plots were then compared at sites having either low (nonreserve) or high (reserve) predator density. The highest rates of survivorship of the bivalve were found in caged plots inside reserves and in all treatments outside reserves. However, inside reserves, open and partially caged treatments exhibited low survivorship. It was possible to specifically attribute much of this mortality to predation by large rock lobsters, due to distinctive marks on the valves of dead *D. subrosea*. This suggests that predation by large rock lobster could indeed account for the distributional patterns previously documented for certain bivalve populations. Our results illustrate that protection afforded by marine reserves is necessary to investigate how depletion through fishing pressure can change the role of upper-level predators and trophic processes between habitats.

Introduction

Biotic interactions across habitat types have been observed to create distinct 'halo' patterns, often indicating foraging by fauna from a shelter to a food habitat (Ogden et al. 1973). Most investigations of these interactions have focused on meso grazing herbivores (Suchanek 1978) or secondary consumers (Fairweather 1988) rather than upper-level predators. 'Haloes' of reduced infaunal abundance have been observed in soft-sediment communities adjacent to rocky reefs and have been attributed to predation by reef-associated fauna (Davis et al. 1982, Posey and Ambrose 1994, Barros et al. 2001). However, these studies have been done with only limited replication over small spatial scales (Davis et al. 1982, Posey and Ambrose 1994) and have shown a lack of significant effects in caging studies designed to investigate predation (Posey and Ambrose 1994). Fully protected marine reserves have been suggested to provide a framework for large-scale experiments in which trophic interactions, involving more natural populations of predators can be observed (Dayton et al. 2000, Bohnsack 2003). Investigations of marine reserves have generally documented the recovery of previously exploited upper-level predators (Kelly et al. 2000, Willis et al. 2003). However, few have identified the trophic implications of increased populations and size distributions of these large, often relatively sedentary predators (Shears and Babcock 2002, Graham et al. 2003) and no previous studies have considered the importance of these trophic interactions across habitats.

Recent investigations in northeastern New Zealand have revealed patterns in soft-sediment communities near reefs that correlate well with the measured densities of two upper-level predators, the snapper, *Pagrus auratus*, and the rock lobster, *Jasus edwardsii* (Langlois et al. 2005). In that study, large-scale differences in abundances of predators found inside versus outside three comparable marine reserves were used to investigate the influence of these reef-associated predators on adjacent soft-sediment fauna. Snapper are generalist predators that take primarily invertebrate prey from both soft-sediment habitats and rocky reefs (Paul 1976, Babcock et al. 1999) and rock lobster, although commonly assumed to spend most of their time on rocky reefs, have been observed to forage over adjacent sandy areas (Kelly et al. 1999). MacDiarmid et al. (1991) found nocturnal foraging by *J. edwardsii* to be spatially limited, suggesting that any control these rock lobster may have on prey populations would be restricted to areas

near day-time shelters. Langlois et al. (2005) found sites with consistently higher densities of snapper and lobster to have ‘haloes’ of lower biomass of several bivalve species adjacent to the reef, in particular *Dosinia subrosea*, the largest and third most abundant species of the infaunal assemblage. This pattern was consistent across the three locations that were separated by hundreds of kilometres. In addition, the comparison of sites with different densities of predators could not be correlated in any systematic way with other measured environmental variables, such as sediment characteristics, densities of bioturbating infauna or predatory infauna. These observations, however, although quantitative and replicated, do not provide conclusive evidence that differences in bivalve densities are due to predation by snapper and rock lobster, as correlation does not provide a basis for causal inference. Experimental caging manipulations are needed to establish that predators are causing observed effects.

Caging manipulations are useful in that they can reduce or remove concerns relating to confounding environmental effects at larger scales. However, such experiments are successful only if there are significant levels of predation in the ‘uncaged’ treatment (Posey and Ambrose 1994, Connell 1997). We used the large-scale differences in density of upper-level predators inside versus outside two marine reserves as part of a large-scale caging manipulation, with replication at three spatial scales. Snapper and rock lobster are both heavily fished in northeastern New Zealand and they have been found to occur at significantly higher densities inside no-take marine reserves. Greater-than-legal-sized snapper (> 270 mm fork length) and rock lobster (> 100 mm carapace length (CL)) have been observed to be 14 times and 3.7 times more abundant, respectively, inside no-take reserves than outside (Babcock et al. 1999). However, the role of predators in structuring soft-sediment systems can be complex (Thrush 1999) and confounded by environmental heterogeneity at larger scales (Legendre et al. 1997). Here, by replicating the caging manipulation both inside and outside reserves, the relative sizes of any effects could be compared between sites of high (reserve) and low (nonreserve) predator densities.

The model proposed was that the differences in the distribution of large bivalves observed inside versus outside marine reserves are due to greater levels of predation inside the reserves. The central hypothesis was that there would be significantly lower survivorship of the bivalve, *D. subrosea*, in uncaged areas (exposed to predation) than in caged areas where predators were excluded. It was also predicted that survivorship of bivalves would be lower in areas open to predators at sites having higher densities of

predators (inside reserves) than in open areas with lower densities of predators (outside reserves).

Laboratory feeding trials of juvenile *J. edwardsii* on the mussel *Perna canaliculus* (James and Tong 1998) have described an innate feeding technique where the mandibles leave a distinctive damage pattern on the posterior margin of bivalve shells. Similarly, aquaria trials indicated that the method used by larger rock lobsters to open and consume *D. subrosea* also leaves distinctive marks on their shells (T. J. Langlois pers. obs.). Furthermore, shells of *D. subrosea* (~50 mm) preyed on by large lobster (> 120 mm CL) exhibit marks distinct from those preyed on by smaller lobster (< 90 mm CL) or other predators. By identifying these distinctive marks on shells of *D. subrosea* in the field, we also tested the hypothesis that predation of *D. subrosea* is primarily due to large rock lobster. Feeding on *Dosinia* species by snapper has been reported (Godfriaux 1970) but has not been widely observed.

Materials and methods

Study sites and sampling methods

Two separate no-take marine reserve locations in northeastern New Zealand were studied between January and March of 2003. The Cape Rodney to Okakari Point (Leigh) Marine Reserve (36° 16' S, 174° 48' E) was gazetted in 1975 and the Tawharanui Marine Park (36° 22' S, 174° 50' E) was declared a no-take area in 1981 (Fig. 4.1). Six sites were designated at each location (three inside and three outside each marine reserve) at 12 meters deep on sand flats adjacent to the extensive subtidal rocky reefs. They were chosen for similar wave exposure and reef / soft-sediment interfaces. To ensure interspersed, nonreserve sites were selected on either side of each reserve at distances of more than 500 m apart (see Fig. 4.1). Within each site, 12 circular plots (each 0.5 m²) were established (5 - 7 m from the reef edge and marked with two steel stakes) within which all *D. subrosea* were removed before the plots were reseeded with 10 live *D. subrosea*. These densities were comparable to densities observed in wild populations outside reserves (Langlois et al. 2005). No plots were more than 25 m away from each other. *Dosinia subrosea* were of similar size (~50 mm) and obtained from local populations. Exclusion cages were constructed over four of these plots, using steel mesh with a cross-mesh measurement of 75 mm, and anchored by steel stakes. Cages were circular, extended 150 mm into the sediment, and protruded 200 mm above. Lids

to the cages were constructed out of the same material and hinged to allow easy access. Over four other plots, cage walls were constructed around half the circumference of the plots but lids were not added, creating partial exposure. The four remaining plots were left open. These three treatments (cage, partial cage and open plots) were haphazardly interspersed across each site. These bivalves are not thought to be highly mobile (Powell 1979) and a pilot study did not find any measurable migration of *D. subrosea* out of the plots (T.J. Langlois unpub. data). All plots were excavated after two weeks to estimate the survivorship of *D. subrosea*. Shells of dead *D. subrosea* were collected from an area of $\sim 250\text{m}^2$ around the plots and along the adjacent reef edge.

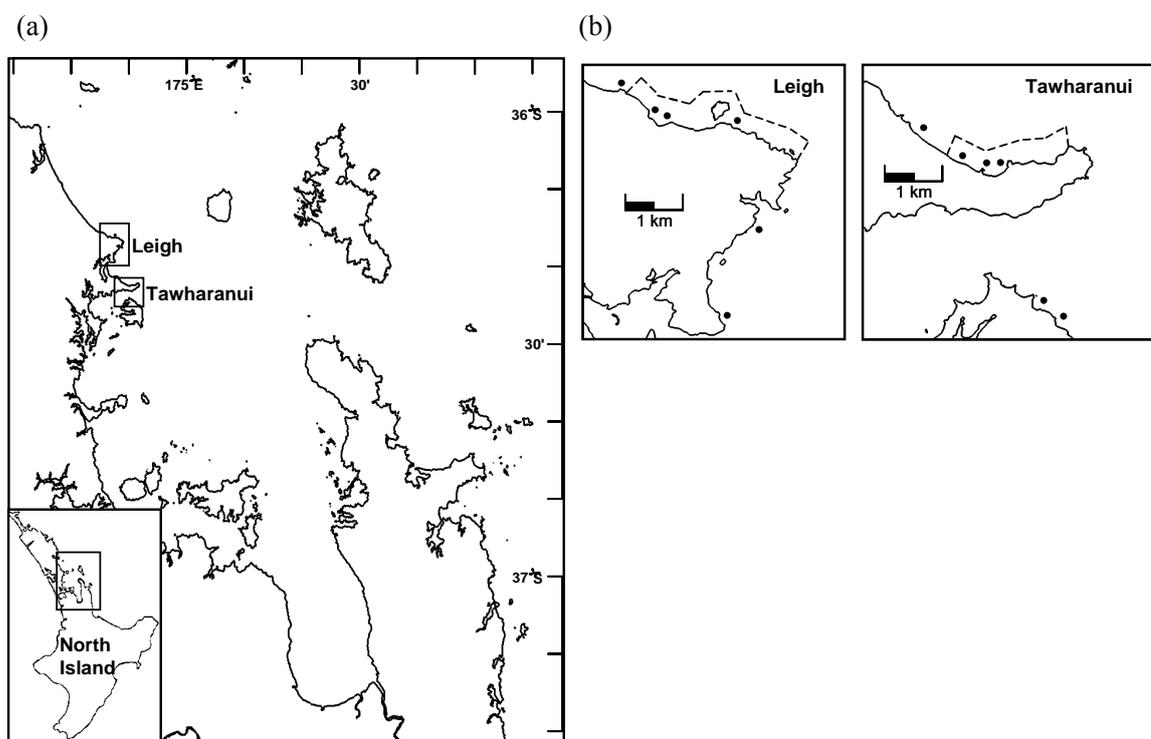


Fig. 4.1. (a) Map of Hauraki Gulf and environs showing the location of the two reserves used in this study. (b) The insets show the reserve boundaries (dashed lines) and experimental sites (filled circles) at the two locations.

Environmental variables

Densities of snapper at the sites were estimated from data collected in April and May of 2002. Relative densities at these locations were shown to be fairly stable between years (Willis et al. 2003). Baited underwater video (BUV) (Willis and Babcock 2000) ($n = 4$) was used at each site to estimate snapper density. Densities of lobster at each site were estimated by underwater visual census (UVC) of 25 m^2 quadrats ($n = 10$) during February and March 2003, and the sizes of lobsters were obtained using a visual

method as described by MacDiarmid (1991). Feeding rates in captive *Jasus edwardsii* from January to March have been observed to be approximately 50% of the peak rates found in November and December (Kelly et al. 1999). Other species known to be predators of soft-sediment fauna (i.e. octopus and rays) were also identified during rock lobster census dives. Pilot studies suggested that caging materials presented a limited area of resistance to water movement within the experimental plots and therefore environmental variables, including grain size and organic content were not expected to change over short time periods. Any confounding effects of the caging were thus considered as likely to be detected by the comparison of survivorship in the partial cages versus that in the open plots.

Statistical analyses

The overall experimental design consisted of four factors: Location (random with two levels: Leigh and Tawharanui), Status (fixed with two levels: inside versus outside a marine reserve), Site (random with three levels, nested within Location \times Status) and Treatment (fixed with three levels: full cage, partial cage and no cage). The density of snapper and rock lobster (greater than legal size) were analysed with a generalized linear model under the assumption of Poisson errors with over-dispersion. The survivorship of *D. subrosea* observed in the plots was analysed using a binomial generalized linear mixed model. Models were fit using the GLIMMIX routine (Littell et al. 1996) in the SAS statistical software package. The tests associated with each of the variance components for all random effects in the model and random interaction terms (i.e., Lo, Si(Lo \times St), Lo \times St, Lo \times Tr, Lo \times St \times Tr, and Tr \times Si(Lo \times St)) had *P*-values > 0.4 . As a consequence, the model was refitted with the fixed effects and their interaction only. Effect sizes were calculated from maximum likelihood estimates from the SAS GLIMMIX procedure (see Willis and Millar 2001).

Shells of dead *D. subrosea* collected from each site were classified into one of three categories: ‘cracked’ (opened by a large lobster, see the short video of a large lobster feeding on *Dosinia subrosea* provided in Appendix 4.A), ‘nibbled’ (opened by either a small lobster or another predator) or ‘ambiguous’ (shell fragments or unmarked valves). The proportion of shells in each category recovered from nonreserve and reserve sites were compared using a chi-squared test.

Results

Within reserves, where there are high densities of large snapper and rock lobster, levels of survivorship were found to be consistently lower for treatments open to predation (Fig. 4.2). At these reserve sites, large rock lobster (> legal size) were found to be consistently and significantly more abundant (Fig. 4.2, $\chi^2_1 = 26.1$, $P < 0.0001$) with no significant interaction of Location and Status. The estimated effect was a 4.6-fold higher

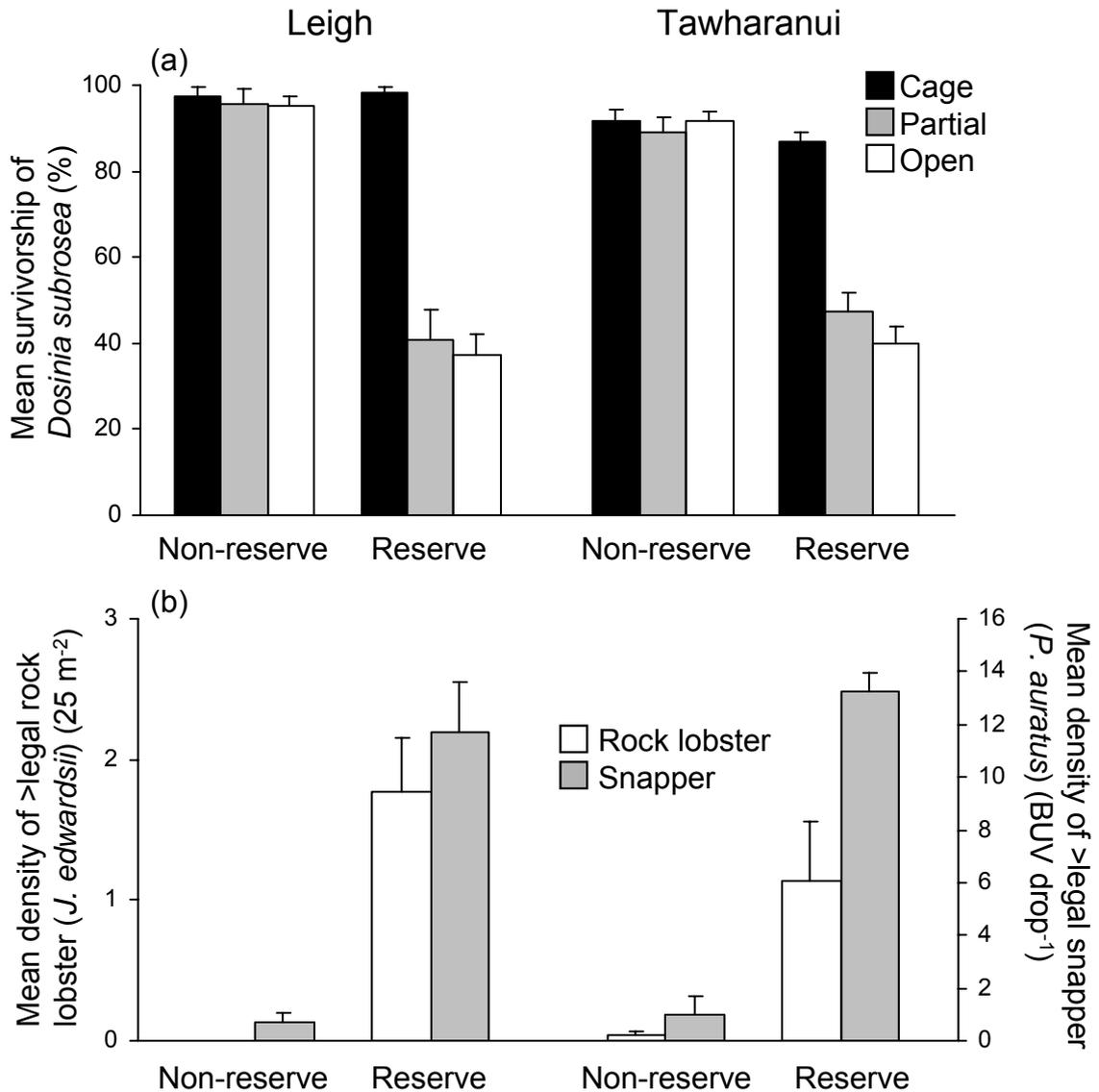


Fig. 4.2. (a) Average (+ 1SE) survivorship of *Dosinia subrosea* ($n = 12$) within each treatment, reserve status and location. (b) Average (+ 1SE) density of legal-size snapper (*Pagrus auratus*) and rock lobster (*Jasus edwardsii*) at reserve and nonreserve sites of each location. All sites and replicates were pooled. No greater-than-legal-sized rock lobster were observed at the nonreserve sites within Leigh.

average density in greater-than-legal-size rock lobster at reserve sites compared to nonreserve sites (with 95% confidence bounds of 3.2 to 7.1). Large snapper (> legal size) were also significantly more abundant at the reserve sites for both locations (Fig. 4.2, $\chi^2_1 = 186.9$, $P < 0.0001$) with no significant interaction between Location and Status. The estimated effect was a 16-fold higher average density in snapper larger than legal size at reserve sites compared to nonreserve sites (with 95% confidence bounds of 4.2 to 41.4). No octopuses or rays were observed during the censuses of rock lobster.

Table 4.1. Tests for the fixed effects of Status (reserve and nonreserve), Treatment (cage, partial and open) and their interaction on percentage survivorship of bivalves.

Fixed factors	df	<i>F</i>	<i>P</i>
Status (St)	1, 137	89.25	0.067
Treatment (Tr)	2, 137	20.2	< 0.001
St×Tr	2, 137	10.65	< 0.001

Analysis of the survivorship of *D. subrosea* found significant interaction of Status and Treatment (Table 4.1, $F_{2, 137} = 10.65$, $P < 0.001$), indicating that the effects of cages on survivorship of *D. subrosea* should be analysed separately inside and outside reserves. Inside reserves, the survivorship of *D. subrosea* was significantly and consistently lower in uncaged plots than in caged plots ($P < 0.0001$, Fig. 4.2a). The estimated probability of survivorship within reserves was 0.39 (with 95% confidence bounds of 0.34 to 0.44) in open plots compared to 0.93 (with 95% confidence bounds of 0.84 to 0.98) in caged treatments. In contrast, there were no effects of either cages or predators on survivorship of *D. subrosea* outside reserves (Fig. 4.2a). Survivorship in plots open to predation outside reserves was estimated to have a probability of 0.94 (with 95% confidence bounds of 0.87 to 0.99) compared to 0.39 inside reserves.

No caging artefacts were detected, as there were no significant differences in survivorship between open plots and partial cages, either inside ($P > 0.31$) or outside marine reserves ($P > 0.27$, Fig. 4.2a). In addition, the lack of any significant differences among any of the treatments outside of marine reserves indicated that (a) there was a conspicuous lack of predation occurring outside reserves and (b) there were no detectable caging artefacts in the absence of predation. The loss of bivalves observed in fully caged plots was attributed to mortality from handling, as intact but empty valves were recovered from these plots.

Of the transplanted shells that did not survive or were missing from the plots at the end of the experiment, 49% were accounted for by the dead shells recovered around the plots and along the adjacent reef edge. Amongst these recovered shells, a significantly greater proportion from reserve sites (64.8%) than from nonreserve sites (8.5%) were cracked distinctly (Fig. 4.3, $\chi^2_1 = 124.5$, $P < 0.0001$), indicating large lobster had preyed on them. A significantly greater proportion of shells at nonreserve sites (23.4%) compared to reserve sites (5.2%) were marked by “nibbles” (Fig. 4.3, $\chi^2_1 = 25$, $P < 0.001$), suggesting either a small lobster or another predator had opened them.

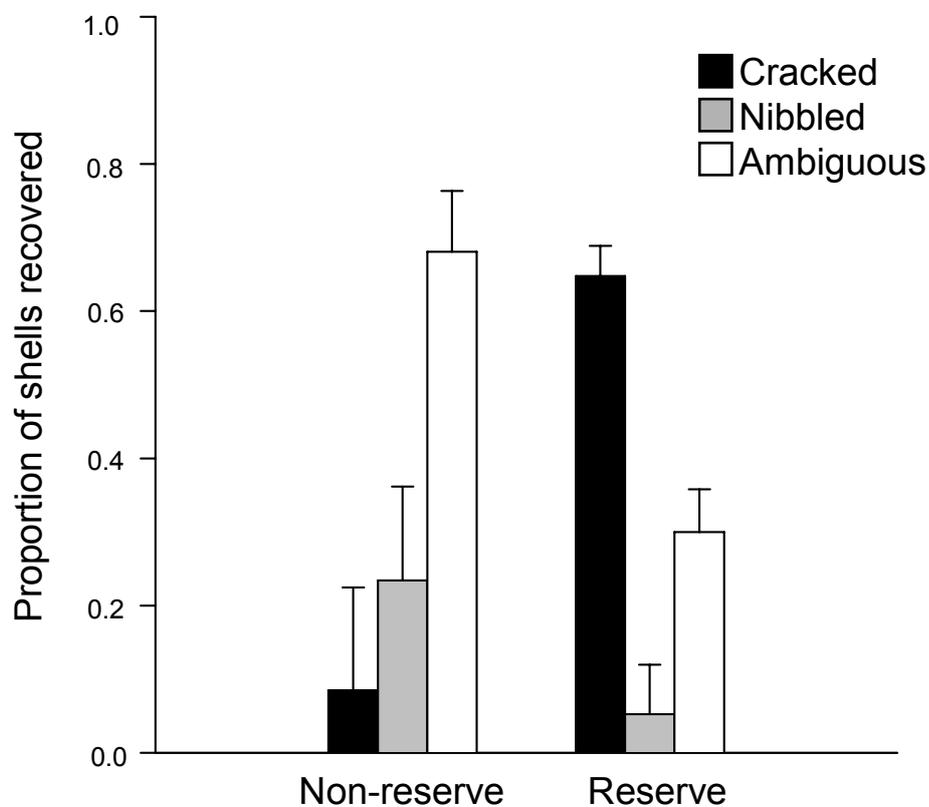


Fig. 4.3. Proportion of dead *Dosinia subrosea* found at the experimental sites, within each reserve status, that exhibited marks consistent with predation by large lobster (Cracked), small lobster (Nibbled) or had no attributable marks (Ambiguous). Locations were pooled.

Discussion

There was no evidence of significant predation from the cage experiment after two weeks at sites where upper-level predators were exploited. However, within the reserves, where the densities of large rock lobster and large snapper were higher,

predation resulted in lower survivorship of bivalves. This difference in the level of survivorship between the reserve and nonreserve sites suggests that the significantly higher densities of rock lobster and snapper within the reserves can have a large influence on soft-sediment bivalve populations.

The majority of dead shells recovered from reserve sites exhibited distinctive markings attributable to predation by large rock lobster. Observations of rock lobster and snapper in aquaria suggest that rock lobsters readily prey on *D. subrosea*, while snapper do not (T. J. Langlois pers. obs.). These bivalves are not thought to be highly mobile (Powell 1979) and so predation by rock lobster or benthivorous fishes that then deposited any shell fragments outside the experimental sites may explain the 51% of shells not recovered. In their natural environment, rock lobster have been observed to forage over adjacent soft-sediments and return to the reef edge with bivalves (MacDiarmid 1991) and also to cover large distances (~km's) along and off the reef edge. This behaviour could have resulted in a wide dispersal of shell fragments.

This study does not provide unequivocal evidence to show that rock lobster predation is the only explanation for patterns previously described in soft sediment communities by Langlois et al. (2005). Snapper and other benthivorous fauna such as rays (Hines et al. 1997) and octopus (Luckens 1991) are also likely to prey on these organisms. However, this study provides strong evidence that predation by rock lobster can be an important factor in the survivorship of adult bivalve populations.

Langlois et al. (2005) and this study illustrate the possible trophic interactions between reef-associated predators and large bivalves in adjacent soft-sediment assemblages. The actions of these predators may result in further indirect effects. Shears and Babcock (2002) describe a trophic cascade of effects on rocky reef habitats in these marine reserves, where snapper affect densities of urchins that in turn affect distributions of kelp forests. Regular disturbance of soft-sediment communities by the feeding activity of decapod crustaceans have been shown to indirectly impact infaunal assemblages (Bonsdorff and Pearson 1997). Feeding disturbance by rays has also been found to indirectly regulate community structure (Thrush et al. 1991). However, the large-scale study by Langlois et al. (2005) found no evidence of further community effects beyond these direct effects of predators on bivalves in soft-sediment habitats at these locations. Such indirect effects may be lost at the large-scale of sampling employed by Langlois et al. (2005) as the inherent spatial variability in soft-sediment assemblages can mask subtler small-scale patterns (Legendre et al. 1997).

Strong evidence exists suggesting that epibenthic predators, such as rock lobster, can use various cues to locate infaunal prey, including chemical signals carried in the exhalent water from bivalve siphons (Vedel 1986, Zimmer et al. 1999). There is also an increasing amount of evidence suggesting relatively sessile prey such as bivalves (Nakaoka 2000) and urchins (Dill et al. 2003) can detect the presence of certain predators. Nakaoka (2000) illustrated how the presence of a specific predator resulted in avoidance behaviour by an infaunal bivalve, including reduced water flow through the siphons. This mechanism of predator avoidance could explain the persistence of small populations of *D. subrosea* in the presence of high densities of rock lobster (Langlois et al. 2005). The high predation rates detected by this study were likely to be the result of density-dependent feeding behaviour (Eggleston et al. 1992, Hines et al. 1997) and epibenthic predators responding to various cues (Zimmer et al. 1999). These cues may have been very strong because the densities of bivalves used were far higher than any previously observed in areas where high densities of rock lobster or snapper occur (Langlois et al. 2005).

The historical fishing pressure for rock lobster (Kelly et al. 2000) suggests that, before the exploitation of this upper-level predator, coastal populations of *D. subrosea* were likely to have been similar to those now found in marine reserves. Centuries of fishing pressure off the western coast of Europe has led to a reduction of predation on benthic ophiuroids and the extension of their beds (Aronson 1989). Similarly, this study suggests the extraction of rock lobster in New Zealand has led to populations of bivalves flourishing in the functional absence of this important predator.

Caging has long been used as a means of understanding predation processes in marine systems, but it can be difficult or impossible to eliminate the possibility that any effects detected might be due to caging artefacts (Connell 1997). Kennelly (1991) devised a means of assessing caging artefacts by examining effects of full and partial cages in the absence of predators. He achieved this by setting up caging experiments inside and outside larger-scaled exclusions. By using “cages inside cages”, his experiment provided a means of assessing artefacts of smaller cages that were independent of their role to exclude predators. In the present study, we replicated caging treatments inside and outside of marine reserves. This allowed the assessment of effects of predators in areas of different predator densities. More particularly, no predation was detected in areas where densities of predators were low (outside reserves), due to exploitation. The lack of any significant effects of cages in these predator-free areas

provided a solid basis for inferring that caging artefacts, if any, did not confound interpretations of results (Kennelly 1991, Connell 1997). It also demonstrated how exploitation of higher-level predators can dramatically affect trophic interactions.

Previous experimental caging studies of predation in soft-sediment communities frequently have not detected direct effects on prey (e.g. Bell and Coull 1978, Thrush 1986, Raffaelli et al. 1989, Hall et al. 1990). Features of soft-sediment communities used to explain the lack of direct negative effects by predators include: the absence of dramatic resource monopolization and the generalist nature of many predators (Peterson 1979), multiple trophic levels (Commito and Ambrose 1985) and the mobility of both predators and prey (Thrush 1986, Frid 1989, Hall et al. 1990). These studies assumed that predation plays a strong role in these systems, an assumption that we are increasingly realising may not be correct, due to the functional extinction of large predators by fishing pressure (Aronson 1989, Dayton et al. 1998). Our study found direct evidence of how fished areas, in comparison with reserves, act as a 'sliding baseline' when investigating the trophic implications of exploitation in marine communities (Pauly et al. 1998, Dayton et al. 2000, Thrush and Dayton 2002).

Our study has benefited from the ability to contrast sites with different densities of predators, ensuring that rates of predation are high enough to be functionally important, and also ensuring that effects detected are not due to caging artefacts. These results indicate that reef-associated predators in this system, and in particular rock lobster, are capable of controlling a dominant species of macrofauna in adjacent soft sediments. Our study estimates that where lobsters are fished this role is reduced, and the estimated probability of survivorship by *D. subrosea* increases from 0.39 to 0.94. This study and Langlois et al. (2005) demonstrate that the comparison of highly protected and exploited areas is necessary to appreciate how predators, that are normally heavily fished, are capable of affecting populations of their prey and how trophic processes can structure adjacent habitats.

Acknowledgements

This research was supported by a scholarship to T. J. Langlois from the Education Committee, States of Jersey, Channel Islands, UK and funds from the University of Auckland. We thank Bill Ballantine and Geordie Murman for ideas and suggestions. We also thank Taylor Heyl, Russell Millar, Simon Thrush, and one

anonymous reviewer for their comments on a previous version of the manuscript.
Michelle Brock provided the supplementary video.

References

- Aronson, R. B. 1989. Brittlestar beds: low-predation anachronisms in the British Isles. *Ecology* **70**:856-865.
- Babcock, R. C., S. Kelly, N. T. Shears, J. W. Walker, and T. J. Willis. 1999. Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series* **189**:125-134.
- Barros, F., A. J. Underwood, and M. Lindegarth. 2001. The influence of rocky reefs on structure of benthic macrofauna in nearby soft-sediments. *Estuarine, Coastal and Shelf Science* **52**:191-199.
- Bell, S. S., and B. C. Coull. 1978. Field evidence that shrimp predation regulates meiofauna. *Oecologia* **35**:141-148.
- Bohnsack, J. A. 2003. Shifting baselines, marine reserves, and Leopold's biotic ethic. *Gulf and Caribbean Research* **14**:1-7.
- Bonsdorff, E., and T. H. Pearson. 1997. The relative impact of physical disturbance and predation by *Crangon crangon* on population density in *Capitella capitata*: an experimental study. *Ophelia* **46**:1-10.
- Commuto, J. A., and W. G. Ambrose. 1985. Multiple trophic levels in soft-bottom communities. *Marine Ecology Progress Series* **26**:289-293.
- Connell, S. D. 1997. Exclusion of predatory fish on a coral reef: the anticipation, pre-emption and evaluation of some caging artefacts. *Journal of Experimental Marine Biology and Ecology* **213**:181-198.
- Davis, N., G. R. VanBlaricom, and P. K. Dayton. 1982. Man-made structures on marine sediments: effects on adjacent benthic communities. *Marine Biology* **70**:295-304.

- Dayton, P. K., E. Sala, M. J. Tegner, and S. F. Thrush. 2000. Marine reserves: parks, baselines, and fishery enhancement. *Bulletin of Marine Science* **66**:617-634.
- Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecological Applications* **8**:309-322.
- Dill, L. M., M. R. Heithaus, and C. J. Walters. 2003. Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecology* **84**:1151-1157.
- Eggleston, D. B., R. N. Lipcius, and A. H. Hines. 1992. Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. *Marine Ecology Progress Series* **85**:55-68.
- Fairweather, P. G. 1988. Predation creates haloes of bare space among prey on rocky seashores in New South Wales. *Journal of Experimental Marine Biology and Ecology* **114**:261-273.
- Frid, C. L. J. 1989. The role of recolonization processes in benthic communities, with special reference to the interpretation of predator-induced effects. *Journal of Experimental Marine Biology and Ecology* **126**:163-171.
- Godfriaux, B. L. 1970. Food of predatory demersal fish in hauraki gulf: part 1 food and feeding habits of snapper. *New Zealand Journal of Marine and Freshwater Research* **3**:518-544.
- Graham, N. A. J., R. D. Evans, and G. R. Russ. 2003. The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. *Environmental Conservation* **30**:200-208.
- Hall, S. J., D. Raffaelli, and W. R. Turrell. 1990. Predator-caging experiments in marine systems: a re-examination of their value. *American Naturalist* **136**:657-672.
- Hines, A. H., R. B. Whitlatch, S. F. Thrush, J. E. Hewitt, V. J. Cummings, P. K. Dayton, and P. Legendre. 1997. Nonlinear foraging response of a large marine predator

- to benthic prey: eagle ray pits and bivalves in a New Zealand sandflat. *Journal of Experimental Marine Biology and Ecology* **216**:191-210.
- James, P. J., and L. J. Tong. 1998. Feeding technique, critical size and size preference of *Jasus edwardsii* fed cultured and wild mussels. *Marine and Freshwater Research* **49**:151-156.
- Kelly, S., A. B. MacDiarmid, and R. C. Babcock. 1999. Characteristics of spiny lobster, *Jasus edwardsii*, aggregations in exposed reef and sandy areas. *Marine and Freshwater Research* **50**:409-416.
- Kelly, S., D. Scott, A. B. MacDiarmid, and R. C. Babcock. 2000. Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. *Biological Conservation* **92**:359-369.
- Kennelly, S. J. 1991. Caging experiments to examine the effects of fishes on understorey species in a sublittoral kelp community. *Journal of Experimental Marine Biology and Ecology* **147**:207-230.
- Langlois, T. J., M. J. Anderson, and R. C. Babcock. 2005. Reef associated predators influence adjacent soft-sediment communities. *Ecology* **86**:1508-1519.
- Legendre, P., S. F. Thrush, V. J. Cummings, P. K. Dayton, J. Grant, J. E. Hewitt, A. H. Hines, B. H. McArdle, R. D. Pridmore, D. C. Schneider, S. J. Turner, R. B. Whitlatch, and M. R. Wilkinson. 1997. Spatial structure of bivalves in a sandflat: scale and generating processes. *Journal of Experimental Marine Biology and Ecology* **216**:99-128.
- Littell, R., G. Milliken, W. Stroup, and R. Wolfinger. 1996. SAS system for mixed models. SAS, Cary, North Carolina, US.
- Luckens, P. A. 1991. Distribution growth rate and death from octopod and gastropod predation of *Tawera bollonsi* (Bivalvia Veneridae) at the Auckland Islands. *New Zealand Journal of Marine and Freshwater Research* **25**:255-268.

- MacDiarmid, A. B. 1991. Seasonal changes in depth distribution, sex ratio and size frequency of spiny lobster (*Jasus edwardsii*) on a coastal reef in northern New Zealand. *Marine Ecology Progress Series* **70**:129-141.
- MacDiarmid, A. B., B. Hickey, and R. A. Maller. 1991. Daily movement patterns of the spiny lobster *Jasus edwardsii* (Hutton) on a shallow reef in northern New Zealand. *Journal of Experimental Marine Biology and Ecology* **147**:185-205.
- Nakaoka, M. 2000. Nonlethal effects of predators on prey populations: predator-mediated change in bivalve growth. *Ecology* **81**:1031-1045.
- Ogden, J. C., R. A. Brown, and N. Salesky. 1973. Grazing by echinoid diadema *Antillarum philippi*: formation of halos around West Indian patch reefs. *Science* **182**:715-717.
- Paul, L. J. 1976. A study on age, growth, and population structure of the snapper, *Chrysophrys auratus* (Foster), in the Hauraki Gulf, New Zealand. New Zealand Ministry of Agriculture and Fisheries, Wellington, New Zealand.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres. 1998. Fishing down marine food webs. *Science* **279**:860-863.
- Peterson, C. H. 1979. Importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey. *Oecologia* **39**:1-24.
- Posey, M. H., and W. G. Ambrose. 1994. Effects of proximity to an offshore hard-bottom reef on infaunal abundances. *Marine Biology* **118**:745-753.
- Powell, A. W. B. 1979. New Zealand mollusca. William Collins Publishers Ltd, Auckland, New Zealand.
- Raffaelli, D., A. Conacher, H. McLachlan, and C. Emes. 1989. The role of epibenthic crustacean predators in an estuarine food web. *Estuarine, Coastal and Shelf Science* **28**:149-160.
- Shears, N. T., and R. C. Babcock. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* **132**:131-142.

- Suchanek, T. H. 1978. The ecology of *Mytilus edulis* in exposed rocky inter tidal communities. *Journal of Experimental Marine Biology and Ecology* **31**:105-120.
- Thrush, S. F. 1986. Community structure on the floor of a sea-lough: are large epibenthic predators important? *Journal of Experimental Marine Biology and Ecology* **104**:171-183.
- Thrush, S. F. 1999. Complex role of predators in structuring soft-sediment macrobenthic communities: implications of changes in spatial scale for experimental studies. *Australian Journal of Ecology* **24**:344-354.
- Thrush, S. F., and P. K. Dayton. 2002. Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. *Annual Review of Ecology and Systematics* **33**:449-473.
- Thrush, S. F., R. D. Pridmore, J. E. Hewitt, and V. J. Cummings. 1991. Impact of ray feeding disturbances on sandflat macrobenthos: do communities dominated by polychaetes or shellfish respond differently? *Marine Ecology Progress Series* **69**:245-252.
- Vedel, J. P. 1986. Morphology and physiology of a hair plate sensory organ located on the antenna of the rock lobster *Palinurus vulgaris*. *Journal of Neurobiology* **17**:65-76.
- Willis, T. J., and R. C. Babcock. 2000. A baited underwater video system for the determination of relative density of carnivorous reef fish. *Marine and Freshwater Research* **51**:755-763.
- Willis, T. J., and R. B. Millar. 2001. Modified hooks reduce incidental mortality of snapper (*Pagrus auratus* : Sparidae) in the New Zealand commercial longline fishery. *International Council for the Exploration of the Sea Journal of Marine Science* **58**:830-841.
- Willis, T. J., R. B. Millar, and R. C. Babcock. 2003. Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *Journal of Applied Ecology* **40**:214-227.

Zimmer, R. K., J. E. Commins, and K. A. Browne. 1999. Regulatory effects of environmental chemical signals on search behavior and foraging success. *Ecology* **80**:1432-1446.

Appendices

Appendix 4.A

Video of a large (155 mm carapace length) rock lobster (*Jasus edwardsii*) cracking open a large (~50 mm) *Dosinia subrosea* shell.

CHAPTER FIVE

Importance of Rock Lobster Size-Structure for Trophic Interactions: Choice of Soft-Sediment Bivalve Prey

Timothy J. Langlois, Marti J. Anderson, Michelle Brock and
Geordie Murman

This chapter has been submitted to *Marine Biology*

Abstract

Ecologists are becoming increasingly interested in how variation in predator demographics influences prey communities. In northeastern New Zealand, the contrasting populations of previously exploited predators in highly protected marine reserves and fished areas have been used to investigate the effects of predation in soft-sediment habitats. However, these experiments have been unable to separate the role of predator size from that of density. This study provides evidence to support the model that foraging by different sizes of the rock lobster *Jasus edwardsii* affects soft-sediment bivalve populations in different ways. Feeding trials were conducted to investigate whether rock lobsters of different sizes vary in their choice of taxa and size of their bivalve prey. Trials with two morphologically similar species, *Dosinia subrosea* and *D. anus*, indicated that lobsters of all sizes choose *D. subrosea* more frequently than the heavier shelled *D. anus*. Further results indicated that both large (> 130 mm carapace length (CL)) and small (< 100 mm CL) lobsters are capable of preying on a wide size-range of *D. subrosea* (20 to 60 mm). However, small lobsters more frequently chose smaller shells (< 30 mm) and large lobsters more frequently chose larger shells (> 40 mm). Patterns in the abundance and size-class distributions of these two bivalve species at protected and fished sites supported the feeding choices observed in the laboratory. These results suggest that populations of rock lobsters with large individuals inside

reserves are capable of controlling the demography of bivalve populations in adjacent soft-sediment systems.

Introduction

The role of large marine predators in population and community-level dynamics has been a focus of many investigations into the ecology of coastal systems (Paine 1974, Robles et al. 1990, Babcock et al. 1999). Where predators have retained substantial populations with large size frequencies, e.g. where there is low fishing mortality or inside marine reserves, they have been demonstrated to constrain the size structure of prey populations (Pollock 1979, Castilla and Duran 1985, Sala and Zabala 1996, Shears and Babcock 2002, Parrish and Boland 2004). Commercial trap fisheries for several rock lobster species have been shown to incidentally target larger individuals (e.g. Ziegler et al. 2002, Acosta and Robertson 2003). Quantitative observations of such differences in predator population structure provide the context and basis for designing manipulative experiments to investigate their role in controlling prey populations (Underwood et al. 2000). The recovery of populations of previously exploited predators inside highly protected marine reserves, such as the panulirid rock lobster *Jasus edwardsii* (Shears and Babcock 2003), provide an experimental opportunity for the investigation of such questions (Langlois and Ballantine 2005).

These models can be investigated in the field by manipulative experiments, which involve the manipulation of predictor variables. However, Peters (1991) suggested that ecologists should test models using a combination of experimental techniques and treat hypotheses that have not stood the test of manipulative experiments with caution. For example, the findings of field and laboratory studies of the southern African rock lobster *Jasus lalandii* both confirmed that larger lobster were likely to prey on a greater range of rocky reef invertebrate fauna (Mayfield et al. 2001). These findings provided a predictive model of the inter-relationship among rock lobsters, sea urchins *Parechinus angulosus* and juvenile abalone *Haliotis midae* (Mayfield and Branch 2000).

Laboratory experiments have been used to investigate the factors that influence bivalve prey choice by decapod predators (Hughes and Seed 1995). In a laboratory study of predation by the shore crab *Carcinus maenas*, Elnor (1978) demonstrated that resistance to crushing in the mussel *Mytilus edulis* is positively correlated with shell

thickness and curvature. Pollock (1979), in a laboratory and field-based study of the predator / prey relationship between the rock lobster *Jasus lalandii* and the mussel *Aulacomya ater*, showed that prey may reach a 'critical size' (relative to the predator's size) above which they cannot be crushed. The importance of predator / prey size ratios has been indicated by studies of rock lobster and other decapod predators (Griffiths and Seiderer 1980, Sanchez-Salazar et al. 1987). In New Zealand, James and Tong (1998) found that juvenile *Jasus edwardsii*, feeding on the mussel *Perna canaliculus*, most frequently chose mussels that were half of their 'critical size'. For other shell-crushing decapod predators, this 'preferred size' has been suggested to yield the greatest energy per unit of handling time (Hughes 1980).

Jasus edwardsii is heavily fished in northeastern New Zealand (Kelly et al. 2000). Langlois et al. (2005a) found rock lobsters larger than legal size (> 100 mm carapace length (CL)) to be 2.4 to 5.9 times more abundant inside three comparable marine reserves. They also observed decreased biomass of several bivalve species, including *Dosinia subrosea*. This bivalve was the largest and third most abundant species found in the soft-sediment habitat near reefs at these three locations. Further manipulative investigations found the percent survivorship for this bivalve, after two-weeks, to be only 39% inside reserves, compared to 93% outside (Langlois et al. 2005b). Areas inside reserves that were protected from predation by cages had a percent survivorship similar to nonreserve areas (96%). These experiments suggested that foraging by predators strongly influences bivalve populations in these habitats. However, these studies did not attempt to separate the effects of predator density from predator size.

At one of the locations sampled by Langlois et al. (2005a), the Tawharanui Marine Park (Fig. 5.1), *Dosinia anus* and *D. subrosea* occurred together. Both species have been reported in shallow exposed subtidal sands around northeastern New Zealand, with *Dosinia anus* being more typical of exposed shores (Morton and Miller 1968). The two *Dosinia* species are morphologically similar and can prove troublesome to identify in the field unless compared simultaneously (Morton and Miller 1968). However the shell of *D. anus* is heavier, with stronger concentric ridges, and has a slightly lamellose area on the dorsal side extending along both the anterior and posterior margins. *Dosinia anus* generally buries itself in the sand to depths of 50 - 100 mm whilst *D. subrosea* is generally found deeper at 100 - 150 mm (Powell 1979). Kitching and Lockwood (1974) studied the prey selection of the shore crab *Hemigrapsus edwardsii* between two thaisid

gastropods of the genus *Lepsiella*. Like the two *Dosinia* species in question, the two *Lepsiella* species co-occurred. The heavier and ribbed shelled of *Lepsiella scobina* was found to be more resistant to attack than the smoother shell of *L. albomarginata*.

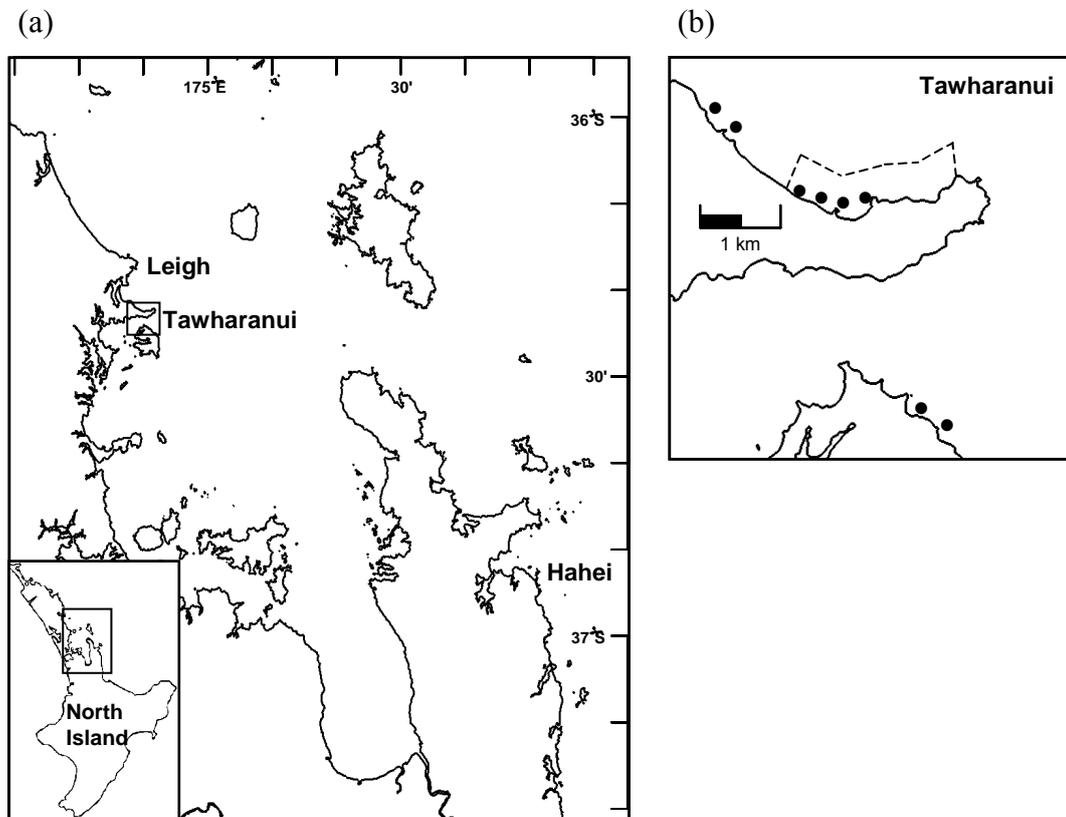


Fig. 5.1. (a) Map of Hauraki Gulf and environs showing the location of the three comparable reserves surveyed by Langlois et al. (2005a). (b) The insets show the reserve boundary (dashed line) and survey sites (solid circles) at Tawharanui (this study).

This study investigated predictive models suggested by previous mensurative and manipulative experiments (Langlois et al. 2005a, Langlois et al. 2005b). First, we hypothesised that *J. edwardsii* of a given size, when simultaneously presented with a *D. subrosea* and a *D. anus* of the same maximum dimension (shell width), would choose to feed upon the less heavily shelled *D. subrosea*. Next, based on the observations of size-selective feeding by Pollock (1979), we hypothesised that greater-than-legal sized *J. edwardsii* (i.e. > 100 mm carapace length) would choose *D. subrosea* of greater maximum dimension than those chosen by sub-legal sized lobsters. We used laboratory food-selection experiments to test these hypotheses. These experiments were designed to give an indication of how rock lobster populations of different size structure may

influence the population structure of bivalves adjacent to rocky reefs. We also examined data collected in a larger survey (Langlois et al. 2005a) to test the hypothesis that, in areas known to have different sizes of predators, the distributional patterns in prey populations would be consistent with choices made by predators of different sizes in the lab.

Methods

Feeding choice experiments

All lobsters (*J. edwardsii*) and bivalves (*D. subrosea* and *D. anus*) were collected from the Hauraki Gulf in northeastern New Zealand (Fig. 5.1). Only male lobsters were used due to dimorphism in feeding pereiopods between sexes and differences observed in the feeding rates (Kelly et al. 1999). Three size classes of lobsters were used ($n = 9$ in each case), based on carapace length: small (sub-legal, < 100 mm), medium (between 100 mm and 125mm) and large (> 130mm). The mean sizes within these classes were 95, 109 and 172 mm, respectively (Fig. 5.2). Lobsters were randomly assigned to replicate 1.5 m² tanks for each trial. The tanks were constructed from sea-seasoned wood and no sand was added, but concrete shelters were provided. Care was taken to minimize disturbance during trials by observing lobsters from a hidden position using red light. At the beginning of each trial the bivalves were introduced to the center of the tank. Two trials of each of the species-choice and size-choice experiments were run on each lobster. All trials were run between January and February 2004.

For each species-choice trial, one *D. subrosea* and one *D. anus* of comparable maximum dimension (shell width ~55 mm) were introduced to each tank. Hourly observations were made throughout the night and the identity of the first bivalve consumed was recorded. Results from each trial were treated separately and, for each lobster size class, the proportions of each species chosen were compared using an exact binomial test (Sokal and Rohlf 1995).

For each size-choice trial, eight *D. subrosea* of incremental size classes (shell width) were introduced to each tank. The eight size classes were in 5 mm increments from 20 mm to 60 mm, representative of size classes observed in the field. Hourly observations were made and the size of the first bivalve consumed was recorded. There were not sufficient replicates from either trial alone to perform separate significance

tests on proportions and so the data were tested for independence between the two trials before pooling observations. Independence of the size-choices made by each lobster from one trial to the next was examined using a test devised and implemented in the statistical programme R (R Development Core Team 2004). A separate test was done for each size class of lobster. The test-statistic compared the proportion of matching choices made by a single lobster in both trials with the proportion of matching choices made from one lobster to the next within either trial. Under the null hypothesis of independence of choice through time a distribution of the test-statistic was generated using 999 permutations. The proportion of matching choices from one trial to the next was not significantly greater than the proportion of matching choices made from one lobster to the next within either trial ($P > 0.7$ in all cases). Therefore, the results from the two trials were considered independent of one another and pooled. The proportion of each bivalve size class chosen by each lobster size class was then compared using Fisher's exact test (Sokal and Rohlf 1995).

Attempts were made to measure the time taken by individual lobsters to open their chosen bivalve, in each feeding trial. However, large variability in these times meant that only a few observations were completed.

Rock lobster and infaunal populations

Field observations were carried out between January and March of 2002. Eight sites of similar wave exposure and reef / soft-sediment interface were chosen, four inside and four outside the Tawharanui Marine Park (36° 22'S, 174° 50'E), which was declared a no-take area in 1981. To ensure interspersed, two of the nonreserve sites were located north and the other two located south of the reserve (see Fig. 5.1). Within each site, estimates of the density of lobsters at the reef edge were obtained by underwater visual census (UVC) of 25 m² quadrats ($n = 10$), and the sizes of lobsters were estimated using a visual method described by MacDiarmid (1991). The median and the inter-quartile range of their size frequencies were used to describe the rock lobster populations.

Infaunal soft-sediment communities, including bivalves (> 4 mm) were sampled at each of four distances from the reef edge: 2, 5, 15 and 30 m at each site. These distance strata were a proxy for distance from the location of surveyed reef-associated predators (for details see Langlois et al. 2005a) and within the likely foraging ranges of rock lobsters (MacDiarmid et al. 1991). At each distance, six replicate samples were

obtained using box-cores measuring 0.5 m² (1 m x 0.5 m) x 13 cm deep (0.065 m³). Sediment was excavated by hand with a metal scoop and sieved in the field using a sieve with a 4 mm mesh. Organisms retained on the sieve were preserved in 5% formalin and later transferred to 70% ethanol. All organisms were identified to the lowest taxonomic resolution possible and patterns in overall community structure have been described elsewhere (Langlois et al. 2005a). The distributional data of *D. subrosea* and *D. anus* abundance contained many zeros and were too overdispersed to consider using either a GLM or a traditional ANOVA on either raw or transformed values. Therefore, we used an ANOVA to partition the variability and obtain *F*-statistics on the original raw data, with all *P*-values obtained using 4999 permutations of the appropriate exchangeable units (Anderson and ter Braak 2003). This avoided making any particular distributional assumptions, apart from additivity of effects and exchangeability of errors, for these analyses. The size frequency distributions of the *D. subrosea* populations from the fished and reserve sites were analysed using a two-sample Kolmogorov-Smirnov test (Sokal and Rohlf 1995).

Results

Feeding choice experiments

In the species-choice experiments, the majority of lobsters from both trials (96%) chose *D. subrosea* when given the choice between *D. subrosea* and *D. anus* of the same shell width (Table 5.1). The only trial that did not find a significant frequency of choice in favour of *D. subrosea* was the second trial with nine medium-sized lobsters. However, seven of these nine legal-sized lobsters chose *D. subrosea* over *D. anus* (7 *D. subrosea* to 2 *D. anus*, $P = 0.1797$). A few large lobsters were observed to open their chosen bivalves within 3 minutes, whereas several small lobsters required repeated attempts over 48 hours before their prey was successfully opened.

Table 5.1. Frequencies of *Dosinia subrosea* and *D. anus* chosen by rock lobster in each of two separate trials ($n = 9$). Three size classes of lobster (small, medium and large) were used and all shells were of comparable size (~55 mm). Statistical significance: * $p < 0.05$, ** $p < 0.01$.

		Small	Medium	Large
Trial 1	<i>Dosinia subrosea</i>	8*	8*	9**
	<i>Dosinia anus</i>	1	1	0
Trial 2	<i>Dosinia subrosea</i>	9**	7	9**
	<i>Dosinia anus</i>	0	2	0

In the size-choice trials, large lobsters most frequently ate *D. subrosea* of 40 - 45 mm shell width (Fig. 5.2). Medium-sized lobsters exhibited a large range of choice, eating both small and large bivalves, with a median of 35 mm. The small lobsters chose no *D. subrosea* greater than 45 mm in width and the median size chosen was 30 mm. However, in the species-choice trials, all lobsters ate *D. subrosea* of 55 mm shell width or greater, demonstrating that small lobsters are capable of opening larger shells. Observations made after the initial bivalve chosen had been consumed indicated that the small lobsters continued to target the smaller-sized bivalves, leaving the larger prey (45 - 60mm) until there was no alternative. A large amount of variability was found in the

time required to open the shells. However, some small lobsters were able to open their chosen bivalves (ca. 30 mm) within 5 minutes.

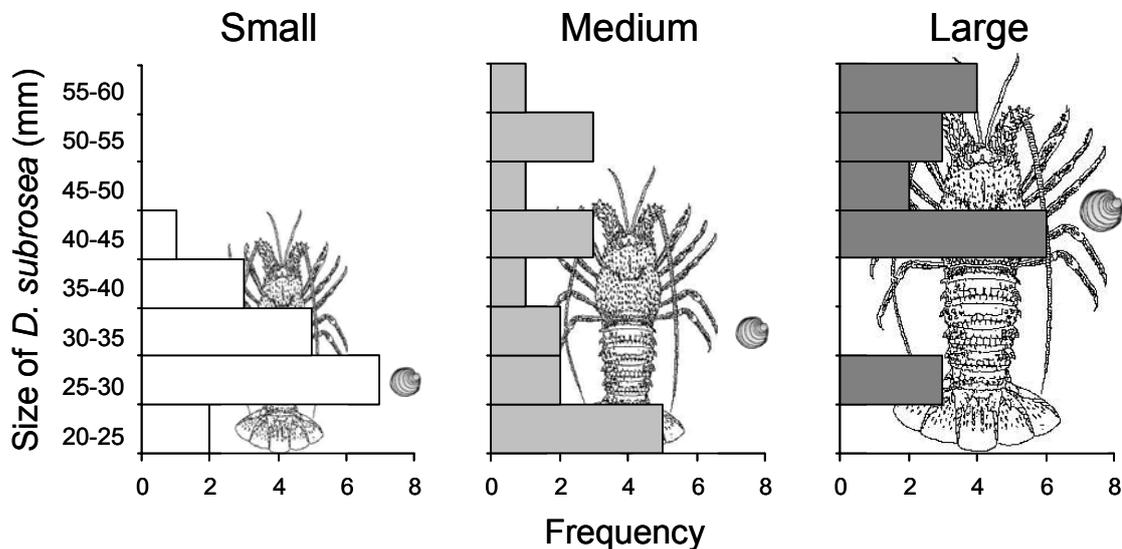


Fig. 5.2. Proportion of eight size classes of *Dosinia subrosea* chosen by rock lobster. Three size classes of lobster (small, medium and large) were used ($n = 18$) and shells were assigned to 5 mm size classes. The mean size of each class of lobster (small = 95 mm, medium = 109 mm and large = 172 mm) and median size of shell chosen (30mm, 35 mm and 40 - 45 mm) are illustrated to scale.

Rock lobster and infaunal populations

The populations of *J. edwardsii* at sites with different protection status (fished and no-take reserve) showed differences in density and size structure (Fig. 5.3). The population at the fished sites was made up of small individuals with a median size of 80 mm CL (inter-quartile range of 75 – 85 mm) and an estimated density of 0.014 m⁻². By comparison, the population observed at the reserve sites was made up of larger individuals, with a median size of 115 mm CL (inter-quartile range of 95 – 125 mm CL) and an estimated density of 0.134 m⁻².

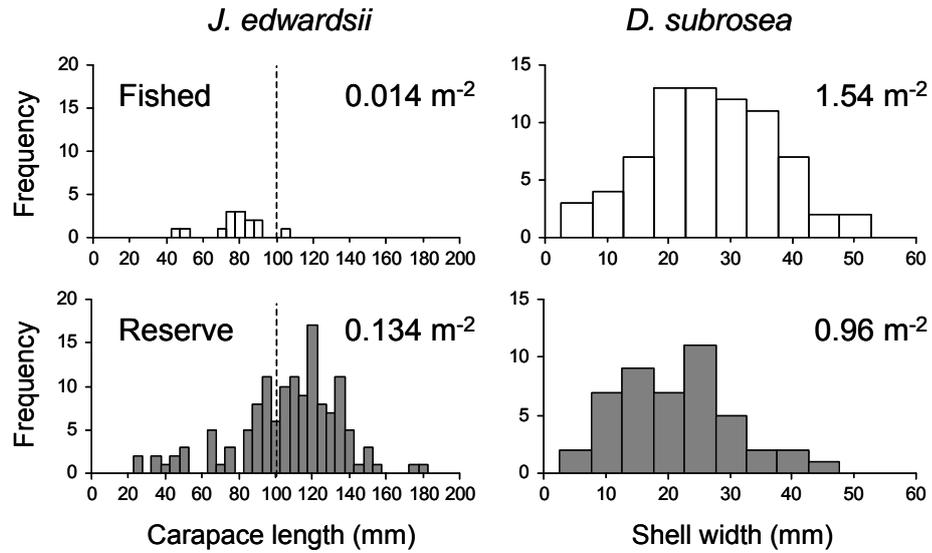


Fig. 5.3. Size frequency distributions and average density (m^{-2}) of *Jasus edwardsii* and *Dosinia subrosea* populations surveyed at reserve and fished sites at Tawharanui. The dashed line represents minimum size for rock lobster fishery.

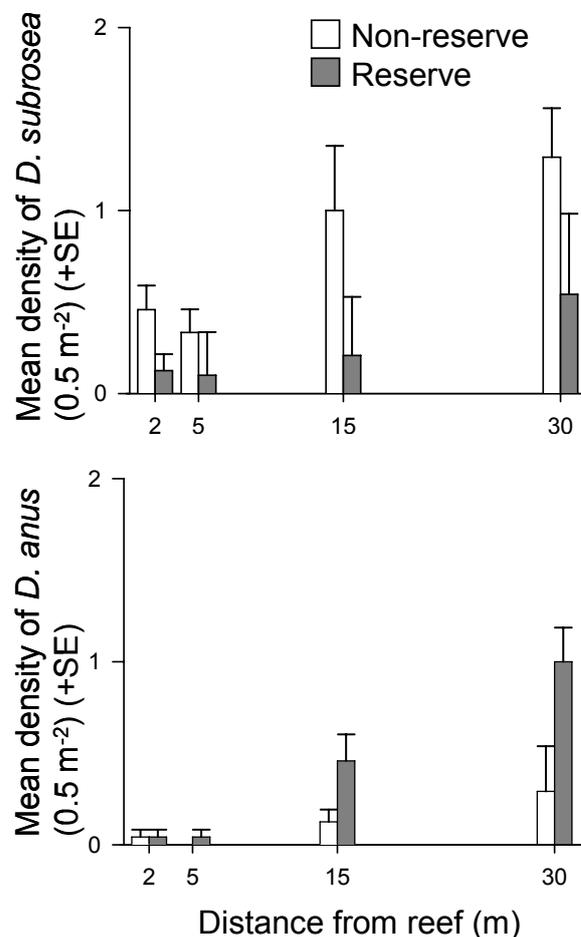
Table 5.2. Results of three-factor permutational ANOVA examining abundance of *Dosinia subrosea* and *Dosinia anus* at Tawharanui in response to site, reserve status and distance from the reef edge.

Exchangeable units used for permutations (Anderson and ter Braak 2003) are indicated by the term used for the denominator for each F -ratio (Denom MS).

Source	df	<i>Dosinia subrosea</i>			<i>Dosinia anus</i>			Denom MS
		MS	F	P	MS	F	P	
Status	1	39.42	13.687	< 0.01	3.52	6.377	< 0.05	Site (St)
Site (St)	6	2.88	5.369	< 0.001	0.55	1.359	0.245	Res
Distance	3	2.45	1.684	0.206	4.07	17.848	< 0.001	Di x Si(St)
St x Di	3	2.64	1.818	0.186	1.28	5.635	< 0.01	Di x Si(St)
Di x Si(St)	18	1.45	2.711	< 0.001	0.23	0.561	0.923	Res
Residual	160	0.54			0.41			
Total	191							

The density of *D. subrosea* varied significantly among sites at different distances from the reef edge, as indicated by the interaction between distance and site in the ANOVA (Table 5.2, $F_{18, 160} = 1.45$, $P < 0.001$). There was, however, a trend of increasing density with distance from the reef edge (Fig. 5.4). *D. subrosea* was also found to be consistently more abundant at fished sites ($F_{1, 6} = 13.69$, $P < 0.05$), with a mean density of 1.54 m^{-2} outside the reserve compared to 0.96 m^{-2} inside the reserve. *Dosinia anus* showed a similar pattern to *D. subrosea* of increasing density with distance from the reef (Fig. 5.4). However, there was a significant status-by-distance interaction, due to small differences among the nonreserve sites but significant differences at reserve sites from 5 m to 15 m ($t_{32} = 7.67$, $P < 0.05$) and also from 15 m to 30 m ($t_{32} = 2.81$, $P < 0.05$). The overall average abundance of *D. anus* was found to be greater at the reserve sites (Fig. 5.4). The highest average densities of *D. subrosea* and *D. anus* were observed at 30 meters from the reef edge (Fig. 5.4).

Fig. 5.4. Average (+ 1SE) density of (top-panel) *Dosinia subrosea* and (bottom-panel) *D. anus* at each distance stratum, inside and outside the reserve at Tawharanui (sites and replicates pooled).



The size structure of *D. subrosea* also differed inside and outside the reserve (Fig. 5.3). At the fished sites, the population was made up of larger individuals compared to inside the reserve, with median sizes of 24 mm and 19 mm respectively. Although comparison of the entire distribution of size frequencies of *D. subrosea* from the fished versus the reserve areas found no statistically significant difference at the level of 0.05 (Kolmogorov-Smirnov test, $P \sim 0.075$), the populations were markedly different for bivalves larger than 30 mm in shell width (Fig. 5.3).

Discussion

Prey selection experiments indicated that *Jasus edwardsii* is more likely to choose *Dosinia subrosea* over comparably sized *D. anus*, irrespective of lobster size, and that small lobsters will choose to eat small *D. subrosea*, whilst large lobsters will choose those that are larger. Densities of *D. subrosea* and *D. anus* observed in the field were low and so caution should be used when interpreting the patterns observed. However, the size structure of *D. subrosea* sampled at the reserve and fished sites were distinctly different above 30 mm shell width, but similar for smaller sizes. This suggests differences are likely to be due to mortality of large *D. subrosea* and not factors acting on small *Dosinia*. Given the findings of the laboratory trials and the natural distribution of *D. subrosea* in the field, it was surprising that *D. anus* was observed to be more abundant at reserve sites, suggesting that recruitment and / or mortality of *D. anus* is different where large rock lobsters and lower densities of *D. subrosea* are found. No consistent patterns were observed in the sediment characteristics between the reserve and nonreserve sites (Langlois et al. 2005a). These laboratory feeding experiments suggest a mechanism to explain the patterns of decreased abundance and survivorship of *D. subrosea* at sites with high densities of large rock lobsters (Langlois et al. 2005a, Langlois et al. 2005b). This new evidence supports the foraging predator model that predicts the top-down control of bivalve populations by lobsters in these habitats.

Laboratory-based experiments have often been criticized for not allowing the natural behaviour of free-living organisms (e.g. Dayton and Oliver 1980, Hilborn and Stearns 1982). In the above trials, the bivalve prey was presented simultaneously to each individual lobster, removing any differences in their natural occurrence. Morton and Miller (1968) indicate that *Dosinia subrosea* generally occur deeper in the sediment

(100 - 150 mm) than *D. anus* (50 - 100 mm). A similar bivalve species, *Paphies ventricosa*, was found to attain a refuge from predation at larger size by virtue of greater burial depth (Haddon et al. 1987). Smith et al. (1999) confirmed how burial depth affords an important refuge from crab predation, significantly increasing handling time and decreasing profitability of individual prey (energy intake per unit handling time). Therefore, the behaviour observed in our laboratory feeding trials may not occur in the field. However, the observations from the field suggest that, despite the shallower burial depth, *D. anus* does not appear to be more vulnerable to predation by large rock lobsters. Also *Jasus edwardsii* occur in social groupings in the wild (MacDiarmid 1991) and studies of comparable predators have demonstrated that the presence of conspecifics can affect prey choice (Salierno et al. 2003).

The complex nervous system of rock lobsters enables them to use a variety of sensory cues to detect, identify and discriminate among food sources (Derby et al. 2001). Odour plumes are used by predatory decapods to find prey (Weissburg and Zimmerfaust 1994) and *J. edwardsii* has been shown to use chemical cues to detect conspecifics (Butler et al. 1999). MacDiarmid (1991) suggested that *J. edwardsii* foraging nocturnally for bivalves could be using chemical cues to locate them. Rock lobsters are also highly adept at detecting small-scale changes in water flow (such as exhalent currents from infaunal bivalves) with the many sensilla distributed over their cuticle and antennae (Vedel 1986). It is likely that *J. edwardsii* uses a combination of mechanical and chemical cues to locate infaunal bivalve prey in the wild.

Jasus edwardsii could be using chemical cues to choose between the species and size classes of *Dosinia*. However, a simpler process may be behind the observed behaviour in the laboratory experiments and patterns in wild populations. The rock lobsters could be using a strategy similar to the crab *Carcinus maenas*, which attacks all encountered prey, but rejects those that remain unbroken after a certain number of opening attempts (Mascaro and Seed 2000). Our study found a similar pattern to that described by Kitching and Lockwood (1974) where the decapod predator chose the lighter shelled species when presented with two similar molluscs of the same genus. The shell of *D. anus* may simply be stronger than *D. subrosea*, and thus more resistant to predation. The minimum dimension of bivalve prey is also an important feature that shell-crushing predators recognize and associate with prey value (Mascaro and Seed 2000). For panulirid lobsters, Robles et al. (1990) described a relationship between the minimum dimension of the bivalve prey and the mandible gape of lobsters; above a

certain minimum dimension, a bivalve attains a ‘critical size’ at which the mandibles of a lobster can no longer exert sufficient pressure to break the shell. In the species-choice trials done here, *Dosinia subrosea* and *D. anus* of comparable maximum dimension (shell width) were also of comparable minimum dimension. However, the stronger concentric ridges and slightly lamellose margins of *D. anus* (Powell 1979) may cause *J. edwardsii* to perceive that *D. anus* has a larger minimum dimension. Therefore, when *J. edwardsii* encountered the two *Dosinia* species, it could have been choosing to prey on the shell of smallest perceived minimum dimension.

Previous studies of rock-lobster predation on bivalves have generally found that smaller size classes are chosen more frequently, or have observed a pattern of decreasing predation with increasing size of prey, suggesting a size refuge from predation is obtained with growth (Pollock 1979, Robles et al. 1990). In this field study, the smaller *D. subrosea* (ca < 30 mm) do not appear to be influenced by the adjacent population of rock lobsters to the extent that large individuals are. The existence of a relatively substantial population of small *D. subrosea* inside the reserve, where there is a high density of both small and large rock lobsters, suggests that these smaller *Dosinia* may have some refuge from predation. If smaller rather than larger rock lobsters choose to prey on small *D. subrosea*; this apparent refuge could be the result of burial depths. The 1st and 2nd pereopods of *J. edwardsii* play an important role in excavating bivalves from the sand (T.J. Langlois *personal observation*) and opening valves (James and Tong 1998). The carapace length of male *J. edwardsii* was found to be equivalent to the length of the 1st pereopod (T.J. Langlois unpub. data). Therefore, small lobsters (< 100 mm CL) will be limited in their ability to excavate a *Dosinia* from more than ~100 mm below the surface of the substrate. In the field, the encounter rate of large lobsters (> 130 mm CL) with such *Dosinia* is also likely to be greater given their range of movement over sandy habitats (Kelly et al. 1999) compared to smaller lobsters that have been observed to generally remain on the reef (MacDiarmid 1991).

The size-frequency distribution of *Jasus lalandii* observed by Pollock (1979), inside the Robben Island rock lobster sanctuary, and the *J. edwardsii* measured in this study are similar. The mussel *Aulacomya ater*, the main prey of *J. lalandii*, appeared to gain a refuge from predation at sizes greater than 60 mm and by the formation of dense clumps of individuals (Pollock 1979). *Dosinia subrosea* have not been observed to reach sizes greater than 60 mm around New Zealand (Powell 1979). At greater shell width, it is possible this bivalve might also gain some refuge from predation. A video

has been published by Langlois et al. (2005b) showing a large *Jasus edwardsii* (155 mm) feeding on large *Dosinia subrosea* (55 mm). The video illustrates the relative ease with which this predator feeds on large individuals of this bivalve species. Other soft-sediment bivalves around New Zealand attain refuges from predation at high density (Haddon et al. 1987), however, the densities of *Dosinia* in this study were always observed to be relatively sparse.

These experiments have demonstrated how large rock lobsters (> 130 mm) are capable of exerting greater control over prey populations than small lobsters (< 100 mm). Thus, it is not only changes in the density of fished populations but also changes in their size-structure that have important trophic implications for soft-sediment communities. It can be predicted from this study that, where fishing pressure impacts rock-lobster populations, they will be less able to exert top-down control over bivalve communities near rocky reefs. Management objectives of fisheries for rock lobster around New Zealand have historically not considered the effects of fishing on non target species. A process is currently underway to consider these objectives within the 'Strategy for managing environmental effects of fishing' (Ministry of Fisheries 2005). Our study provides novel information about the coastal system of northeastern New Zealand that would allow additional aims involving ecosystem processes (i.e. top-down control of a predator on its prey) to be integrated into predictive management models.

Acknowledgements

This research was supported by a scholarship to T. J. Langlois from the Education Committee, States of Jersey, Channel Islands and funds from the University of Auckland. Thanks to R. C. Babcock, W. J. Ballantine, C. Honeywill and R. B. Ford for ideas and valuable discussion.

References

Acosta, C. A., and D. N. Robertson. 2003. Comparative spatial ecology of fished spiny lobsters *Panulirus argus* and an unfished congener *P. guttatus* in an isolated marine reserve at Glover's Reef atoll, Belize. *Coral Reefs* **22**:1-9.

- Anderson, M. J., and C. J. F. ter Braak. 2003. Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* **73**:85-113.
- Babcock, R. C., S. Kelly, N. T. Shears, J. W. Walker, and T. J. Willis. 1999. Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series* **189**:125-134.
- Butler, M. J., A. B. MacDiarmid, and J. D. Booth. 1999. The cause and consequence of ontogenetic changes in social aggregation in New Zealand spiny lobsters. *Marine Ecology Progress Series* **188**:179-191.
- Castilla, J. C., and L. R. Duran. 1985. Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). *Oikos* **45**:391-399.
- Dayton, P. K., and J. S. Oliver. 1980. An evaluation of experimental analyses of population and community patterns in benthic marine communities. *in* K. R. Tenore and B. C. Coull, editors. *Marine Benthic Diversity*. University of South Carolina Press, Georgetown, US.
- Derby, C. D., P. Steullet, A. J. Horner, and H. S. Cate. 2001. The sensory basis of feeding behaviour in the Caribbean spiny lobster, *Panulirus argus*. *Marine and Freshwater Research* **52**:1339-1350.
- Elnor, R. W. 1978. Mechanics of predation by shore crab, *Carcinus maenas* (L.), on edible mussel, *Mytilus edulis* (L.). *Oecologia* **36**:333-344.
- Griffiths, C. L., and J. L. Seiderer. 1980. Rock lobsters and mussels: limitations and preferences in a predator-prey interaction. *Journal of Experimental Marine Biology and Ecology* **44**:95-109.
- Haddon, M., R. G. Wear, and H. A. Packer. 1987. Depth and density of burial by the bivalve *Paphies ventricosa* as refuges from predation by the crab *Ovalipes catharus*. *Marine Biology* **94**:25-30.

- Hilborn, R., and S. C. Stearns. 1982. On inference in ecology and evolutionary biology: the problem of multiple causes. *Acta Biotheoretica* **31**:145-164.
- Hughes, R. N. 1980. Optimal foraging theory in the marine context. *Oceanography and Marine Biology. An Annual Review* **18**:423-481.
- Hughes, R. N., and R. Seed. 1995. Behavioural mechanisms of prey selection in crabs. *Journal of Experimental Marine Biology and Ecology* **193**:225-238.
- James, P. J., and L. J. Tong. 1998. Feeding technique, critical size and size preference of *Jasus edwardsii* fed cultured and wild mussels. *Marine and Freshwater Research* **49**:151-156.
- Kelly, S., A. B. MacDiarmid, and R. C. Babcock. 1999. Characteristics of spiny lobster, *Jasus edwardsii*, aggregations in exposed reef and sandy areas. *Marine and Freshwater Research* **50**:409-416.
- Kelly, S., D. Scott, A. B. MacDiarmid, and R. C. Babcock. 2000. Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. *Biological Conservation* **92**:359-369.
- Kitching, J. A., and J. Lockwood. 1974. Observations on shell form and its ecological significance in Thaisid gastropods of genus *Lepsiella* in New Zealand. *Marine Biology* **28**:131-144.
- Langlois, T. J., M. J. Anderson, and R. C. Babcock. 2005a. Reef associated predators influence adjacent soft-sediment communities. *Ecology* **86**:1508-1519.
- Langlois, T. J., M. J. Anderson, R. C. Babcock, and S. Kato. 2005b. Marine reserves demonstrate trophic interactions across habitats. *Oecologia*:in press.
- Langlois, T. J., and W. J. Ballantine. 2005. Marine ecological research in New Zealand: developing predictive models using no-take marine reserves. *Conservation Biology*:in press.
- MacDiarmid, A. B. 1991. Seasonal changes in depth distribution, sex ratio and size frequency of spiny lobster (*Jasus edwardsii*) on a coastal reef in northern New Zealand. *Marine Ecology Progress Series* **70**:129-141.

- MacDiarmid, A. B., B. Hickey, and R. A. Maller. 1991. Daily movement patterns of the spiny lobster *Jasus edwardsii* (Hutton) on a shallow reef in northern New Zealand. *Journal of Experimental Marine Biology and Ecology* **147**:185-205.
- Mascaro, M., and R. Seed. 2000. Foraging behavior of *Carcinus maenas* (L.): comparisons of size-selective predation on four species of bivalve prey. *Journal of Shellfish Research* **19**:283-291.
- Mayfield, S., and G. M. Branch. 2000. Inter-relationships among rock lobster, sea urchins and juvenile abalone: implications for community management. *Canadian Journal of Fisheries and Aquatic Sciences* **57**:2175-2187.
- Mayfield, S., E. de Beer, and G. M. Branch. 2001. Prey preference and the consumption of sea urchins and juvenile abalone by captive rock lobsters (*Jasus lalandii*). *Marine and Freshwater Research* **52**:773-780.
- Ministry of Fisheries. 2005. Strategy for managing the environmental effects of fishing. Ministry of Fisheries, Wellington, New Zealand.
- Morton, J., and M. Miller. 1968. *The New Zealand Sea Shore*, 2nd edition. Collins, Auckland.
- Paine, R. T. 1974. Intertidal community structure: experimental studies on relationship between a dominant competitor and its principal predator. *Oecologia* **15**:93-120.
- Parrish, F. A., and R. C. Boland. 2004. Habitat and reef-fish assemblages of banks in the Northwestern Hawaiian Islands. *Marine Biology* **144**:1065-1073.
- Pollock, D. E. 1979. Predator-prey relationships between the rock lobster *Jasus lalandii* and the mussel *Aulacomya ater* at Robben Island on the Cape West Coast of Africa. *Marine Biology* **52**:347-356.
- Powell, A. W. B. 1979. *New Zealand mollusca*. William Collins Publishers Ltd, Auckland, New Zealand.
- R Development Core Team. 2004. R: a language and environment for statistical computing. *in*. R Foundation for Statistical Computing, Vienna, Austria.

- Robles, C., D. Sweetnam, and J. Eminike. 1990. Lobster predation on mussels: shore-level differences in prey vulnerability and predator preference. *Ecology* **71**:1564-1577.
- Sala, E., and M. Zabala. 1996. Fish predation and the structure of the sea urchin *Paracentrotus lividus* populations in the NW Mediterranean. *Marine Ecology Progress Series* **140**:71-81.
- Salierno, J. D., S. Rebach, and M. C. Christman. 2003. The effects of interspecific competition and prey odor on foraging behavior in the rock crab, *Cancer irroratus* (Say). *Journal of Experimental Marine Biology and Ecology* **287**:249-260.
- Sanchez-Salazar, M. E., C. L. Griffiths, and R. Seed. 1987. The effect size and temperature on the predation of cockles *Cerastoderma edule* (L.) by the shore crab *Carcinus maenas* (L.). *Journal of Experimental Marine Biology and Ecology* **111**:181-193.
- Shears, N. T., and R. C. Babcock. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* **132**:131-142.
- Shears, N. T., and R. C. Babcock. 2003. Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Marine Ecology Progress Series* **246**:1-16.
- Smith, T. E., R. C. Ydenberg, and R. W. Elner. 1999. Foraging behaviour of an excavating predator, the red rock crab (*Cancer productus* Randall) on soft-shell clam (*Mya arenaria* L.). *Journal of Experimental Marine Biology and Ecology* **238**:185-197.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. W. H. Freeman and Company, New York.
- Underwood, A. J., M. G. Chapman, and S. D. Connell. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology* **250**:97-115.

Vedel, J. P. 1986. Morphology and physiology of a hair plate sensory organ located on the antenna of the rock lobster *Palinurus vulgaris*. *Journal of Neurobiology* **17**:65-76.

Weissburg, M. J., and R. K. Zimmerfaust. 1994. Odor plumes and how blue crabs use them in finding prey. *Journal of Experimental Biology* **197**:349-375.

Ziegler, P. E., C. R. Johnson, S. D. Frusher, and C. Gardner. 2002. Catchability of the southern rock lobster *Jasus edwardsii*. II. Effects of size. *Marine and Freshwater Research* **53**:1149-1159.

CHAPTER SIX

General Discussion

Influence of Reefs on Nearby Soft-Sediment Systems

This thesis investigated how reef-associated predators influence infauna in adjacent sandy habitats. Field studies were done at each of three comparable locations in northeastern New Zealand, representative of shallow soft-sediment habitats near coastal reefs (Fig. 6.1). Differences in community structure were compared among sites in protected and fished areas. Sampling was conducted at several distance strata from the reef edge. The individual studies in the thesis have been written as separate manuscripts for publication (Chapters 2, 3, 4 & 5). In these chapters separate discussions can be found dealing with the detailed results of each study. This general discussion synthesises these findings and gives examples of how marine reserves can assist the research-led management of marine systems.

Consistency and Predictability

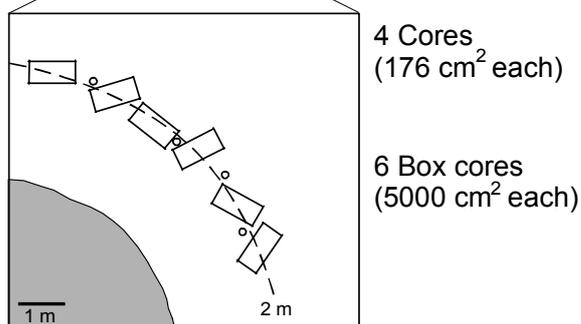
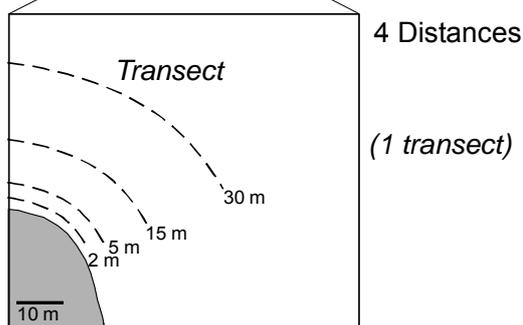
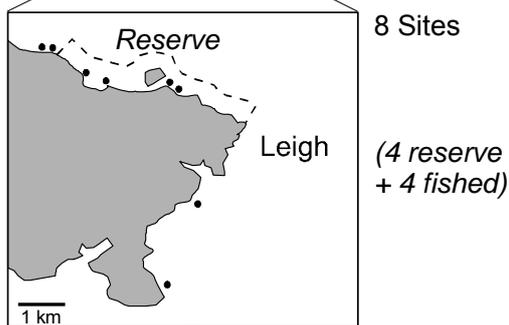
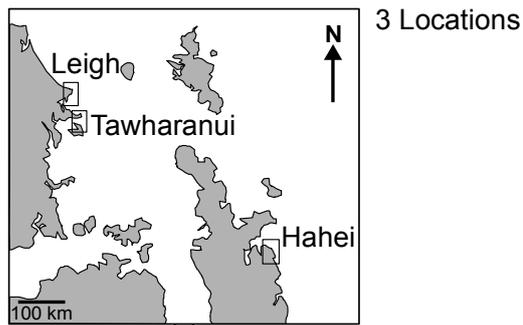
Some patterns were reasonably predictable for particular reef-associated predators and large-bodied infauna (> 4 mm), within the habitats and spatial scales considered. A summary of consistent results are as follows:

1) There was predictability in the density of reef-associated predators, the snapper *Pagrus auratus* and rock lobster *Jasus edwardsii*, across the three comparable locations sampled in this thesis. Snapper and rock lobster greater than legal size were found to be consistently more abundant at protected compared to fished sites.

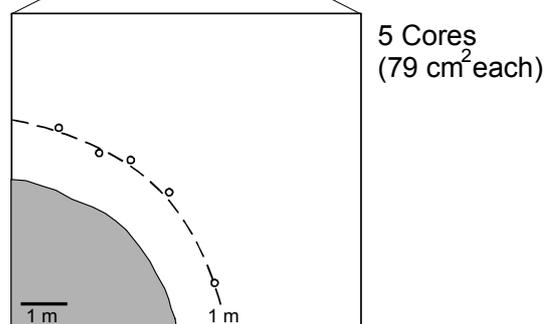
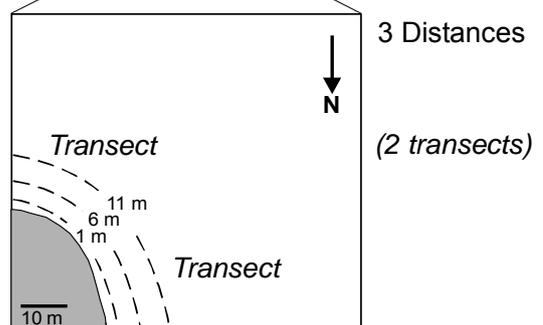
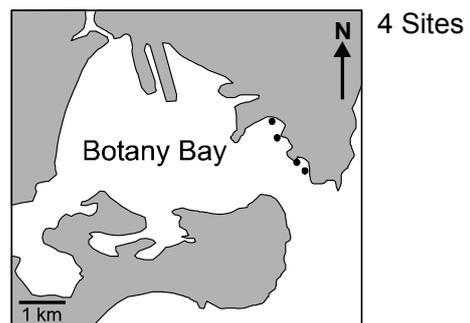
2) The distribution of some large-bodied infauna were found to correlate with sediment texture (Chapter 3, Appendix 3.E). For example, the most abundant species, the opisthobranch *Amalda novaezelandiae*, had a positive relationship with the percentage of fine sediments.

3) The abundance and biomass of several large-bodied species were observed to change consistently with distance from the reef edge (Chapter 3). For example *Dosinia subrosea* and the heart urchin *Echinocardium cordatum* were found to increase in

A. This study



B. Barros et al. (2001)



	<u>Cores</u>	<u>Box Cores</u>	<u>Cores</u>
Total number	384	576	120
Total area (m ²)	5.09	288	0.95

Fig. 6.1.

Fig. 6.1. The spatial extent of sampling undertaken by: (A) this thesis and (B) a comparable study with the next greatest spatial extent of sampling (Barros et al. 2001). (A) Map of the Hauraki Gulf and environs showing the three locations (Leigh, Tawharanui and Hahei) sampled, map of Leigh showing the reserve boundaries (dashed lines) and eight survey sites (solid circles), four distance strata sampled at each site, and the random allocation of the two sampling methods at each distance stratum (132.7 cm² cores and 5000 cm² box-cores). (B) Map of Botany Bay showing the four survey sites (solid circles), three distance strata and two transects sampled at each site, and the random allocation of the one sampling method at each distance stratum (79 cm² cores). The total number of samples obtained by each study is also given.

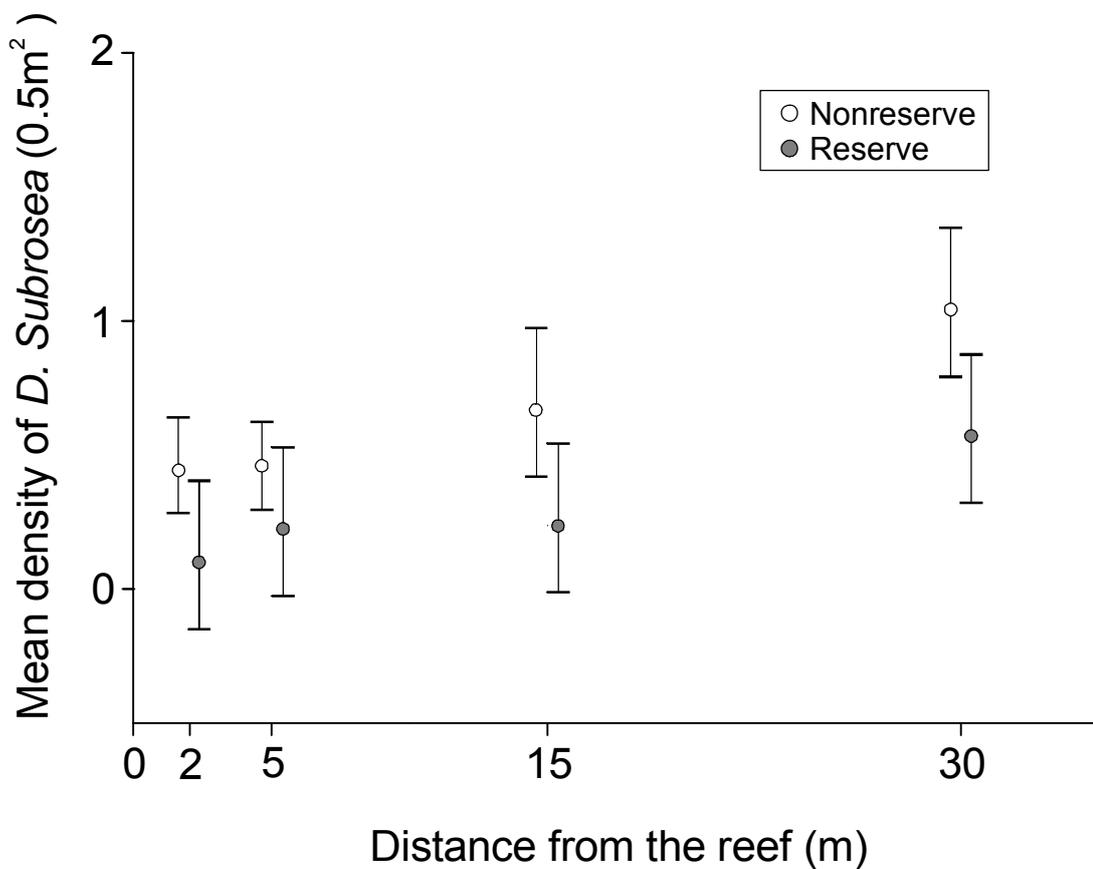


Fig. 6.2. Average (\pm 95% CI) density of *Dosinia subrosea* observed at each distance stratum sampled from either reserve or nonreserve areas (locations, sites and replicates pooled).

abundance with distance from the reef edge, but the reverse pattern was also observed, particularly for the hermit crab *Pagurus novizelandiae*.

4) There were also consistent differences in relative abundance for some infauna between fished and protected areas. Several large bivalve species were lower in biomass, on average, at reserve sites (Chapter 3). The most conspicuous bivalves to exhibit this distribution were the third and fifth most abundant large-bodied taxa: *Dosinia subrosea* and *Myadora striata*, respectively.

Due to the patterns observed (1 - 4) in the soft-sediment communities near to coastal reefs, a general conceptual model of these systems can be considered. The density of large reef-associated predators, in particular rock lobster, can be used to predict the community structure of some large-bodied soft-sediment fauna near coastal reefs. Distance from the reef edge can also be used to predict the distribution of some large-bodied infauna, some of which are influenced by predator density whilst others are not. A 'foraging predator model' (*sensu* Fairweather 1988) would explain how these patterns will be created by predators foraging given distances from a 'shelter habitat' out into a 'food habitat'. The density of *D. subrosea* observed at each distance stratum sampled from either reserve or nonreserve areas was found to support the 'foraging predator model' (Fig. 6.2). However, the distribution of *D. subrosea* also suggests that the influence of proximity to the reef edge is consistent regardless of the densities of predator populations.

5) The 'foraging predator model' was further supported by a manipulative experiment (Chapter 4). This involved a density and caging manipulation across two comparable locations, using *D. subrosea* as prey. The percentage survivorship for this bivalve (over the two-week experiment) was 39% in reserves and 93% in fished areas. Direct evidence was collected (broken shells) to indicate that predation by large rock lobster accounted for the majority of mortality of *D. subrosea* in uncaged plots.

6) Reserve sites not only had greater densities of rock lobster but also a greater size range, with more individuals being greater-than-legal size, whilst rock lobster populations at fished sites were predominantly made up of sub-legal-size animals. Trophic implications of different predator populations were investigated using feeding experiments (Chapter 5). In these laboratory experiments, feeding choice was found to

change with lobster size. This choice correlated with differences observed in populations of two bivalve species at reserve and fished sites.

The consistent patterns observed by this thesis are summarised in Figure 6.3. This includes the ‘foraging predator model’, response of *D. subrosea*, and also the distribution of the other three most abundant species.

Variation and the Limits of Predictability

Prior to this investigation there was no information regarding the distribution of infauna or sediment characteristics near reefs in northeastern New Zealand. Despite the apparent success of the ‘foraging predator model’ in predicting the patterns just described for certain fauna, not all the components of this system responded as expected, particularly smaller bodied infauna (0.5 mm – 4 mm). There are also several other conceptual models regarding the distribution of biotic and abiotic variables for which no support was found. Particular examples of fine-scale variation and unexpected outcomes are summarised as follows:

- 1) Consistent patterns in abundance or biomass with distance from the reef or with reserve status was not apparent from many large-bodied fauna nor for any small-bodied fauna. For example the most abundant large-bodied species (Chapter 3), the opisthobranch *Amalda novaezelandiae*, did not show any consistent pattern with predator density or distance from the reef (Fig. 6.3).

- 2) There were no consistent patterns observed in any of the measured environmental variables among locations, with respect to reserve status or with distance from the reef edge (Chapter 2 and 3).

- 3) No strong correlations were observed between the biomass of small-bodied infauna and any of the environmental variables measured (Chapter 2). However, grain sizes of sediments appeared to be somewhat important in structuring the community (Fig. 2.4).

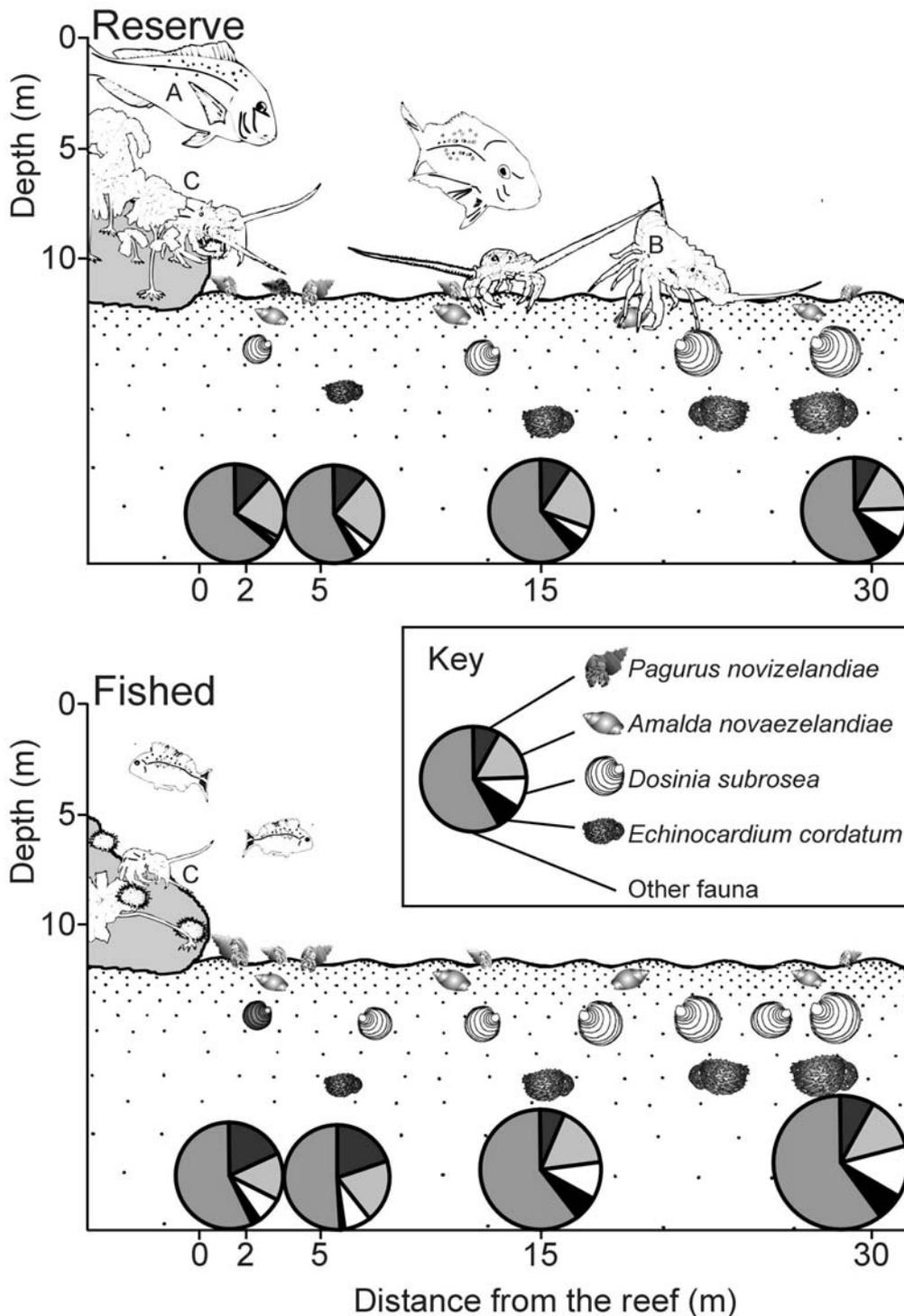


Fig. 6.3. Conceptual model of the influence of proximity to the reef and foraging predators on the four most abundant species and other large-bodied (> 4 mm) macrofaunal species in adjacent sediments. The (A) snapper (*Pagrus auratus*) and (B) rock lobster (*Jasus edwardsii*) were the predators considered. The distribution of infauna is shown with pie charts scaled to the abundance of each species at each distance stratum and between reserve and nonreserve areas. The abundance of each taxon is pooled (locations, sites and box-cores) and the size of the pie chart is proportional to the total number of all large-bodied infauna. The (C) trophic cascade in reef communities described by Shears and Babcock (2002) is also illustrated.

Spatial Patterns of Infauna near Reefs

Variability in small-bodied infauna

Processes governing the distribution of infauna have previously been discussed at length (see, Ambrose 1984) and, in general, variability has been found to be common across scales (Schlacher et al. 1998, Thrush 1999). Legendre et al. (1997) suggested that small-scale variability in soft-sediment systems can mask the influence of infaunal interactions when communities are sampled at larger scales. Despite this small-scale variation, physical properties of sediments have been suggested to be important in determining community composition (e.g. grain-size, Gray 1974, Reise 2002). Several workers have described gradients in sediment characteristics (e.g. Ambrose and Anderson 1990, Barros et al. 2004) and predicted biotic variables to change with distance from the reef (e.g. organic content, Dahlgren et al. 1999). The lack of any consistent patterns in sediment characteristics at the locations studied suggests that any evidence supporting the 'foraging predator model' is unlikely to be confounded by gradients in these variables.

The Role of Physical Disturbance in Soft-Sediment Systems

Small-scale disturbances of relatively stable sediment systems have been demonstrated to increase the vulnerability of prey to epibenthic predators (e.g. Flach and Debruin 1994, Eriksson et al. 2005). At the locations sampled for this thesis (Fig. 6.1), the sediments are described as mobile and have been observed to be frequently turned over by storm events (Hilton and Hesp 1996). This disturbance has been regularly recorded in 25 m of water, twice the depth of the sampling conducted in this thesis (10 - 12 m). Studies of shallow water sediments frequently disturbed by wave action and current flow have found associated communities to be relatively impoverished (DeFelice and Parrish 2001). These habitats can also support high diversity communities associated with long lived biogenic reef forming organisms that do not recover quickly from trawl disturbance (Lenihan and Peterson 1998, Fossa et al. 2002). It has also been observed that communities inhabiting mobile sediments in high-energy environments can recover quickly from mechanical disturbance such as trawling (MacDonald et al. 1996, Kaiser et al. 1998). The apparently resilient nature of these communities (Dernie

2002) has been suggested to be due to infauna being continually redistributed by hydrodynamic forces (Hewitt et al. 1997).

The patterns observed in Chapters 2 and 3 suggested a model of community structure dependent on hydrodynamic forces in these habitats. Larger infauna are likely to be more resistant to physical disturbance in these dynamic habitats (Olafsson et al. 1994), whereas smaller-bodied infauna are likely to be dominated by physical forces as opposed to biological controls (*sensu* Menge and Sutherland 1987). This may be one reason why the influence of predation in such wave-exposed communities was only detected in large-bodied infauna in this study.

Formation of Haloes

Despite detecting consistent gradients in the abundance and biomass of a limited subset of large-bodied infauna (Fig. 6.3), this thesis did not find evidence to support many of the models predicting the formation of ‘haloes’. It is also interesting to note that ‘haloes’ of increasing biomass with increasing distance from the reef were not observed to level off (*Dosinia subrosea*, Fig. 6.2 and *Pagurus novizelandiae*, *Echinocardium cordatum*, Fig. 6.3), suggesting that the processes creating these patterns extend further than the extent of sampling undertaken in this thesis (30 m).

Various mechanisms for the creation of these ‘haloes’ have been suggested. For example, the decreased abundance of the bivalve *Dosinia subrosea* and heart urchin *Echinocardium cordatum* near the reef edge could be due to variation in hydrodynamic forces. Barros et al. (2004) showed that the concentration of reflected wave energy near to a reef edge can alter the microtopographic structure of sediments and their associated fauna. Increased physical disturbance near the reef may also result in changes in feeding efficiency (Pilditch and Grant 1999, Ward and Shumway 2004) or increased physiological stress on infauna (Friedrichs et al. 2000, Crimaldi et al. 2002). Reported patterns of increased abundance of certain taxa near reefs, such as the deposit-feeding holothurian *Holothuria princeps* (Dahlgren et al. 1999) and the scavenging / suspension-feeding hermit crab *P. novizelandiae* (Chapter 3), may be the result of food matter derived from the reef. Previous studies have found reef-derived organic matter to correlate with the infaunal biomass of sandy beach (Soares et al. 1997) and off-shore (Duggins et al. 1989) communities. In northeastern New Zealand the recovery of predators in reserves has lead to the concomitant recovery of shallow kelp beds (Fig. 6.2), which are predicted to result in the increased production of organic matter

(Babcock et al. 1999). The increased abundance of hermit crabs near reefs may have resulted from greater production of particulate organic matter in reserves. However, no consistent patterns were observed in the distribution of organic matter in the sediments sampled; and the distribution of hermit crabs did not differ significantly between reserve and nonreserve sites (Fig. 6.3). Therefore, this mechanism of increased particulate matter in reserves sustaining greater populations of hermit crabs seems unlikely.

Investigation of Haloes

The observation of ‘halo’ patterns across three comparable locations has allowed a predictive model to be formed regarding their occurrence in these habitats. However, no generalisations can as yet be made about the processes creating ‘haloes’. Further experiments are needed to investigate ‘halo’ patterns with respect other factors and variables. Alternative methods have been developed for measuring small-scale variability in organic content (see Eglinton et al. 1996) and sediment grain size (Gibbs 1974, McArdle 1992). Other variables, not yet considered, may also be useful to further investigations. For example, isotope analysis may be used to investigate the trophic pathways supporting certain fauna in these assemblages (see Soares et al. 1997). Such studies would aid the development of existing models and suggest new avenues for investigation.

Alternatives to the Predation Model

Several alternative hypotheses have been considered in the development of the ‘foraging predator model’. Models of large-scale processes such as recruitment (e.g. supply-side, Lewin 1986, Witman et al. 2003) and food supply (Menge et al. 1999, Paiva 2001) were not explicitly tested in this study. Instead, the use of multiple comparable locations and the interspersed treatments in the mensurative and manipulative experiments allowed the generality of any patterns to be tested over several spatial scales (Fig. 6.1). In New Zealand’s coastal habitats the influence of ‘supply-side’ or bottom-up’ processes are expected to be apparent between bioregions (Menge et al. 1999) or along strong environmental gradients (Lundquist et al. 2004). At the scales sampled, no patterns were found that might suggest any consistent influence of these processes on community structure (Chapters 2 & 3). A variety of models concerning smaller-scale processes were explicitly tested. These included the influence of various biotic factors including infaunal predation (e.g. Ambrose 1984, Desroy et al. 1998) and bioturbation (e.g. Thrush et al. 1991, Dahlgren et al. 1999). The distribution

of these infauna did not strongly correlate to the community structure of any other small or large-bodied infauna. Also, no consistent correlations were found between any other infauna in the assemblage, suggesting competition was not an important factor (e.g. Peterson 1979, Legendre et al. 1997). A correlation between the community structure of large-bodied infauna and sediment grain-size was detected, but this did not confound the comparison of reserve and fished areas (Chapter 3, Appendix 3.E).

Placing this Study in Perspective

Predator Populations

Snapper occur across the continental shelf from estuarine habitats to depths > 100 m (Paul 1976) and are observed to concentrate in coastal areas for spawning (Kingett and Choat 1981, Willis et al. 2003). Recent movement studies investigating populations within protected areas have indicated how large snapper can become resident on coastal reefs (Willis et al. 2001, Parsons et al. 2003). A variety of movement patterns have been observed (Parsons and Egli 2005), including frequent sorties by resident reef fish to and over soft-sediment areas (Fig. 6.1). Detailed observational and gut content studies have confirmed that snapper are generalist predators that take a large variety of prey from both reef and soft-sediment habitats (Colman 1972, Berquist 1994, Babcock et al. 1999). Less is known about the diet of *Jasus edwardsii* in these habitats. However, they have been observed to forage along the reef edge (Fig. 6.3) and take large-bodied bivalve prey (MacDiarmid 1991). Detailed tracking studies have also found large rock lobster to regularly move to adjacent sand flats and migrate distances up to 1 km over sandy habitats (Kelly et al. 1999).

Size-Structure of Populations

The field experiments in this thesis used the contrasting populations of reef-associated predators inside and outside reserves to investigate the top-down control of fauna in nearby sandy habitats (Chapters 2, 3 and 4). At the locations studied it was not only the density of predators that differed with reserve status but also the size-structure, with a greater proportion of the population being larger than their respective legal sizes inside reserves (see Chapter 5). Many studies of the effect of predator / prey size ratios on rates of predation have shown the size of predators to be very important (e.g. Shelbourne 1962, Evans 1976). For example studies of predation by the blue crab

Callinectes sapidus on soft-sediment bivalves have suggested that populations of large crab predators result in direct increases in predation pressure, depending on habitat type and prey size (Arnold 1984, Seitz et al. 2001). This thesis used contrasting predator populations that differed in terms of both density and size to investigate effects of predation.

In Chapter 5 the implications of different predator populations for trophic linkages were investigated in a laboratory experiment using rock lobster and two soft-sediment bivalves. Lobster of all sizes consistently chose *Dosinia subrosea* over *Dosinia anus*. This is consistent with the greater average abundance of *D. anus* found at sites with greater density of rock lobster. This study showed that large rock lobster preyed on a much larger size-range of *D. subrosea* than smaller lobster. It appears that populations of large *D. subrosea* in fished areas are subject to lower levels of predation pressure from rock lobster. It was also observed that foraging by smaller lobster would be limited by their smaller movement patterns (Kelly et al. 1999) and the morphology of their feeding pereopods (Chapter 5).

Commercial trap fisheries for rock lobster have been shown to preferentially remove larger individuals (e.g. Ziegler et al. 2002, Acosta and Robertson 2003) and commercial fishing for snapper has resulted in drastic changes in the size-structure of exploited populations (Hauser et al. 2002). The trophic implications of such changes in predator populations have been investigated in theoretical studies and small-scale field experiments (e.g. Stevens et al. 2000, Jennings et al. 2002, Thrush and Dayton 2002). This thesis provides empirical evidence, from experimental studies over a variety of scales, of the effects of fishing activities on the structure of predator and prey communities. To further investigate the importance of size-structure versus the density of predator populations it would be necessary to design manipulative experiments in which these two factors could be separated. Such information could suggest how to maintain the top-down control of community structure by sustaining sufficient populations of higher-order predators.

Limitations of Predictive Models

There are over 10 distinct bio-geographic regions around the coast of New Zealand (Babcock and Shears 2003). This thesis has tested the generality of models by considering comparable locations as random factors (Beck 1997), at locations representative of coastal reefs with adjacent shallow sandy habitats in the northeastern

bioregion. This comparison has allowed predictions to be made regarding similar habitats in this region but predictive models should not be extended to other habitats and regions until appropriate tests have been conducted (e.g. Walters and Hilborn 1978). Previous investigations of various marine reserves in different bioregions have found variation in the recovery of previously exploited predators (Babcock 2003). For example, in the Poor Knights Islands Marine Reserve snapper populations have recovered rapidly (Denny et al. 2004) but rock lobster have not. At the Poor Knights *Jasus edwardsii* populations are likely to be limited by larval supply due to oceanographic features (Booth et al. 2000). In contrast, rock lobster populations in two newly established reserves in the southeastern bioregion of the north island have increased dramatically whilst snapper and other previously exploited predators have not (D. Freeman Pers. Com.). These contrasting results from newly established marine reserves suggest top-down processes may vary between bioregions. For example, the trophic cascade (Fig. 6.3) demonstrated by Shears and Babcock (2002) has so far only been detected inside two marine reserves in the northeastern bioregion and subsequent surveys of reserves in other bioregions have found no strong evidence of this top-down process (Shears 2003). This has been attributed to bio-geographic differences in the macroalgal and invertebrate community structure around New Zealand, but may also be due to differences in predator populations.

New Tools for Soft-Sediment Ecology

Shallow-water soft-sediment communities have been shown to be highly productive habitats (e.g. Edgar and Shaw 1995, Cahoon 1999). However, their systems have been recognised as highly complex (e.g. Thrush 1999, Barros 2005) and it has been suggested that various scales of investigation are required to link patterns to processes in these communities (e.g. Thrush et al. 1997, Underwood et al. 2000). This thesis used a novel approach of combining mensurative experiments with existing manipulations of predator density in no-take areas. Marine reserves provided a novel contrast in predator populations with which to investigate the top-down control of community structure. Prior to this thesis, no investigation of such communities near reefs was able to corroborate the results of different ecological tools over a variety of spatial scales (Barros 2005).

Marine Reserves as Ecological Tools

A variety of studies have demonstrated the direct effects of certain fishing methods (e.g. trawling and dredging) on soft-sediment community structure (e.g. Jennings et al. 2001, Thrush and Dayton 2002). Investigations of indirect effects of fishing on food-webs in these communities have proved difficult (Coleman and Williams 2002) in part due to the complex nature of soft-sediment systems (Schlacher et al. 1998, Thrush 1999). Pinnegar et al. (2000) suggested that if protected areas, such as marine reserves, were available for study then cascades of indirect effects of fishing might be found in soft-sediment systems.

Ideally an investigation of the effects of fishing would begin with an unfished (natural) situation (Jackson and Sala 2001). The influence of fishing could then be investigated with a before / after and control / impact (BACI) study (*sensu* Underwood 1994). The controls in such a study would be provided by marine reserves. Given the historical and widespread effects of fishing that have been recognised worldwide (e.g. Jackson et al. 2001, Thrush and Dayton 2002) and the recent establishment of no-take areas (Roberts 2003) a BACI study is not now possible. Investigations using marine reserves to study the effects of fishing are now obliged to work backwards, by observing what changes occur when fishing stops. Importantly, the historical trophic changes resulting from exploiting higher-order predators are not likely to be symmetrical with the recovery of populations of these predators and the reestablishment of top-down processes in marine reserves (e.g. Jennings and Polunin 1997, Frid et al. 1999). For example the removal of large predators by fishing can occur quickly (Chiappone et al. 2000, Acosta and Robertson 2003) but the reestablishment of comparable adult populations without immigration can take much longer (Newman and Pollock 1974, Millar et al. 1999). Therefore, it is possible that food-webs studied within established marine reserves, where exploited populations are recovering, may have never occurred before.

Improving on Previous Studies

To specifically investigate the top-down control of soft-sediment communities researchers have used geographical ranges of predators (e.g. Kvitek et al. 1992, Skilleter 1994). This approach was not used in this thesis as existing gradients for snapper (Francis 2003) and rock lobster (Breen and Kendrick 1997) in New Zealand occur across bioregions and studies along these continuous gradients would have lacked the

necessary control for processes occurring at intermediate scales (*sensu* Hurlbert 1984). Previous mensurative studies of soft-sediment communities near reefs have suggested trophic interactions (Davis et al. 1982, Posey and Ambrose 1994, Dahlgren et al. 1999). However, investigations of processes have often been complicated by various problems. For example, observations have been confounded by gradients in sediment characteristics (Ambrose and Anderson 1990, Barros et al. 2001), interactions between infauna (Dahlgren et al. 1999) and limited replication over relevant spatial scales (Barros 2005). The spatial extent of sampling undertaken by this thesis and a comparable study with the next greatest spatial extent of sampling (Barros et al. 2001) is illustrated in Fig. 6.1.

By using marine reserves interspersed across several locations (Fig. 6.1), this study has been able to avoid these problems and investigate the role of predators. In the absence of any before / after investigations this thesis has demonstrated existing marine reserves to be useful as ecosystem-based experiments to investigate food-webs (*sensu* Carpenter et al. 1995). By considering reserve locations and sample sizes as random factors this study has been able to test the generality of the effects measured (Beck 1997). Compared to fished areas these reserves are less disturbed systems in which the natural processes are recovering from the historical effects of fishing pressure (*sensu* Bohnsack 2003). This comparison has also allowed investigations of consistent patterns in community structure that occur regardless of predator density.

Ecosystem management

This thesis has provided novel information regarding trophic interactions between reef-associated predators and adjacent soft-sediment communities (Chapters 3, 4 & 5). These studies also provided evidence of how the exploitation of a predator, in particular the rock lobster *Jasus edwardsii*, can lead to compensatory effects in prey communities. Such information is seen as essential for the construction of reliable food-web models and ecosystem-based management (Bradford-Grieve et al. 2003, Christensen and Walters 2004).

Rock (or spiny) lobsters support some of the largest commercial fisheries worldwide (Lipcius and Cobb 1994) and, therefore, there is a need for effective fisheries management strategies. Since 1990 the management of the New Zealand rock lobster has been held up as a success story for fisheries scientists (Breen and Kendrick 1997). However, recent stock assessments have indicated that certain management areas

around New Zealand are overfished. This has led managers to reduce quotas of some areas by up to 30% (NZPA 2005). Over the same period the management of the Australian western rock lobster, *Panulirus cygnus*, has been credited with the recovery of stocks (Hall and Chubb 2001). Given the health of the fishery in Western Australia it has even been suggested that quotas could be increased (Donohue 2000). Since 1990 various controls of the fishery, including a maximum legal size, have been used in Australia that has not been adopted in New Zealand.

Modelling studies have suggested that, to sustain fisheries yields, large breeding adults are essential to preserve the natural genetic variation in populations (Conover and Munch 2002). Investigations of rock lobster in New Zealand have also indicated that large individuals of both sexes are important for maintaining the reproductive output of populations (MacDiarmid and Butler 1999). The introduction of the maximum legal size in the *P. cygnus* fishery in Western Australia has been suggested to have led to an increase in egg production (Hall and Chubb 2001).

If the New Zealand rock lobster fishery adopted a maximum legal-size regulation, a similar increase in egg production could result. However, due to the efficient nature of most rock lobster fisheries (Ziegler et al. 2002) the vast majority of animals in a fishery are unlikely to reach a maximum legal size. If a system of marine reserves existed around New Zealand, these would provide a refuge for populations of large-bodied rock lobster and maintain any long-term benefits of a maximum-legal-size regulation. Such a system of reserves would also provide a comparative framework with which to test the generality of the conceptual model proposed in this thesis (Fig. 6.3). Contrasting prey population structures between sites with different populations of predators, as done in this thesis, would allow experiments to be devised to directly test hypotheses of top-down processes across bioregions (Agardy 2000).

Reliable Models

If a model of a food-web had been created for the coastal ecosystem of northeastern New Zealand prior to this study, the model would have included trophic processes between reef-associated predators and the soft-sediment community (MacDiarmid 1991, Kelly et al. 1999). However, the nature and strength of these interactions would not have been estimated accurately. This thesis has illustrated how reserves can provide useful controls for research and adaptive management. It is the role of ecologists to suggest management actions that can provide for the further testing of

ecological models (*sensu* Underwood 1995). To maximise the possible benefits for research and management of marine systems, it is essential that comparable systems of reserves are created and that these reserves are representative of all habitats and bioregions.

In conclusion, despite variability, reliable models have been developed in this thesis for several large-bodied infauna near reefs. The assemblage of small-bodied fauna in this system has, however, proved more complex. More investigative work is needed before predictive models can be posed and tested for smaller macrofauna. Despite this, using the information in this thesis, it is now possible to reliably predict how fishing for rock lobster and distance from the reef edge will affect several soft-sediment fauna near reefs in northeastern New Zealand.

References

- Acosta, C. A., and D. N. Robertson. 2003. Comparative spatial ecology of fished spiny lobsters *Panulirus argus* and an unfished congener *P. guttatus* in an isolated marine reserve at Glover's Reef atoll, Belize. *Coral Reefs* **22**:1-9.
- Agardy, T. 2000. Effects of fisheries on marine ecosystems: a conservationist's perspective. *International Council for the Exploration of the Sea Journal of Marine Science* **57**:761-765.
- Ambrose, R. F., and T. W. Anderson. 1990. Influence of an artificial reef on the surrounding infaunal community. *Marine Biology* **107**:41-52.
- Ambrose, W. G. 1984. Role of predatory infauna in structuring marine soft-bottom communities. *Marine Ecology Progress Series* **17**:109-115.
- Arnold, W. S. 1984. The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus* (Rathbun), on the hard clam, *Mercenaria mercenaria* (Linne). *Journal of Experimental Marine Biology and Ecology* **80**:207-219.
- Babcock, R. C. 2003. The New Zealand marine reserve experience: the science behind the politics. Pages 108-119 in P. Hutchings and D. Lunney, editors. *Conserving*

marine environments. Out of sight out of mind? Royal Zoological Society of New South Wales, Mosman, New South Wales.

- Babcock, R. C., S. Kelly, N. T. Shears, J. W. Walker, and T. J. Willis. 1999. Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series* **189**:125-134.
- Babcock, R. C., and N. T. Shears. 2003. Rocky coastal marine habitat coastal protection in New Zealand: requirements and implications. Report to the Department of Conservation. Uniservices, Auckland, New Zealand.
- Barros, F. 2005. Evaluating the importance of predation on subtidal benthic assemblages in sandy habitats around rocky reefs. *Acta Oecologia* **27**:211-223.
- Barros, F., A. J. Underwood, and P. Archambault. 2004. The influence of troughs and crests of ripple marks on the structure of subtidal benthic assemblages around rocky reefs. *Estuarine, Coastal and Shelf Science* **60**:781-790.
- Barros, F., A. J. Underwood, and M. Lindegarth. 2001. The influence of rocky reefs on structure of benthic macrofauna in nearby soft-sediments. *Estuarine, Coastal and Shelf Science* **52**:191-199.
- Beck, M. W. 1997. Inference and generality in ecology: current problems and an experimental solution. *Oikos* **78**:265-273.
- Berquist, R. M. 1994. Patterns of activity and movement in New Zealand snapper, *Pagrus auratus*. MSc Thesis, University of Auckland, Auckland.
- Bohnsack, J. A. 2003. Shifting baselines, marine reserves, and Leopold's biotic ethic. *Gulf and Caribbean Research* **14**:1-7.
- Booth, J. D., E. Bradford, and J. Renwick. 2000. *Jasus edwardsii* puerulus settlement levels examined in relation to the ocean environment and to subsequent juvenile and recruit abundance. Ministry of Fisheries, Wellington, New Zealand.
- Bradford-Grieve, J. M., P. K. Probert, S. D. Nodder, D. Thompson, J. Hall, S. Hanchet, P. Boyd, J. Zeldis, A. N. Baker, H. A. Best, N. Broekhuizen, S. Childerhouse, M. Clark, M. Hadfield, K. Safi, and I. Wilkinson. 2003. Pilot trophic model for

- subantarctic water over the Southern Plateau, New Zealand: a low biomass, high transfer efficiency system. *Journal of Experimental Marine Biology and Ecology* **289**:223-262.
- Breen, P. A., and T. H. Kendrick. 1997. A fisheries management success story: the Gisborne, New Zealand, fishery for red rock lobsters (*Jasus edwardsii*). *Marine and Freshwater Research* **48**:1103-1110.
- Cahoon, L. B. 1999. The role of benthic microalgae in neritic ecosystems. Pages 47-86 *in* *Oceanography and Marine Biology*, Vol 37.
- Carpenter, S. R., S. W. Chisholm, C. J. Krebs, D. W. Schindler, and R. F. Wright. 1995. Ecosystem experiments. *Science* **269**:324-327.
- Chiappone, M., R. Sluka, and K. S. Sealey. 2000. Groupers (Pisces: Serranidae) in fished and protected areas of the Florida Keys, Bahamas and northern Caribbean. *Marine Ecology Progress Series* **198**:261-272.
- Christensen, V., and C. J. Walters. 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* **172**:109-139.
- Coleman, F. C., and S. L. Williams. 2002. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *Trends in Ecology & Evolution* **17**:40-44.
- Colman, J. A. 1972. Food of snapper, *Chrysophrys auratus* (Forster), in the Hauraki Gulf, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **6**:221-239.
- Conover, D. O., and S. B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. *Science* **297**:94-96.
- Crimaldi, J. P., J. K. Thompson, J. H. Rosman, R. J. Lowe, and J. R. Koseff. 2002. Hydrodynamics of larval settlement: The influence of turbulent stress events at potential recruitment sites. *Limnology and Oceanography* **47**:1137-1151.

- Dahlgren, C. P., M. H. Posey, and A. W. Hulbert. 1999. The effects of bioturbation on the infaunal community adjacent to an offshore hardbottom reef. *Bulletin of Marine Science* **64**:21-34.
- Davis, N., G. R. VanBlaricom, and P. K. Dayton. 1982. Man-made structures on marine sediments: effects on adjacent benthic communities. *Marine Biology* **70**:295-304.
- DeFelice, R. C., and J. D. Parrish. 2001. Physical processes dominate in shaping invertebrate assemblages in reef-associated sediments of an exposed Hawaiian coast. *Marine Ecology Progress Series* **215**:121-131.
- Denny, C. M., T. J. Willis, and R. C. Babcock. 2004. Rapid recolonisation of snapper *Pagrus auratus*: Sparidae within an offshore island marine reserve after implementation of no-take status. *Marine Ecology Progress Series* **272**:183-190.
- Dernie, K. M. 2002. Predicting post-disturbance recovery of soft-sediment communities. *Marine Ecology Progress Series* **215**:121-131.
- Desroy, N., C. Retiere, and E. Thiebaut. 1998. Infaunal predation regulates benthic recruitment: an experimental study of the influence of the predator *Nephtys hombergii* (Savigny) on recruits of *Nereis diversicolor* (Muller). *Journal of Experimental Marine Biology and Ecology* **228**:257-272.
- Donohue, K. 2000. Western Rock Lobster Management for seasons 2001/2002 and 2002/2003. Fisheries Management Paper, Fisheries WA, Australia.
- Duggins, D. O., C. A. Simenstad, and J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* **245**:170-173.
- Edgar, G. J., and C. Shaw. 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia. 3. General relationships between sediments, seagrasses, invertebrates and fishes. *Journal of Experimental Marine Biology and Ecology* **194**:107-131.

- Eglinton, T. I., J. J. Boon, E. C. Minor, and R. J. Olson. 1996. Microscale characterization of algal and related particulate organic matter by direct temperature-resolved mass spectrometry. *Marine Chemistry* **52**:27-54.
- Eriksson, S. P., H. Wennhage, J. Norkko, and A. Norkko. 2005. Episodic disturbance events modify predator-prey interactions in soft sediments. *Estuarine, Coastal and Shelf Science* **64**:289-294.
- Evans, H. F. 1976. Role of predator-prey size ratio in determining efficiency of capture by *Anthocoris nemorum* and escape reactions of its prey, *Acyrtosiphon pisum*. *Ecological Entomology* **1**:85-90.
- Fairweather, P. G. 1988. Predation creates haloes of bare space among prey on rocky seashores in New South Wales. *Journal of Experimental Marine Biology and Ecology* **114**:261-273.
- Flach, E. C., and W. Debruin. 1994. Does the activity of cockles, *Cerastoderma edule* (L.) and lugworms, *Arenicola marina* L., make *Corophium volutator* Pallas more vulnerable to epibenthic predators: a case of interaction modification. *Journal of Experimental Marine Biology and Ecology* **182**:265-285.
- Fossa, J. H., P. B. Mortensen, and D. M. Furevik. 2002. The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. *Hydrobiologia* **471**:1-12.
- Francis, M. 2003. Snapper. Pages 186-191 in N. L. Andrew and F. M., editors. *The living reef*. Craig Potton Publishing, Nelson.
- Frid, C. L. J., S. Hansson, S. A. Ragnarsson, A. Rijnsdorp, and S. A. Steingrimsson. 1999. Changing levels of predation on benthos as a result of exploitation of fish populations. *Ambio* **28**:578-582.
- Friedrichs, M., G. Graf, and B. Springer. 2000. Skimming flow induced over a simulated polychaete tube lawn at low population densities. *Marine Ecology Progress Series* **31**:219-228.

- Gibbs, R. J. 1974. A settling tube for sand-size analysis. *Journal of Sedimentary Petrology* **44**:538-588.
- Gray, J. S. 1974. Animal-sediment relationships. *Oceanography and Marine Biology. An Annual Review* **12**:707-722.
- Hall, N., and C. Chubb. 2001. The status of the western rock lobster, *Panulirus cygnus*, fishery and the effectiveness of management controls in increasing the egg production of the stock. *Marine and Freshwater Research* **52**:1657-1667.
- Hauser, L., G. J. Adcock, P. J. Smith, J. H. B. Ramirez, and G. R. Carvalho. 2002. Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (*Pagrus auratus*). *Proceedings of the National Academy of Sciences of the United States of America* **99**:11742-11747.
- Hewitt, J. E., R. D. Pridmore, S. F. Thrush, and V. J. Cummings. 1997. Assessing the short-term stability of spatial patterns of macrobenthos in a dynamic estuarine system. *Limnology and Oceanography* **42**:282-288.
- Hilton, M. J., and P. Hesp. 1996. Determining the limits of beach-nearshore sand systems and the impact of offshore coastal sand mining. *Journal of Coastal Research* **12**:496-519.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**:187-212.
- Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**:629-638.
- Jackson, J. B. C., and E. Sala. 2001. Unnatural oceans. *Scientia Marina* **65**:273-281.
- Jennings, S., S. P. R. Greenstreet, L. Hill, G. J. Piet, J. K. Pinnegar, and K. J. Warr. 2002. Long-term trends in the trophic structure of the North Sea fish community:

- evidence from stable-isotope analysis, size-spectra and community metrics. *Marine Biology* **141**:1085-1097.
- Jennings, S., J. K. Pinnegar, N. V. C. Polunin, and K. J. Warr. 2001. Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. *Marine Ecology Progress Series* **213**:127-142.
- Jennings, S., and N. V. C. Polunin. 1997. Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. *Coral Reefs* **16**:71-82.
- Kaiser, M. J., D. B. Edwards, P. J. Armstrong, K. Radford, N. E. L. Lough, R. P. Flatt, and H. D. Jones. 1998. Changes in megafaunal benthic communities in different habitats after trawling disturbance. *International Council for the Exploration of the Sea Journal of Marine Science* **55**:353-361.
- Kelly, S., A. B. MacDiarmid, and R. C. Babcock. 1999. Characteristics of spiny lobster, *Jasus edwardsii*, aggregations in exposed reef and sandy areas. *Marine and Freshwater Research* **50**:409-416.
- Kingett, P. D., and J. H. Choat. 1981. Analysis of density and distribution patterns in *Chrysopharys auratus* (Pisces: Sparidae) within a reef environment: an experimental approach. *Marine Ecology Progress Series* **5**:283-290.
- Kvitek, R. G., J. S. Oliver, A. R. Degange, and B. S. Anderson. 1992. Changes in Alaskan soft-bottom prey communities along a gradient in sea otter predation. *Ecology* **73**:413-428.
- Legendre, P., S. F. Thrush, V. J. Cummings, P. K. Dayton, J. Grant, J. E. Hewitt, A. H. Hines, B. H. McArdle, R. D. Pridmore, D. C. Schneider, S. J. Turner, R. B. Whitlatch, and M. R. Wilkinson. 1997. Spatial structure of bivalves in a sandflat: scale and generating processes. *Journal of Experimental Marine Biology and Ecology* **216**:99-128.
- Lenihan, H. S., and C. H. Peterson. 1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecological Applications* **8**:128-140.

- Lewin, R. 1986. Supply-side ecology. *Science* **234**:25-27.
- Lipcius, R. N., and J. S. Cobb. 1994. Ecology and fishery biology of spiny lobster. Pages 5-15 in P. B. F, C. J. S, and K. J, editors. *Spiny lobster management*. Blackwell Scientific, Victoria, Australia.
- Lundquist, C. J., S. F. Thrush, J. W. Oldman, and A. K. Senior. 2004. Limited transport and recolonization potential in shallow tidal estuaries. *Limnology and Oceanography* **49**:386-395.
- MacDiarmid, A. B. 1991. Seasonal changes in depth distribution, sex ratio and size frequency of spiny lobster (*Jasus edwardsii*) on a coastal reef in northern New Zealand. *Marine Ecology Progress Series* **70**:129-141.
- MacDiarmid, A. B., and M. J. Butler. 1999. Sperm economy and limitation in spiny lobsters. *Behavioral Ecology and Sociobiology* **46**:14-24.
- MacDonald, D. S., M. Little, N. C. Eno, and K. Hiscock. 1996. Disturbance of benthic species by fishing activities: a sensitivity index. *Aquatic Conservation* **6**:257-268.
- McArdle, S. B. 1992. Sand beach ecology: swash features relevant to the macrofauna. *Journal of Coastal Research* **8**:398-407.
- Menge, B. A., B. A. Daley, J. Lubchenco, E. Sanford, E. Dahlhoff, P. M. Halpin, G. Hudson, and J. L. Burnaford. 1999. Top-down and bottom-up regulation of New Zealand rocky intertidal communities. *Ecological Monographs* **69**:297-330.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental-stress and recruitment. *American Naturalist* **130**:730-757.
- Millar, R. B., B. H. McArdle, and S. J. Harley. 1999. Modeling the size of snapper (*Pagrus auratus*) using temperature-modified growth curves. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:1278-1284.
- Newman, G. G., and D. E. Pollock. 1974. Growth of rock lobster *Jasus lalandii* and its relationship to benthos. *Marine Biology* **24**:339-346.

- NZPA (New Zealand Press Association). 2005. Rock lobster catch slashed by 30pc. Pages 5 in *The New Zealand Herald*, Auckland.
- Olafsson, E. B., C. H. Peterson, and W. G. Ambrose, Jr. 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes. *Oceanography and Marine Biology. An Annual Review* **32**:19-32.
- Paiva, P. C. 2001. Spatial and temporal variation of a nearshore benthic community in southern Brazil: implications for the design of monitoring programs. *Estuarine, Coastal and Shelf Science* **52**:423-433.
- Parsons, D., and D. Egli. 2005. Fish movement in a temperate marine reserve: new insights through application of acoustic tracking. *Marine Technology Society Journal* **39**:15-22.
- Parsons, D. M., R. C. Babcock, R. K. S. Hankin, T. J. Willis, J. P. Aitken, R. K. O'Dor, and G. D. Jackson. 2003. Snapper *Pagrus auratus* (Sparidae) home range dynamics: acoustic tagging studies in a marine reserve. *Marine Ecology Progress Series* **262**:253-265.
- Paul, L. J. 1976. A study on age, growth, and population structure of the snapper, *Chrysophrys auratus* (Foster), in the Hauraki Gulf, New Zealand. New Zealand Ministry of Agriculture and Fisheries, Wellington, New Zealand.
- Peterson, C. H. 1979. Approaches to the study of competition in benthic communities in soft sediments. Proceedings of the Fifth Biennial International Estuarine Research Conference; Jekyll Island.
- Pilditch, C. A., and J. Grant. 1999. Effect of variations in flow velocity and phytoplankton concentration on sea scallop (*Placopecten magellanicus*) grazing rates. *Journal of Experimental Marine Biology and Ecology* **240**:111-136.
- Pinnegar, J. K., N. V. C. Polunin, P. Francour, F. Badalamenti, R. Chemello, M. L. Harmelin-Vivien, B. Hereu, M. Milazzo, M. Zabala, G. D'Anna, and C. Pipitone. 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environmental Conservation* **27**:179-200.

- Posey, M. H., and W. G. Ambrose. 1994. Effects of proximity to an offshore hard-bottom reef on infaunal abundances. *Marine Biology* **118**:745-753.
- Reise, K. 2002. Sediment mediated species interactions in coastal waters. *Journal of Sea Research* **48**:127-141.
- Roberts, C. M. 2003. Our shifting perspectives on the ocean. *Oryx* **37**:166-177.
- Schlacher, T. A., P. Newell, J. Clavier, M. A. Schlacher-Hoenlinger, C. Chevillon, and J. Britton. 1998. Soft-sediment benthic community structure in a coral reef lagoon: the prominence of spatial heterogeneity and 'spot endemism'. *Marine Ecology Progress Series* **174**:159-174.
- Seitz, R. D., R. N. Lipcius, A. H. Hines, and D. B. Eggleston. 2001. Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. *Ecology* **82**:2435-2451.
- Shears, N. T. 2003. Response of shallow subtidal reef communities to marine reserve protection in northeastern New Zealand. PhD thesis, University of Auckland, Auckland, New Zealand.
- Shears, N. T., and R. C. Babcock. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* **132**:131-142.
- Shelbourne, J. E. 1962. Predator-prey size relationship for plaice larvae feeding on oikopleura. *Journal of the Marine Biological Association of the United Kingdom* **42**:243-252.
- Skilleter, G. A. 1994. Refuges from predation and the persistence of estuarine clam populations. *Marine Ecology Progress Series* **109**:29-42.
- Soares, A. G., T. A. Schlacher, and A. McLachlan. 1997. Carbon and nitrogen exchange between sandy beach clams (*Donax serra*) and kelp beds in the Benguela coastal upwelling region. *Marine Biology* **127**:657-664.
- Stevens, J. D., R. Bonfil, N. K. Dulvy, and P. A. Walker. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine

- ecosystems. *International Council for the Exploration of the Sea Journal of Marine Science* **57**:476-494.
- Thrush, S. F. 1999. Complex role of predators in structuring soft-sediment macrobenthic communities: implications of changes in spatial scale for experimental studies. *Australian Journal of Ecology* **24**:344-354.
- Thrush, S. F., and P. K. Dayton. 2002. Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. *Annual Review of Ecology and Systematics* **33**:449-473.
- Thrush, S. F., R. D. Pridmore, J. E. Hewitt, and V. J. Cummings. 1991. Impact of ray feeding disturbances on sandflat macrobenthos: do communities dominated by polychaetes or shellfish respond differently? *Marine Ecology Progress Series* **69**:245-252.
- Thrush, S. F., D. C. Schneider, P. Legendre, R. B. Whitlatch, P. K. Dayton, J. E. Hewitt, A. H. Hines, V. J. Cummings, S. M. Lawrie, J. Grant, R. D. Pridmore, S. J. Turner, and B. H. McArdle. 1997. Scaling-up from experiments to complex ecological systems: where to next? *Journal of Experimental Marine Biology and Ecology* **216**:243-254.
- Underwood, A. J. 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. *Ecological Applications* **4**:3-15.
- Underwood, A. J. 1995. Ecological research and (and research into) environmental management. *Ecological Applications* **5**:232-247.
- Underwood, A. J., M. G. Chapman, and S. D. Connell. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology* **250**:97-115.
- Walters, C. J., and R. Hilborn. 1978. Ecological optimization and adaptive management. *Annual Review of Ecology and Systematics* **9**:157-188.

- Ward, J. E., and S. E. Shumway. 2004. Separating the grain from the chaff: particle selection in suspension- and deposit-feeding bivalves. *Journal of Experimental Marine Biology and Ecology* **300**:83-130.
- Willis, T. J., R. B. Millar, and R. C. Babcock. 2003. Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *Journal of Applied Ecology* **40**:214-227.
- Willis, T. J., D. M. Parsons, and R. C. Babcock. 2001. Evidence for long-term site fidelity of snapper (*Pagrus auratus*) within a marine reserve. *New Zealand Journal of Marine and Freshwater Research* **35**:581-590.
- Witman, J. D., S. J. Genovese, J. F. Bruno, J. W. McLaughlin, and B. I. Pavlin. 2003. Massive prey recruitment and the control of rocky subtidal communities on large spatial scales. *Ecological Monographs* **73**:441-462.
- Ziegler, P. E., C. R. Johnson, S. D. Frusher, and C. Gardner. 2002. Catchability of the southern rock lobster *Jasus edwardsii*. II. Effects of size. *Marine and Freshwater Research* **53**:1149-1159.