

# **Examining the ecological complexities of blackfoot paua demography and habitat requirements in the scope of marine reserve protection**

BY

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## Abstract

A critical question for ecologists and fisheries managers is what drives the demographic processes that dictate the abundance and size structure of ecologically and commercially important species. Marine Reserves (MRs) provide an opportunity to examine species in the absence of human disturbance (i.e. no fishing) and to investigate how habitat type, quantity and condition contribute to yield large individuals and dense aggregations that are typical of a more natural state. However, an improved understanding of the efficacy of marine reserves requires a robust examination of habitats inside and outside reserves to distinguish any reserve effect from a potential confounding habitat effect. Abalone are a valuable nearshore fishery in many parts of the world and many stocks have been overexploited to the point of collapse. Countries striving to rebuild their abalone stocks are utilizing MRs to support viable populations and focusing on habitat requirements that produce large aggregations and individuals. The abalone commonly referred to as the blackfoot paua (*Haliotis iris*) is a culturally and ecologically important New Zealand (NZ) species and is the focus of customary, recreational and commercial fisheries. However, the demography and growth rates of paua populations are highly variable, with pockets of “stunted” populations occurring throughout NZ. Density-dependent processes, differential juvenile success, variable habitat quality and fishing pressure have all been suggested to influence the fitness of individuals and the demography of paua populations.

My research utilizes MRs to control for fishing activity and thereby to investigate ecological patterns and the effects of habitat on paua abundance and size variability. The main objectives of this thesis were to quantify the response of paua to MR status, distinguish habitat effect from a reserve effect and understand the contribution of habitat variables on demography and growth. Research was conducted within and surrounding five MRs in central NZ. The habitats in and outside MRs were not significantly different in physical and biogenic characteristics, but paua occurred in significantly greater densities and were significantly larger within four MRs compared with outside, illustrating that marine reserves do afford protection for paua. Paua within MRs were significantly more dense and larger in areas of relatively higher wave exposure and dense macroalgal cover.

Despite protection, paua were found to be undersized or “stunted” at Long Island and Horoirangi MRs. I conducted surveys to evaluate the effect of density and the contribution of habitat variables on paua size at two spatial scales across environmental gradients. To further test the hypothesis that habitat effects growth a 12 month translocation experiment was conducted at Long Island MR. The surveys revealed that environmental gradients exist at small and large scales and explained how paua size varied along these gradients. The habitat variables which supported larger size individuals were consistent across both locations, where paua were significantly larger in areas that were exposed with high algal cover than those at

sheltered areas with low algal cover. This result was further confirmed by the translocation experiment which revealed that paua translocated from a stunted environment to a normal environment grew significantly more than conspecifics placed at the stunted environment.

To further explore the response of paua to protection and see if patterns were consistent across bioregions in areas with “normal” size paua I conducted research at the Taputeranga MR on the Wellington South Coast to evaluate juvenile and adult population densities and examine stage-specific habitat requirements. Juvenile paua were found in higher densities at fished sites in areas that were sheltered from wave exposure and dominated by cobbles and boulder fields. Adult paua were found in greater densities and were larger in size within the reserve than outside, which was the opposite finding to the baseline survey illustrating reserve effectiveness. Although within the reserve there were large aggregations and individual adults which may support population reproductive success, juvenile and adult population densities were not correlated. Results from this study indicate that marine reserve implementation does have an impact on adult populations but that habitat is more important for juvenile success.

Although this thesis focused on paua within the scope of protection, MRs are placed in NZ to protect a suite of species. To thoroughly investigate habitats I conducted a rigorous inside-outside habitat analysis utilizing multibeam bathymetric data and video footage from drop camera surveys at Taputeranga MR. Habitat maps produced by NIWA were utilized to plan drop camera sampling locations and 278 drops were conducted across 8 sites associated with TMR. Analysis revealed that habitats within fished and reserve sites were comparable in physical and biogenic habitat quantities, although the reserve had greater topographic relief. However, when examining only a subsample of fished sites there were pronounced habitat differences between in and outside the reserve, where the western fished sites have significantly more rocky reef with greater algal cover than the reserve and eastern sites. These results illustrate the need for quantification of habitat when siting fished (control) areas and conducting inside versus outside reserve comparisons.

This research has determined that MRs do afford protection for paua in central NZ. The differentiation between habitat and reserve effects that I have identified has direct relevance to current and future MRs in NZ and highlights the need for studies to examine habitat effect in MR spatial planning at a global level. Furthermore, this research highlights the importance of considering stage-specific habitat requirements when designing the spatial arrangement of MRs by protecting juvenile habitat as well as adults to increase chances of recovery. These abalone-habitat associations, showing the importance of exposure and macroalgal cover for growth, can be used to assist in management decisions within NZ such as considerations for siting management areas and potential translocations and are directly applicable to abalone conservation, management concerns and recovery efforts across the world.

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## Chapter 1. Introduction

### 1.1.General Introduction

The ever increasing impacts and demand on marine resources through fishing, coastal development and detrimental land-sea interactions such as habitat degradation and sedimentation has sparked a global movement to implement marine reserves (MRs) and marine protected areas (MPAs). MRs and MPAs are designated areas in the coastal zone and ocean where extractive human use (mainly fishing) is restricted and other forms of human disturbance are minimized. The need for protected areas is often in response to overfishing or destruction of habitats in the coastal oceans. Design of the protected area placement, size, boundaries, spacing between reserves and the aim of the designation (fisheries, biodiversity) is often developed through community-based processes with input from local stakeholder groups (Halpern and Warner 2003). Type of protection, jurisdiction, enforcement and compliance varies based on location. Marine protected areas have some form of protection and are quite common in marine spatial management whereas marine reserves are typically “no-take”(no fishing or removal of materials), have no direct disturbance and are starting to become more prevalent at a global level (Lester et al. 2009, Eddy et al. 2014a). This thesis will focus on “no-take” marine reserves.

MRs are often placed with the aim of enhancing fisheries, protecting biodiversity and establishing a space for scientific research. MRs are typically set up to protect unique habitat and/or are targeted for economically important species (Lubchenco et al. 2003, Lester et al. 2009). They are often set up as networks and designed as ecosystem-based management tools, protecting fished and un-fished species and habitats. Individual reserves afford enhanced protection to species that have limited dispersal and limited adult movement patterns, whereas networks provide opportunity for spill-over and protection for species with larger home ranges through connectivity (Botsford et al. 2001, Moffitt et al. 2009, Claudet 2011). MRs and MPAs are one spatial management tool that permits examination of how and at what rate populations recover to a more natural state after being depleted and/or affected

by anthropogenic impacts (Micheli 2004, Edgar et al. 2014). MRs also permit the examination of indirect effects of fishing, trophic interactions and shifting habitats to restore ecosystems to a more natural, pre-fishing state (Shears and Babcock 2002, Pederson et al. 2008, Shears et al. 2008, Leleu et al. 2012). Furthermore, MRs may provide a safeguard to extreme environmental changes such as hypoxia, land-slides and storm events and as a buffer to climate change (Allison et al. 2003, Harley et al. 2006, Micheli et al. 2012).

Fish and invertebrates that are fished commercially or recreationally and have relatively small home ranges are often chosen as biological response variables to detect a marine reserve effect. Important near-shore fisheries such as abalone and lobsters globally, the rockfish species complex in North America, and subtidal reef fish in Australasia are some examples of species or species groups that have potential to benefit from protection (Rogers-Bennett et al. 2000, Anderson and Millar 2004, Edgar et al. 2014). Historically, MR studies were conducted post-closure where in the absence of baseline data, the majority of MR studies compared species biological response variables (density, size, biomass) inside to outside, termed control impact (CI) studies, which may be replicated over time or may be a one time “snapshot” study (Micheli et al. 2004, Aburto-Oropeza et al. 2011). When a baseline is available scientists often use a Before After Control Impact (BACI) design, in which studies are conducted before and after closure and monitoring at areas inside and outside (controls) the reserve to examine the effect of fishing directly on the target species and indirectly on ecosystems (Stewart-Oaten et al. 1986, Halpern 2003, Eddy et al. 2014a).

There is a growing body of evidence showing the positive response of populations to protection, where fished species’ density, size and biomass within marine reserves are greater than outside: this is often referred to as the ‘reserve effect’ (Halpern 2003, Claudet et al. 2008, Edgar et al. 2014). However, assessing if MRs are effective in protection is difficult because deficiencies that may confound MR efficacy can include reserve placement, design and size, inappropriate ecological control sites (i.e. habitat differences) and proper sampling designs (Halpern 2003, Huntington et al. 2010, Edgar et al. 2014). The BACI method attempts to control for spatial and temporal change but is often flawed by assuming that habitats and environmental variables in and outside the reserve are comparable and often attributes biological responses to reserve status without assessing habitats. Evaluation and

quantification of habitats to test if they are comparable is essential as a difference in quantity or quality of habitat may affect the magnitude of species responses and this must be controlled for in the ecological analysis when examining potential reserve effects. Although scientists strive to pick control areas that are as similar as possible to reserve sites in regard to species' assemblages, habitat, oceanography and fishing pressure, habitats are seldom quantified to examine if habitats in and outside are comparable (García-Charton et al. 2004, Pande and Gardner 2009). MRs are often placed in areas that support high levels of biodiversity or are heavily fished such as offshore islands, sea stacks, high energy sites, large reefs and atolls. Given the placement in unique habitat it is often challenging to assign appropriate control sites with similar environmental variables. However, data on physical and biogenic habitats, exposure and other environmental variables are essential when assigning control sites and setting baselines.

Appropriate placement of MRs highlights the need for accurate physical and biogenic habitat maps for marine spatial management and to improve the evaluation of marine reserves. Despite the knowledge that seascape heterogeneity is a common feature of the marine environment and all sites are not equal, once MR and control sites are assigned, habitat types are seldom quantitatively analysed (Huntington et al. 2010, Eddy et al. 2014a). However, classification and spatial description of habitat types is essential for understanding the patterns and processes dictating organismal distribution patterns and size structure (Andrew and Mapstone 1987, Underwood et al. 2000) and when habitat is not examined, natural spatial variability in the physical environment may confound a potential 'reserve effect' with a 'habitat effect' (Charton and Ruzafa 1999, García-Charton et al. 2004, Huntington et al. 2010, Eddy et al. 2014a). Therefore, an improved understanding of the efficacy of marine reserves requires a robust examination of habitats inside and outside reserves to distinguish any reserve effect from a potential confounding habitat effect. It has been shown that detecting differences in target species abundance or size in MR evaluation has been confounded by site-specific differences in habitat (Anderson and Millar 2004, Claudet et al. 2010, Huntington et al. 2010).

Marine reserves in New Zealand (NZ) are defined as complete "no-take" and are established under the Marine Reserves Act, 1971 (Pande and Gardner 2009). Within NZ, reserves are

established to protect all species and representative coastal habitats and create places for scientific research (Carter 2005). There are currently 44 marine reserves in New Zealand on the North and South main islands and offshore Islands (Fig. 1.1) managed and under the jurisdiction of the Department of Conservation (DOC); by international standards this is considered a large and comprehensive network (Willis 2013). DOC and the Ministry of Primary Industries enforces no fishing in the reserves and although there may be limited poaching these areas are assumed to have no extraction. The Cape Rodney to Okakari Point Marine Reserve (CROP - also called the Leigh MR) was established in 1975 as New Zealand's first marine reserve and is one of the oldest no-take reserves in the world. In 2010, New Zealand's Department of Conservation and the Ministry of Primary Industries developed a New Zealand MPA policy in which they stated that the goal is "to protect marine biodiversity by establishing a network of MPAs that is comprehensive and representative of New Zealand's marine habitats and ecosystems". The reserves have a wide latitudinal range and therefore encompass a range of habitat types, including estuaries, intertidal and subtidal rocky reefs, sand flats and offshore islands.

The majority of NZ reserves have had some level of scientific research and monitoring, some have annual monitoring to develop a long term time series and Taputeranga located on the Wellington South Coast is one of the first to have a baseline data set collected prior to closure (Pande and Gardner 2009, Willis 2013). Within NZ, MR "success" or recovery of a MR area is often determined or measured by recovery of exploited species (Willis 2013). Studies focus primarily on the shallow subtidal and examine exploited species of reef fish, blue cod, rock lobster and kina (urchin), and to a lesser extent, paua (abalone). Through various research agencies and PhD and Masters research theses it has been shown that NZ marine reserves afford protection for *Jasus edwardsii* (rock lobster), *Pagrus auratus* (snapper), *Parapercis colias* (blue cod) and various reef fish (Davidson et al. 2002, Pande et al. 2008, Davidson 2009, Freeman et al. 2009, Dias Guisado et al. 2011, Gardner and Struthers 2013, Rojas Nazar 2013, Eddy et al. 2014b). Furthermore, it has been documented that the recovery of these species has led to shifts in community structure, through trophic cascades resulting in changes to macroalgal habitats and distributions of cryptic reef fish (Babcock et al. 1999, Willis and Anderson 2003, Shears et al. 2008, Leleu et al. 2012). Historically in NZ, research focused on the intertidal (species or habitats), and habitat mapping across tidal zones is rarely conducted.



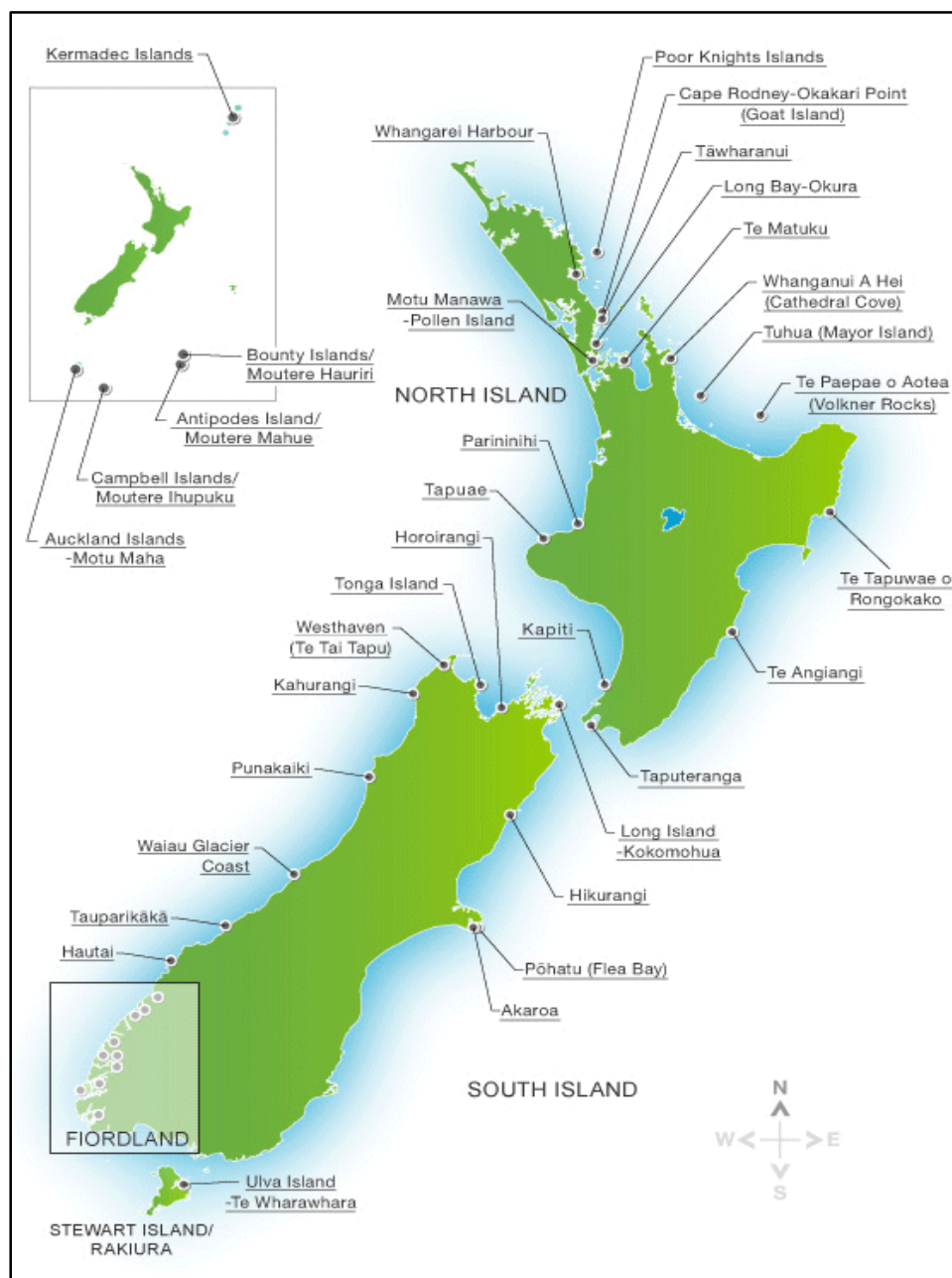


Figure 1.1 Map of New Zealand Marine Reserves

<http://www.doc.govt.nz/nature/habitats/marine/marine-reserves-a-z/marine-map/>

reserves-

Knowledge of what dictates the abundance and size structure of ecologically and commercially important species is critical for effective fisheries management and conservation of the species. Marine reserves provide an opportunity to examine commercially important species in the scope of protection to investigate what habitat types, quantities and qualities are required to yield large individuals and dense aggregations. Abalone (Haliotids) are an important commercial fishery in North America, Japan, South Africa, Australia and New Zealand and many stocks have been overexploited to the point of collapse (Werner et al. 1995, Rogers-Bennett et al. 2002, Prince 2005). The life history characteristics of abalone include a short pelagic larval duration, limited adult movement patterns, forms dense aggregations and is long lived (Davies 2006, Aguirre and McNaught 2010). Given the aggregating nature of abalone the species group is vulnerable to overfishing; countries striving to rebuild stocks recognize the need to protect broodstock (Werner et al. 1995, Rogers-Bennett et al. 2002, Prince 2005). Fertilisation and recruitment success in many abalone species is limited by low spawner density which has a critical threshold in the range of 0.15-1 abalone m<sup>-2</sup> to be successful (Babcock and Keesing 1999, Miner et al. 2006a, Catton and Rogers-Bennett 2013).

Regardless of location or level of fishing pressure, the demography, morphology and growth rates of abalone are highly variable at broad and fine spatial scales (Breen et al. 1982, McShane 1994, McShane and Naylor 1995a, Naylor et al. 2006). Abalone demographics are dictated by several factors: density dependence where fertilisation success is limited by low spawner density, larval supply, post-settlement success, resource (food and habitat) availability and predation pressure (McShane and Naylor 1995a, Babcock and Keesing 1999, Miner et al. 2006a, Aguirre and McNaught 2012). An examination of abalone populations within MRs permits a test of the effect of MR protection on biological response variables such as mean abundance, mean size, and also gives opportunity to examine the potential affect habitat characteristics have on these indices. The life history traits of abalone (limited larval dispersal and adult movement patterns, long lived) predict a positive response to marine reserve implementation, making overfished abalone ideal candidates for marine reserve protection (Prince et al. 1987, McShane et al. 1994b, Botsford et al. 2001, Prince 2004).

Abalone have increased in abundance and mean size within marine reserves compared to outside in many areas in the world. Following six years of protection at Maria Island MR, Tasmania, large *H. rubra* significantly increased in abundance relative to outside (Edgar and Barrett 1999). The northern abalone (*H. kamtschatkana*) was significantly more abundant and larger (on average 16 mm larger) in MRs after 40 years of protection (Wallace 1999). Black abalone (*H. cracherodii*) were bigger in size within MRs in central California (legal size individuals only observed within reserves), but did not reach sizes that were present before the collapse of the fishery (Micheli et al. 2008). Pink abalone (*H. corrugata*) in California were significantly more abundant within no take MRs and had 30% more commercial- size abalone than the fished site (Rogers-Bennett et al. 2002). Not surprisingly, red abalone (*H. rufescens*) showed a significant decrease in mean size and a profound change in size structure when a MR was opened to fishing (Rogers-Bennett et al. 2013). These findings combined strongly suggest that MRs do afford protection for abalone species allowing them to increase in mean density and size.

New Zealand has three endemic species of abalone, the yellow-foot abalone, *H. australis*, the white-foot abalone, *H. virginea* and the blackfoot abalone, *Haliotis iris*, commonly referred to as the blackfoot paua (hereafter referred to as paua) (Poore 1972). Blackfoot paua can be found on both main islands of New Zealand as well as the Chathams, Stewart and the Snares Islands (Sainsbury 1982). Blackfoot paua inhabit intertidal and shallow subtidal rocky reefs and are the focus of important customary, recreational and commercial fisheries. Paua are respected as a taonga (treasured) species to the Maori culture and many New Zealanders recreationally collect the limit of 10 per day (McCarthy et al. 2014). The minimum legal size of paua is 125 mm and paua cannot be collected via SCUBA. The commercial fishery is managed through the “Quota Management System” through the Fisheries Amendment Act 1986. There are eleven paua quota management areas (Fig. 1.2). The QMS allocates a “Total Allowable Catch” (TAC), the TAC makes allowances for Maori and recreational users and the remainder is for the commercial sector, Total Allowable Commercial Catch (TACC). The tonnage of the TACC is variable dependent on quota management area. Paua are distributed around the country in a somewhat irregular distribution with the commercial fishery focused on the South, Stewart and Chatham Islands. Although paua populations are managed under the QMS, there are still areas where exploitation rates are high with 50% of estimated stock

removed each year (i.e. QMA PAU7) (Shellfish Working Group, personal communication) and in the future there may be a need to utilise MRs or other forms of management areas to protect this iconic species.

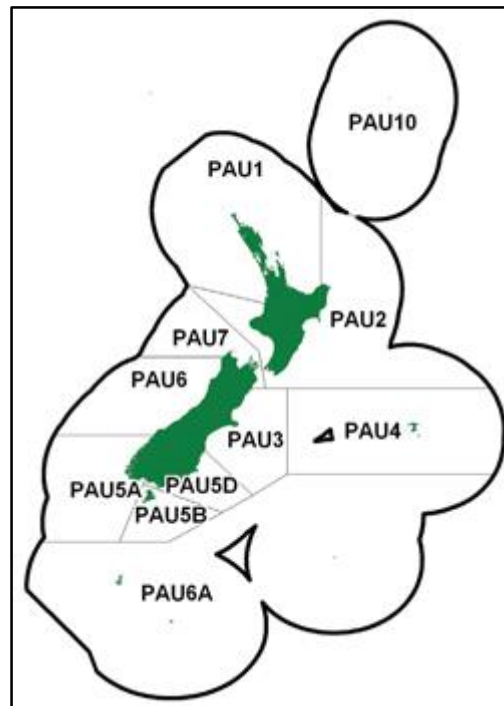


Figure 1.2. Map of New Zealand showing Paua Quota Management Areas (adapted from Ministry of Primary Industries 2014).

Historically, paua populations have seldom been examined in the context of MRs. This may be due in part to the fact that a great deal of the MR monitoring occurs in northern NZ, where paua are scarce and rarely reach minimum legal size and therefore do not experience fishing pressure and are not a monitored species. Within central New Zealand, studies focused on paua have been conducted prior to marine reserve establishment and paua were included in species surveyed to set the baseline for the Taputeranga Marine Reserve, Wellington South Coast, central New Zealand (Pande and Gardner 2009, Aguirre and McNaught 2012). A study at the Kapiti MR in central NZ showed paua did not exhibit a positive response to protection after eight years; however the sampling was limited and one site had significant habitat

differences to the other sites, potentially confounding the results (Pande and Gardner 2012, Eddy et al. 2014a).

Given that paua are important across stakeholder groups, including the commercial sector, much research has focused on reproduction, settlement, growth, diet, population size structure and spatial distributions. Paua have separate sexes, are broadcast spawners and spawning typically occurs in late summer and autumn (Poore 1972). After successful fertilisation, larvae develop into a trochophore stage and then metamorphose into a veliger larvae over the course of 7-10 days when they become competent to settle (Tong et al. 1992). Larvae settle by chemical cue on crustose coralline algae and typically settle on *Lithothamnion* spp. in 6-9 m depth (Shepherd et al. 1992, Aguirre and McNaught 2012). Juvenile paua up to 10 mm feed on diatoms then move into the intertidal and shallow water, typically less than 3 m depth, and live underneath boulders and feed on macroalgae (Davies 2006, Aguirre and McNaught 2012). When paua reach maturity at 60-70 mm, at 3-5 years of age, they move out from underneath boulders and into less cryptic habitat in deeper water (Poore 1972, Schiel and Breen 1991, Aguirre and McNaught 2012). Adult paua have limited movement patterns and are distributed from 0-10 m depth, although typically more abundant in less than 5 m and live in dense aggregations on rocky reef, surge channel and boulder habitats. Physical and biogenic habitat variables effect the distribution of adult abalone, to the extent that their abundance is positively correlated with areas of canopy macroalgae and negatively correlated with understory algae (Andrew and O'Neill 2000, Sasaki and Shepherd 2001, Aguirre and McNaught 2012). Adult paua feed on attached and drift algae; their diet is thought to be dependent on localised algal supply, not on algal preference (Poore 1972, Day and Fleming 1992, Allen et al. 2006).

Density and size of adult paua are highly variable on spatial scales that are fine, from reef to reef (<10 m), to broad across bays and headlands (km). These patterns are observed in areas of commercial fishing and in protected areas, such as marine reserves and customary closure areas (Breen et al. 1982, McShane 1994, McShane and Naylor 1995a, Naylor et al. 2006). It has been suggested that juvenile success, density of conspecifics, habitat, food availability and fishing pressure may be the main drivers of demographic variability of paua populations, but despite this habitat is rarely examined in demographic studies (McShane and Naylor 1995b, Sasaki and Shepherd 2001, Coates et al. 2013). Examination of paua populations

within the scope of protection enables a more realistic view (controlling for fishing) of the potential effect habitat characteristics have on abundance and size and spatial distribution.

Countries striving to rebuild their abalone stocks have examined what habitats yield dense adult aggregations and large individuals for reseeded and recovery purposes (Lessard and Campbell 2007, Donnellan 2015). However, there are clear differences in habitat requirements for the juvenile and adult stages that enable each to be successful and efforts should therefore be made to place adults in areas adjacent to where there is suitable juvenile habitat (Davies 2006, Aguirre and McNaught 2012). Juvenile abundance, distribution and mortality are critical factors to consider as they can strongly effect adult population abundances and distributions (Rowley 1989, McShane and Naylor 1995a). Variation in juvenile abundance and success, that is the ability to mature into sub-adults and adults, has been attributed to depth, sedimentation, habitat quality, wave exposure and predation (McShane and Naylor 1995b, Aguirre and McNaught 2010). Within NZ, the paua industry recognises the contribution of juveniles to the future fishery and has undertaken reseeded projects to support fisheries by placing juvenile paua in low intertidal and very shallow subtidal habitats adjacent to areas that have habitats that support adults in the hope of successful recruitment into the fishery (Tom McCowan, Paua Industry Council, personal communication).

MRs, where paua populations are protected and can reach densities and sizes that are similar to natural levels (i.e., in the absence of human disturbance), are an ideal tool to examine natural species-habitat associations and demographic processes. A positive response to protection should yield more larvae (because of increased numbers of individuals and also because bigger individuals produce disproportionately more offspring than smaller individuals), and for an organism that has a short larval duration may result in larger juvenile populations in close proximity to adults. However, given the often comparatively small size of MRs, the close proximity of control sites and local oceanography, these potentially productive populations may be seeding populations outside the reserve via larval export rather than directly adjacent areas (Micheli et al. 2012). The combination of potential larval export, recruitment dynamics, and different stage-specific habitat requirements is a complex system that warrants further investigation (McShane and Naylor 1996, Sasaki and Shepherd 2001).

Despite the importance of juvenile populations for adult success and the recognition of differences in stage-specific habitat suitability, very few studies, and none to my knowledge in New Zealand, have focused on both juvenile and adult stages and their respective habitat associations in adjacent tidal zones within the context of MRs. Results from the literature on juvenile adult relationships are conflicting. A Californian study examining four abalone species reported high densities of juveniles adjacent to large adult populations and low densities of juveniles adjacent to low adult densities (Rogers-Bennett et al. 2011). Through a manipulative experiment in Australia, a positive relationship between adults and juveniles has been shown for *H. rubra* (Prince et al. 1988). However, there are also reports of negative correlations, for northern hemisphere species (*H. rufescens* and *H. walallensis*) and southern hemisphere species (*H. iris* and *H. rubra*) populations (Schiel and Breen 1991, Shepherd et al. 1992, Rogers-Bennett et al. 2000). Low juvenile densities are often attributed to low adult densities and recruitment failure (Tegner 1993, Rogers-Bennett et al. 2011). Additionally, habitat quantity and quality are suggested to be important contributing factors to juvenile success and ultimately to productive adult aggregations for multiple abalone species (Tegner 1993, Miner et al. 2006a, Aguirre and McNaught 2012). To aid in the understanding of demographic processes researchers need to look at both ontogenetic stages and their respective habitat requirements and it is highly beneficial to examine these processes within the scope of MRs as they provide a more natural setting.

A lack of knowledge about paua responses to habitat variability is a contributing factor to both ongoing fisheries management uncertainty and how best to implement management actions to contribute to paua conservation. Understanding what dictates growth and ultimately size structure of paua populations is critical for effective fisheries management. Unlike other abalone species, growth rings are not currently able to be used to measure age for *H. iris* (Naylor et al. 2006, Naylor et al. 2007). Therefore, growth under wild conditions is often measured using mark-recapture methods. There are specific areas along the North and South Islands of New Zealand where paua populations do not reach the minimum legal size limit of 125 mm; these are referred to as “stunted” populations (McShane et al. 1994c, Naylor et al. 2006). Stunting in abalone occurs in many species and compared to standard abalone, stunted abalone are smaller, with shorter shells that are higher, wider and thicker (Nash 1995, Saunders et al. 2008). Although this morphological variation is ubiquitous (in many species

and locations) the underlying mechanism(s) that limits growth is not well understood. It is commonly suggested that morphological variability amongst abalone is a phenotypic response to the environment, and to a lesser extent to genetic differentiation of discrete populations (McShane et al. 1994c, Saunders et al. 2009, Mundy 2010). Understanding what promotes growth and causes stunting is essential for fisheries management.

Genetic research on *H. iris* has found four phylogeographic breaks within New Zealand (Will et al. 2011), but these do not delineate the stunted stocks found in all areas of the country. Therefore, it has been suggested that density-dependent processes, food availability, habitat and fishing pressure are the main factors dictating growth (McShane and Naylor 1995a, Sasaki and Shepherd 2001, Coates et al. 2013). Finer scale genetic work within the Marlborough Sounds (top of the South Island) revealed an absence of population structure from reef to reef up to 6 km distant and a minimal population genetic structure up to 300 km distant (McCowan 2013), further supporting the contention that morphological variation is not a result of genetic variation.

Given that abalone form large aggregations it is often hypothesised that growth is density-dependent through intraspecific competition for food (McShane and Naylor 1995a, Dixon and Day 2004a). However, the results of research examining density-dependent growth are variable and may be species-specific. Within aquaculture experiments, growth has been shown to be negatively correlated with density for juvenile *H. rubra* and *H. tuberculata* and for adult *H. asinina* (Hunt et al. 1995, Mgaya and Mercer 1995, Capinpin et al. 1999). In field experiments, growth has been shown to be negatively correlated with density for *H. laevis*, whereas in a controlled field experiment where densities were increased, growth was independent of density for *H. iris* (McShane and Naylor 1995a, Dixon and Day 2004a). For *H. iris*, a study utilising a “fish-down” experiment (a method where populations are systematically fished to reduce density to examine effects) showed no density effect on growth at the “fish-down” sites compared to controls where density was constant (Naylor and Andrew 2004). Although there is some evidence for density to negatively affect growth (and this topic warrants further investigation), a robust examination of the contribution of habitat variables is important to better understand what is dictating relatively slower growth in these stunted populations.



Stunted populations are typically found in dense aggregations on reefs that are protected from wave action (Schiel and Breen 1991, McShane and Naylor 1995a, Naylor et al. 2006). In a study at 34 locations across NZ, sea surface temperature and relative wave exposure explained a significant amount of variation in mean paua length among areas (McShane et al. 1994c). Subsequently, paua that were translocated over small spatial scales (<200 m) from sheltered bays to exposed headlands within NZ grew more than controls placed back into bays (McShane and Naylor 1995a). In these sheltered areas it was postulated that low water movement limits the amount of drift algae (an important food source) delivered to paua (i.e., contributes to food limitation) and this has been suggested as a possible mechanism underlying the existence of stunted stocks (Day and Fleming 1992, Shepherd et al. 1992, McShane and Naylor 1995a).

Abalone translocations have been used to examine the effect of density and the contribution of habitat variables on growth, and for enhancing populations (Dixon and Day 2004a, Lessard and Campbell 2007, Mundy 2010, Taniguchi et al. 2013). Translocating stunted abalone to an area of typical sized abalone results in increased growth rates and suggests that the favourable response in growth is a plastic (phenotypic) response to better quality environment (Emmett and Jamieson 1989, McShane and Naylor 1995a, Dixon and Day 2004a). In an Australian study, where abalone density was kept constant, a reciprocal transplant experiment of *H. rubra* showed that stunted individuals grew faster in non-stunted areas and non-stunted individuals grew slower in stunted areas. This was explained by stunted populations occurring in areas of low food availability and reduced topographic complexity, whereas non-stunted populations had more food available and increased topographic complexity (cracks and crevices may collect drift algae better than flat surfaces) (Saunders et al. 2009). These studies demonstrate the potential importance of environment in the biological mechanism of abalone stunting and highlight the need for a detailed examination of the habitats of stunted and productive growth areas. Understanding growth and habitat associations of normal and stunted stocks will contribute to explaining paua demography. This knowledge can be utilised in effective fisheries management by setting appropriate location-specific minimum legal size limits and in conservation by the designation of closure areas such as marine reserves and customary closures.

The present study utilises marine reserves to control for fishing activity and thereby to investigate ecological patterns and the effects of habitat on paua abundance and size variability. Although poaching may occur, it is assumed that there is very limited if any fishing in these reserves. A focus is on habitat characteristics and demographic processes that may underlie observed patterns of variation in abundance, individual size and growth. This research contributes to the efficacy of marine reserves for an important species group and is unique in that it examines an abalone species' habitat association that has not had detrimental fishing pressure to the point of collapse (compared to international standards). The findings of paua-habitat associations within the scope of protection can be used to assist in management decisions within NZ such as considerations for siting management areas and potential translocations and are directly applicable to abalone conservation, management concerns and recovery efforts across the world.

## 1.2 Thesis Objectives

Objective 1: To evaluate if MRs provide protection for paua; are populations denser and is mean length greater within than outside marine reserves. Research was conducted at four marine reserves in central New Zealand: Kapiti, Long Island-Kokomohua, Tonga Island and Horoirangi. A seascape habitat assessment was utilised to quantify habitats in and outside reserves and determine if paua response was attributed to a reserve effect or confounded by a habitat effect.

Objective 2: To quantify density, length, distribution and habitat requirements of the juvenile and adult stages of paua at the Taputeranga Marine Reserve. This research examined habitat in and outside Taputeranga Marine Reserve to determine if juvenile populations were more abundant in areas adjacent to productive adult populations or if habitat suitability was more important for juvenile success.

Objective 3: To examine the role of physical and biogenic habitat variables on paua size, specifically on stunted populations. The study evaluated the effect of density and the contribution of habitat variables on paua size by conducting an assessment across environmental gradients at Long Island Marine Reserve (Marlborough Sounds) and Tasman

Bay (central New Zealand). Additionally, to test experimentally the effect of changing habitat on growth, a reciprocal translocation experiment was employed whereby paua from a “stunted” growth site were translocated to a productive “normal” growth site and *vice versa* within the protection of Long Island MR.

Objective 4: To determine if habitats inside and outside Taputeranga Marine Reserve were comparable in quantity (spatial extent) and composition. Utilising both acoustics and video from drop camera the substratum, geomorphology and biogenic habitat types were quantified at three sites within and five sites outside the reserve to ascertain if habitats were similar with the overall aim of detecting a habitat effect in future quantification of reserve.

### 1.3 Thesis Layout

Each of the four objectives outlined above is addressed in a separate chapter (chapters 2-5) to allow ease of publication at a later date. Each chapter has an introduction, specific methodologies and maps of study areas that pertains to the chapter, analysis, results and a discussion of the results found and future applications. Given the interlinked nature of these research topics and individual studies there have been parts where unavoidable repetition in the introduction and discussion of these chapters has occurred. In the methodology sections, although habitat classifications may seem similar the methods are slightly different for each chapter and as such, have been written in detail for each chapter.

Chapter Six, the discussion consists of a summary overview and conclusions focusing on the findings from the previous four chapters. It discusses paua response to protection and highlights habitat associations that support large aggregations and individuals. I present some of my own ideas about paua specific closure areas within New Zealand and how these ideas can be applied to abalone fisheries globally for management and conservation of the species group.

Note: My research permit did not allow any extraction or lethal sampling within marine reserves.

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## Chapter 2. Distinguishing and Quantifying the ‘Reserve Effect’ from the ‘Habitat Effect’ on Abalone (*Haliotis iris*) Populations in Central New Zealand

### 2.1 Abstract

Marine reserves provide an opportunity to examine commercially important species in the absence of human disturbance by prohibiting extractive use (i.e. fishing) and to investigate what habitat types, quantities and condition are required to yield large individuals and dense aggregations that are typical of the natural state. However, an improved understanding of the efficacy of marine reserves requires a robust examination of habitats inside and outside reserves to distinguish any reserve effect from a potential confounding habitat effect. The goal of this research was to distinguish and quantify a ‘reserve effect’ from a ‘habitat effect’ on abalone, *Haliotis iris*, populations and identify any species-habitat associations that could assist with future placement of management areas for the success and recovery of the populations. I evaluated the abundance and length structure response of *H. iris* (commonly referred to as the black-foot pua) to marine reserve protection. To increase the robustness of reserve evaluation and distinguish between management effects and potentially confounding habitat differences, I included a seascape habitat assessment. In the austral summers of 2013 and 2014, surveys of pua and habitat types were conducted via SCUBA at four marine reserves in central New Zealand. The habitats in and outside marine reserves were not significantly different in physical and biogenic characteristics, but pua occurred in significantly greater densities and were significantly larger within three marine reserves compared with outside, although one location had higher densities and lengths outside. However, when all the data were combined, analyses revealed that pua were denser and larger within than outside, illustrating that marine reserves do afford protection for pua. In addition, pua were significantly more dense and larger in areas of relatively higher wave exposure and dense macroalgal cover. The differentiation between habitat and reserve effects that I have identified has direct relevance to current and future marine reserves in New Zealand and highlights the need for studies to examine habitat effect (i.e., environmental differences inside and outside in marine reserve planning at a global level. In addition, these species-habitat associations showing the importance of exposure and macroalgal cover assist in management decisions within New Zealand and are directly applicable to abalone conservation, management concerns and recovery efforts across the world.

## 2.2 Introduction

The ever increasing impacts and demand on marine resources through fishing, coastal development and detrimental land-sea interactions has sparked a global movement to implement marine reserves (MRs) and marine protected areas (MPAs), spaces where fishing is not allowed or is restricted, and where other forms of human disturbance are minimised (Micheli et al. 2004, Eddy et al. 2014a). Internationally, MRs are typically set up for a specific group of economically important species, to protect biodiversity or unique habitat; often areas of high diversity are supported by dynamic and diverse habitat structure (Lubchenco et al. 2003, Lester et al. 2009). In New Zealand (NZ), full no-take MRs are established to protect all species and representative coastal habitats and create places for scientific research. Regardless of the objective, usually this enforced cessation of extractive activities allows the populations of formerly exploited species to recover or rebound to what is considered to be a more natural state. There is a growing body of evidence showing the positive response of populations, where fished species density, size and biomass within marine reserves are higher than outside: this is often referred to as the ‘reserve effect’ (Halpern 2003, Claudet et al. 2008, Edgar et al. 2014).

In the absence of baseline data, the majority of MR studies compare species biological response variables (density, size, biomass) from inside to outside, termed control impact (CI) studies, which may be replicated over time or may be a one time “snapshot” study (Micheli et al. 2004, Aburto-Oropeza et al. 2011). This method assumes that habitats and environmental variables in and outside the reserve are comparable and often attributes species responses to reserve status. However, given the placement of MRs in unique habitat it is often challenging to assign appropriate control sites with similar physical and biogenic habitats. Despite the knowledge that seascape heterogeneity is a common feature of the marine environment and all sites are not equal, once MR and control sites are assigned, habitat types are seldom quantitatively analysed (Huntington et al. 2010, Eddy et al. 2014a). When habitat is not examined, natural spatial variability in the physical environment may confound a potential ‘reserve effect’ with a ‘habitat effect’ (Charton and Ruzafa 1999, García-Charton et al. 2004, Huntington et al. 2010, Eddy et al. 2014a). It has been shown that detecting differences in target species abundance or size in MR evaluation has been

confounded by site-specific differences in habitat (Anderson and Millar 2004, Claudet et al. 2010, Huntington et al. 2010).

New Zealand's temperate marine environment is a complex system composed of dynamic geology and biogenic habitats that often vary across spatial scales. The physical reef is heterogeneous in composition (bedrock forms, outcroppings, greywacke reef, boulder and cobble fields), size of particular substrata (patch size) and spatial arrangement. The biogenic community is largely composed of habitat-forming algal groups, dominated by large brown macroalgae (kelps) with understories of foliose reds and browns and a large turf community (Schiel 1990, Shears et al. 2004). These biogenic habitats vary in abundance and species composition across spatial scales associated with the underlying physical habitat (Schiel 1990, Shears et al. 2004, Pérez-Matus and Shima 2010). Given that biogenic habitats provide an important structural component and food source, organism response to habitat heterogeneity varies across spatial scales depending on habitat requirements of the organism (e.g. for food and shelter). Classification and spatial description of habitat types is essential in understanding the patterns and processes dictating organism distribution patterns and size structure (Andrew and Mapstone 1987, Underwood et al. 2000), but is often absent from studies of organismal responses to marine reserves.

In NZ, the abalone, *Haliotis iris*, commonly referred to as the black-foot paua (hereafter referred to as paua) inhabits intertidal and shallow subtidal rocky reefs, and supports important customary, recreational and commercial fisheries (Schiel and Breen 1991, Aguirre and McNaught 2012). The life history characteristics of paua include a short pelagic larval duration, has limited adult movement patterns, and is long lived (Davies 2006, Aguirre and McNaught 2010). These traits, combined with being a heavily fished species highlights the vulnerability of paua to human-mediated disturbance and makes them ideal candidates for marine reserve protection. As paua develop their depth distribution changes, which is directly related to and dictated by habitat associations (Aguirre and McNaught 2012). Adult paua are most commonly distributed from 0-10 m depth (most abundant at <5 m), and live in dense aggregations on rocky reefs, surge channels and boulder habitats (Poore 1972, Choat and Schiel 1982, McShane and Naylor 1995a). Physical and biogenic habitat variables effect the distribution of adult abalone species, to the extent that their abundance is positively correlated with areas of canopy macroalgae and negatively correlated with understory algae

(Andrew and O'Neill 2000, Sasaki and Shepherd 2001, Aguirre and McNaught 2012). Adult paua feed on attached and drift algae; their diet is thought to be dependent on localised algal supply, not on algal preference (Poore 1972, Day and Fleming 1992, Allen et al. 2006). Because responses to variability in habitat and food availability are so pronounced, paua demography is highly variable on broad and fine spatial scales, including within fisheries management areas (Breen et al. 1982, McShane et al. 1994b, McShane and Naylor 1995b, Naylor et al. 2006). Although it has been suggested that habitat variability and fishing pressure may be the main drivers of paua demographic variability, habitat type is seldom examined in demographic studies (McShane and Naylor 1995a, Sasaki and Shepherd 2001, Coates et al. 2013). A lack of knowledge about paua responses to habitat variability is therefore a contributing factor to both ongoing fisheries management uncertainty and how best to implement management actions to contribute to paua conservation.

An examination of paua populations within MRs permits a test of the effect of MR protection on biological response variables such as mean abundance, mean size, and also gives opportunity to examine the potential affect habitat characteristics have on these indices. In many areas of the world, abalone populations have increased in abundance and mean size within marine reserves (Edgar and Barrett 1999, Wallace 1999, Rogers-Bennett et al. 2013). In NZ, paua populations have rarely been examined in the context of MRs. This may be due in part to the fact that a great deal of the MR monitoring occurs in northern NZ, where paua are scarce and rarely reach mean legal size and therefore do not experience fishing pressure and are not a monitored species. One study at the Kapiti MR in central NZ showed paua did not exhibit a positive response to protection after eight years; however the sampling was limited and one site had significant habitat differences to the other sites, potentially confounding the results (Pande and Gardner 2012, Eddy et al. 2014a).

Using paua as a model organism this research was conducted to quantify the relative contributions of 'reserve effect' and 'habitat effect' in four no-take MRs in central NZ. To increase the robustness of reserve evaluation and distinguish between management effects and potential confounding habitat differences, I included a seascape habitat assessment. Classifying habitat at the seascape level enables the rapid classification of large areas so that the observed ecological patterns can be scaled to the area of defined habitat (Shears et al. 2004, Lessard and Campbell 2007). The goals of this study were to evaluate: 1) If MRs provide

protection for paua; are populations more dense and is mean length greater within than outside reserves? 2) If habitat type inside and outside individual reserves is comparable so that paua responses are attributable to a ‘reserve effect’ rather than a ‘habitat effect’; and 3) How and to what extent habitat variables are associated with paua density and mean length within marine reserves. I hypothesised that paua would be more abundant and larger in length within marine reserves than outside due to protection afforded by the reserve if habitats were similar in and outside the reserves. I quantified the contribution of key habitat variables to determine if habitat affects the abundance and size response variables nested within protection. This research contributes to the efficacy of marine reserves for an important species group and is unique in that it examines an abalone species’ habitat association that has not had major fishing pressure.

## 2.3 Methods

Underwater visual surveys (carried out via SCUBA) of paua populations and habitat types were conducted at four MR locations in central NZ in the Austral summer of 2013 and 2014. Reserves surveyed included Kapiti, Long Island-Kokomohua, Tonga Island and Horoirangi (Fig.1, Table 1). These four MRs were selected because they are representative of the “Abel” bioregion (Shears et al., 2007). Reserve and associated control sites (hereafter referred to as “fished” sites) were assigned as per the existing and long term monitoring areas rigorously chosen during baseline surveys; where scientists aimed to choose areas that were as similar as possible with respect to habitat, oceanography and species composition (Battershill et al. 1993, Davidson et al. 2002, Davidson 2009, Davidson 2013).

### 2.3.1 Marine Reserve Locations

Table 2.1 Characteristics of marine reserves, including size, number of MR sites, number of “fished sites” and date gazetted.

Marine Reserve	Size (ha)	# Reserve sites	# Fished sites	Gazetted
Kapiti	2167	2	2	1992
Long Island	619	9	6	1993
Tonga Island	1835	5	4	1993
Horoirangi	904	6	6	2006

**Kapiti Marine Reserve** is 30 km north of Wellington and 5 km offshore. The reserve has two parts, the eastern reserve, which is 1825 ha and extends to the mainland and the western section, which is 342 ha. A baseline subtidal survey was conducted around Kapiti Island in 1992, to identify habitats and to collect data about fish and invertebrate population densities and size from which to compare change over time. The western reserve was composed of extensive boulder reefs, whereas the eastern reserve was composed of boulder and cobble fields (Baxter 1987, Battershill et al. 1993). Shears and Babcock (2007) reported ecological differences between the two sides of the reserve, with the eastern side being relatively wave-protected, mainly composed of boulder and cobble habitats and being dominated by *Carpophyllum* spp. whereas the western side was much more wave-exposed, composed of rugose greywacke reef covered with brown macroalgal stands, and dominated by *Ecklonia radiata*. To control for known habitat differences between the two reserves, surveys were conducted only on the eastern side of the reserve; two sites within and two sites outside (Fig.2.1).

**Long Island-Kokomohua Marine Reserve** is 6.5 km in length, 619 ha in area and extends approximately 460 m offshore from Long and Kokomohua islands. Long Island is located in Queen Charlotte Sound and is in a transition zone between the wave-protected inner Sound and exposed, dynamic Cook Strait. Sites at the wave-protected end are composed of cobble and boulder and are dominated by *Carpophyllum* spp., whereas sites at the more wave-exposed end are composed of large boulders and rocky reef that is dominated by rich multi-species macroalgal habitats (Shears and Babcock 2007, Davidson 2009). Nine sites within and six sites outside the reserve (on surrounding islands and mainland) were sampled (Fig.2.1).

**Tonga Island Marine Reserve** is 1835 ha in area and extends approximately 1.8 km offshore. The reserve is adjacent to Abel Tasman National Park within Tasman Bay and is composed of granite and bedrock substratum. This area receives substantial sediment input from the Motueka River, resulting in turbid waters (Rob Davidson, Davidson Environmental Ltd, personal communication). It is classified as a wave-sheltered location and has low to moderate levels of abundance of *Carpophyllum* spp., but no *Ecklonia radiata*. Paua surveys were conducted at this marine reserve location for the first time in 2013. Nine sites were chosen for sampling, five within and four outside the reserve (Fig. 2.1).

**Horoirangi Marine Reserve** is 904 ha in area and is situated along a rocky coastline 11 km north of Nelson within Tasman Bay. The reserve is contiguous with the Nelson Boulder Bank and is moderately exposed to sea conditions. *Carpophyllum maschalocarpum* is the dominant macroalgal species and is restricted to shallow depths (Davidson 2013). Twelve sites were chosen for sampling, six within and six outside the reserve (Fig.2.1).

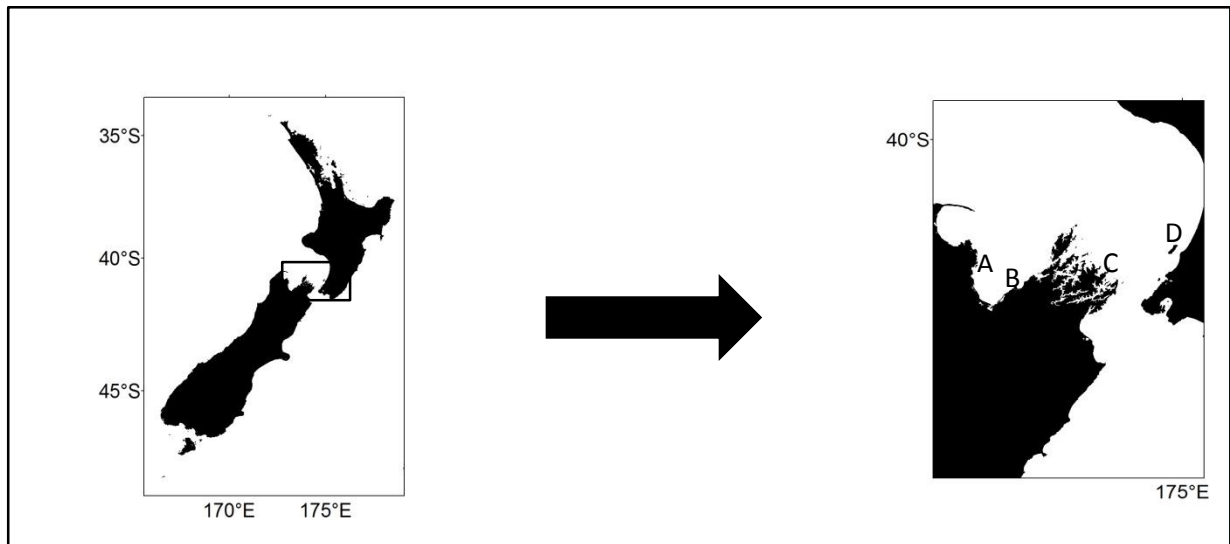


Figure 2.1. Map of four marine reserve locations in central New Zealand: (A) Tonga Island, (B) Horoirangi (C) Long Island and (D) Kapiti.

### 2.3.2 Survey Methods

At all locations, both inside and outside the reserve, paua density and individual size data were collected by two SCUBA divers in depths of 0-4 m. Divers surveyed in reef and boulder habitats that were approximately 300 m alongshore. One diver haphazardly placed  $30 \times 1 \text{ m}^2$  quadrats on the substratum and all paua visible inside each quadrat were counted (haphazard placement was chosen to be consistent with prior MR monitoring). Boulders were not flipped over to look for cryptic or juvenile paua. The other diver measured (*in situ*) up to 60 paua for maximum shell length to the nearest millimetre using standard or electronic calipers (<http://www.zebra-tech.co.nz>) from the same area as density data were collected. The minimum number of paua sampled was dependent on availability of paua at the site.

Habitat was classified at each site to include exposure level, physical substratum type and biogenic habitat categorical variables. These variables were chosen because they affect the abundance of abalone (Andrew and Underwood 1992, Sasaki and Shepherd 2001, Aguirre and

McNaught 2012). To compare among sites, relative exposure to prevailing wind and swell was subjectively assessed and defined on a three-point scale: exposed, moderate and sheltered as in McShane et al. (1994). The visual classification system to determine physical and biogenic habitats was designed for rapid visual assessment by SCUBA divers; habitats were categorised visually at each site as the relative amount of cover. The diver visually assessed the site and recorded primary (>50%) and secondary (<50%) physical substrata according to the JNCC and CMCES classification schemes, as outlined in Table 2 (Connor et al. 2004, Madden et al. 2009).

Algal information was recorded into four functional groups based on height and growth patterns (Steneck and Dethier 1994): (1) Articulated Coralline Algae (ACA), (2) Crustose Coralline Algae (CCA), (3) understory (blades at  $\leq 125$  mm height above the substratum) and (4) canopy (blades  $\geq 125$  mm height above substratum). Visual estimates of the relative abundance (low 0-30%, moderate 31-70%, high 71-100% cover) of each of the four algal functional groups were recorded for each site. Dominant canopy species were recorded to determine macroalgal assemblage type at each site. Total algal cover (i.e. the sum of canopy, understory CCA and ACA) was classified into low, moderate or high for each site. This simple classification system does not take into account differences in size of individual plants, health, morphology or presence of epiphytes. It does, however, provide a quick, semi-quantitative and cost efficient index for use in habitat assessment studies.

Table 2.2. Physical substratum descriptors based on JNCC (2004) CMCES (2009) classification schemes.

Substratum Type	Definition
Bedrock	Continuous rock
Large Boulder	>512 mm
Small Boulder	256-512 mm
Cobble	64-255 mm
Gravel/Pebble	4-64 mm
Sand	<4 mm



### 2.3.3 Statistical Analysis

Data analysis was carried out using the software packages IBM SPSS Statistics 20 and STATISTICA. Location (Kapiti, Long Island, Tonga Island, Horoirangi) and status (reserve vs. fished) were treated as fixed factors and site was treated as a random factor nested within status. The response of paua to protection was compared based on the response variables of mean density (per 1 m<sup>2</sup>) (included quadrats with zero counts) and mean length (mm) of paua at all sites (pooled) within the reserve compared to all sites outside the reserve (pooled) (“fished” areas).

Paua density data were highly skewed and contained a great number of zeros, and length data often did not meet the assumption of equal variances, making traditional parametric analyses (which assume normality and do not deal well with over-dispersion) unsuitable. As a consequence, non-parametric methods were employed for analysis when assumptions were not met. Wilcoxon signed rank tests were employed to test the null hypothesis that there was no difference in paua mean density and mean length between the reserve versus fished sites for each location and across pooled locations. The technique of calculating Response Ratios (RR) was employed to examine location-specific responses and also for comparison across locations (Halpern and Warner 2002, Halpern 2003, Lester et al. 2009, Dias Guisado et al. 2011). RRs were calculated by dividing the mean density or mean length from inside the reserve (sites pooled) by that outside the reserve (sites pooled) at each location and pooled across all locations. Values greater than one indicate the populations are more abundant or larger within the reserve than outside.

Due to its commercial importance it is often debated why paua do not reach mean legal size at some sites or locations. One argument put forward is density dependent growth, based on the competition of food and fishing pressure, not allowing populations to attain legal size. To examine the relationship between mean density and mean length within reserves non-parametric Spearman’s rank correlation tests were utilised, within fished sites and across all sites at Long Island and Horoirangi locations, (sample sizes were insufficient at Kapiti and Tonga Island to conduct the analysis).

Fisher’s exact  $\chi^2$  test of independence was employed to test if habitat types were different inside and outside each reserve. Habitats consisted of multiple variables, including: primary

substratum, secondary substratum, dominant macroalgal type, combined algal cover and exposure. Given that there was only one habitat (each variable) assessment per site, it may yield type II errors (missing patterns in the data); therefore, I choose not to make any correction for the multiple statistical tests (i.e. the sequential Bonferroni correction). Such tests tend to be overly conservative when there are many statistical tests, which could lead to disregarding patterns that are really present in the data (Moran 2003, García 2004). The  $\chi^2$  test results coupled with a qualitative description of habitats inside versus outside allowed the examination of a potential 'habitat effect' or a 'reserve effect' explained observed differences in paua mean density and length at each reserve location.

To control for the effects of fishing, reserve only paua populations were examined to understand the role of habitat variables on density and length. The non-parametric Kruskal-Wallis test was employed to test for significant differences in mean density and/or mean length as a function of each habitat variable category (i.e. to see if paua were more dense or larger on certain substrata, or associated with dominant macroalgal species, combined algal cover or exposure). Although all length location data did not have normal distributions, two out of four locations did and therefore a General Linear Model (GLM) assuming a Gaussian (normal) distribution error structure with main effects was employed to examine which habitat variables were having the main effect on paua length: interactions amongst the main effects were not tested because the variables were co-linear. Density data did not meet assumptions of variance or normal distributions due to the large amount of zeros and a GLM was not employed to examine habitat variables effect on density.

## 2.4 Results

### 2.4.1 Paua Metrics

Testing for statistically significant differences in paua responses between individual MRs and their associated fished sites (sites within pooled and outside pooled) revealed that paua had a higher mean density inside reserves than outside at Horoirangi (Wilcoxon:  $z=-4.39$ ,  $p=0.0001$ ), Kapiti (Wilcoxon:  $z=-3.77$ ,  $p=0.0002$ ) and Long Island (ANOVA:  $F_{1,452}=65.41$ ,  $p=0.0318$ ), but not at Tonga Island where there was no significant difference (Wilcoxon:  $z=0.61$ ,  $p=0.54$ ) (Fig. 2.2, Table 2.3). When pooling all reserve versus all fished sites across

locations, paua were significantly denser within MRs (Table 2.3). Kapiti had the highest densities overall, with mean densities of 4.2 m<sup>2</sup> inside and 2.0 m<sup>2</sup> outside the reserve. Densities at the other reserve locations were substantially lower (Table 2.3). RR indices were greater than one for Horoirangi (RR=1.7), Kapiti (RR=2.1) Long Island (RR=1.4), however, RR at Tonga Island was less than one (0.92). Regardless of Tonga Island having higher density outside when combining all locations, RR indices were greater than one (RR=1.4) illustrating that paua were more dense inside than outside reserves.

Statistically significant differences in mean length were observed between fished and reserve sites, with greater mean lengths inside at Kapiti (Wilcoxon:  $z=2.799$   $p=0.0051$ ), Long Island (ANOVA:  $F_{1, 768} = 65.41$ ,  $p=0.0001$ ) and Tonga Island (Wilcoxon:  $z= -3.322$   $p=0.0009$ ) (Fig. 2.3, Table 2.4). Paua were noticeably smaller at Horoirangi (mean length = 73 mm) than the other reserve locations (Table 2.4) and they were significantly larger outside than inside the reserve (Wilcoxon:  $z= 5.434$ ,  $p= 0.0001$ ). The largest paua were found at exposed sites at Kapiti (mean length = 110 mm) and Long Island (mean length = 110 mm), whereas the smallest paua were, on average, found at Horoirangi. RR indices were greater than one for Kapiti (RR=1.1) Long Island (RR=1.1) Tonga Island (RR=1.1), however at Horoirangi were less than one (RR=0.9). All locations combined (RR=1.1) illustrated that paua were larger inside than outside reserves.

To investigate if length is a function of density, non-parametric Spearman's rho correlations were calculated based on mean length and mean density at Long Island and Horoirangi marine reserves (insufficient data were available to carry out this testing for Tonga and Kapiti). Long Island (all sites) exhibited a significant positive correlation (Spearman correlation:  $\rho=.601$ ,  $p=0.018$ ), yielding larger paua when density was greater. There was no correlation between density and length at Horoirangi sites (Spearman correlation:  $\rho=.564$ ,  $p=0.071$ ).

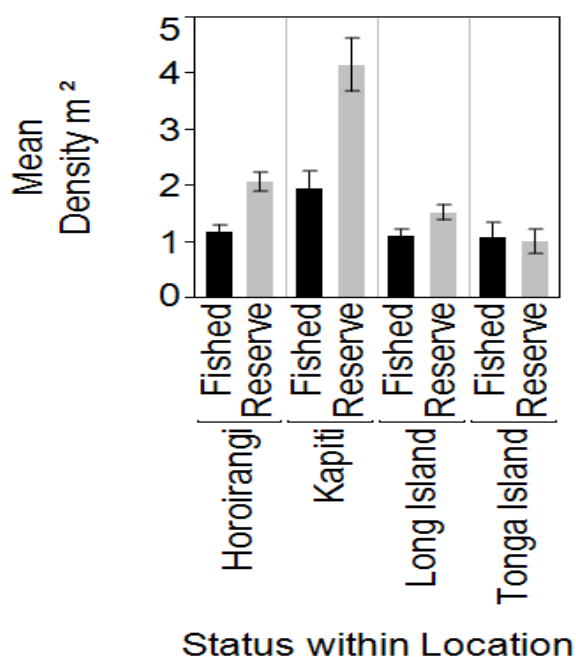


Figure 2.2. Mean ( $\pm$  SE) paua density for each marine reserve location as a function of status (fished versus reserve). 30 quadrats per site. Horoirangi: fished sites  $n=6$ , reserve sites  $n=6$ , Kapiti fished sites  $n=2$ , reserve sites  $n=2$ ; Long Island: fished sites  $n=6$ , reserve sites  $n=9$ ; Tonga Island: fished sites  $n=4$ , reserve sites  $n=5$ .

Table 2.3 Mean ( $\pm$ SE) paua density at each location for reserve and fished sites. 30 quadrats per site. Horoirangi: fished sites  $n=6$ , reserve sites  $n=6$ , Kapiti fished sites  $n=2$ , reserve sites  $n=2$ ; Long Island: fished sites  $n=6$ , reserve sites  $n=9$ ; Tonga Island: fished sites  $n=4$ , reserve sites  $n=5$ . Result of non-parametric Wilcoxon rank result for difference between fished and reserve sites for each marine reserve location. Z; Wilcoxon test statistic, p; Wilcoxon test probability. ANOVA results for Long Island.

Location	Reserve sites mean density 1 m <sup>2</sup> ( $\pm$ SE)	Fished sites mean density 1 m <sup>2</sup> ( $\pm$ SE)	Test-specific statistic Wilcoxon Z or ANOVA F & DF	p
Horoirangi	2.08 (0.14)	1.19 (0.14)	-4.39	<0.0001
Kapiti	4.16 (0.40)	1.95 (0.40)	-3.778	0.0002
Long Island	1.53 (0.13)	1.11 (0.15)	65.41, DF=1, 452	0.0318
Tonga Island	1.02 (0.26)	1.10 (0.22)	0.608	0.5415
All Locations	1.90 (0.09)	1.30 (0.10)	-5.265	<0.0001

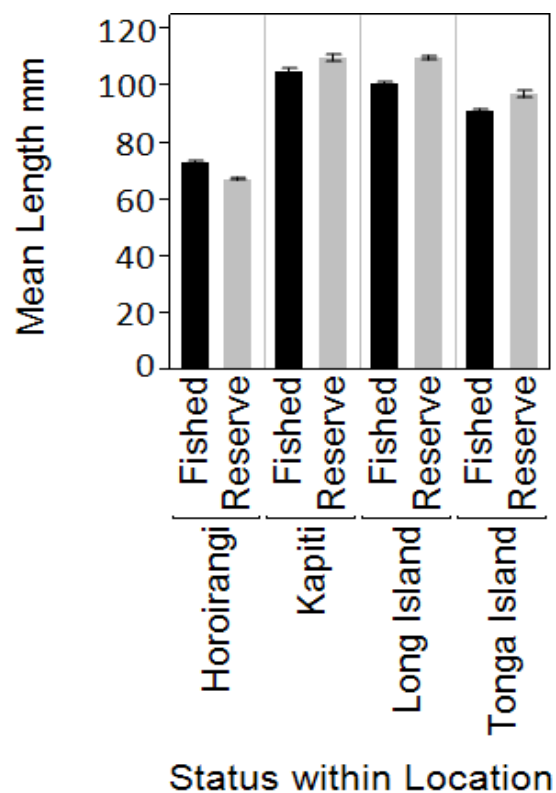


Figure 2.3. Mean ( $\pm$  SE) pua length for each marine reserve location as a function of status (fished versus reserve). Horoirangi: fished sites  $n=6$ , reserve sites  $n=6$ , Kapiti fished sites  $n=2$ , reserve sites  $n=2$ ; Long Island: fished sites  $n=6$ , reserve sites  $n=9$ ; Tonga Island: fished sites  $n=4$ , reserve sites  $n=5$ .

Table 2.4. Mean ( $\pm$ SE) length at each location for reserve and fished sites. Result of non-parametric Wilcoxon rank result for difference between fished and reserve sites mean length for each marine reserve location; Z: Wilcoxon test statistic, p: Wilcoxon test probability. ANOVA results for Long Island.

Location	Reserve sites mean length mm ( $\pm$ SE,n)	Fished sites mean length mm ( $\pm$ SE,n)	Test-specific statistic Wilcoxon Z or ANOVA F & DF	P
Horoirangi	67.29 (0.57, 252)	72.91 (0.71,389)	5.434	<0.0001
Kapiti	110.02 (1.27,118)	104.82 (1.27,120)	2.799	0.0051
Long Island	109.90 (0.72,295)	100.60 (0.97,472)	65.41 DF: 1, 768	<0.0001
Tonga Island	97.15 (1.1,120)	91.03 (1.1,121)	-3.322	0.0009
All Locations	93.51 (0.66,675)	90.89 (0.78,1102)	-2.867	0.0041

### 2.4.2 Habitat

All Fisher's exact  $\chi^2$  tests revealed that there was no significant difference inside versus outside each reserve in the proportion of habitat types (Table 2.5). However, due to low sample sizes (one habitat category per site) this test had low power to detect significant differences in habitat types between sites. To provide further evaluation, a descriptive qualitative assessment was conducted that further confirmed that habitats inside and outside each reserve were not significantly different (i.e. are similar).

Horoirangi MR and associated fished sites were mainly composed of boulder habitats with a moderate level of combined algal cover. *Carpophyllum* spp. was the dominant macroalgal group and the understory was mainly *Ulva* spp. This green algal band was constrained to a shallow and narrow strip in 0-5 m depth, alongshore. Testing revealed that the fished sites CB1 and CB2 were different in that they were more exposed to the swell, the dominant substratum was bedrock rather than boulder and they supported a higher algal diversity and cover.

Long Island MR and associated fished sites were all similar in habitat composition. However, there was a distinct difference in habitat type between sites located near the Cook Strait versus sites located in inner Queen Charlotte Sound. Regardless of status, sites located near the Cook Strait end were composed of bedrock and large boulders, and were exposed to swell. Large stands of macroalgae, composed of a mix of *Ecklonia radiata* and *Carpophyllum* spp. dominated these sites. In contrast, sites located at the inner end of the Sound were composed of boulders and cobbles, were more protected and have low to moderate combined algal cover dominated by *Carpophyllum* spp. and *Ulva* spp. Thus, on average, sites inside and outside the reserve were similar but sites did vary along the environmental gradient within Queen Charlotte Sound.

Kapiti and associated fished sites were all similar in habitat composition. Sites were moderately exposed, made up of boulder habitats with a moderate to high level of combined algal cover, composed of *Carpophyllum* spp. In addition, all sites had well developed understories of brown and foliose red algae.

Tonga Island MR and associated fished sites were composed of large boulders and areas of bedrock. *Carpophyllum* spp. was the dominant macroalgal group and was constrained to a narrow depth band of 0-5 m with mainly moderate cover. Mussel beds were well developed in the shallows and large volumes of deposited sediment were present at all sites. Most sites were exposed to the swell, being north or northwest facing.

Table 2.5. Fisher's exact  $\chi^2$  significance levels (p values), testing the difference between habitat variables by status (reserve or fished) at each reserve location. Horoirangi: fished sites n=6, reserve sites n=6, Kapiti fished sites n=2, reserve sites n=2; Long Island: fished sites n=6, reserve sites=9; Tonga Island: fished sites n= 4, reserve sites n=5.

Habitat Variable	Horoirangi	Long Island	Kapiti	Tonga Island
Primary substratum	0.50	0.59	0.50	0.72
Secondary substratum	0.06	1.00	1.00	1.00
Dominant macroalgae	0.45	0.82	NA	1.00
Combined algal cover	NA	0.92	NA	NA
Exposure	0.48	0.55	NA	0.29

NA =  $\chi^2$  could not be calculated because the variable was constant

To examine and define habitat differences between MR locations  $\chi^2$  tests were run for each habitat variable. The proportions of primary substratum, secondary substratum, dominant algae, algal cover and exposure were different based on MR location. Substratum at Horoirangi and Kapiti were dominated by boulder habitats, whereas at Long Island and Tonga Island substrata were dominated by bedrock (Fig. 2.4). At Horoirangi and Tonga Island the dominant macroalgal group was *Carpophyllum* spp., whereas at Kapiti it was mixed and at Long Island sites all algal categories were present. Kapiti had considerably more algal cover than all other reserve locations (Fig. 2.5). MR locations varied in exposure. Horoirangi was the most sheltered, Tonga Island had some sheltered sites and sites facing northwest were moderately exposed. Sites at Kapiti were all moderately exposed. Long Island had a mix of

sites with some very protected on the eastern Queen Charlotte end and the most exposed sites at the Cook Strait end across the whole study.

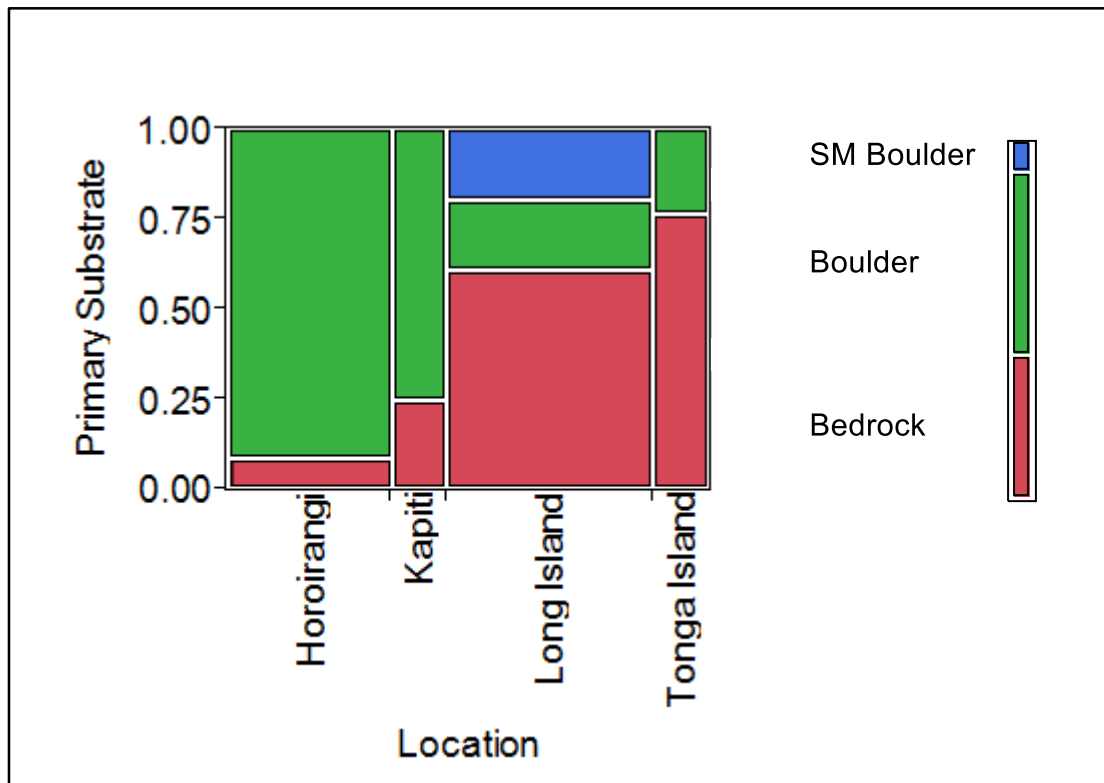


Figure 2.4. Proportion of primary substratum from all site (pooled reserve and fished sites) at each marine reserve location: Horoirangi: n=12, Kapiti: n=2; Long Island: n=15; Tonga Island: n=9.



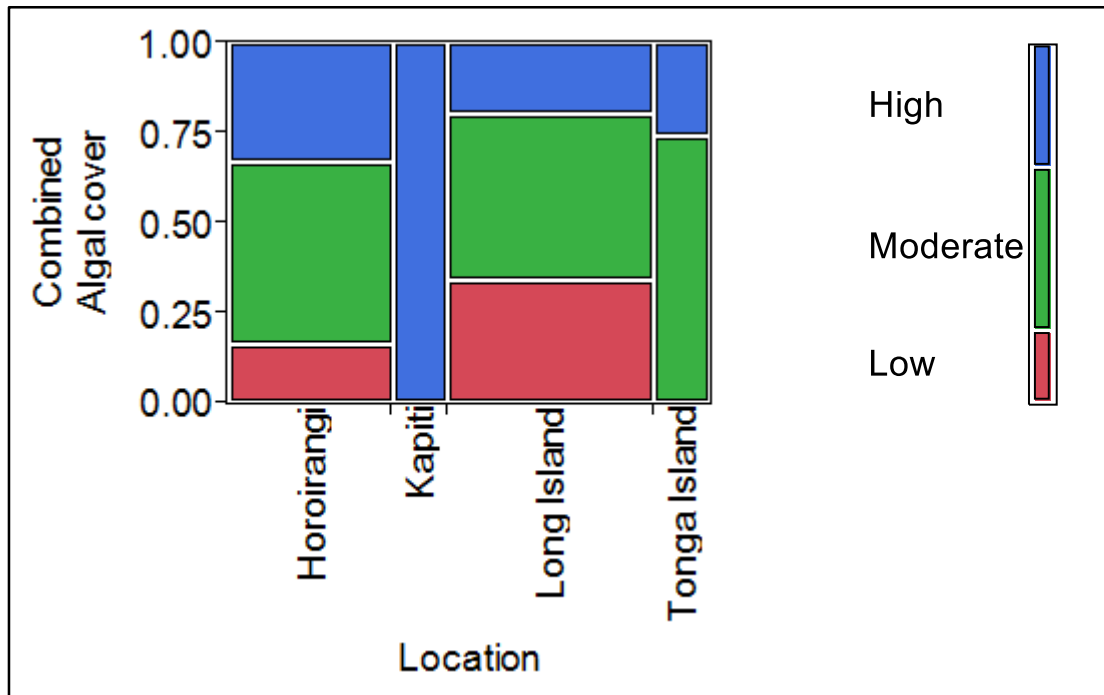


Figure 2.5. Proportion of combined algal cover from pooled reserve and fished sites at each marine reserve location. Horoirangi: n=12, Kapiti: n=4; Long Island: n=15; Tonga Island: n=9.

#### 2.4.3 Paua-Habitat Associations

To control for the effects of fishing, reserve-only populations were examined to better understand the role of habitat variables on paua density and length. Paua at Long Island MR were significantly denser at moderately exposed boulder habitats with crustose coralline algae (CCA) and were significantly larger in exposed bedrock sites with high amounts of *Ecklonia radiata* (Table 2.6). Horoirangi MR habitat variables were mainly continuous across sites; paua were significantly more dense and larger in areas with higher combined algal cover (Table 2.7). Kapiti and Tonga Island had continuous habitat variables across their reserve sites and consequently paua were not significantly denser or larger based on habitat variables. All reserve sites were combined to examine the effect of habitat on paua density and length at a broader scale. Across all MR sites paua were significantly more dense in boulder habitats with higher combined algal cover. Paua were significantly larger in areas that are wave exposed with high algal cover of *Ecklonia radiata* mixed with *Carpophyllum* spp. (Table 2.8, Fig. 2.6).

Table 2.6. Long Island MR non-parametric Kruskal-Wallis results for differences in paua density and paua length by habitat classifications.

Habitat Classification	Density P value	Preference	Length P value	Preference
Primary substratum	0.0001	Boulder	0.0492	Bedrock
Secondary substratum	NS	NA	0.0001	Bedrock
Dominant algae	0.0011	CCA	0.0001	<i>Ecklonia radiata</i>
Combined algal cover	NS	NA	0.0001	High Cover
Exposure	0.0001	Moderate	0.001	Exposed

NA: test could not be run because variable was continuous

Table 2.7. Horoirangi MR non-parametric Kruskal-Wallis results for differences in paua density and paua length by habitat classifications.

Habitat Classification	Density P value	Preference	Length P value	Preference
Primary substratum	NA	NA	NA	NA
Secondary substratum	NA	NA	NA	NA
Dominant algae	NA	NA	NA	NA
Combined algal cover	0.0002	High Cover	0.0167	High Cover
Exposure	NS	NA	NS	NA

NA: test could not be run because variable was continuous

Table 2.8. All MR sites at all four locations combined, non-parametric Kruskal-Wallis results for differences in paua density and paua length by habitat variables.

Habitat Classification	Density P value	Preference	Length P value	Preference
Primary substratum	0.0001	Boulder	0.0001	Bedrock
Secondary substratum	NS	NA	NS	NA
Dominant algae	NS	NA	0.0001	<i>Ecklonia radiata</i> & “mixed”
Combined algal cover	0.0001	High Cover	0.0001	High Cover
Exposure	NS	NA	0.0001	Exposed

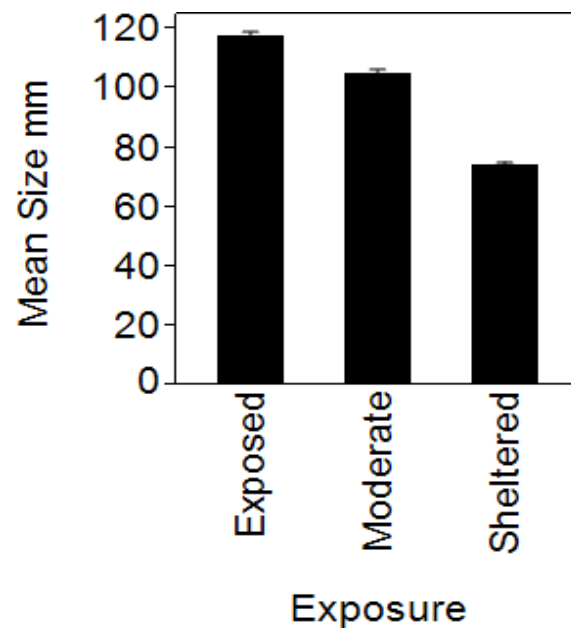


Figure 2.6. Paua mean ( $\pm$ SE) size in mm by exposure level across all MR locations.

In the Kruskal Wallis analysis, secondary substratum did not explain significant variation in paua length and therefore was removed prior to the GLM analysis. GLM testing revealed that paua length was significantly affected by primary substratum ( $df=2, F=9.027, p=0.007$ ), dominant algal cover ( $df=3, F=4.962, p=0.027$ ), combined algal cover ( $df=2, F=13.908, p=0.0002$ ); exposure had the most significant effect on length ( $df=2, F=24.561, p=0.0001$ ). These results are consistent with the Kruskal-Wallis results.

## 2.5 Discussion

Understanding if and to what extent MRs provide protection for any abalone species, an historically exploited species, is critical for their conservation. An improved understanding of the efficacy of marine reserves requires a robust examination of habitats inside and outside reserves to distinguish any reserve effect from a potential confounding habitat effect. Furthermore, studies conducted at several MRs within a biogeographic region increase rigour and enable a broader understanding and further application of results (Shears et al. 2008). The goal of this research was to quantify and distinguish any 'reserve effect' from any 'habitat effect' on paua populations and obtain additional information on paua-habitat associations. These habitat association results can be used to assist with future placement of management areas for the success and recovery of populations within New Zealand and contribute knowledge to other countries that are striving to rebuild their *Haliotid* stocks. Research at the MR, habitat and paua-habitat association level, illustrates how MRs can provide protection for an economically important species under fishing pressure.

### 2.5.1 Paua Metrics

Within New Zealand, MRs are not placed to solely protect *Haliotis iris*, they are placed in representative coastal habitats with the goal of protecting a suite of species (and for scientific research). Albeit these MRs were not designed for paua, analyses revealed paua were, on average, significantly denser and larger within MRs than outside. This is the first study to examine paua and habitat associations in the context of multiple MRs in central New Zealand and contributes to the small amount of international studies on abalone at multiple marine reserves. This study also provides opportunity to examine an abalone species that is the focus of a major fishery but has not suffered extreme exploitation (relative to other abalone fisheries), which may provide a clearer understanding of species habitat associations and

natural demographic processes. These positive results to protection are consistent with the literature; that for certain species marine reserves do support populations that are larger and more abundant within their boundaries, the so-called 'reserve effect' (Halpern 2003, Micheli et al. 2008, Pande et al. 2008, Lester et al. 2009), and with positive abalone response to MR protection world-wide (Wallace 1999, Rogers-Bennett et al. 2000, Barrett et al. 2009).

Fertilisation and recruitment success in many abalone species is limited by low spawner density and has a critical density threshold in the range of 0.15-1 abalone m<sup>-2</sup> to be successful (Babcock and Keesing 1999, Miner et al. 2006b). Paua were significantly more dense within MRs at three of four locations and reached density thresholds for reproductive success. The highest densities were found at Kapiti, both in and outside the reserve. These higher densities may be attributed to Kapiti Island being more difficult than other MR locations to access for recreational fishers. This was the first time that paua were surveyed at Tonga Island MR and densities were found to be similar inside and outside the reserve. Tonga Island is located on the popular Abel Tasman coast, which historically has not been a site for recreational paua fishing, as they are hard to find and other species are in greater abundance (Rob Davidson, Davidson Environmental Ltd, personal communication). Due to the lack of fishing pressure at this site I did not expect to see a direct reserve effect.

Paua were significantly larger within MRs at three of the four locations. However, paua were significantly larger outside the reserve at Horoirangi; this may be attributed to habitat differences of two out of the six fished sites. These two sites were composed of bedrock with large cracks and more exposed than the other sampling sites. Overall, the largest paua were found at Long Island and Kapiti. These sites are exposed which may be favourable habitat for paua growth and the locations are difficult to access for recreational fishers.

Individual location results and response ratio indices of greater density and length within MRs versus fished areas supports other findings that MRs afford protection for abalone. Following six years of protection at Maria Island MR, Tasmania, large *H. rubra* increased in abundance (Edgar and Barrett 1999). The northern abalone (*H. kamtschatkana*) was significantly more abundant and larger in MRs after 40 years of protection (Wallace 1999). Black abalone (*H. cracherodii*) were found to be bigger in size within MRs in central California, but did not reach sizes that were present before the collapse of the fishery (Micheli et al. 2008). Red abalone

(*H. rufescens*) were found in greater abundance within no take MRs and the authors suggest that MRs afforded protection and enabled resilience of the species in the face of a major fishery collapse (Rogers-Bennett et al. 2002, Micheli et al. 2008). Not surprisingly, red abalone (*H. rufescens*) showed a significant decrease in size structure (fewer large abalone) when a MR was opened to fishing (Rogers-Bennett et al. 2013). These findings combined strongly suggest that MRs do afford protection for abalone species allowing them to increase in mean density and size.

It is often argued that paua density and or fishing pressure are the two factors affecting paua size structure. This research showed that fishing pressure affected size (the paua were smaller outside reserves where fishing occurs). Given that paua often form large aggregations and have limited movement patterns one would expect to see intraspecific competition for food. Density length correlations were examined and analyses confirmed that there was no negative correlation of density and length. One possible explanation for the positive correlation between density and length at Long Island, is food may be abundant enough at this location to support healthy and fast growing populations. I conclude that density is not limiting length in central NZ and hypothesise that fishing pressure and habitat variables, specifically exposure to waves play a critical role in length.

### 2.5.2 Habitat

To examine the effect of protection, the main variables measured were paua abundance and size, however the research also focused on quantifying habitats in and outside MRs to assess if there was suitable and comparable paua habitat. In New Zealand, managers strive to place MRs in areas of representative coastal habitats (Carter 2005). However, nearshore temperate reef habitats are complex, seascape heterogeneity is prevalent and due to resource limitation habitats are seldom quantified or monitored. Potential habitat differences in and outside reserves can have a confounding effect on a reserve effect if not taken into account in the analysis of a species response to protection (Charton and Ruzafa 1999, García-Charton et al. 2004, Huntington et al. 2010, Eddy et al. 2014). This investigation enabled the examination of the relative importance of habitat and how it might influence paua metrics and explain effects of protection. I hypothesised that if habitats were comparable then paua would be denser and larger within the reserve than outside. Statistical testing combined with a descriptive qualitative assessment revealed that habitats inside and outside each reserve

location were similar in regards to substratum, algal cover, dominant macroalgae and exposure. This finding indicates that appropriate associated “fished” sites were chosen for monitoring and that habitat within the reserve is not more favourable for paua. Habitat similarity between in and outside reserves confirms that populations at higher density and larger individual paua within MRs are attributable to a ‘reserve effect’ and not a ‘habitat effect’.

### **2.5.3 Paua-Habitat Associations**

Around the world abalone populations have suffered overexploitation, causing fisheries to collapse in many regions (Wallace 1999). For reseeded or recovery purposes much research is focused on what habitats yield dense aggregations and large individuals (Lessard and Campbell 2007, Donnellan 2015). However, it is well documented that abalone have large demographic variability and that density and size can vary on small to large spatial scales (Shepherd and Hearn 1983, Day and Fleming 1992, McShane and Naylor 1995a, Wells and Mulvey 1995, Naylor et al. 2006, Prince et al. 2008, Saunders et al. 2008). Because of this demographic variability abalone-habitat associations should be furthered explored.

In New Zealand, paua populations support a fishery that is managed thorough a Quota Management System with a Total Allowable Catch. Although the fishery is operating (i.e. not crashed) and may be deemed well managed, it still warrants investigation to better understand and manage populations. Fishing pressure and habitat are suggested to limit density and fishing pressure, density and habitat to limit size structure. In this study, length was independent of density at the two locations tested and to control for effects of fishing, MR sites only were used to examine the role of habitat variables of substratum, algal cover, dominant macroalgae and exposure on paua density and length. This research considered each paua metric (density or length) individually to examine what and if the same habitat variables were supporting large aggregations or individuals.

Paua density is recognised as being highly variable, yet the drivers behind this variation are unclear (Prince et al. 1987, Sloan and Breen 1988, Nash 1992, Naylor and Andrew 2004). Density variation may be due to: recruitment failure due to low adult density, thus self-perpetuating low densities (Babcock and Keesing 1999, Miner et al. 2006b), recruitment being variable across populations (McShane and Smith 1991), the habitat that juveniles encounter

may determine the success of recruitment into adult populations (Aguirre and McNaught 2012) and limited adult movement patterns (McShane and Naylor 1997). This study revealed that paua were more dense in boulder habitats with high algal cover (macroalgal and CCA) across all locations. One hypothesis to explain this pattern is that adult abalone are more secure on boulders that are unlikely to roll around in wave conditions and this may be why greater paua abundance is found in boulder habitats (Sousa 1979, Aguirre and McNaught 2012). High densities in areas of high algal cover is consistent with findings of high densities in areas of high CCA in controlled field experiments (McShane and Naylor 1995b, Aguirre and McNaught 2012) and in high macroalgal cover in natural field surveys (Lessard and Campbell 2007, Pande and Gardner 2009).

Paua were significantly larger in areas exposed to swell and wind and with high algal cover dominated by a mixed macroalgal habitat of *Ecklonia radiata* and *Carpophyllum* spp. The largest paua were found at the most exposed sites across all MR locations. These findings are consistent with previous research in which a positive relationship between length, growth and exposure has been reported and that exposure was a significant source of variation in mean length (McShane et al. 1994a, McShane and Naylor 1995a). In addition, *H. iris* individuals from headlands have been found to have higher incremental growth and obtain larger maximum size than individuals in nearby sheltered bays (McShane and Naylor 1995a).

Finding large paua in areas of dense macroalgal stands, their main food supply, was not surprising and is consistent with the literature. For the red abalone (*H. rufescens*) decline in growth was explained by low food availability due to warm water and El Niño events affecting macroalgal growth (Haaker et al. 1998, Tegner et al. 2001). Saunders et al. (2008) found that small or “stunted” populations of *H. rubra* were related to low algal cover and topographic simplicity whereas “normal” populations were related to high algal abundance and topographic complexity. It is suggested that variation in paua growth is attributed to type and availability of food (Sainsbury 1982, Shepherd and Hearn 1983, Day and Fleming 1992). In NZ it is thought that paua prefer to feed on drift rather than attached algae, although (to my knowledge) it has not been shown in the field. In controlled laboratory experiments paua showed a preference for drift over attached algae and during high flow conditions paua were able to trap drift algae but grazing ceased on attached algae (Cornwall et al. 2009). Unfortunately, due to logistical restraints I was unable to measure drift algae concentrations.



However, much would be gained from examining drift algae quality and type and *in situ* paua feeding rates.

Macroalgal cover was a significant explanatory variable for both paua density and length. Food availability is affected by density of conspecifics, water movement, algal cover, drift algal supply and substratum. In central NZ, exposed areas are often dominated by dense macroalgal stands, because the grazers are dislodged by turbulence. It has been hypothesised that a certain amount of water motion is needed to supply food and an increased amount of water movement would increase drift algal supply to the area and also reduce sedimentation which can smother abalone (Sainsbury 1982, Schiel 1990). This research's findings suggest that exposure level and areas with high macroalgal cover may be working in concert to yield large individual paua, potentially indirectly by supplying large amounts of drift algae. Although exposure may be ideal for growth it may hinder large aggregations of paua to form as smaller individuals may be dislodged; therefore an intermediate level of exposure may be optimal to support aggregations and growth (Ward and Stanford 1983, Roxburgh et al. 2004). I propose that a balance between exposure and food supply is required to allow large aggregations of paua to form in the absence of fishing pressure. Large macroalgal stands would dampen exposure allowing smaller paua to adhere and boulder habitats may be preferable for smaller paua in high exposure conditions. Manipulative experiments are needed to test various densities and sizes in varying levels of exposure, substratum and macroalgal habitats to further understand the mechanism of how these environmental variables interact and affect the demography of paua populations.

## 2.6 Conclusion

Marine reserves as a conservation tool for fisheries and biodiversity are starting to flourish and be used effectively across the globe; however, there is still a strong need for baseline data and more studies which investigate how environmental variables may confound and or contribute to reserve effects. By international standards New Zealand has an extensive network of MRs, which encompasses representative habitats across its bioregions. New Zealand's paua populations represent an opportunity to examine an abalone species that is not as stressed by fisheries exploitation as its global cousins and MRs are an ideal tool to examine natural species-habitat associations. These results that *H. iris* are more dense and larger within reserves confirms that MRs do afford protection for paua in central NZ and

provide evidence that MRs are an effective tool for recovery efforts of *Haliotids*. This study was able to successfully distinguish the interaction of 'habitat effect' and 'reserve effect' and confirm paua response to protection is indeed a 'reserve effect'. This research illustrates the importance of examining habitat variables when assessing MR efficacy, and contributes to a better understanding of the conservation role of MRs by showing how a heavily exploited fishery species can benefit from protection. The habitat associations shown here, that wave exposed areas with high macroalgal cover produce large individuals and aggregations assist in management decisions within New Zealand and are directly applicable to reseeded and recovery efforts in the United States and British Colombia.

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## Chapter 3. Ontogenetic changes in habitat requirements for a highly fished species: implications for marine reserve planning

### 3.1 Abstract

A critical question for ecologists and fisheries managers is what drives the demographic processes that dictate the abundance and size structure of ecologically and commercially important species. Abalone (called paua in New Zealand) support valuable nearshore fisheries in many parts of the world and many stocks have been overexploited to the point of collapse. Countries striving to rebuild their abalone stocks are utilizing marine reserves to produce large aggregations and individuals and focusing on habitat requirements which support viable adult populations. In New Zealand, despite the fact that the demography of paua populations is highly variable across spatial scales the abalone, *Haliotis iris*, is the focus of an operating fishery managed through a quota management system. Habitat variability and fishing pressure are suggested to be the main drivers of demographic variation but of equal importance may be post-settlement juvenile success. To examine which variables are having the greatest effect on population structure I evaluated the relationship between physical and biogenic habitat types and the densities and sizes of juvenile and adult *H. iris*. To examine stage-specific habitat requirements in a more natural setting, research was conducted at the Taputeranga Marine Reserve, New Zealand. The goals of this research were to quantify juvenile and adult population densities and examine stage-specific habitat requirements in the context of protection. The design allowed me to test if juvenile populations were more abundant in areas adjacent to productive adult populations. In the austral summers of 2013 to 2015, intertidal and subtidal surveys were conducted of habitat type and paua populations. Juvenile paua were found at higher densities in areas that were sheltered from wave exposure and dominated by cobbles and boulder fields, which provide safe habitat for juveniles. The 2013 storm event had the largest impact on paua densities at the exposed sites, further confirming that sheltered areas may be a critical component for juvenile stage success. Adult paua were found in greater densities and were larger in size within the reserve than outside which was the opposite finding to baseline surveys. The sharp contrast before and after reserve establishment in adult paua density and size indicates that the reserve is affording protection. Although within the reserve there were large aggregations and individual adults which may support reproductive success, juvenile and adult densities were not correlated. Results from this study suggest that marine reserve implementation does have a positive



impact on adult populations but that habitat is more important for juvenile success. The results from this study strongly suggest that when designing individual marine reserves or systems, it is important to consider species-specific habitat requirements of multiple life history stages, by protecting juvenile habitat as well as adults to increase chances of successful recovery.

### 3.2 Introduction

A critical question for ecologists and fisheries managers is what drives the demographic processes that dictate the abundance and size structure of ecologically and commercially important species. Heavy extraction can have direct effects on a species' recruitment dynamics, adult abundance, size structure and spatial distribution as well as effects on the general ecology of an area. Abalone support important nearshore fisheries around the world and many stocks have been overexploited to the point of collapse (Werner et al. 1995, Rogers-Bennett et al. 2002, Prince 2005). Regardless of location or level of fishing pressure, demography, morphology and growth rates of abalone are highly variable at broad and fine spatial scales (Breen et al. 1982, McShane 1994, McShane and Naylor 1995a, Naylor et al. 2006). Abalone demographics are dictated by several factors: density dependence where fertilisation success is limited by low spawner density, larval supply, post-settlement success, resource (food and habitat) availability and predation pressure (McShane and Naylor 1995a, Babcock and Keesing 1999, Miner et al. 2006b, Aguirre and McNaught 2012).

In NZ, the abalone, *Haliotis iris*, commonly referred to as the blackfoot paua (hereafter referred to as paua) inhabits intertidal and shallow subtidal rocky reefs and is the focus of important customary, recreational and commercial fisheries (Schiel and Breen 1991, Aguirre and McNaught 2012). Density and size of paua are highly variable on spatial scales that are fine from reef to reef (<10 m) to broad across bays and headlands (km). These patterns are observed in areas of commercial fishing (managed through a quota management system) and in protected areas, such as marine reserves and customary closures (Breen et al. 1982, McShane 1994, McShane and Naylor 1995a, Naylor et al. 2006). It has been suggested that habitat, food availability and fishing pressure may be the main drivers of demographic variability of paua populations (McShane and Naylor 1995b, Sasaki and Shepherd 2001, Coates et al. 2013). Potentially of equal importance is post-settlement success, whereby

juveniles that recruit into suitable habitat with appropriate food sources have a better chance to develop into dense adult populations than juveniles that recruit into less desirable conditions. Variation in juvenile abundance and success has been attributed to depth, sedimentation, habitat quality, wave exposure and predation (McShane and Naylor 1995b, Aguirre and McNaught 2010).

Paua have a short larval duration (~ 72 h) and studies suggest they are mostly self-recruiting (Prince et al. 1987, Sloan and Breen 1988, Nash 1992). Juvenile paua recruit and settle onto crustose coralline algae in the intertidal zone down to approximately 10 meters in depth and feed mainly on diatoms and micro-filamentous algae (Tong et al. 1992). Once paua reach approximately 10 mm in length they tend to congregate in shallow water (<3 m), living under boulders or in cryptic habitats, and their dietary requirements slowly change to macroalgae (Pederson et al. 2008, Aguirre and McNaught 2012). They reside in shallow water for three to five years until they reach 70-90 mm in length, at which size they become more emergent being large enough to persist against predation pressures and are commonly found in 1-10 meters water depth (Schiel and Breen 1991, Tong et al. 1992, Aguirre and McNaught 2012). Adult paua are most abundant in the shallow subtidal (<10 m depth), have limited movement, live in dense aggregations on rocky reefs, surge channels and boulder habitats and feed on attached and drift macroalgae (Day and Fleming 1992, McShane 1994, Allen et al. 2006). Adult abalone (*H. rubra* in Australia and *H. iris* in NZ) abundance is positively correlated with areas of canopy macroalgae and negatively correlated with understory algae (Andrew and Underwood 1992, Sasaki and Shepherd 2001, Aguirre and McNaught 2010, 2012).

There are clear differences in habitat requirements for the juveniles and adult stages that enable them to be successful. Countries striving to rebuild their abalone stocks are utilizing marine reserves and much research is focused on what habitats yield dense adult aggregations and large individuals for reseeded and recovery purposes (Lessard and Campbell 2007, Donnellan 2015). However, efforts should also be made to place adults in areas adjacent to where there is suitable juvenile habitat because juvenile abundance, distribution and mortality are critical factors to consider as they can strongly affect adult population abundances and distributions (Rowley 1989, McShane and Naylor 1995a). Within NZ, the paua industry, quota holders and researchers recognize the importance of juvenile populations and have undertaken reseeded projects to support fisheries by placing juvenile

paua in low intertidal and very shallow subtidal habitats adjacent to areas that have habitats that support adults in hopes of successful recruitment into the fishery (Paua Industry Council, Personal Communication(Booth and Cox 2003, Roberts et al. 2007).

The life history characteristics of paua, combined with being a heavily fished species, exacerbates the vulnerability of paua to human-mediated disturbance and makes them ideal candidates for marine reserve (MR) protection. There is a growing body of evidence showing the positive response of populations to protection, where fished species' density, size and biomass within MRs are higher than outside: this is often referred to as the 'reserve effect' (Halpern 2003, Micheli et al. 2004, Barrett et al. 2009, Lester et al. 2009, Eddy et al. 2014a). Additionally, MRs have been shown to provide protection for abalone in many countries, including New Zealand (see Chapter 2, this thesis), resulting in higher densities and larger individuals (Edgar and Barrett 1999, Wallace 1999, Rogers-Bennett et al. 2002, Barrett et al. 2009). MRs, where densities and sizes have the protection to obtain more normal levels are an ideal tool to examine natural species-habitat associations and demographic processes. A positive response to protection should yield more larvae (because of increased numbers of individuals and also because bigger individuals produce disproportionately more offspring than smaller individuals), and in an organism with short larval duration and localized recruitment, potentially result in larger juvenile populations in close proximity to adults. However, knowledge of larval dispersal and population structure at this fine scale has not been determined for the Wellington South Coast. Given the often comparatively small size of MRs, the close proximity of control sites and local oceanography, these potentially productive populations may be seeding populations outside the reserve via larval spillover (Micheli et al. 2012). The combination of potential spillover, recruitment dynamics, and different stage-specific tidal/habitat requirements is a complex system that warrants further investigation (McShane and Naylor 1996, Sasaki and Shepherd 2001).

Despite the importance of juvenile populations for adult success and the recognition of differences in stage-specific habitat suitability, very few studies (and none to my knowledge) in the southern hemisphere have focused on both juvenile and adult stages and their respective habitat associations in adjacent tidal zones within the context of MRs. The few studies in California, USA, have found a species specific response, where green abalone juvenile abundance was positively correlated with adult abundance whereas red abalone

juvenile abundance was negatively correlated with adult abundance. To aid in the understanding of demographic processes researchers need to look at both ontogenetic stages and their respective habitat requirements and it is highly beneficial to examine these processes within the scope of MRs as they provide a more natural setting.

This study focused on the relationship between physical and biogenic habitat types and the abundance of juvenile paua in the intertidal zone and adult paua in the shallow subtidal zone. The research was conducted at the Taputeranga Marine Reserve (TMR) on Wellington's south coast (WSC), New Zealand to examine a potential reserve effect and to investigate stage-specific habitat associations in a setting with more natural densities and sizes (due to reserve designation). This area of the coast has been closed to commercial paua fishing since 1986, and therefore should exhibit one of the best natural environments in regard to paua populations in New Zealand. The goals of this study were to evaluate in and outside the reserve: 1) Biological response variables density and length and the distribution of juvenile paua in the intertidal and adult paua in the subtidal zones; 2) Habitat types (classifications) in both tidal zones; and 3) How and to what extent the density of ontogenetic stage-specific paua populations were associated with habitat variables. I hypothesized that adult paua would be more abundant and larger in size within TMR than outside due to protection afforded by the reserve. The surveys quantified intertidal and subtidal habitat types to better understand the habitat preference and requirements of both ontogenetic stages of paua. This research examined if juvenile populations were more abundant in areas adjacent to productive adult populations to help understand if adult populations (i.e. high densities) or habitat suitability was more important for juvenile success.

### **3.3 Methods**

#### **3.3.1 Study Area**

TMR was gazetted in August 2008, is 855 hectares in area and runs along 12 km of coastline on WSC. The WSC is located on the dynamically active Cook Strait (Harris 1990). There is a natural environmental gradient in terms of water chemistry and nutrients along the WSC from west (low concentrations) to east (high concentrations) that affects biological community

composition (Gardner 2000, Pande and Gardner 2009). The geomorphology of the WSC is characterized by a highly indented and uneven greywacke reef and the coastline encompasses a large number and diversity of shallow and emerging reefs and nearshore structures (Lewis 1979). The tidal zone is composed of rugose bedrock reefs, large patches of boulders, cobble fields and areas of gravel and sand.

The south coast supports a diverse macroalgal community (Shears and Babcock 2007, Nelson 2008). The immediate subtidal zone is composed of large stands of the brown kelps *Carpophyllum maschalocarpum* and *Carpophyllum flexuosum*, whereas deeper areas are dominated by *Ecklonia radiata* and *Lessonia variegata* (Shears and Babcock 2007). All depths are composed of a diverse understory of red algae and the green algae *Ulva* spp. and *Caulerpa* spp. (Shears and Babcock 2007). Crustose coralline algae form the dominant cover, interspersed with turf algae. Diverse assemblages of encrusting and globular sponges are also an important component of the benthic community on the south coast (Berman and Bell 2010). To establish long term monitoring sites for TMR, a baseline survey of greywacke reef locations was conducted, and revealed sites differing in macrobiotic community structure were often spatially separated (Pande and Gardner 2009).

### 3.3.2 Survey Methods

#### **Paua Surveys**

Underwater visual surveys (carried out via SCUBA) of paua populations and habitat types were conducted in the austral summer (January-March) and winter seasons (June-August) of 2013-2015 at six sites associated within TMR, WSC, New Zealand. Three “reserve” sites (Yung Pen, Sirens, Princess Bay) and three “fished” sites (Red Rocks, Palmer Head, Breaker Bay) were chosen for sampling because they had intertidal and subtidal habitats appropriate for the assessment of juvenile and adult paua populations (Fig. 3.1). At all sites paua density, individual size and habitat classification data were collected in the intertidal zone for juvenile paua and the shallow subtidal zone for adult paua.

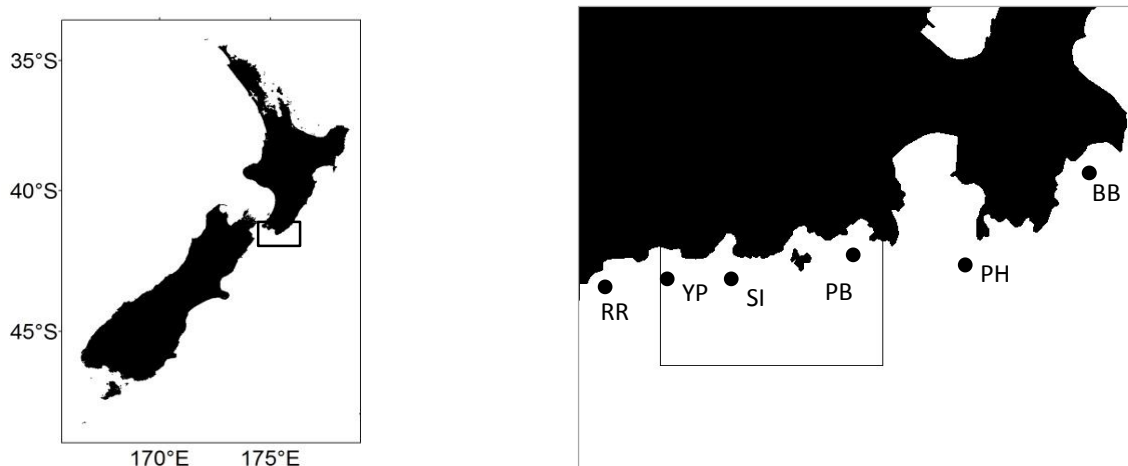


Figure 3.1. Location of study sites. Map of New Zealand with enlarged map of Wellington South Coast. Solid line indicates Taputeranga Marine Reserve boundary. Solid circles indicate study sites: RR (Red Rocks), YP (Yung Pen), SI (Sirens), PB (Princess Bay), PH (Palmer Head), BB (Breaker Bay).

Juvenile paua density and size data were collected by researchers on foot with an underwater viewing platform in the intertidal at low tide (0.4-0.6 m above CD). At each site, three areas of boulder and cobble habitats were identified in < 1 m water depth. At each area, a transect tape was rolled out and a 1 m<sup>2</sup> quadrat was placed at each of five predetermined random numbers on the transect tape. Based on surveys conducted by NIWA in the Wellington region, it was determined that 15 × 1 m<sup>2</sup> quadrats are needed per site to collect a representative sample of the population (Reyn Naylor 2008). When each quadrat was placed, the area was determined to be suitable if it was composed of boulders and/or cobbles, but rejected if composed of sand, bare rock or gravel. The quadrat was searched and boulders flipped to find all juvenile paua within the quadrat. Paua were counted and measured along the longest shell axis to the nearest millimetre with standard callipers to determine the density and length frequency of the population at each site. It has been shown that abalone habitat associations, emergent behaviour and diet all vary depending on paua size or age and that these biotic interactions change as the individual reaches reproductive maturity (McShane and Naylor 1995a, Naylor et al. 2006, Prince et al. 2008, Aguirre and McNaught 2012). The study focused on juveniles rather than recruits (defined by size) as they are a better indicator of what will succeed to adults. Although it is recognized that *Halioti iris* <10 mm are early juveniles, 11-30

mm are late juveniles and 31-90 mm are sub-adults (Aguirre and McNaught 2012), for the purpose of this study all paua between 0-90 mm were grouped into a single “juvenile” category. Paua larger than 90 mm (assumed to be reproductively mature) were classed as “adults” and enumerated for each quadrat.

Adult paua density and individual size data were collected by two SCUBA divers in depths 0-4 m. Divers surveyed in reef and boulder habitats that were approximately 300 m alongshore. One diver haphazardly placed 30 x 1 m<sup>2</sup> quadrats on the substratum and all paua visible inside each quadrat were counted. Boulders were not flipped over to look for cryptic or juvenile paua. The other diver measured (*in situ*) between one and up to a maximum of 60 paua for maximum shell length to the nearest 0.5 millimetre using electronic calipers (Zebra-Tech - <http://www.zebra-tech.co.nz/>) from the same area as density data were collected. The minimum number of paua sampled was dependent on availability of paua at the site (i.e. if less than 60 then all paua were measured).

### **Habitat Surveys**

Habitat was classified at the quadrat level for both the intertidal and subtidal surveys. Classification of physical substratum type, biogenic communities, and relative wave exposure were employed. These variables were chosen for examination because they have been shown to affect the abundance of abalone (Andrew and Underwood 1992, Sasaki and Shepherd 2001, Aguirre and McNaught 2010, 2012). The visual classification system to determine physical and biogenic subtidal habitats was designed for rapid visual assessment by a SCUBA diver. At each quadrat (intertidal or subtidal) the researcher visually assessed and determined primary (>50%) and secondary (<50%) physical substratum type according to the JNCC (2004) and CMCES (2009) classification schemes as outlined in Table 3.1 (Connor et al. 2004, Madden et al. 2009).

Table 3.1. Physical substratum descriptors based on the JNCC (2004) and CMCES (2009) classification schemes.

Substratum type	Definition
Bedrock	Continuous rock
Large Boulder	>512 mm
Small Boulder	256-512 mm
Cobble	64-255 mm
Gravel/Pebble	4-64 mm
Sand	<4 mm

Algal information was recorded into four functional groups based on height and growth patterns (Steneck and Dethier 1994): (1) Articulated Coralline Algae (ACA), (2) Crustose Coralline Algae (CCA), (3) understory (blades at <125 mm height above the substratum) and (4) canopy (blades at >125 mm height above substratum). Visual estimates of the relative abundance (absent, rare <10%, moderate 10-60%, abundant 70-100% cover) of each of the four algal functional groups were recorded for each quadrat. The dominant macroalgal category was noted for the subtidal surveys. This simple classification system does not take into account differences in size of individual plants, their health, morphology or presence of epiphytes. It does however provide a quick semi-quantitative and cost efficient index for use in habitat assessment studies. To compare among sites, relative exposure to prevailing wind and swell was subjectively assessed as wave exposure and defined on a three point scale: exposed, moderate and sheltered (McShane et al. 1994a).

On June 21<sup>st</sup>, 2013, Wellington experienced a very large storm system with Cook Strait wave heights of 15 m and winds exceeding 200 km h<sup>-1</sup>. The storm had a profound effect on the intertidal zone of the south coast, with much debris thrown up on to the shore and portions of the road removed, but did not appear to affect too greatly the subtidal zone (personal observation). To assess the effects of a massive storm event and the potential shifting of intertidal habitats on juvenile paua, two marine reserve (Sirens, Yung Pen) and two fished sites (Palmer Head, Breaker Bay) were chosen for re-sampling in the weeks immediately following the storm.



### 3.3.3 Statistical Analysis

Data analysis was carried out using the software packages IBM SPSS Statistics 20, Statistica and PRIMER. Status (reserve vs. fished) was treated as a fixed factor and site was treated as a random factor nested within status. I wanted to test if there were differences in habitat types between the intertidal sites and between the subtidal sites by status. Habitat classifications consisted of multiple variables: wave exposure, primary and secondary substratum relative abundance of CCA, ACA, understory and macroalgae. To test if there were habitat differences between sites within a tidal zone I utilized two approaches: 1) Community analysis using the software PRIMER (v.6.1) and 2) standard  $\chi^2$  tests. Resemblance matrices for environmental variables based on Euclidean distance were calculated and Multi-Dimensional Scaling (MDS) plots were utilized to examine the spatial relationships of sites based on environmental data. Principle Component Analysis (PCA) was used as an exploratory tool to examine which habitat variables had the greatest effect on structuring the habitat. Categorical habitat variables were transformed to an ordinal scale so there was no need to standardize data for PCA analysis. Based on PCA results the  $\chi^2$  test was employed to test each specific habitat variable effect on paua size and density.

The response of paua to protection in the intertidal zone was compared based on the response variable of mean density ( $1 \text{ m}^{-2}$ ) (included quadrats with zero counts) and in the subtidal zone was compared based on the response variable of mean density ( $1 \text{ m}^{-2}$ ) (included quadrats with zero counts) and mean length (mm) of paua at all sites within the reserve (sites pooled) compared to all sites outside the reserve (sites pooled) (“fished” areas). Paua density data were highly skewed and contained a great number of zeros making traditional parametric analyses (which assume normality and do not deal with over-dispersion particularly well) unsuitable. I did consider transforming the data, however based on the nature of the data, where dispersion was high and counts were low; transformations have been shown to perform poorly (on this type of data) and therefore I rejected transforming the data (O’hara and Kotze 2010). As a consequence, non-parametric methods were employed. Mann-Whitney U tests were employed to test the null hypothesis that there was no difference in mean density at the reserve versus fished sites for both juveniles and adults. Kruskal-Wallis tests were used to examine differences in density between fished and between reserves sites for both juveniles and adults. Adult paua length data met assumptions of

normality and therefore parametric ANOVA was used to test the null hypothesis that there was no difference in adult paua mean length at reserve versus fished sites and used to test for differences in length between the three fished sites and between the three reserves sites. To examine the effect of the storm matched pair t-tests were employed to test for differences in juvenile densities and habitat variables by site before and after the storm (A two way ANOVA was not utilized as the data did not meet assumptions).

The non-parametric Kruskal-Wallis test was employed to test for significant differences in mean juvenile densities and mean adult densities as a function of each habitat variable category (i.e. to see if paua were denser at certain substrata, dominant macroalgae species, combined algal cover, exposure or relief). Because adult length data were not collected at the experimental unit level of quadrat it was not possible to test for habitat type associations with length.

## 3.4 Results

### 3.4.1 Intertidal Assessment

#### Habitat

The MDS plot (Fig. 3.2A) shows a degree of similarity among samples at a given site. The MDS plot (Fig. 3.2B) shows evidence of environmental dissimilarity based on status (reserve versus fished), and the ANOSIM test results indicated that status was significant in describing the habitat structure ( $R=0.107$ ,  $p=0.01$ ). The PCA plot explained 94.6% of the total variation and showed that primary substratum, abundance of ACA and canopy algae were the three primary factors and understory, CCA and exposure are the three secondary factors that contribute to differences among sites (Fig. 3.3). A  $\chi^2$  test revealed a significant difference in primary substratum type between fished and reserve sites ( $p=0.0006$ ), with the fished sites being dominated by cobble and small boulder whereas the reserve sites were a more heterogeneous mix of substratum types (Fig. 3.4). The presence of drift algae was found significantly more often in quadrats at the fished sites than at the reserve sites ( $p=0.0010$ ). The reserve sites, being situated on the western end of the Wellington South Coast were significantly more exposed to wind and swell conditions than the fished sites ( $p=0.0001$ ). There were no significant differences in habitat variables (i.e substrates, algal cover) among reserve sites. Among fished sites there was a significant difference in primary

( $p=0.0024$ ) and secondary substratum ( $p=0.0108$ ), where Palmer Head was primarily a cobble environment whereas Red Rocks and Breaker Bay were a mix of cobbles and small boulders. Algal variables were not significantly different in abundance across all sites regardless of MR status. Outside TMR, exposure was significantly different, where Red Rocks and Palmer Head are exposed and Breaker Bay is sheltered in comparison ( $p=0.0001$ ).

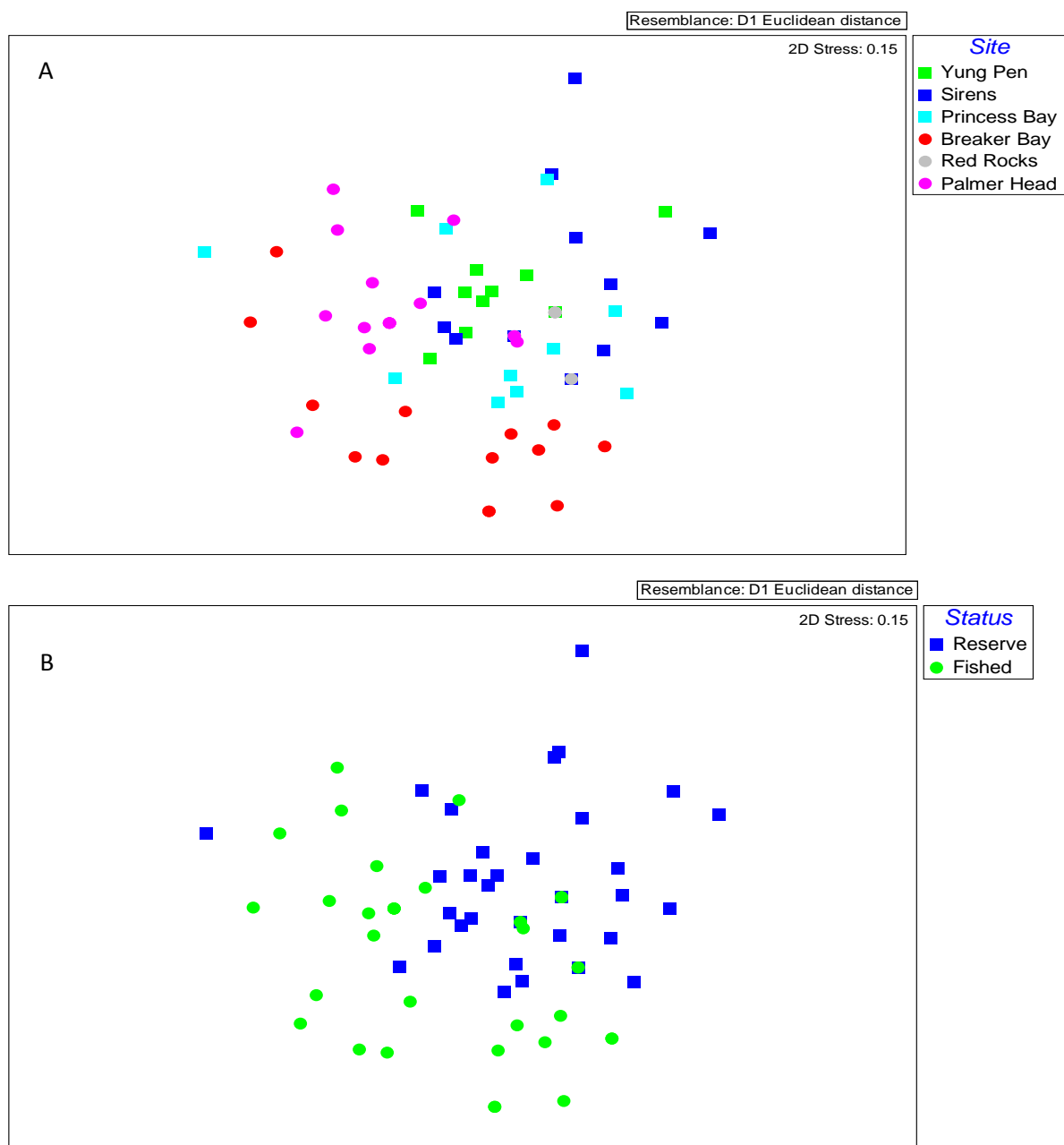


Figure 3.2. MDS plots showing the correspondence between intertidal environmental variables and sites (A) and status (B).

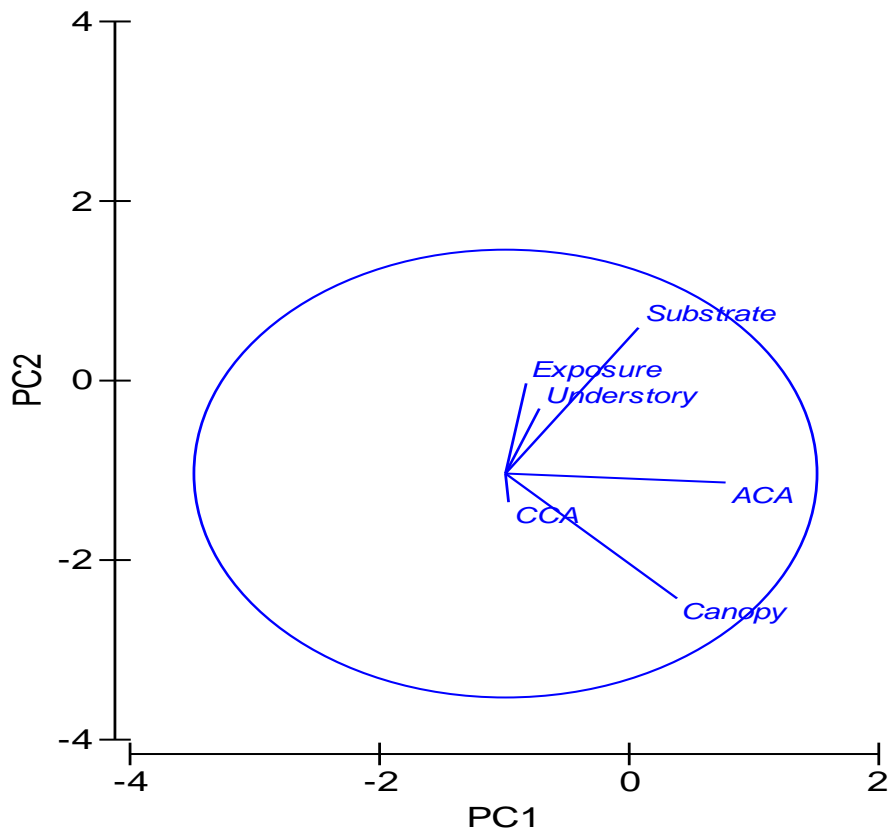


Figure 3.3. PCA plot showing contribution of intertidal habitat variables to environmental composition.

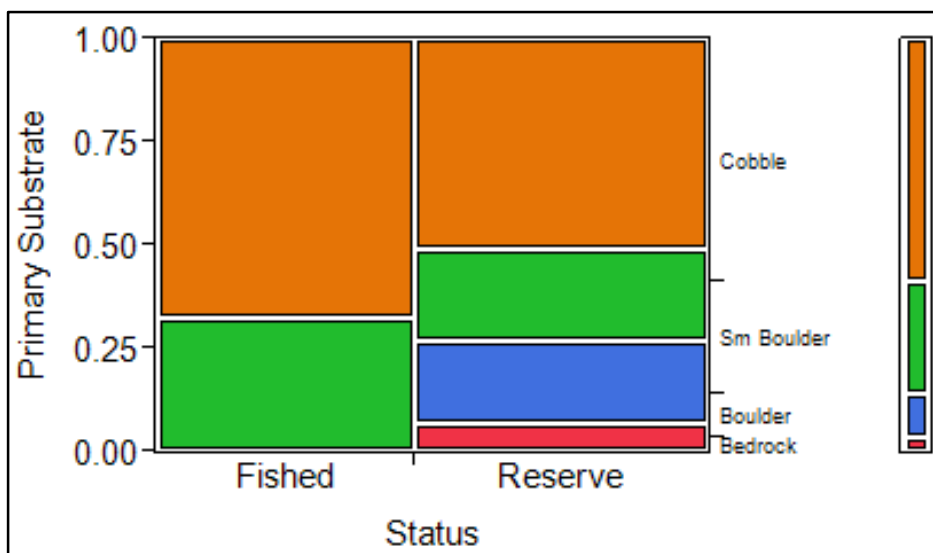


Figure 3.4. Proportion of intertidal primary substratum by status (fished versus reserve). 15 quadrats per site, 3 fished sites, 3 reserve sites.

## Intertidal Paua Metrics

Juvenile paua mean density was significantly greater at fished intertidal sites than at reserve intertidal sites (Mann-Whitney U Test,  $Z=-3.40$ ,  $p=0.0005$ , Fig. 5). Breaker Bay had the highest mean density of  $3.7 \text{ m}^{-2}$ , a value that was significantly higher than the other sites (Kruskal-Wallis  $H=5$ ;  $p=0.0047$ , Fig. 3.6). Kruskal-Wallis analysis revealed that paua density was not significantly different among sites based on primary or secondary substratum or any algal variable. However, paua were significantly more dense in areas that were sheltered from exposure compared to those areas that were moderately exposed (Kruskal-Wallis  $H=2$ ;  $p=0.0012$ , Fig. 3.7).

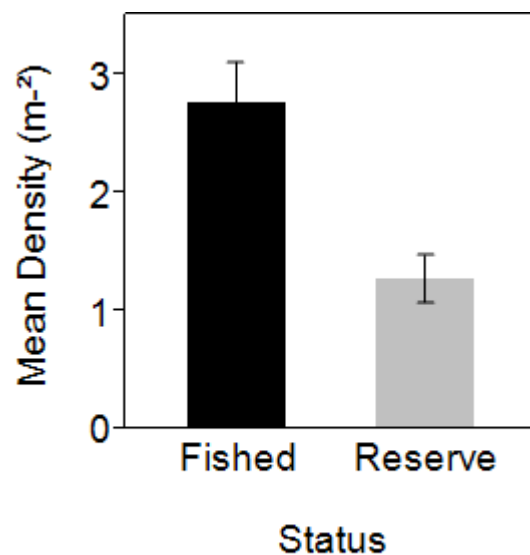


Figure 3.5. Mean ( $\pm$ SE) juvenile paua density as a function of status (fished versus reserve) within the intertidal zone. 15 quadrats per site, 3 fished sites pooled, 3 reserve sites pooled.

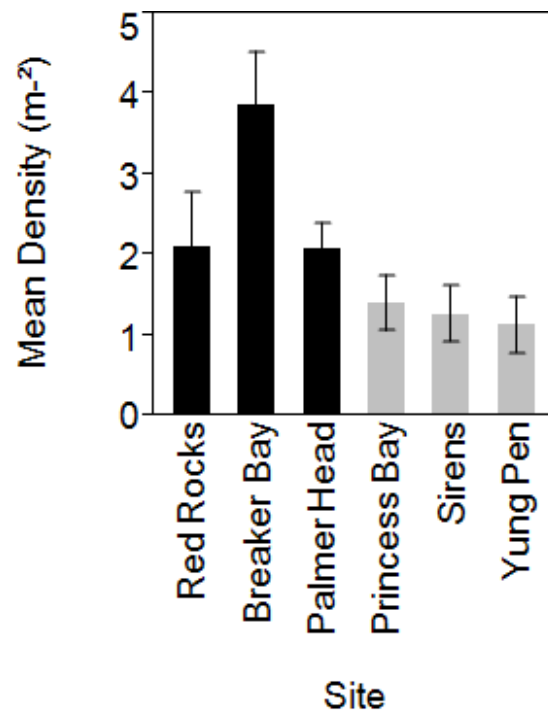


Figure 3.6. Mean ( $\pm$ SE) juvenile paua density as a function of intertidal site: black bars are fished sites, grey bars are reserve sites. n= 15 quadrats per site.

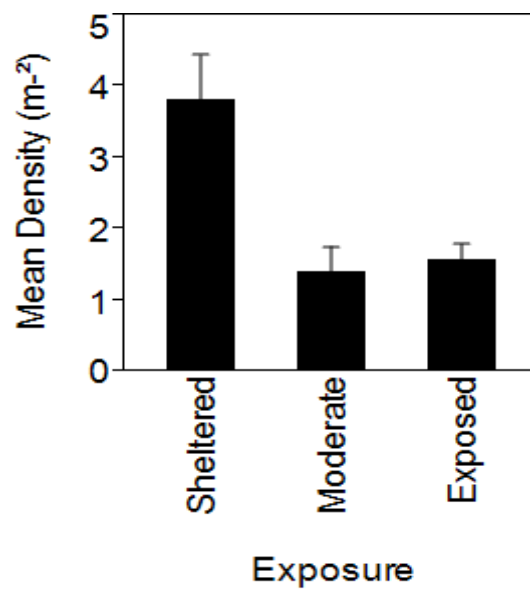


Figure 3.7. Mean ( $\pm$ SE) juvenile paua density as a function of intertidal exposure.

## Storm Effect

Paua were significantly less abundant after the storm at all four sites and this effect was statistically significant at Palmer Head ( $p=0.0381$ ), Sirens ( $p=0.0293$ ), and Yung Pen ( $p=0.0273$ ) (Fig. 3.8). A matched paired test of habitat variables before and after the storm across all sites revealed no significant differences due to the storm event, but there was a shift in primary substratum at these sites with more cobbles and the addition of brick and concrete debris presumably from higher up on the shore.

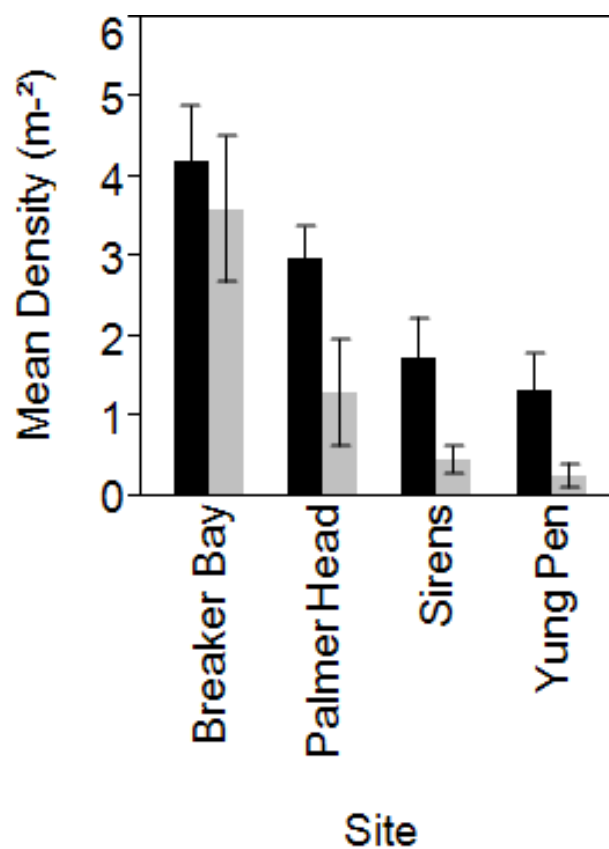


Figure 3.8. Mean ( $\pm$ SE) juvenile paua density by intertidal site as a function of before (black) and after (grey) storm event.  $n=15$  quadrats per site at each sampling interval (before vs. after).

### 3.4.2 Subtidal Assessment

#### Habitat

The MDS plot (Fig. 3.9A) shows a degree of similarity among samples at a given site. The MDS plot (Fig. 3.9B) shows evidence of separation based on status (fished versus reserve), and the ANOSIM test results indicated that status was significant in describing the habitat structure ( $R=0.05$ ,  $p=0.01$ ). The PCA plot explained 92.4% of the total variation and showed that exposure, primary substratum and abundance of ACA were the three primary factors whereas understory, canopy and CCA were the three secondary factors that contribute to differences among sites (Fig. 3.10). A  $\chi^2$  test revealed a significant difference in primary substratum type between fished and reserve sites, with the reserve sites being dominated by bedrock whereas the fished sites had approximate proportions of all substrata ( $p=0.0001$ , Fig. 3.11). Secondary substratum was different by status, reserve sites had components of all substratum, whereas the fished sites were mainly small boulder and cobble ( $p=0.015$ ). Understory algae were found significantly more in quadrats at the reserve sites than the fished sites ( $p=0.0002$ ). Within reserve sites there was no significant difference in any habitat variable between sites. Within fished sites there was significant difference in primary substratum ( $p=0.0001$ ), where Red Rocks was dominated by large boulders and Breaker Bay was dominated by bedrock. There was no significant difference in canopy cover or understory cover at these sites, however there was a significant difference in CCA cover ( $p=0.0031$ ), with less at Red Rocks and a significant difference in ACA cover with more at Breaker Bay ( $p=0.0011$ ).



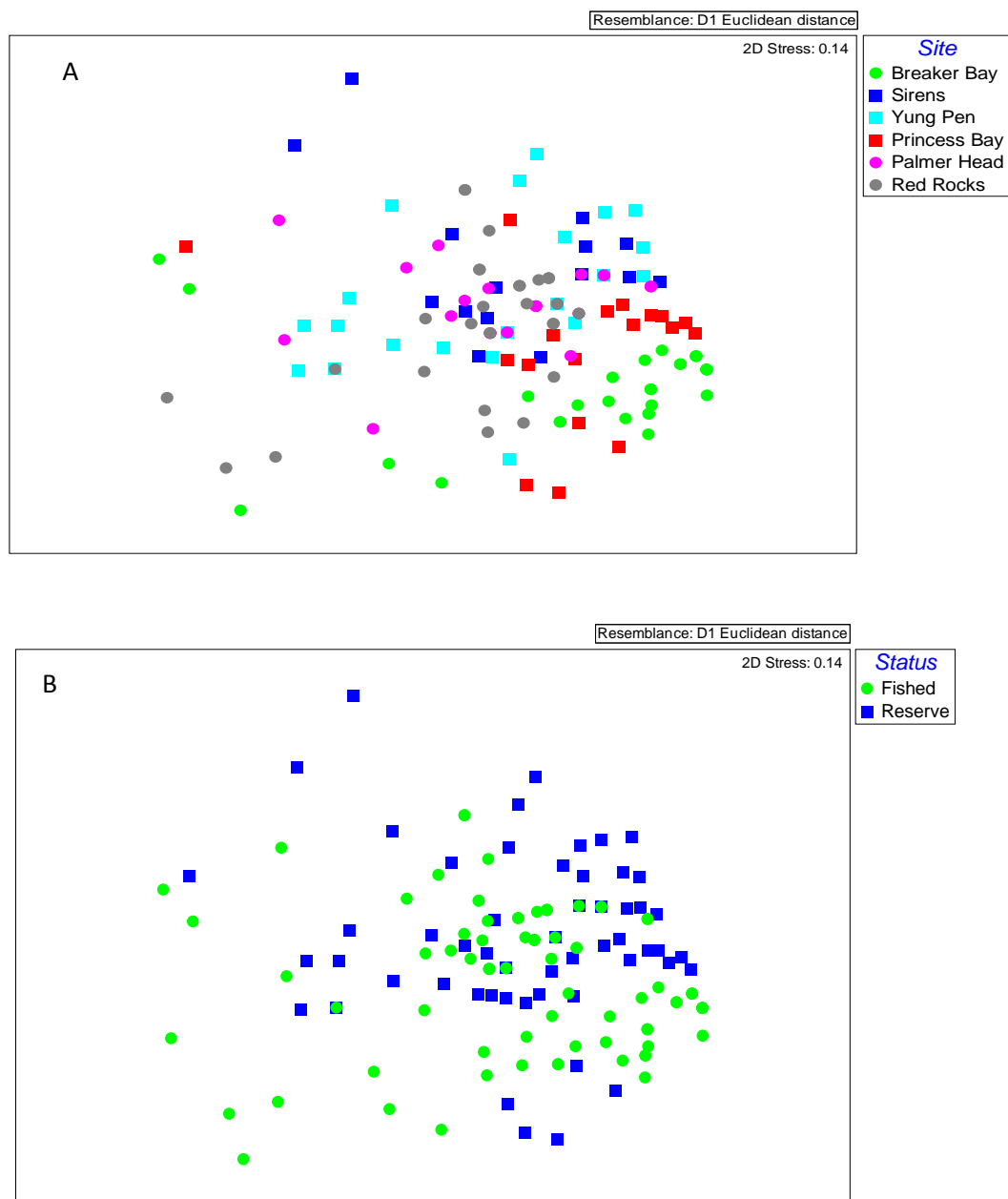


Figure 3.9. MDS plot showing the correspondence between subtidal environmental variables and site (A) and status (B).

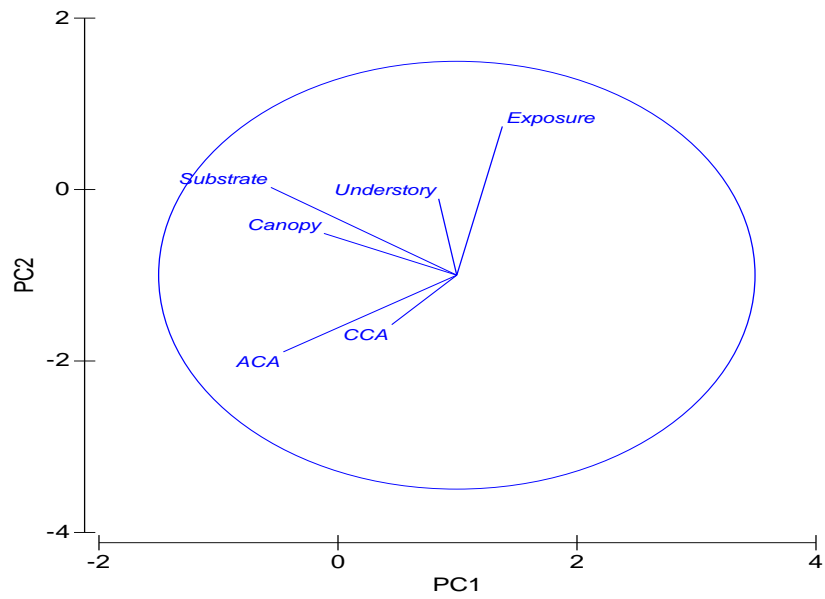


Figure 3.10. PCA plot showing contribution of subtidal habitat variables to environmental composition.

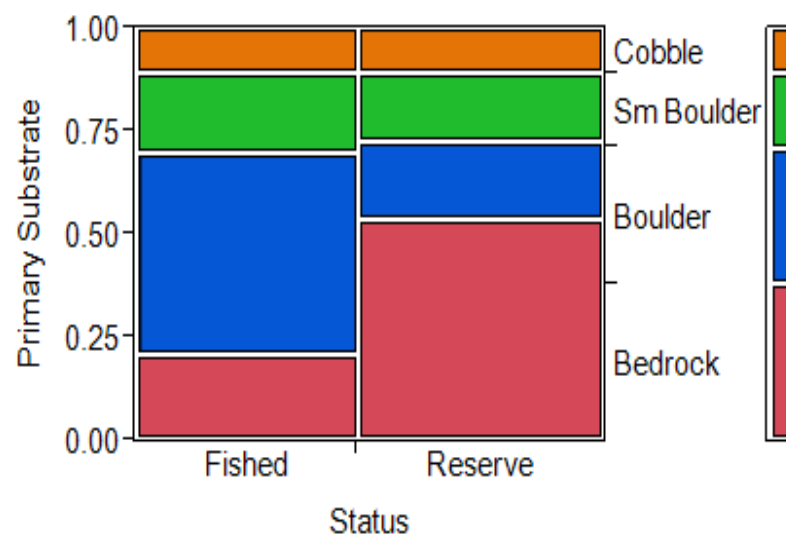


Figure 3.11. Proportion of subtidal primary substratum by status (fished versus reserve). n= 30 quadrats per site, 3 fished sites pooled, 3 reserve sites pooled.

### Subtidal Paua Metrics

Adult paua from subtidal reserves sites were significantly more dense than paua at fished sites (Mann Whitney U Test:  $Z = 4.49$ ,  $p < 0.0001$ , Fig. 3.12). Adult paua within reserve sites were significantly more dense at Sirens than the other two sites, with a density of  $3.2 \text{ m}^{-2}$  (Kruskal-Wallis  $H=2$ ;  $p=0.0001$ , Fig. 3.13). Paua occurred at similar densities at fished sites (Kruskal-Wallis  $H=2$ ;  $p=0.11$ , Fig. 3.13). Only one individual paua was located and measured at Palmer Head (fished site), therefore this site was removed from the length analysis. Paua were significantly larger within reserves sites than within fished sites (ANOVA:  $DF: 1,229$ ,  $F_{155}$ ,  $p < 0.0001$ , Figs. 3.14 & 3.15). Within the reserve 88% of the paua measured were above mean legal size (MLS) of 125mm whereas 42% of the paua measured from the fished sites were above MLS. Adult paua within reserve sites were significantly smaller at Yung Pen (ANOVA,  $DF: 2,164$ ,  $F_{40.16}$ ,  $p < 0.0001$ , Fig. 3.15). Paua at fished sites were not significantly different in mean size (ANOVA:  $DF 1, 61$ ,  $F_{2.20}$ ,  $p=0.1431$ , Fig. 3.15).

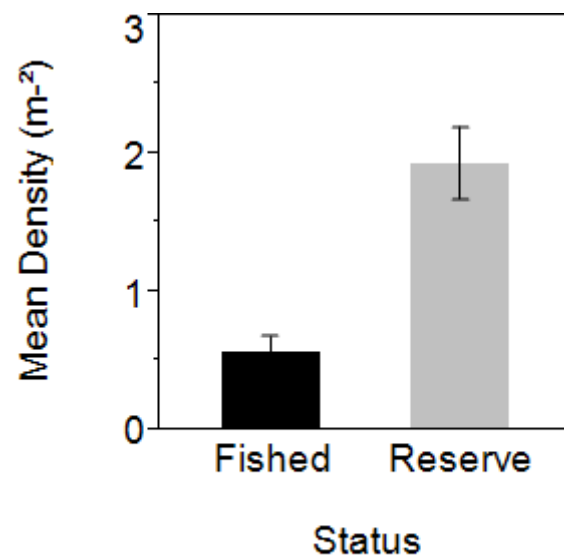


Figure 3.12. Mean ( $\pm$ SE) adult paua density in the subtidal zone as a function of status (fished versus reserve).  $n = 30$  quadrats per site, 3 fished sites pooled, 3 reserve sites pooled.

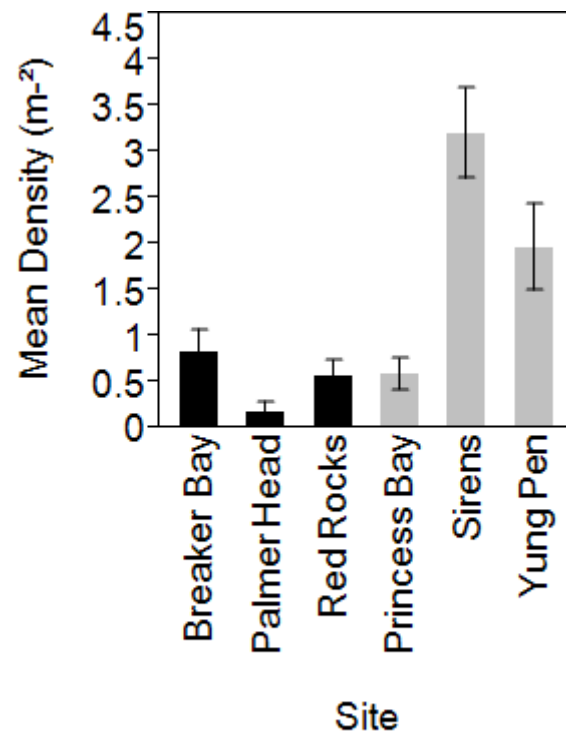


Figure 3.13. Mean ( $\pm$ SE) adult paua density as a function of subtidal site, black bars are fished sites, grey bars are reserve sites.  $n=30$  quadrats per site.

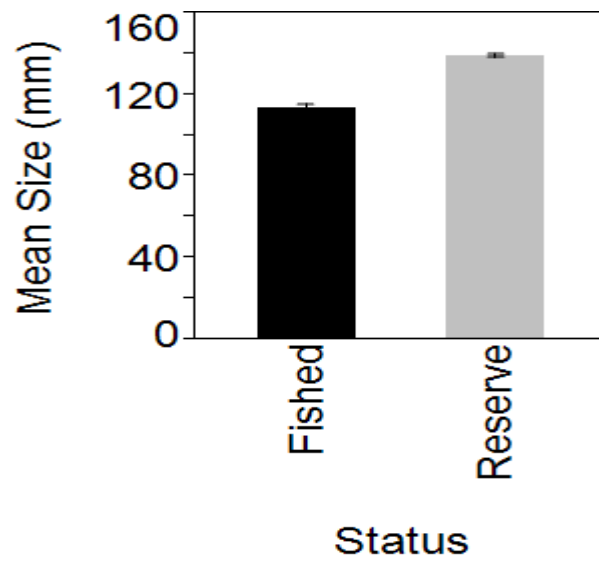
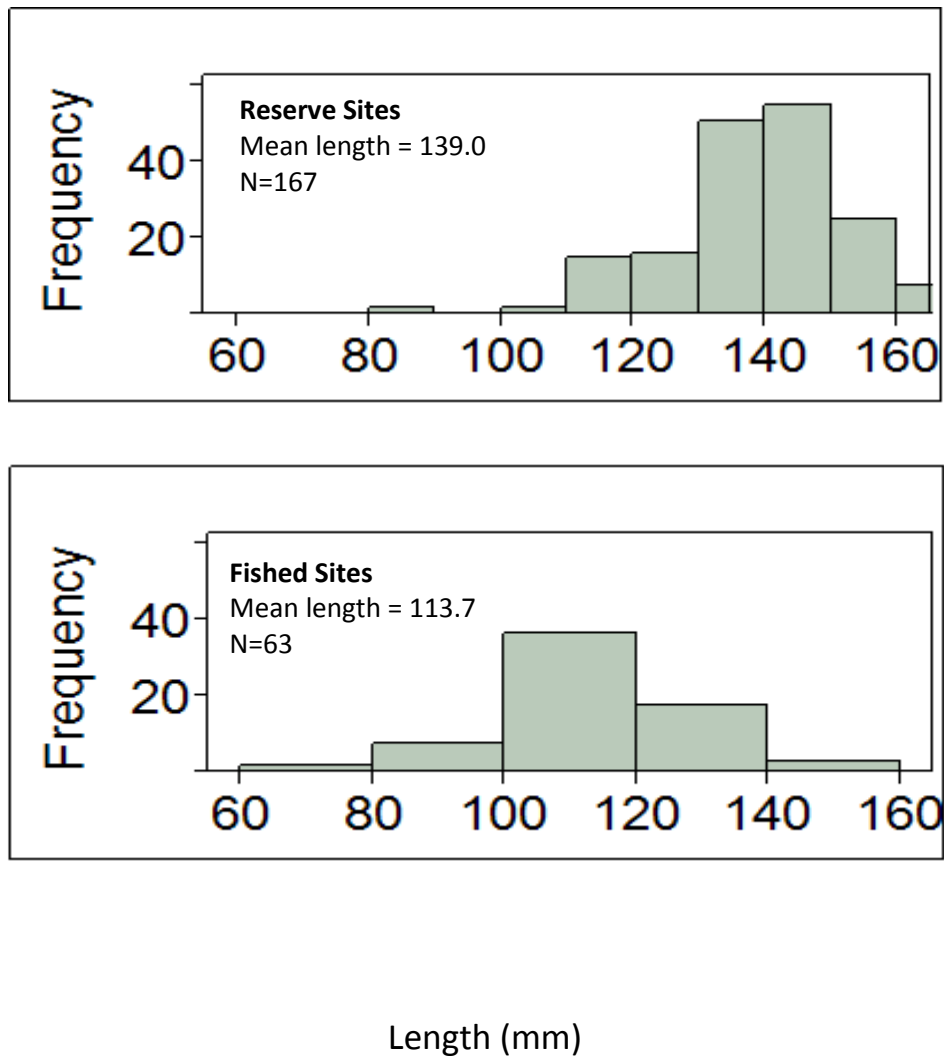


Figure 3.14. Mean ( $\pm$ SE) adult paua size as a function of status. Fished sites pooled,  $n=63$ ; reserve sites pooled  $n=167$ .



**Figure 3.15.** Size-frequency distributions of adult paua at reserve and fished sites based on shell length.

Independent Kruskal-Wallis testing revealed that within fished and reserve sites paua density was not significantly different based on exposure, primary or secondary substratum or any algal variable. However, when all data were pooled regardless of status a significant amount of the variation in density was attributed to bedrock being the primary substratum (Kruskal-Wallis  $H=4$ ,  $p=0.0010$ ).

### 3.4.3 Intertidal versus Subtidal Assessment

Not surprisingly, intertidal and subtidal habitats were significantly different. Intertidal habitats across status were dominated by cobbles and small boulders, whereas subtidal habitat was composed of boulders and bedrock ( $\chi^2$  test,  $p=0.0001$ ). There was significantly more canopy and articulate coralline algae in the subtidal zone and more crustose coralline algae in the intertidal zone ( $\chi^2$  test,  $p=0.001$ ). There was no difference in the amount of understory cover in both zones ( $\chi^2$  test,  $p=0.3278$ ).

Comparison of the relationships between density of paua as a function of zone (intertidal versus subtidal) and status (fished versus reserve) revealed pronounced differences. Juveniles were denser in areas with more cobbles and small boulders at the fished sites than at the reserves sites. Adults were more dense and larger within the reserve than the fished sites and denser at sites with bedrock. This density difference is attributed to a reserve effect. These results reveal contrasting responses of paua density to status and to tidal zone (Fig. 3.16).

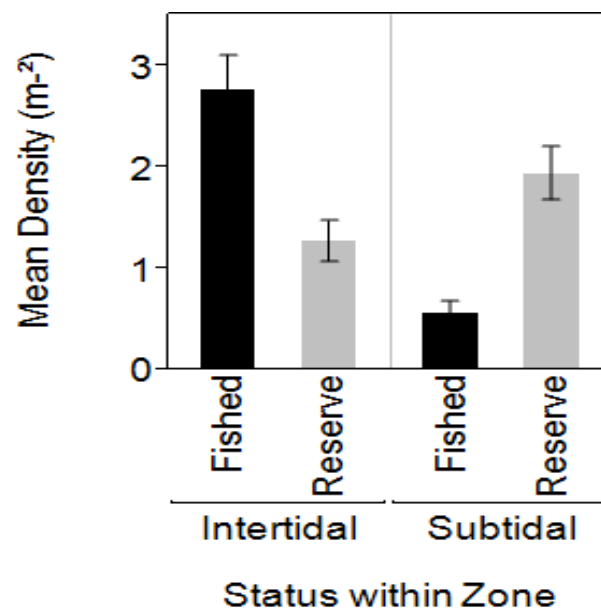


Figure 3.16. Mean ( $\pm$ SE) paua density as a function of status (fished versus reserve, sites pooled) and tidal zone.

### 3.5 Discussion

The many factors that dictate the spatial distributions of an economically important species and also produce large aggregations and individuals are of critical importance to a fishery and ultimately to the conservation of the species. Abalone are an important nearshore fishery around the world and many stocks have been overexploited to the point of collapse (Werner et al. 1995, Rogers-Bennett et al. 2002). Countries striving to rebuild their abalone stocks are utilizing MRs and Marine Protected Areas (MPAs) and are focusing on habitat requirements that support viable adult populations. MRs and MPAs provide opportunity to examine commercially important species in the (theoretical) absence of human disturbance and to investigate what habitats are required to yield large individuals and dense aggregations that are typical of a more natural state.

The goals of this research were to quantify juvenile and adult population densities and examine stage-specific habitat requirements that could then be considered in the context of protection. The surveyed answered if adjacent juvenile and adult populations were correlated and determine habitat requirements for both stages. In New Zealand, this is the first study to examine both ontogenetic stages of paua within the context of MRs; this study also contributes internationally to the paucity of MR research examining commercially valuable abalone at both life history stages.

MR and MPA size and spacing are often designed around protecting the adult organisms of economic and ecological importance. Dense and large individually sized adult populations are needed for reproductive success, however post settlement juvenile success is equally important to the stability of the local population. In this study, juvenile paua occurred in higher densities at fished sites compared to reserve sites. This result can at first seem to be counter intuitive because we might expect higher densities of juveniles adjacent to large adult populations (given the short larval duration and suggestion they are self-recruiting). However, the data suggest this result may be attributed to the pronounced differences in habitat by status. Fished sites were composed of cobbles and small boulders, substratum types that may provide valuable cryptic habitat for the vulnerable juvenile life history stage (Schiel 1993, Aguirre and McNaught 2012). The highest densities of juvenile paua were found at the most sheltered site, consistent with previous reports of higher densities of paua in sheltered bays than exposed areas (Naylor and McShane 2001). The 2013 storm event had the largest impact



on juvenile paua densities at the exposed sites, further confirming that sheltered areas may be a critical component for juvenile stage success. This result is consistent with a study examining survival of juvenile *H.iris* (from a reseeded effort), where the lowest survival was found at sites that were affected by substrate movement during storms (Roberts et al. 2007). Although not quantified, subtidal habitat composition and distribution and adult paua densities appeared to be similar after the storm event, and no substantial mortality was observed (personal observation).

In this study, adult paua were found in greater densities and to be larger in size, within the reserve than outside. Furthermore, a larger percent of paua above MLS were found inside the reserve compared to outside, illustrating the strength of the reserve effect. In the baseline survey, there was no difference in mean paua size based on site but interestingly there were greater densities of paua outside the reserve at the eastern end which was attributed to higher nutrient and algal levels (Pande and Gardner 2009). The present study suggests the successful emigration of sub-adults into the subtidal may have also contributed to greater densities at these sites. Regardless, the sharp contrast before and after reserve establishment in mean density and mean size strongly suggests that the reserve is affording protection. Within reserve sites, the highest densities were found at Sirens, which may be attributed to better habitat and or food supply. Victoria University's Coastal Ecology Laboratory is adjacent to this site and may be an added deterrent to poachers fishing at this specific site within the reserve (although I expect poaching to be rather limited at all sites). Within the reserve the lowest densities were found at Princess Bay (these densities were similar to fished areas), this site is on the reserve boundary where potential illegal take is higher (personal observation). Within fished sites paua densities and sizes were similar and below minimum legal size; given this area is closed to commercial fishing and there is rarely customary take these results are likely due to consistent recreational fishing pressure. This study's findings of greater adult densities and larger individuals within reserve sites are consistent with the literature; that is, for certain species marine reserves do produce populations that are larger and more abundant within their boundaries, the 'reserve effect' (Halpern and Warner 2002, Halpern 2003, Micheli et al. 2004, Pande et al. 2008, Lester et al. 2009, Horta e Costa et al. 2013) and with positive abalone response to MR protection world-

wide (Tegner 1993, Edgar and Barrett 1999, Wallace 1999, Rogers-Bennett et al. 2000, Rogers-Bennett and Pearse 2001, Rogers-Bennett et al. 2002).

Although TMR has large paua aggregations and individuals which may support reproductive success (Dayton et al. 1995), juvenile and adult population densities were not correlated and does not support a discrete stock recruitment relationship. Results from the literature on juvenile adult relationships are conflicting. A Californian study examining four abalone species reported high densities of juveniles adjacent to large adult populations and low densities of juveniles adjacent to low adult densities (Rogers-Bennett et al. 2011). Through a manipulative experiment in Australia, a positive relationship between adults and juveniles has been shown for *H. rubra* (Prince et al. 1988). However, there are also reports of negative correlations, for northern hemisphere species (*H. rufescens* and *H. walallensis*) and southern hemisphere species (*H. iris* and *H. rubra*) populations (Schiel and Breen 1991, Shepherd et al. 1992, Rogers-Bennett et al. 2000). Low juvenile densities are often attributed to low adult densities and recruitment failure (Tegner 1993, Rogers-Bennett et al. 2011). However, larval dispersal and local oceanography may be a driving factor for localized recruitment. Additionally, habitat quantity and quality are suggested to be an important contributing factors to juvenile success and ultimately to productive adult aggregations for multiple abalone species (Tegner 1993, Miner et al. 2006b, Aguirre and McNaught 2012). This research suggests that habitat appears to be more important for juvenile stage success than adjacent productive populations. However, this study would be greatly improved by examining paua larval dispersal, recruitment and local oceanographic processes to assist in quantification of local recruitment processes.

At a global level, fishing pressure has caused dramatic declines of the world's abalone populations (Campbell 2000). In countries where fisheries have collapsed, managers and scientists are utilizing MRs and MPAs targeted specifically for abalone for recovery and rebuilding efforts. Evidence of recruitment failure has been recognized and rebuilding efforts are often focused on broodstock (adult) protection. Managers are considering optimal adult habitat that would support large aggregations of adults when planning and designing protected areas (Lessard and Campbell 2007, Micheli et al. 2008). However, when designing MRs for abalone that have contrasting life histories, designs should include habitat

requirements for both stage which will assist in the successful transition from juveniles to adults.

Results from this study suggest that MR implementation has a positive impact on abalone population dynamics and illustrates the need for MRs to be designed to protect habitats required for juveniles as well. In locations where marine reserves are placed to protect biodiversity and or ecosystems, managers should also consider habitats required for multiple life history stages of all species. In locations where protected areas are utilized as a fisheries management tool they have even more opportunity to design areas with the target species stage specific habitat requirements in mind. The results of this study strongly support and suggest that when designing individual marine reserves or systems, regardless of the goal, (fisheries or biodiversity protection) habitat suitability for the species within is an essential requirement to increase chances of successful protection or recovery. Countries that are striving to rebuild their Haliotid stocks will benefit from this study's results and the recognition of the importance of ontogenetic stage specific habitat requirements for success.

### 3.6 Literature

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## Chapter 4. Habitat related differences in the size structure and growth response of the New Zealand abalone *Haliotis iris*: implications for conservation and fisheries

### 4.1 Abstract

Understanding what dictates growth and ultimately size structure of a species is critical for effective fisheries management. Abalone (Halitoids) are a valuable nearshore fishery in many parts of the world and many stocks have been overexploited to the point of collapse. Size and growth rates of abalone are highly variable on broad and fine spatial scales, yet the underlying mechanism(s) that promote or restrain growth are not well understood. Across abalone species there are occurrences of populations that do not reach their full growth potential, referred to as “stunted” populations. In New Zealand, the abalone, *Haliotis iris*, is the focus of an operating fishery and also has stunted populations in specific areas. It has been suggested that stunted populations result from density-dependent processes, fishing pressure and poor habitat quality. The aim of this study was to quantify and evaluate the effect of density and the contribution of habitat variables on abalone size (shell length) at two spatial scales across two environmental gradients. In the austral summer of 2014, a survey was conducted of habitat type and *H. iris* populations in Tasman Bay and at Long Island Marine Reserve, central New Zealand. To further explore the effect of habitat type on growth a translocation experiment was conducted at Long Island Marine Reserve. The survey determined environmental gradients existed at small (<10 km) and large scales (>80 km) and explained how paua size varied along these gradients. The habitat variables that supported larger sized individuals were consistent across both locations, where paua were significantly larger in areas that were more exposed and with greater algal cover than those at sheltered areas with low algal cover. This result was further confirmed by translocation experiment results, where paua that were translocated from a stunted environment to a normal environment grew significantly more than conspecifics placed at the stunted environment. The habitat association results from both the survey and translocation can be used to assist with fisheries and conservation management decisions in New Zealand, such as considerations for potential translocations and closure areas and may contribute knowledge to other countries that are working to rebuild or sustain economically important abalone fisheries.



## 4.2 Introduction

Understanding what dictates growth and ultimately size structure of an economically important species is critical for effective fisheries management. Abalone, an important nearshore fishery in many areas of the world, exhibit highly variable demography, morphology and growth rates on broad and fine spatial scales (Breen et al. 1982, McShane 1994, McShane and Naylor 1995a, Naylor et al. 2006). Across abalone species there are occurrences of populations that do not reach their full growth potential, referred to as “stunted” populations (Nash 1992, McShane et al. 1994a, Wells and Mulvay 1995). Compared to standard abalone, stunted abalone are smaller, with shorter shells that are higher, wider and thicker (Nash 1995, Saunders et al. 2008). Although this morphological variation is ubiquitous (across species and locations) the underlying mechanism(s) that promote or restrain growth are not well understood. In places with commercial abalone fisheries, such as New Zealand and Australia, it is often debated why abalone at certain locations do not reach Mean Legal Size (MLS). It is commonly suggested that morphological variability in abalone is a phenotypic response to the environment, and to a lesser extent genetic differentiation of discrete populations is suggested to dictate differences in morphology (McShane et al. 1994c, Saunders et al. 2009, Mundy 2010).

In New Zealand (NZ), the abalone, *Haliotis iris*, commonly referred to as the blackfoot paua (hereafter referred to as paua) inhabits intertidal and shallow subtidal rocky reefs and is the focus of important customary, recreational and commercial fisheries. There are specific areas along the North and South Islands of NZ where the paua populations do not reach the minimum legal size (MLS) limit of 125 mm. Genetic research on *H. iris* has found four phylogeographic breaks within New Zealand (Will et al. 2011), but these do not delineate the stunted stocks found in all areas of the country. Finer scale genetic work within Marlborough Sounds, top of the South Island, revealed an absence of population structure from reef to reef up to 6 km and minimal population genetic structure existed up to 300 km (McCowan 2013). Therefore, it has been suggested that density-dependent processes, food availability, habitat and fishing pressure are the main factors dictating growth (McShane and Naylor 1995a, Sasaki and Shepherd 2001, Coates et al. 2013).

Given that abalone form large aggregations it is often hypothesised that growth is density-dependent through interspecific competition for food (McShane and Naylor 1995a, Dixon and Day 2004a). However, the results of research examining density-dependent growth are variable and may be species-specific. Within aquaculture experiments, growth has been shown to be negatively correlated with density for juvenile *H. rubra* and *H. tuberculata* and for adult *H. asinina* (Hunt et al. 1995, Mgaya and Mercer 1995, Capinpin et al. 1999). In field experiments, growth has been shown to be negatively correlated with density for *H. laevis*, whereas in a controlled field experiment where densities were increased, growth was independent of density for *H. iris* (McShane and Naylor 1995a, Dixon and Day 2004a). In a NZ study of *H. iris*, utilizing a “fish-down” experiment (a method where populations are systematically fished to reduce density to examine effects) no effect of reducing density on growth at the “fish-down” sites compared to controls was observed. However, the authors noted that fishing intensity may not have been at a large enough scale to see significant results (Naylor and Andrew 2004). Although there is some evidence for density to negatively affect growth (and this topic warrants further investigation), a robust examination of the contribution of habitat variables is perhaps more important to better understand what is dictating relatively slower growth in these stunted populations. Unlike other abalone species, growth rings are not currently able to be used to measure age for *H. iris* (Naylor et al. 2006, Naylor et al. 2007). Therefore, growth is often measured from mark-recapture methods, where growth is defined as change in size over time. Stunted populations are typically found in dense aggregations on reefs that are protected from wave action (Schiel and Breen 1991, McShane and Naylor 1995a, Naylor et al. 2006). In a study at 34 locations across NZ, focused on collecting paua biometric data for stock assessments, sea surface temperature and relative wave exposure explained a significant amount of variation in mean paua length among areas (McShane et al. 1994c). Within NZ, paua that were translocated over small spatial scales (<200 m) from sheltered bays to exposed headlands grew more than controls placed back into bays (McShane and Naylor 1995a). In these sheltered areas it was postulated that low water movement limits amounts of drift algae which is an important food source to the abalone (i.e., contributes to food limitation), which has been suggested as a possible mechanism underlying the establishment of stunted stocks (Day and Fleming 1992, Shepherd et al. 1992, McShane and Naylor 1995a).

Abalone translocations have been used to examine the effect of density and the contribution of habitat variables on growth, and for enhancing populations (Dixon and Day 2004a, Lessard and Campbell 2007, Mundy 2010, Taniguchi et al. 2013). Typically, such translocations alter density and are not reciprocal, meaning that abalone are translocated in one direction only and to more optimal habitat. Regardless of density alterations, translocating stunted abalone to an area of typical sized abalone results in increased growth rates and suggests that the favourable response in growth is a plastic (phenotypic) response to better quality environment (Emmett and Jamieson 1989, McShane and Naylor 1995a, Dixon and Day 2004a). In an Australian study, where density was kept constant, a reciprocal transplant experiment of *H. rubra* showed that stunted individuals grew faster in non-stunted areas and non-stunted individuals grew slower in stunted areas. This was explained by stunted populations occurring in areas of low food availability and reduced topographic complexity whereas non-stunted populations had more food available and increased topographic complexity (cracks and crevices may collect bits of drift algae better than flat surfaces) (Saunders et al. 2009). These studies, in combination, demonstrate the potential importance of environment in the biological mechanism of abalone stunting.

It is well known that environmental gradients can influence, dictate and limit marine communities and species distributions, and that classification and spatial description of habitat types is essential to the understanding of patterns and processes dictating organism distributions and size structure (Andrew and Mapstone 1987, Underwood et al. 2000). However, environmental variables are often overlooked when fisheries assessments are conducted. (Naylor et al. 2006) showed that demographic variation of paua populations was partially due to an environmental gradient in sea surface temperature, where paua grew faster in areas with colder water. Surveys at Long Island Marine Reserve (MR) have revealed that paua are significantly larger at the northern Cook Strait end of the island versus the southern upper Queen Charlotte Sound end, a mere six kilometres away (Chapter 2, this thesis). A similar pattern is observed in Tasman Bay, where paua typically do not reach MLS in the upper bay near Nelson but have historically supported a commercial fishery at the Cook Strait end of Tasman Bay, a distance of approximately 80 km. These patterns raise an interesting question: in the wild within a narrow temperature band what other environmental gradients may be affecting paua size and that may result in stunted populations?

Although stunted abalone populations occur in several places in the world, very little work has been done to investigate the role of environment on stunting whilst keeping density constant. In NZ, stunted paua do not reach MLS and cannot therefore be fished. As such, stunted paua provide a unique opportunity to examine populations at densities that are closer to the natural situation in the absence of extractive pressure. Furthermore, conducting studies within marine reserves (MRs) enables examination of a commercially important species in the absence of human disturbance and permits investigation of what habitats are required to yield large individuals that are typical of a more natural state. Investigation of stunted populations within the scope of protection may therefore reveal the influence of environment on the plasticity of stunting.

The main goal of this study was to examine the role of physical and biogenic habitat variables on paua size, specifically on stunted populations. The study evaluated the effect of density and the contribution of habitat variables on paua size by conducting an assessment across potential environmental gradients in central New Zealand. To increase robustness of the study and to see if patterns were persistent across locations, the assessment was conducted at two different scales; at a small scale (<10 km) at Long Island MR in the Marlborough Sounds and at a large scale (>80 km) within Tasman Bay (Fig. 4.1). The assessment was designed to test the following hypotheses; 1) Is length of paua a density-dependent response? 2) What habitat variables support larger size paua? 3) Are there environmental gradients at these locations and if so do paua vary across these gradients? Additionally, to test experimentally the effect of changing habitat on growth (change in size over time) a constant density, reciprocal translocation experiment was employed whereby paua from a “stunted” site were translocated to a productive “normal” growth site and *vice versa* within the protection of Long Island MR. I hypothesised that regardless of natal origin, paua would grow more at the normal growth site than the stunted site i.e., they would show a plastic response to the environment. The results from this study will contribute to a greater understanding of the contribution of environmental variation to abalone stunting which will enable an improved management of this important shellfish group.

### 4.3 Methods

Underwater visual surveys (carried out via SCUBA) of paua populations and habitat types were conducted at Long Island MR within the Marlborough Sounds and at sites within Tasman Bay in central New Zealand in the austral summer of 2014 (Fig. 4.1). These locations were chosen because they have similar environmental gradients, although at different spatial scales (Long Island MR is <10 km, Tasman Bay >70 km). These locations sit within New Zealand's PauaMac 3 management area (part of New Zealand's Quota Management System) which is an area that has historically experienced heavy fishing pressure (McShane and Naylor 1995a). A reciprocal translocation experiment was conducted at Long Island MR to investigate the effects of changing habitat type on paua growth (change in size over time). This research would have benefited from studies examining size at maturity, however my permit did not allow any extractive/lethal sampling, which would be required to determine reproductive status.

#### 4.3.1 Study Sites

**Long Island-Kokomohua Marine Reserve** is 6.5 km in length, 619 ha in area and extends approximately 460 m offshore from Long and Kokomohua islands. Long Island is located in Queen Charlotte Sound and is a transition zone between the wave-protected inner Sound and exposed, dynamic Cook Strait. Sites at the wave-protected end are composed of cobble and boulder and are dominated by *Carpophyllum* spp., whereas sites at the more wave-exposed end are composed of large boulders and rocky reef that is dominated by rich multi-species macroalgal habitats (Shears and Babcock 2007, Davidson 2009). Fourteen sites around the island were chosen for sampling, including eight long-term MR monitoring sites (Fig. 4.1).

**Tasman Bay** is a large bay at the north end of New Zealand's South Island. It stretches along 120 km of coastline and is 70 km across at its widest point. This study focused on the eastern side of the Bay, with 14 surveys sites spread from the Boulder Bank north of Nelson, along D'Urville Island out to Stephens Island in the Cook Strait (Fig. 4.1). This area has a range of habitats: the head of the Bay is made up of cobble and boulders with sparse algal habitats, whereas D'Urville Island and the area towards Cook Strait is composed of large boulder fields and rocky reef and it hosts rich multispecies macroalgal stands dominated by *Carpophyllum maschalocarpum* and *Ecklonia radiata* (McShane and Naylor 1995a, Shears and Babcock

2007). Historically, sites on D’Uurville Island have been important for commercial paua fishing (McShane and Naylor 1995a).

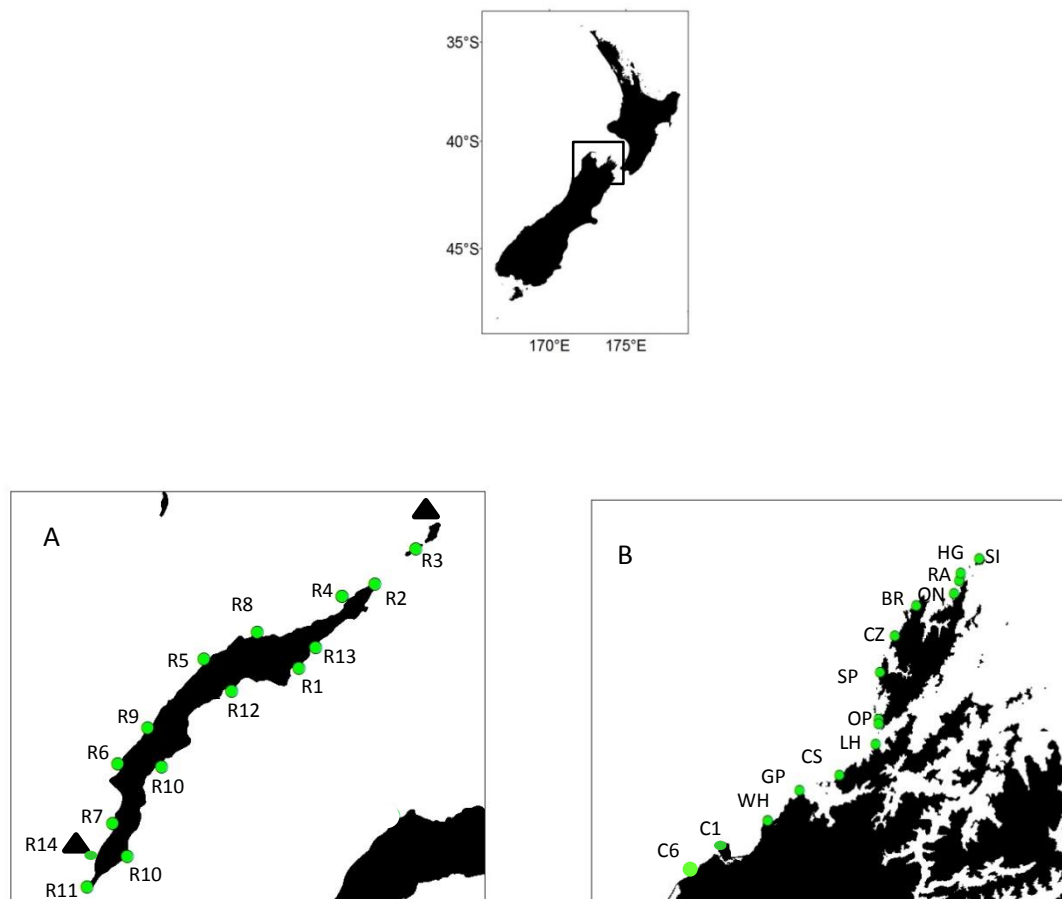


Figure 4.1. Location of study sites. Map of New Zealand with enlarged map of Long Island Marine Reserve (A) and Tasman Bay (B). Solid circles indicate survey sites. Triangles indicate translocation sites at Long Island.

#### 4.3.2 Survey Assessment

At each site, paua density and individual size data were collected by two SCUBA divers in depths of 0-4 m. Divers surveyed in areas of boulder and reef substratum that were approximately 300 m alongshore. One diver haphazardly placed 30 × 1 m<sup>2</sup> quadrats on the substratum and all paua visible inside each quadrat were counted. Boulders were not flipped over to look for cryptic or juvenile paua. The other diver measured (*in situ*) between 60 and 80 paua for maximum shell length to the nearest millimetre using standard or electronic calipers (<http://www.zebra-tech.co.nz>) from the same area as density data were collected. The minimum number of paua sampled was dependent on availability of paua at the site.

Habitat was classified at each site to include exposure level, physical substratum type and biogenic habitat categorical variables. These variables were chosen because they affect the abundance and size of abalone (Andrew and Underwood 1992, Sasaki and Shepherd 2001, Aguirre and McNaught 2012). To compare among sites, relative exposure to prevailing wind and swell was subjectively assessed and defined on a three-point scale: exposed, moderate and sheltered as in McShane et al. (1994). The visual classification system to determine physical and biogenic habitats was designed for rapid visual assessment by SCUBA divers; habitats were categorised visually at each site as the relative amount of cover. The diver (always the author for consistency purposes) visually assessed the site and recorded primary (>50%) and secondary (<50%) physical substrata according to the JNCC and CMCES classification schemes, as outlined in Table 4.1 (Connor et al. 2004, Madden et al. 2009). To further define the physical properties of the area and compare and contrast between sites a physical “reef type” was assigned to the site and is described in Table 4.2.

Algal information was recorded into four functional groups based on height and growth patterns (Steneck and Dethier 1994): (1) Articulated Coralline Algae (ACA), (2) Crustose Coralline Algae (CCA), (3) understory (blades at ≤125 mm height above the substratum) and (4) canopy (blades ≥125 mm height above substratum). Visual estimates of the relative abundance (low 0-30%, moderate 30-70%, high 70-100% cover) of each of the four algal functional groups were recorded for each site. Total algal cover (i.e. the sum of canopy, understory CCA and ACA) was classified into low, moderate or high for each site. One discrete

“algal habitat type” based on a visual assessment of the dominant species or species group was assigned for each site; categories included: *Ecklonia radiata*, *Carpophyllum* spp., “mixed” (includes both *Ecklonia radiata* and *Carpophyllum* spp.), red foliose, understory browns, *Ulva lactuca*, turf and CCA. This simple classification system does not take into account differences in size of individual plants, health, morphology or presence of epiphytes. It does however provide a quick, semi-quantitative and cost efficient index for use in habitat assessment studies. The presence of habitat forming invertebrates such as sponge flats and or mussel beds and the presence of urchin barrens was noted because they have been shown to indirectly and indirectly affect the density of paua. A general visual assessment of vertical relief, based on height was classed as an ordinal categorical variable for each site (1= 0-1 m, 2=1-3 m, 3=3+ m).

**Table 4.1.** Physical substratum descriptors based on JNCC (2004) and CMCES (2009) classification schemes.

Substratum	Definition
<b>Bedrock</b>	Continuous rock
<b>Large Boulder</b>	>512 mm
<b>Small Boulder</b>	256-512 mm
<b>Cobble</b>	64-255 mm
<b>Gravel/Pebble</b>	4-64 mm
<b>Sand</b>	<4 mm

**Table 4.2.** Description of physical reef types classified in this study

Reef Type	Definition
<b>Wall Reef</b>	Vertical continuous rock, often covered in encrusting invertebrates and turf algae with large macroalgal stands
<b>Rocky Reef</b>	Rocky outcroppings, some vertical walls, large areas of continuous bedrock and grey wacke reef and large boulders. A mix of large macroalgal stands and areas of foliose reds & browns
<b>Boulder Reef</b>	Areas mainly composed of small and large boulders, mainly dominated by CCA and turfing algae
<b>Patch Reef</b>	Large boulders and bedrock surrounded by large patches of gravel, shell hash or sand
<b>Cobbles</b>	Reef composed of cobbles, rather unstable to wave exposure



#### 4.3.3 Translocation

The survey assessment revealed distinct differences in paua length between the inner sound and Cook Strait end of Long Island. On 27 & 28 August 2014, a translocation experiment was employed to further explore the differences in length and test experimentally the effect of changing habitat type on growth. Two snorkelers searched for one “normal” and one “stunted” growth site at each end of the island. The “normal” growth site was defined as having paua that had large mean size and typical (normal) shell growth as well as large quantities of macroalgae in exposed areas. The “stunted” site was defined as having paua that had a small mean length with higher shells (atypical growth form), small quantities of macroalgae and was sheltered from wind and prevailing swell (relative to the normal site) that were fairly sheltered. The Department of Conservation allowed the collection of 400 paua per site and mandated that sites needed to be 300 m away from MR monitoring sites. Since initial size is expected to affect incremental growth, paua were collected from a size range of 80-115 mm, to limit or remove the effect of initial size on growth. In total, 668 paua were tagged at Long Island: 400 were tagged from the stunted site and 268 from the normal site. All paua were removed from the water for the translocation process. To minimise stress, all paua were carefully removed from the substrate with a paua hook by experienced commercial paua divers (Kina Scollay and Trevor Robb), transferred into collecting bags (approximately 50 per bag) and held in seawater until all paua from that growth site had been collected. All measuring and tagging was done on board the fishing vessel. Paua were prepared for tagging by gently scraping epibiota off the shell, at the anterior aspect of the high point of the shell (with a butter knife until the shell was showing), and then a small (5 mm) coloured polythene individually numbered tag was glued (“Sellys Quick FIX SUPA GLUE”) to the shell. Tagged paua were then measured manually using electronic calipers, to determine shell length to the nearest 0.5 mm. An apparatus was used to measure shell height from the ventral plane to the highest part of the shell (McShane et al. 1994c). At both sites (normal versus stunted), half were placed back on their natal reef (control) and the other half was translocated to reefs at the reciprocal site. Paua were hand placed on the reef and great care was taken to ensure all paua had a chance to properly attach to the substrate. Tagged paua were visually inspected in situ in November 2014 for tag health (i.e. was the tag readable?) and collected on April 23 & 24, 2015 (eight months after placement) to measure growth, retagged if necessary and placed back into respective treatment sites. Final collection

was conducted on October 10, 2015 (13.5 months after placement) to measure growth and to replaced paua into their respective treatment sites so they can be monitored for growth by the Department of Conservation.

#### 4.3.4 Statistical Analysis

##### **Survey Assessment**

Data analysis was carried out using the software packages JMP, Statistica and Primer. Location (Tasman Bay, Long Island) was treated as fixed a factor and site was treated as a random factor nested within location. Community analysis using the software PRIMER (v.6.1) was employed to test if there were habitat differences between sites within a location (Tasman Bay and Long Island). Habitats consisted of multiple variables, including: primary substratum, secondary substratum, reef type, dominant macroalgal type, combined algal cover and wave exposure. Resemblance matrices for environmental variables based on Euclidean distance were calculated and Multi-Dimensional Scaling (MDS) ordination plots were utilised to examine the spatial relationships of sites based on environmental data. Principle Component Analysis (PCA) was used as an exploratory tool to examine which habitat variables had the greatest effect on structuring the habitat and what variables might be interacting or co-linear. Categorical habitat variables were transformed to an ordinal scale so there was no need to standardise data for PCA analysis. A canonical analysis of principle coordinates (CAP) defines an axis through a “multivariate cloud of points” that has a correlation with a gradient. CAP was utilized to investigate if there was a geographical gradient in the multivariate environmental dataset within Tasman Bay. For this analysis, the general order of sites from outer to inner bay (Stephens Island=1, Hells Gate=2, etc.) was used rather than geographical distance. At Long Island prior analyses on habitat data collected during marine reserve monitoring revealed there was an environmental gradient within Queen Charlotte Sound (Davidson 2009). To examine this existing gradient and include the potential sheltering effect of the island form which may affect habitat types an overall exposure score (regardless of which side of the island or end of the sound) was applied to be used in a CAP analysis.

The response of paua to site, location and habitat variables was compared based on the mean response variables of density (per 1 m<sup>2</sup>) and length (mm) of all sites. Paua density data were highly skewed and contained a great number of zeros making traditional parametric analyses (which assume normality and do not deal with over-dispersion particularly well) unsuitable. As a consequence, non-parametric methods were employed. Kruskal-Wallis tests were employed to test the null hypothesis that there was no difference in mean density or mean length between sites within locations and the Wilcoxon test was used to test for differences in metrics between locations. Non-parametric Kolmogorov-Smirnov tests were employed to examine length frequency distributions by site. Non-parametric Spearman's rank correlation tests were utilized to examine the relationship between paua mean density and paua mean length across all sites at both locations to test the hypothesis that length was not a function of density.

The non-parametric Kruskal-Wallis test was employed to test for significant differences in mean density or length at both locations as a function of each habitat variable category (i.e. to see if paua were more dense on or at certain substrates, reef types, dominant macroalgae species, combined algal cover, exposure or vertical relief). Due to limitations in the data (i.e. not meeting assumptions) it was deemed inappropriate to conduct further analysis such as General Linear Model to examine habitat variables together.

## **Translocation**

Paua shell height data were discarded and not analysed due to inconsistencies in measurement. Amount of encrusting algal growth on the shell and whether the foot was relaxed or not, affected the height of the paua and contributed to measurement error. Due to very low recovery rates during the October 2015 recovery effort these data were not analysed and growth analysis was only conducted on the data collected from the April 2015 recovery period (8 months after placement). Paua have been shown to vary in growth rates dependent on initial size or place in growth history (Shepherd and Hearn 1983, Dixon and Day 2004b). As such, ANOVA was utilized to test for differences in average initial length of paua between study sites. Furthermore, a one-way analysis of covariance (ANCOVA) was utilized to test for the effect of site on growth while controlling for initial length; where growth was

the independent variable, initial length was the covariate and site was the treatment. Given that initial mean length did not vary between sites and paua were at liberty for the same amount of time it was determined that estimates of mean annual growth are biologically more meaningful than von Bertalanffy growth curve estimations (Francis 1988, Hooker et al. 1997, Naylor et al. 2006). The design of the translocation study tested the following predictions: (1) All tagged paua at the normal site would grow more than at the stunted site, (2) within a site paua growth would not differ based on natal origin (i.e. a plastic response), (3) paua from the normal site would grow faster at their natal site than those translocated to the stunted site and (4) paua from the stunted site would grow faster when translocated to the normal site than those placed at their natal site. To test *a priori* planned contrasts, ANOVA and non-parametric Wilcoxon tests (in cases where data did not meet assumptions tests) were utilised.

## 4.4 Results

### 4.4.1 Environment

#### Long Island

The two dimensional MDS plot (with a low stress level of 0.08) is evidence of environmental variability separation based on sites within Long Island (LI) (Fig. 4.2). The PCA plot explained 95.6% of the total variation and showed that secondary substratum, reef type and algal cover were the primary factors that contribute to differences among sites (Fig. 4.3). CAP analysis revealed that an exposure gradient exists along the length of the island ( $\delta^2 = 0.88$ ,  $p = 0.001$ , Fig. 4.4).

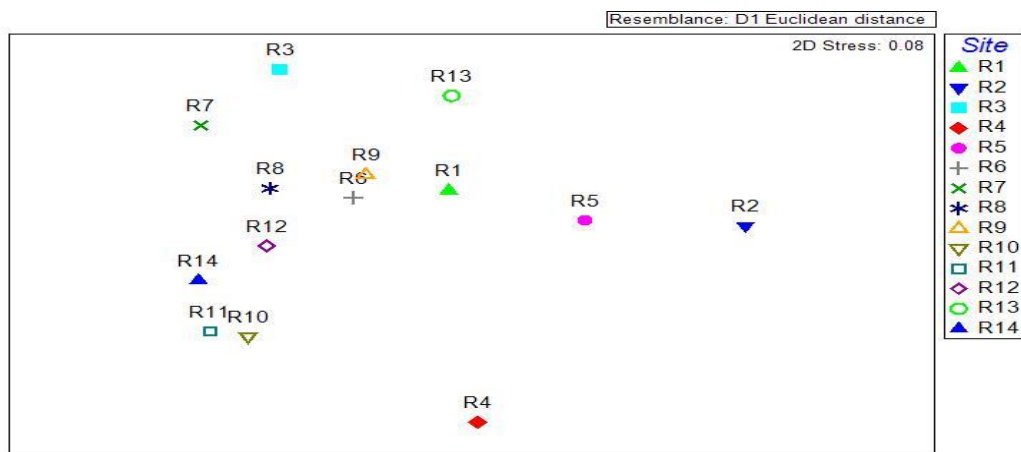


Figure 4.2. MDS plot of multivariate environmental data from sites at Long Island.

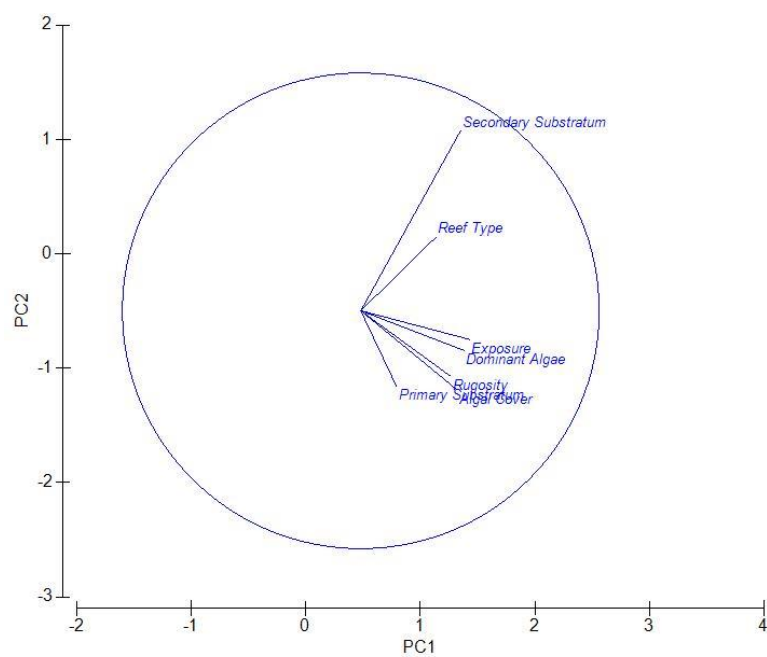


Figure 4.3. PCA plot showing contribution of habitat variables to environmental composition within Long Island.

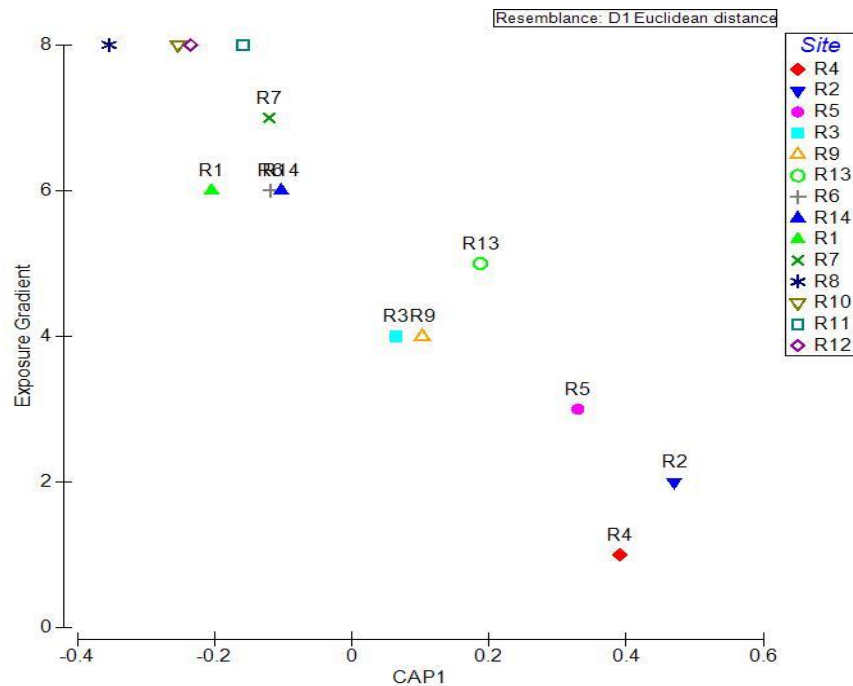


Figure 4.4. CAP plot for sites along an exposure gradient. The sites in the legend coincide with the exposure gradient from most exposed to sheltered.

### Tasman Bay

Evidence of environmental variability separation based on site within Tasman Bay (TB) is shown in the MDS plot with a low stress level of 0.06 (Fig. 4.5). The PCA plot explained 97.1% of the total variation and showed that secondary substratum, algal cover and reef type were the three primary factors and primary substratum, exposure, rugosity and dominant macroalgae were the secondary factors that contributed to differences among sites (Fig. 4.6). CAP analysis revealed that a geographical gradient exists from the outer bay to the inner bay ( $\delta^2=0.92$ ,  $p=0.001$ , Fig. 4.7).

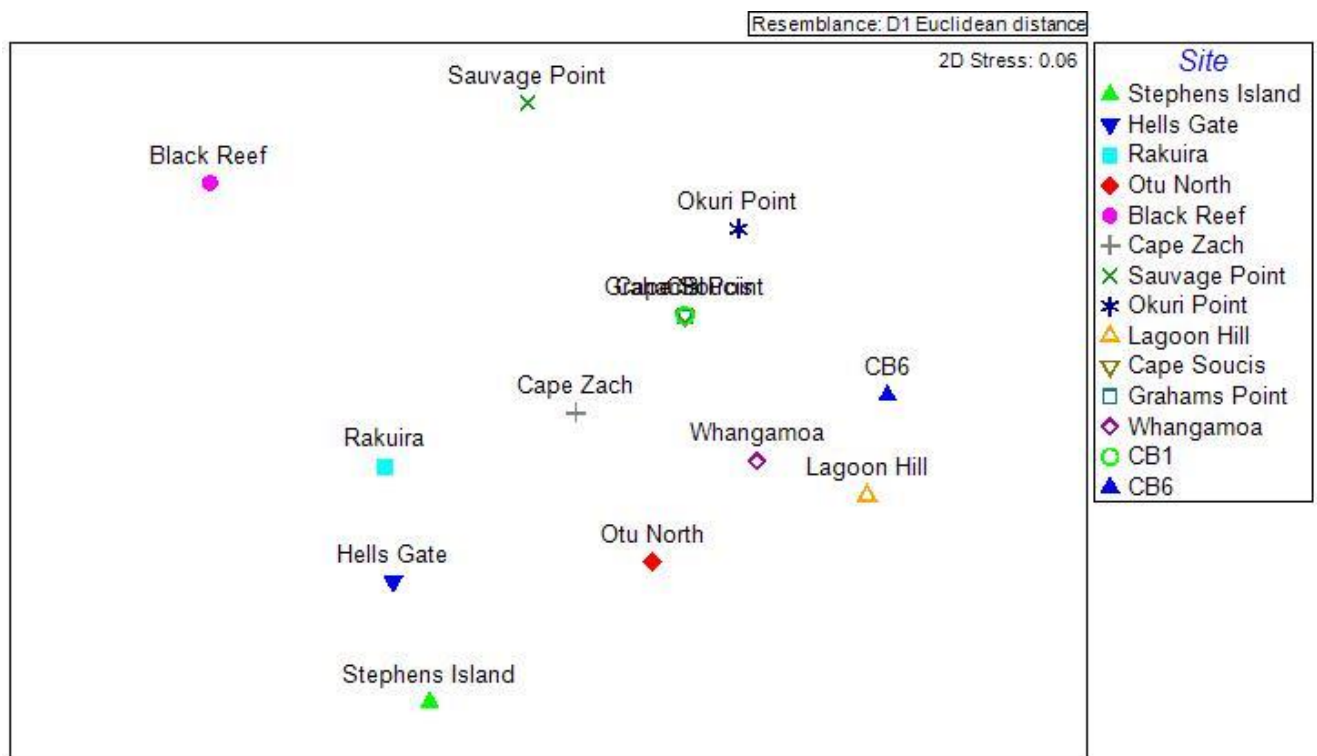


Figure 4.5. MDS plot of multivariate environmental data from sites within Tasman Bay

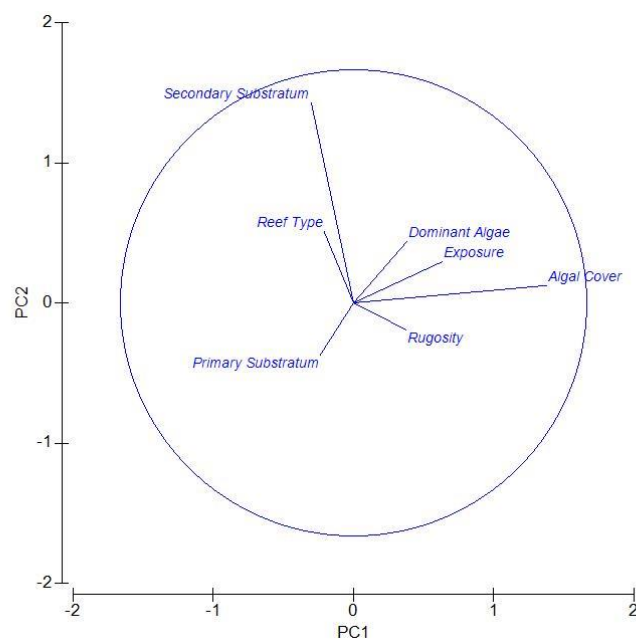


Figure 4.6. PCA plot showing contribution of habitat variables to environmental composition at Tasman Bay.

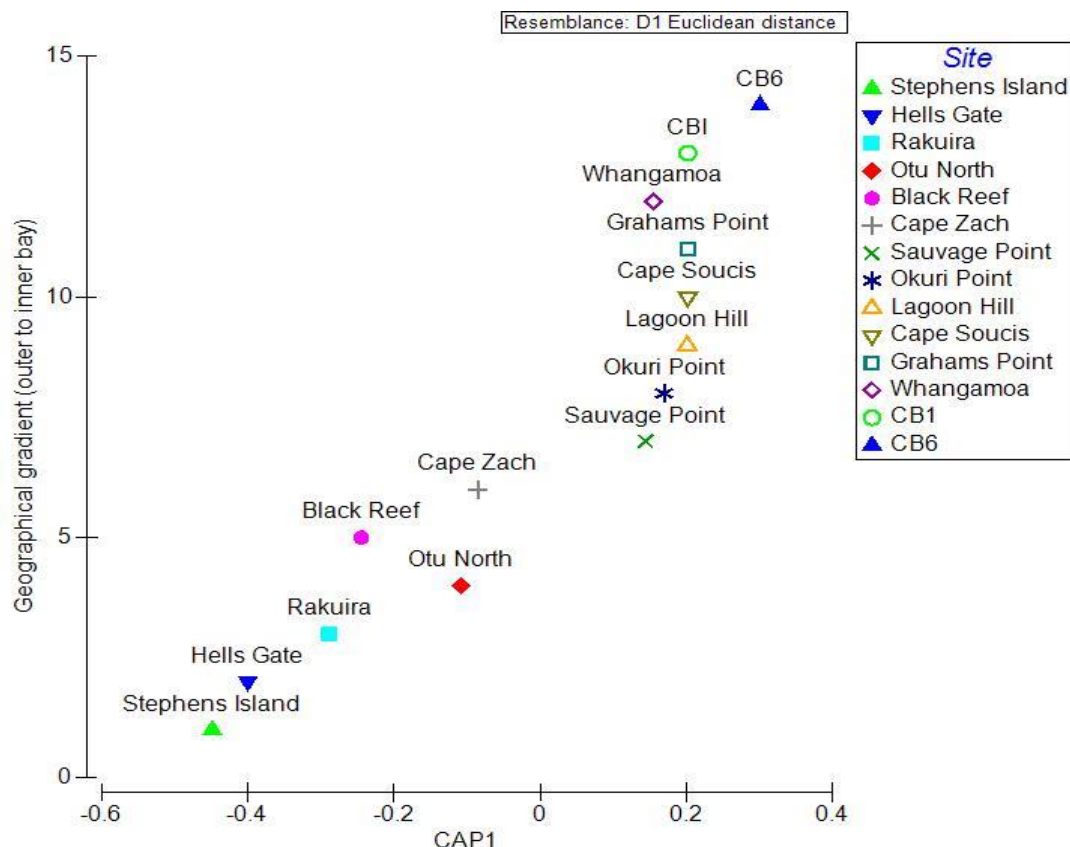


Figure 4.7. CAP plot for sites along a geographical gradient. The order in the legend coincides with the geographical position from outer to inner bay.

#### 4.4.2 Paua Metrics

At both LI and TB mean paua density was significantly different by site (Kruskal-Wallis: LI,  $p < 0.0001$ ; TB,  $p < 0.0001$ ; Figs. 4.8 & 4.9). Although paua densities were not statistically different by location, LI did have higher concentrations of paua than TB (Wilcoxon:  $p = 0.1037$ , Fig. 4.10). Mean paua length was significantly different by site at LI and TB (Kruskal-Wallis: LI,  $p < 0.0001$ ; TB,  $p < 0.0001$ ; Figs. 4.11 & 4.12). Paua were significantly larger at LI than TB (Wilcoxon:  $p < 0.0001$ , Fig. 4.13). Figure 4.14 illustrates the length frequency distributions of paua at both locations and non-parametric Kolmogorov-Smirnov testing revealed that length frequencies were statistically different by location (KS:  $p = 0.001$ ).

To investigate if length is a function of density, non-parametric Spearman's rho correlations were calculated based on mean length and mean density at both locations. There was no correlation between density and length at LI (Spearman correlation,  $p = 0.060$ ). TB exhibited a



significant positive correlation (Spearman correlation,  $p = 0.003$ ), yielding larger paua when density was greater.

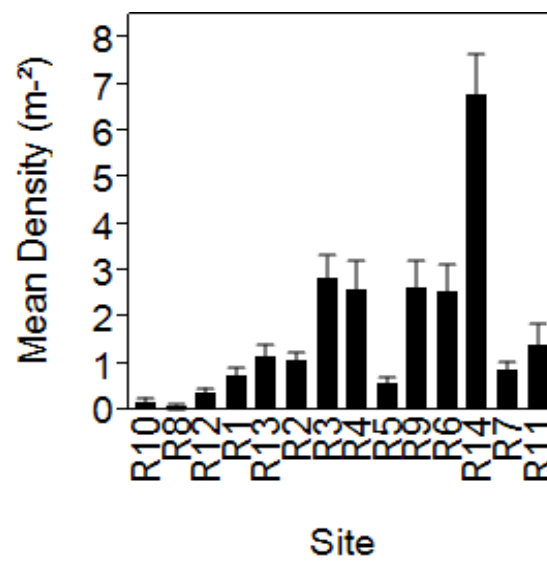


Figure 4.8. Mean ( $\pm$ SE) paua density as a function of site at Long Island. Sites are ordered starting from the southeastern side of the island in a counterclockwise direction (refer to map Fig. 1).  $n=30$  quadrats per site.

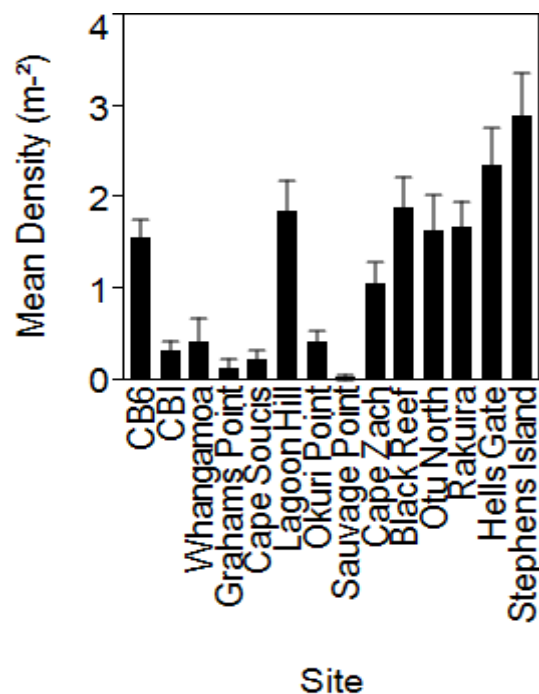


Figure 4.9. Mean ( $\pm$ SE) paua density as a function of site within Tasman Bay.  $n=30$  quadrats per site.

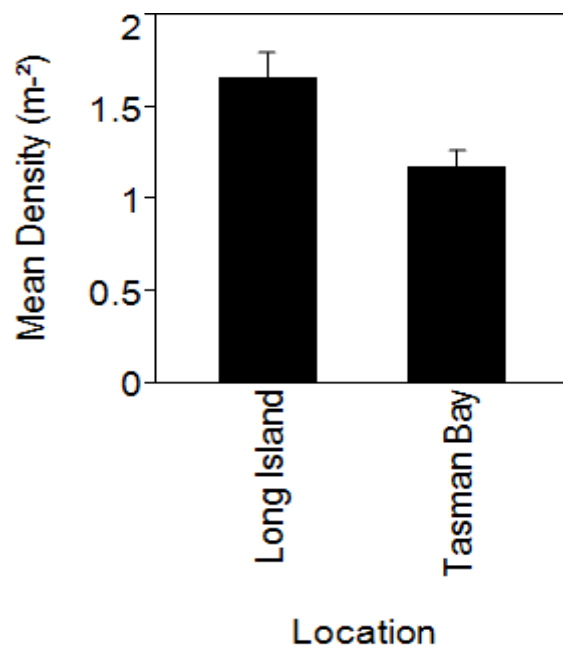


Figure 4.10. Mean ( $\pm$ SE) paua density as a function of location.  $n=14$  sites at each location, 30 quadrats per site.

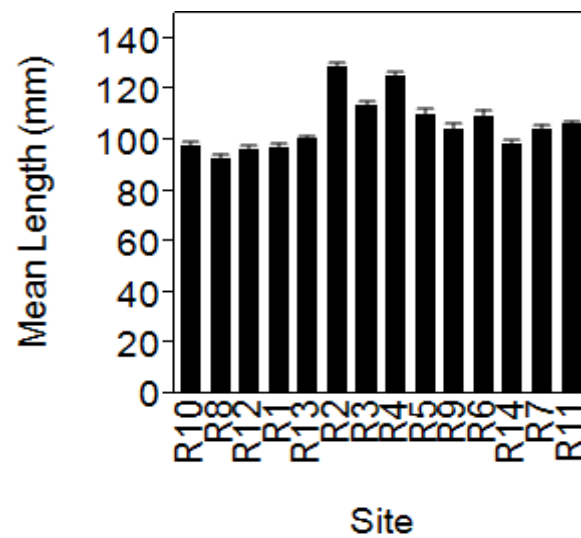


Figure 4.11. Mean ( $\pm$ SE) paua length as a function of site at Long Island. Sites are ordered starting from the southeastern side of the island in a counterclockwise direction (refer to map Fig. 4. 1).

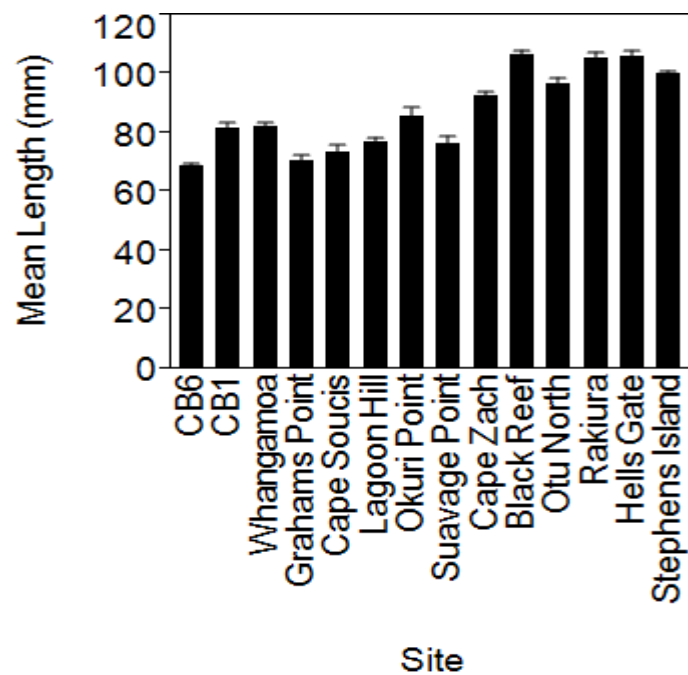


Figure 4.12. Mean ( $\pm$ SE) paua length as a function of site within Tasman Bay.

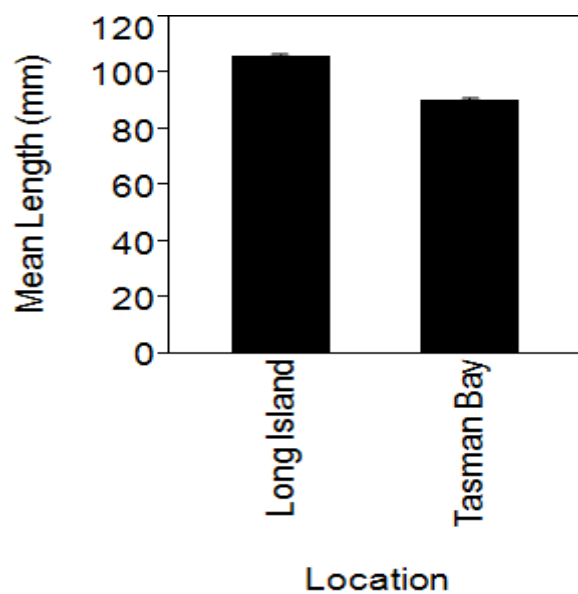


Figure 4.13. Mean ( $\pm$  SE) paua length as a function of location, Long Island  $n=800$ , Tasman Bay  $n= 809$ .

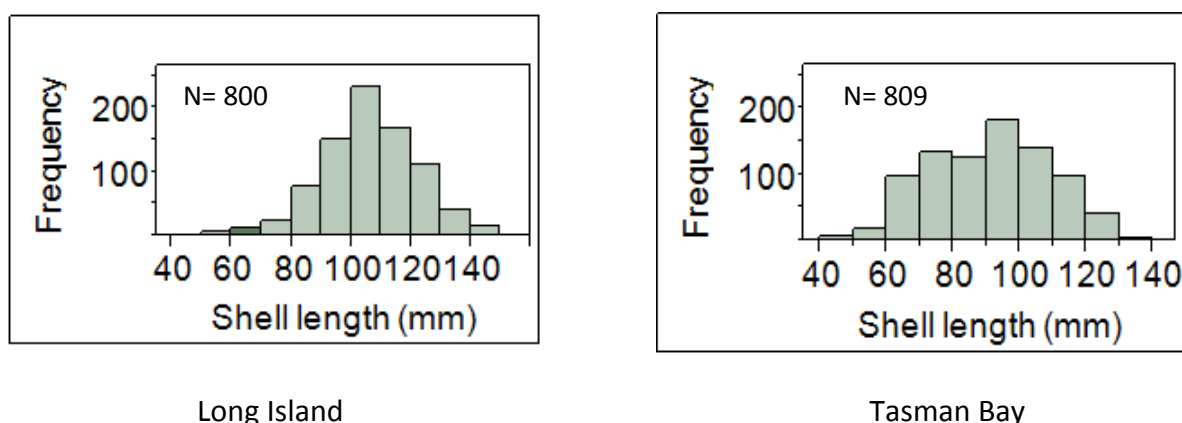


Figure 4.14. Size-frequency distributions of paua at both locations based on shell length (mm).

#### 4.4.3 Paua-Habitat Associations

For both locations non-parametric Kruskal-Wallis tests were employed to test for significant differences in mean density and mean length by each habitat variable category (i.e. to see if paua were more dense or bigger on or in certain substrates, reef type, dominant macroalgae species, combined algal cover and or exposure). Across both locations, paua were significantly more dense at moderately exposed boulder habitats with a high combined algal cover ( $p < 0.0001$  in all cases). Differences between locations were paua were more dense in areas with CCA at LI ( $p < 0.0001$  in all cases) whereas they were more dense in “mixed” algae habitats at TB ( $p = 0.0011$ ). At LI paua were significantly larger in exposed rocky reef sites with high amounts of *Ecklonia radiata* ( $p < 0.0001$  in all cases). Whereas, paua within TB were significantly larger in areas with high cover of “mixed” algae on patch reefs composed of boulders with surrounding sand in exposed areas ( $p < 0.0001$  in all cases).

#### 4.4.4 Translocation

On 27 & 28 August 2014 a total of 668 paua were tagged at Long Island: 400 were tagged from the stunted site and 268 from the normal site. Paua were recovered on April 23 & 24 (8 months after placement), total combined (both treatments) recovery rate at the normal site was 21%, whereas the total combined recovery rate at the stunted site was 6%. Shells were noticeably clean to the point of being polished at the stunted site. Individual treatment numbers and percent recovery are illustrated in Table 4.5. Although these recovery rates are low, they are comparable with other tagging studies for paua within New Zealand (Naylor et al. 2006). Low recovery of tagged paua may be attributed to overgrowth of the tag by crustose

coralline algae, migration of the animals out of the site or into highly cryptic areas of the reef (i.e. paua moved under boulders or ledges). A final recovery effort was made on October 10, but because recovery rates were less than five percent at both sites, these data were not analysed.

Animals recovered (April 2015) and used in analysis did not differ significantly in initial mean shell length by site (ANOVA:  $F=0.1814$ ,  $p=0.6712$ ). However, growth did vary dependent on initial length of the paua, where typically smaller paua grew more than larger paua; this is expected and consistent with the literature (Shepherd and Hearn 1983, Dixon and Day 2004b). ANCOVA testing revealed a significant effect of site on growth after accounting for potential variation in initial length (covariate) (ANCOVA;  $F_{1,86}=29.36$ ,  $p<0.0001$ ). Regardless of natal origin, paua grew significantly more at the normal site than the stunted site (Wilcoxon:  $p<0.0001$ , Fig. 4.15). Within a site paua did not differ in growth based on natal origin (ANOVA: Normal site  $f=0.461$ ,  $p=0.499$ ; Stunted site  $f=0.014$ ,  $p=0.906$ ). Paua from the normal site that were returned to their natal site grew significantly more than paua translocated to the stunted site (ANOVA:  $f=4.67$ ,  $p=0.0393$ , Fig. 4.16). Paua from the stunted site that were returned to their natal site grew significantly less than those translocated to the normal site (Wilcoxon= $0.0001$ , Fig. 4.16).

Table 4.3. Number of tagged paua by treatment, number recovered and percent recovered after eight months at liberty.

Treatment	Code	N Tagged	N Recovered	% Recovered
Normal Control	NC	134	26	19
Normal Translocated	NT	134	4	3
Stunted Control	SC	200	16	8
Stunted Translocated	ST	200	43	22

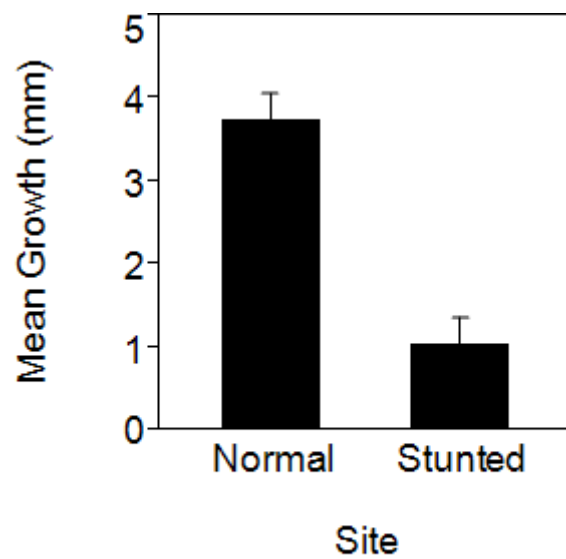


Figure 4.15. Mean ( $\pm$  SE) paau growth as a function of site.

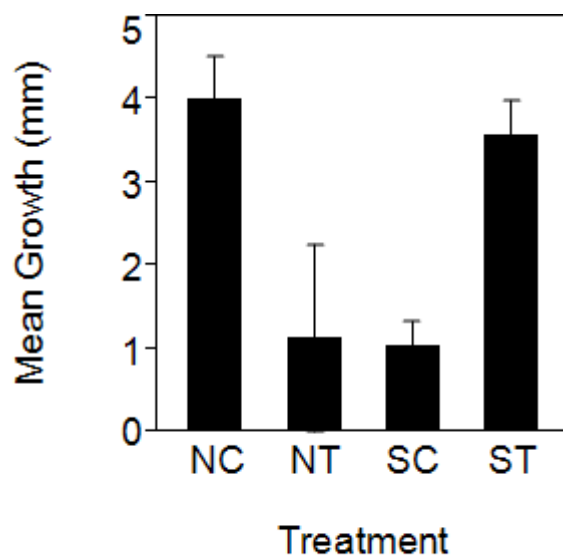


Figure 4.16. Mean ( $\pm$  SE) paau growth as a function of treatment; where NC=Normal Control, NT=Normal Translocated, SC=Stunted Control and ST=Stunted Translocated.

## 4.5 Discussion

Understanding what restrains growth, resulting in stunted populations versus what supports normal growth resulting in “normal” populations of any abalone species is critical for successful fisheries management of the species group. In New Zealand, paua populations support a fishery that is managed through a Quota Management System with a Total Allowable Catch (TAC). The TAC makes allowances for Customary and recreational users and the remainder is for the commercial sector, that tonnage of the TACC is variable dependent on quota management area. Although the fishery is operating (i.e. TAC and TACC are still being allocated based on stock assessment) and may be deemed to be well managed, it still warrants investigation to better understand demographic and size variability and manage populations. The aim of this study was to quantify and evaluate the effect of paua density and the contribution of habitat variables on paua size (growth rate) at two spatial scales across environmental gradients. The survey determined environmental gradients existed at small and large scales and explained how paua size varied along these gradients. The habitat variables which supported larger size individuals were consistent across both locations, where paua were significantly larger in areas that were exposed with high algal cover than those at sheltered areas with low algal cover. This result was further confirmed by translocations experiment results where paua that were translocated from a stunted environment to a normal environment grew significantly more than conspecifics placed at the stunted environment. The habitat association results from both the survey and translocation experiment can be used to assist with fisheries management decisions in New Zealand, such as setting appropriate size limits, considerations for potential translocations and contribute knowledge to other countries that are working to rebuild or sustain economically important abalone fisheries.

Given that majority of paua examined were protected from fishing, either by being under MLS or within a MR (where it is assumed there is no fishing), it provided an opportunity to examine species-habitat associations and demographic processes in a more natural environment with more realistic densities. In addition to habitat, it is often suggested that fishing pressure and density affect size of abalone and should be closely examined. This research suggests that fishing pressure affected size, whereby paua were larger at Long Island MR than at Tasman Bay. In Tasman Bay paua were found to be larger at sites that were more exposed with higher

quantities of algae in the outer bay, however they were still below MLS, suggesting that a combination of habitat variables and potential fishing pressure may be prohibiting paua from obtaining larger sizes. Regardless of location, majority of paua did not reach MLS (except at a few sites at Long Island) suggesting there are other variables contributing to growth than fishing, such as a possible density dependence effect. Given the aggregating nature of abalone one would expect to see intraspecific competition for food (Dixon and Day 2004a, Mundy 2010). Density-length correlations were examined and analyses confirmed that there was no negative correlation between density and length. Based on these results I conclude that density is not limiting length (growth) at either of these locations and suggest that habitat variables and environmental gradients are playing a critical role in length and growth.

Environmental gradients of exposure and algal cover where algal cover was higher in more exposed areas existed at both Long Island and Tasman Bay. Paua size varied as a function of these environmental gradients. Paua were significantly larger at sites in both locations that were exposed with high algal cover, dominated by a mixed macroalgal habitat of *Ecklonia radiata* and *Carpophyllum* spp. The largest paua were found at the most exposed sites at both locations. These findings are consistent with previous research in which a positive relationship between growth and exposure has been reported and that exposure was a significant source of variation in mean length (McShane et al. 1994a, McShane and Naylor 1995a). In addition, *H. iris* individuals from headlands have been found to have higher incremental growth and obtain larger maximum size than individuals in nearby sheltered bays (McShane and Naylor 1995a).

Finding large paua in areas of macroalgal stands, their main food supply is consistent with the literature. For the red abalone (*H. rufescens*) decline in growth was explained by low food availability due to warm water and El Niño events affecting macroalgal growth and small size abalone *H. rubra* were correlated with low algal abundance (Haaker et al. 1998, Tegner et al. 2001, Saunders et al. 2009). It is suggested that variation in paua growth is attributed to type and availability of food and they are thought to prefer drift algae (Sainsbury 1982, Shepherd and Hearn 1983, Day and Fleming 1992, Cornwall et al. 2009). Food availability is affected by density of conspecifics, interspecific competition water movement, algal cover, drift algal supply and substratum. In central NZ, exposed areas are often dominated by dense macroalgal stands, because the grazers are dislodged by turbulence. It has been hypothesised



that a certain amount of water motion is needed to supply food and an increased amount of water movement would increase drift algal supply to the area and also reduce sedimentation which can smother abalone (Sainsbury 1982, Schiel 1990). This research's findings suggest that exposure level and areas with high macroalgal cover may be working in concert to yield large individual paua, potentially indirectly by supplying large amounts of drift algae.

Given that Long Island has been protected for 22 years I assumed that paua size was not confounded by fishing pressure and that paua were responding in a more natural way to their environment than in Tasman Bay where present day fishing pressure still exists and historically was quite high. Furthermore, the variation of paua size across an environmental gradient at such a fine scale as Long Island prompted the translocation experiment. This is the first study (to the best of my knowledge) to conduct a reciprocal translocation of paua in New Zealand and contributes to the one other translocation experiment where density is constant and habitat is investigated (Saunders et al. 2009).

This translocation experiment showed that regardless of natal origin, paua grew more at the normal site than at the stunted site. Additionally, there was no difference in growth based on natal history at the normal site or the stunted site. This positive result in growth at the normal site was attributed to a plastic response to better quality environment. The environment was more suitable for paua growth at the normal site, which was exposed, dominated by high abundance of macroalgal cover whereas the stunted site was sheltered with low algal cover. Higher growth at more exposed sites has been found in New Zealand where *H. iris* individuals from headlands have been found to have higher incremental growth and obtain larger maximum size than individuals in nearby sheltered bays (McShane and Naylor 1995a). It has been shown that biomass is higher for abalone in exposed areas; these areas have increased water flow and turbulence that may break up canopy macroalgae, creating greater amounts of drift algae food supply (McShane and Naylor 1995b, Donovan and Taylor 2008). My results are consistent with Saunders et al. (2009), where they found that small or "stunted" populations were related to low algal cover and topographic simplicity whereas "normal" populations were related to high algal abundance and topographic complexity and attributed this difference to a plastic response in the environment and not abalone history.

Translocation of adult abalone has been suggested and trialled (in Tasmania) as a tool by industry and fisheries managers to develop populations for spawning or for fast growth to support the fishery (Campbell 2000, Mundy 2010, Taniguchi et al. 2013). My results suggest that translocating stunted abalone from poor habitat (sheltered with low algal cover) to areas with more optimal habitat (exposed with high algal cover) will increase growth rates, which may be used as evidence to support translocations for stock enhancement. However, when considering translocations to enhance populations, there must be a surfeit amount of reproductively mature adults, otherwise there is a risk of reducing these populations to the point where they cannot reproduce. Additionally, if translocation is used as a means to increase standing stock for fishing or to protect spawning biomass then other factors such as densities of the stunted populations and juvenile habitat requirements must be taken into account.

Despite the fact that abalone have limited larval dispersal and populations are thought to be mainly self-recruiting (Prince et al. 1987, Nash 1992), the contribution of larvae from stunted populations recruiting into these higher quality habitats and exhibiting normal growth is unknown. These stunted populations, which are reproductively mature, could be an important larval source for normal populations (McShane and Naylor 1995a, Micheli et al. 2008). Therefore if stunted populations were to be targeted for the purpose of translocation, densities of stunted populations need to maintain a critical density to ensure reproductive success (Babcock and Keesing 1999, Miner et al. 2006b). If translocations of stunted populations were conducted to solely increase spawning biomass, then juvenile habitat requirements must be considered for the populations to be successful. Many abalone industries recognize the importance of juvenile populations and have undertaken reseeded projects to support fisheries by placing juvenile paua adjacent to areas that have habitats that support adults. Reseeding is very costly and the success rate is often low; this may be due to the differences in habitat requirements of juveniles and adult abalone (Mundy 2010, Aguirre and McNaught 2012)Chapter 3, this thesis). Therefore, translocation may be a more cost effective method to bolster spawning biomass but juvenile habitat requirements must be taken into account when designing a translocation.

## 4.6 Conclusion

Around the world abalone populations have suffered overexploitation, causing fisheries to collapse in many regions (Wallace 1999). In places where abalone stocks have collapsed much research is focused on what habitats yield dense aggregations and large individuals for reseeded or recovery purposes (Lessard and Campbell 2007, Taniguchi et al. 2013, Donnellan 2015). Results from this study suggest it is equally beneficial to take into account what habitats produce stunted populations as well as normal ones along environmental gradients, to better understand what is promoting or restraining growth. The survey assessment and translocation results strongly suggest that habitat variables of exposure and algal cover are the major contributing factors in abalone size structure and growth and inversely the main driver behind the production of stunted populations. Translocation of stunted abalone to better habitat environments where populations may grow rapidly is appealing and potentially more cost effective. However, scientists need to be thoughtful and consider existing stunted stock densities, habitat requirements of juvenile stages in the translocated environment and short and long term benefits. Albeit these results may support translocations of abalone to enhance populations, more field research needs to be conducted to examine larval dispersal, juvenile and adult habitat requirements, the effect of type and availability of food, and additional translocation experiments in areas with fishing pressure before successful translocations can be conducted.

## 4.7 Literature

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## **Chapter 5. Utilization of Multi-beam and Video Data to Classify Complex Subtidal Habitat to Evaluate Efficacy of Marine Reserves: A Case Study from Taputeranga Marine Reserve, New Zealand.**

### **5.1 Abstract**

With increasing human pressures, marine reserves are now often utilized as a tool to conserve species and habitats. Appropriate placement of MRs highlights the need for accurate physical and biogenic habitat maps for marine spatial management and to improve the evaluation of marine reserves. To produce habitat maps for management purposes the Wellington South Coast (New Zealand) was acoustically surveyed by the National Institute of Water and Atmosphere (NIWA) and these data were utilized for siting the Taputeranga Marine Reserve (TMR), gazetted in 2008. Since TMR designation a quantitative assessment of habitats in and outside the reserve has not been conducted. Furthermore, the mapping has not been ground-truthed i.e., there has been no confirmation of substrates with visual assessment. The main objective of this study was to determine if physical and biogenic habitat quantity and composition are similar in and outside TMR. Maps depicting backscatter from the 2005 acoustic survey were utilized to plan drop camera stations at three sites within the reserve and five sites outside (two on the western side, three on the eastern side). From the 279 usable camera drops video was reviewed and substratum, geomorphology and biogenic habitat types were classified (as per JNCC and CMCES classification scheme) and quantified at all sites. Analysis revealed that habitats in and outside reserve sites were comparable in physical and biogenic habitat quantities and composition, although sites in the reserve had significantly greater topographic relief than sites outside. Further analysis was conducted on only a subset of outside sites revealing pronounced habitat differences between in and outside the reserve, where the western outside sites were significantly more rocky with greater macroalgal cover than the reserve and eastern outside sites. This study, at TMR, illustrates why quantification of habitats is critical when evaluating MRs, shows how choice of control sites can drastically change research outcomes and encourages managers to recognize differences in future quantification.

## 5.2 Introduction

With increasing human pressure, marine reserves (MRs) and marine protected areas (MPAs), spaces where fishing is not allowed or is restricted, are being increasingly utilized as a tool to conserve and protect species and habitats around the world (Micheli et al. 2004, Eddy et al. 2014a). In many countries, MRs are typically set up for a specific group of economically important species, to protect biodiversity or unique habitat (Lubchenco et al. 2003, Jordan et al. 2005, Lester et al. 2009). The majority of MR studies compare species response variables (density, size, biomass) from inside to outside, termed control impact studies (Lubchenco et al. 2003, Micheli et al. 2004, Aburto-Oropeza et al. 2011). Typically, MR studies attribute positive species' responses to reserve status without taking into account or integrating habitat assessments at similar spatial scales (Huntington et al. 2010). However, given the placement of MRs in unique habitat or in areas to protect biodiversity, it is often challenging to assign appropriate control sites with similar physical and biogenic habitats and when habitat is not examined, natural spatial variability in the physical environment may confound a potential 'reserve effect' with a 'habitat effect' (Charton and Ruzafa 1999, García-Charton et al. 2004, Huntington et al. 2010, Eddy et al. 2014a). Despite the knowledge that seascape heterogeneity is a common feature of the marine environment and that all sites are not equal, once MR and control sites are assigned, habitat types are rarely quantitatively analysed which can result in confounding habitat effects (Huntington et al. 2010, Eddy et al. 2014a).

Given the existing pressures on the marine environment and the implementation of protected areas, the need for accurate habitat maps is critical. Mapping the physical seabed at several spatial scales is being utilized to identify and spatially describe habitats and the identification of associated biogenic communities is being increasingly conducted to understand marine ecosystems. In the last decade, habitat maps have been employed as a marine spatial management tool to assist in the designing and siting of MRs and to monitor biological responses due to reserve status (Costello et al. 2006, Leleu et al. 2012, Buhl-Mortensen et al. 2014, Henriques et al. 2014). An improved quantification of the effect of MR designation requires an examination of physical and biogenic habitats at similar spatial scales to distinguish management effects from potential existing habitat differences. Identifying the geomorphology and biogenic habitats of an area are key to understanding species' distributions and ecological interactions. Often areas of high biodiversity are a function of



dynamic and diverse habitat structure and habitat types may be able to be applied as a “surrogate” for species diversity (Lubchenco et al. 2003, Jordan et al. 2005, Lester et al. 2009). For example, in temperate reefs, areas with more complex habitat and higher topographic relief have higher species diversity and higher densities and diversity of reef fishes (Ebeling et al. 1980, Levin and Hay 1996, Willis and Anderson 2003, Jordan et al. 2005). Macroalgal assemblages are often used as habitat descriptors and are, in part, dictated by the underlying substratum, both macroalgal and substratum can be used as surrogates for biodiversity (Patton et al. 1994, Shears et al. 2004, Tuya et al. 2008). Examination of habitat is critically important and it has been shown that detecting differences in target species’ metrics in MR evaluations has been confounded by site-specific differences in habitat (Anderson and Millar 2004, Claudet et al. 2010, Huntington et al. 2010).

In New Zealand (NZ) full no-take MRs are established to protect all species and representative coastal habitats (and to create places for scientific research) (Carter 2005). Examination of habitats with visual surveys via SCUBA is costly, time consuming, provides limited spatial coverage and historically has been secondary to the priority of sampling biological response variables in MR studies. However, in the last decade, the use of acoustics to rapidly examine physical habitats over large spatial extents has been implemented as a tool to map MRs within NZ (Wright et al. 2006, Lamarche and 2015). In 2005, the Wellington South Coast (WSC) on the lower North Island was mapped by the National Institute of Water and Atmosphere (NIWA) with one objective being that data acquired would be utilized for MR design and siting of the Taputeranga Marine Reserve (TMR).

There are however, inherent challenges with mapping habitats via acoustics. Survey equipment cannot always decipher substratum differences to a fine level (e.g., differences between cobble and gravel) or map the extent of boundaries or transition zones which may be important for species’ life history strategies and distributions (Tuya et al. 2008, Malcolm et al. 2010). Importantly, habitat maps need to be validated because they represent spatial depiction of data generated from models using statistical methodologies. This validation is usually done through ground-truthing, either through physical collection of substrates or visual surveys. Additionally, boat-based multibeam surveys are limited by water depth and often leave an area nearshore unmapped, referred to as the “white zone”. The white zone is often a critical area for species because of ontogenetic stage habitat requirements, foraging

and predation avoidance. Drop cameras, which provide an affordable and efficient platform from which to ground-truth acoustic data, are therefore often employed to define boundary habitats and obtain data from the white zone.

Prior to and during the same time frame as the WSC was acoustically surveyed, visual surveys via SCUBA focused on finfish, invertebrate (paua, kina, crayfish) and macroalgal abundances and distributions to establish a baseline prior to reserve establishment. Analyses along the WSC revealed that sites differed in macrobiotic community structure along an environmental gradient from east to west, the authors noted that sites that differed were spatially separated but that physical habitats were fundamentally similar between sites (Pande and Gardner 2009). Another study, prior to reserve establishment, utilizing a drop camera, identified the physical characteristics of the WSC and reported no gradient in substratum type along the WSC (Byfield 2013). A specific study to quantify geomorphology and biogenic habitats to determine quantity and composition within and outside TMR has not been conducted post-establishment of the reserve.

The objectives of this study were multifaceted, with the primary aim being to determine if habitats inside and outside the reserve were comparable in quantity (spatial extent) and composition. Substratum, geomorphology and biogenic habitat types were quantified at three sites within and five sites outside the reserve to ascertain if habitats were similar. Secondly, the drop camera was utilized as a tool to collect data in areas that the multibeam was not able to survey i.e., in the white zone. Finally, the video collected here was the first to ground-truth and cross validate the multibeam survey, backscatter and subsequent classification scheme conducted by NIWA. A long term objective (although not part of the work discussed in this chapter) is to compare these results with the habitat baseline (Byfield 2013) to assess potential change in habitats due to reserve designation.

## 5.3 Methods

### 5.3.1 Study Area

To quantify habitat types in and outside the Taputeranga Marine Reserve (TMR) and validate the accuracy of habitats from the NIWA multibeam map, video surveys were conducted in the austral summers of 2014 and 2015 at eight sites associated with TMR, WSC, central New Zealand (Fig. 5.1). TMR was gazetted in August 2008, is 855 hectares in area and runs along

12 km of coastline on WSC. The WSC is located on the dynamically active Cook Strait, which experiences strong physical forcing, high winds and wave heights, severe storms and powerful tidal currents (Lewis 1979, Carter et al. 2002). The geomorphology of the WSC is characterized by a highly indented and uneven greywacke reef and the coastline encompasses a large number and diversity of shallow and emerging reefs and nearshore structures (Lewis 1979, Campbell 2008). The nearshore subtidal zone is composed of rugose bedrock reefs, large patches of boulders, cobble fields and areas of gravel and sand (Campbell 2008).

The south coast encompasses a diverse macroalgal community (Choat and Schiel 1982, Shears and Babcock 2007, Nelson 2008). The immediate subtidal zone is composed of large stands of the brown kelps *Carpophyllum maschalocarpum* and *Carpophyllum flexuosum*, whereas deeper areas are dominated by *Ecklonia radiata* and *Lessonia variegata* (Shears and Babcock 2007, Byfield 2013). The subtidal zone (0-30 m) is composed of a diverse understory of red algae and the green algae *Ulva* spp. and *Caulerpa* spp. (Shears and Babcock 2007). Crustose coralline algae form the dominant cover, interspersed with turf algae. Diverse assemblages of encrusting and globular sponges are also an important component of the benthic community (Berman and Bell 2010).

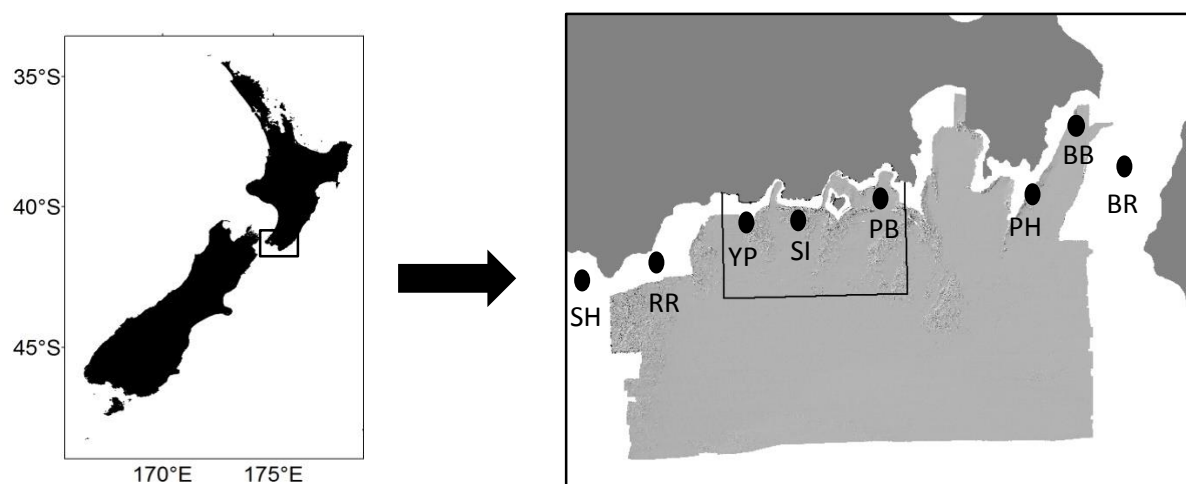


Figure 5.1. Location of study sites. Map of New Zealand with enlarged map of Wellington South Coast. Solid black line in right hand panel indicates Taputeranga Marine Reserve boundary. Solid circles indicate study sites: SH (Sinclair Head), RR (Red Rocks), YP (Yung Pen), SI (Sirens), PB (Princess Bay), PH (Palmer Head), BR (Barrett Reef), BB (Breaker Bay).

### 5.3.2 Video Data Collection and Review

At each site, nearshore areas (0-15 m) that have been used for MR monitoring and directly adjacent deeper water (15-30 m) were identified on a map for drop camera sampling. Utilizing ARCGIS v 10.2 and National Park Service Alaskapak v 2.2 software programs, these areas were encircled with polygons and fifty random points were generated within each polygon. The drop camera used was a simple autonomous underwater video system designed and built for use in high topographic relief rocky habitats. The drop camera is composed of an aluminium circular frame, paired lasers, and a Go-Pro 3.5 Hero camera in underwater housing which collects high definition video. The drop camera was deployed at each sample station and video was collected for 120 seconds, which was sufficient time for sediment to settle after the camera reached the substratum and for surge to dislodge macroalgae covering the view. The camera was downward facing and positioned 0.5 m above the substratum. Latitude, longitude and water depth were recorded at each video lander sample location.

Following the field work, videos were reviewed in the laboratory and habitat was classified for each sample (video drop) to include substratum type and biogenic habitat categorical variables. The visual classification system to determine substratum and biogenic habitats was designed for rapid visual assessment by SCUBA divers for other components of my PhD research and is used here to be consistent with my other thesis chapters. Habitats were categorized visually for each sample as the relative amount of cover. The video was visually assessed for each drop: primary (>50%) and secondary (<50%) physical substrata (when present) were recorded according to the JNCC and CMCES classification schemes (Connor et al. 2004, Madden et al. 2009), as outlined in Table 5.1. Although the New Zealand Marine Habitat Classification Scheme (NZMHCS) developed for the purpose of classifying habitat from drop camera footage was not finished at the time of my research, the classification scheme used here is aligned with this new scheme (I discussed and advised the author on its development (Dohner 2013). It is important to note that video samples classified were based on what was observed not what was inferred, following advice from NIWA biologists (e.g. there may have been algae in sand, suggesting hard bottom underneath the sand but this could not be confirmed from visual assessment). To further define the physical properties of the sample a physical “reef type” was assigned, as described in Table 5.2. (vertical continuous rock was identified on the descent and ascent of the camera). Topographic vertical relief was

visually assessed based on height on the camera's descent and ascent, and was classed as an ordinal categorical variable for each drop (1=0-1 m, 2=1-3 m, 3=3+ m).

Algal type information was recorded into four functional groups based on height and growth patterns (Steneck and Dethier 1994): (1) Articulated Coralline Algae (ACA), (2) Crustose Coralline Algae (CCA), (3) understory (blades at  $\leq 125$  mm height above the substratum) and (4) canopy (blades  $\geq 125$  mm height above substratum). Visual estimates of the relative abundance (none 0%, sparse 1-30%, moderate 31-70%, dense 71-100% cover) of each of the four algal functional groups were recorded for each drop. This simple classification system does not take into account differences in size of individual plants, health, morphology or presence of epiphytes. It does however, provide a quick, semi-quantitative and cost efficient index for use in habitat assessment studies. The sample was categorized as either colonized or not and the presence of habitat forming invertebrates such as sponges was recorded.

Table 5.1. Physical substratum descriptors based on JNCC (2004) and CMCES (2009) classification schemes.

Substratum	Definition
<b>Bedrock</b>	Continuous rock
<b>Large Boulder</b>	>512 mm
<b>Small Boulder</b>	256-512 mm
<b>Cobble</b>	64-255 mm
<b>Gravel/Pebble</b>	4-64 mm
<b>Sand</b>	<4 mm

Table 5.2. Description of physical reef types classified in this study.

Reef Type	Definition
<b>Wall Reef</b>	Vertical continuous rock, often covered in encrusting invertebrates and turf algae with large macroalgal stands
<b>Rocky Reef</b>	Rocky outcroppings, some vertical walls, large areas of continuous bedrock and grey wacke reef and large boulders. A mix of large macroalgal stands and areas of foliose reds & browns
<b>Boulder Reef</b>	Areas mainly composed of small and large boulders, mainly dominated by CCA and turfing algae
<b>Patch Reef</b>	Large boulders and bedrock surrounded by large patches of gravel, shell hash or sand
<b>Cobbles</b>	Reef composed of cobbles, rather unstable to wave exposure
<b>Sand/Gravel</b>	Sand and Gravel, unstable to wave exposure
<b>UCRR</b>	Unconsolidated (sand, gravel, cobbles) over rocky reef

### 5.3.3 Analysis

The habitat maps were developed from multibeam echosounder (MBES) survey data collected by NIWA using a Kongsberg EM3000D MBES. The data were processed by NIWA using Caris HIPS software generating a Digital Elevation Model (DTM) with a grid cell size of 2 m. This DTM was used in ESRI ArcGIS to generate various derivatives for habitat analysis and classification. The backscatter is a secondary signal collected during multibeam surveys and can be used as proxy for substrate type and was the best choice to compare video footage data. Drop camera footage was entered into an Access database and then joined into ESRI ArcGIS version 10.1 for mapping purposes. Primary substratum characterized from the video was visually compared to the backscatter (overlain on “hillshade” to improve the visual effect) to determine if habitat outputs were similar.

Data analysis was carried out using the software packages JmP and STATISTICA. Status (inside vs. outside) and site (Sinclair Head, Red Rocks, Yung Pen, Sirens, Princess Bay, Palmer Head, Barrett Reef, Breaker Bay) nested within status were treated as fixed factors and drop camera sample was treated as a random factor nested within site. Fisher’s exact  $\chi^2$  test of independence and the non-parametric Wilcoxon test were employed to test if habitat types

were different between sites and by status. Habitats consisted of multiple variables, including: primary substratum, secondary substratum, reef type, topographic relief, and relative cover of macroalgae.

Sinclair Head and Red Rocks, the two western-most outside sites, are often difficult sites to access and present strenuous working conditions such as high current and low visibility. Because of these conditions, these two fished sites were sometimes not sampled by researchers during their studies that have examined the impact of the MR. As such, as an exercise to better understand the contribution of these two sites to the overall control (outside) impact (inside the reserve) design, I conducted two additional analyses. In the first analysis (to replicate a common scenario) Sinclair Head and Red Rocks were excluded and eastern sites only were examined whereas in the second analysis both Sinclair Head and Red Rocks were included but the non-reserve sites to the east of TMR were excluded.

## 5.4 Results

In total, 279 usable camera drops were completed in 2.1-27.5 m water depth over 12 days at sea over the austral summers of 2014 and 2015. There were 151 video drops in the white zone and 128 video drops within the multibeam swath. There were 28 to 43 drop camera sample stations conducted per site; variation in number of stations across site was due to weather and sea conditions (Table 5.3). Video drop locations across the eight sites with associated backscatter are depicted in Fig. 5.2. The multibeam swath at the western outside sites did not cover inshore MR associated monitoring areas. Therefore, drops were conducted in shore of the multibeam swath at these sites to keep depths consistent (3-28 m) across all sampling locations. Primary substratum observations made from review of drop camera footage were visually compared with backscatter generated from multibeam survey habitat classification and are shown for western outside sites (Sinclair Head and Red Rocks) (Fig. 5.3), reserve sites (Yung Pen, Sirens and Princess Bay) (Fig. 5.4) and eastern outside sites (Palmer Head, Breaker Bay, Barrett Reef) (Fig. 5.5).

Table 5.3. Drop camera stations conducted at each site.

Site	Drop Camera Stations
Sinclair Head	30
Red Rocks	28
Yung Pen	34
Sirens	39
Princess Bay	37
Palmer Head	36
Barrett Reef	43
Breaker Bay	31



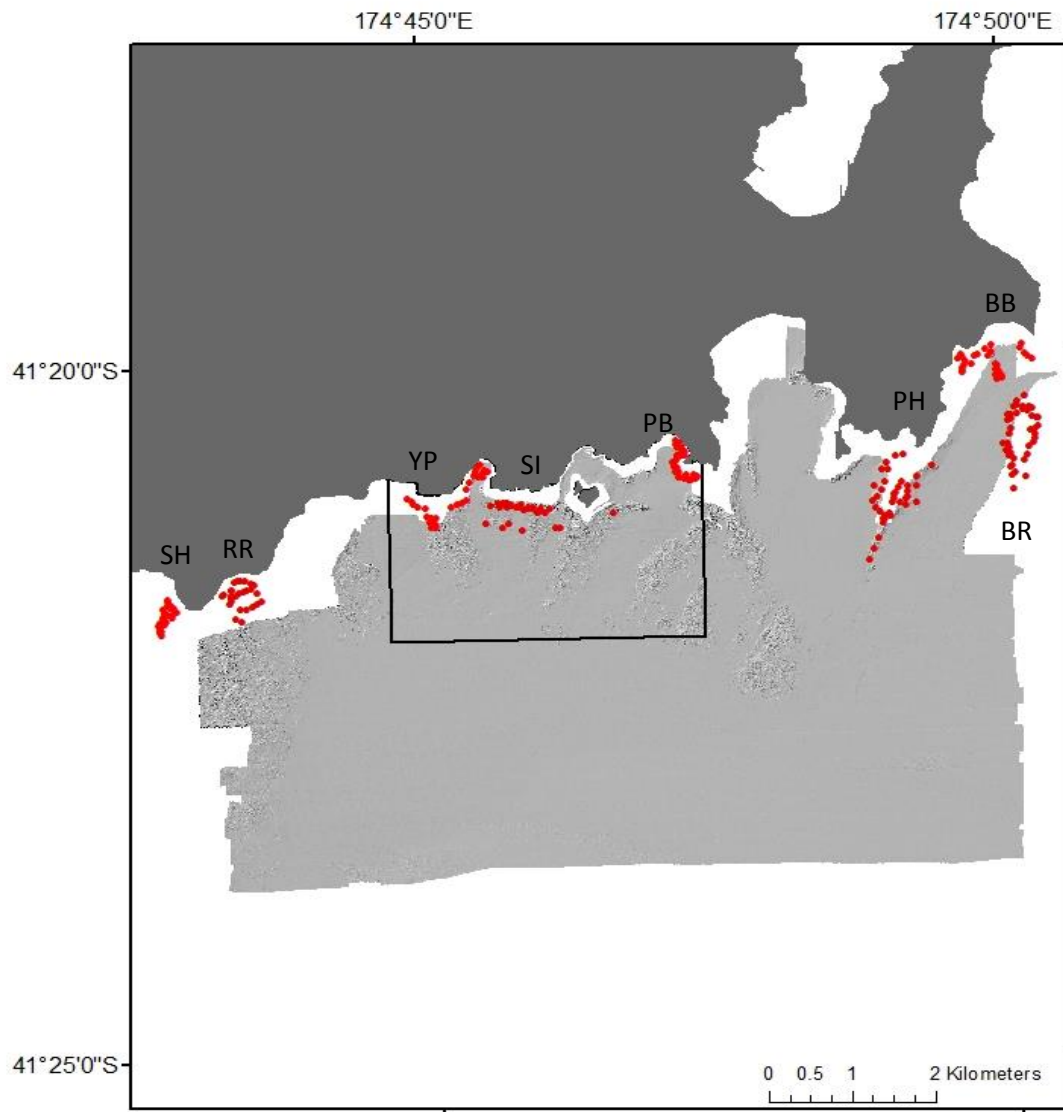


Figure 5.2. Sampling locations depicted by solid red circles within sites: SH (Sinclair Head), RR (Red Rocks), YP (Yung Pen), SI (Sirens), PB (Princess Bay), PH (Palmer Head), BB (Breaker Bay), BR (Barrett Reef). Solid black line indicates Taputeranga Marine Reserve boundary. Backscatter layer generated from the 2005 multibeam survey (Wright et al. 2006).

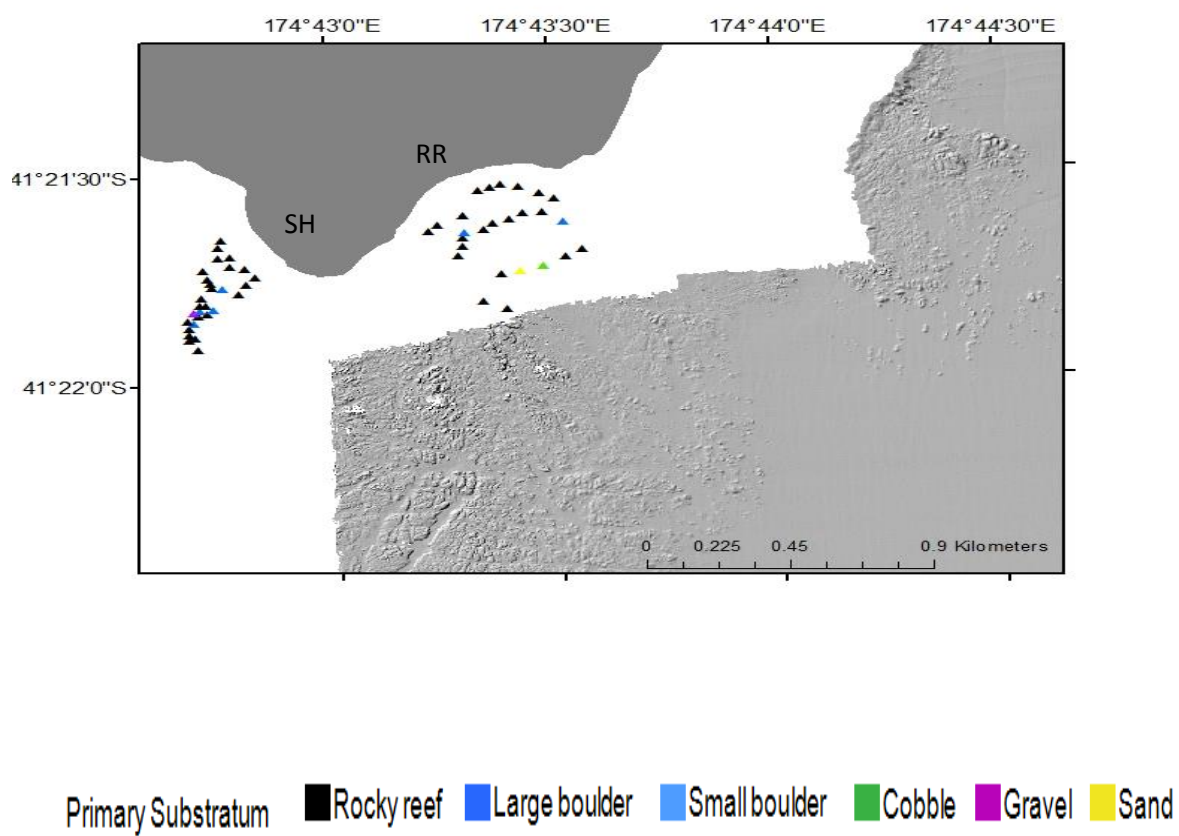
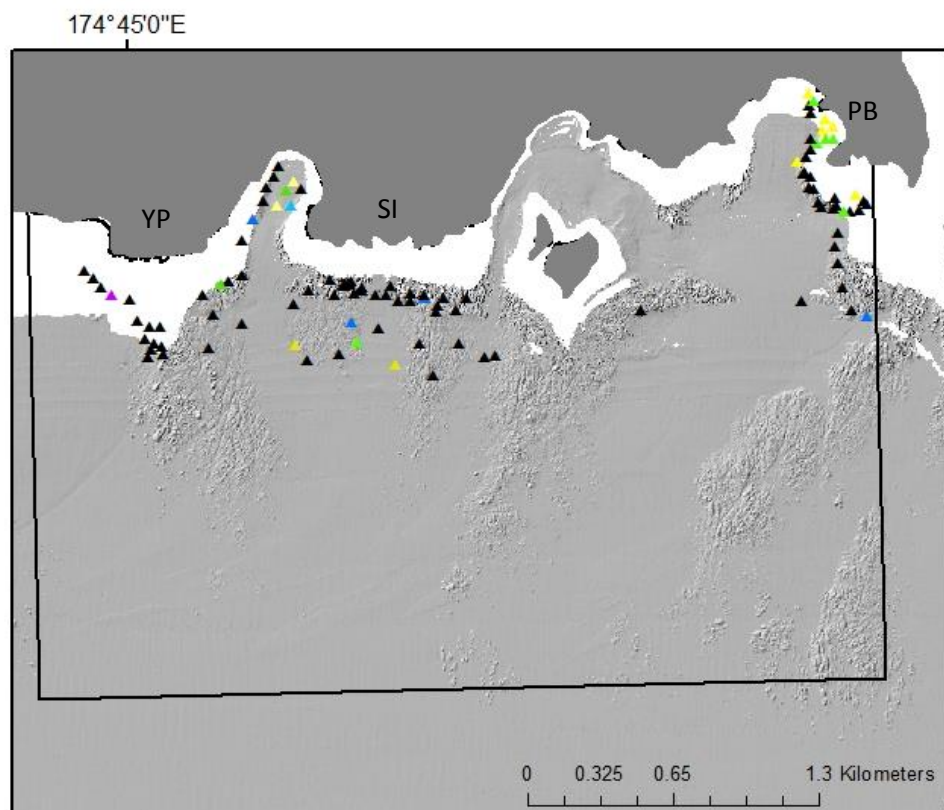
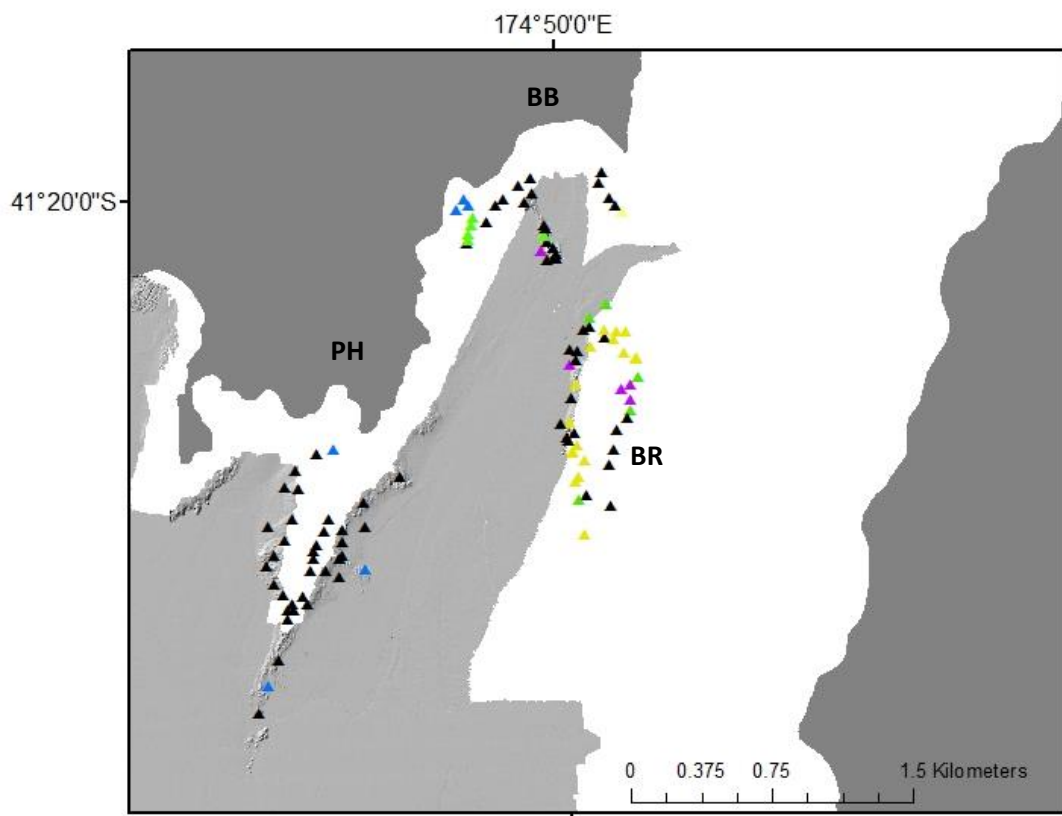


Figure 5.3. Primary substratum at western outside sites Sinclair Head (SH) and Red Rocks (RR). Backscatter layer generated from the 2005 multibeam survey (Wright et al., 2006).



Primary Substratum    ■ Rocky reef   ■ Large boulder   ■ Small boulder   ■ Cobble   ■ Gravel   ■ Sand

Figure 5.4 Primary substratum at reserve sites Yung Pen (YP), Sirens (SI) and Princess Bay (PB). Solid black line denotes Marine Reserve boundary. Backscatter layer generated from the 2005 multibeam survey (Wright et al., 2006).



Primary Substratum    ■ Rocky reef   ■ Large boulder   ■ Small boulder   ■ Cobble   ■ Gravel   ■ Sand

Figure 5.5. Primary substratum at eastern outside sites, Palmer Head (PH), Breaker Bay (BB) and Barrett Reef (BR). Backscatter layer generated from the 2005 multibeam survey (Wright et al. 2006).

Habitat classification from drop camera footage across the eight sites on the WSC revealed that sites were composed of differing physical attributes where primary substratum, secondary substratum and reef type were significantly different by site ( $\chi^2$ : in all cases  $p < 0.0001$ , Fig. 5.6). Primary substratum composition by area is depicted in Figure 5.6. Despite differences between sites, rocky reef was the most abundant habitat type for both primary (72.4%) and secondary (55.2%) substratum across all sites. Sand was the second most frequent primary substratum (12.2%) and large boulder was the second most frequent secondary substratum (12.5%). However, when combining the results of secondary substratum classifications for sand and shell hash (which may be functionally similar for organisms) it summed to 15.8%, which exceeded large boulder cover. Reef type was dominated by rocky reef (53.8%) with the second most frequent reef type being sand gravel cover. Highest percentages were recorded for sand patch reef (6.9%) and cobble patch reef (5.7%). There was a large number of drops where relative cover of understory, turfing and CCA could not be determined and therefore these were removed from the analysis. Relative cover of canopy algae was significantly different between sites ( $\chi^2$ :  $p < 0.0001$ ).

To compare and analyse habitats between outside and reserve sites, data from the five outside sites (Sinclair Head, Red Rocks, Palmer Head, Barrett Reef, Breaker Bay) were combined and data from the three reserve sites (Yung Pen, Sirens, Princess Bay) were combined. Habitat classification comparing the outside versus reserve sites revealed that sites were not significantly different in primary substratum, secondary substratum or reef type (primary substratum  $\chi^2$ :  $p = 0.155$ ; secondary substratum  $\chi^2$ :  $p = 0.398$ ; reef type  $\chi^2$ :  $p = 0.062$ ). Primary substratum composition and reef type for outside versus reserve sites is illustrated in Fig. 5.7 & 5.8. Rocky reef was the most abundant habitat type for both primary and secondary substrata at the outside sites (primary=42.3%, secondary=30.8%) and at the reserve sites (primary=30.1%, secondary=24.4%). Sand was the second most frequent primary substratum at the outside sites (7.2%) and reserve sites (5.0%). Large Boulder was the second most frequent secondary substratum at the outside sites (7.9%) and reserve sites (4.7%). Reef type was dominated by rocky reef at all sites but with notably more at the outside sites (33.7%) than reserves sites (20.1%) with the second most frequent reef type being sand gravel cover. There was considerably more patch reef in the reserve than at the fished sites. Reserve sites had significantly more high relief samples than outside sites and this difference

may be reflected in the presence of wall crevice reef types within the reserve (Wilcoxon:  $p=0.006$ ). Relative cover of canopy algae was not significantly different between reserve and fished sites ( $\chi^2$ :  $p=0.778$ ).

To better understand the differences in habitat composition and distinguish between a reserve effect and a potential confounding habitat effect additional analyses were conducted on a subset of fished sites. Analysis of western outside sites versus reserve sites showed that sites were significantly different by status, with outside sites having significantly rockier reef ( $\chi^2$ :  $p=0.0037$ ) and more canopy algal cover ( $\chi^2$ :  $p=0.0484$ ) than reserve sites (Fig. 5.9). Analysis of eastern outside sites versus reserve sites showed that reserve sites were significantly different from outside sites, where reserves sites were composed of significantly rockier reef primary substratum ( $\chi^2$ :  $p=0.0004$ ) with denser canopy algal habitats ( $\chi^2$ :  $p=0.0022$ ) than outside sites.

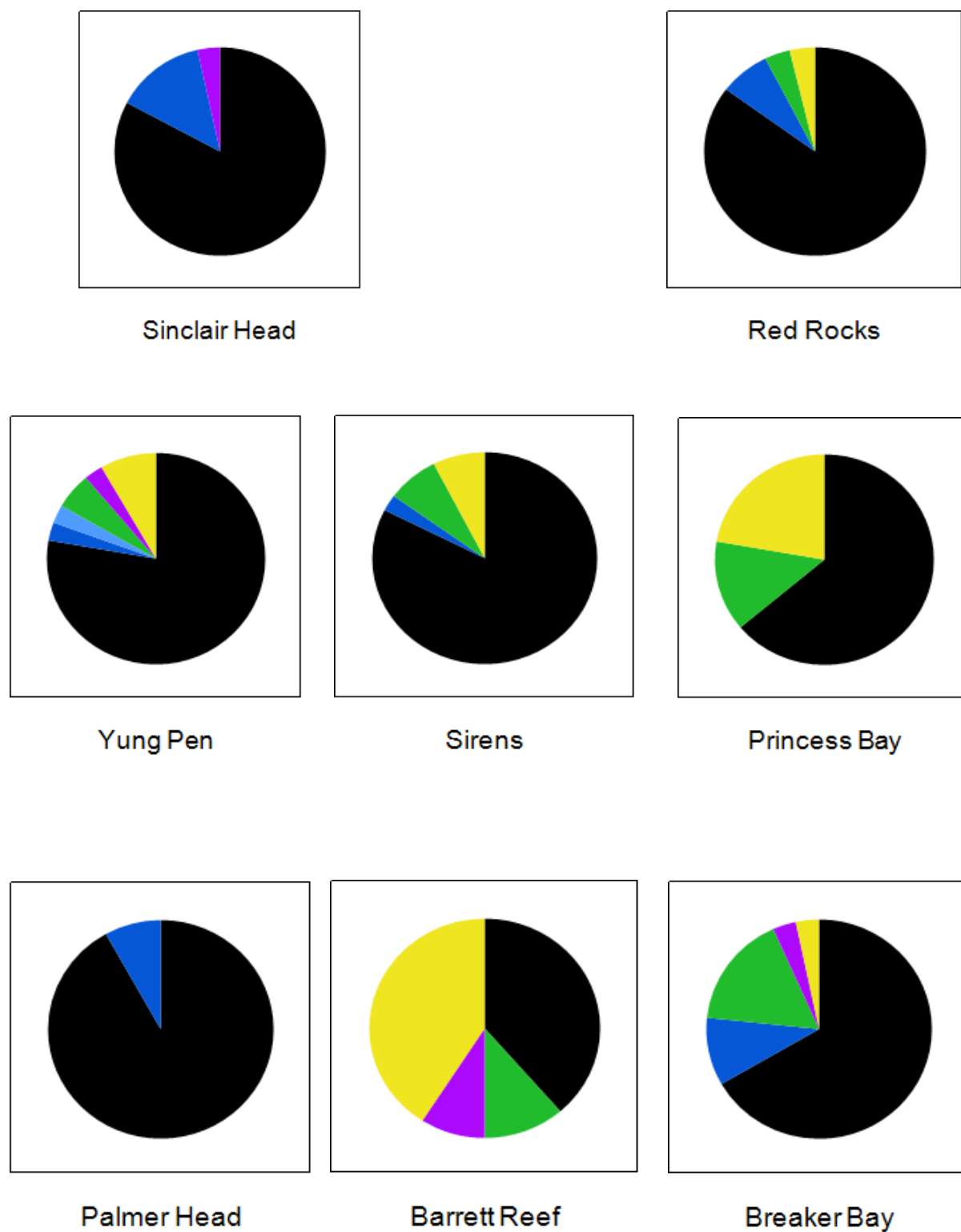
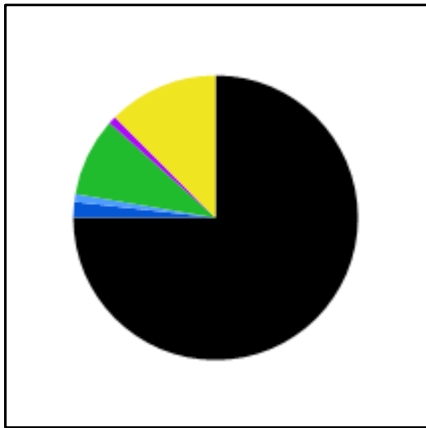
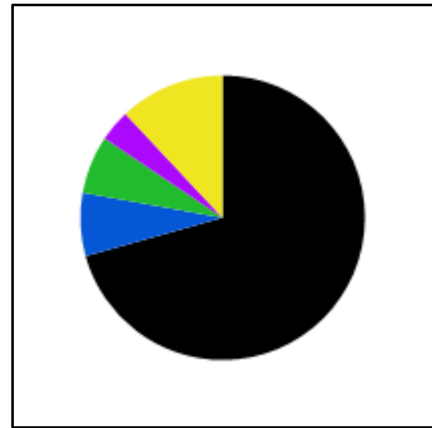


Figure 5.6. Primary substratum composition for each site in order from west to east along the Wellington South Coast.



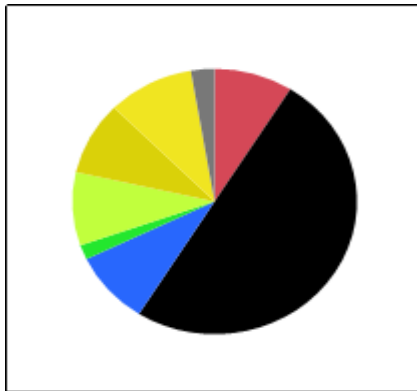
Reserve Sites



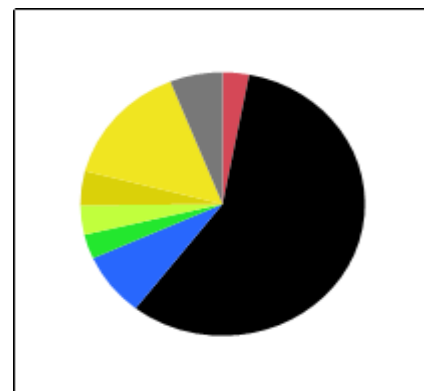
Outside Sites

Primary Substratum    ■ Rocky reef   ■ Large boulder   ■ Small boulder   ■ Cobble   ■ Gravel   ■ Sand

Figure 5.7. Primary substratum composition for reserve and outside sites.



Reserve Sites

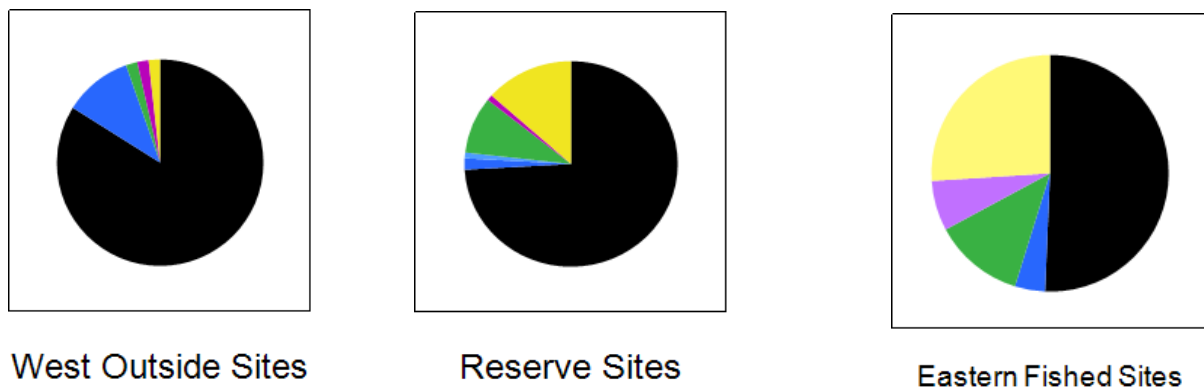


Outside Sites

Reef Type    ■ Wall crevice   ■ Rocky Reef   ■ Boulder Reef   ■ Cobble   ■ Cobble patch reef   ■ Sand patch reef   ■ Sand/gravel   ■ UCRR

Figure 5.8. Reef type for reserve and outside sites.





Primary Substratum    ■ Rocky reef   ■ Large boulder   ■ Small boulder   ■ Cobble   ■ Gravel   ■ Sand

Figure 5.9. Primary substratum at western outside sites, reserves sites and eastern outside sites.

## 5.5 Discussion

Temperate marine nearshore systems are complex and highly variable in regards to reef type, composition and spatial arrangement. As such, habitat mapping (physical and biogenic) is being increasingly utilized as a tool for marine spatial planning and management of many systems. Spatially describing habitats combined with the knowledge of species-habitat associations enables managers to protect habitats that support species groups of interest. Within New Zealand, this is one of the first studies to utilize drop camera footage to ground-truth multibeam surveys and provides a platform from which to design and direct additional ground-truthing exercises at other locations. The work here illustrates the ease and accuracy of drop cameras for ground-truthing methodologies for marine geologists, conservation and fisheries managers. A multidisciplinary approach enabled habitat data collection across an ecological corridor from the shallow nearshore subtidal (white zone) to the deeper transition and reserve boundary habitats. This study collected valuable physical and biogenic habitat

data and highlighted the importance of habitat and control site selection in the quantification and accuracy of marine reserve evaluation.

This research identified which substrate types can be accurately identified from acoustic surveys and which substrate types would benefit from ground-truthing and further investigation using these tools in NZ's temperate system. Visual comparisons of primary substratum between drop camera footage and the backscatter produced from the multibeam survey were consistent and positively identified areas of rocky reef, boulders and sand. The assurance that acoustics can accurately identify spatially differentiated reef structures is very beneficial, where the majority of MR studies are focused on hard bottom areas which support large macroalgal stands, macroinvertebrates and finfish that are the focus of MR monitoring (Pande et al. 2008, Pande and Gardner 2009, Edgar et al. 2014). Furthermore, given that acoustic surveys rapidly cover large areas, acoustic data are of great utility for marine spatial management, siting of MRs and from which MR monitoring efforts can be best planned (Ward et al. 1999).

Inconsistencies between the multibeam data and the video footage were in transitional habitats or patch reef, where the echo-sounder is likely obtaining a signal from multiple substrate types. These inconsistencies between the two methods are commonly reported within the literature and are mainly attributed to scale (Brown et al. 2011, Hasan et al. 2012). That is, the drop camera provides a view over a small area but allows for a clear depiction of transition zones or patch reef, whereas the backscatter cannot always define habitats in such fine detail. Acoustic surveys however, allow extensive spatial coverage of habitats and scope of habitat continuity. Combined, these two tools allow for a thorough understanding of habitat type, composition and continuity and can be applied directly, for example, to plan ground-truthing locations on the 2015 survey of Kapiti Island MR, NZ. Internationally, these concepts and results of comparing habitats and utilizing drop camera for ground-truthing can be applied to other temperate systems with similar habitats.

This survey collected a large swath of habitat data from the very shallow nearshore white zone, an area vessels using acoustic survey technology typically cannot access. During standard MR monitoring, dive surveys to collect data on biological response variables (e.g., abundance, size and biomass of finfish, macro-invertebrates, macroalgae) are conducted in

this zone, however habitats are rarely assessed due to ship time and diver air constraints. Although habitats are often not the primary focus, much research is focused on species-specific habitat associations within the scope of protection (Willis and Anderson 2003, Shears et al. 2004, Freeman et al. 2009). Knowledge of species-habitat associations enables habitats to act as proxies for species' distributions and allows for predictive mapping of species' distributions (Ward et al. 1999, Anderson et al. 2009). The combination of drop camera samples within the white zone and in the deeper adjacent subtidal zone has provided information on habitats across this ecological corridor at all sites within and outside the reserve. It has been demonstrated that habitat continuity across depths and across MR boundaries is an important factor in assessing MR effectiveness (Forcada et al. 2008, Freeman et al. 2009, Edgar et al. 2014).

The data collected here revealed that the choice of outside (control) sites resulted in comparable physical habitat and macroalgal cover in (3 sites) and outside (5 sites) the reserve. Across the WSC, the nearshore was mainly rocky reef; moderate depths (8-15 m) were dominated by patch reef and boulder fields, indented with cobble fields or sand and the deepest habitats were dominated by gravel and sand. Macroalgal cover was similar across sites, with dense beds of *Carpophyllum* spp. in the shallows extending into *Ecklonia radiata* fields. However, topographic relief was not similar in and outside the reserve, where reserve sites had significantly greater relief and was reflected in the presence of notably more wall reef and vertical patch reefs. High relief reefs, which provide structural refuge, have been shown to support areas of higher biodiversity, higher densities of cryptic reef fish in the scope of protection and are of critical importance for lobsters (Willis and Anderson 2003, Jordan et al. 2005, Eggleston and Parsons 2008, Freeman et al. 2009). The recognition of differences in relief between the reserve and associated control sites needs to be considered in future analysis of ecological impacts of the reserve and specifically the difference this habitat structure may have for organisms that seek topographic complexity (e.g., to avoid predation).

Although habitats in and outside the reserve were mainly comparable, when only a subset of control sites was included in analysis the results were vastly different. Western outside sites were significantly rockier with greater macroalgal cover than reserves sites and eastern outside sites. This analysis illustrates the importance of choosing control sites with similar physical substratum composition, which in large part dictates macroalgal distribution and

therefore may strongly affect the ecological structure of the site (Patton et al. 1994, Tuya et al. 2008). Given that MRs are often placed in areas of complex habitat it may be challenging to choose comparable control sites. Differences in habitat quantity or quality between reserve and control sites can muddle the interpretation of change in biological response variables from MR designation and must be taken into account so these differences do not confound a reserve effect (Huntington et al. 2010, Eddy et al. 2014a, Edgar et al. 2014). This study, at TMR, is an example of why consideration and quantification of habitats is critical when evaluating MRs and that choice of control sites can drastically change research outcomes and conclusions. Unfortunately, it is quite common that MRs are designated without baseline data (acoustic or visual), and in the absence of baseline data I recommend that habitats are quantified early on in evaluation and if differences are present, be recognized in subsequent analysis of the impact of marine reserve designation.

## 5.6 Conclusion

This research encourages scientists and managers to use a multidisciplinary approach, acoustics and drop camera to spatially describe habitats. These field surveys enabled collection of habitat data, from very nearshore to 30 m depth, across the Wellington South Coast from which MR monitoring can be guided. Although at this time a quantitative assessment comparing these data to the baseline dataset cannot be conducted it is important to note that a gradient of rocky reef was shown in this study that was not apparent in former baseline studies (Pande and Gardner 2009, Byfield 2013). In the future this habitat information can be compared to the baseline survey to assess long term change in physical or biogenic habitats, to see if there are changes from reserve designation such as trophic cascades (Shears and Babcock 2002, Leleu et al. 2012, Eddy et al. 2014b). Most significantly, these results highlight the importance of habitat quantification and the recognition that habitat differences must be taken into account in future analysis of ecological impacts and the evaluation of the efficacy of marine reserve designation.

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## Chapter 6. General Discussion

My PhD research was designed to address three main questions and test subsequent hypothesis: 1) Do marine reserves afford protection for the abalone, *Haliotis iris*, the blackfoot paua? That is, on average, are they more dense and larger within marine reserves than outside? 2) Are habitats in and outside MRs comparable? This distinction is important to distinguish and quantify a reserve effect from a potential confounding habitat effect. 3) What physical and biogenic habitats support large aggregations and individuals of paua? This investigation of the response of paua to marine reserve protection advances our understanding of the efficacy of marine reserves and what habitats may underpin demographic processes yielding large populations.

Abalone are an important nearshore fishery around the world yet many stocks have been overexploited to the point of collapse (Werner et al. 1995, Rogers-Bennett et al. 2002). As such, countries are implementing protected areas to try and help populations recover (Lessard and Campbell 2007, Micheli et al. 2008). Understanding if and to what extent MRs provide protection for any abalone species, and what habitats promote productive populations, is critical for the conservation of the species group. This study examined an abalone species that is the focus of a major fishery but has not suffered extreme exploitation (relative to other abalone fisheries) to the point of being closed which may provide a clearer understanding of abalone habitat associations and natural demographic processes. Furthermore, MRs enable examination of paua whilst controlling for fishing to investigate what habitats are required to yield large individuals and dense aggregations, which is essential for effective fisheries management.

This is the first study to examine paua and habitat associations in the context of multiple MRs in New Zealand, contributes to the limited international studies on abalone at multiple marine reserves and is unique when compared to the international literature because NZ paua populations are stable relative to populations of other abalone species (in that a TAC and TACC are being allocated). Results from Chapters 2 and 3 showed that paua responded positively to marine reserve protection. Paua were significantly more dense within MRs at four of five locations and reached density thresholds necessary for reproductive success



(Babcock and Keesing 1999). Paua were significantly larger within MRs at four of the five locations. Large paua were found at Long Island, Kapiti and Taputeranga Marine Reserves, sites that are wave exposed which may be favourable habitat for paua growth. Overall, the largest paua were found at the Taputeranga MR. Although the Wellington South Coast has been closed to commercial fishing since 1986, the area experiences a very high level of recreational and customary fishing pressure. Taputeranga MR was established in 2008 and the data collected here of dense and large paua within the reserve compared to outside are in sharp contrast to the results from the baseline prior to establishment (Pande and Gardner 2009); this before versus after difference strongly suggests that the reserve is affording protection for paua.

My findings of positive response to protection are consistent with responses reported in the literature; MRs do support for certain species individuals that are larger and more abundant within their boundaries, the so-called 'reserve effect' (Halpern 2003, Micheli et al. 2008, Pande et al. 2008, Lester et al. 2009). Individual location-specific results and response ratio indices of greater paua density and length within MRs versus fished areas support findings from other countries that MRs afford protection for abalone (Wallace 1999, Rogers-Bennett et al. 2000, Barrett et al. 2009). The northern abalone (*H. kamtschatkana*) was significantly more abundant and larger (on average 16 mm larger) in MRs after 40 years of protection (Wallace 1999). Pink abalone (*H. corrugata*) in California were significantly more abundant within no take MRs and had 30% more commercial sized abalone than the fished site (Rogers-Bennett et al. 2002). Black abalone (*H. cracherodii*) were bigger in size within MRs in central California (legal size individuals only observed within reserves), but did not reach sizes that were present before the collapse of the fishery (Micheli et al. 2008). Although these are positive results, often these studies focus on the persistence of these populations, rather than full recovery of the populations, with the authors suggesting that MRs afford protection and promote resilience of the species in the face of a major fishery collapse but did not provide evidence of a full recovery (Rogers-Bennett et al. 2002, Micheli et al. 2008). My research adds to the persistence argument but provides important evidence that paua can rebound to density and size levels that exceed what was present prior to closure because of reserve designation (Chapter 3, this thesis).

To examine the effect of protection, the main variables measured were adult paua abundance and size. However, the research also focused on assessing if there was suitable and comparable paua habitat in and outside MRs. In New Zealand, managers strive to place MRs in areas of representative coastal habitats that will protect a suite of species (Carter 2005, Willis 2013). However, nearshore temperate reef habitats are complex, seascape heterogeneity is prevalent and due to resource limitation the habitats are seldom quantified or monitored. I hypothesised that if habitats were comparable in and outside reserves then paua would be more dense and larger within the reserve than outside. Statistical testing combined with a descriptive qualitative assessment revealed that habitats inside and outside each of the five reserve locations were similar in regards to substratum, algal cover, dominant macroalgae and exposure. This finding indicates that appropriate associated “fished” sites were chosen for monitoring and that habitat within the reserve is not more favourable for paua. Habitat similarity between in and outside reserves confirms that populations at higher density and larger individual paua within MRs are attributable to a ‘reserve effect’ and not a ‘habitat effect’.

To further explore paua response to protection and the role of habitat, focused studies of juvenile populations (Chapter 3) and habitats across depth ranges (Chapter 5) were conducted at the Taputeranga Marine Reserve (TMR). Adult paua within TMR were significantly more dense and larger within the reserve than at fished sites, suggesting that there is effectively protected broodstock for reproductive success. Fertilisation and recruitment success in many abalone species is limited by low spawner density and has a critical density threshold in the range of 0.15-1 abalone m<sup>-2</sup> to be successful: therefore MR size and spacing are often designed around protecting the adult organisms (Babcock and Keesing 1999, Miner et al. 2006b). Although dense adult populations are needed to support viable populations, post settlement juvenile success is equally important to the stability of the local population. My research at TMR showed that juvenile paua occurred in higher densities at fished sites compared to reserve sites. This result was at first surprising, as I had expected higher densities of juveniles adjacent to large adult populations. However, this result was attributable to the pronounced differences in habitat in the intertidal zone in and outside the reserve. Fished sites were composed of cobbles and small boulders, substratum types that may provide valuable cryptic habitat for the vulnerable juvenile life history stage (Schiel 1993,

Aguirre and McNaught 2012). The highest densities of juvenile paua were found at the most sheltered site, consistent with previous reports of higher densities of paua in sheltered bays than exposed areas (Naylor and McShane 2001).

Although TMR has large paua aggregations and individuals which may support reproductive success (Dayton et al. 1995), juvenile and adult population densities were not correlated. Reports in the literature about juvenile-adult relationships are conflicting. A Californian study examining four abalone species reported high densities of juveniles adjacent to large adult populations and low densities of juveniles adjacent to low adult densities (Rogers-Bennett et al. 2011). Through a manipulative experiment in Australia, a positive relationship between adults and juveniles has been shown for *H. rubra* (Prince et al. 1988). However, there are also reports of negative correlations, for Northern hemisphere species (*H. rufescens* and *H. walallensis*) and Southern hemisphere species (*H. iris* and *H. rubra*) populations (Schiel and Breen 1991, Shepherd et al. 1992, Rogers-Bennett et al. 2000). Low juvenile densities are often attributed to low adult densities and recruitment failure (Tegner 1993, Rogers-Bennett et al. 2011). Additionally, habitat quantity and quality are suggested to be an important contributing factors to juvenile success and ultimately to productive adult aggregations for multiple abalone species (Tegner 1993, Miner et al. 2006b, Aguirre and McNaught 2012).

My study determined that juvenile success was not limited by adult densities and strongly suggests that habitat quality is more important to juvenile success than adjacent productive adult populations: it illustrates the need for MRs to be designed to protect habitats required for juveniles as well as adults. In locations where MRs are placed to protect biodiversity and or ecosystems, managers should also consider habitats required for multiple life history stages of species. In locations where protected areas are utilised as a fisheries management tool they have even more opportunity to design areas with the target species stage-specific habitat requirements in mind. The results of this study strongly indicate that when designing individual marine reserves or systems, regardless of the goal, (fisheries or biodiversity protection) habitat suitability for all of the life history stages of species within is an essential requirement to increase chances of successful protection or recovery.

Given the result of habitat differences at TMR in the intertidal zone found during the juvenile assessment I thought it was prudent to examine deeper habitats adjacent to paua surveyed

areas, in and outside the reserve. Visual surveys via drop camera confirmed that habitats in and outside were mainly the same (with the exception that vertical relief was significantly greater in the reserve). However, when only a subset of control sites was included in analysis the results were vastly different. Western outside sites had significantly more rocky reef with greater macroalgal cover than reserves sites and eastern outside sites. This analysis illustrates the importance of choosing control sites with similar physical substratum composition, which in large part dictates macroalgal distribution and therefore may strongly affect the ecological structure of the site (Patton et al. 1994, Tuya et al. 2008). Given that temperate MRs are often placed in areas of complex rocky reef habitat it may be challenging to choose comparable control sites. Differences in habitat quantity or quality between reserve and control sites can muddle the interpretation of change in biological response variables from MR designation and must be taken into account so these differences do not confound a reserve effect (Huntington et al. 2010, Eddy et al. 2014a, Edgar et al. 2014). The study at TMR is an example of why consideration and quantification of habitats is critical when evaluating MRs and that choice of control sites can drastically change research conclusions and management outcomes.

Although marine reserves within New Zealand are not established to facilitate species-specific protection, my results that showed that paua do respond positively to protection can be utilised to help in future MR placement. The results illustrated a need to protect habitats of both adults and juvenile populations when designing MRs. This research showed the importance of quantifying habitats in MR evaluation and encourages managers to examine habitats when siting control sites and conducting baselines. There are currently (winter 2016) discussions being undertaken by the South East Marine Protection Forum to place MPA's from Timaru to Waipapa Pt., which includes the Southland, Otago and Canterbury Coasts on the South Island (<http://www.doc.govt.nz/get-involved/have-your-say/all-consultations/2013/otago-marine-protection-forum/>). There is significantly more fishing pressure for paua in this part of the country than in central NZ. Given the heavy extraction rate, paua will be chosen as one of the indicator species to measure change as a consequence of reserve status. This study can assist with that placement, and spatial design by examining habitats for both juveniles and adults. If a MR is placed in Otago it will be interesting to ascertain if the paua response to protection is positive and/or of a similar magnitude to the

response in central New Zealand. I postulate that the response in Otago will be of greater positive proportion relative to my findings because of the cessation of the increased amount of fishing pressure (I would expect a heightened effect) and the Otago coast has optimal paua habitat (personal observation). Furthermore, in the event there is a desire, to make paua-specific closure areas either via future legislation or customary closures, these data will be advantageous for site selection.

In open access areas the paua fishery is very active and although managed through the QMS, the industry recognizes the stress the fishing is putting on wild populations. The Paua Industry Council (PIC) is starting to conduct research on density dependent effects and want to investigate habitat requirements for growth to better understand what is producing large individuals. Knowledge of species-habitat associations leads to the understanding of where large aggregations and individuals are spatially distributed which is critical for successful fisheries management of the species group. It is well documented that abalone have large demographic variability and that mean density and mean size can vary on small to large spatial scales (Shepherd and Hearn 1983, Day and Fleming 1992, McShane and Naylor 1995a, Wells and Mulvay 1995, Naylor et al. 2006, Prince et al. 2008, Saunders et al. 2008). Because of this variability paua habitat associations still warrant investigation to better understand what habitat requirements are necessary to produce healthy populations and to inform management of populations. This research examined paua habitat associations within the scope of protection within Chapters 2 and 3. Despite protection, the majority of paua at four of the five marine reserves were under the Minimum Legal Size (MLS) of 125 mm, which prompted me to investigate habitat associations across environmental gradients to examine what habitat variables produced stunted and normal growth populations (Chapter 4).

Typically, in MR monitoring within New Zealand, organisms such as paua are counted and measured but habitat associations are seldom if ever quantified in relation to organismal spatial distribution. My research is one of the first studies to examine the role of habitat variables (substratum, algal cover, dominant macroalgae and exposure) on paua density and size within the scope of protection. This research considered both paua metrics (density or size) individually to examine what and if the same habitat variables were supporting large aggregations or individuals. Paua were more dense in boulder habitats with high algal cover across all locations. One hypothesis to explain this pattern is that adult abalone are more

secure on boulders that are unlikely to roll around in wave conditions and this may be greater paua abundance is found in boulder habitats (Sousa 1979, Aguirre and McNaught 2012). High densities in areas of high algal cover is consistent with findings of high densities in areas of high CCA in controlled field experiments (McShane and Naylor 1995b, Aguirre and McNaught 2012) and in high macroalgal cover in natural field surveys (Lessard and Campbell 2007, Pande and Gardner 2009). Paua were significantly larger in areas exposed to swell and wind and with high algal cover dominated by a mixed macroalgae habitat of *Ecklonia radiata* and *Carpophyllum* spp. The largest paua were found at the most exposed sites across all MR locations. These findings are consistent with previous research in which a positive relationship between growth and exposure has been reported and that exposure was a significant source of variation in mean length (McShane et al. 1994a, McShane and Naylor 1995a). In addition, *H. iris* from headlands have been found to have higher incremental growth and obtain larger maximum size than individuals in nearby sheltered bays (McShane and Naylor 1995a).

Finding large paua in areas of dense macroalgal stands, their main food supply, was not surprising and is consistent with the literature. For the red abalone (*H. rufescens*) decline in growth was explained by low food availability due to warm water and El Niño events affecting macroalgal growth (Haaker et al. 1998, Tegner et al. 2001). Saunders et al. (2008) found that small or “stunted” populations of *H. rubra* were related to low algal cover and topographic simplicity whereas “normal” populations were related to high algal abundance and topographic complexity. It is suggested that variation in paua growth is attributed to type and availability of food (Sainsbury 1982, Shepherd and Hearn 1983, Day and Fleming 1992). In NZ it is thought that paua prefer to feed on drift rather than attached algae, although (to my knowledge) this has not been shown in the field. In controlled laboratory experiments paua showed a preference for drift over attached algae and during high flow conditions paua were able to trap drift algae but grazing ceased on attached algae (Cornwall et al. 2009). Unfortunately, due to logistical restraints I was unable to measure drift algal concentrations. However, much would be gained from examining drift algal quality and type and *in situ* paua feeding rates.

Macroalgal cover was a significant explanatory variable for both paua density and length. Food availability is affected by density of conspecifics, water movement, algal cover, drift algal supply and substratum. In central NZ, exposed areas are often dominated by rich macroalgal

stands, because the grazers are dislodged by turbulence. It has been hypothesised that a certain amount of water motion is needed to supply food and an increased amount of water movement would increase drift algal supply to the area and also reduce sedimentation which can smother abalone (Sainsbury 1982, Schiel 1990). This research's findings suggest that exposure level and areas with high macroalgal cover may be working in concert to yield large individual paua, potentially indirectly by supplying large amounts of drift algae. Although exposure may be ideal for growth it may hinder large aggregations of paua from forming because smaller individuals may be dislodged. I propose that a balance between exposure and food supply is required to allow large aggregations of paua to form in the absence of fishing pressure. Large macroalgal stands are expected to dampen exposure allowing smaller paua to adhere to the substratum, and boulder habitats may be preferable for smaller paua in high exposure conditions. Manipulative experiments are needed to test densities and sizes in varying levels of exposure, substratum and macroalgal habitats to further understand the mechanism of how these environmental variables interact and affect the demography of paua populations.

To further explore the effect of habitat on size I quantified and evaluated the contribution of habitat variables on paua size at two spatial scales across environmental gradients. The survey revealed that environmental gradients existed at small (within the Long Island MR) and large scales (across Tasman Bay) and explained how paua size varied along these gradients. The habitat variables that supported larger sized individuals were consistent across both locations, where paua were significantly larger in areas that were exposed with high algal cover than those at sheltered areas with low algal cover. These findings are consistent with previous research in which a positive relationship between growth and exposure has been reported and that exposure was a significant source of variation in mean length (McShane et al. 1994a, McShane and Naylor 1995a). In addition, *H. iris* individuals from headlands have been found to have greater incremental growth and to obtain larger maximum size than individuals in nearby sheltered bays (McShane and Naylor 1995a). The results from Chapter 4 corroborate the findings of paua habitat associations within the scope of marine reserve protection reported in Chapters 2 and 3.

Given the aggregating nature of abalone one would expect to see intraspecific competition for food (Dixon and Day 2004a, Mundy 2010). Density-length correlations were examined and

analyses confirmed that there was no correlation between density and length (Chapters 2 and 4). Based on these results I conclude that density is not limiting length (growth) at either of these locations and further confirm that habitat variables are playing a critical role in length and growth. This is important information for fisheries managers; it is often hypothesised that density has a negative effect on growth and this argument has historically been used in discussions to reduce the MLS, apply for permits for fish down experiments and translocations. My results that density does not have a negative effect on growth, argues against the hypothesis and encourages fisheries managers to examine habitat effects on growth.

Abalone translocations have been used to examine the effect of density and the contribution of habitat variables on growth, and for enhancing populations (Dixon and Day 2004a, Lessard and Campbell 2007, Mundy 2010, Taniguchi et al. 2013). Typically, such translocations alter density and are not reciprocal, meaning that abalone are translocated in one direction only and to more optimal habitat. To experimentally test the effect of changing habitat on growth, I conducted a translocation experiment at Long Island MR. This was (to the best of my knowledge) the first density constant reciprocal translocation experiment conducted in New Zealand. It showed that regardless of natal origin, paua grew more at the normal site than at the stunted site. Additionally, there was no difference in growth based on natal history at the normal site or the stunted site. This positive result in growth at the normal site was attributed to a plastic response to better quality environment. The environment was more suitable for paua growth at the normal site, which was exposed, dominated by high abundance of macroalgal cover whereas the stunted site was sheltered with low algal cover. Greater growth rates at more exposed sites have been found in New Zealand where *H. iris* individuals from headlands have higher incremental growth and obtain larger maximum size than individuals in nearby sheltered bays (McShane and Naylor 1995a). My results are consistent with those of Saunders et al. (2009) who reported that small or “stunted” populations were related to low algal cover and topographic simplicity whereas “normal” populations were related to high algal abundance and topographic complexity. This difference was attributed to a plastic response to the environment and not to abalone history.

Translocation of adult abalone has been suggested in many locations and trialled in Tasmania as a tool by industry and fisheries managers to develop populations for spawning or for fast



growth to support the fishery (Campbell 2000, Mundy 2010, Taniguchi et al. 2013). My results suggest that translocating stunted abalone from poor habitat (sheltered with low algal cover) to areas with more optimal habitat (exposed with high algal cover) will increase growth rates, which may be used as evidence to support translocations for stock enhancement. Translocation of stunted abalone to better habitat environments where populations may grow rapidly is appealing and potentially cost effective. However, scientists and fisheries managers need to be thoughtful and consider existing stunted stock densities and habitat requirements of juvenile stages in the translocated environment. Currently in New Zealand the PIC is considering conducting translocations of paua to fast growth sites for direct fishing and potentially to areas where they would be “protected” to provide broodstock (personal communication, Tom McCowan, PIC). Whilst my results may support translocations of abalone to enhance populations, more field research needs to be conducted to examine larval dispersal, juvenile and adult habitat requirements, the effect of type and availability of food, and additional translocation experiments in areas with fishing pressure before translocations can be conducted. The habitat association results from both the survey and translocation experiment can be used to assist with fisheries management decisions in New Zealand, such as setting appropriate size limits, considerations for potential translocations and contributing knowledge to other countries that are working to rebuild or sustain economically important abalone fisheries.

## 6.2 Conclusion

By international standards New Zealand has an extensive network of MRs that encompasses representative habitat types across its bioregions. Although, MRs are not placed to solely protect *Haliotis iris*, they are providing protection, where paua are significantly more dense and larger within than outside reserves. Paua are an iconic NZ species, they are culturally very important and that may be in part why this fishery has been well managed to date. . However, conservation and fisheries managers can learn from other abalone fisheries and continue best management practices to ensure that the resource is not exploited to a point of no return. In California, abalone populations are persisting within the protection of MRs but are not able to obtain levels that were present before collapse of the fishery (Rogers-Bennett et al. 2002, Micheli et al. 2008). Managers can reap knowledge from other abalone

fisheries and the knowledge from this study to be proactive rather than reactive to extreme exploitations, such as setting aside areas to specifically protect paua, if the need should arise.

The results from this study show that protection enables paua to be successful and supports paua-specific closure areas. The habitat association results from this study can be used to assist with future placement of management areas for the success and recovery of populations within New Zealand and may contribute knowledge to other countries that are striving to rebuild their Haliotid stocks. This research illustrated the need to consider stage-specific habitat requirements when designing MRs for abalone because of their contrasting life histories (juveniles versus adults). Designs should include habitat requirements for both stages which will assist in the successful transition from juveniles to adults. Furthermore, fisheries managers can use the knowledge gathered in this research to inform potential translocations of stunted abalone to better habitat environments where populations may grow rapidly or act as seed banks. New Zealand's paua populations are unique, that is, not as stressed by fisheries exploitation as its global cousins, but it will take continued informed management to ensure the success of this valuable resource. The findings of my PhD research are directly applicable to MR management within New Zealand, and to abalone conservation and management globally.

## 6.3 Literature

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