



Seagrass Meadows as Biodiversity and Productivity Hotspots

New Zealand Aquatic Environment and Biodiversity Report No 137.

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ISSN 1179-6480 (online)
ISBN 978-0-478-43764-5 (online)

October 2014



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EXECUTIVE SUMMARY

Morrison, M.A.; Lowe, M.L.; Grant, C.M.; Smith, P.J.; Carbines, G.; Reed, J.; Bury, S.J.; Brown, J. (2014). Seagrass meadows as biodiversity and productivity hotspots.

New Zealand Aquatic Environment and Biodiversity Report No. 137. 147 p.

A large scale survey of the communities associated with seagrass (*Zostera muelleri*) meadows and adjacent bare sediments for both fish and infaunal/epifaunal assemblages was undertaken across New Zealand to investigate any potential trends in biodiversity and secondary production with latitude or bioregion.

Fish assemblages sampled from the nine locations revealed that subtidal seagrass meadows from northern New Zealand were important juvenile fish nurseries, particularly for species such as snapper and trevally. However, the relative fish nursery value of seagrass meadows varied strongly, dependent upon depth (tidal position), coast, landscape setting and latitude. South of Cook Strait, only spotties and piper were present, while seagrass meadows in Southland supported higher abundances of pipefish and juvenile leather jackets. From a strictly fisheries based view-point, this means that northern subtidal seagrass meadows are of much higher economic value. A small number of species such as yellow-eyed mullet and mottled triplefin had more universal distributions. These results show that the value of a given habitat type is contextual, being affected by factors such as biogeography and local setting, as well as habitat quality (e.g., seagrass blade height and density, water depth, and patchiness).

Ontogenetic dietary shifts were evident for the majority of fish species, with meiofaunal crustaceans (0.5–1 mm) predominating in the diet for fish less than 25 mm in size. Newly recruited fish exhibited an obligatory planktivorous stage, with a gradual transition to a diet of larger crustaceans such as gammaridean amphipods (particularly for subtidal meadows), mysids and caridean shrimps and crabs. Habitat-related differences in diet were also evident, reflecting benthic prey availability and diversity.

The role of seagrass habitat on the composition of faunal invertebrate communities (both infaunal and epifaunal) is complex and highly variable spatially. The presence of seagrass does not always equate to higher abundance, species richness or secondary production when compared to local bare or sand habitats. In terms of secondary production derived from seagrass compared to bare habitats, no consistent latitudinal trends were apparent for associated invertebrate communities. Subtidal seagrass sites were not identified as having higher secondary production values when compared to their intertidal seagrass counterparts, in contrast to its fish nursery values (north of Cook Strait).

Random amplified polymorphic DNA (RAPD) markers were evaluated for detecting genetic variation in *Z. muelleri*, the seagrass species found in New Zealand, and subsequently used to estimate genetic variation within and among regions. Significant genetic differentiation was found among seven regional populations. There was no evidence for a simple isolation by distance model at the national level, or within the east coast, or North Island sites. The high level of regional genetic differentiation is indicative of limited gene flow, with little long distance (over 100 km) dispersal of seeds or vegetative parts of plants between widely separated geographic regions. At the local scale (less than 1 km) the majority of genetic variation was found within sites (over 86%) and there were shared composite genotypes among sites, indicative of clonal reproductive strategy.

Investigation of the stable isotope signatures of seagrasses along with other sources of primary production from a relatively pristine harbour (Rangaunu Harbour) and a harbour which is known to be influenced by anthropogenic pollution sources (Kaipara Harbour), provided preliminary results that indicate that seagrass was not the main ecosystem fuel for either of these harbours, as higher order

consumers had stable isotope values for carbon which fell in between those for seagrass and phytoplankton sources.

An ecological appraisal framework is provided to aid managers in objectively ranking seagrass meadows of varying ecological value based on the findings of this current report.

1. OBJECTIVES

- 1 Complete a national bio-geographic assessment of seagrass associated biodiversity.
- 2 Quantify seagrass connectivity with surrounding marine landscapes through nursery functions and detritus export.
- 3 Quantify seagrass replication/connectivity mechanisms: reproductive or clonal?
- 4 Develop an appraisal model for seagrass systems in New Zealand.

2. A GENERAL INTRODUCTION TO SEAGRASS SYSTEMS

2.1 Global understanding

Seagrasses are a unique group of flowering plants that exist fully submerged in the sea. Seagrasses are distributed globally, but unlike terrestrial angiosperms exhibit low taxonomic diversity (approximately 60 species worldwide), with 12 genera. All species share similar architecture and physiology, and perform similar ecosystem functions. Seagrasses are a characteristic component of many coastal areas ranging from subarctic to temperate and equatorial regions, reaching their most southerly global distribution at Stewart Island, New Zealand (Hemminga & Duarte 2000, Turner & Schwarz 2006).

Seagrasses commonly occur in sheltered areas, away from strong currents and wave action, on a variety of substrata ranging from mud through to sand and bedrock (Hemminga & Duarte 2000, Green & Short 2003). However, the most extensive meadows are found on soft substrata, often forming continuous expanses over several square kilometres. Alternatively, they can form mosaics of discrete patches (often in areas with more wind-generated wave exposure) (Inglis 2003, M.L. & M.M., NIWA, pers. obs.). Seagrasses are typically found in intertidal (to mid tide level) and shallow subtidal waters at depths between 2 and 12 m, but can occur down to 50–60 m, depending on water clarity (Turner & Schwarz 2004). Seagrasses require some of the highest light levels of any plant group (about 25% incident radiation compared to up to 1% for other angiosperms; Dennison et al., 1993). Seagrasses are thus acutely responsive to environmental changes, especially those altering water clarity and are considered ‘sentinels’ for these types of environmental changes.

Seagrass meadows are considered to be one of the most productive ecosystems in the world, ranked ahead of coral reefs (Constanza et al. 1997, Grech et al. 2012, Matheson & Wadhwa 2012), yet they are relatively unknown and often under appreciated by the general public. Whilst prior research has shown that seagrasses provide a variety of ecosystem services encompassing both economic and ecological functions, the relative importance of these functions can vary appreciably between different estuarine and coastal systems (Beck et al. 2001, Orth et al. 2002, Heck Jr et al. 2003).

Ecosystem services provided by seagrasses include high primary productivity to both detrital and grazing food webs (Keough & Jenkins 1995, Turner & Schwarz 2004, 2006, Connolly et al. 2005), nutrient recycling (see review Turner & Schwarz 2006), attenuating water flow (Eckman 1987, Foncesca & Koehl 2006, Widdows et al. 2008), trapping and stabilisation of bottom sediments (Foncesca et al. 1983, Gacia & Duarte 2001), providing refuge from predation (Attrill et al. 2000, Hindell et al. 2000, 2001), increasing biodiversity and providing crucial nursery habitat (including feeding/foraging) for a variety of taxonomic and functional groups, including the juveniles of important recreational and commercial fisheries species (Orth et al. 2006, Grech et al. 2012). Other important services performed by seagrasses include being a significant repository for what is termed “blue carbon” (i.e., as a marine primary producer) (Matheson & Wadhwa 2012), the release of oxygen, and the trapping of nutrients (Figure 1).

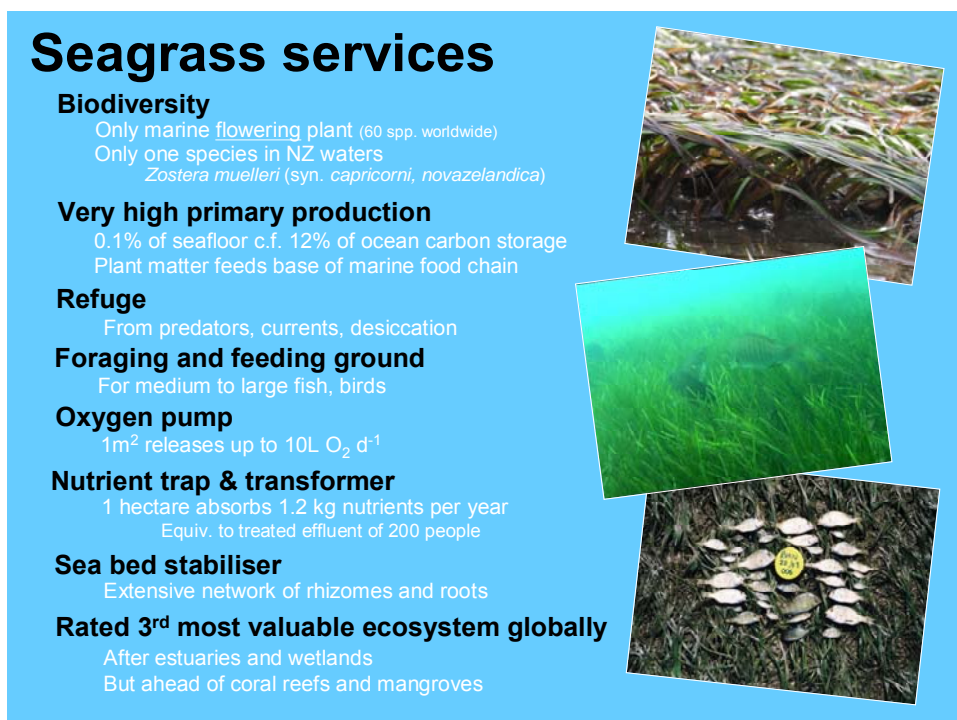


Figure 1: Summary of ecosystem services provided by seagrass meadows (Source: Matheson & Wadhwa 2012).

However, rapid large scale seagrass losses reported in both tropical and temperate regions have increased almost tenfold over the past 40 years (Orth et al. 2006). Worldwide, seagrass meadows declined at a rate of 110 km² yr⁻¹ between 1980 and 2006, with 15% of seagrass species now considered threatened (Waycott et al. 2009, Short et al. 2011, cited in Grech et al. 2012). Biological, environmental, and extreme weather events have been identified as causes of seagrass losses which can interact at varying temporal and spatial scales (Orth et al. 2006). Nonetheless, a recent global review of the 6 seagrass bioregions acknowledged that anthropogenic activities including urban/industrial runoff, urban/port infrastructure development, agricultural runoff, and dredging had the greatest impact on seagrasses worldwide (Grech et al. 2012). These terrestrially based activities highlight the need for land-based coastal management to be incorporated into conservation and protection of seagrass habitat.

2.2 New Zealand state of knowledge for *Zostera muelleri*

Two comprehensive New Zealand focused reviews have been undertaken with respect to taxonomy, growth requirements, distribution, threats, and habitat characterisation of seagrasses in New Zealand; one by Turner & Schwarz (2006), and the other by Schwarz & Sutherland (2012). Both reviews acknowledge that their assessment of hotspots of biodiversity and areas of particular vulnerability are potentially biased, due to incomplete knowledge of seagrass systems in many parts of the country. Most seagrass research has been centred around the main urban population centres – e.g. Auckland, Christchurch and Otago, with research focusing on demography, ecology and physiology, seagrass associated fauna, and seagrass distribution at local scales. Only limited research has been undertaken to address the impacts of anthropogenic activities (Schwarz & Sutherland 2012).

Limited historical evidence suggests that New Zealand has experienced extensive declines in seagrass habitats since the late nineteenth and early twentieth centuries (Inglis 2003). Analysis has largely been restricted to the past 40 to 50 year period, due to the limited availability of qualitative survey/photographic data (Inglis 2003, Turner & Schwarz 2006). Spatial and temporal dynamics of intertidal *Zostera* has been documented within the Manukau and Whangapoua Harbours (Turner et al.

1997), Tauranga Harbour (Parks 1999), on some Kaikoura reef areas (Ramage & Schiel 1999), and in Otago Harbour (Ismail 2001), while in Tauranga Harbour both intertidal and subtidal seagrass has been assessed (Park 1999), along with subtidal seagrass in the Bay of Islands (Matheson et al. 2010), the southern Kaipara Harbour (Morrison et al. 2014b), and Parengarenga and Rangaunu harbours (Morrison/Lowe et al., unpubl. data).

A seasonal pattern in biomass/cover has been suggested from some studies, with an above-ground mass minima recorded over winter from both the Coromandel Peninsula (Turner & Schwarz, 2006) and Otago Harbour (Ismail 2001). The spatial extent of seagrass has also been shown to vary over periods as short as one year (Ismail, 2001). Both of the New Zealand reviews identified the need to quantify changes in seagrass communities (e.g., for rhizome demography, patch expansion/contraction and landscape patterns) over appropriate space and time scales concurrently (Turner & Schwarz 2006, Schwarz & Sutherland 2012). This would in turn allow for the meaningful interpretation of any subsequent snapshots utilizing techniques such as remote sensing. However, they acknowledged that large areas within New Zealand were yet to be surveyed for seagrass, with scant attention being paid to historical distributions (over decadal scales) and the development of suitable mapping techniques (Schwarz & Sutherland 2012).

Environmental constraints imposed on seagrass growth have been highlighted with recent research undertaken on water clarity (Schwarz 2004, Turner & Schwarz 2006, Matheson & Wadhwa 2012), suitability of sediments (Schwarz et al. 2004, Matheson & Schwarz 2007), and nutrients (Ismail 2001, Turner & Schwarz 2006). Seagrass beds have also been shown to be characterised by intensive internal nutrient cycling, with nitrogen fixation shown to occur within seagrass sediments (Hicks & Silvester 1990).

Seagrasses in New Zealand have been shown to have an effect on macrofaunal communities, which differ from surrounding unvegetated sediments (van Houte-Howes et al. 2004). Studies of the communities associated with seagrasses have described both meiofauna (e.g. Hicks 1986, 1989, Bell & Hicks 1991) and macrofauna (e.g. Henriques 1980, , Woods & Schiel 1997, Turner et al. 1999).

The role of seagrass meadows as nursery areas for fishery species has only recently been acknowledged and investigated within New Zealand. New Zealand wide estuarine fish surveys undertaken by Francis et al. (2005, 2011) first identified the association of small snapper, trevally, parore, spotties and other species associations with subtidal seagrass, followed by further work on subtidal meadows from Slipper and Mercury Islands, off the Coromandel Peninsula (Schwarz et al. 2006). These studies showed that subtidal seagrass (i.e., that permanently submerged) was the important seagrass component, with a much less pronounced effect (if any, in some circumstances) when only intertidal seagrass was present. Beyond the simple division of intertidal and subtidal seagrass, international studies have shown that other seagrass related factors including landscape metrics (e.g. patch size, perimeter to area ratios) (Boström et al. 2006), and within patch metrics of seagrass condition (e.g. blade density & height) (Horinouchi 2007) also influence fish usage of seagrass. Fine scale observational and experimental work in New Zealand is limited. Morrison et al. (unpubl. data) utilized artificial seagrass units (ASU) in Whangapoua Harbour, Coromandel, and showed that increasing blade densities were associated with increasing fish densities (although the patterns of response varied across species) and species diversity (see summary in Morrison et al. 2014b). Further research by Parsons et al. (2013) confirmed the effect of blade density, and also found that the position of the ASU's within the harbour (i.e. upper/lower) affected the abundance of juvenile fish (notably snapper and spottys) with greater densities found towards the mouth of the harbour. The body condition of juvenile snapper was also greatest in ASU units with the highest blade densities. Given that one of the initial responses of seagrass meadows to environmental degradation (prior to complete loss) is a reduction in blade density, this habitat quality effect (i.e. seagrass blade density) is an important component to consider in the healthy functioning of seagrass meadows as fish nurseries (Morrison et al. 2014a–c). Recent experimental research on factors affecting settlement dynamics and olfactory cues within seagrass and other habitats for larval snapper has also been undertaken (Radford et al. 2012, Sim-Smith et al. 2012, 2013). Tank experiments revealed that larvae preferentially swam

towards water taken from over seagrass beds, versus water that had been taken from the harbour entrance, or over artificial seawater (chemically created 'pure' saltwater without prior biological influence) in which seagrass had been soaked. Results strongly suggested that biological chemical cues from sources other than seagrass, such as from prey or conspecifics present in the seagrass habitat, may also be involved.

There have been several small scale seagrass restoration studies undertaken within New Zealand. Attempts within the Manukau Harbour had limited success (Turner 1995), but subsequent seagrass restoration in Whangarei Harbour has been more successful with recent anecdotal reports of the reestablishment and expansion of seagrass meadows (Reed et al. 2004, Matheson et al., in prep.). However, the significant seagrass expansion, including 3.5 km² of patchy subtidal seagrass (D. Parsons, NIWA, pers. comm), while starting around the same time period (2008) as the small-scale transplants, is too widespread to have been generated by the effect of the transplants alone.

A widely recognised function of seagrass beds is the provision of sheltered habitats and elevated food supplies for fish and macrofaunal communities. Seagrasses in New Zealand have been shown to have an effect on macrofaunal communities which differs from surrounding unvegetated sediments (e.g. van Houte-Howes et al. 2004). Henriques (1980), showed that seagrass habitats in the Manukau Harbour had a higher species diversity and abundance of macrofauna than comparable non-vegetated habitat. Other studies of the animal communities associated with seagrasses include meiofauna (e.g. Hicks 1986, 1989; Bell & Hicks, 1991) and macrofauna (e.g. Henriques 1980, Alderson 1997, Woods & Schiel 1997, Turner et al. 1999; Schwarz et al. 2006). Higher macrofaunal density/biomass/productivity has also been observed for subtidal relative to intertidal seagrass in northern (Ellis et al. 2004; van Houte-Howes et al. 2004; Alfaro 2006; Schwarz et al. 2006) and southern New Zealand (e.g. Mills & Berkenbusch 2009). This may be a result of the large fluctuations in environmental conditions (i.e. periodic desiccation and fluctuating temperatures), experienced by intertidal habitats, resulting in stunted growth (shorter blade lengths), and lower overall diversity and productivity (Schwarz et al. 2006). In contrast, subtidal habitats are more environmentally benign and stable (i.e. reduce effects of currents/waves; provide shelter from predation; support larval settlement), and are characterized by more complex structure, with higher density and longer stems providing up to 20 times more surface area for epifaunal animals to graze (Schwarz et al., 2006).

2.3 Seagrass connectivity and role as an ecosystem fuel

Seagrass beds are significant producers of primary productivity, which may subsequently be exported into the surrounding landscape through both movement of detrital material, and export via animals that have used seagrass directly and/or indirectly as part of their food intake (Hemminga & Mateo 1996). Thus seagrass beds can 'fuel' other ecosystem elements spatially removed from the seagrass beds themselves, through a range of trophic linkages. These linkages are very difficult to show through traditional approaches such as gut analyses for groups such as invertebrates, but can be investigated using food web tracers such as stable isotopes.

The complex interplay of physical, biological and chemical processes in the environment produces distinct isotopic signatures in naturally occurring materials. These natural abundance signatures are increasingly used as tracers in environmental studies. Carbon and nitrogen isotope ratios can track nutrient fluxes between ecosystems and determine the trophic structure level of organisms within ecosystems. Carbon isotopes are a powerful tool for identifying carbon sources and fluxes within ecosystems (Fry & Sherr 1984, Peterson & Fry 1987), whilst nitrogen isotope ratios show distinct enrichments (i.e. increases in $\delta^{15}\text{N}$) of up to 3‰ per successive trophic level and have strong applications in food web and dietary studies (DeNiro & Epstein 1978, Minagawa & Wada 1984, Vander Zanden & Rasmussen 2001). Seagrass beds have very distinct $\delta^{13}\text{C}$ values, averaging -10 to -11 ‰, compared to most C3 land plants (which include mangroves) which exhibit values of between -35 to -23 ‰ (Hemminga & Mateo 1996).

2.4 Seagrass replication and connectivity mechanisms

Seagrasses are clonal marine angiosperms found on all continents except Antarctica, and form extensive beds in tropical and temperate coastal regions (Anon 1973, Green & Short 2003, Hartog 1970). Seagrasses provide key ecological services in intertidal and sub-tidal regions by creating complex structures that support numerous associated species (Williams & Heck Jr 2001), but are under increasing threat from habitat loss and degradation in coastal environments (Orth et al. 2006). Consequently there is a growing awareness of the need for the protection and restoration of depleted seagrass meadows (Duarte 2002, Orth et al. 2006), which requires base-line information on population genetic structure within and among seagrass meadows (Reusch 2003).

The genetic structure of seagrass meadows is influenced by a balance between seedling recruitment and clonal propagation, with the former introducing new genotypes and the latter spreading single genotypes (Diekmann et al. 2005). Sexual reproduction may not play a major role in seagrass propagation due to low pollination success and the limited dispersal of pollen and seeds (see Diekmann et al. 2005), and clones have been reported in populations of *Zostera noltii*, *Zostera marina*, and *Cymodocea nodosa* in the Northeast-Atlantic Ocean and Baltic, Black, and Mediterranean seas (Coyer et al. 2004, Olsen et al. 2004, Alberto 2005). Recruitment most likely occurs through rafting of shoots rather than dispersal of fruits and seeds (Harwell & Orth 2002). Extensive dispersal has been reported in the eelgrass *Zostera marina*. Vegetative shoots with attached roots and rhizomes of *Z. marina* have been observed floating at the water surface and can potentially disperse long distances (Ewanchuk & Williams 1996). Floating reproductive shoots with mature seeds remain positively buoyant for up to two weeks and reproductive fragments with viable seeds have been found on shorelines up to 34 km from established natural beds. The establishment of new patches of *Z. marina* in different regions of Chesapeake Bay up to 100 km from source populations indicated rapid natural colonization (Harwell & Orth 2002).

Genetic studies of seagrasses applying a range of molecular techniques (allozymes, AFLPs, RAPDs, and microsatellites) have revealed significant genetic differentiation at the 100–150 km scale among North Atlantic Ocean and Mediterranean Sea populations of *Z. noltii* and *Z. marina* (Reusch et al. 2000, Coyer et al. 2004, Olsen et al. 2004). Genetic diversity may be important for survival and recovery of seagrass meadows (Hughes & Stachowicz 2004, Reusch et al. 2005, Diaz-Almela et al. 2007).

Currently one seagrass taxon *Zostera muelleri* is recognised in New Zealand waters (Les et al. 2002, Jacobs et al. 2006). *Z. muelleri* meadows are found on littoral and sub-littoral sandflats and rocky shore platforms in estuaries and sheltered bays around New Zealand, and as with seagrass meadows in other regions of the world, are in local decline (Turner & Schwarz 2006). The spatial scale of *Z. muelleri* beds varies from rhizomes and shoot groups (centimetres to metres), to patches (metres to tens of metres), to landscapes (tens of metres to kilometres); the patches exhibit both spatial and temporal variation reflecting recruitment dynamics and, indirectly, dispersal potentials (Turner et al. 1999).

Z. muelleri reproduces both sexually and vegetatively, but seed production is not likely to be important; it has been observed once in South Island populations (Ramage & Schiel 1998), and never in extensive surveys of North Island populations (Turner & Schwarz 2006). Around Kaikoura, large reproductive shoots were located only on the lower shore and not in meadows high on the shore (Ramage & Schiel 1998).

Random amplified polymorphic DNA (RAPD) markers have been used to determine genetic relationships among geographically separated populations in a variety of marine taxa (Smith 2005), and have been widely used as population markers in botanical studies, including sea grasses (Franconi et al. 1995, Waycott 1995, Procaccini et al. 1996, Alberto et al. 2001, Micheli et al. 2005,) and *Z. muelleri* in New Zealand (Jones et al. 2008). In seagrass (a marine angiosperm) populations which are able to reproduce both sexually and asexually (i.e. via clones) there may be geographic differences

with regard to the relative importance of the two modes of reproduction, with genotypic diversity often used to express the relative contribution of each mode. Seagrass genetics can help us to gain a better understanding of the potential reproductive connectivity between New Zealand seagrass meadows at a range of spatial scales, the potential for depleted populations to recover through connectivity with other beds/populations via the exchange of drift algae or seeds, and what the best approaches are to take in terms of restoration; where genetic material needs to be sourced from areas outside of the spatial area to be restored (the original beds either being absent, or too limited to provide donor material) (as described in Williams 2001).

3. METHODOLOGY

3.1 Biogeographic Survey Work

Context and Spatial Sampling Design

Seagrass meadows are found around both of New Zealand's main islands, as well as Stewart and the Chatham Islands (Turner & Schwarz 2006, Morrison et al. 2014b). While only one seagrass species is present, it spans a wide range of environments, including the intertidal and subtidal (to 7 m), estuarine and coastal systems, and soft sediment and rocky reef substrates. The combination of this adaptability, along with a latitudinal range of more than 1900 km (from warm sub-tropical to cool temperate environments) that crosses different bio-geographic species pools, means that the assemblages associated with seagrass will vary across New Zealand. To 'capture' this spatial variability/change, we adopted a spatial sampling framework which maximised the spatial range and type of seagrass meadow setting sampled (Table 1). The known current biogeographic distribution of seagrass was used to select four geographic sampling regions: the upper west coast North Island, east coast North Island, upper northern-western coast South Island, and the lower south-eastern coast South Island. Within each region, we looked for seagrass meadows in association with the following setting: a large estuary, a small estuary, a coastal island, and an intertidal rock platform. In the large estuaries, the system was further split into upper and lower seagrass meadow positions (i.e. upper meadows being furthest from the estuary mouth, lower seagrass meadows being closer to the open sea) to further investigate whether seagrass meadow position in an estuary had any effect on the associated assemblages. Published literature, contacts within the New Zealand marine science network, and previous field knowledge were used to identify these seagrass locations, as no comprehensive inventory of seagrass occurrence and extent exists. As seagrass distribution and associated settings are not uniformly distributed around the New Zealand coastline, not all settings/replicates could be found in each of the four sampling regions. Seagrass on intertidal rocky reefs in particular appeared quite regionally disjunct from estuarine meadows, with the known/reported regions of abundance being along the Gisborne and Kaikoura coastlines; neither of which have substantive estuaries. Coastal seagrass settings were rare, and to the best of our knowledge located largely only along the north-eastern coast of the North Island (see Schwarz et al. 2006). A reported sub-tidal bed at Ruapuke Island, Foveaux Strait, was not able to be assessed during field work operations due to the very exposed nature of the Strait, and the limitations of the small boats available for use. Subtidal seagrass was preferentially targeted where present, based on prior knowledge of its elevated ecological roles over intertidal seagrass (e.g. Schwarz et al. 2004). However, this did not eventuate in intertidal sites being 'dropped' during field operations, as subtidal seagrass either only occurred in the larger estuaries, or in the case of Waikawa, in the absence of intertidal meadows.

Table 1: Summary of sampling regions, locations targeted, whether the locations were intertidal or subtidal, and the number of seagrass and adjacent bare sites sampled in each. N/A, not available.

Region	Large Harbour (Upper/Lower)	Small Harbour	Coastal Island	Rocky Reef
East coast North Island	Rangaunu Intertidal (1+1) Subtidal (2+2)	Tairua Intertidal (1+1) (very narrow subtidal fringe)	Urapukapuka Is. (Bay of Islands) Subtidal (1+1)	Gisborne Intertidal (1)
Upper west coast North Island	Kaipara Intertidal (2+2) Subtidal (1+1)	Kawhia Intertidal (1+1)	N/A	N/A
Upper north- western coast South Island	Farewell Spit Intertidal (2+2)	Whanganui Inlet Intertidal (1+1)	N/A	Kaikoura (east coast) Intertidal (1+1)
South east coast South Island	Bluff/Awarua Intertidal (1+1) Subtidal (1+1)	Waikawa Subtidal (1+1)	N/A	N/A

3.2 Field operations

Given the wide geographic spread, and associated high logistical costs of getting to these areas (including the need to hire local boats) it was not possible to visit the sampling areas prior to the arrival of the full field team. Sampling periods were chosen to maximise the timing and extent of the low tide time windows available. At the start of each day, the team arrived at the site roughly two hours after high tide, and as the tide dropped selected the best sites possible to meet the outlined objectives. Sites were assigned as either subtidal or intertidal. Each site extended a sufficient along-shore extent to permit the completion of four beach seine tows (tows being about 50 m in length) within each assigned habitat, and for seagrass sites, held sufficient seagrass cover to constitute a ‘meadow’ (arbitrarily defined as having at least 90% coverage, with average blade lengths of at least 5 cm (with intertidal seagrass generally having blade lengths less than 18 cm and subtidal seagrass more than 18 cm in length). To maintain as much consistency as practical, seagrass sites were centred on where the dominant ‘mass’ of the seagrass meadow was concentrated, to minimise potential confounding issues such as highly fragmented seagrass mosaics, and/or large interspersed strips/patches of bare sediment. Within each seagrass meadow site, maximum blade lengths of five haphazardly selected individual blades were measured, and this was repeated at each of the four replicated sites within a specific location. Contrasting bare sediment sites were selected as close as practical to the seagrass sites, with a minimum distance of 100 m separation to avoid potential habitat halo-effects (especially for fish). However, the strong dominance of seagrass in some estuarine locations resulted in some of the sampled bare sediment sites being much larger distances away (several hundreds to a thousand metres). Due to the time and distance constraints of traversing intertidal flats on foot, all intertidal samples were collected within 200 m of the low tide mark. Beach seine tows were made sequentially, parallel to the shore, while the benthic core and strip transect samples were haphazardly distributed across the defined survey site (about 250 by up to 200 m in area).

Sampling was undertaken in eight New Zealand estuaries (Rangaunu, Kaipara, Tairua, Kawhia, Farewell Spit, Whanganui Inlet, Waikawa and Bluff); along with one island location (Bay of Islands) and two strictly coastal rock platform sites (Gisborne and Kaikoura), giving eleven locations in total, along a 1900 km latitudinal gradient (from north to south) (Figure 2). The eleven locations differed

considerably with respect to their morphology, size, hydrology and degree of exposure. A summary of the key environmental characteristics of each estuary is given in Table 2.

Samples were collected from 33 sites comprising seagrass (intertidal/subtidal), and sand/bare (intertidal/subtidal) habitats (Table 1).

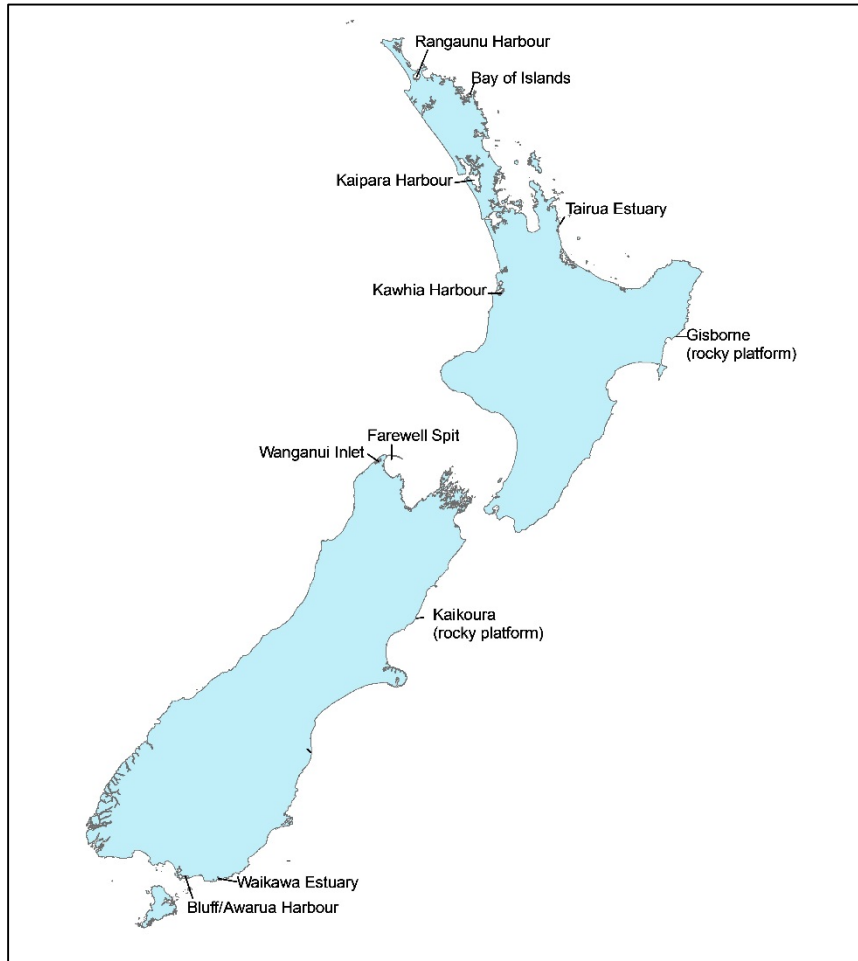


Figure 2: Sampling locations used in the biogeographic survey of New Zealand seagrass meadows. Location and site selection approach is given in Section 3.3.

Table 2: Physical characteristics and habitat composition of the eleven locations surveyed for this study (adapted from T. Hume, NIWA Estuary Environment Classification database). ‘Type’ abbreviations used: DV, drowned valley; TL, tidal lagoon; HW, high water, IS, island, SP, spit, RS, rocky shore.

Harbour	Coast	Type	Area (km ²)	Catchment Area (km ²)	Average Depth (m)	Intertidal Area (% of HW)	Sand Area (% of HW)	Mud Area (% of HW)	Mangrove Area (% of HW)	Seagrass Area (km ²)	Natural Land Cover (%) catchment)	Pastoral Land Cover (% catchment)	Exotic Forest Land Cover (% catchment)	Urban Land Cover (% catchment)	Misc Land Cover (%) catchment)
NORTH															
Is.															
Rangaunu	East	TL	101.7	552	2	78	51	50	25.8	20	30.0	67.8	1.9	0.5	0.3
Bay of Islands	East	IS	2.65	2.65	5	—	—	—	0	0.047	—	—	—	—	—
Kaipara	West	DV	743.1	6266	5	41.9	34	29	8.3	51.28	17.9	70.5	11.3	0.2	0.1
Tairua	East	DV	6.0	282	1	51	51	51	—	~1.25	70.4	15.9	12.4	1.2	0.0
Kawhia	West	DV	67.6	499	2	74	74	73	0	7.93	46.1	53.8	0.1	0.0	0.0
Gisborne	East	RS	—	—	—	—	—	—	—	—	—	—	—	—	—
SOUTH															
Is.															
Farewell Spit	West	SP	—	—	—	—	—	—	—	—	—	—	—	—	—
Whanganui Inlet	West	DV	25.08	87.5	2	79	79	78	0	8.6	89.9	7.7	1.3	0	1.1
Kaikoura	East	RS	—	—	—	—	—	—	—	—	—	—	—	—	—
Waikawa	South	TL	0.11	241	2	53.7	53.7	0	0	0.07	44.8	54.8	0.29	0	0.1
Bluff	South	TL	54.6	99.17	2	52.2	46.8	46.8	0	7.5	78.1	14.9	1.3	4.7	1.1

Fish sampling

Fish were sampled at each location (with the exception of Gisborne and Kaikoura) using beach seine tows. Along with all other sampling, beach seine tows were undertaken between January and April 2006, when recently settled juvenile fish are at their most abundant, and the highest number of fish species are present in estuaries. Tows were made within a tidal window 2.5 hours each side of low tide. For each site, a seagrass and a bare area were identified, and four replicate tows made in each. The net(s) used was 11 m wide and 2.3 m high, with 9 mm mesh and a 4 m long cod end, with a five meter bridle and 15 m sweep attached to each end of the net for hand hauling. When fishing, a sweep/bridle angle of about 25–35° produced a net mouth width of about 9 m, considered to be most effective for fish retention, as specified in Morrison et al. (2002). With a nominal net width of 9 m (Morrison et al. 2002), each tow swept about 450 m² of seafloor. The nets were hauled alongshore (parallel to the shore) by two people for a distance of 50 m, and then the net mouth was closed under tow, and the net pulled onto the adjacent shore-line. At the completion of a tow, the net was shaken down, and all fish removed and placed into labelled plastic bags. Where there was no adjacent shore-line, such as in the subtidal lower Kaipara, and Farewell Spit, the net was pursed together at the end of the tow while still under tow to prevent fish escapement, and then lifted up into a waiting support boat. Sequential tow end and start points were spaced at least 50 m apart, to minimise potential issues of fish disturbance in subsequent tow areas. In the Bay of Islands, the approximately 4 m water depth prevented hand hauling. Long rope warps (100 m) were attached to the net; one warp was run out from the shore, the net set parallel to the shore-line, and the second warp run back to the shoreline. The net was then hand-hauled to the shore, with sufficient separation between the haulers to ensure the net stayed open (as described in Schwarz et al. 2006). The extra rope length was required to account for the bare sediment area between the inner edge of the seagrass meadows, and the shoreline.

At a few sites where very large catches were made of some species (e.g. one tow with about 2000 small snapper in Rangaunu Harbour), a random sub-sample of 50 fish was kept for length analysis, and the remainder counted and released alive. Where possible, larger fish (over 100 mm) such as flounders, snapper, trevally, and eagle rays, were also measured and released alive. All retained fish samples were held on ice until return to land, where they were frozen until processing.

A target of up to ten individuals of each fish species were taken from the aggregate tows for a given site/habitat for dietary gut analysis; selected to cover the size range present at the time. These fish were injected with 10% buffered formalin to preserve prey items in the gut for later microscopic analysis.

We note that using beach seines for subtidal sampling during low tide samples both fish that have migrated from the adjacent intertidal flat during low tide periods, and fish that are permanently ‘resident’ in the subtidal area. Previous work has shown that such movement occurs for some species (Morrison et al. 2002), and that distinct fish ‘habitat signals’ can be seen between sites very close together sampled at low tide (i.e. between intertidal and subtidal seagrass, Whangapoua Harbour, Morrison et al. unpubl. data), implying direct vertical tidal movements on and off the intertidal flats. Effectively, this means that while subtidal seagrass meadows and bare sediment areas are sampled directly, the intertidal seagrass meadows and bare sediment sites are sampled on the assumption that fish retreat from these habitats during low tide and reside in the adjacent low tide zone. In effect, the intertidal and subtidal bare sediment tows are the same as each other, with the only difference usually being where they are positioned in the estuary (e.g. bare intertidal beach seines were positioned next to intertidal banks, while bare subtidal beach seines were positioned away from any lowtide banks). While other sampling methods have been developed since this field programme was completed, none allow the sampling of both intertidal and subtidal beds over high tide periods; and they also require detailed habitat and bathymetry maps to allow for specific habitat types to be targeted. It should be noted here that all sampling was conducted during daylight hours and as such may have undersampled those fish species which move into a habitat during the night; some fish may also have higher vulnerabilities to capture at night (Morrison et al. 2002).

Sampling of infaunal invertebrates

At each site, small hand deployed benthic corers (13 cm diameter) were used to sample the benthic infauna and small epifauna (i.e. those nominally under 10 mm) to a sediment depth of about 15 cm. Cores were sampled haphazardly across the sampling site, either on foot (for intertidal and shallow sub-tidal sites) or by diver (for deeper sub-tidal sites). Four replicate cores per site were collected. The contents of each core were sieved through a 1 mm sieve, and the live material retained on this sieve was preserved in 10% buffered formalin solution. While most sites were generally discrete as either seagrass or bare sediment, in the case of Urapukapuka Island (Bay of Islands), the patchy nature of the seagrass present and the fact that it occupied virtually all of the bay meant that bare sediment core samples had to be interspersed between seagrass patches, with bare cores being taken at a distance at least 10 m from the nearest seagrass patch. Sediment grain size analysis from these benthic cores was not carried out due to logistical constraints. Sampling of the bare habitats at Kaikoura was actually of trapped sediment held in what were presumed to be dead seagrass matts, though there was no evidence of blades; what appeared to be decayed root masses bound the sediment together as low mounds.

Sampling of epifaunal invertebrates

Fifty metre long by 2 metre wide strip transects (subsequently reduced to 20 m long after the first field trip for logistical reasons) were used to sample the larger epifauna (i.e. nominally those over 10 mm) living on the seagrass and bare sediment habitats. Positions for these strip transects were haphazardly chosen within the appropriate habitat (either seagrass or bare sand) and a fibreglass measuring tape was used to delineate the search area (i.e., 40 m²) which was then visually searched for organisms. For subtidal strip transects, a diver laid out a tape for 20 m while avoiding disturbing the sediment surface, and then returned to the start point. With a companion diver, they moved slowly along either side of the tape visually searching for organisms which were placed inside a plastic bag, while using a light steel rod 1 m wide to identify the search area edge. Four replicate strip transects were conducted at each site. At the end of the transect all of the organisms collected were placed into one plastic bag, which was taken back to the boat, labelled and stored on ice, and frozen on return to land.

Seagrass blade length and biomass

In the laboratory, seagrass material collected in the cores was separated from any sediment and thoroughly rinsed through a 1 mm sieve to ensure that all benthic invertebrates were removed. The maximum length of the first five plants haphazardly selected from within each core was recorded. Seagrass material was subsequently separated into above (blades) and below (roots) ground categories and oven dried at 60°C for 48 h. Samples were then cooled in a desiccator and weighed. Biomass was expressed as g dry weight (DW) / core.

Bird counts

Although bird counts were originally suggested as part of the methodology to be employed in this project, these proved impossible to carry out in the field; largely due to the short timeframe for sampling around the low tide window, including water being over the habitats at the time of arriving at a site, and the human activity being thought to inhibit the activities of birds in the area.

3.3 Laboratory Methods

Fish identification and enumeration

Each beach seine sample was thawed, and the catch sorted to species. All fish for each species were enumerated, and measured for length (either fork length or total length, depending on the species). Where a species was present in large numbers, 50 to 100 fish were sub-sampled for length, and these lengths were scaled up to estimate the length frequency for the full sample.

Fish prey utilisation

To ascertain resource utilisation of the benthos by fish species present in each beach seine trawl, prey items consumed by each fish species were identified by analysis of gut contents. Foreguts were

removed and the contents were identified to genus or species level (where possible) under a dissecting microscope. In order to estimate biomass and directly compare the size distribution of ingested prey items with invertebrate size structure identified from the benthic core sampling, animals were allocated to sieve size-classes by eye using a graticule in the microscope, and a reference collection consisting of a mixture of species retained by different sized sieves as described by Edgar et al. (1994). The percent occurrence of detritus, macroalgae and sessile organisms (e.g. sponges and bryozoans) was estimated by volume (i.e., via the % cover when squashed flat to about 1 mm height on a petri dish). Organisms unable to be identified to the species level (e.g., due to heavy erosion of the shell or algal/invertebrate encrustation) were recorded as unidentified species.

Data on the mean ash-free dry weight (AFDW) of animals retained by different sieve sizes, as calculated from the regression equations listed in table 2 of Edgar (1990a) were used to estimate the biomass of individual prey items consumed. This allowed the proportional biomass of each prey species found within the stomach contents of each fish species to be calculated. We acknowledge that some prey items are digested faster than others and this may affect the apparent dietary composition; however no solution exists for such potential effects.

To determine resource utilisation of the benthos by the fish assemblages, prey items were grouped into 12 general categories (Table 3) for analysis. Categories were selected to reflect different feeding modes (i.e. benthic/pelagic), and dominance as a prey item, and are not taxonomically equivalent. For example, amphipods, mysids and 'other pericarids', although all are crustaceans, were given individual categories due to their dominances as prey items. Similarly, zooplankton was separated to denote the pelagic component. Statistical analysis was limited to 16 of the 32 taxa examined due to inadequate total sample sizes ($n < 20$, many only $n=1, 2$) for the other 16 taxa (note: broad dietary components are graphically presented for all 32 taxa).

The mean percentage volumetric contributions (biomass) to the different dietary categories for each dietary sample were calculated and square root transformed, as is appropriate for percentage data (Platell & Potter 2001). Principal Components Analysis (PCA) was used to determine size-related ontogenetic differences in diet for individual fish species, utilizing the length frequency data.

Table 3: Prey categories used in dietary analyses.

Category	Description
Amphipods	Predominantly gammarid amphipods
Decapods	Crabs
Pericarids (other)	Predominantly cumaceans, some isopods and tanaids
Crustacea (other)	All crustaceans excluding copepods, decapod pericarids and mysids
Mysids	All mysid shrimps
Plankton	Calanoid/harpacticoid cyclopoid copepods, cladocerans, barnacle cyprids, decapod zoeae
Fishes	All fishes including larvae
Polychaetes	Worms
Other	Nematodes, oligochaetes, ophiuroids, insects and eggs
Bivalves	All bivalves including siphons
Gastropods	
Plants and Detritus	

Infaunal invertebrate identification and enumeration

Benthic core samples were degassed, preserved in 70% isopropyl alcohol, and stained with 6.2% rose-bengal solution. Samples were washed through a log series of sieves (1.0, 1.4, 2.0, 2.8, 4.0, 5.6, 8.0, 11.2, 16.0, and 22.0 nominal mesh sizes) using the methods described by Edgar (1990a). Organisms were then identified to the lowest taxonomic level possible and the abundance for each sieve size class recorded. All seagrass material was removed and stored separately.

Infaunal community biomass and secondary production

For biomass calculations, data on the mean ash-free dry weight (AFDW) of animals retained by different sieve sizes, as calculated from the regression equations listed in table 2 of Edgar (1990a) were used to estimate the biomass of individual species identified. This allowed the proportional biomass of each infaunal species to be calculated per core. Productivity of the benthic infauna was then estimated using the biomass estimates obtained above and the equation

$$P = 0.0049 * B^{0.80} T^{0.89} \quad (\text{Edgar 1990a})$$

which relates daily macrobenthic productivity P ($\mu\text{g/day}$) to AFDW B (μg) and water temperature T ($^{\circ}\text{C}$) (Edgar 1990a). Estimation of the secondary productivity of the macrobenthic component provides an index of the contribution this community makes to the flux of energy and materials within these habitats (Edgar 1990a).

Epifaunal invertebrate identification and enumeration

Each individual strip transect sample was preserved in 10% buffered formalin solution and then subsequently degassed, preserved in 70% isopropyl alcohol, and stained with 6.2% rose-bengal solution. For each strip transect, individual organisms were identified to the lowest taxonomic level possible and enumerated.

3.4 Data analysis

Fish

In order to standardise for differences in area sampled between different beach seine replicates, and make them comparable with other studies, fish abundances were expressed as number of individuals per 100 m².

Univariate data analysis on fish species richness and total abundance were conducted using a nested ANOVA, followed by Tukey HSD *post hoc* pairwise comparisons (SYSTAT 13, 2009). Data were log10 transformed, and a constant was added to ensure that all values were greater than zero. We note that given the large number of significance tests completed, the possibility of Type II error is increased. No corrections such as that of Bonferonni were applied, as such tests are extremely conservative. The reader is reminded to be aware of the possible occurrence of such errors.

Spatial variations in fish community structure were analysed on fish abundance data using the PERMANOVA multivariate approach as provided for in Primer-E 6.1.13 (Clarke & Warwick 2001) and PERMANOVA+ (1.0.3) (Anderson et al. 2008). Species composition data were fourth root transformed to downweight the influence of highly abundant species. The Bray Curtis similarity matrix was used as the best fit for biological assemblage data. The PERMANOVA design contained the following factors:

Island:

North, South

Location:

North: Rangaunu Harbour, Bay of Islands, Kaipara Harbour, Tairua Harbour, Kawhia Harbour

South: Farewell Spit, Whanganui Inlet, Waikawa Harbour, Bluff Harbour

Position:

Upper or Lower

North: Rangaunu Harbour, Kaipara Harbour

South: Farewell Spit, Bluff Harbour

Habitat:

Bare intertidal (BI), Seagrass intertidal (SI), Bare subtidal (BS), Seagrass subtidal (SS).

PERMANOVA utilises permutations based on dissimilarities and does not assume a normal distribution for the original variables, making it a useful tool for analysing ecological community datasets (Anderson et al. 2008). Further pair-wise tests were also conducted to detect which group differences contributed to any significant result using PERMANOVA. Monte Carlo tests were undertaken in the pair-wise test function in PERMANOVA if low permutations were obtained. The Monte Carlo (*P*) value is better suited and more reliable when there are not enough possible permutations (i.e. fewer than 100) to get a decent test (Anderson et al. 2008).

Following the PERMANOVA analysis the contributions of particular fish species to any identified significant differences in community assemblages were assessed using a SIMPER analysis (Clarke & Gorley 2006).

Infaunal invertebrate analysis

Benthic core infaunal invertebrate data are reported as the number of individuals, species richness, biomass, and secondary production per core. Univariate data analysis of these measures were conducted using a nested ANOVA, followed by Tukey HSD *post hoc* pairwise comparisons (SYSTAT 13, 2009). Data were log10 transformed, and a constant was added to ensure that all values were greater than zero.

To determine the diversity and evenness of invertebrate species composition at all sites, three different diversity indices were calculated (Shannon-Wiener index, Pielou's evenness and Simpson's index) based on the total number of individuals (*N*) from the number of species (*S*). The Shannon-Wiener

index identifies greater species diversity with an index number closer to one. Pielou's index identifies the equitability of species presence at each site where a larger number indicates less evenness and Simpson's index is a measure of ecological diversity with infinite diversity decreasing from zero to one, indicating dominance of single species (Clarke & Warwick 2001).

Spatial variations in infaunal invertebrate community composition were analysed in the same fashion as that previously described in the "fish analysis" section. The above analysis was also repeated in its entirety using taxonomic groupings by class, rather than for individual invertebrate species.

The nursery role of seagrass habitats for bivalve species was also explored via descriptive analysis of the infaunal invertebrate dataset, where numbers of an individual species allowed this. Statistical analysis was not carried out due to the modest numbers of shellfish harvested.

Epifaunal invertebrate analysis

In order to standardise for the difference in area sampled between different strip transects, invertebrate abundances were expressed as number of individuals per 100 m². At the Farewell Spit (upper) bare intertidal habitat no organisms were found in any of the strip transect runs, so this site is excluded from the analyses.

Univariate data analysis on epifaunal invertebrate species richness and total abundance were conducted using a nested ANOVA, followed by Tukey HSD *post hoc* pairwise comparisons (SYSTAT 13, 2009). Data were log10 transformed, and a constant was added to ensure that all values were greater than zero. The multivariate analysis was the same as that described above for infaunal invertebrates.

3.5 Seagrass as an ecosystem fuel (isotopic analysis)

Sample field collection

Primary (plants) and secondary (animal) producer samples were collected in both Rangaunu (a relatively pristine estuary) and Kaipara (a harbour known to be influenced by anthropogenic inputs) harbours to encapsulate the anticipated flow of seagrass associated carbon and nitrogen through different trophic levels of these seagrass related foodwebs.

For phytoplankton samples, replicate 20 L volumes of seawater were filtered through pre-ashed GF filters and stored frozen for further analysis. Various primary producers (macroalgae (red and green), epiphytes, mangrove litter and seagrass) were also sampled and again stored frozen for isotopic analysis. Faunal samples including: bryozoans, sponges, ascidians, bivalves, gastropods, echinoderms, crustaceans and fish were also collected and stored frozen for later isotopic analysis.

Sample preparation

Phytoplankton on pre-ashed GF Filters: Whole filters plus filtered phytoplankton were folded and placed into tin boats in preparation for combustion on the NA1500 CHN analyser linked to the Delta^{plus} mass spectrometer (see below for mass spectrometer details). For each batch run of filters + phytoplankton samples a set of filter blanks were run so that the %C, %N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signal from the filter paper blank could be subtracted from the filter+sample signal.

Plants (red and green macroalgae, epiphytes, mangrove litter and seagrass)

Sub-samples of all plants collected were dried, ground and weighed out into tin boats ready for analysis on the mass spectrometer.

Fauna (bryozoans, sponges, ascidians, bivalves, gastropods, echinoderms, crustaceans and fish)

Small portions of the whole organism were taken from the bryozoans, sponges and ascidians, which were then processed in the same way as the remaining fauna. For all other larger organisms small pieces of muscle (less than 10 mg) were sub-sampled and prepared for lipid extraction. Both muscle and whole organism tissue contain a mixture of protein and lipid, which can cause problems when interpreting isotopic data. Lipid synthesis strongly discriminates against the ^{13}C isotope (De Niro & Epstein 1977, 1978) leading to more negative $\delta^{13}\text{C}$ in lipid-rich tissues that is independent of the organism's diet. Lipids are therefore known to be ^{13}C depleted relative to protein and carbohydrate (Rounick & Winterbourn 1986). Lipids and proteins, or tissues such as fat and muscle, have been shown to have $\delta^{13}\text{C}$ values that differ by as much as 2 ‰ or more (Parker 1964, van der Merwe 1982) and more recent studies show that lipid $\delta^{13}\text{C}$ values can differ by as much as 3–8 ‰ (Schell 2002, Jardine & Cunjak 2006, Logan & Lutcavage 2006). It is well known that the proportion of lipid in muscle samples varies with a number of physiological factors of the individual animal, including for example, age, sex, reproductive stage, and condition. The presence of lipid biases the results of stable isotope analysis in a way which is not straightforward to correct retrospectively. Lipid extraction of the sample therefore needs to be carried out before the isotopic signature of the sample is analysed. All fauna sub-samples were therefore placed in labelled 1.5 ml eppendorf tubes, freeze dried and then lipid-extracted prior to being crushed and weighed out into tin boats for mass spectrometer analysis.

Lipid extraction

Lipid extraction was performed on a DIONEX 200 accelerated solvent extraction system (ASE), which is an approved Environmental Protection Agency (EPA) method for the extraction of lipid soluble contaminants in solid matrices, e.g. marine biota (Greg Olsen, *pers. comm.*). Samples were transferred to 22 mL s/s ASE cells and extracted three times with dichloromethane at 70 °C and 1500 psi for a static hold time of 5 minutes. Standard reference materials were run to monitor lipid recovery rates using the ASE method, which were in excess of 95 % following the second cycle of extraction (Greg Olsen, *pers. comm.*). Following extraction, samples were then heated to 40 °C in an oven overnight to evaporate any traces of solvent. Samples were dried in an oven at 50 °C in their GF/C envelopes for 24 hrs. After drying, samples were put in a desiccator until weighing for isotope analysis.

Mass spectrometer stable isotope analysis

All stable isotope analyses were carried out on NIWA's Delta^{Plus} (Thermo-Finnigan, Bremen, Germany) continuous flow, isotope ratio mass spectrometer (Bury 1999). Solid samples were weighed out into tin boats and combusted in an NA 1500N (Fisons Instruments, Rodano, Italy) elemental analyser combustion furnace at 1020 °C in a flow of oxygen and helium carrier gas. Oxides of nitrogen were converted to N_2 gas in a reduction furnace at 640 °C. N_2 and CO_2 gases were separated on a Porapak Q gas chromatograph column before being introduced to the mass spectrometer detector via an open split Conflo II interface (Thermo-Finnigan, Bremen, Germany). CO_2 and N_2 reference gas standards were introduced to the mass spectrometer with every sample analysis. ISODAT (Thermo-Finnigan) software was used to calculate $\delta^{15}\text{N}$ values against atmospheric air, and $\delta^{13}\text{C}$ values against the CO_2 reference gas relative to PDB, correcting for ^{17}O . Percent C and % N values were calculated relative to a solid laboratory reference standard of DL-Leucine (DL-2-Amino-4-methylpentanoic acid, $\text{C}_6\text{H}_{13}\text{NO}_2$, Lot 127H1084, Sigma, Australia) at the beginning of each run. Internal standards were routinely checked against National Institute of Standards and Technology (NIST) standards. Accuracy and precision data for NIST standard analyses, and repeat analyses of DL-Leucine standards during batch analysis, are given in Appendix 1. Repeat analysis of NIST standards produces data accurate to within 0.1–0.5 ‰ for $\delta^{15}\text{N}$ and 0.3–0.4 ‰ for $\delta^{13}\text{C}$ and a precision of better than 0.5 ‰ for N and 0.25 ‰ for C. For % N and C content, data are accurate to within 0.4%, with a precision usually better than 0.3% for N and 0.2% for C.

3.6 Seagrass replication mechanisms

Sample collection

Seagrass samples were collected for genetic analyses at two spatial scales: specific locations, and New Zealand wide, as an integrated part of the fieldwork programme. Sampling locations were: North Island – Bay of Islands, Kaipara Harbour, Kawhia Harbour, Gisborne (rocky reef); and South Island – Farewell Spit, Kaikoura (rocky reef) and Bluff Harbour (Figure 2). At each location, four sites were sampled at approximately 0, 10, 100, and 1000 m, either within an extensive seagrass meadow or between patches. Sampling at nationwide scales was designed to test genetic differentiation either side of large scale current boundaries, such as Cook Strait where the D’Urville and Wairarapa coastal currents appear to restrict gene flow in snapper and some invertebrates (Apte & Gardner 2002, Ayers & Waters 2005, Bernal-Ramirez et al. 2003, Goldstein et al. 2006). Seagrass samples were collected at four sites in each of the following regions: the Bay of Islands (BI), Kaipara (KP), Gisborne (GI), Farewell Spit (FS), Kaikoura (KK), and Bluff (BF), and at five sites at Kawhia (KW), 0, 10, 100, 900, and 1000 m.

At each site leaf samples were collected from live plants within an approximate one metre radius, by gently pulling on the leaves to reveal the rhizome. The top portion of each leaf was discarded and the lower 3–4 cm of the leaf cut off near the leaf sheath on the rhizome. Each leaf sample was placed in a separate tube pre-filled with 90% ethanol and placed in a plastic clip-top bag labelled with region name and site.

DNA extraction and amplification

Three DNA extraction methods were evaluated in an initial set of samples:

- Homogenisation and digestion with proteinase-K at 55 °C for 4 h, followed by phenol/chloroform extraction, then chloroform/isoamyl alcohol, and precipitation with 70% ethanol at –20 °C;
- Homogenisation with the Qiagen Dneasy™ isolation kit, following manufacturer’s instructions (Qiagen Inc., United States); and
- Digestion and incubation in CTAB (cetyl trimethyl ammonium bromide) extraction buffer, followed by chloroform/isoamyl alcohol extraction, and precipitation with 70% ethanol.

Only the CTAB DNA extraction method resulted in DNA products that amplified with RAPD primers in the initial tests, so this method was used for subsequent DNA extractions, details of which are given here. DNA extractions followed those used for seagrass (Procaccini et al. 1996) using a modified CTAB protocol (Doyle & Doyle 1987, Martin et al. 1999). A small amount of clean shoot tissue (0.5 g) was rinsed in de-ionised water, minced with scissors, placed in an eppendorf centrifuge tube with 500 µl 2% CTAB and 20 µl proteinase K, and incubated at 60° C for a minimum of 4 h. Following incubation 500 µl of chloroform/isoamyl alcohol (24:1) was added, mixed by inversion and centrifuged at 12000g for 10 min, after which the clear supernatant was pipetted into a clean eppendorf tube. The DNA was precipitated by adding 500 µl cold (4°C) 70% ethanol, followed by centrifugation at 12000g for 10 min. The DNA pellet was washed in 70% ethanol and then air dried before being re-dissolved in 40 µl sterile deionised water and stored at –20 °C.

PCR reactions were performed in 50 µl volumes in a Cetus 9600 DNA thermocycler (PerkinElmer Inc., Boston, USA), and followed those used at NIWA for RAPDs (Smith et al. 1997, Smith 2005, Smith et al. 1996). Each sample was amplified separately with a 10-base oligonucleotide primer from Operon Technologies, Alameda (Appendix 2). These primers were randomly selected, but have a G+C content of 60–70%. Serial dilutions of DNA samples were tested to determine optimum DNA concentration for amplification. Subsequently, the DNA concentration in each sample was estimated fluorometrically, using a Qubit fluorometer (Invitrogen) to ensure consistency among amplifications. The optimum primer and MgCl₂ concentrations were tested experimentally. Amplification reactions contained approximately 50 ng DNA template in 10 mM Tris HCl pH8.3, 30 ng single 10-base primer, 50 mM KCl, 2 mM MgCl₂, 100 mM each of *d*ATP, *d*CTP, *d*GTP, and *d*TTP, and 1 unit Taq DNA

polymerase in Perkin Elmer PCR buffer. Blank controls were run with the DNA template replaced by de-ionised water.

Amplifications were carried out for 40 cycles of 1 min at 94 °C to denature the DNA, 1 min at 36 °C to allow the primers to anneal to their complementary sequence, and 2 min at 72 °C to extend the annealed primers; followed by a final step of 5–10 min at 70–75 °C to allow complete extension. The amplification products were separated in 1.4% agarose gels, along with a DNA size ladder and a blank control (no DNA template), and detected with ethidium bromide staining under a UV light (312 nm). The raw data were captured with a digital gel documentation system, and line drawings made of fragments.

Studies of RAPDs in aquatic species have noted that changes in PCR parameters (in particular concentration of primer, concentration of template, annealing temperature, and concentration of magnesium ions) or quality of the DNA sample can alter RAPD fragment patterns (Smith 2005). Potential problems with reproducibility of seagrass RAPDs were minimised by determining the optimum amplification conditions and using the same thermocycler, amplification protocol, and batch of reagents throughout the study. Each selected primer was re-amplified to test for repeatability of DNA fragments.

A suite of 59 10-mer RAPD primers (Appendix 2) were screened in a sub-set of 3 pooled samples from a wide geographic range (one pooled sample from each of the Bay of Islands, Farewell Spit, and Bluff) to find appropriate primers for population studies. Primers producing repeatable fragment patterns in the initial screening were tested in 5 specimens per site at two spatial scales (0 and 1000 m) in five areas (Bay of Islands, Gisborne, Farewell Spit, Kaikoura, and Bluff). The few primers producing consistent fragment patterns in this larger population sample were tested in additional population samples. Distinct well-stained and repeatable fragments between 200 and 2000 bp were scored and numbered with the primer code and the fragment number. The total fragment pattern (presence/absence) of each individual specimen was treated as the RAPD phenotype or composite genotype.

The homology of selected fragments of the same size in different populations was tested by sequencing. Selected fragments were band stabbed from the agarose gels (Bjourson & Cooper 1992) and re-amplified. The re-amplified products were separated in 1.4% agarose gels in a TBE buffer (25 mM Tris, 0.5 mM EDTA, and 25 mM boric acid), stained with ethidium bromide, and viewed under ultraviolet (UV) light. Samples that produced a single amplified product of appropriate size were purified using the QIAquick gel extraction kit (Qiagen Inc United States), and sequences determined using the ABI Taq DyeDeoxyTM Terminator Cycle Sequencing Kit according to manufacturer's directions (Applied Biosystems Inc., California, United States) and analysed on an ABI prism autosequencer. DNA sequences were edited in CHROMAS (Technelysium, Queensland), aligned in CLUSTAL in MEGA version 4 (Kumar et al. 2004), and a similarity matrix calculated in BIOEDIT (Hall 1999).

RAPD analyses

Hierarchical structure in the data was tested by partitioning variance components within and among regions with an analysis of molecular variance, AMOVA (Excoffier et al. 2005) using the Arlequin (v 3.1) package (Schneider et al. 2000). AMOVA generates an F_{ST} or standardized genetic variance (Wright 1949) based on the frequency of composite genotypes. The AMOVA was developed for RFLP haplotypes but can be applied to RAPD's where the multi-locus RAPD phenotypes (i.e. composite genotypes) are considered as haplotypes (Excoffier et al. 2005).

Isolation by distance was tested with a Mantel test in the IBDWS web program (Jensen et al. 2005), by testing genetic distance (measured as F_{ST}) against geographic distance both within regions and between neighbouring regions. A genetic distance matrix based on F_{ST} values was estimated with Arlequin v 3.1, and pair-wise genetic distances regressed against log transformed straight-line shortest sea distances.

Genetic distances within and among regions were visualised in a tree generated by UPGMA with bootstrapping in the Tools for Population Genetic Analyses (TFPGA) programme v 1.3 (Miller 1997). Bootstrap values greater than 75% are generally considered to be significant (Hillis & Bull 1993).

4. RESULTS

4.1 Biodiversity of fish associated with seagrass across New Zealand

Fish Community Structure

Overall, a total of 103 beach seine tows were completed around New Zealand, which sampled 40 447 individuals, from 34 fish species, along with 12 individuals from 2 squid species (Table 4). The five most abundant families, based on total abundance were Mugilidae (40.9%), Gobiidae (17.9%), Pleuronectidae (27.3%), Clupeidae (10%) and Hemiramphidae (8.6%) accounting for 60% of the total catch. Ninety three percent of all individuals were juveniles or adults of small sized demersal species, comprised of nine species. These included in order of respective importance, yellow-eyed mullet (40%), snapper (10%), sand goby (9%), garfish (9%), exquisite goby (9%), mottled triplefin (7%), smelt (4%), spotty (3%), sand flounder (2%), and parore (2%). A further four species contributed 1% each (speckled sole, jack mackerel, grey mullet and anchovy). Individuals of the remaining 20 species were captured in modest numbers only.

Ecological fish guilds (i.e., a group of fish which biologically use an estuary in a similar fashion), were dominated by marine migrants, comprising estuarine opportunist (MMO) species 45%, followed by marine estuarine dependent (MMD) 17%, and marine stragglers (17%). Resident species made up 14%. Smelt was the only anadromous species.

Spatial variation in fish abundance

Overall, fish abundance showed strong spatial variability along the latitudinal gradient (north to south), between the east and west coast harbours (North Island only), and between habitat types within estuaries (Figure 3). Species richness was less variable (Figure 3). The highest fish densities were recorded at Rangaunu, the northernmost harbour, particularly for upper subtidal seagrass sites where densities reached 254.8 ± 134.8 fish per 100 m^2 (dominated by juvenile snapper). Sand habitats generally returned lower catch rates compared to both intertidal/subtidal seagrass sites, in the North Island, ranging from 5 ± 0.47 to 14.7 ± 3.8 fish per 100 m^2 for Rangaunu and Kaipara respectively. Conversely, southern sites showed the reverse trend (with the exception of Whanganui Inlet), with four out of the five harbours showing equivalent or higher fish abundances over sand than for seagrass habitats. South Island densities ranged from a high of 137.3 ± 195.9 (Whanganui Inlet) to a low of 10.9 ± 11.1 fish per 100 m^2 (Waikawa). An ANOVA comparison revealed significant differences in fish densities for the same habitat (e.g. intertidal seagrass) across position and between islands (*d.f.* 6, *f* 2.345, $P < 0.037$) (Figure 4a). A second ANOVA analysis of fish densities between habitats within one position, between islands, was not significant (*d.f.* 8, *f* 1.797, $P < 0.088$) (Figure 4a). Tukey HSD *post hoc* analysis of these ANOVA results show that upper intertidal seagrass (North Island) had significantly higher densities than for equivalent South Island sites (Figure 4a). Additionally, lower South Island intertidal bare sites had significantly higher densities than for all other position across island combinations. Of note for this analysis, was the lack of a comparable upper subtidal seagrass habitat as recorded for Rangaunu Harbour, at any of the other locations (thought to be due to the relative 'pristineness' of this harbour).

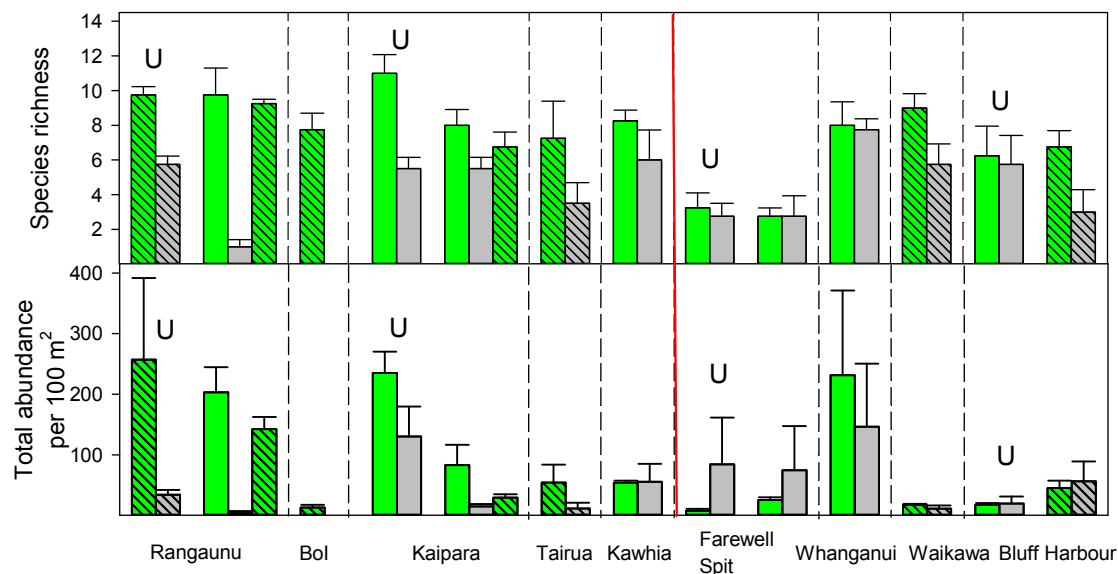


Figure 3: Species richness (top) and total abundance (bottom) of all fish species caught by beach seine from seagrass and sand habitats from nine locations in the North and South Island. U = upper harbour sites, all other sites are by default lower harbour sites. Green shading, seagrass; grey shading, bare sediments; hatching, subtidal, no-hatching, intertidal. Red line denotes break between North and South Islands.

Spatial variation in fish species richness

Overall, species richness was relatively low, ranging from 1.3 to 11.5 per tow (Figure 3). This was unexpected given the total species pool (36 species) of sampled estuarine fish. Seagrass habitats pooled over all North Island sites had double the number of species counts than for sand habitats (8.8 compared to 4.2), while differences between habitats in the South Island were less pronounced (7.6 compared to 5.7) (Figure 4). An ANOVA comparison revealed significant differences in species richness for the same habitat (e.g. seagrass intertidal) across position (upper or lower) and between islands combinations ($d.f. 6, f 2.219, P < 0.048$) (Figure 4a).

Table 4: Mean density and richness per 100 m² (± s.e.), of all fish species collected from bare and seagrass habitats by beach seines at 27 sites from nine locations in the North and South Islands. Species order is ranked by abundance from north to south.

Location	Rangaunu Harbour										Bay of Islands		Kaipara Harbour						Tairua Harbour				Kawhia Harbour							
Position	Upper					Lower					Upper						Lower													
Habitat	SS		BI		SI		BI		SS		SS		BI		SI		SI		SS		BS		SS		BS		SI		BS	
Species richness	9.80	[0.5]	5.80	[0.5]	9.80	[1.5]	1.00	[0.4]	9.30	[0.3]	7.80	[0.9]	5.50	[0.6]	11.00	[1.1]	8.00	[0.9]	6.80	[0.9]	5.50	[0.6]	7.30	[2.1]	3.50	[1.2]	8.30	[0.6]	6.00	[1.7]
Overall fish density	256.86	[155.4]	33.80	[15.7]	203.11	[80.1]	4.24	[3.4]	142.26	[64.8]	12.80	[4.6]	129.95	[49.6]	234.80	[35.4]	83.09	[33.4]	29.10	[5.8]	14.72	[3.8]	53.87	[29.9]	11.44	[9.5]	53.63	[3.5]	55.22	[29.5]
Broad squid	–	–	–	–	–	–	–	0.03	[0.03]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Koheru	0.17	[0.2]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pilchard	–	–	–	–	0.06	[0.1]	–	–	0.03	[0.03]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Jack mackerel	16.33	[16.3]	–	–	–	–	–	–	0.34	[0.3]	–	–	–	–	0.06	[0.1]	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sand goby	10.28	[7.3]	7.11	[2.5]	135.55	[45.0]	2.74	[1.9]	28.15	[16.4]	–	–	0.61	[0.5]	2.44	[0.7]	0.17	[0.1]	0.08	[0.05]	–	–	–	–	–	–	–	–	–	–
Snapper	159.14	[105.2]	6.67	[1.8]	2.56	[1.0]	–	–	21.57	[5.2]	4.89	[1.6]	–	–	0.22	[0.2]	–	–	5.18	[1.0]	0.61	[0.2]	0.11	[0.1]	–	–	0.06	[0.1]	0.11	[0.1]
Red mullet	0.39	[0.1]	0.06	[0.1]	–	–	–	–	0.25	[0.1]	0.50	[0.3]	–	–	–	–	–	–	–	–	–	–	0.06	[0.1]	–	–	0.03	[0.03]	–	–
Exquisite goby	7.89	[3.2]	10.94	[5.7]	25.83	[9.4]	1.50	[1.5]	18.06	[8.8]	0.17	[0.1]	0.44	[0.4]	35.44	[17.6]	58.93	[28.2]	9.52	[3.3]	3.56	[0.6]	0.33	[0.3]	–	–	3.67	[1.1]	0.09	[0.1]
Anchovy	–	–	–	–	0.06	[0.1]	–	–	–	–	–	–	2.06	[2.1]	0.67	[0.5]	–	–	–	–	8.72	[3.7]	–	–	–	–	–	–	–	–
Trevally	1.72	[1.0]	–	–	0.11	[0.1]	–	–	0.12	[0.1]	0.33	[0.2]	–	–	0.56	[0.3]	0.67	[0.2]	4.49	[1.7]	0.06	[0.1]	0.50	[0.2]	–	–	0.11	[0.1]	–	–
Grey mullet	–	–	–	–	–	–	–	–	–	–	–	–	0.06	[0.1]	10.17	[3.4]	1.11	[0.5]	–	–	–	–	0.28	[0.3]	–	–	0.22	[0.2]	–	–
Striped clingfish	–	–	–	–	0.06	[0.1]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.06	[0.1]	
Kahawai	–	–	–	–	0.06	[0.1]	–	–	–	–	–	–	0.11	[0.1]	1.33	[0.6]	1.06	[1.0]	0.06	[0.1]	0.06	[0.1]	–	–	0.39	[0.4]	0.44	[0.4]	1.78	[1.6]
Estuarine triplefin	1.89	[0.4]	0.83	[0.6]	1.94	[0.7]	–	–	–	–	0.67	[0.4]	–	–	–	–	–	–	–	–	–	–	4.33	[2.4]	–	–	–	–	–	–
Spotty	40.72	[15.1]	1.11	[1.0]	0.50	[0.3]	–	–	8.70	[1.4]	2.17	[1.3]	–	–	–	–	–	–	0.06	[0.1]	–	–	2.11	[1.3]	–	–	–	–	–	–
Parore	–	–	–	–	0.50	[0.3]	–	–	–	–	0.22	[0.1]	–	–	–	–	0.06	[0.1]	–	–	–	–	39.87	[23.2]	–	–	–	–	–	–
Short-finned eel	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.06	[0.1]	–	–	–	–	–	–	–
Bumble bee squid	–	–	–	–	–	–	–	–	0.50	[0.3]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Yellow-belly flounder	–	–	–	–	–	–	–	–	–	–	–	–	2.11	[2.5]	0.78	[0.3]	0.33	[0.2]	–	–	0.06	[0.1]	–	–	–	–	1.56	[0.6]	–	–
Yellow-eyed mullet	–	–	–	–	32.83	[21.5]	–	–	2.96	[3.0]	0.44	[0.3]	106.95	[43.0]	176.77	[28.6]	12.67	[3.2]	–	–	–	–	4.67	[2.7]	13.19	[8.7]	36.94	[5.9]	46.31	[32.4]
Speckled sole	–	–	–	–	0.06	[0.1]	–	–	–	–	–	–	7.67	[6.2]	0.50	[0.4]	6.39	[3.9]	0.22	[0.1]	0.89	[0.5]	0.06	[0.1]	0.44	[0.2]	3.89	[0.4]	0.52	[0.2]
Garfish	12.83	[5.3]	5.67	[3.2]	1.33	[0.7]	–	–	30.71	[15.7]	2.00	[1.0]	–	–	2.22	[2.2]	–	–	6.14	[2.9]	0.44	[0.3]	0.11	[0.1]	–	–	0.11	[0.1]	5.75	[5.6]
Red gurnard	–	–	–	–	–	–	–	–	–	–	–	–	0.06	[0.1]	–	–	0.06	[0.1]	–	–	–	–	–	–	–	–	0.11	[0.1]	0.03	[0.03]
Black pipefish	–	–	0.06	[0.1]	0.56	[0.3]	–	–	0.09	[0.1]	0.11	[0.1]	–	–	0.06	[0.1]	0.17	[0.1]	–	–	0.06	[0.1]	0.50	[0.3]	–	–	0.06	[0.1]	0.03	[0.03]
Sand flounder	0.06	[0.1]	–	–	–	–	–	–	–	–	–	–	9.89	[1.9]	3.50	[1.2]	1.44	[0.6]	–	–	0.06	[0.1]	0.06	[0.1]	0.22	[0.1]	6.11	[1.1]	0.35	[0.2]
Slender sprat	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Slender stargazer	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sand atargazer	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Speckled pipefish	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.11	[0.1]	–	–	0.10	[0.1]	–	–	–	–	–	–	0.03	[0.03]	–	–
Estuarine stargazer	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.44	[0.3]	–	–	–	–
Mottled triplefin	5.44	[1.1]	1.39	[0.7]	1.11	[0.5]	–	–	31.23	[13.8]	0.67	[0.6]	–	–	–	–	0.06	[0.1]	3.25	[1.3]	0.22	[0.2]	0.78	[0.8]	–	–	–	–	0.18	[0.1]
Smelt	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leatherjacket	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Spotted stargazer	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.28	[0.1]	–	–
Smooth pipefish	–	–	–	–	–	–	–	–	–	–	0.11	[0.1]	–	–	–	–	–	–	–	–	–	–	0.06	[0.1]	–	–	–	–	–	–
Red cod	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Table 4 continued.

Location	Farewell Spit								Whanganui Inlet				Waikawa Harbour				Bluff Harbour							
Position	Upper				Lower												Upper				Lower			
Habitat	SI		BI		SI		BI		SI		BI		SS		BS		SI		BI		SS		BS	
Species richness	3.30	[0.9]	2.80	[0.8]	2.80	[0.5]	2.80	[1.2]	8.00	[1.4]	7.80	[0.6]	9.00	[0.8]	5.80	[1.2]	6.30	[1.7]	5.80	[1.7]	6.80	[0.9]	3.00	[1.3]
Overall fish density	7.48	[3.1]	84.32	[77.0]	25.22	[4.5]	74.44	[72.9]	231.29	[139.5]	146.32	[103.8]	17.14	[1.9]	10.92	[5.6]	17.04	[3.2]	19.64	[11.4]	45.11	[12.11]	56.19	[32.8]
Broad squid	–		–		–		–		–		–		–		–		–		–		–		–	
Koheru	–		–		–		–		–		–		–		–		–		–		–		–	
Pilchard	–		–		–		–		–		–		–		–		–		–		–		–	
Jack mackerel	–		–		–		–		–		–		–		–		–		–		–		–	
Sand goby	–		–		–		–		–		–		–		–		–		–		–		–	
Snapper	–		–		–		–		–		–		–		–		–		–		–		–	
Red mullet	–		–		–		–		–		–		–		–		–		–		–		–	
Exquisite goby	–		–		–		–		–		–		–		–		–		–		–		–	
Anchovy	–		–		–		–		–		–		–		–		–		–		–		–	
Trevally	–		–		–		–		–		–		–		–		–		–		–		–	
Grey mullet	–		–		–		–		–		–		–		–		–		–		–		–	
Striped clingfish	–		–		–		–		–		–		–		–		–		–		–		–	
Kahawai	–		–		–		–		–		–		–		–		–		–		–		–	
Estuarine triplefin	–		–		–		–		0.74	[0.4]	0.06	[0.1]	–		0.04	[0.04]	–		–		–		–	
Spotty	–		–		–		–		1.22	[0.4]	–		1.42	[0.5]	2.21	[0.5]	0.37	[0.3]	1.75	[1.2]	–		–	
Parore	–		–		–		–		–		–		–		–		–		–		–		–	
Short-finned eel	–		–		–		–		–		–		–		–		–		–		–		–	
Bumble bee squid	–		–		–		–		–		–		–		–		–		–		0.11	[0.1]	–	
Yellow-belly flounder	–		–		–		–		1.21	[0.8]	0.06	[0.1]	0.21	[0.1]	0.26	[0.3]	–		–		0.22	[0.1]	–	
Yellow-eyed mullet	0.93	[0.9]	78.27	[78.23]	4.22	[3.5]	10.28	[10.3]	194.70	[119.6]	116.26	[100.0]	–		–		0.37	[0.2]	1.27	[1.0]	–		0.06	[0.1]
Speckled sole	0.48	[0.4]	1.50	[0.5]	–		0.37	[0.3]	0.12	[0.1]	0.44	[0.3]	0.42	[0.1]	0.04	[0.04]	2.85	[0.9]	0.52	[0.3]	1.78	[0.8]	0.06	[0.1]
Garfish	4.91	[2.8]	4.44	[2.9]	20.33	[7.4]	62.40	[62.4]	1.17	[0.6]	19.61	[7.4]	1.61	[1.3]	3.06	[2.9]	0.28	[0.3]	0.32	[0.2]	3.78	[2.8]	0.06	[0.1]
Red gurnard	–		–		–		–		0.08	[0.05]	0.56	[0.3]	–		–		–		–		–		–	
Black pipefish	–		–		–		–		–		–		0.51	[0.4]	0.07	[0.1]	0.21	[0.1]	–		0.06	[0.1]	–	
Sand flounder	0.57	[0.2]	0.06	[0.1]	0.22	[0.1]	0.37	[0.2]	3.37	[1.5]	7.17	[2.4]	0.33	[0.2]	1.50	[0.5]	6.67	[3.0]	0.32	[0.3]	2.67	[1.0]	0.11	[0.1]
Slender sprat	0.48	[0.5]	–		–		–		–		–		–		–		–		0.08	[0.1]	–		–	
Slender stargazer	–		–		–		–		–		0.39	[0.2]	–		–		–		–		–		–	
Sand stargazer	–		–		–		–		–		0.28	[0.3]	–		–		–		–		–		–	
Speckled pipefish	–		–		–		–		–		–		0.03	[0.03]	–		0.07	[0.1]	0.08	[0.05]	–		–	
Estuarine stargazer	–		–		–		–		–		1.11	[0.8]	0.42	[0.3]	0.04	[0.04]	0.28	[0.2]	0.20	[0.1]	–		–	
Mottled triplefin	0.05	[0.05]	–		–		0.28	[0.3]	0.80	[0.4]	0.22	[0.1]	10.12	[2.2]	3.56	[1.6]	5.74	[2.3]	12.74	[7.4]	34.78	[11.9]	1.67	[1.0]
Smelt	–		–		–		–		27.83	[18.3]	0.06	[0.1]	0.18	[0.1]	0.11	[0.1]	–		–		0.50	[0.3]	53.53	[31.3]
Leatherjacket	–		–		–		–		0.06	[0.1]	0.06	[0.1]	1.58	[0.6]	–		–		1.51	[1.0]	0.17	[0.2]	0.11	[0.1]
Spotted stargazer	0.07	[0.04]	–		0.44	[0.2]	0.74	[0.5]	–		0.06	[0.1]	0.06	[0.1]	0.04	[0.04]	0.14	[0.1]	0.12	[0.1]	5.72	[0.1]	0.06	[0.1]
Smooth pipefish	–		0.06	[0.1]	–		–		–		–		0.26	[0.2]	–		0.07	[0.1]	0.71	[0.7]	0.89	[0.7]	0.56	[0.6]
Red cod	–		–		–		–		–		–		–		–		–		0.04	[0.04]	–		–	

Fish species richness was also significantly different between habitats within one position (upper or lower) between islands (*d.f.* 9, *f* 3.241, *P* < 0.002). Tukey HSD *post hoc* analysis of these ANOVA results show that for within position and between island comparisons, North Island (lower) intertidal and subtidal seagrass sites had significantly higher species richness than bare intertidal sites (Figure 4).

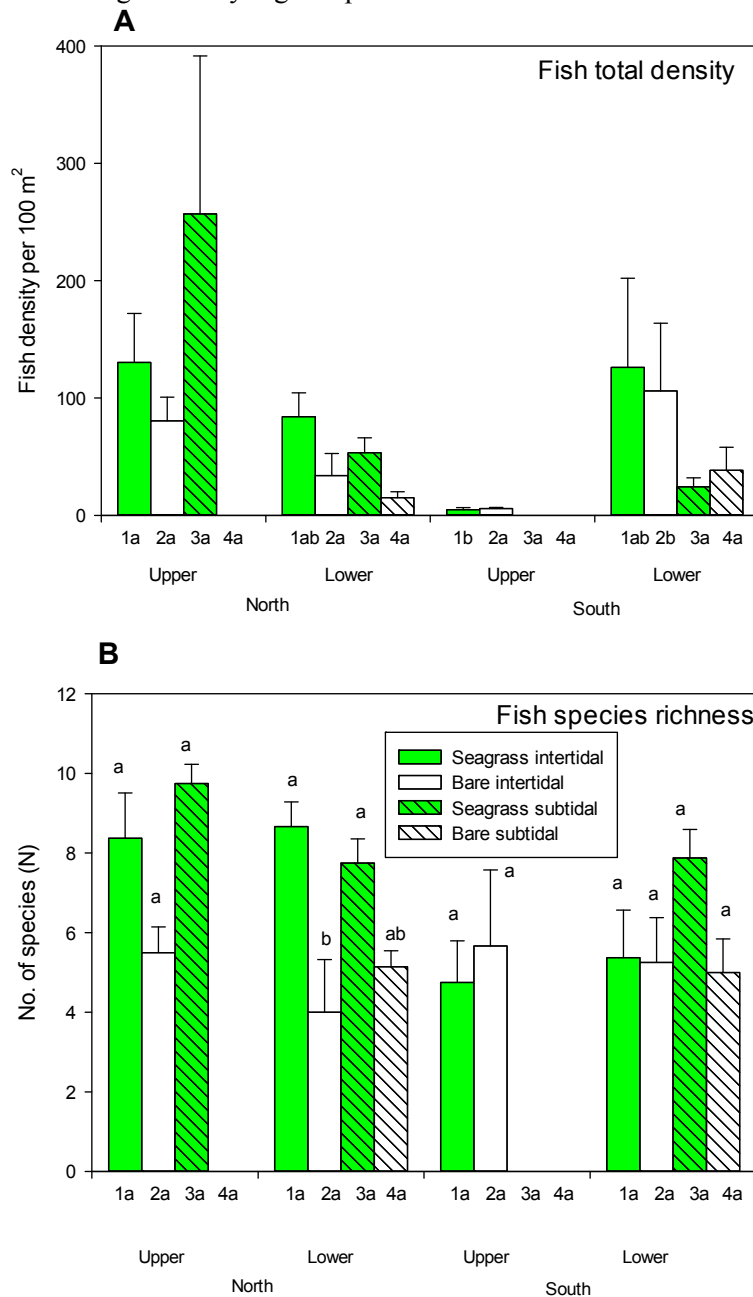


Figure 4: Graphical representation of Tukey HSD analysis for fish samples, a) fish density per 100 m² and b) species richness per tow, displayed by habitat type (SS, BS, SI, BI) within position (upper or lower) within island (North and South Island). Annotation: letters above bars denote any differences for the habitat comparisons within each position by island combination, letters beneath bars denote same habitat comparisons across each position by island combination.

4.2 Spatial variations in composition and fish length of dominant species

There was a clear latitudinal change in the presence/absence of some species, with a group of relatively abundant species (snapper, trevally, jack mackerel, sand and exquisite goby, anchovy, grey mullet, kahawai and parore) only being found north of Cook Strait, whilst fewer species (smelt, leatherjackets, sand and slender stargazer, and slender sprat) were sampled exclusively south of Cook Strait (Table 4, Figure 5).

Other species such as yellow-eyed mullet, garfish, sand flounder, speckled sole, and mottled triplefins were more cosmopolitan in their geographical distribution. We emphasise that the absence of some species in this survey does not necessarily imply true absence in the region, but rather absence from the habitats sampled (seagrass and associated bare sand sediments) (e.g., leatherjackets occur around New Zealand, Morrison et al. 2014a)

Fish abundances varied among habitats with some species showing strong habitat associations (Figures 5 and 6). Northeastern harbours, particularly subtidal seagrass habitats, were dominated by high numbers of juvenile snapper, along with moderate numbers of garfish, jack mackerel, trevally, parore (east coast only), and spotty, in addition to estuarine resident species adults such as exquisite and sand gobies, and mottled triplefin. In contrast, intertidal seagrass was characterized by gobies in northeastern estuaries, with large catches of yellow-eyed mullet from Kawhia and the upper Kaipara, along with modest numbers of speckled sole and sand flounder. Similarly, intertidal sandflat (bare) assemblages in the northeastern harbours were dominated by low numbers of gobies and by pelagic schooling species such as yellow-eyed mullet; and anchovy on the subtidal sandflats, particularly on the west coast.

By contrast, there was little differentiation of fish assemblages between intertidal sand and seagrass sites for the upper South Island (Farewell Spit and Whanganui). Both habitats were dominated by high numbers of yellow-eyed mullet (e.g. 194.7 ± 119.4 fish per 100 m² for Whanganui) and garfish, with more modest numbers of smelt, sand flounder and speckled sole (Figures 5 and 6). The southernmost sites (Waikawa and Bluff), recorded higher numbers of mottled triplefin, particularly for subtidal seagrass, along with modest numbers of garfish, sand flounder and speckled sole. Leather jackets, spotty and two pipefish species (smooth and black) were also collected in both habitats. Smelt were caught in high numbers over subtidal sand at Bluff.

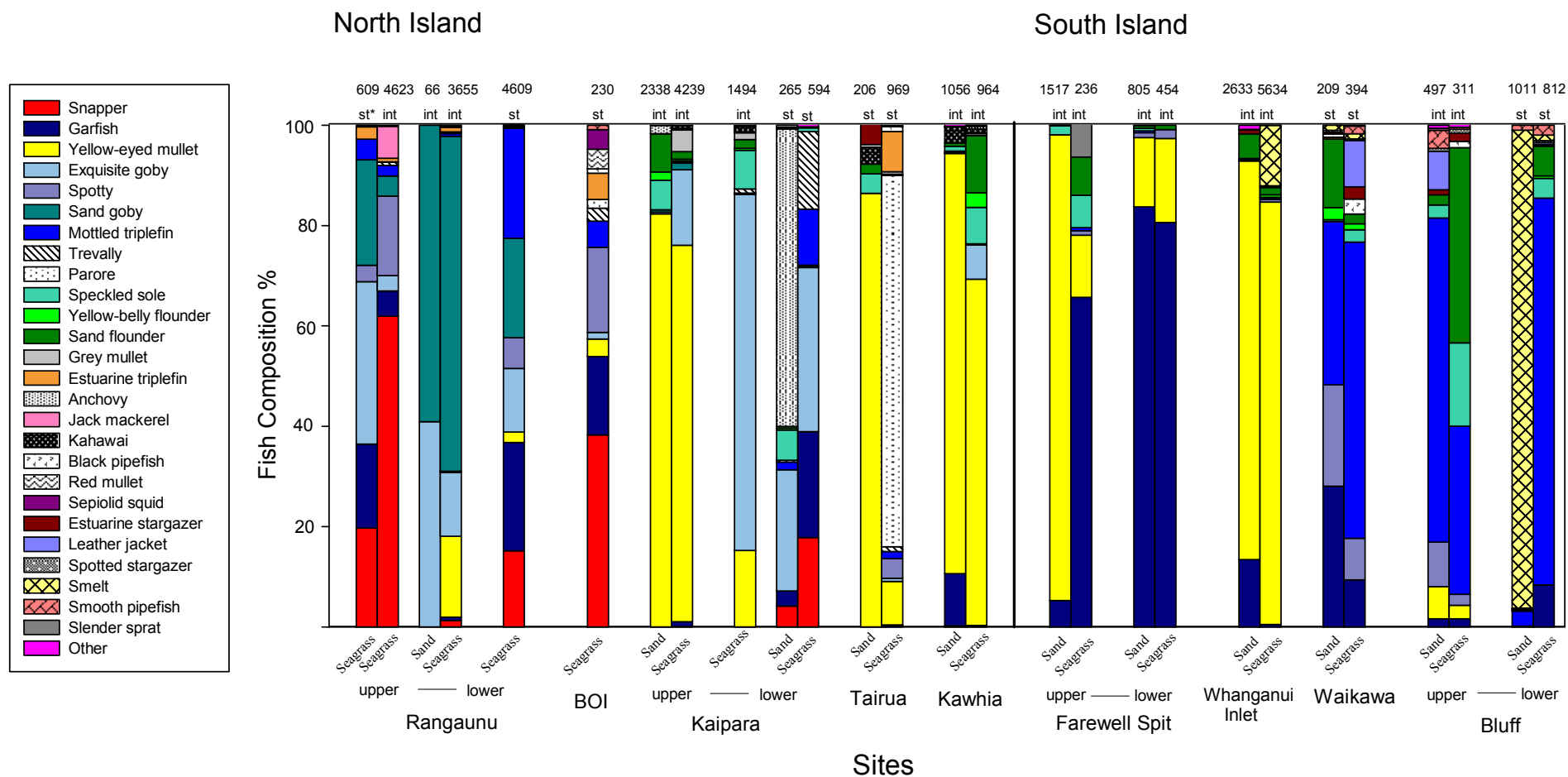


Figure 5: Composition and proportional abundance of the fish assemblage at each of the four habitats from 27 sites at five North Island and four South Island locations. (NB. 'Other' category contributing less than 1%: slender sprat, sand stargazer, red cod, koheru, short-finned eel, striped clingfish, red gurnard, striped pipefish, and pilchards) Numbers above bars are total numbers of fish caught, st = subtidal, int = intertidal.

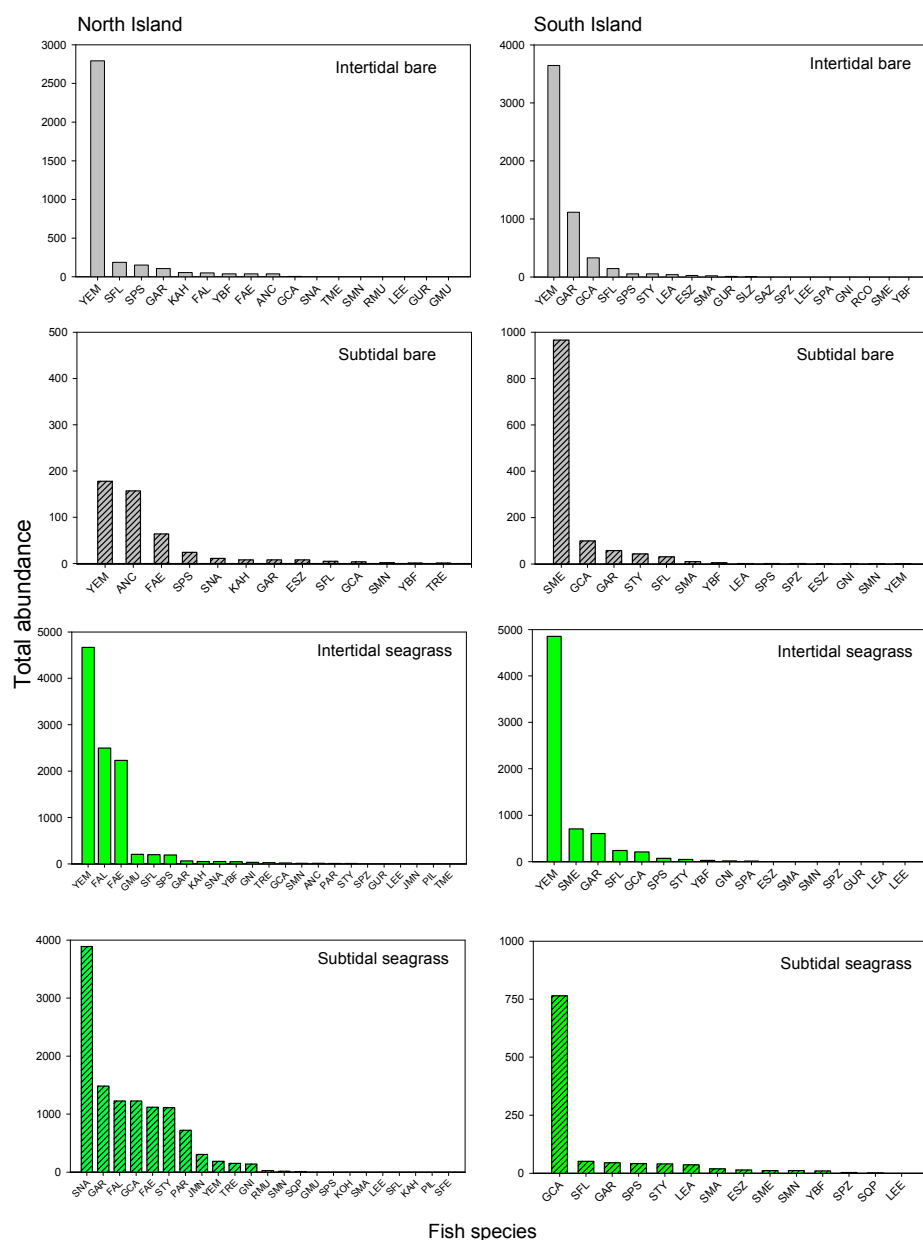


Figure 6: Total abundance of fish species caught by beach seine from seagrass or sand, habitats at 27 sites (from five North Island and four South Island locations). Standard MPI species codes are used, as defined in the table below.

ANC: Anchovy	JMN: Jack mackerel	SAZ: Sand stargazer	SPS: Speckled sole
ESZ: Estuarine stargazer	KAH: Kahawai	SFE: Short-finned eel	SPZ: Spotted stargazer
FAE: Exquisite goby	KOH: Koheru	SFL: Sand flounder	STY: Spotty
FAL: Sand goby	LEA: Leather jacket	SLZ: Slender stargazer	SQP: Sepiolid squid
GAR: Garfish	LEE: Speckled pipefish	SMA: Smooth pipefish	SQX: Squid
GCA: Mottled triplefin	PAR: Parore	SME: Smelt	TME: Striped clingfish
GMU: Grey mullet	PIL: Pilchard	SMN: Black pipefish	TRE: Trevally
GNI: Estuarine triplefin	RCO: Red cod	SNA: Snapper	YBF: Yellow-belly flounder
GUR: Gurnard	RMU: Red mullet	SPA: Slender sprat	YEM: Yellow-eyed mullet

4.3 Nursery role of seagrass for fish species

Size-frequency distributions of the 22 dominant species (Figures 7–10) show that all habitats were dominated by juveniles under 125 mm (excluding garfish) or adults of small sized species (98.2% combined). Overall there was little evidence for latitudinal or across coast (west versus east) variation in length frequencies. Higher abundances of fish greater than 125 mm were caught only at Urupukapuka Island (Bay of Islands), the most open coastal of all the locations sampled (e.g., 52% of snapper caught there were over 125 mm). Juvenile snapper showed some spatial size variation within Rangaunu Harbour: with higher numbers of juveniles (15–25 mm) collected from the lower harbour sites for both intertidal and subtidal seagrass; while upper subtidal seagrass juvenile snapper were slightly larger, averaging 40–60 mm FL (Figure 7). Garfish exhibited a bimodal size distribution within Rangaunu subtidal seagrass beds, with the majority of juveniles measuring 80 mm, followed by a smaller peak of older juveniles at about 225 mm. Other seagrass associated species such as trevally, kahawai, grey mullet, and parore all returned predominantly small juvenile size frequencies (about 20–60 mm). Yellow-belly flounder was the only species to record larger size frequencies for the more southern South Island sites, with 45% of the total catch being over 125 mm in length.

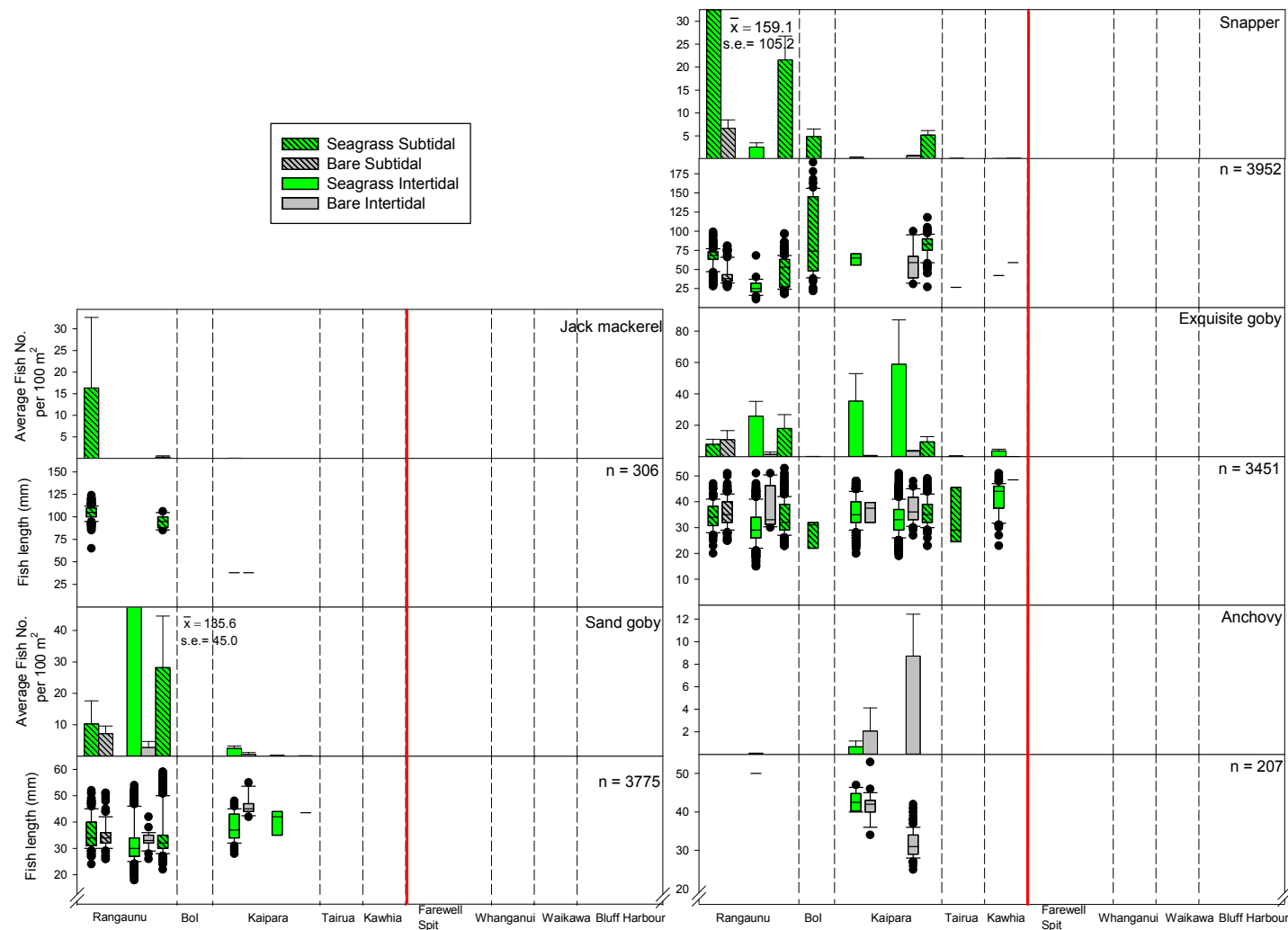


Figure 7: Length frequency box plots of common fish species collected by beach seine from sand and seagrass habitats from nine locations in the North and South Islands. Locations run north to south from left to right. The red line denotes the North to South Island break. Upper and Lower positions within harbours are as in Figure 4a.

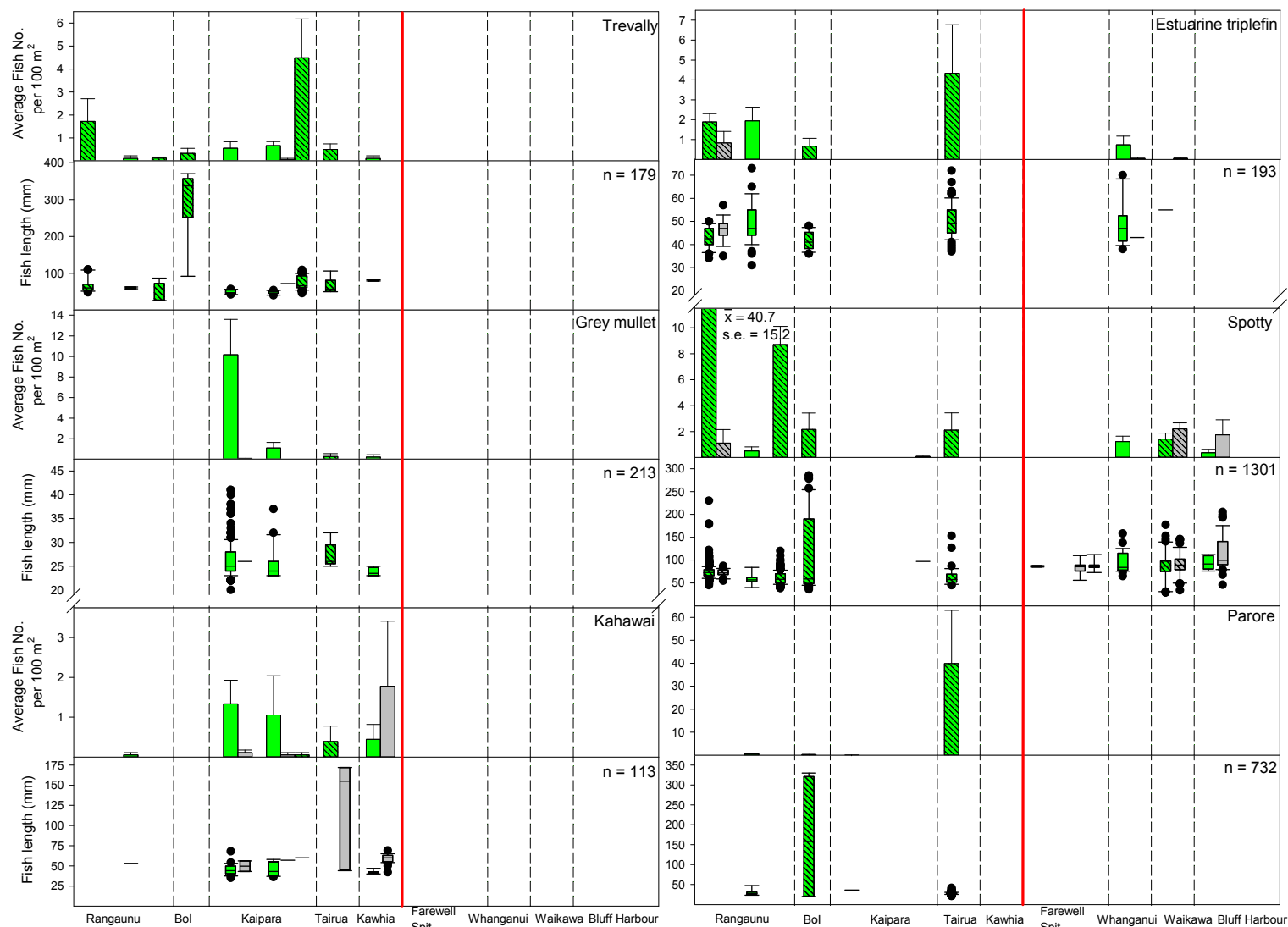


Figure 8: Length frequency box plots for common fish species collected by beach seine from sand and seagrass habitats from nine locations in the North and South Islands. Locations run north to south from left to right. The red line denotes the North to South Island break. Upper and Lower positions within harbours are as in Figure 4a.

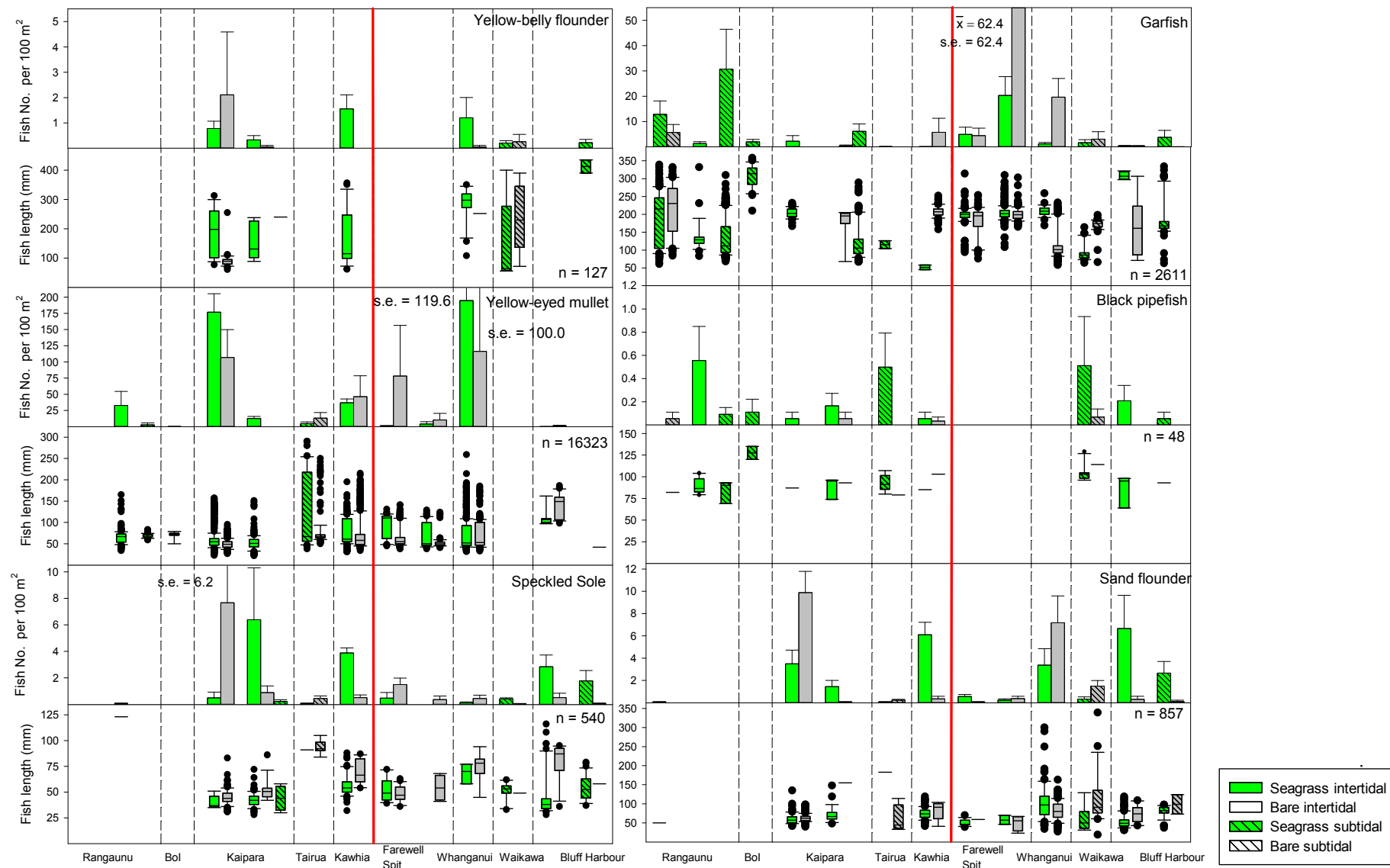


Figure 9: Length frequency box plots for common fish species collected by beach seine from sand and seagrass habitats from nine locations in the North and South Islands. Locations run north to south from left to right. The red line denotes the North to South Island break. Upper and Lower positions within harbours are as in Figure 4a.

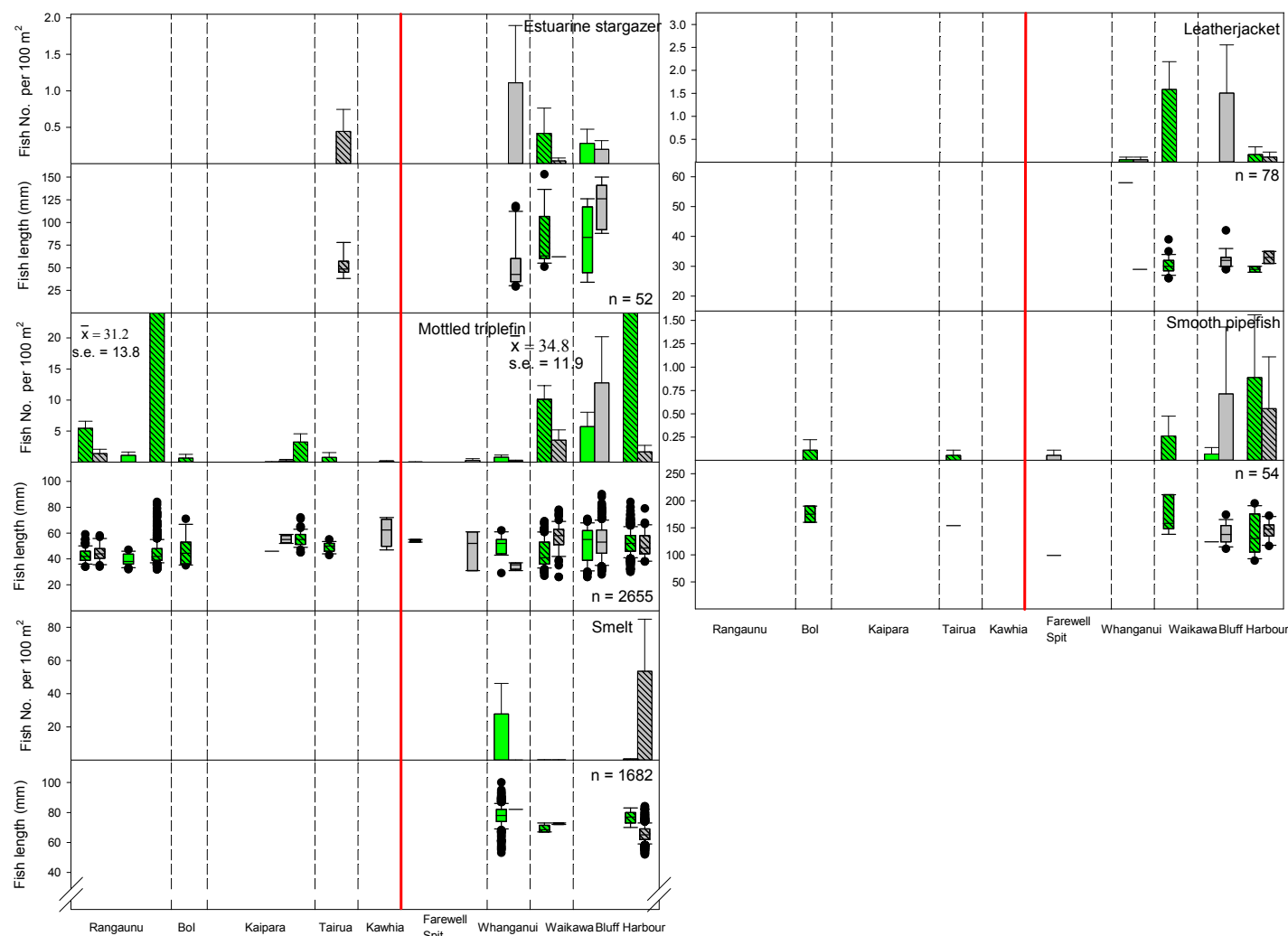


Figure 10: Length frequency box plots for common fish species collected by beach seine from sand and seagrass habitats from nine locations in the North and South Islands. Locations run north to south from left to right. The red line denotes the North to South Island break. Upper and Lower positions within harbours are as in Figure 4a.

4.4 Seagrass characteristics

Overall, seagrass blade length for the North Island sites varied with tidal position (Table 5). This was consistent across both coasts. Intertidal seagrass averaged 9.6 ± 0.12 cm, while blade lengths for subtidal meadows were significantly longer at 22.8 ± 2.4 cm. However, density and coverage varied geographically. Subtidal meadows (extending to about 3–4 m below low tide datum depth) in the lower Rangaunu Harbour were the most verdant and dense of all the northern harbours sampled, although cover became thinner and patchier towards the lower depth boundary (Table 5, Figure 11, M.M. pers. obs.). Medium densities were recorded for the remaining northeastern harbours (both intertidal and subtidal sites), with either ‘continuous’ or ‘patchy’ coverage observed. In contrast, seagrass coverage at the more exposed west coast harbour meadows of Kaipara and Kawhia was relatively sparse. Southern harbours exhibited similar trends in intertidal seagrass blade heights, averaging 11.1 ± 1.5 cm. However, subtidal seagrass recorded shorter overall lengths compared to northern sites, at 15.6 ± 2.6 cm. Whanganui Inlet held the densest and most continuous seagrass cover, whilst the two larger estuarine systems (Farewell Spit and Bluff) supported medium density, but patchy, seagrass cover. Intertidal rocky platforms (Gisborne and Kaikoura) were notable for their dense coverage (more akin to terrestrial grass turf) and high root biomass (dry weight) (Figure 12), with blade lengths averaging 15 ± 1.4 cm. Lower Farewell Spit was also noteworthy for high below ground biomass (g DW) compared to other South Island seagrass meadows (with the exception of Kaikoura’s rocky reef platform).



A. Subtidal seagrass continuous cover - lush



B. Medium density seagrass - sparse



C. Intertidal seagrass – medium density short



Subtidal seagrass meadow (darker shaded area) Urupukapuka. (Bay of Islands)

Figure 11: Examples of seagrass meadow characteristics used in the survey. Estimated percentage seagrass cover (A= over 75%; B = 26–50%; C = 51–75%), as specified in cover scale of appendix 1 of Schwarz et al. (2006). The Urupukapuka Island (Bay of Islands) subtidal seagrass site (NB: photograph is not from the time of sampling).

Table 5: Physical characteristics of the seagrass meadows and environment of the nine locations sampled for fish and two intertidal rocky platforms sampled for benthos only (Gisborne and Kaikoura). See Figure 11 for examples of seagrass coverage characteristics. Water clarities as specified in Lowe (2013).

Harbour	Depth (m)	Blade length (cm) ± s.e.	Density/Coverage	Exposure	Coast	Water clarity (NTU)	Substrate
North Island							
Rangaunu (upper)	Intertidal	9.4	Medium/Continuous	Sheltered	East	1	Fine sand
Rangaunu (upper)	c. 1	17.3 ± 0.7	Medium	Sheltered	East	< 1	Fine sand
Rangaunu (lower)	Intertidal	10.7 ± 1.5	Medium/Patchy	Sheltered	East	1	Fine sand
Rangaunu (lower)	c. 2.5	21.8 ± 2.9	Lush/Thick	Sheltered	East	< 1	Fine sand
Urapukapuka Is, Bol	3.5	26.3 ± 3.0	Medium/Patchy	Coastal sea	East	0.39	Sandy
Kaipara (upper)	Intertidal	12.9 ± 1.1	Medium/Continuous	Exposed	West	c. 16	Fine sand
Kaipara (lower)	Intertidal	9.5 ± 1.1	Sparse	Exposed	West	c. 16	Fine sand
Kaipara (lower)	c. 1.3	25.9 ± 2.5	Sparse	Exposed	West	c. 13	Coarse sand
Tairua	c. 1 (fringe)	14 ± 2.4	Medium/Continuous	Semi-sheltered	East	8	Coarse sand
Kawhia	Intertidal	9.5 ± 0.8	Sparse/Patchy	Exposed	West	c. 21	Fine iron sand muddy clay
South Island							
Farewell Spit (upper)	Intertidal	9.6 ± 0.5	Medium/Patchy	Exposed	West		Fine sand
Farewell Spit (lower)	Intertidal	15 ± 1.4	Medium/Patchy	Exposed	West		Fine sand
Whanganui Inlet	Intertidal	8.6 ± 0.5	Dense/Continuous	Sheltered	West		Fine sand
Waikawa	c. 3	19.8 ± 1.9	Medium/Continuous	Sheltered	East		Fine sand
Bluff (upper)	c. 0.2	10.8 ± 0.7	Sparse/Patchy	Exposed			Sandy
Bluff (lower)	c. 1.5	16.2 ± 2.2	Sparse/Patchy	Exposed			Sandy
Intertidal rock platforms							
Gisborne (North Island)	Intertidal	13.6 ± 1.4	Dense/Continuous	Exposed	East		Bedrock
Kaikoura (South Island)	Intertidal	16.4 ± 2.7	Dense/Patchy	Exposed	East		Bedrock

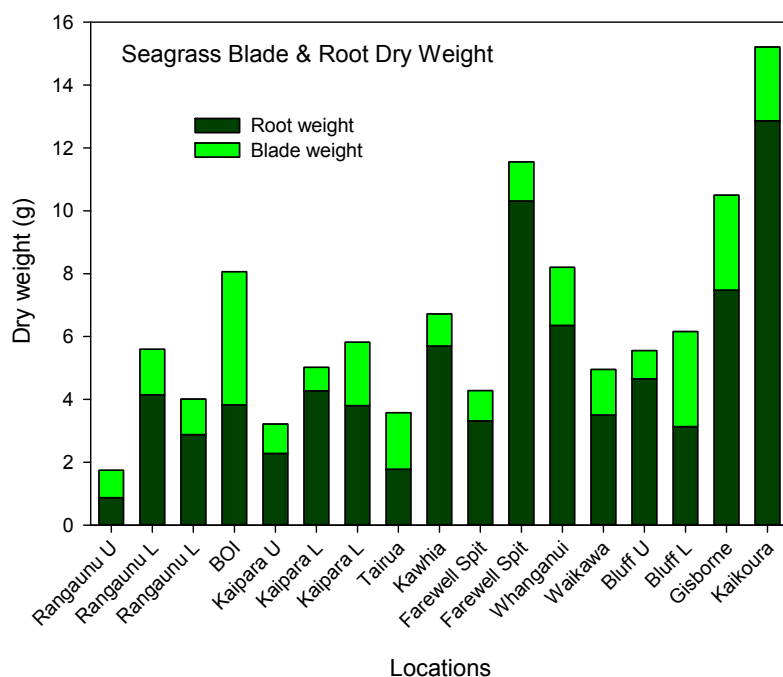


Figure 12: Seagrass root and blade biomass (g DW) per benthic core collected from each location.

4.5 Multivariate community analysis of fish assemblages

Habitat variation between islands

An MDS ordination plot on the overall fish assemblage data shows the northern sites (1–5) clustering to the left hand side of the data cluster, while those from the South Island (6–9) tended to cluster on the right side (Figure 13). At the broadest spatial scale, PERMANOVA analysis revealed there was a significant difference between habitats of the North and South Island fish assemblages (Table 6a). Pairwise tests show only lower intertidal bare habitats to have non-significant differences between the North and South Island fish assemblages (Table 6b). SIMPER analysis revealed that 8–9 species collectively contributed about 60% towards the dissimilarity between islands. However, the contribution of individual species to the dissimilarities was low to moderate, ranging from about 5–25%. These included in order of decreasing importance, yellow-eyed mullet, mottled triplefin, snapper, garfish, exquisite goby and sand goby.

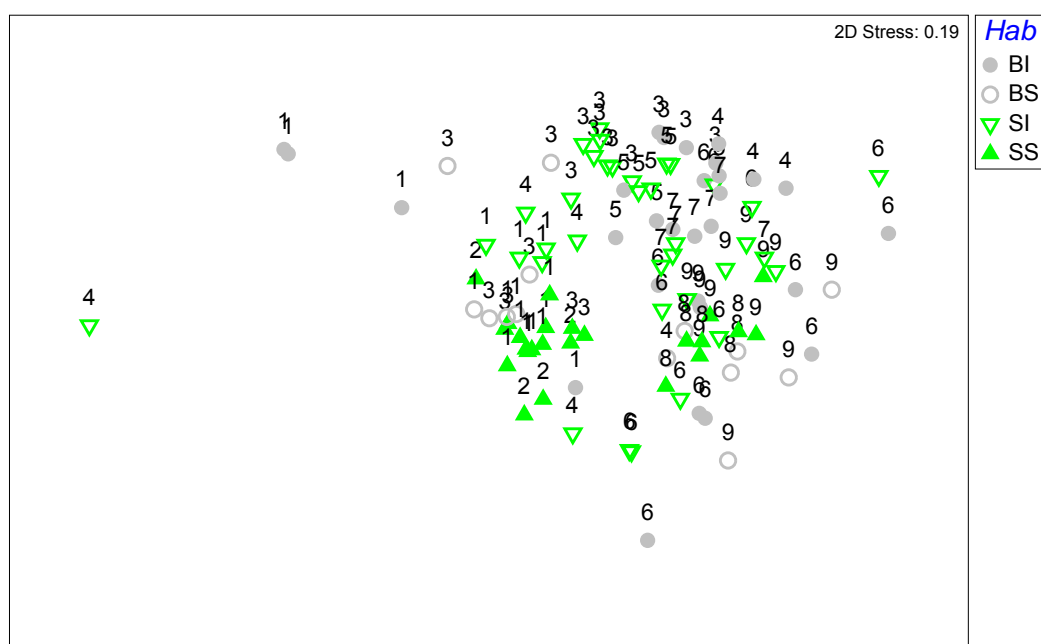


Figure 13: MDS ordination of all fish assemblage data plotted by location and habitat. Sampling locations numerically labelled from North to South; Rangaunu (1), Bay of Islands (2), Kaipara (3), Tairua (4), Kawhia (5), Farewell Spit (6), Whanganui (7), Waikawa (8), Bluff (9). The North/South Island split occurs between numbers 5 and 6. BI, bare intertidal; BS bare subtidal; SI seagrass intertidal; SS seagrass subtidal.

Table 6: a): PERMANOVA test for differences in the composition of fish assemblages recorded for each Island (North/South), nested within position (upper/lower) and habitat, P (perm) values which are significant are shown in bold; b) Pairwise tests for differences in the composition of fish assemblages recorded for each Island (North/South), nested within position (upper/lower) and habitat. P(perm) values which are significant are shown in bold.

a)				
Source		df	Pseudo-F	P(perm)
Habitat		3	6.9777	0.001
Position (Habitat)		3	1.9457	0.009
Island (Position (Habitat))		6	6.5297	0.001
b)				
Habitat	Position	Groups	t	P(perm)
SS	Upper	Nth, Sth	N/A	N/A
	Lower	Nth, Sth	3.3927	0.001
SI	Upper	Nth, Sth	2.7471	0.002
	Lower	Nth, Sth	2.9592	0.001
BS	Upper	Nth, Sth	N/A	N/A
	Lower	Nth, Sth	2.3402	0.001
BI	Upper	Nth, Sth	2.4431	0.012
	Lower	Nth, Sth	1.4490	0.068

Habitat variation within islands

PERMANOVA analysis revealed that fish assemblages were also significantly different between habitats nested within position (upper/lower) and island (North/South) (Table 7a). Pairwise tests revealed that the majority of fish assemblages were significantly different, with the exception of upper North Island subtidal/intertidal seagrass; and lower intertidal bare habitats paired with intertidal bare and subtidal seagrass respectively (Table 7b). Within the South Island, lower intertidal seagrass and

intertidal bare sites were not significantly different. Important discriminating species for the northern subtidal seagrass meadows (in descending order of importance) included snapper, garfish, exquisite goby, mottled triplefin and trevally, whilst southern sites saw the dominance of mottled triplefin, as well as leather jacket.

Table 7: a) PERMANOVA test for differences in the composition of fish assemblages recorded between island (North/South), nested within position (upper/lower) and habitat. P(perm) values which are significant are shown in bold. b) Pairwise tests for differences in the composition of fish assemblages recorded for each habitat, nested within position (upper/lower) and Island (North/South). P(perm) values which are significant are shown in bold. * denotes that Monte Carlo simulations were used to obtain more permutations where the original comparison returned fewer than 100 permutations.

a)

Source	df	Pseudo-F	P(perm)
Island	1	22.3090	0.001
Position(Island)	2	2.2182	0.005
Habitat(Position(Island))	9	4.3559	0.001

b)

Island	Position	Groups	t	P(perm)
North	Upper	SS, BS	N/A	N/A
		SS, SI	1.7917	0.084
		SS, BI	6.4929	0.001*
		BS, SI	N/A	N/A
		BS, BI	N/A	N/A
		SI, BI	2.4115	0.011
North	Lower	SS, BS	1.6173	0.034
		SS, SI	2.8712	0.001
		SS, BI	2.2339	0.001
		BS, SI	1.8746	0.004
		BS, BI	1.3735	0.119
		SI, BI	0.9170	0.526
South	Upper	SI, BI	1.5804	0.048
South	Lower	SS, BS	1.6173	0.034
		SS, SI	2.8712	0.001
		SS, BI	2.1573	0.002
		BS, SI	1.8746	0.004
		BS, BI	1.6988	0.009
		SI, BI	0.9170	0.526

(C) Habitat variation across locations

PERMANOVA analysis revealed significant differences between fish assemblages between all locations (harbour) within position (upper/lower) and habitats (Table 8a). Pairwise tests revealed that 87% of all fish assemblages between locations within habitats/positions were significantly different (Table 8b).

Table 8: a) PERMANOVA test for differences in the composition of fish assemblages recorded for each Location (harbour), nested within position (upper/lower) and habitat type. P(perm) values which are significant are shown in bold; b) Pairwise tests for differences in the composition of fish assemblages recorded for each Location (harbour), nested within position (upper/lower) and habitat type. *denotes that Monte Carlo simulations were used to obtain more permutation where the original comparison returned fewer than 100 permutations. P(perm) values which are significant are shown in bold.

a)

Source	df	Pseudo-F	P(perm)
Habitat	3	12.8190	0.001
Position(Habitat)	3	3.5744	0.001
Location(Position(Habitat))	20	8.0657	0.001

b)

Habitat	Position	Groups	t	P(perm)
SS	Upper	N/A		
SS	Lower	BISL, BLUFF	3.5648	0.002
		BISL, KAP	2.3843	0.011
		BISL, RUN	2.2831	0.016
		BISL, TAI	1.4963	0.136
		BISL, WAK	3.2383	0.004
		BLUFF, KAP	3.9027	0.001
		BLUFF, RUN	4.3073	0.002
		BLUFF, TAI	2.6637	0.006
		BLUFF, WAK	1.8240	0.027
		KAP, RUN	2.7399	0.004
		KAP, TAI	2.5665	0.007
		KAP, WAK	4.2755	0.001
		RUN, TAI	2.4123	0.012
		RUN, WAK	4.3307	0.001
		TAI, WAK	2.3853	0.009
SI	Upper	BLUFF, FWP	1.7073	0.067
		BLUFF, KAP	4.7788	0.002
		BLUFF, RUN	3.9308	0.001
		FWP, KAP	2.8330	0.006
		FWP, RUN	2.5239	0.006
		KAP, RUN	4.1151	0.001
SI	Lower	FWP, KAP	3.6776	0.002
		FWP, KAW	3.8587	0.002
		FWP, RUN	3.5471	0.003
		FWP, WNU	2.0648	0.038
		KAP, KAW	2.0545	0.018
		KAP, RUN	3.3663	0.002
		KAP, WNU	2.7260	0.004
		KAW, RUN	4.5187	0.002
		KAW, WNU	2.3571	0.006
		RUN, WNU	2.9330	0.005
BS	Upper	N/A		
BS	Lower	BLUFF, KAP	2.6143	0.009
		BLUFF, TAI	2.2723	0.04
		BLUFF, WAK	1.7133	0.085
		KAP, TAI	4.1679	0.005
		KAP, WAK	4.0304	0.002
		TAI, WAK	3.8508	0.001
BI	Upper	BLUFF, FWP	2.4532	0.027
		BLUFF, KAP	3.6398	0.006

		FWP, KAP	3.1423	0.009
BI	Lower	FWP, KAW	1.5531	0.084
		FWP, RUN	2.1468	0.02
		FWP, WNU	1.8723	0.053
		KAW, RUN	2.9253	0.01
		KAW, WNU	1.4692	0.117
		RUN, WNU	3.7284	0.003

Habitat variation within locations

PERMANOVA analysis showed that fish assemblages were also significantly different between habitats (BI, BS, SI, SS) nested within position (upper/lower) and location (harbours) (Table 9a). Pairwise comparisons of fish assemblages revealed significant differences between 17 of the 27 sampling sites (Table 9b). Overall contribution of individual species to the dissimilarities was moderate (about 7–20%). All North Island sites were significantly different with the exception of intertidal and subtidal seagrass habitats within upper Rangaunu Harbour, characterized by snapper, spotty, trevally and gobies (sand and exquisite) (Table 9b). Tairua subtidal seagrass (fringe) was characterized by parore, contributing 17% to dissimilarity, while flounder and exquisite goby dominated (36%) intertidal seagrass in Kawhia. Important discriminating species for upper Kaipara subtidal seagrass meadows included trevally, mottled triple fin, garfish and snapper. Lower subtidal seagrass beds were characterized by snapper, yellow-eyed mullet and garfish, and upper intertidal seagrass by grey mullet and exquisite goby.

In contrast, only one South Island harbour (Waikawa) showed significantly different fish assemblages between bare and seagrass habitats. SIMPER analysis revealed that leather jacket, sole, smelt and pipefish (smooth and black) characterized subtidal seagrass habitat in Waikawa Harbour, and contributed about 36% towards dissimilarity between habitats.

Table 9: a) PERMANOVA results of the main test of differences for composition of fish assemblages. Factors used include: Location (Harbour), Position (upper/lower) and Habitat. b) Pairwise tests on the composition of fish assemblages recorded between habitats nested within position (upper/lower), and locations (harbour). Significant pairwise comparisons are given in bold (*denotes that Monte Carlo simulations were used to obtain more permutation where the original comparison returned fewer than 100 permutations).

a)

Source	df	Pseudo-F	P(perm)
Location	8	15.5080	0.001
Position(Location)	4	5.5031	0.001
Habitat(Position(Location))	14	4.6010	0.001

b)

Location	Position	Groups	t	P(perm)*
Rangaunu	Upper	SS, SI	1.8114	0.059
	Lower	SS, BI	3.6644	0.003
		SS, SI	2.6061	0.012
		BI, SI	3.2807	0.004
Kaipara	Upper	BI, SI	2.5624	0.001
	Lower	SS, BS	2.670	0.007
		SS, SI	4.0438	0.001
		BS, SI	3.3935	0.003
Tairua	Lower	BS, SS	2.3974	0.009
Kawhia	Lower	BI, SI	1.8222	0.039
Farewell Spit	Upper	BI, SI	1.7051	0.069
	Lower	BI, SI	1.4503	0.155
Whanganui	Lower	BI, SI	1.6347	0.074
Waikawa	Lower	BS, SS	1.9476	0.037
Bluff	Upper	BI, SI	2.0255	0.092
	Lower	BS, SS	1.4839	0.141

4.6 Diet

Prey utilization

Broad dietary composition

Diets of the 29 most abundant fish species were investigated. Stomach contents of 1225 fish were examined, of which 128 were empty. Ninety two prey taxa were identified, with the majority of fish (88%) feeding on small epibenthic crustaceans (Figure 14). Proportions of major dietary items varied between islands, with consumption of amphipods declining from 26% of total biomass in the north to 13% in the South Island, with an inverse increase in the proportion of mysids consumed for the south (25%) compared to the north (about 15%). Similarly, plankton comprised 23% of total biomass consumed in the north, while only representing 11% of southern fish diets.

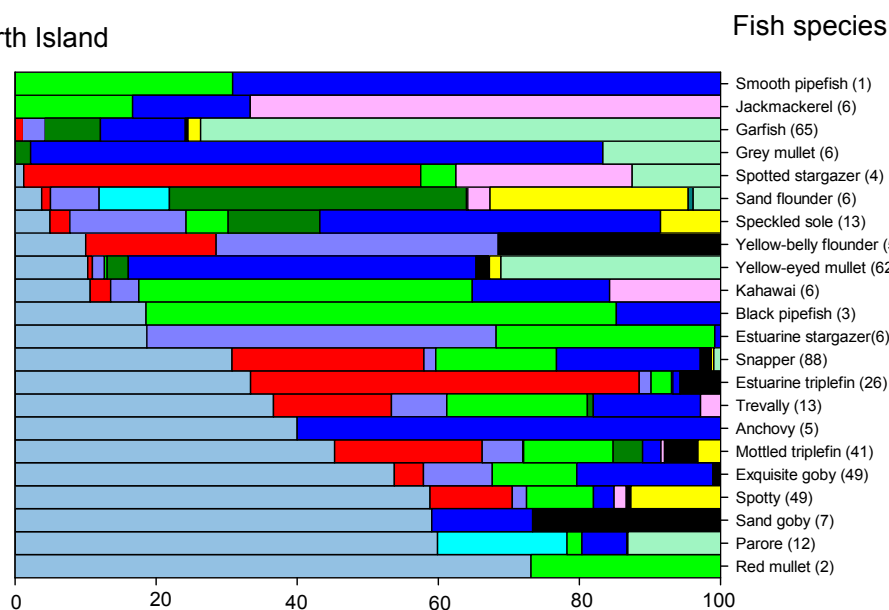
Species with atypical diets included spotted stargazer which was largely piscivorous (fish-eating); leather jacket which consumed gastropods in addition to bryozoa; grey mullet which fed predominantly on detritus/fine algae and plankton; yellow-eyed mullet which consumed red/green algae (*Polysiphonia* sp. and *Ulva* sp.) along with detritus, and garfish which was the only species to consume substantial quantities of seagrass in addition to zooplankton. Few species fed predominantly on infaunal animals such as polychaetes and bivalves, apart from mottled triplefin and spotty.

Bivalves and bivalve siphons were taken in significant numbers by the two flounder species, while speckled sole consumed high numbers of cumaceans.

Dietary variation with habitat

There were habitat related differences in diet. For example, within the North Island, diets of those species highly associated with seagrass (e.g. snapper, trevally, parore and spotty) were dominated by gammaridean amphipods (35–73% of the total gut biomass), followed by mysids (19%), decapods (12%) and plankton (7%), whilst individuals collected over sand (e.g. sand goby) consumed larger proportions of infaunal species. However, in terms of numerical abundance, copepods dominated (about 75%) the diets of fish collected from intertidal seagrass for both Rangaunu (especially *Paracalanus indicus*) and Kaipara Harbours (especially *Euterpina acutifrons*), while gammarid amphipods dominated prey consumed over subtidal seagrass sites for both harbours (particularly for the Kaipara, 89%). In contrast, diets (biomass) from bare southern sites were dominated by mysids (23%) and plankton (20%), in addition to infaunal species such as nematodes (category ‘other’) contributing 18%, of total gut biomass. (Note: South Island percentages were calculated once the mean biomass of small ingested fish was removed, due to the disproportionate contribution of a few individuals (n=6) to this category). Diets of South Island fish collected over seagrass were similarly dominated by decapods (45% of total invertebrate gut biomass) due to larger size classes, with more modest contributions of amphipods.

A. North Island



B. South Island

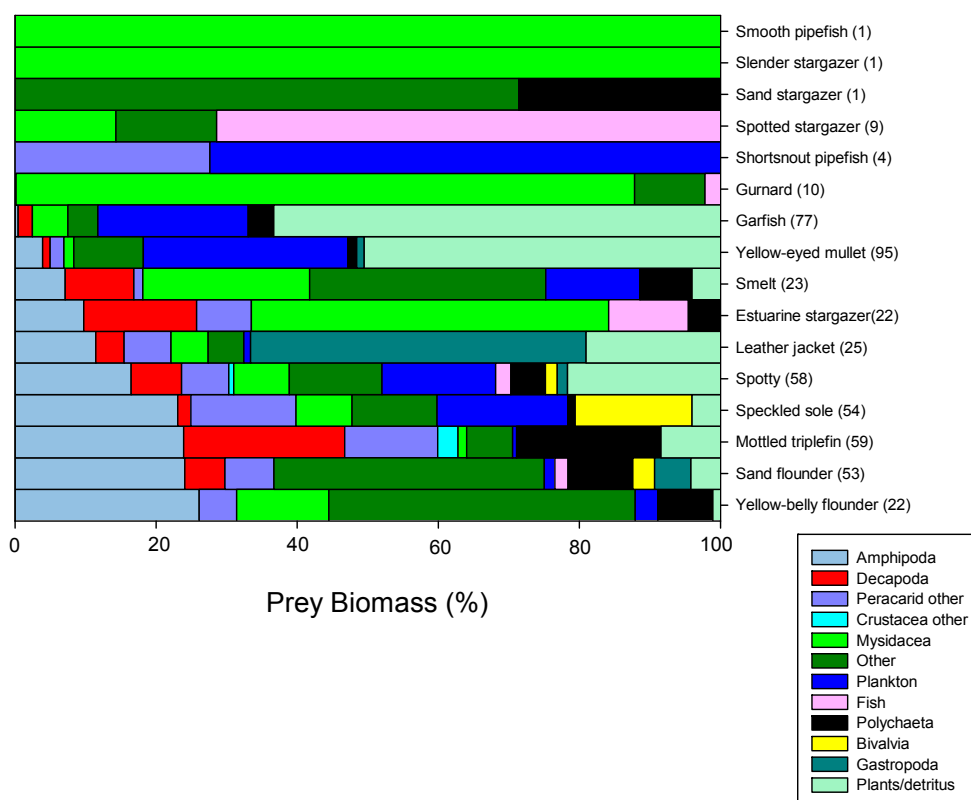


Figure 14: Average proportional abundance of the major dietary categories in fish diets consumed across all habitats, locations and fish sizes. Sample sizes are given in parentheses after species name.

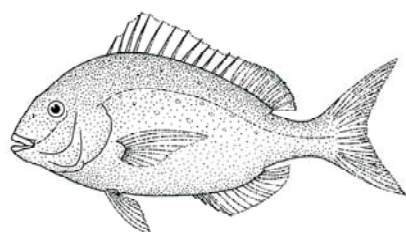
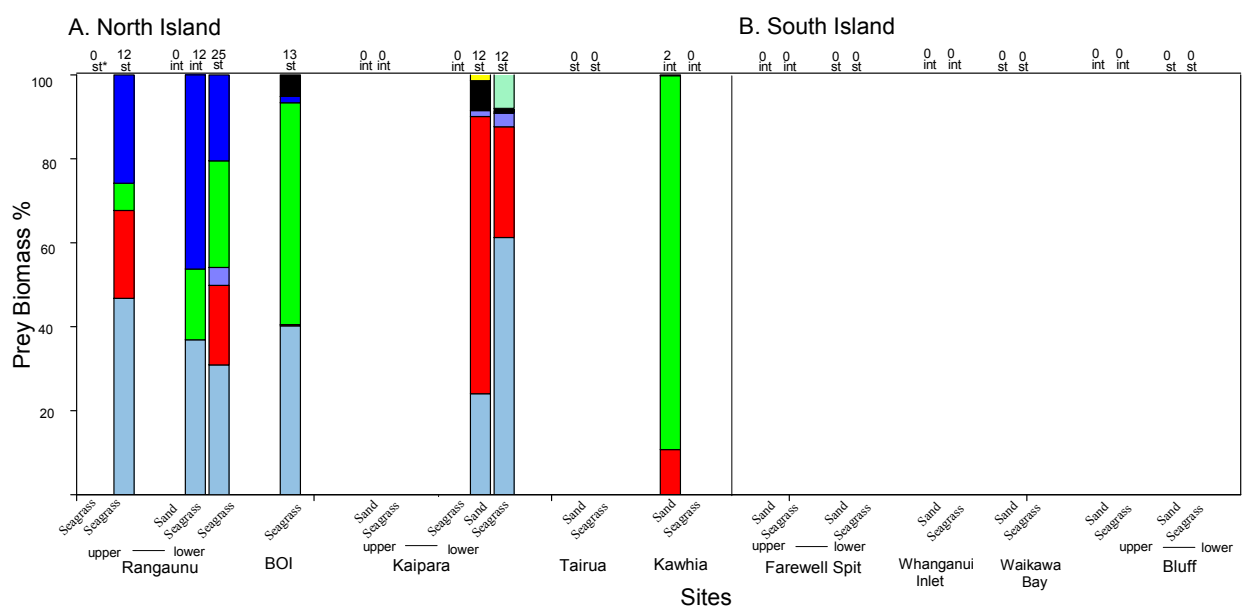
4.7 Dietary changes with fish size and habitat

The diets of 13 of the most abundant species characterizing each of the habitats sampled for fish in both northern and southern estuaries are summarized for each of the nine harbours (see Figures 15–26).

Snapper (*Pagrus auratus*) North Island only

Ontogenetic shifts in snapper diet were clearly evident, with 83.7% of the variation explained by the first two axes of the PCA (Figure 15d). Newly settled recruits (20–29 mm) preyed primarily on calanoid copepods (*Paracalanus indicus*) which were the numerically dominant prey item, constituting 44% of the total stomach contents, with consumption gradually declining to 1% after juveniles reached 70 mm (Figure 15c). Although plankton was consumed at all sites, its importance declined from east to west coast sites. Gammarid amphipods (e.g. *Paracalliope novaezealandiae*) and mysids similarly declined with increasing length, averaging 35% and 25% respectively of total stomach contents for the 20–80 mm size classes. Conversely, there was an increase in the contribution of larger and more mobile decapods, namely *Halicarcinus* sp., juvenile crabs and the shrimps *Palaemon affinis* and *Pontophilus australis* for juveniles ranging between 50 to 100 mm. Modest numbers of polychaetes (*Neanthes* sp., *Eunicid* sp.) and cumaceans were also eaten when fish grew beyond 40 mm long.

Differences in prey composition between habitats were not especially marked. Prey ingested from sand habitats showed an increased infaunal component (i.e. polychaetes; bivalves). Plankton consumption defined seagrass sites (Rangaunu), particularly the lower intertidal, whilst Kaipara snapper also consumed small amounts of plant material and cumaceans. Prey diversity was 22 for seagrass versus 6 for sand sites. Similarly, diets from sandy sites (Kaipara only) had an increased infaunal component (cumaceans; polychaetes), in addition to bivalve siphons. No significant differences in diet were detected (ANOSIM analysis) between upper/lower ($R=0.034$, $p<0.326$) and intertidal/subtidal ($R=0.129$, $p<0.987$) seagrass sites within Rangaunu Harbour, or within Kaipara Harbour (sand and seagrass sites) ($R=0.128$, $p<0.07$). However, there was a significant geographic effect, albeit small, between Rangaunu and Kaipara subtidal seagrass sites ($R=0.201$, $p<0.001$), and similarly between the Bay of Islands and Kaipara ($R=0.361$, $p<0.001$). Kaipara snapper had the highest consumption of amphipods (e.g. *Aora* sp. and *P. novaezealandiae*), both for biomass (60%) and abundance (83%), with plankton constituting only 3% (total numbers); while mysids and zooplankton dominated prey eaten in Rangaunu (44–48% total stomach contents). However, results may be confounded with fish size, as Rangaunu sites had higher numbers of snapper between 20 and 40 mm in length.



Snapper
(*Pagrus auratus*)

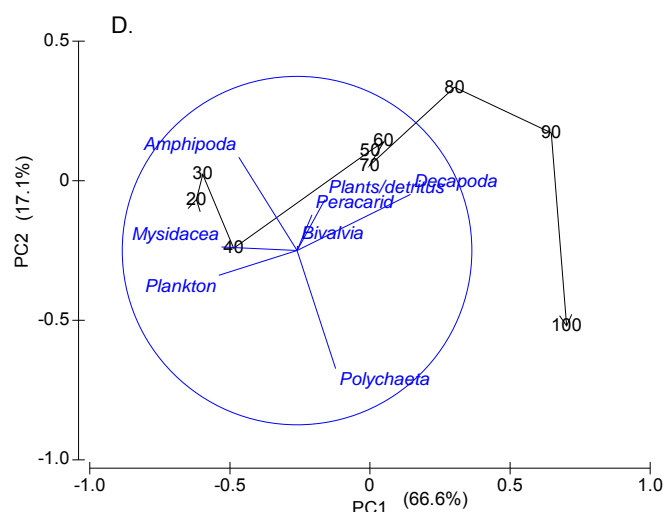
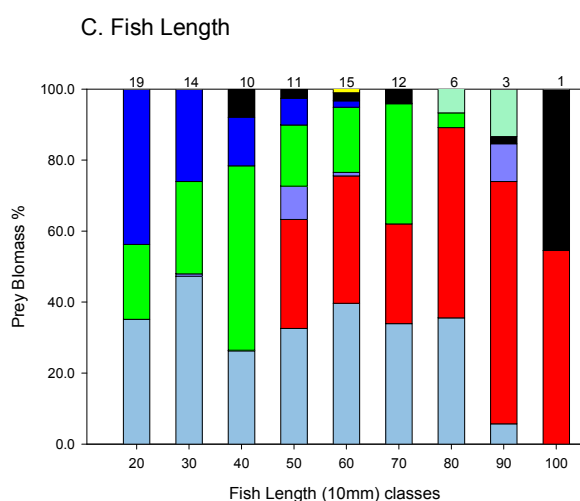
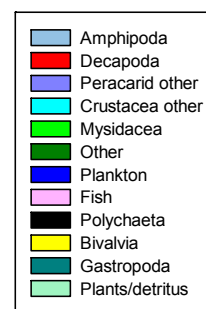


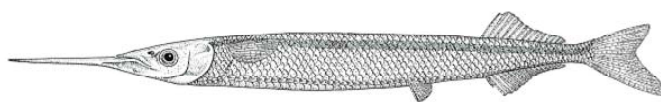
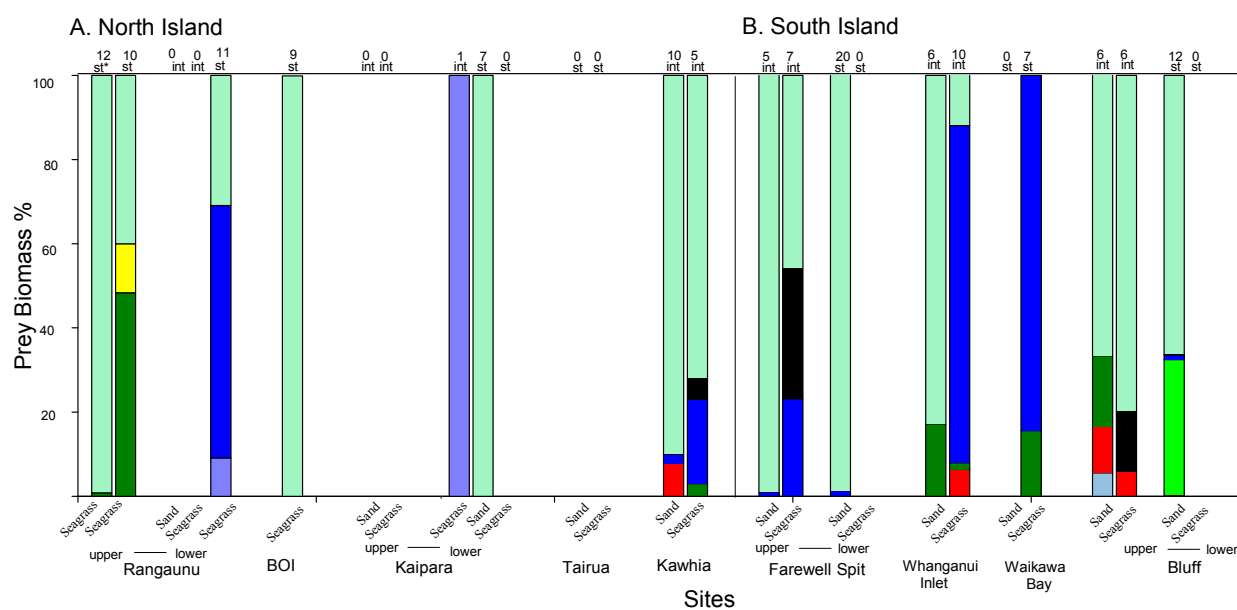
Figure 15: Proportional abundance of major dietary categories consumed by snapper across all habitats and harbours (A–B); by (10 mm) length class (C); PCA trajectory score plots of major dietary categories consumed by (10 mm) length class (D); *Peracarid=Peracarid other. Number of guts analysed are shown above each histogram.

Garfish (*Hyporhamphus ihi*) Both Islands

Garfish had the narrowest diet range (10 taxa) of seagrass associated species (as defined by most sampled fish coming from seagrass) and were predominantly herbivorous, with 70% of their total stomach contents consisting of seagrass fragments followed by zooplankton (16%) and *Hymenoptera* sp. (6%) (Figure 16a, b). Early juveniles (80–119 mm) fed primarily on calanoid copepods, along with *Hymenoptera* sp. (category ‘Other’) gathered from the water surface (Figure 16c, d), along with smaller numbers of cumaceans. Consumption of plant material increased with size, along with mysids in Bluff. The same three dietary categories explained 75% of dietary variation for the first two axes of the PCA analysis (Figure 16d).

Trevally (*Psuedocaranx dentex*) North Island only

Gammarid amphipods (*Paracalliope novaezealandiae*, *Aora* sp.) and mysids were consumed by all size classes, dominating the stomach contents by 55% and 27% respectively. Larger fish size classes (80–119 mm) also included cumaceans, fish scales and zooplankton in their stomachs (Figure 17a–d). Dietary variation between some harbours (seagrass only) could not be analyzed due to the small sample size. However, Kaipara differed from Rangaunu and Kawhia by virtue of trevally almost exclusively eating gammarid amphipods (about 81% biomass), while mysids characterized the latter two harbours.



Garfish
(*Hyporhamphus ihi*)

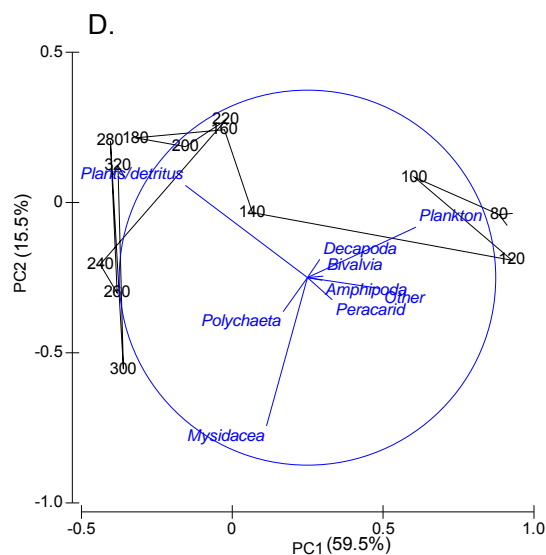
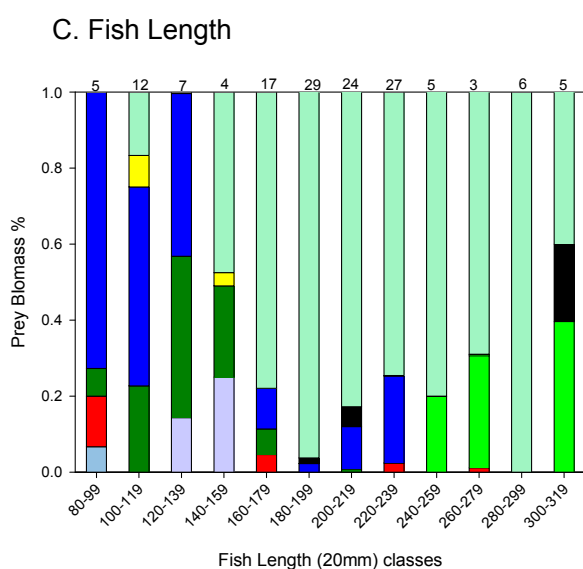


Figure 16: Proportional abundance of major dietary categories consumed by garfish across all habitats and harbours (A–B); by (20 mm) length class (C); PCA trajectory score plots of major dietary categories consumed by (20 mm) length class (D); * Peracarid=Peracarid other. Number of guts analysed are shown above each histogram.

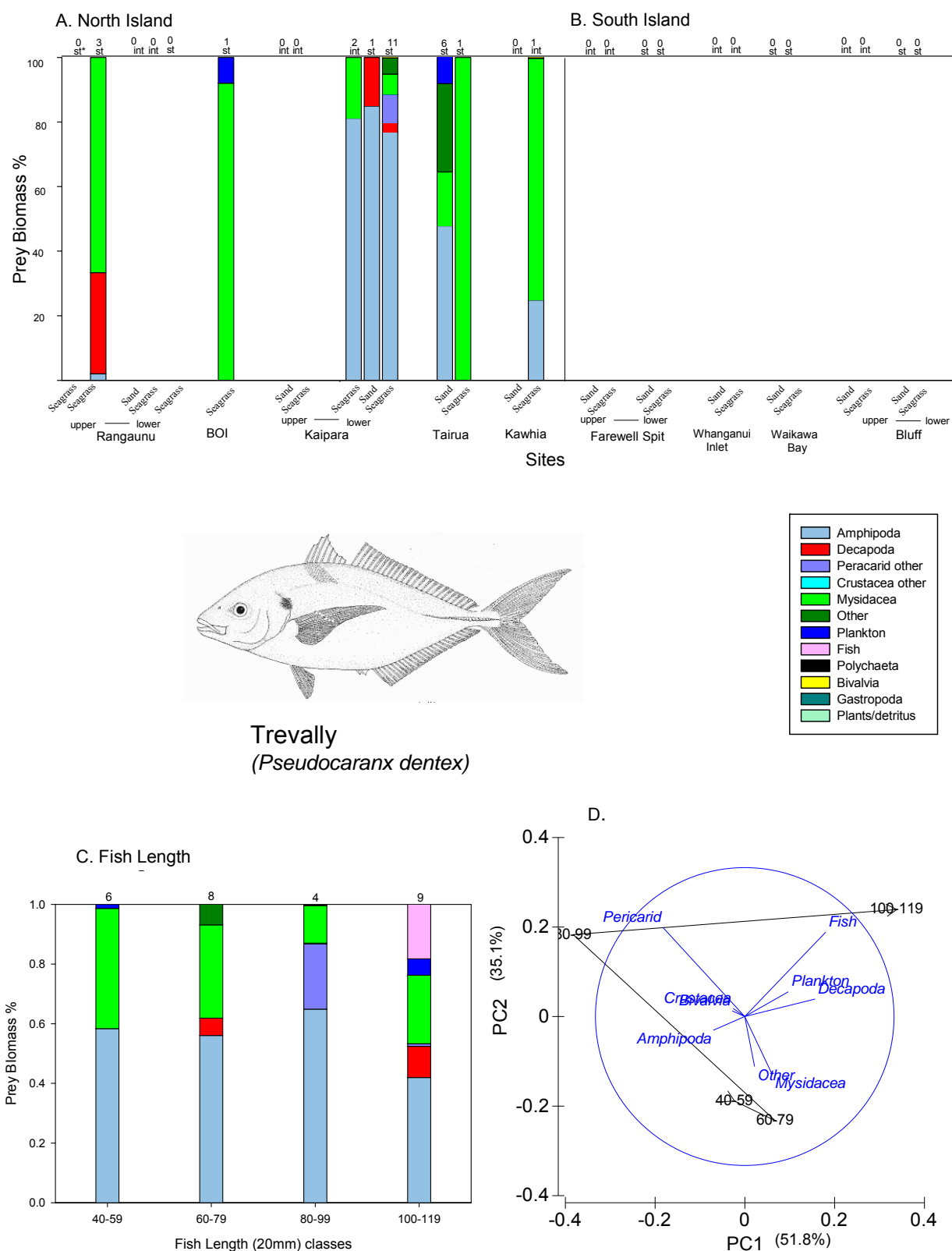


Figure 17: Proportional abundance of major dietary categories consumed by trevally across all habitats and harbours (A–C); by (20 mm) length class (D); PCA trajectory score plots of major dietary categories consumed by (20 mm) length class (E); *Peracarid=Peracarid other. Number of guts analysed are shown above each histogram.

Spotty (*Notolabrus celidotus*) Both Islands

Prey biomass was dominated by amphipods (38%), decapods (10%), plankton (9.55%) and mysids (9%). PCA analysis showed a clear ontogenetic shift with size, with 67.9% of dietary variance explained by the first two axes (Figure 18c–d). New recruits of 19–79 mm consumed plankton, isopods and mysid. Amphipods (seven species; both epifaunal and infaunal) dominated the diet, particularly for size classes 40–79 mm, thereafter declining substantially with a corresponding increase in the contribution of crabs (*H. whitei*). Modest numbers of bivalves (about 0.5 mm), gastropods and fish scales were also eaten. Sea anemone ('other') was also consumed within southern harbours.

Mottled triplefin (*Grahamina capito*) Both Islands

Amphipods were the principal prey, accounting for 31% of the total biomass, followed by decapods (25%) and mysids (14%). Plankton, isopods and amphipods comprised the diet of the smaller size class (20 mm), followed by a transition to mysids and an increasing infaunal component comprising polychaetes and bivalves at 30 mm (Figure 19a–c). Numbers of amphipods gradually declined with increasing size, whilst decapods, polychaetes and algae increased in importance. Ontogenetic change was evident in the PCA with a progression from left to right, with increasing size classes (Figure 19d).

Exquisite goby (*Favonigobius exquisitus*) North Island only

Clear ontogenetic shifts in diet were shown in the PCA with 100% of total variation explained by the first two axes, showing an obvious progression of increasing lengths from left to right (Figure 20d). Biomass was dominated by amphipods (53%) and zooplankton (21%) respectively, which was also reflected in the diet of smallest size class (20%), in addition to modest numbers of cumaceans, mysids and crab species (*Haliscarcinus* sp.) (Figure 20c). Increased ingestion of infaunal species (e.g. cumaceans) characterised prey consumed for sand habitats by exquisite goby (note however that only a few sand sites returned samples).

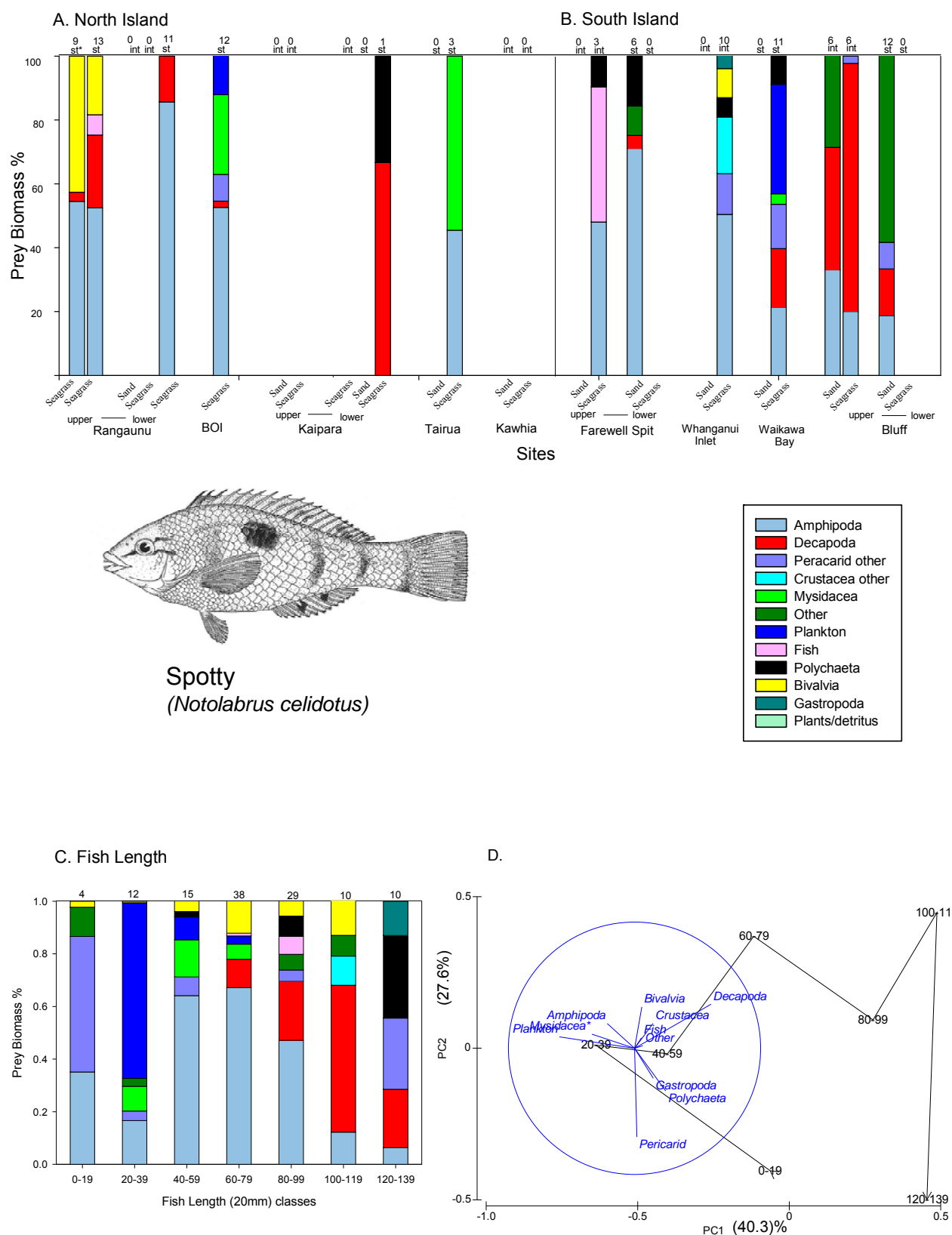
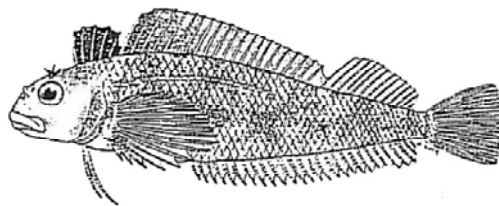
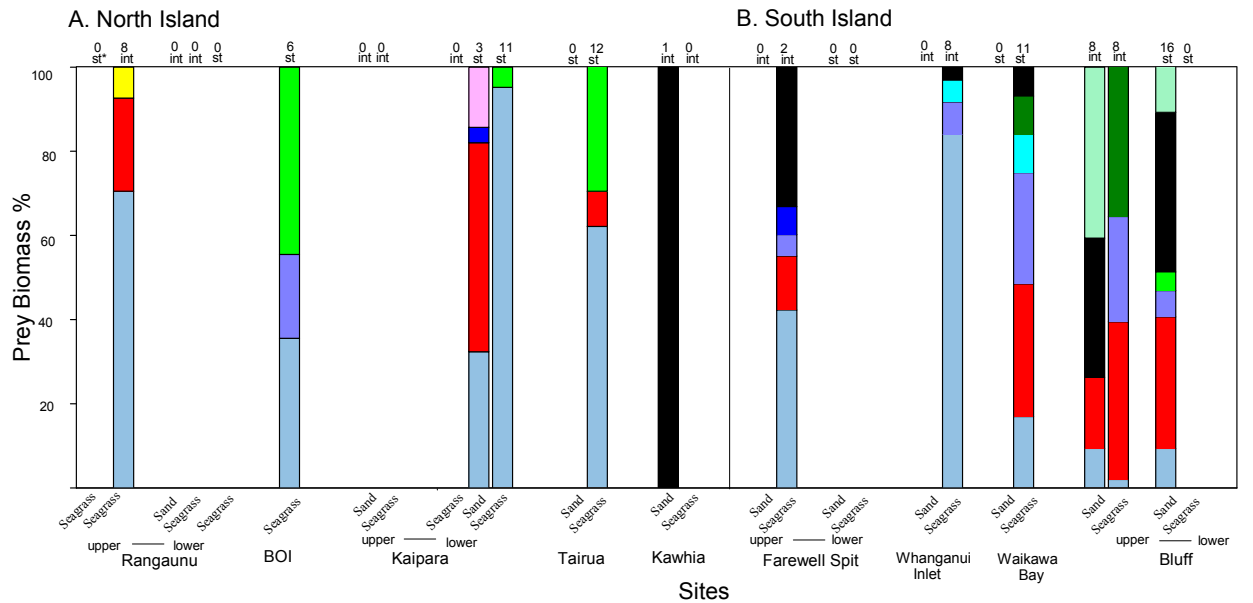


Figure 18: Proportional abundance of major dietary categories consumed by spotty across all habitats and harbours (A–B); by (20 mm) length class (C); PCA trajectory score plots of major dietary categories consumed by (20 mm) length class (D); *Peracarid=Peracarid other. Fish=fish scales. Number of guts analysed are shown above each histogram.



Mottled triplefin
(*Grahamina capito*)

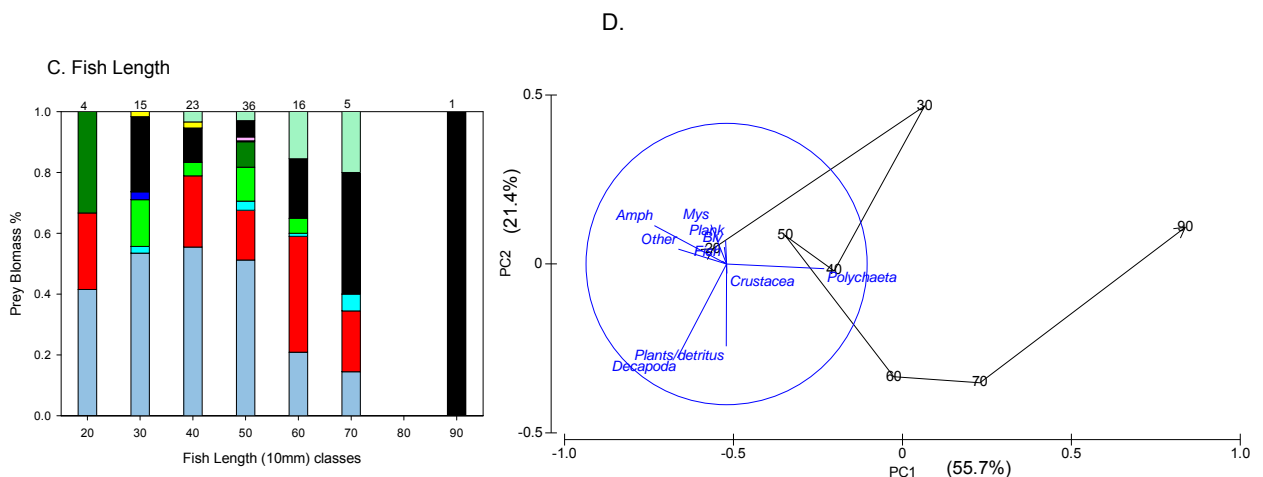
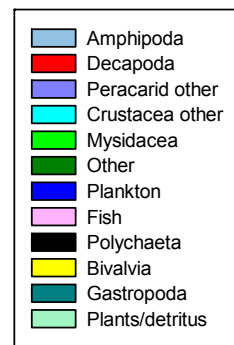
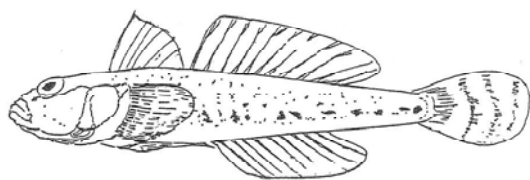
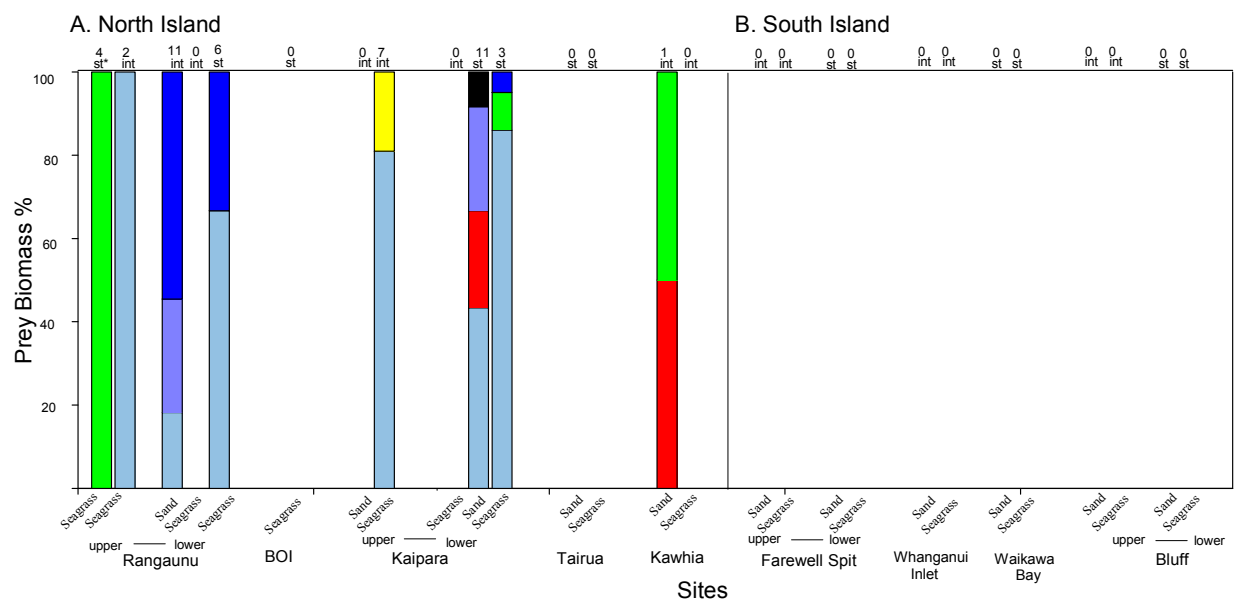
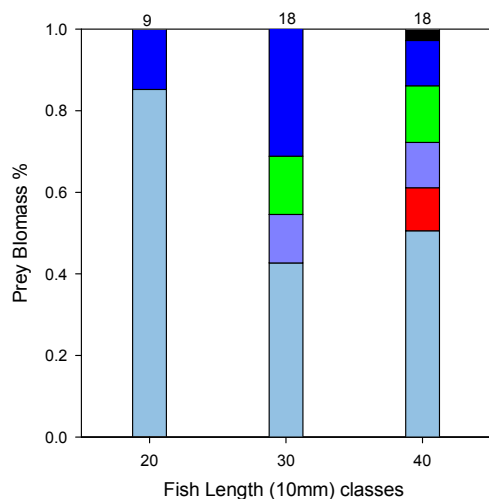


Figure 19: Proportional abundance of major dietary categories in mottled triplefin fish guts consumed across all habitats and harbours (A–B); by (10 mm) length class (C); PCA trajectory score plots of major dietary categories consumed by (10 mm) length class (D); Amp=Amphipoda; Mys=Mysidacea; Dietary category overlap at 20 mm: Plank=plankton; Biv=Bivalvia; Fish. Number of guts analyzed are shown above each histogram.



Exquisite goby
(*Favonigobius exquisitus*)

C. Fish Length



D.

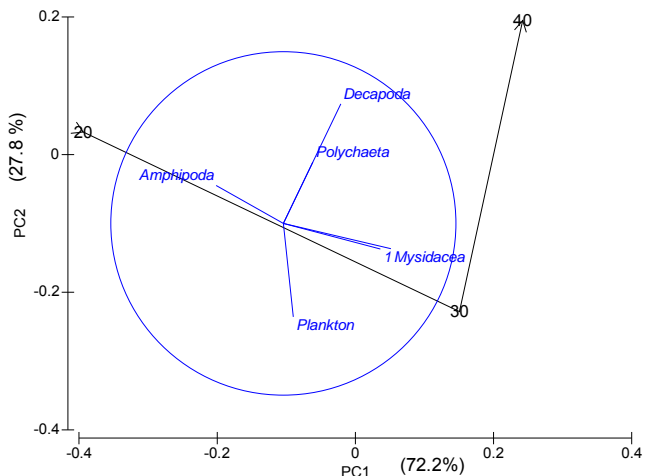


Figure 20: Proportional abundance of major dietary categories in exquisite goby fish guts consumed across all habitats and harbours (A–B); by (10 mm) length class (C); PCA trajectory score plots of major dietary categories consumed by (10 mm) length class (D); *1=Peracarid other. Number of guts analysed are shown above each histogram.

Yellow-eyed mullet (*Aldrichetta forsteri*) Both Islands

Yellow-eyed mullet were highly dependent on copepods (*P. indicus*) during post-settlement (20–59 mm), with the highest mean number of prey (1200 individuals per gut) recorded for this study in seagrass at Urupukapuka Island (Bay of Islands) (Figure 21a–c). Increasing quantities of algae/detritus and *Polysiphonia* sp. /*Ulva* sp. (seagrass sites) were consumed with increasing length (more than 59 mm), in addition to modest numbers of mysids, amphipods, and insect larvae (Chironomidae). PCA analysis showed a clear ontogenetic change with size, with the first two axes explaining 86.5% of the variation (Figure 21d). Diet across seagrass sites only was distinguished by higher numbers of plankton ingested, while sand sites had more benthic prey items (i.e. ‘other’ nematodes, plant and/or detritus).

Yellow-belly flounder (*Rhombosolea leporina*) Both Islands

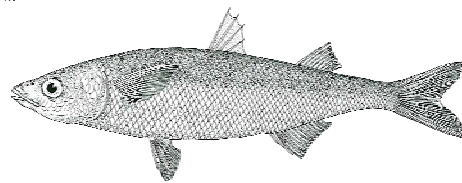
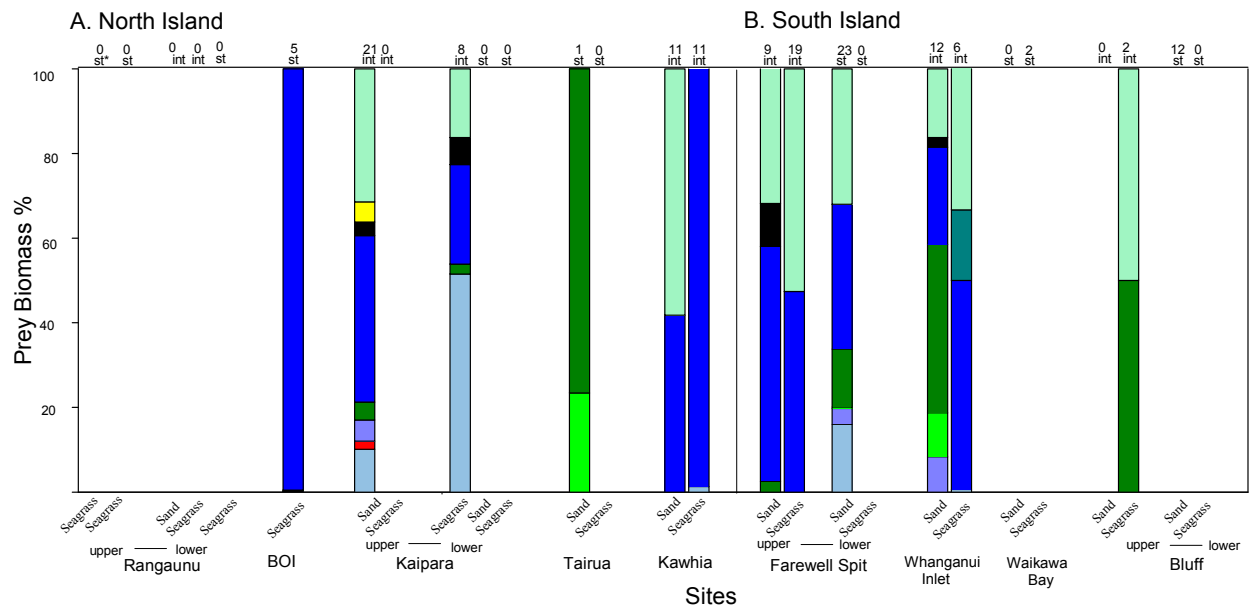
Mysids and amphipods were the major prey item for early juvenile (50 mm) yellow-belly flounder (Figure 22a–c). Infaunal species such as nematodes (‘other’), cumaceans and polychaetes (e.g. *Neanthes* sp.) became increasingly important above 60–79 mm. PCA analysis of the major prey categories revealed that 75.2% of variability was explained by the first two axes (Figure 22d), revealing a clear ontogenetic dietary shift (although large size fish sample sizes were low)

Sand flounder (*Rhombosolea plebeia*) Both Islands

Diet of juvenile sand flounder (25–39 mm TL) was dominated by amphipods (Figure 23a–b) which progressively declined in importance with size. Mussels were consumed in moderate numbers between 40 and 79 mm. The dominance of nematodes (category ‘Other’) increased with size class. The largest sized sand flounder consumed 100% juvenile crabs. Seagrass-associated fish consumed the highest diversity of prey items (i.e., Kawhia).

Speckled sole (*Peltorhampus latus*) Both Islands

Speckled sole preyed primarily on cumaceans (*C. lemurana*), constituting 43% of the total stomach contents, particularly for the larger size-classes (20–99 mm), followed by bivalves (22%), (Figure 24d, e). PCA analysis explained 80.2% (first two axes) of the variance with the smaller size classes showing an association with zooplankton and mysid eigen-vectors along the first axis. Mussels distinguished the prey over sandy habitats (Figure 24a, b). As with sand flounder, the largest sized sand flounder consumed predominantly decapods.



Yellow-eyed mullet
(*Aldrichetta forsteri*)

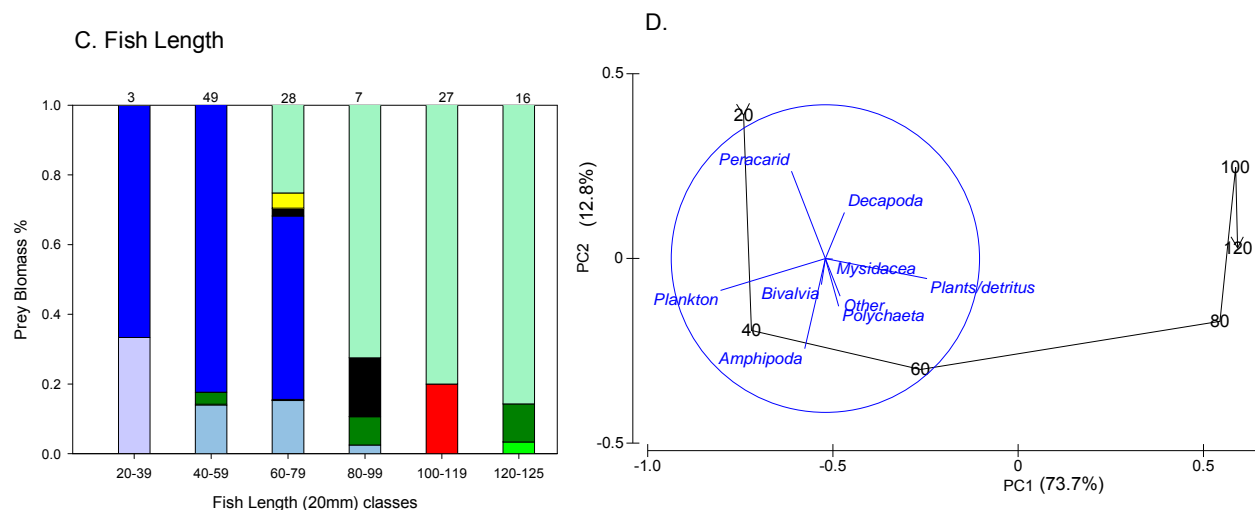
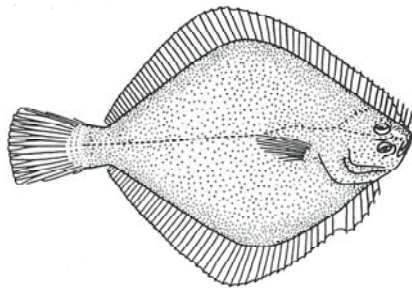
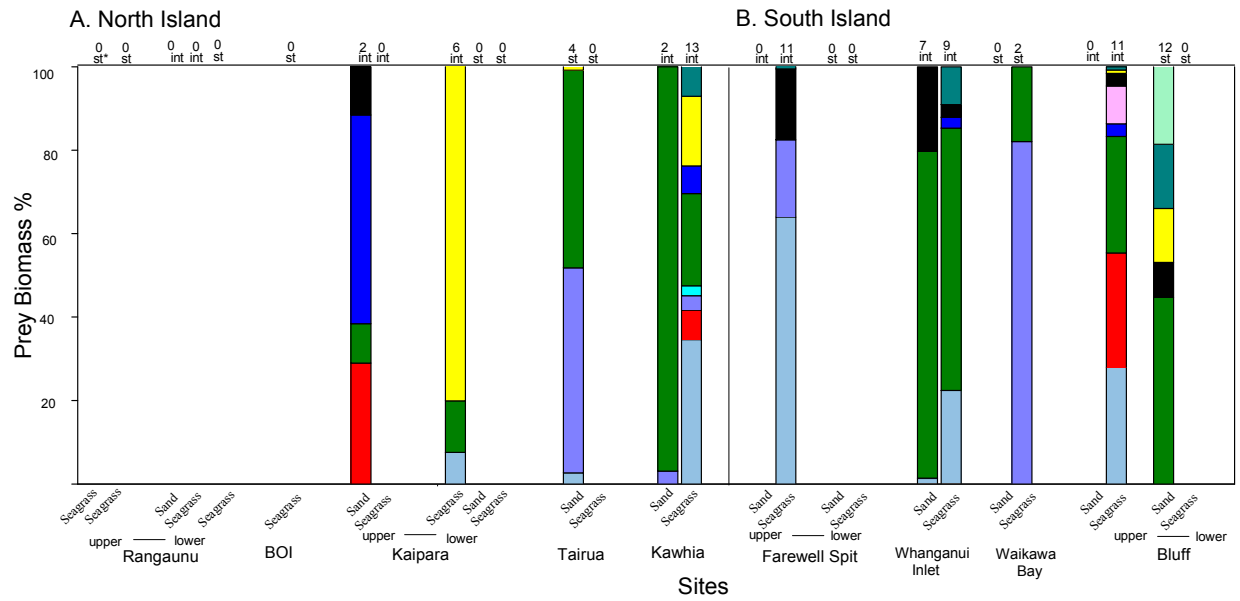


Figure 21: Proportional abundance of major dietary categories consumed by goby across all habitats and harbours (A–B); by (20 mm) length class (C); PCA trajectory score plots of major dietary categories consumed by (10 mm) length class (D); Peracarid=Peracarid other. Number of guts analysed are shown above each histogram



Sand flounder
(*Rhombosolea plebeia*)

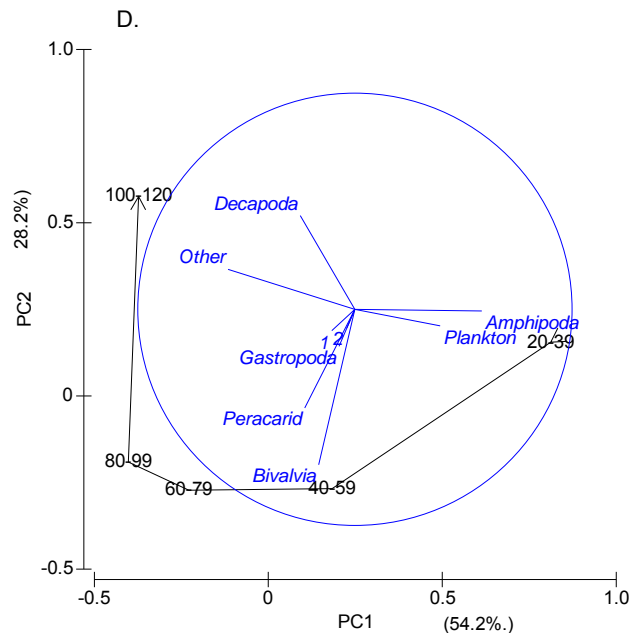
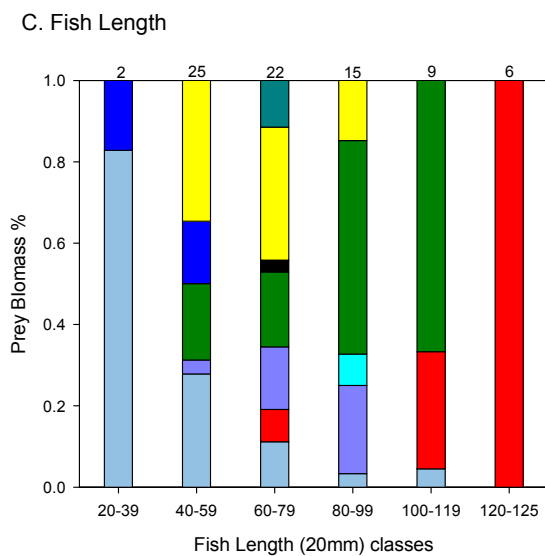
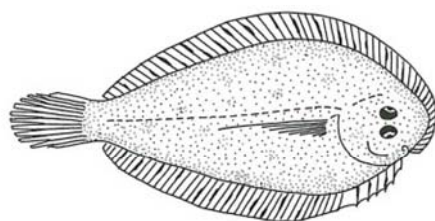
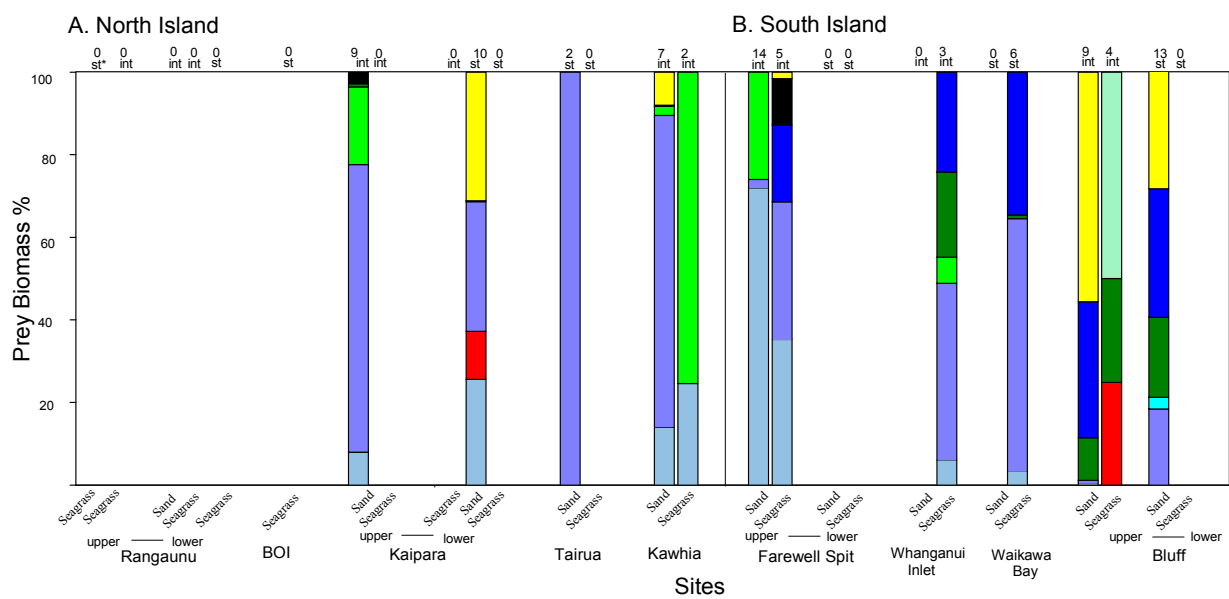


Figure 23: Proportional abundance of major dietary categories consumed by sand flounder across all habitats and harbours (A–B); by (20 mm) length class (C); PCA trajectory score plots of major dietary categories consumed by (20 mm) length class (D). 1=Polychaeta; 2=Crustacea other; Peracarid=Peracarid other. Number of guts analysed are shown above each histogram.



Speckled sole
(*Peltorhamphus latus*)

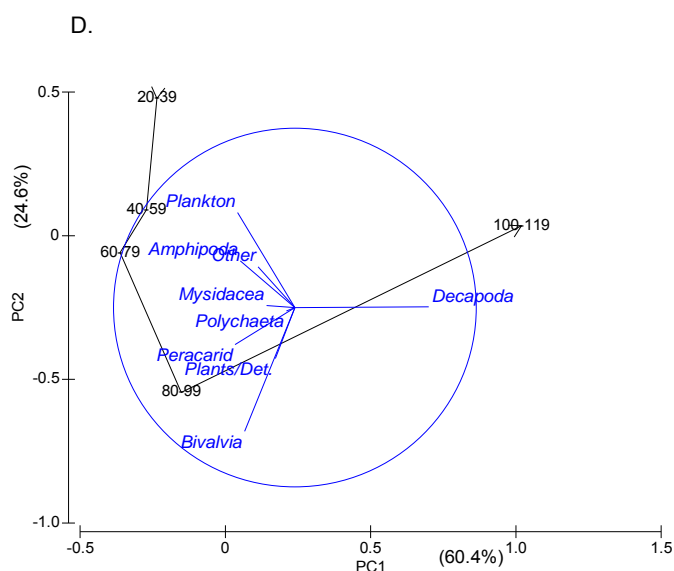
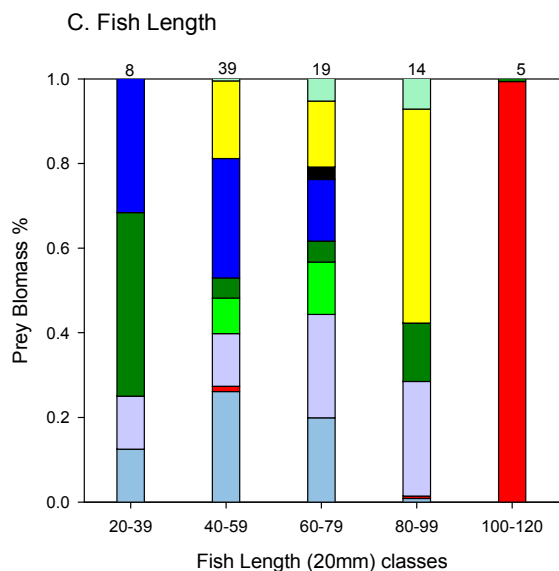
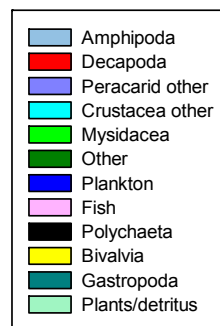


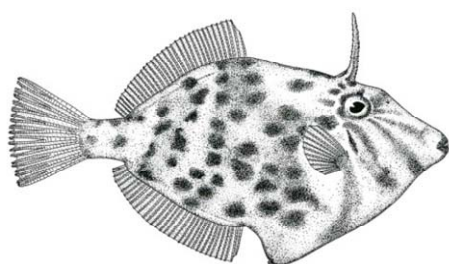
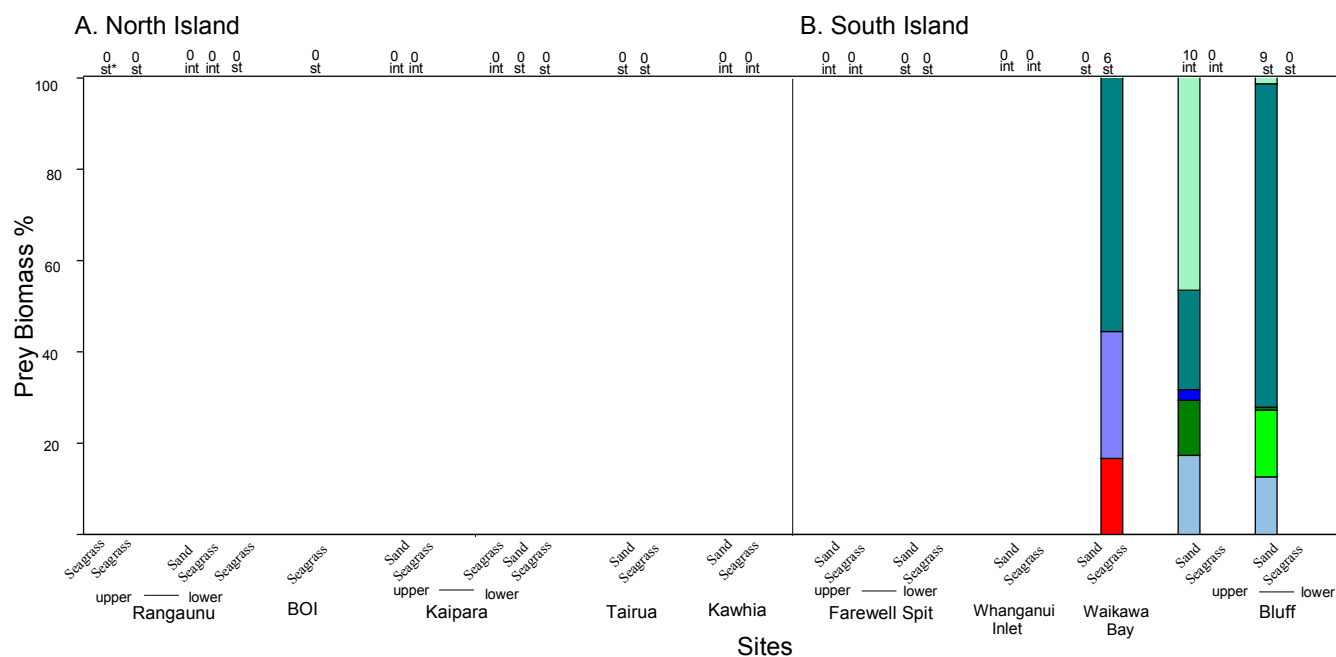
Figure 24: Proportional abundance of major dietary categories consumed by speckled sole across all habitats and harbours (A–B); by (20 mm) length class (C); PCA trajectory score plots of major dietary categories consumed by (10 mm) length class (D); *Peracarid=Peracarid other. Number of guts analysed are shown above each histogram.

Leather jacket (*Parika scaber*) South Island only

Gastropods (*Eatoneella* sp.) along with algae/bryozoa dominated the early juvenile leather jacket diet along with moderate numbers of mysids and amphipods (Figure 25b–c). Larger juveniles (30–39 mm) saw the addition of small crab species and isopods to their diet.

Smelt (*Retropinna retropinna*) South Island only

Mysids and nematodes (‘other’) were the major prey items for 60 mm smelts, with nematodes increasing in importance with size along with modest contributions of crab species, polychaetes and isopods. PCA analysis of the major prey categories revealed that 100% of the variability was explained by the first two axes (Figure 26d), revealing a clear ontogenetic dietary shift from a mysid and plankton dominated diet to a decapod dominated diet as the size of the fish increased.



Leatherjacket
(*Parika scaber*)

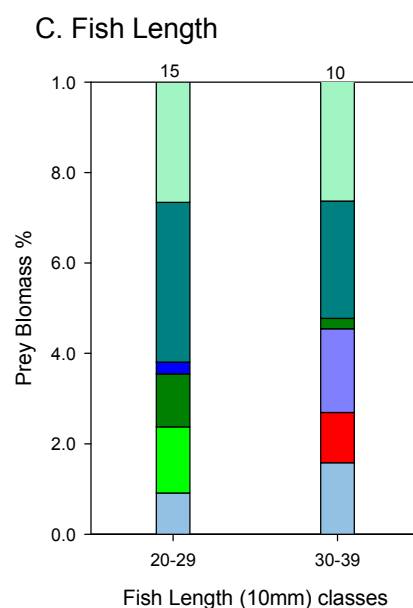


Figure 25: Proportional abundance of major dietary categories consumed by leatherjacket across all habitats and harbours (A–B); by (10 mm) length class (C). Number of guts analysed are shown above each histogram.

4.8 Biodiversity of invertebrates associated with seagrass across New Zealand

Infaunal invertebrate community structure

A total of 132 benthic cores were processed, including some location/habitat combinations unable to be sampled for the fish community analysis (namely the Gisborne and Kaikoura rocky reef sites, along with bare subtidal samples from upper and lower Rangaunu Harbour and lower Kaipara Harbour). All samples from Tairua Harbour were intertidal. Two hundred and thirty two (232) operational taxonomic units were identified; henceforth referred to as species for convenience (Appendix 3).

Spatial variation in infaunal invertebrate abundance

Combined mean densities of all species found (i.e. total density, Figure 27c) within a particular Location/Habitat combination showed a greater degree of variation than species richness (Figure 27b), ranging from ten up to about 240 individuals per core. Most of the higher densities were recorded from seagrass sites, both intertidal and subtidal (although sites from Kaikoura appeared to be an exception to this, see below). The highest densities were seen at the subtidal seagrass sites of lower Rangaunu Harbour, the Bay of Islands, Waikawa and lower Bluff Harbour, along with intertidal seagrass sites at Tairua, upper Farewell Spit, and Whanganui Inlet. At Kaikoura high numbers of individuals were found in the bare habitat (actually the remnants of dead seagrass forming a structure into which the sand had become bound), as well as in the intertidal seagrass.

An ANOVA comparison revealed significant differences in infaunal invertebrate abundances for the same habitat (e.g. intertidal seagrass) across position and between islands (*d.f.* 6, *f* 4.198, *P* < 0.001). A second ANOVA comparison of infaunal invertebrate abundance between habitats within one position between islands was also significant (*d.f.* 10, *f* 5.558, *P* < 0.000) (Figure 28a), Tukey HSD *post hoc* analysis of these ANOVA results identified that lower North Island, subtidal seagrass sites had significantly higher total infaunal invertebrate abundance than bare intertidal or bare subtidal sites (Figure 28b). Lower South Island intertidal seagrass sites had significantly higher total infaunal invertebrate abundance than bare subtidal sites.

Infaunal invertebrate species richness (N) and species diversity

The number of species per core (N or 'richness') (Figure 27b) varied from 3 to 44, with the highest species richness being found in the north, in association with subtidal seagrass habitats in lower Rangaunu Harbour, and in the subtidal seagrass of Urupukapuka Island, Bay of Islands. Aside from these two sites, there was no general trend in infaunal invertebrate richness from north to south, with most locations averaging between 10 and 20 species per core. Generally, seagrass habitats, whether intertidal or subtidal, held more species per core than their adjacent 'bare' counterparts, and blade lengths were longer in the subtidal versus intertidal (Figure 27a, b). In the Kaipara Harbour there was little difference between the intertidal seagrass and bare sites, except for the subtidal component. Species richness was higher than seagrass in the bare habitat at the upper Farewell Spit sites. In the South Island species richness was relatively constant across sites for both seagrass and bare sites respectively.

An ANOVA comparison investigating infaunal invertebrate richness for the same habitat (e.g. seagrass intertidal) across position and between islands was not significant (*d.f.* 6, *f* 2.017, *P* < 0.068). Infaunal invertebrate richness was significantly different between habitats within one position (upper or lower) between islands (*d.f.* 10, *f* 7.493, *P* < 0.000). Tukey HSD *post hoc* analysis of these ANOVA results show that for within position and between island comparisons, lower North Island, subtidal seagrass sites had significantly higher infaunal invertebrate richness than intertidal seagrass or bare subtidal sites, which in turn had higher infaunal invertebrate richness than bare intertidal sites (Figure 28a). Lower South Island, intertidal seagrass sites had significantly higher infaunal invertebrate richness than bare intertidal sites.

The species diversity indices calculated for infaunal invertebrates across the various locations throughout New Zealand identified a total species number ranging between 8 species (upper Farewell

Spit, bare intertidal) and 83 species (lower Rangaunu Harbour, seagrass subtidal) (Table 10), when all cores are combined. In general, the Shannon-Weiner Index was closer to 1 for the South Island locations, indicating greater species diversity at these locations. The Simpson's Index was high for many locations indicating dominance of a relatively few species at these sites.

Table 10: Diversity indices for infaunal invertebrate community composition (all cores combined) from locations sampled throughout New Zealand (locations displayed North to South) in 2006. Habitats sampled include: SS – Seagrass Subtidal, SI – Seagrass Intertidal, BS – Bare Subtidal and BI – Bare Intertidal.

Location × Position × Habitat	S (Total No. of Species)	N (Total No. of Individuals)	Pielou's Evenness Index	Shannon –Weiner Index	Simpson Index
RUNU U SS	39	140	0.8477	3.106	0.9331
RUNU U BS	26	110	0.7549	2.459	0.8594
RUNU L SI	44	330	0.6004	2.272	0.7903
RUNU L BI	24	47	0.9155	2.910	0.9473
RUNU L SS	83	882	0.7012	3.099	0.8835
RUNU L BS	40	110	0.8993	3.317	0.9586
BISL L SS	65	873	0.6179	2.579	0.8353
BISL L BS	41	210	0.8132	3.020	0.9158
KAIP U SI	29	371	0.6436	2.167	0.8180
KAIP U BI	25	136	0.7819	2.517	0.8882
KAIP L SI	32	116	0.8579	2.973	0.9355
KAIP L BI	26	137	0.7344	2.393	0.8228
KAIP L SS	47	236	0.8727	3.360	0.9545
KAIP L BS	25	89	0.8526	2.744	0.9099
TAIR L SI	29	662	0.3887	1.309	0.4709
TAIR L BI	14	73	0.8149	2.151	0.8550
KAWH L SI	36	199	0.7565	2.711	0.8924
KAWH L BI	26	232	0.6310	2.056	0.7465
GISB L SI	28	180	0.8175	2.724	0.8958
FWSP U SI	29	434	0.7541	2.539	0.8989
FWSP U BI	8	65	0.4641	0.965	0.4053
FWSP L SI	31	608	0.7872	2.703	0.9110
FWSP L BI	22	420	0.6292	1.945	0.8115
WNUI L SI	31	633	0.6056	2.080	0.8035
WNUI L BI	19	235	0.6620	1.949	0.7770
KAIK L SI	33	817	0.5683	1.987	0.7064
KAIK L BI	24	953	0.5456	1.734	0.7323
WAKW L SS	25	572	0.5554	1.788	0.7109
WAKW L BS	25	120	0.7918	2.549	0.8697
BLUF U SI	21	165	0.6539	1.991	0.7635
BLUF U BI	26	138	0.7721	2.516	0.8615
BLUF L SS	23	521	0.3673	1.152	0.4009
BLUF L BS	35	219	0.8348	2.968	0.9309

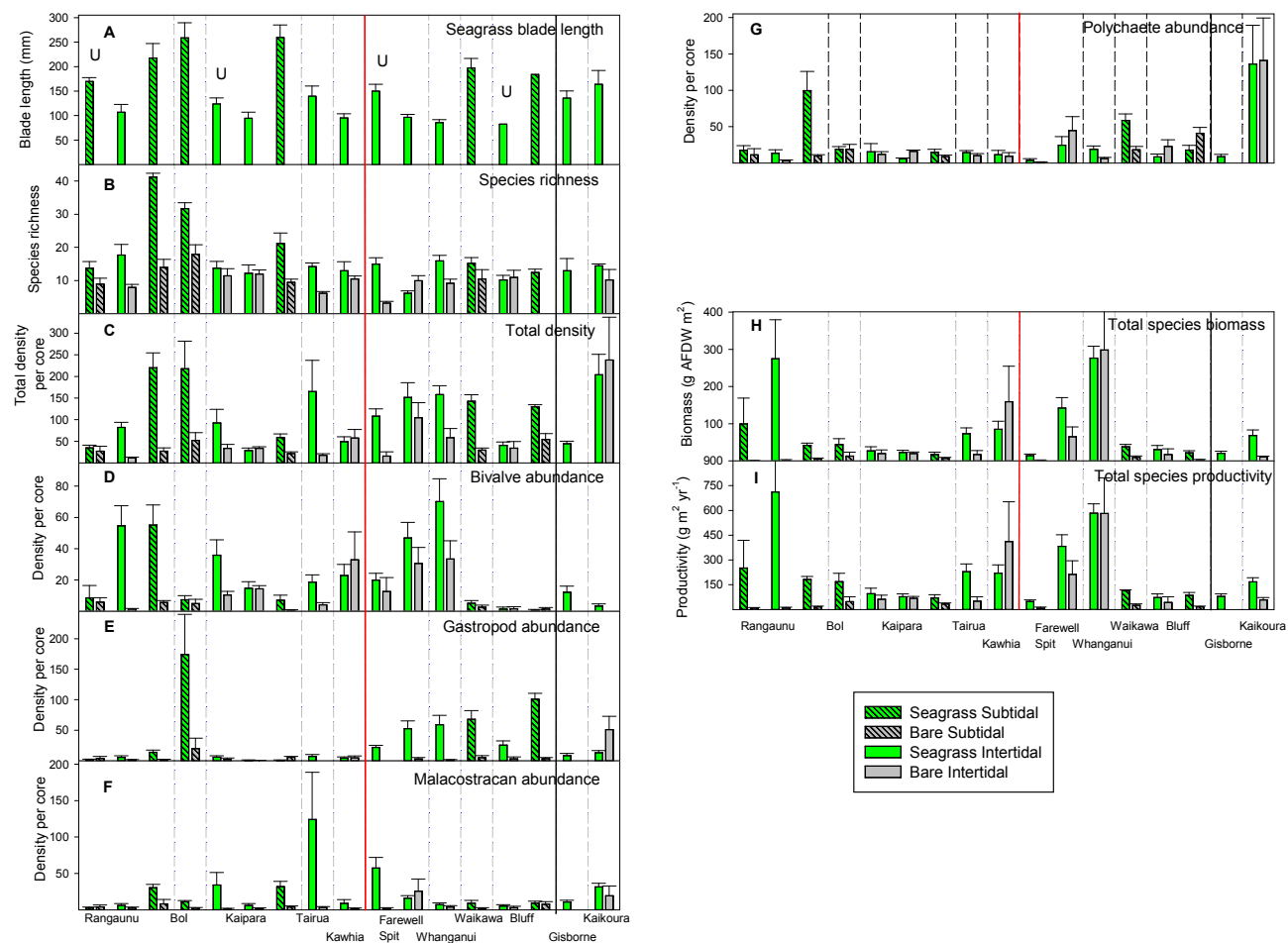


Figure 27: Graphs summarising the key components of the infaunal invertebrate assemblage (nominally under 10 mm in size) for eleven locations sampled throughout New Zealand. Locations run north to south from left to right, apart from the two rocky reef sites which are positioned at the far right. The red line denotes the North to South Island break. The black line denotes intertidal rocky reef sites. For each Location, seagrass and bare sites are paired in the following order, upper (U), then lower intertidal, then lower subtidal. A) average seagrass blade length (\pm s.e.), B) average species richness (\pm s.e.), C) total species abundance (\pm s.e.), D) average bivalve abundance per location (\pm s.e.), E) average gastropod abundance per location (\pm s.e.), F) average malacostracan abundance per location (\pm s.e.), G) average polychaete abundance per location (\pm s.e.), H) average total invertebrate biomass (\pm s.e.), and I) average invertebrate secondary production (\pm s.e.).

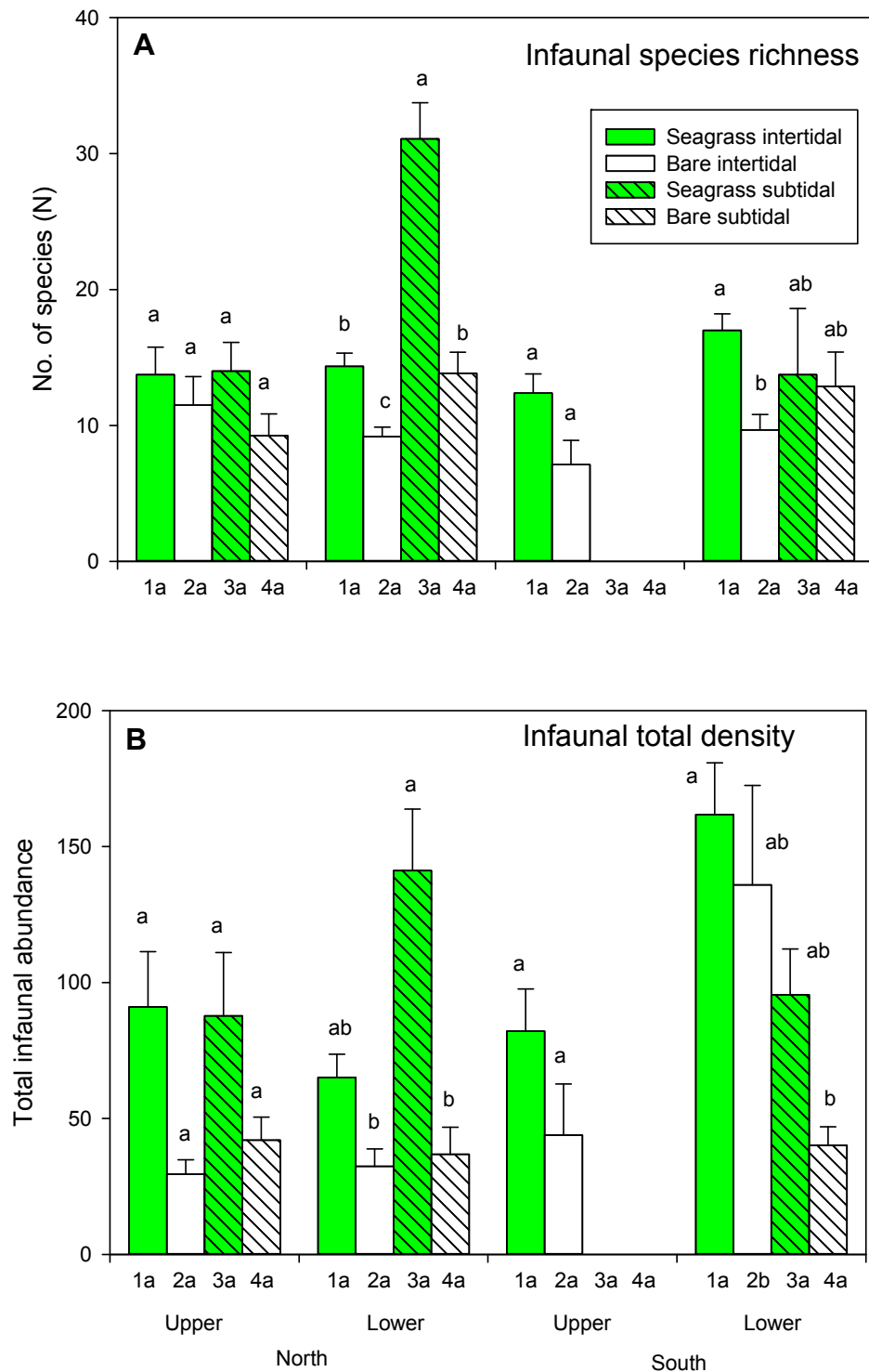


Figure 28: Graphical representation of Tukey HSD analysis for infaunal samples, A) average species richness (\pm s.e.) and B) mean total density per core (\pm s.e.), displayed by habitat type (SS, BS, SI, BI) within position (upper or lower) by island (North and South Islands). Annotation: letters above bars denote any differences for the habitat comparisons within each position by island combination, letters beneath bars denote same habitat comparisons across each position by island combination.

Invertebrate community contributions at the taxonomic group level

Seagrass habitats across the survey were characterised by four main taxonomic groups: gastropods (with a mean percentage contribution across all locations of 25%), malacostracans (22%), bivalves (24%), and polychaetes (24%) (Figure 27d, e). Bare habitats across the survey were dominated by polychaetes (42%), following by gastropods (11%), malacostracans (13%) and bivalves (25%). Across the spatial range sampled, bivalves were patchy in their distribution, and were present in low numbers only at the two most southern sites of Waikawa and Bluff harbours. In lower Rangaunu Harbour, the highest bivalve abundances were seen in the intertidal and subtidal seagrass sites, and were much greater than the densities in the adjacent bare substrates. Densities were generally lower across the remainder of the North Island locations, aside from the intertidal seagrass site in the (upper) Kaipara Harbour, and both the intertidal bare and seagrass sites in Kawhia Harbour. Bivalves were also highly abundant in several locations from the South Island, namely lower Farewell Spit and Whanganui Inlet, although the contrast between seagrass and bare sites at these locations was not as defined as for some northern locations.

Gastropods showed a broadly inverse pattern to bivalves (Figure 27e), occurring at relatively low densities in the North Island, with the exception of large numbers at the Bay of Islands subtidal seagrass site. Starting from Farewell Spit, they became much more common, and were largely associated with seagrass habitats, both intertidal and subtidal. Relatively, very few were present in the bare sediment sites.

Malacostracans (crustaceans) occurred at variable densities across the full range of locations and sites sampled (Figure 27f), with no clear geographic pattern. Higher densities were associated with subtidal seagrass in lower Rangaunu and lower Kaipara harbours, but the highest densities overall were seen in the intertidal seagrass sites of Tairua and upper Farewell Spit. The intertidal bare and seagrass habitats on the rocky reefs at Kaikoura also contained relatively high numbers of malacostracans.

Polychaetes were more evenly distributed across the entire geographic range (Figure 27g), but showed elevated abundances in the subtidal seagrass of lower Rangaunu and Waikawa harbours, as well as the subtidal bare habitat of lower Bluff Harbour. The highest densities recorded were on the intertidal bare and seagrass sites of the rocky reef platform at Kaikoura, where they averaged about 125 individuals per core.

Infaunal invertebrate biomass (seagrass versus bare).

The invertebrate biomass associated with seagrass habitats was generally higher than that for bare sand sites throughout the country (Figure 27h), although this was not true for all locations (e.g. Kaipara Harbour, Kawhia Harbour, and Whanganui Inlet). Interestingly, the locations with the highest infaunal invertebrate biomass were predominantly intertidal seagrass or bare sites, as opposed to the subtidal seagrass sites. A further breakdown of these biomass estimates clearly identifies the large contribution that bivalves make to these estimates at many locations (Figure 29a). Displaying the biomass data minus the highly influential bivalve component (Figure 29b), allows a better visual comparison of the role other major invertebrate assemblage taxa make at each location, namely gastropods, malacostracans and polychaetes.

An ANOVA comparison revealed significant differences in infaunal invertebrate biomass for the same habitat (e.g. intertidal seagrass) across position and between islands (*d.f.* 6, *f* 2.809, *P* < 0.014). A second ANOVA comparison of infaunal invertebrate biomass between the habitats within one position between islands was also significant (*d.f.* 10, *f* 8.404, *P* < 0.000). Tukey HSD *post hoc* analysis of these ANOVA results are graphically summarised in Figure 30a. Within position between islands comparisons identified that upper North Island, subtidal seagrass sites, had significantly higher infaunal invertebrate biomass than bare subtidal sites. Lower North Island, intertidal seagrass sites had significantly higher infaunal invertebrate biomass than bare subtidal sites. Lower South Island, intertidal seagrass and bare intertidal sites had significantly higher biomass than bare subtidal sites.

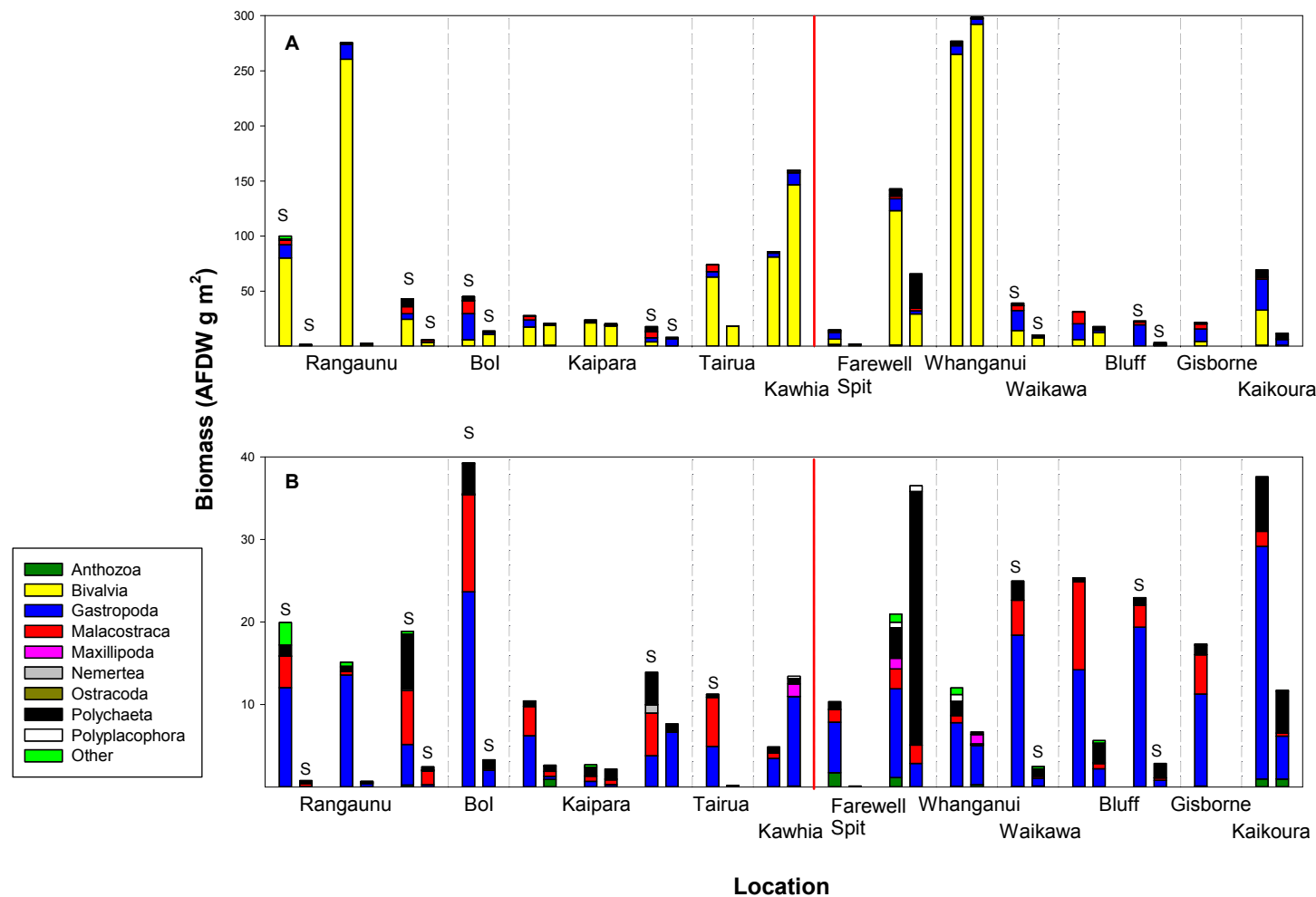


Figure 29: Graphs summarising the biomass contribution of the major taxonomic groups of the infaunal invertebrate species assemblage (nominally under 10 mm in size) for eleven locations sampled throughout New Zealand. Locations run north to south from left to right, apart from the two rocky reef sites which are positioned at the far right. The red line denotes the North to South Island break. An S denotes the subtidal sites. In each pair the seagrass site is presented first followed by the bare site. A) Mean biomass, B) Mean biomass – bivalve contribution removed.

Infaunal invertebrate secondary production (seagrass versus bare).

The estimates of invertebrate secondary production associated with seagrass habitats were generally higher than those for bare sand sites throughout the country (Figures 27i, 31), although not always (e.g. Kaipara Harbour, Kawhia Harbour, and Whanganui Inlet) (Figure 27i). Interestingly, the locations with the highest infaunal invertebrate secondary production were predominantly intertidal seagrass or bare sites, as opposed to the subtidal seagrass sites.

An ANOVA comparison of infaunal invertebrate secondary production for the same habitat (e.g. intertidal seagrass) across position and between islands was significant (*d.f.* 6, *f* 3.165, $P < 0.007$). A second ANOVA comparison of infaunal invertebrate secondary production between habitats within one position between islands was also significant (*d.f.* 10, *f* 8.736, $P < 0.000$). Tukey HSD *post hoc* analysis of these ANOVA results show that upper North Island, subtidal seagrass sites had significantly higher levels of secondary production than bare subtidal sites (Figure 32b). And lower North Island, intertidal seagrass sites had significantly higher levels of infaunal invertebrate secondary production than bare subtidal sites. For the upper South Island, intertidal seagrass sites had significantly higher levels of infaunal invertebrate secondary production than bare intertidal sites. For the lower South Island, intertidal seagrass and bare sites had significantly higher levels of secondary production than bare subtidal sites.

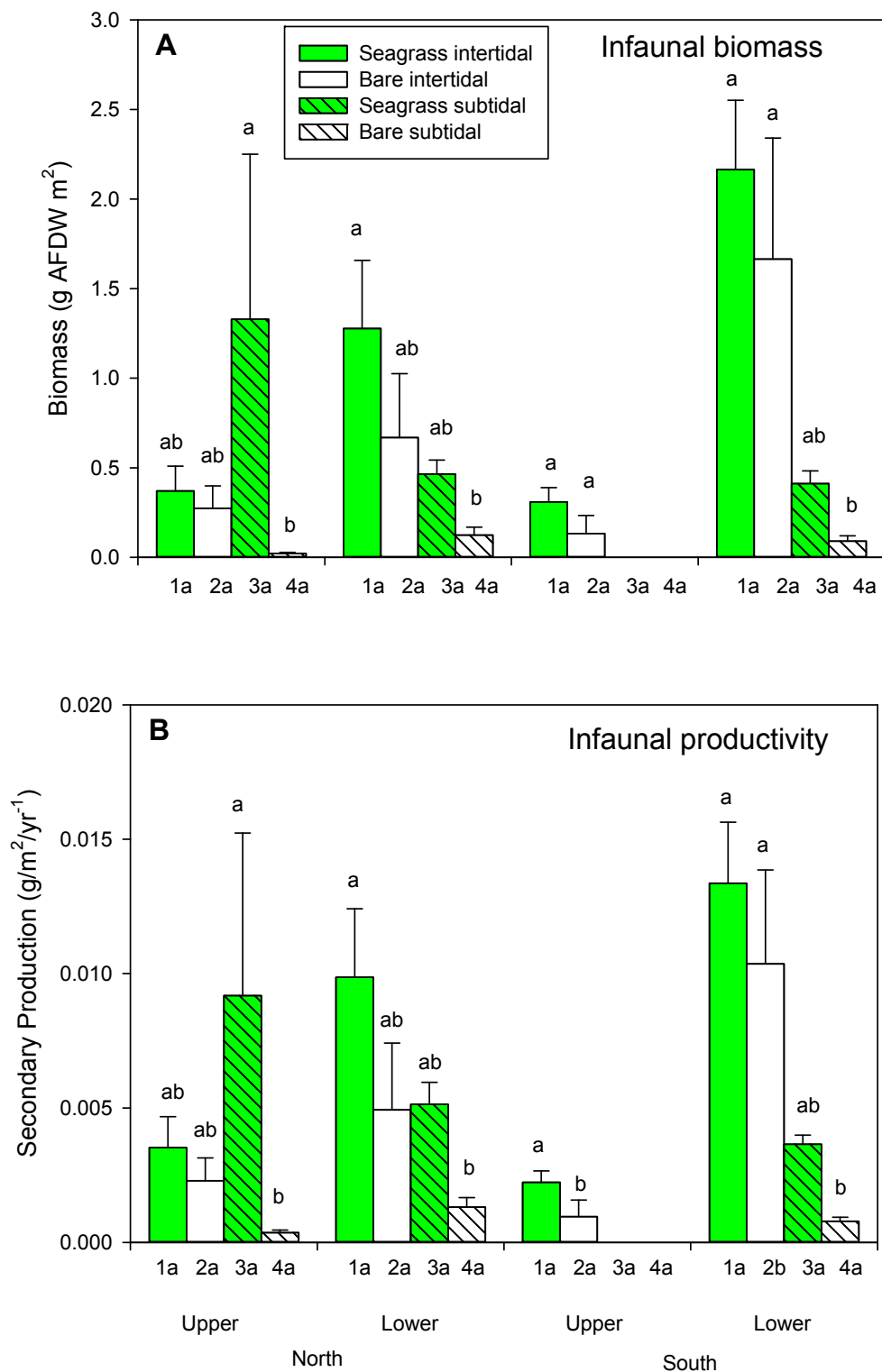


Figure 30: Graphical representation of Tukey HSD analysis for infaunal samples, A) Biomass (g AFDW m⁻²), and B) Secondary production (g/m²/yr⁻¹), displayed by habitat type (SS, BS, SI, BI) within position (upper or lower) within island (North and South Islands). Annotation: letters above bars denote any differences for the habitat comparisons within each position × island combination, letters beneath bars denote same habitat comparisons across each position by island combination.

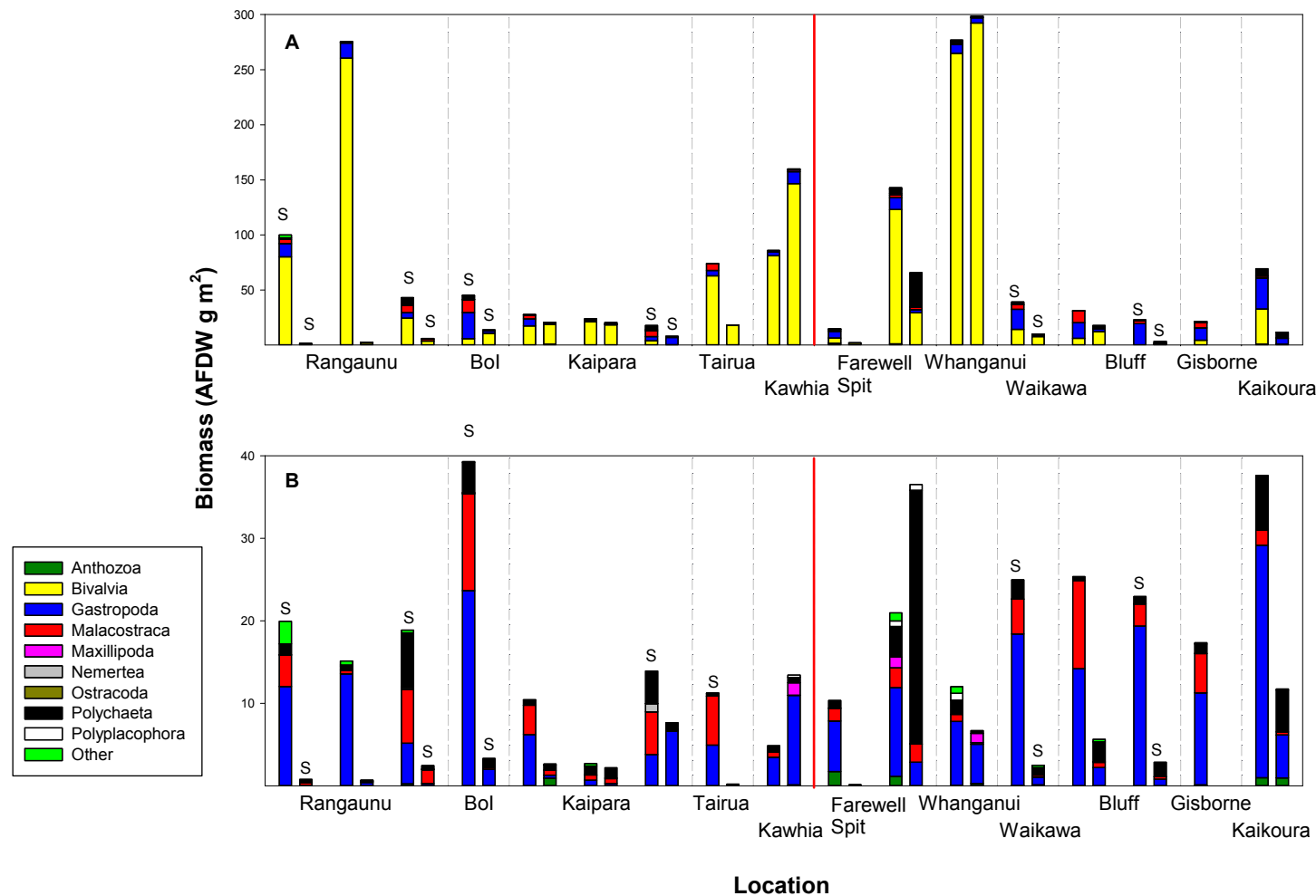
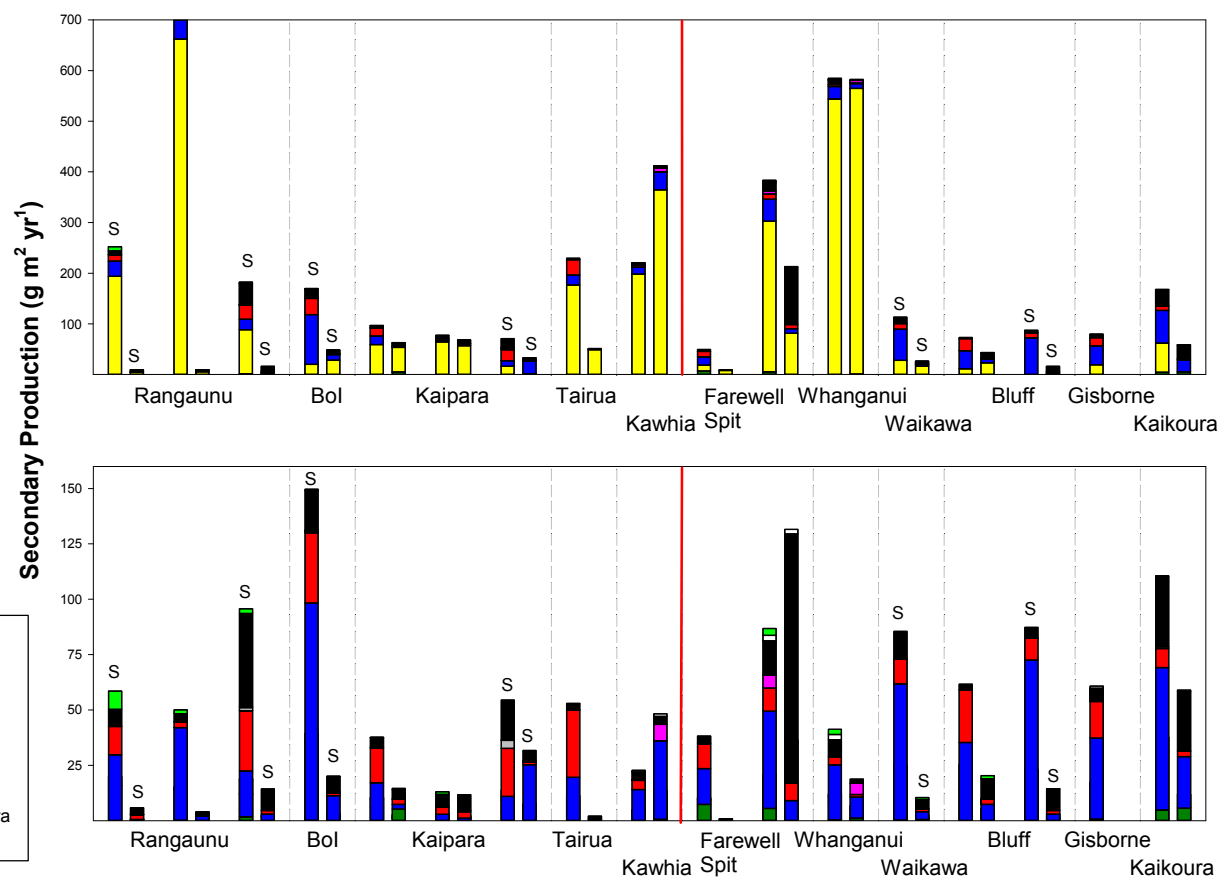


Figure 31: Graphs summarising the biomass contribution of the major taxonomic groups of the infaunal invertebrate species assemblage (nominally under 10 mm in size) for eleven locations sampled throughout New Zealand. Locations run north to south from left to right, apart from the two rocky reef sites which are positioned at the far right. The red line denotes the North to South Island break. An S denotes the subtidal sites. In each pair the seagrass site is presented first followed by the bare site. A) Mean biomass, B) Mean biomass – bivalve contribution removed.



Location

Figure 32: Graphs summarising the contribution to secondary production of the major taxonomic groups of the infaunal invertebrate species assemblage (nominally under 10 mm in size) for eleven locations sampled throughout New Zealand. Locations run north to south from left to right, apart from the two rocky reef sites which are positioned at the far right. The red line denotes the North to South Island break. An S denotes the subtidal sites. In each pair the seagrass site is presented first followed by the bare site: A) mean productivity, B) mean productivity with bivalve contribution removed.

4.9 Seagrass associated infaunal invertebrate communities – multivariate

MDS Ordination

An MDS ordination plot of all benthic cores sampled identified groupings by latitude and habitat type for the infaunal invertebrate assemblage (Figure 33). Increasing the number of restarts for this ordination did not produce a lower stress two-dimensional ordination of this dataset. The North to South Island split is between numbers 5 and 6. The ordination shows that North Island locations fell towards the left of the data cluster while South Island locations fell towards the right of the data cluster.

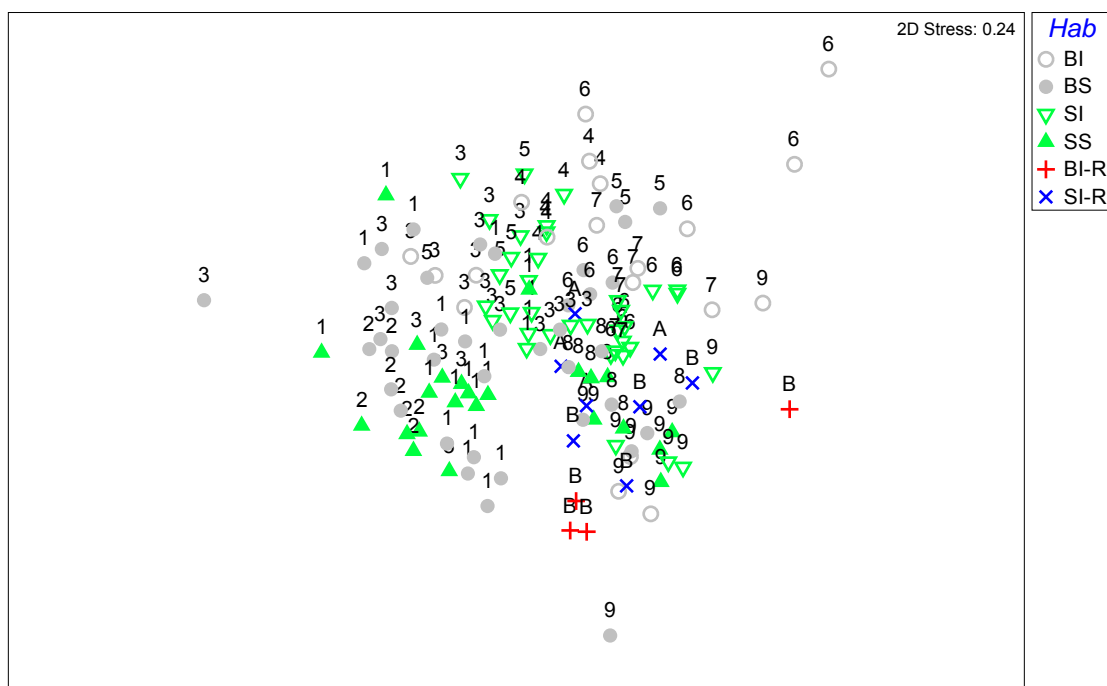


Figure 33: MDS ordination of infaunal invertebrate species assemblage. Sampling locations labelled from North to South as follows; North – Rangaunu (1), Bay of Islands (2), Kaipara (3), Tairua (4), Kawhia (5), South – Farewell Spit (6), Whanganui (7), Waikawa (8), Bluff (9), then Gisborne (AX) and Kaikoura (BX, B+). The North/South Island split occurs between 5 and 6. BI, bare intertidal; BS, bare subtidal; SI, seagrass intertidal; SS, seagrass subtidal.

Infaunal invertebrate community composition – by species composition

At the broadest spatial scale, PERMANOVA analysis revealed that there was a significant difference between habitats for North and South Island infaunal invertebrates (Table 11a). Pairwise tests identified that all the habitats were significantly different when compared between the North and South islands (see Appendix 4, Table 1).

A comparison between habitats nested within position (upper/lower) and Island (North/South) found significant differences (Table 11b). Pairwise tests revealed that all the possible habitat combinations returned significant results within either the North or South Island, with the exception of North Island (upper) subtidal seagrass/bare subtidal (Appendix 4, Table 2) (Rangaunu Harbour).

A comparison between all locations (harbour) within position (upper/lower) and habitats revealed significant differences (Table 11c). Pairwise test revealed that the majority of possible Location combinations returned significant results within every Habitat: with the exception of the Kaipara/Kawhia and Kawhia/lower Rangaunu combination for seagrass intertidal; the lower Rangaunu/Bay of Islands combination for bare subtidal; and the Kawhia/lower Rangaunu,

Kawhia/Tairua, and Kawhia/lower Whanganui Inlet combinations for bare intertidal (Appendix 4, Table 3).

A comparison between habitats (BI, BS, SI, SS) nested within position (upper/lower) and Location (harbours) was also significantly different (Table 11d). Pairwise comparisons for all the possible habitat combinations returned significant results for each Location: with the exception of subtidal seagrass/bare subtidal (upper Rangaunu Harbour), bare subtidal/bare intertidal, seagrass intertidal/bare intertidal (lower Rangaunu Harbour), and seagrass intertidal/bare intertidal (Kawhia Harbour) (Appendix 4, Table 4).

Table 11: PERMANOVA results of infaunal invertebrate community composition (by species), for various habitat comparisons nested by Island, and/or Position.

Source	df	Pseudo-F	P(perm)
a) Between the North and South Islands for each particular habitat			
Ha	3	5.4133	0.001
Po(Ha)	4	3.3034	0.001
Is(Po(Ha))	6	5.2444	0.001
b) Habitat variation within an Island			
Is	1	14.601	0.001
Po(Is)	2	3.6022	0.001
Ha(Po(Is))	10	3.9115	0.001
c) Habitat variation across Locations			
Ha	3	8.5681	0.001
Po(Ha)	4	5.2285	0.001
Lo(Po(Ha))	25	5.5029	0.001
d) Habitat variation within Locations			
Lo	10	9.5736	0.001
Po(Lo)	4	4.838	0.001
Ha(Po(Lo))	18	3.839	0.001

No comparisons were made between the East and West coasts of the North Island as only one west coast location was sampled, meaning that all east coast sites would simply be being compared against the Kaipara Harbour, and this has already been done in the above analysis.

Infaunal invertebrate community composition – by class group

The infaunal invertebrate community composition was also analysed using PERMANOVA analysis at the Class group level. This was deemed appropriate to allow a broader perspective to be obtained in relation to changes in community composition between locations and habitats. Class groups included: Anthozoa, Ascidae, Asteroidea, Bivalvia, Clitellata, Echinoidea, Enteropneusta, Gastropoda, Holothuroidea, Insecta, Malacostraca, Maxillipoda, Nematoda, Nemertea, Oligochaeta, Ophiuroidea, Ostracoda, Pantopoda, Phoronida, Polychaeta, Polycladida, Polyplacophora, Sipunculidea and Other. The exact analysis carried out above was therefore repeated on this taxonomically grouped dataset.

At the broadest spatial scale, PERMANOVA analysis revealed that there was significant difference in infaunal invertebrate community composition (by class group) between habitats of the North and South Island (Table 12a). A posteriori pairwise tests identified that all habitats were significantly different when compared between the North and South Island (Appendix 4, Table 5).

A comparison was also significantly different between habitats nested within position (upper/lower) and Island (North/South) (Table 12b). Pairwise tests revealed that the majority of comparisons in the South Island were significantly different (Appendix 4, Table 6). However, comparison of habitats in the upper North Island identified that only the intertidal seagrass versus bare intertidal comparison was significant, while in the lower North Island only bare intertidal and bare subtidal habitats were not significantly different. In the lower South Island, both bare subtidal versus bare intertidal and seagrass intertidal versus bare intertidal were not significantly different.

A comparison between all locations (harbour) within position (upper/lower) and habitats revealed significant differences between infaunal invertebrate community composition between all locations (harbour) within position (upper/lower) and habitat (Table 12c). Pairwise tests revealed that several lower South Island bare subtidal and bare intertidal combinations returned non-significant results (Appendix 4, Table 7).

A comparison between habitats (BI, BS, SI, SS) nested within position (upper/lower) and Location (harbours) revealed that infaunal invertebrate community composition was also significantly different between habitats (BI, BS, SI, SS) nested within position (upper/lower) and Location (harbours) (Table 12d). Pairwise comparisons of infaunal invertebrate community composition revealed that the following pairs were not significantly different (Appendix 4, Table 8); upper Rangaunu Harbour subtidal seagrass versus bare subtidal; lower Rangaunu Harbour bare subtidal versus bare intertidal, Bay of Islands subtidal seagrass versus bare subtidal, lower Kaipara Harbour subtidal seagrass versus bare subtidal, subtidal versus intertidal seagrass, subtidal seagrass versus bare intertidal, and intertidal seagrass versus bare intertidal; Kawhia Harbour seagrass versus bare intertidal; Kaikoura seagrass versus bare intertidal; Waikawa subtidal seagrass versus bare subtidal; and lower Bluff Harbour subtidal seagrass versus bare subtidal.

Table 12: PERMANOVA results of infaunal invertebrate community composition (by class), for various habitat comparisons nested by Island, and/or Position.

Source	df	Pseudo-F	P(perm)
a) Between the North and South Islands for each particular habitat			
Ha	3	8.0620	0.001
Po(Ha)	4	2.5606	0.001
Is(Po(Ha))	6	4.1138	0.001
b) Habitat variation within an Island			
Is	1	8.8460	0.001
Po(Is)	2	3.5695	0.001
Ha(Po(Is))	10	4.3127	0.001
c) Habitat variation across Locations			
Ha	3	11.751	0.001
Po(Ha)	4	3.7325	0.001
Lo(Po(Ha))	25	4.3592	0.001
d) Habitat variation within Locations			
Lo	10	6.5214	0.001
Po(Lo)	4	3.4012	0.001
Ha(Po(Lo))	18	4.4637	0.001

No comparisons were made between the East and West coasts of the North Island as only one west coast location was sampled, meaning that all east coast sites would simply be being compared against the Kaipara Harbour, and this has already been done in the above analysis.

Seagrass associated epifaunal invertebrate communities – univariate

A total of 126 strip transects were processed, including some location × habitat combinations unable to be sampled for the fish community analysis (namely the Gisborne and Kaikoura rocky reef sites, along with bare subtidal samples from Rangaunu Harbour (upper and lower) and Kaipara Harbour (lower)). Samples from Tairua Harbour were intertidal. Samples for Farewell Spit (upper) BI did not contain any fauna in any of the replicates. Eighty eight (88) operational taxonomic units were identified; henceforth referred to as species for convenience (see Appendix 5).

Total species densities

Combined mean densities of all species found (i.e. total density, Figure 34c) within a particular Location/Habitat combination showed a greater degree of variation than species richness (Figure 34b), ranging from fifteen up to about 5900 individuals per 100 m². The higher densities were recorded at a mix of locations combining both bare and seagrass sites. At Kaikoura high numbers of individuals were found in the bare habitat (actually the remnants of dead seagrass forming the structure for binding up of sand), as well as in the intertidal seagrass present.

An ANOVA comparison revealed significant differences in epifaunal invertebrate density for the same habitat (e.g. intertidal seagrass) across position and between islands (*d.f.* 6, *f* 6.929, *P* < 0.000). A second ANOVA analysis of epifaunal invertebrate density between the different habitats, within one position between islands was also significant (*d.f.* 10, *f* 3.936, *P* < 0.000). Tukey HSD *post hoc* comparisons (Figure 34a) revealed the following differences; upper North Island bare subtidal sites had significantly lower epifaunal invertebrate densities than lower South Island bare subtidal sites. Upper North Island, bare subtidal sites had significantly lower total epifaunal invertebrate densities than bare intertidal and subtidal seagrass sites. Lower North Island bare subtidal sites had significantly lower epifaunal invertebrate densities than bare intertidal sites. And finally, lower South Island bare subtidal sites had significantly lower epifaunal invertebrate densities than bare intertidal sites.

Species richness (N) and species diversity

The number of species per 100 m² of habitat (N or ‘richness’) (Figure 34b, 35) varied from a mean of 2.5 to 13.5, with the highest species richness being found in the south, in association with intertidal seagrass habitat at lower Farewell Spit. There was no general trend in epifaunal species richness running from the north to the south. Generally, seagrass habitats, whether intertidal or subtidal, held more epifaunal species per 100 m² than their adjacent ‘bare’ counterparts.

An ANOVA revealed significant differences in epifaunal invertebrate richness for the same habitat (e.g. intertidal seagrass) across position between islands (*d.f.* 6, *f* 4.536, *P* < 0.000). A second ANOVA comparison of epifaunal invertebrate richness between habitats within one position between islands was also significant (*d.f.* 10, *f* 3.812, *P* < 0.000). Tukey HSD *post hoc* comparisons of epifaunal invertebrate richness identified that lower North Island intertidal seagrass compared against subtidal seagrass sites, had both significantly higher epifaunal invertebrate richness than bare intertidal and bare subtidal sites (Figure 35b).

The species diversity indices calculated for epifaunal invertebrates across the various locations throughout New Zealand identified a total number of species ranging between 4 (Rangaunu Harbour, lower, BS) and 22 (Farewell Spit, upper, SI) (Table 13), when all transects were combined. There were no obvious trends in any of these indices with respect to a North/South Island gradient of locations.

Table 13: Diversity indices for epifaunal invertebrate community composition from locations sampled throughout New Zealand (locations displayed North to South). Habitats sampled include: SS – Seagrass Subtidal, SI – Seagrass Intertidal, BS – Bare Subtidal and BI – Bare Intertidal.

Location × Position × Habitat	S (Total No. of species)	N (Total No. of individuals)	Pielou's Evenness Index	Shannon – Weiner Index	Simpson Index
RUNU U SS	8	3388	0.3477	0.723	0.3702
RUNU U BS	5	155	0.7960	1.281	0.6912
RUNU L SI	16	1935	0.4411	1.223	0.5409
RUNU L BI	7	113	0.6666	1.297	0.6318
RUNU L SS	15	1410	0.5814	1.575	0.6969
RUNU L BS	4	30	0.8250	1.144	0.6609
BISL L SS	20	543	0.7074	2.119	0.8289
BISL L BS	8	183	0.7398	1.538	0.7344
KAIP U SI	14	780	0.5461	1.441	0.6696
KAIP U BI	6	3070	0.4667	0.836	0.4130
KAIP L SI	13	1229	0.4884	1.253	0.6011
KAIP L BI	11	385	0.5932	1.422	0.6401
KAIP L SS	15	165	0.7584	2.054	0.7881
KAIP L BS	11	218	0.8567	2.054	0.8532
TAIR L SI	11	6215	0.4779	1.146	0.5830
TAIR L BI	6	1010	0.2192	0.392	0.1586
KAWH L SI	18	4679	0.4945	1.429	0.7057
KAWH L BI	8	17689	0.7705	1.602	0.7748
GISB L SI	18	1155	0.7149	2.066	0.8058
GISB L BI	14	745	0.5302	1.399	0.6071
FWSP U SI	22	3485	0.5103	1.577	0.6780
FWSP L SI	21	4335	0.4973	1.514	0.6832
FWSP L BI	18	4744	0.4411	1.275	0.6467
WNUI L SI	18	465	0.8026	2.320	0.8671
WNUI L BI	18	6337	0.3609	1.043	0.4386
KAIK L BI	14	2346	0.5413	1.429	0.7119
KAIK L SI	5	305	0.4093	0.658	0.2940
WAKW L SS	8	2059	0.2034	0.423	0.1745
WAKW L BS	11	2155	0.1703	0.408	0.1595
BLUF U SI	14	2367	0.3929	1.037	0.4033
BLUF U BI	17	1788	0.5664	1.605	0.7231
BLUF SS	16	1880	0.5078	1.408	0.6089
BLUF L BS	12	768	0.5809	1.444	0.6730

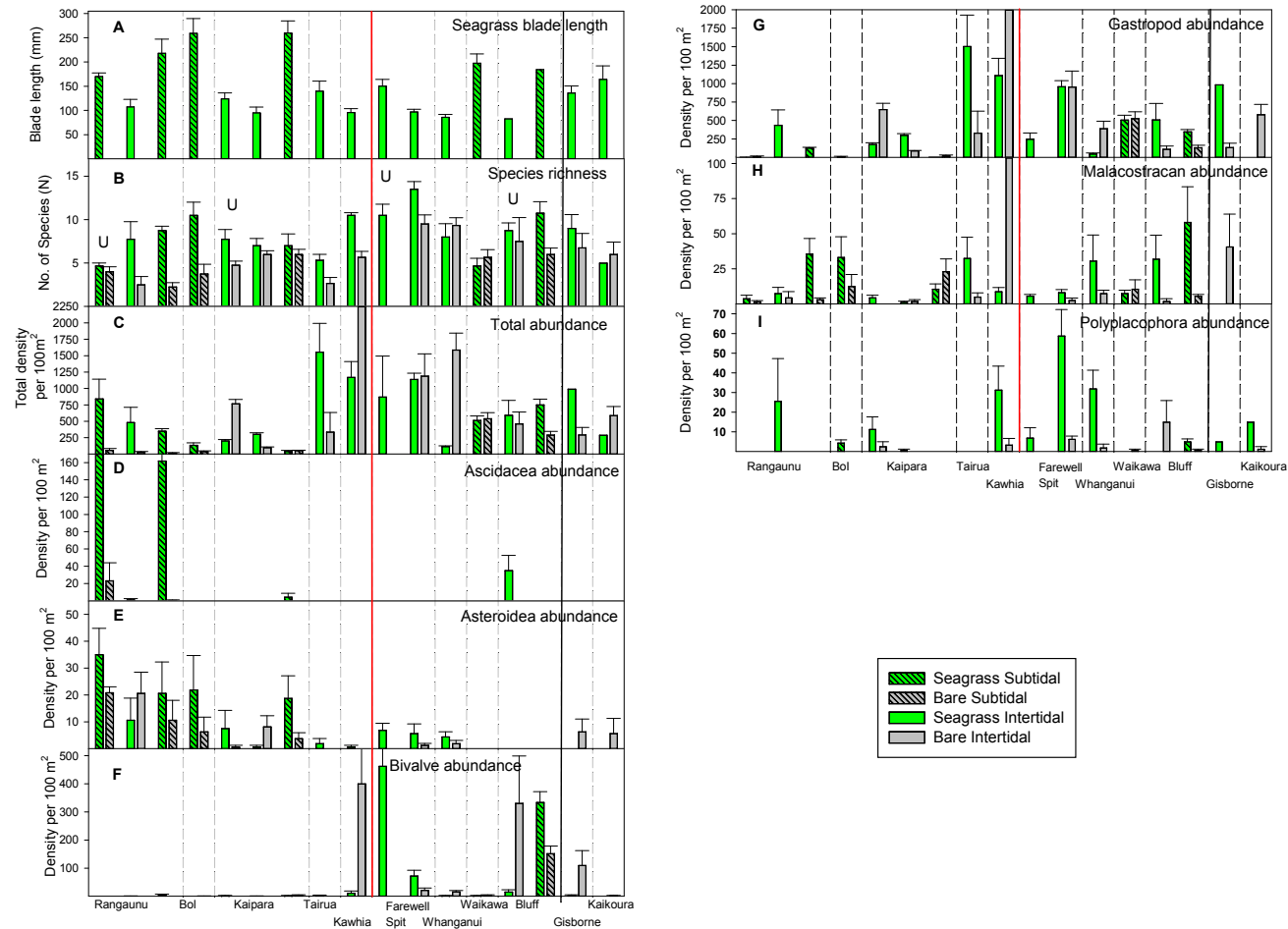


Figure 34: Graphs summarising the key components of the epifaunal invertebrate assemblage (nominally over 10 mm in size) for eleven locations sampled throughout New Zealand. Locations run north to south from left to right, apart from the two rocky reef sites which are positioned at the far right. The red line denotes the North to South Island break. The black line denotes the rocky reef site. For each location seagrass and bare sites are paired in the following order, upper, then lower intertidal, then lower subtidal. A) Mean seagrass blade length (\pm s.e.), B) Species richness (N) (\pm s.e.), C) Total abundance (\pm s.e.), D) Ascidian abundance (\pm s.e.), E) Asteroidea abundance (\pm s.e.), F) Bivalve abundance (\pm s.e.), G) Gastropod abundance (\pm s.e.), H) Malacostracan abundance (\pm s.e.), and I) Polyplacophoran abundance (\pm s.e.)

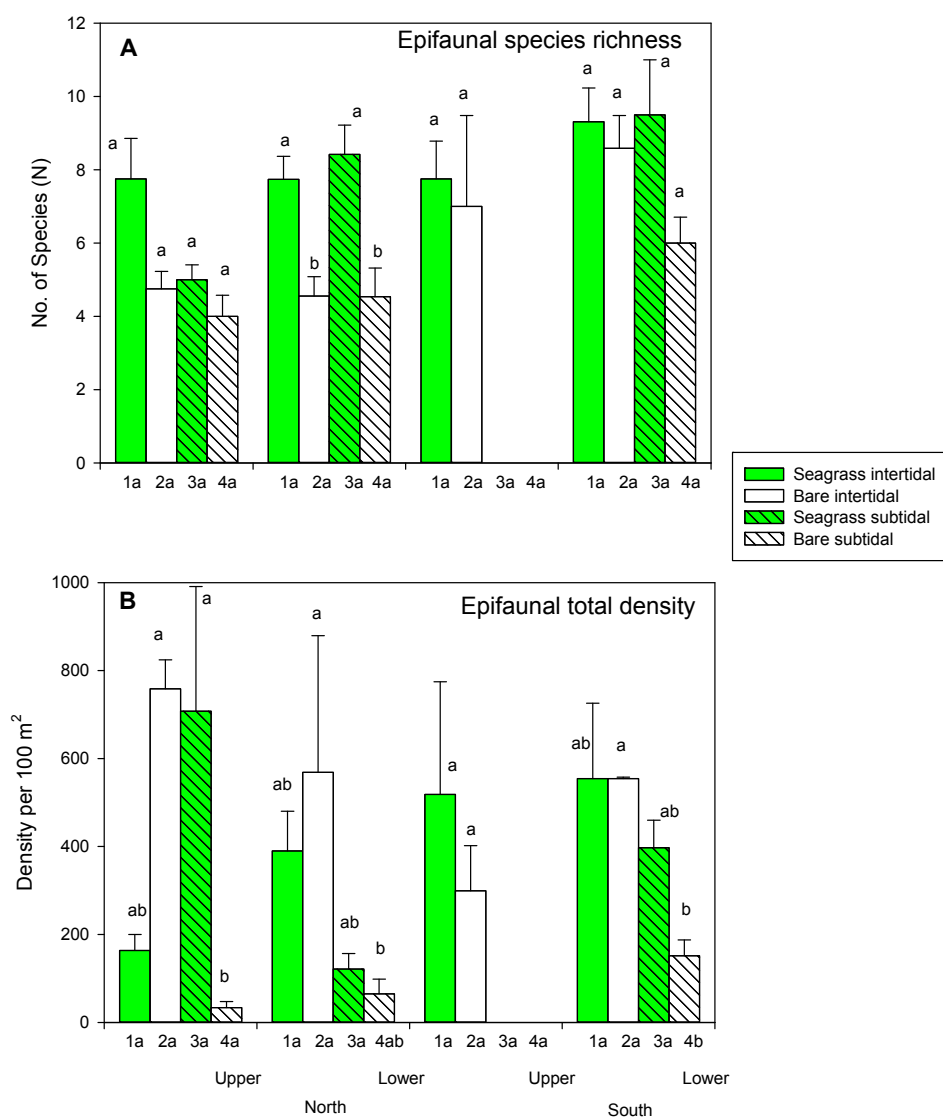


Figure 35: Graphical representation of Tukey HSD analysis for epifaunal samples, A) Species Richness and B) Average number of species per 100 m², displayed by habitat type (SS, BS, SI, BI) within Position (upper or lower) within Island (North and South Islands). Annotation: letters above bars denote any differences for the habitat comparisons within each position × island combination, letters beneath bars denote same habitat comparisons across each position by Island.

Invertebrate community contributions at the taxonomic group level

Ascideans (in Rangaunu Harbour), but more broadly gastropods, contributed the greatest proportion of individuals to the overall densities of epifaunal invertebrates sampled across New Zealand (Figure 34d), and were sampled by this method in far higher numbers than via the infaunal sampling. Bivalves were not a dominant feature of the epifaunal community assemblage when compared with their role in the infaunal community. Malacostracan abundances were highly variable across locations, while polyplacophoran abundances were predominantly highest from intertidal seagrass habitats.

Seagrass associated epifaunal invertebrate communities – multivariate

MDS Ordination

An MDS ordination plot of all epifaunal invertebrate communities sampled (Figure 36) identified groupings by latitude and habitat type for epifaunal community assemblage composition. The North to South Island split is between numbers 5 and 6. The ordination shows that the upper North Island locations (Rangaunu, Bay of Islands, and the subtidal seagrass Kaipara sites) grouped towards the right hand side of the ordination while all the other locations were grouped towards the left hand side. Several outliers were also obvious in the ordination.

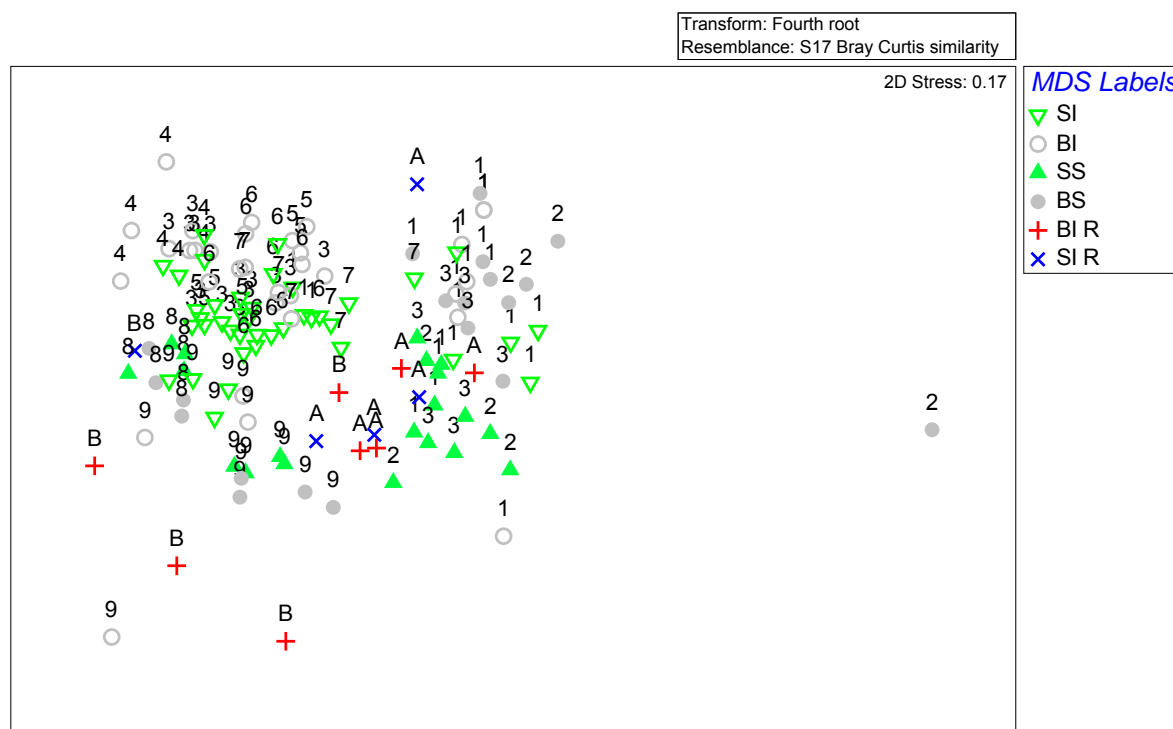


Figure 36: MDS ordination of epifaunal invertebrate species assemblage. Sampling locations labelled from North to South as follows; North – Rangaunu (1), Bay of Islands (2), Kaipara (3), Tairua (4), Kawhia (5); South – Farewell Spit (6), Whanganui (7), Waikawa (8), Bluff (9), then Gisborne (AX, A+) and Kaikoura (BX, B+). The North/South Island split occurs between 5 and 6. BI, Bare Intertidal; BS, Bare Subtidal; SI, Seagrass Intertidal; SS, Seagrass Subtidal.

Epifaunal invertebrate community analysis

Analysis by species

At the broadest spatial scale, PERMANOVA analysis revealed there was a significant difference between habitats for North and South Island epifaunal invertebrates (Table 14a). Pairwise tests identified that all the habitats were significantly different when compared between the North and South islands, except for upper, intertidal seagrass (Appendix 6, Table 1).

A comparison between habitats nested within position (upper/lower) and Island (North/South) found epifaunal invertebrate compositions to be significantly different (Table 14b). Pairwise tests revealed the majority of epifaunal invertebrate communities were significantly different with the exception of seagrass subtidal versus bare subtidal in the lower South Island (Appendix 6, Table 2).

A comparison between all locations (harbour) within position (upper/lower) and habitats revealed significant differences (Table 14c). Pairwise tests revealed that the majority of possible location combinations returned significant results for each habitat, with the exception of the Gisborne/Kaikoura, Kaikoura/Rangaunu, Kaikoura/Whanganui Inlet and lower Rangaunu/lower Whanganui Inlet intertidal seagrass comparisons, along with lower Farewell Spit/Tairua, and Kaipara/Tairua bare intertidal (Appendix 6, Table 3).

A comparison between habitats (BI, BS, SI, SS) nested within position (upper/lower) and Location (harbours) of epifaunal invertebrate community composition was also significantly different (Table 14d). Pairwise tests revealed that the majority of the possible habitat combinations returned significant results for each Location, with the exception of bare subtidal versus bare intertidal (lower Rangaunu Harbour), and seagrass versus bare intertidal (lower Kaipara Harbour, Tairua, and Gisborne respectively), and seagrass versus bare subtidal (Waikawa Harbour) (Appendix 6, Table 4).

Table 14: PERMANOVA results of epifaunal invertebrate community composition (by species), for various habitat comparisons nested by Island, and/or Position.

Source	df	Pseudo-F	P(perm)
a) Between the North and South Islands for each particular habitat			
Ha	3	9.5096	0.001
Po(Ha)	4	4.1000	0.001
Is(Po(Ha))	6	5.7830	0.001
b) Habitat variation within an Island			
Is	1	12.7290	0.001
Po(Ha)	2	2.3717	0.001
Is(Po(Ha))	10	6.2155	0.001
c) Habitat variation across Locations			
Ha	3	20.485	0.001
Po(Ha)	4	8.8321	0.001
Lo(Po(Ha))	25	8.9205	0.001
d) Habitat variation within Locations			
Lo	10	18.345	0.001
Po(Lo)	4	7.1618	0.001
Ha(Po(Lo))	18	5.983	0.001

No comparisons were made between the East and West coasts of the North Island as only one west coast location was sampled, meaning that all east coast sites would simply be being compared against the Kaipara Harbour, and this has already been done in the above analysis.

Seagrass as a nursery habitat for bivalves

Upon exploratory analysis of the infaunal invertebrate dataset derived from the benthic core sampling it was clear that the combination of the core diameter used and the limited number of replicates analysed per site, produced only limited information about bivalve shellfish associations with seagrass and bare sand habitats.

Only two bivalve species (the cockle *Austrovenus stutchburyi*, and the nutshell *Nucula hartvigiana*) were recorded in large enough numbers to investigate the potential for seagrass to be acting as a nursery habitat for these species. For *A. stutchburyi* (Figure 37), two of the sites (Rangaunu and Farewell Spit, Lower) tentatively suggested that seagrass may be providing a nursery habitat for this species when compared against the surrounding bare sand sites. Most cockles were in the 5.6–16 mm size range (as measured by increasing sieve sizes): sexual maturity in cockles starts at about 18 mm length. However, the other two sites (Kawhia and Whanganui Harbours) appear to show the opposite pattern, with bare sand providing as much if not more nursery habitat value as the seagrass sites. For *Nucula hartvigiana* (Figure 38) both Rangaunu and lower Farewell Spit suggested that bare sand and seagrass provided equal opportunity as a nursery area, while in Whanganui Harbour seagrass appears to play a more important nursery role. The modest data encapsulated by this sampling regime does not allow an adequate analysis of the role seagrass may play as a nursery habitat for bivalve species.

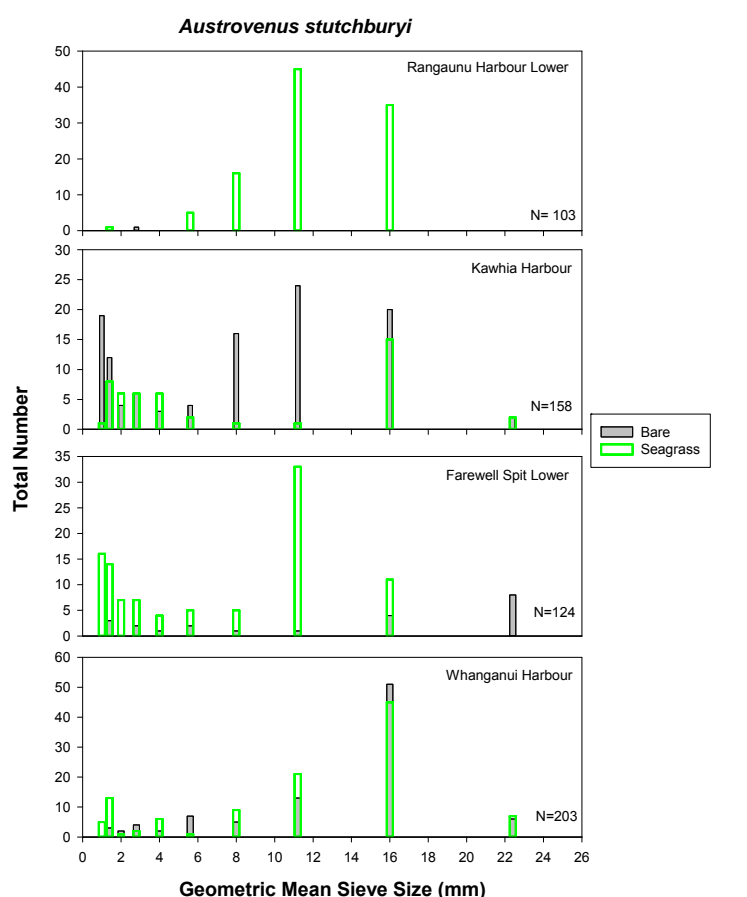


Figure 37: Size frequency graphs for the cockle *Austrovenus stutchburyi*, demonstrating the potential role that bare sand versus seagrass habitats provide in terms of nursery habitat for this species.

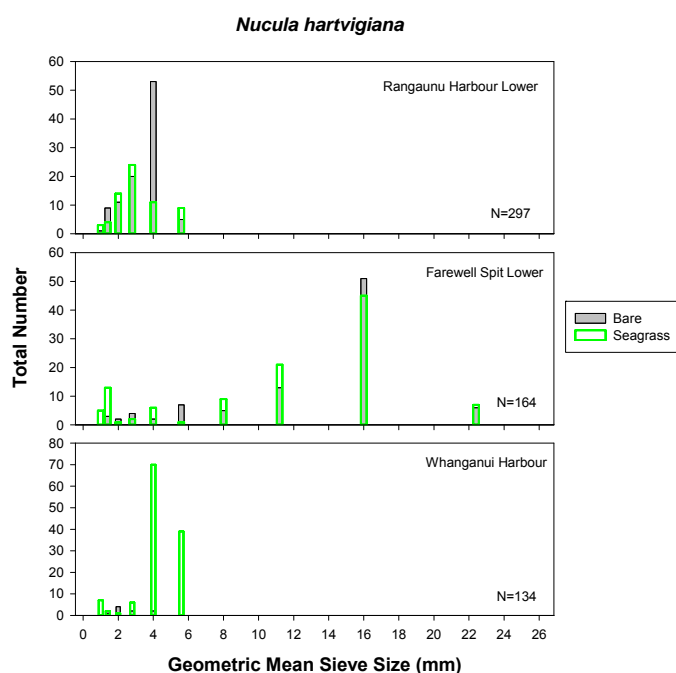


Figure 38: Size frequency graphs for the nut shell *Nucula hartvigiana*, demonstrating the potential role that bare sand versus seagrass habitats provide in terms of nursery habitat for this species.

4.10 Seagrass as an ecosystem fuel component

Primary producer stable isotope signatures

The stable isotope signatures of the primary producers and the higher trophic order consumers sampled from either Rangaunu or Kaipara Harbour are reported in Figures 39 to 42. All mangrove samples analysed had $\delta^{13}\text{C}$ values in the previously published range of -30 to -24 (Hemminga & Mateo, 1996) and $\delta^{15}\text{N}$ values similar to those identified for mangroves in south Australian estuaries (i.e. 2.2. to 8.8, for *Avicinnia marina*, Boon et al. 1997). Phytoplankton samples were also in the expected range for $\delta^{13}\text{C}$ values when compared to phytoplankton samples taken from the Hauraki Gulf (-26 to -19, S. Bury, NIWA, unpubl. data), however, two phytoplankton samples from Rangaunu Harbour (Figure 36a, Bare; Figure 36b, Seagrass), were significantly lower in terms of $\delta^{13}\text{C}$ at -15. Phytoplankton $\delta^{15}\text{N}$ values were also within the expected range when compared to data previously collected in the Hauraki Gulf (S. Bury, NIWA, unpubl. data). Benthic green and red algal isotopic signatures were more variable across the different harbours but were generally within the range expected from previously reported studies (i.e. -20 to -15 for $\delta^{13}\text{C}$ and 2 to 5 for $\delta^{15}\text{N}$, Boon et al. 1997, Nagelkerken & Van der Velde, 2004), although a very high $\delta^{15}\text{N}$ value of 11.5 was recorded for red algae at the Kaipara seagrass site. Seagrass carbon isotopic signatures were far lower (-12 to -10) than other primary producers measured in the two harbours. Seagrasses have stable carbon isotope signatures that are typically less depleted in ^{13}C than those of other groups of aquatic primary producers (Hemminga & Mateo, 1996) with median values falling around -10 to -11 (however the spread in values ranged from -23 to -3).

It was originally planned to run these data through a mixing model such as SIAR to estimate what proportion of each secondary consumer contributed to secondary producers. However, this proved not possible due to a lack of knowledge of the number of intermediate prey steps, some relatively unusual primary producer ranges (e.g. for some phytoplankton and red algae), and issues of secondary consumers not necessarily falling within the 'bounding' box of primary producers.

Higher consumers (animals) all had enriched ^{15}N values, related to their higher trophic levels. For the Rangaunu Bare site (Figure 39a), oysters and gastropods had the lowest values of the consumers, followed by a more enriched group of demersal fish, crustaceans, echinoderms, and cephalopods. A

similar pattern was seen at the Rangaunu Seagrass Site (Figure 39b), although there was a greater spread between the groups (more species detail is given in Figure 40). Pelagic fish were also present, with the highest ^{15}N values of all of the consumer groups, along with bivalves, which fell relatively close to demersal fish. Solitary and colonial ascidians had lower values, much closer to the primary producers, suggesting that they consumed them directly, with few or no intermediary steps. The bryozoan and sponge sampled (one individual of each) also had relatively low values.

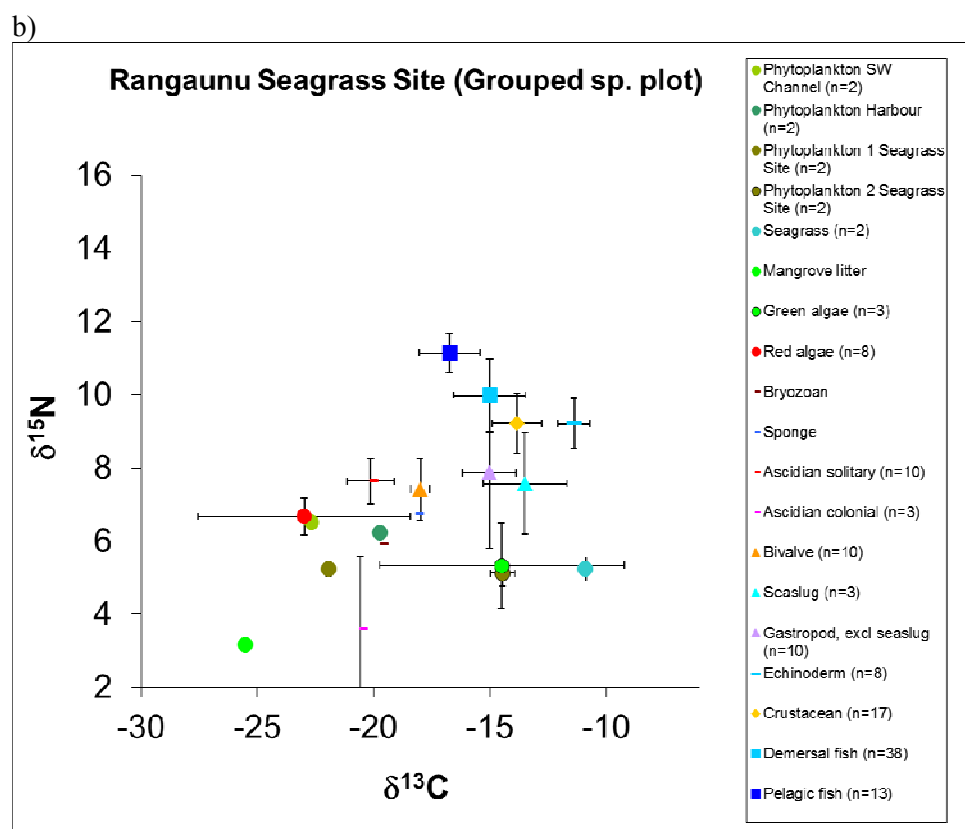
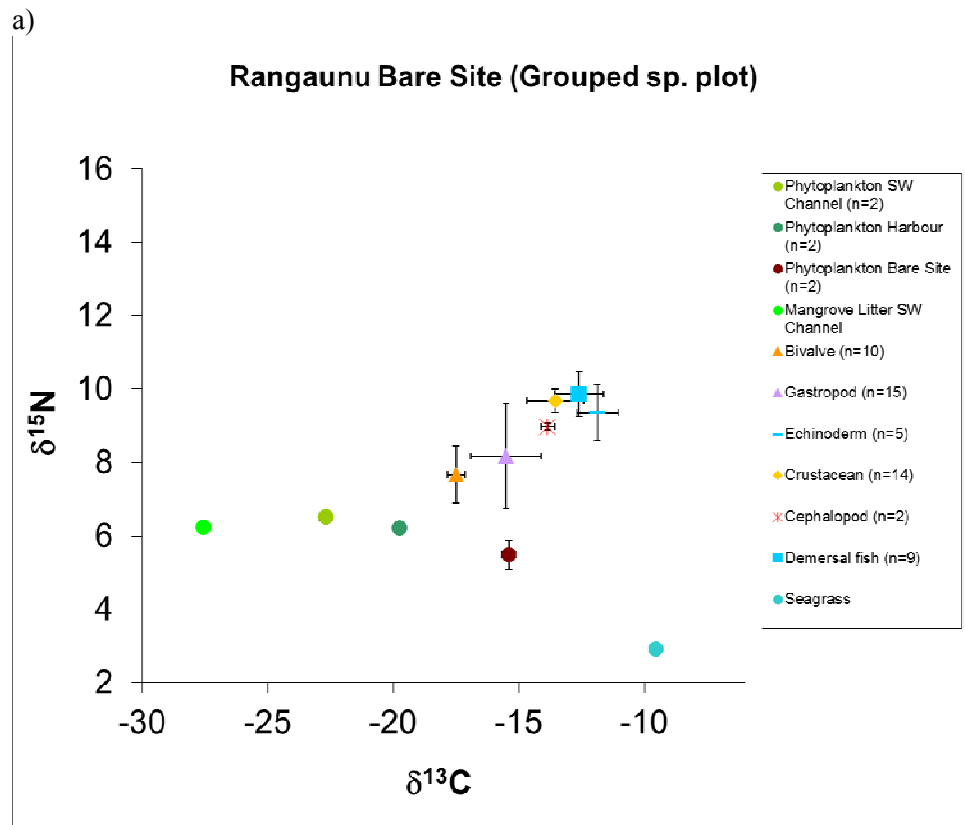


Figure 39: Pooled mean \pm s.e. stable carbon and nitrogen isotope values for primary producers and higher trophic order consumers (filter feeders, grazers and fish species) from Rangaunu Harbour, a) bare site and b) seagrass site.

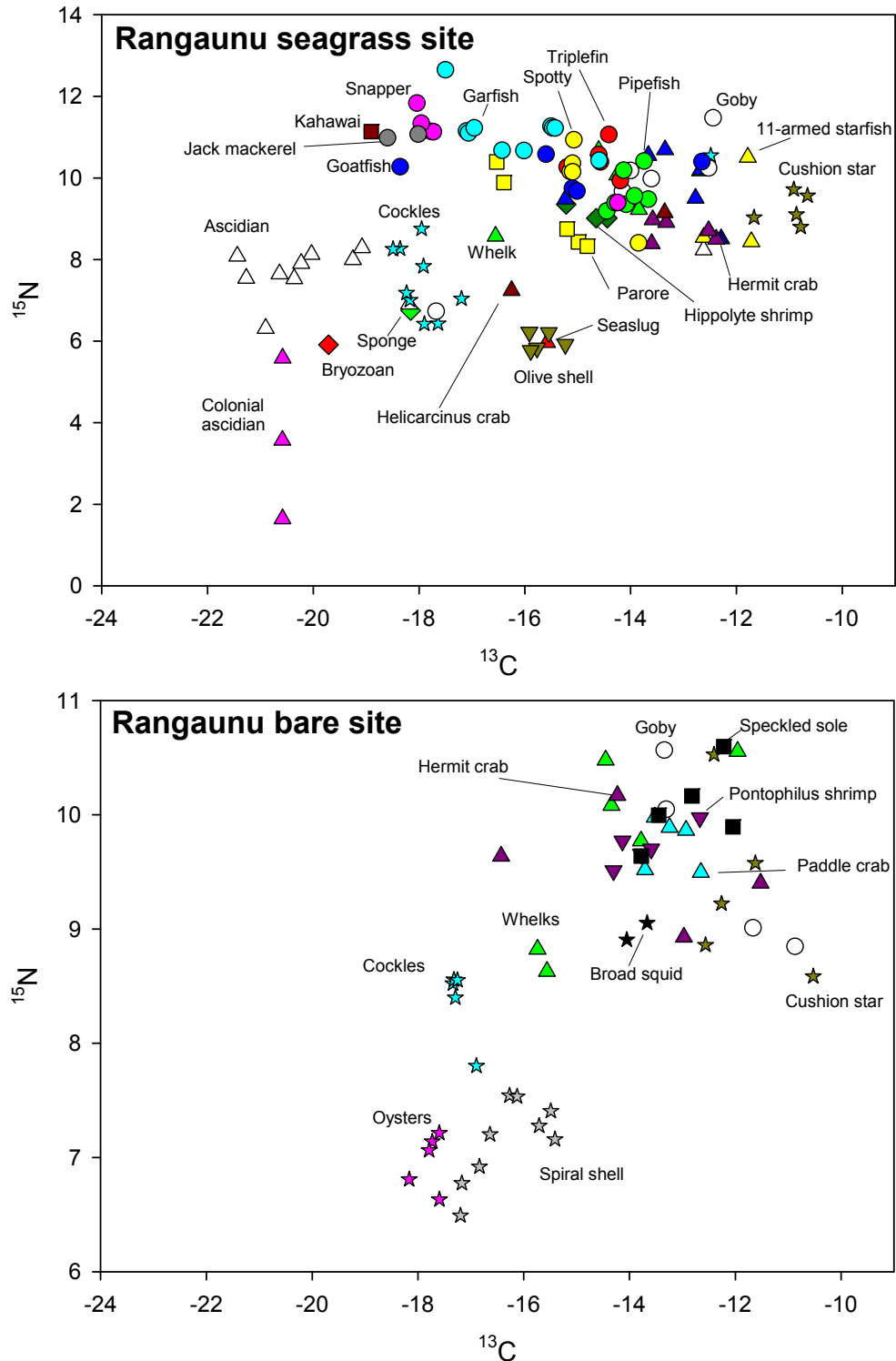
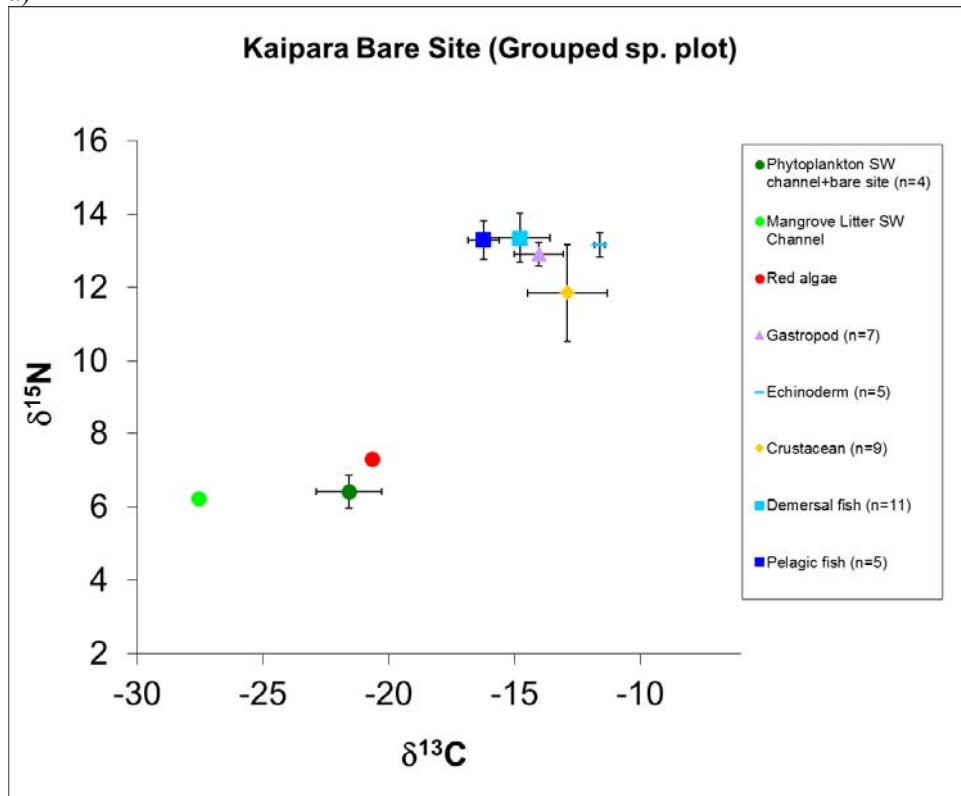


Figure 40: Individual stable carbon and nitrogen isotope values for higher trophic order consumers (filter feeders, grazers and fish species) from Rangaunu Harbour, a) bare site, b) seagrass site.

a)



b)

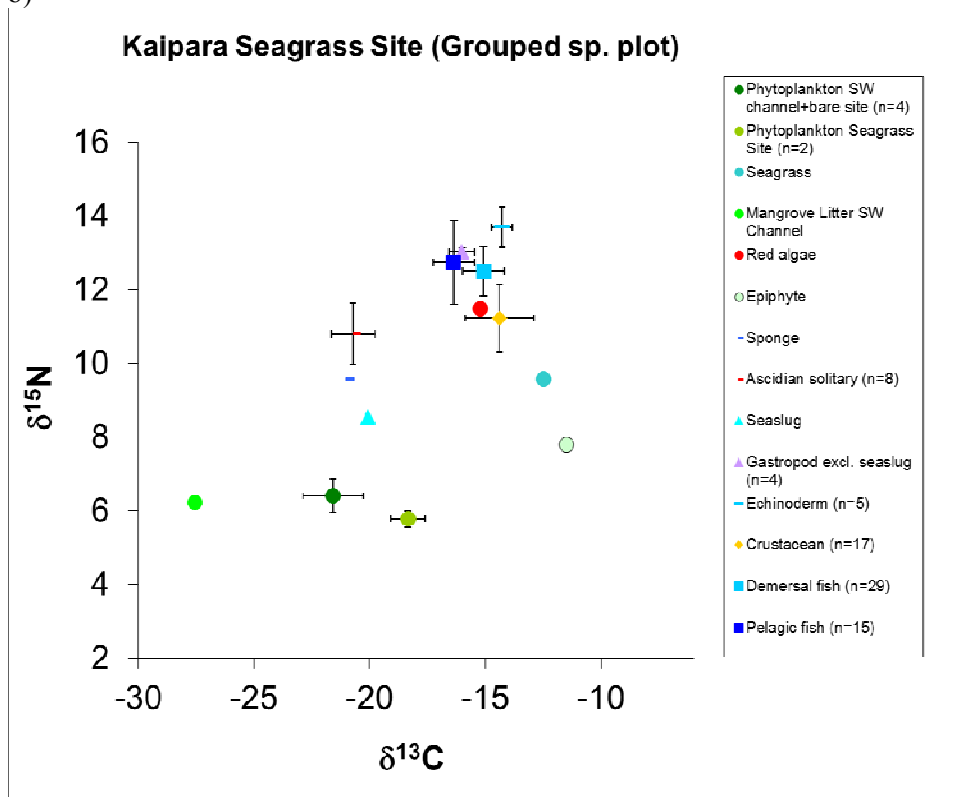


Figure 41: Pooled mean \pm s.e. stable carbon and nitrogen isotope values for primary producers and higher trophic order consumers (filter feeders, grazers and fish species) from Kaipara Harbour, A) bare site and B) seagrass site.

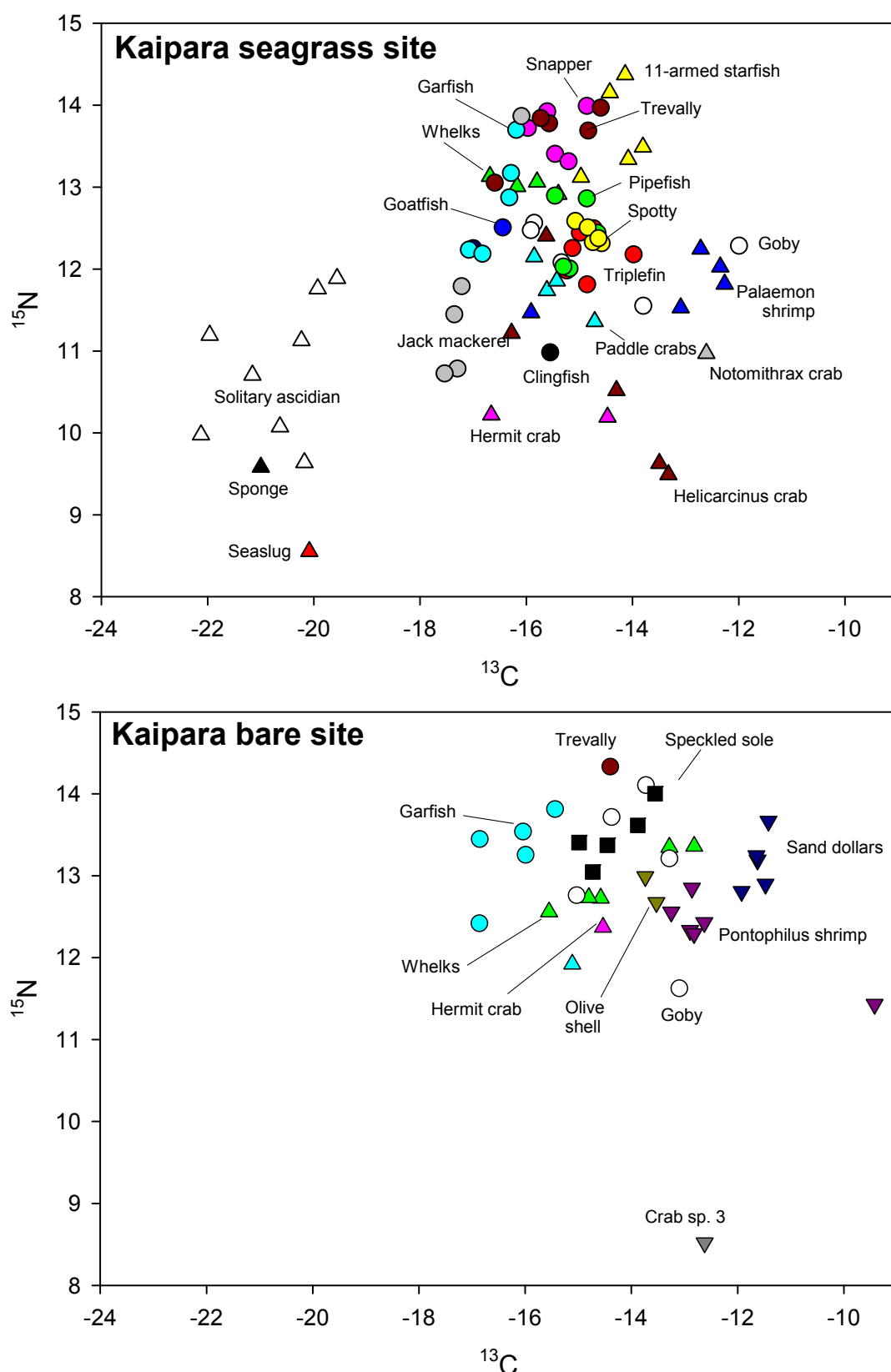


Figure 42: Individual stable carbon and nitrogen isotope values for higher trophic order consumers (filter feeders, grazers and fish species) from Rangaunu Harbour, a) bare site, b) seagrass site.

For the Kaipara Bare site (Figure 41a), secondary consumers had higher ^{15}N values than those of the Rangaunu Bare site (Figure 41a), potentially suggesting a more complex food web in terms of intermediary prey steps. Crustaceans had slightly lower values than those of demersal and pelagic

fish, gastropods, echinoderms, and crustaceans. For the Kaipara seagrass site (Figure 41b), consumers again had higher ^{15}N values than those of the Rangaunu Bare site (Figure 41b), and were also more tightly clumped in terms of both ^{15}N and ^{13}C values. Figure 42 provides a more detailed look at the values for individual species. Fish occupied the highest trophic level, although fish ^{15}N values were higher than those of Rangaunu Harbour, possibly suggesting a more complicated trophic food web structure (i.e. more intermediary prey steps between primary producers and fish).

4.11 Seagrass replication mechanisms

Primer evaluation

The majority of the 59 primers tested in the initial screening produced either no fragments or large numbers of weakly staining fragments, and were discarded from further analyses. Five primers produced consistent fragment patterns with a total of 21 well stained fragments that were scored as either present or absent (Table 15) to produce the RAPD phenotypes or composite genotypes.

Table 15: Operon 10-base oligonucleotide primers tested on populations of *Z. muelleri* around New Zealand.

Primer Code No	Sequence 5'-3'	No. fragments scored
W10	TCGCATCCCT	5
W12	TGGGCAGAAG	4
W13	CACAGCGACA	3
D07	TTGGCACGGG	4
D11	AGCGCCATTG	5

Genetic variation at the New Zealand wide scale

Genetic variation, partitioned with a nested AMOVA, was distributed among regions (about 39%) and within populations (about 62%), with a non-significant level of variation (about 2%) among populations within regions in the total data set (Table 16). This pattern of significant genetic variation partitioned among regions and within populations, but not among populations within a region, was repeated at smaller spatial scales within the North Island, South Island, east coast, and west coast sub-regions (Table 16). There were no shared composite genotypes among regions.

There was no significant relationship between genetic distance and geographic distance in the total data set (Figure 43: genetic distance and log geographic distance: mantel test $Z = 23.67$, $r^2 = 0.088$, $P = 0.164$), where geographic distance was estimated as the shortest sea distance (with Cook Strait open); or within North Island or within east coast sub-sets of samples (Table 17). The west coast and South Island subsets were not tested due to the limited number of samples (3) within each sub-area. The UPGMA analysis revealed strong regional structure (with bootstrap support over 70% for most regional populations), but no evidence for a major genetic break between the North and South Island, or east and west coast populations (Figure 44).

Table 16: Hierarchical analysis of molecular variance in *Z. muelleri* RAPD genotypes within and among regions.

Source of variation	d.f.	Sum of squares	Variance components	% of variation	<i>P</i>
Among all regions	6	177.46	1.336	39.36	<0.001
Among populations within regions	22	43.31	-0.034	-1.80	0.714
Within populations	116	243.20	2.097	61.69	<0.001
Among NI regions	3	88.01	1.296	41.43	<0.001
Among NI pops within regions	13	24.56	-0.014	0.46	0.400
Within populations	68	123.60	1.818	58.1	<0.001
Among SI regions	2	59.43	1.387	36.75	<0.001
Among SI pops within regions	9	17.75	-0.104	-2.75	0.853
Within populations	48	119.60	2.3492	66.00	<0.001
Among EC regions	3	99.00	1.554	43.23	<0.001
Among EC pops within regions	12	22.90	-0.033	-0.93	0.615
Within populations	64	132.80	2.075	57.70	<0.001
Among WC regions	2	49.24	1.053	33.54	<0.001
Among WC pops within regions	10	19.41	-0.036	-1.16	0.598
Within populations	52	110.40	2.123	67.62	<0.001

Table 17: Correlation between genetic distance and log geographic distance between regions for *Z. muelleri*.

Area	<i>Z</i>	<i>r</i> ²	<i>P</i>
All	23.677	0.088	0.164
North Island	6.8839	0.021	0.407
East Coast	7.582	0.084	0.297

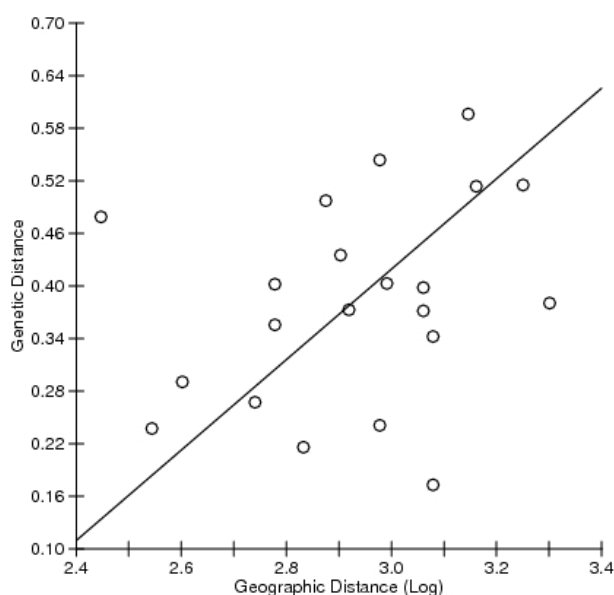


Figure 43: Genetic distance and log geographic distance in the total *Z. muelleri* RAPD data set.

Genetic variation at the local scale

The number of composite genotypes observed at each site ranged from 3–5 (Table 18), and collectively are indicative of a high level of genetic diversity within regions and within sites. Forty-four composite genotypes each occurred only once. At several sites there were 3 or 4 unique composite genotypes.

Contrary to the New Zealand wide scale results, where there were no shared composite genotypes among regions, there were shared composite genotypes among local populations (sites) within each region. Thirty-one composite genotypes occurred at two or more sites, while a further two occurred in two or three specimens at single sites. Three individual Bluff specimens shared an identical and site-unique genotype (BF100 54), and two Kaipara specimens shared another site-unique genotype (KP100 14) and are indicative of single clones.

Genetic variation, partitioned with a nested AMOVA within regions showed that the majority of genetic variation was found within a local population within a region (more than 86% Table 19). Only in one region, Kaipara, was there weak evidence for a significant proportion ($P = 0.054$) of the variation found among populations (13%, Table 19), but was non-significant using a Bonferroni modified P for multiple tests. There was no significant relationship between genetic distance and geographic distance in any of the seven regions, tested independently (Table 20).

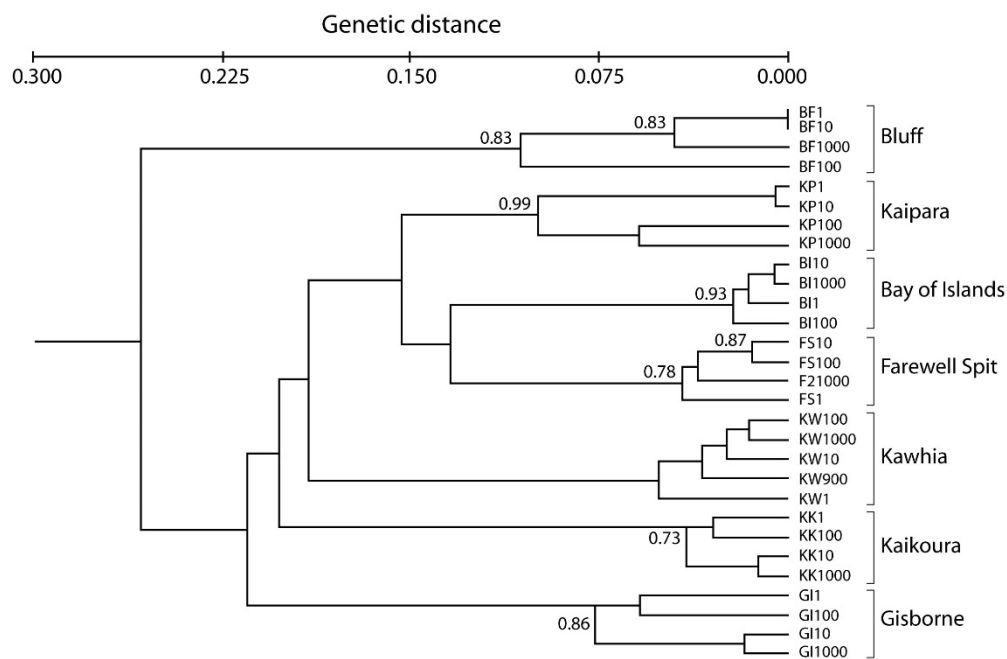


Figure 44: UPGMA tree based on F_{ST} among *Z. muelleri* samples from New Zealand. Numbers at nodes represent bootstrap values for 70%. Each label comprises a shortened site code, e.g. Bluff=BF, then the distance away from the main seagrass meadow the samples were taken from, e.g. 1, 10, 100, 1000 metres distant.

Table 18: RAPD composite genotypes counted in regional samples of *Z. muelleri*. Note: the total number of genotypes in each column is not the sum of genotypes at each site because some genotypes were shared among sites. BI=Bay of Islands, KP=Kaipara, GI=Gisborne, FS=Farewell Spit, KK=Kaikoura, BF=Bluff, KW=Kawhia. NT=not tested.

Site (m)	BI	KP	GI	FS	KK	BF	KW
1	3	3	3	4	5	3	4
10	5	3	4	4	4	3	5
100	5	3	2	4	4	3	5
900	NT	NT	NT	NT	NT	NT	5
1000	5	5	5	5	5	5	5
Total	10	9	10	10	10	9	19

Table 19. Hierarchical analysis of molecular variance in *Z. muelleri* RAPD composite genotypes within regions.

Region	Source of variation	df	Sum of squares	% of variation	<i>P</i>
B. Islands	Among populations	3	4.65	-9.44	0.926
	Within populations	16	43.60	109.44	
Kaipara	Among populations	3	8.25	13.41	0.054
	Within populations	16	24.80	86.59	
Gisborne	Among populations	3	6.70	6.60	0.220
	Within populations	16	26.40	93.40	
Kawhia	Among populations	4	4.96	-2.86	0.724
	Within populations	20	28.80	102.86	
Kaikoura	Among populations	3	3.35	-10.92	0.959
	Within populations	16	35.20	110.92	
Farwell S	Among populations	3	6.20	-9.12	0.904
	Within populations	16	56.80	109.12	
Bluff	Among populations	3	8.20	10.47	0.107
	Within populations	16	27.60	89.53	

Table 20: Correlation between genetic distance (GD) and geographic distance (GgD) and log geographic distance (LogGgD) between sites within regions for *Z. muelleri*.

Region	GD/GgD			GD/LogGgD		
	<i>Z</i>	<i>r</i>	<i>P</i>	<i>Z</i>	<i>r</i>	<i>P</i>
B. Islands	-0.3944	-0.738	0.880	0.2590	-0.566	0.840
Kaipara	0.6100	0.176	0.205	0.0995	0.400	0.131
Kawhia	-0.6297	-0.293	0.739	0.0855	-0.269	0.743
Gisborne	-0.0707	-0.719	0.874	-0.5597	-0.464	0.843
Kaikoura	-0.0703	0.453	0.529	0.6542	0.528	0.131
Farewell S	-0.304	-0.145	0.408	0.3158	-0.305	0.568
Bluff	0.0322	-0.264	0.488	-0.1188	0.126	0.339

Sequencing selected fragments

Two selected fragments (W13-2 and D07-3) were sequenced, and for the D07-3 fragment 641 base pairs of unambiguously aligned sequence and for W13-2 501 bp of unambiguously aligned sequence were compared.

There was a high sequence identity within fragments (97%+) from the three widely separated regions indicating that the fragments were homologous (Table 21). The low level of divergence observed reflects genetic variation, but additional specimens would need to be sequenced to determine if there is regional differentiation among homologous fragments.

There were no close matches for the sequenced regions in Genbank, as might be expected for RAPDs which amplify a random region of the genome.

Table 21: Sequence identity matrix for fragment D07-3 (below diagonal) and fragment W13-2 (above diagonal) for *Z. muelleri* from three regions.

Region	BI 1	BI 2	FS 1	FS 2	BF 1	BF 2
B. Island 1		1.00	0.97	0.97	0.98	0.98
B. Island 2	1.0		0.97	0.97	0.98	0.98
Farewell S 1	0.98	0.98		0.99	0.99	0.99
Farewell S 2	0.98	0.98	1.0		0.99	0.99
Bluff 1	0.97	0.97	0.98	0.98		1.00
Bluff 2	0.97	0.97	0.98	0.98	1.00	

5. DISCUSSION

5.1 Nursery role of seagrass habitats – fish

Spatial variation in fish abundance

Fish abundance in this survey showed significant spatial variability along the latitudinal gradient, (north to south) with the exception of Whanganui Inlet; between east and west coast harbours (North Island only), and between habitat types (i.e. seagrass versus sand) within estuaries. However, position within the estuary (upper/lower) was not significant. Rangaunu Harbour, the northernmost pristine sheltered estuary, with continuous extensive seagrass meadows and high water clarity, recorded the highest densities of the survey, peaking at 661.3 fish per 100 m² for one tow at an inner subtidal seagrass site. It must be noted that Rangaunu Harbour was the only location to have upper harbour subtidal seagrass sites, which was an unexpected habitat. There are no equivalent habitat comparisons across other locations. The presence of subtidal seagrass in the upper harbour reflects the ‘comparitively pristine’ condition of this location and has recently also been observed in some arms of Parengarenga Harbour (M.L., pers. obs.). Densities of fish within subtidal meadows declined eightfold in the more exposed west coast Kaipara Harbour, with associated sparse/patchy seagrass coverage, and higher turbidities. Urupukapuka Island (Bay of Islands), the only offshore subtidal seagrass site, was an exception, recording the lowest density of juvenile fish despite higher water clarity and the longest blade lengths. Bay of Islands was characterized by higher numbers of fish over 125 mm (e.g. snapper 52%) rather than new fish recruits. This may be in part due to the site’s exposure and depth (more than 4 m) resulting in closer proximity and greater densities of larger predators, lower directional current flows over the meadows (bringing less planktonic food), and longer blade lengths hindering fish foraging efficiency (Heck & Thoman 1981; Stoner 1982 cited in Jenkins & Hamer 2001; Motta et al. 1995 and references therein). These results concur with research from other offshore seagrass sites both within New Zealand (e.g. Slipper Island, Bay of Plenty; Schwarz et al., 2006) and Tanzania (Kimirei et al., 2011) which also recorded lower juvenile

densities. This suggests that offshore seagrass beds may provide less fitness benefits for smaller predation-prone individuals than shallower, estuarine locations that afford refuge for small fish from larger predators (Kimirei et al. 2011, Kimirei 2012).

Non vegetated habitats are generally characterized by comparatively low species diversity and abundance of fish species (e.g. Australia: Bell & Pollard 1989, Conolly 1994, Gray et al. 1996, Bloomfield & Gillanders 2005; New Zealand, Francis et al. 2005, 2011). In this survey, sand habitats generally returned significantly lower densities compared to both intertidal/subtidal seagrass sites in the North Island, excluding Kawhia, which recorded a slightly higher catch rate for sand than for seagrass. However, catches for both habitats within Kawhia were dominated by high abundances of yellow-eyed mullet, a more cosmopolitan, schooling species, prone to large variations in abundance. South Island sites showed the reverse trend with four out of five harbours showing equivalent or higher fish abundances over sand than for seagrass habitats. Southern lower intertidal seagrass and bare sites were not significantly different from each other. Overall, species richness was relatively low, ranging from 1.3 to 11.5 species per tow. Significant differences in richness were recorded between lower seagrass habitats and bare intertidal sites within the North Island. Seagrass habitats pooled over all North Island sites had double the species richness than for sand habitats (8.8 compared to 4.2), while little difference was recorded between habitats in the South Island recording 7.6 and 5.7 species per tow for seagrass and sand respectively.

Results from the North Island (only) reinforce prior research within New Zealand (Francis et al. 2005, 2011, Schwarz et al. 2006, Morrison et al. 2007, Miller 2011, unpubl. data), Australia and America (e.g. Orth & Heck 1980, Orth et al. 1984, Bell & Pollard 1989, Murphey & Fonseca 1995), with seagrass, particularly subtidal meadows with higher blade densities, continuous cover, longer blade lengths and associated higher water clarities (e.g. Rangaunu), recording higher overall fish densities and juvenile fish than unvegetated sites. It has been suggested that such variations may be due to spatio-temporal environmental differences between beds (e.g. intertidal sites comprising only a temporarily available habitat, Heck Jr & Orth 1980, Bell & Westoby 1986, Worthington et al. 1992); but may also relate to depth distribution of pre settlement larvae (Murphy et al. 2011), in addition to greater food availability and refuge relative to intertidal seagrass/sand habitats (Bell & Pollard 1989, Gray et al. 1996).

Spatial variation in composition and length of dominant species

There was a significant latitudinal change in the presence/absence of some species with a group of relatively abundant species (snapper, trevally, jack mackerel, sand and exquisite goby, anchovy, grey mullet, kahawai and parore) only found north of the Cook Strait. Fewer species were sampled exclusively from south of Cook Strait. These included smelt, leatherjackets, sand and slender stargazer and slender sprat. Other species were more cosmopolitan in their distribution (yellow-eyed mullet, garfish, mottled triplefin, sole and sand flounder).

Fish assemblages varied significantly between habitats, within position (upper/lower), and between the North and South islands. Additionally, there were significant differences in fish assemblages between habitats across locations, with the exception of Farewell Spit and Whanganui Inlet (both dominated by yellow-eyed mullet). Only one South Island harbour (Waikawa) showed significantly different fish assemblages between bare and seagrass habitats. In the north, only Rangaunu upper subtidal/intertidal seagrass assemblages showed no significant difference between habitats.

Juveniles of many species had discernable habitat affinities, with snapper for example being almost exclusively found in high densities within subtidal meadows. Densities were the highest recorded relative to a variety of other estuarine and coastal biogenic habitats (Table 22), suggesting a significant conservation value as a nursery habitat. Other discriminating species for northeastern subtidal meadows included garfish, jack mackerel, parore (east coast), spotties, gobies (exquisite/sand) and triplefins. Additional species such as trevally, and speckled sole, were recorded for west coast assemblages. Important discriminating species for the South Island subtidal seagrass habitats were leather jackets, smelt, pipefish (smooth and black) and sole.

There was little evidence for latitudinal or coastal variation in length frequencies, with all habitats dominated (98%) by juveniles (under 125 mm; excluding garfish). Snapper showed some spatial ontogenetic variation with Rangaunu Harbour, with greater numbers of juveniles (15–25 mm) collected from the lower harbour sites for both intertidal/subtidal seagrass sites, whilst upper subtidal seagrass snapper were slightly larger (40–60 mm).

Table 22: Comparative studies on density of juvenile snapper (fish per 100 m²) collected in shallow coastal habitats of northern New Zealand (Source: Lowe 2013)

Habitat	Species	Locality	Density No. per 100 m ²	Source
Sand		Kaipara Harbour / Kawhia Harbour	0.4	Present study
Turf	Coralline algae and sedimentary flats next to rocky reef/algae	Leigh	27 Kingett & Choat (1981) 50 Choat & Kingett (1982)	
Reef/sand interface		Leigh	5.6–10.4	Ross et al. (2007)
Sponge gardens	Includes <i>Polymastia granulosa</i> , <i>Aaptos aaptos</i> , <i>Rapsaila topsenti</i> , <i>Axinella</i> n sp., <i>Cinachyra</i> n sp.	Leigh	4.6	Battershill (1987)
Seagrass (intertidal)	<i>Zostera muelleri</i>	Rangaunu Harbour (lower)	2.5	Present study
Seagrass (subtidal)	<i>Zostera muelleri</i>	Slipper Island, Coromandel	40	Schwarz et al. (2006)
		Rangaunu Harbour (upper)	159	Present study
		(max. per tow, 473)		
		Rangaunu Harbour (lower)	21.6	Present study
		Kaipara Harbour (lower)	5.2	Present study
		Whangapoua Harbour, Coromandel	5	M.M., unpubl. data
		Whangarei Harbour	2.8	D. Parsons, NIWA, unpubl. data
Seagrass (subtidal)	Artificial seagrass (plastic plants) (3 m ² patches)	Whangapoua	670–1 650	M.M., unpubl. data
Horse mussels (subtidal)	Artificial horse mussels and epifauna (plastic casts)	Mahurangi	40–120	Usmar (2009)

Fish diet

Grazing amphipods are ubiquitous in marine benthic communities and are often the dominant primary consumers within seagrass meadows (Duffy & Hay 2000, Cowles et al. 2009). They have been recognized (along with other epifaunal crustaceans, e.g., mysids) as critical players in near shore trophic transfer due to their small size, high abundance, short generation times and high rates of secondary production (Edgar & Aoki 1993, Motta et al. 1995, Duffy & Hay 2000, Jenkins et al. 2011).

Fish displayed omnivory and broad dietary overlap (particularly for seagrass associated fish), characteristics typical of estuarine fishes (Sanchez-Jerez et al. 2002, Nunn et al. 2011). Results of this survey revealed epifaunal crustaceans (gammaridean amphipods) were a major food source for fish, particularly within northern seagrass meadows, followed by mysids, decapods and plankton, and concurs with prior studies (e.g. Edgar & Shaw, 1995, Horonouchi & Sano 2000, Gillanders 2006, Jenkins et al. 2011, Nunn et al. 2011). However, proportions of major dietary items varied between islands with consumption of both plankton and amphipods declining by about 50% for southern sites (reflecting benthic availability of amphipods), with a reverse trend for mysids. Infaunal benthos was of much lesser importance, with species such as spotty, triplefin and sand flounder consuming modest numbers of bivalves/siphons over intertidal seagrass. Additionally, polychaetes and cumaceans were consumed by gobies, triplefins and flounder over sandy habitats. No species were exclusively piscivorous as recorded in Port Phillip Bay, Australia (Hindell et al. 2000). However, sites were not

located near reefs (apart from the Bay of Islands) where larger predators are more common (Bell & Pollard 1989). Seagrass itself was hardly utilized, being consumed by only one species (garfish). Diets broadly overlapped at the level of prey species, with common species of amphipods (e.g. *Aora* sp., *Paradexamine* sp.) consumed by numerous fish species. This is consistent with findings from Edgar & Shaw's (1995) survey at Western Port, Victoria.

Ontogenetic changes in diet

Ontogenetic dietary shifts were evident for the majority of the 29 species surveyed with the majority of fishes preying on meiofaunal crustaceans 0.5–1 mm in length. Zooplankton (*P. indicus*; *E. acutifrons*), dominated the diets of new recruits (20–40 mm), particularly for seagrass associated species. Consumption of mysids and gammaridean amphipods increased progressively with growth to be subsequently replaced with the ingestion of larger crustaceans such as caridean shrimps and crabs (*Haliparcinus* sp., *Helice crassa*). Mullet species changed from plankton to fine algae/detritus and garfish switched from plankton to seagrass material. In contrast, diet for flounder species shifted from plankton and mysids (20–30 mm) to include infaunal species before progressing to crabs. These findings concur with other surveys (e.g. Day 1981, Holbrook & Schmitt 1989, Edgar & Shaw 1995, Horinouchi & Sano 2000, Platell & Potter 2001, Kanou et al. 2002: see reviews by Hemminga & Duarte 2000, Nunn et al. 2011).

Meiofaunal crustaceans, particularly harpacticoid and calanoid copepods, gammaridean amphipods, and mysids were overwhelmingly more important than molluscs/polychaetes in linking primary production to fishes (Jenkins et al. 2011). Further research is warranted into the demography and dynamics of these three key trophic groups, particularly given their sensitivity to changing environmental conditions (i.e., increasing turbidity, Lowe 2012).

Habitat related changes in diet

Overall, stomach content (prey biomass) also varied with habitat and tended to reflect the overall relative abundance of prey in the environment. For example, endobenthic prey such as polychaetes, bivalves/siphons, cumaceans and infaunal amphipods characterized prey for fish collected mainly over sand. In contrast, diets of those species highly associated with seagrass (e.g. snapper, trevally) were dominated by mobile epibenthic prey such as gammaridean amphipods, mysids, decapods, and to a lesser extent plankton. These results are consistent with prior research (e.g. Linke et al. 2001, Platell & Potter 2001, Jenkins et al. 2011, Nunn et al. 2011). Benthic infauna, although abundant within seagrass habitats, was largely under-utilized as a food source in accordance with prior studies (Pollard 1984).

There was little discernable dietary difference across multiple habitats for the more cosmopolitan species (e.g. mottled triplefins). Rather, trends were more reflective of prey availability in the benthos, suggesting opportunistic and/or flexible feeding strategies (Day 1981). For example exquisite goby and mottled triplefins consumed more infaunal prey when caught over sand than in seagrass where more epifaunal amphipods, mysids and zooplankton were consumed. This concurs with Edgar's (1999) research on two goby species in Western Port Australia. However, schooling species feeding predominantly on zooplankton (e.g. early juvenile yellow-eyed mullet) showed no marked dietary differences between habitats (sand/seagrass), which would be expected given their pelagic feeding strategy (Bloomfield & Gillanders 2005).

Prey diversity

Overall, dietary breadth reflected benthic biodiversity of prey species less than or equal to 5.6 mm. Higher prey diversities were recorded from those fish species occupying habitats with more structurally complex biogenic structure, i.e., subtidal seagrass (e.g. snapper, 51 taxa). This was particularly evident for the pristine northeastern harbours with longer blade lengths, providing greater surface area for foraging invertebrates) and/or refuge (e.g. Rangaunu, Bay of Islands), followed by

intertidal seagrass. Trends were not as marked for southern sites which overall returned low numbers of amphipods. Lowest prey diversity was recorded from sand habitats (5) for sand goby. These results concur with Jiang & Carabines' (2002) survey in Foveaux Strait, where biodiversity of the epibenthos over complex three dimensional biogenic habitats was positively correlated to diversity in the blue cod (*Parapercis colias*) diet. Although not measured in this study, stomach fullness was generally greater in the more complex seagrass habitats (M.L., pers. obs.). Increased food consumption may be a response to relaxed predator avoidance behaviours, (Allen-Ankins et al. 2012), and/or a reflection of increased food availability.

Variation of diet within seagrass meadows

Prey items varied in composition/size with tidal position within northern seagrass meadows. Zooplankton (*E. acutifrons*) numerically dominated the diets of fish caught from intertidal sites for both Kaipara and Rangaunu Harbours, whilst amphipods were the preferred prey from Kaipara (89%) and Rangaunu (63%) subtidal meadows. Amphipods consumed within subtidal seagrass were larger (i.e., 50% over 1 mm) than those ingested over intertidal sites about 12% over 1 mm) and reflected benthic size frequencies. This was also reflected in sizes of fish caught within these habitats. For example, small bodied species such as exquisite goby and sand goby (25–30 mm FL) dominated intertidal seagrass assemblages. In contrast, larger snapper (about 50–70 mm FL) predominated at subtidal seagrass sites, whilst newly settled snapper (i.e. 20 mm) primarily consumed plankton from the lower Rangaunu Harbour (nearer entrance) intertidal seagrass sites. The dominance of planktonic prey suggests that post larval snapper are initially using seagrass primarily as a refuge. Visual observations observed snapper emerging from the seagrass, holding position in the currents, and foraging on plankton entrained in the passing water (M.L., pers. obs.).

Overall, northern New Zealand seagrass meadows, particularly subtidal meadows, supported a relatively diverse and abundant juvenile fish assemblage, including high numbers of several species that are commercially important (e.g. snapper, trevally) and is supportive of the paradigm that seagrasses provide an enhanced nursery habitat (for this region). Results suggest a close association between the abundance of fish and productivity within northern estuaries of macro invertebrates less than or equal to 5.6 mm (see figures 4.14 and 4.15, Lowe 2012), particularly crustaceans which comprised the major dietary item which also co varied with seagrass biomass (blade length/density). These results support associated studies both in New Zealand (Schwarz et al. 2006), and Australia (Marais 1984, Connolly 1994, Edgar & Shaw 1995, Edgar 1999, Bloomfield & Gillanders 2005).

Geographical setting: are all seagrass meadows equal?

With seagrass landscape attributes such as bed fragmentation, continuity of cover, size and shape along with structure of the plants themselves (i.e., biomass, density, blade length) displaying strong relationships to the physical setting of an area (Turner et al. 1999 and references therein, Connolly & Hindell 2006, Jelbart et al. 2007, Mills & Berkenbusch 2009), the overall coastal differences in abundance, evident for the North Island sites in this study may reflect climatic and geological differences at the landscape level. Northern west coast estuaries are more exposed to wind and waves, and soils are generally softer and more erodible, resulting in higher silt/clay loadings and concomitant elevated turbidities within estuaries, leading to less optimal growing conditions for seagrass (Vant, pers. comm, Gibbs et al. 2012). Conversely, east coast estuaries tend to be more sheltered. Geology tends to be comprised more of volcanic rock, less susceptible to erosion with resultant lower turbidities and fine sands predominating (Vant, pers. comm), providing more benign conditions for seagrass growth (particularly at depth) and fish recruitment. However, given the paucity of sheltered areas along the exposed west coast of the North Island, the value of subtidal seagrass is disproportionately greater for species such as snapper and trevally. For example, Kaipara harbour, with 432 km² of subtidal area may provide the majority of recruits for the coastal snapper stock (Morrison et al. 2009). Thus, deterioration in estuaries within this region (i.e. increased turbidity/sedimentation) may have far greater impacts on levels of snapper recruitment into coastal fisheries.

Results of this survey revealed latitudinal variation, with overall declining densities of fish from the North to South Island, with the exception of large catches of yellow-eyed mullet at Whanganui Inlet. Snapper, trevally, grey mullet and parore were absent as juveniles from seagrass meadows south of Cook Strait, whilst spotties were still recorded in high abundances south to Farewell Spit. These species were subsequently supplanted by leatherjackets and pipefish species extending into Southland. These results collectively demonstrate that the accepted paradigm of seagrass meadows providing important juvenile finfish nurseries, varies for individual species across latitudinal and coastal scales and with tidal position within estuaries for New Zealand. Similarly, overseas reviews note that given the unique characteristics of each estuary, universal generalizations are difficult (Hemminga & Duarte 2000, Heck et al. 2003, Heck & Orth 2006, Horonouchi 2007). Results support increasing evidence that usage of different habitats by juvenile fish is dependent upon environmental context, and that gross physical attributes of habitats may not always be of predictive value in fisheries ecology (Jenkins et al. 2011 and references therein).

Exclusivity of seagrass as nursery areas

The ‘nursery function’ of seagrass is a widely accepted paradigm. It is largely derived from extensive studies detailing higher densities of juvenile fish and invertebrates compared to adjacent unvegetated habitat (see reviews by Heck et al. 2003, Hemminga & Duarte 2000, Gillanders 2006). Few studies have compared the potential range of alternative habitats available, or possible linkages through ontogenetic movement between habitats (but see Parrish 1989, Gillanders & Kingsford 1996, Bloomfield & Gillanders 2005, Lowe, 2012). A review by Heck et al. (2003) challenged the exclusivity of seagrass beds as nursery areas, finding that although density, growth and survival were greater in seagrass than non-vegetated habitats, there were few significant differences when seagrass was compared to other structured habitats (oyster and cobble reefs, macroalgal beds, mangroves) and that structure *per se*, rather than type of structure may determine nursery habitat value.

The review found that densities of fish in northern hemisphere seagrass (i.e., North America) relative to unvegetated sediments were greater in 75% of surveys, compared to 36% for southern hemisphere (i.e., Australia). However, this data set covered a wide range of different seagrass species, with many (45) of the comparisons coming from a single paper reporting visual fish censuses from tropical mangrove/seagrass systems of the Caribbean (Nagelkerken et al. 2000) which are notably different from temperate New Zealand environs. Additionally, visual counts are inappropriate for identifying small juvenile fish (Bloomfield & Gillanders 2005). The use of varying sampling techniques reflects the inherent difficulties of utilizing appropriate sampling methods between multiple habitats, making generality at large biogeographic scales difficult (Gillanders 2006).

While the spatial extent of this present study was broad, encompassing latitudinal, coastal and estuarine differences, sampling was only undertaken on one occasion. Due to the large scale geographic nature of the study, issues of field logistics and especially cost constrained sampling to be a one-off event, during the known highest juvenile fish densities season (February–April). It therefore represents a single ‘snapshot’ of the dietary preferences of the fish species and distribution over late summer. Nonetheless, earlier temperate studies have indicated that assemblage structure of both fish and benthos is mainly governed by seasonal dynamics, while inter annual variation is low (Stål et al. 2007, Hailes & Hewitt 2012, Morrison, unpubl. data). Thus, given the strong seasonal changes in diet documented for temperate ecosystems (Layman & Silliman 2002, Akin & Winemiller 2006, Lowe 2012) and associated benthos (Taylor 1998, Choat & Kingett 1982) future research needs to include temporal variation in food web analyses. It is acknowledged that some factors influencing prey selectivity (i.e., capture efficiency, handling time, digestion rate of prey items), were not accounted for. Additionally, core sampling revealed low capture rates for mysids, a dominant prey item. This species group is problematic to sample well, given their mobile nature and close association with the seafloor water layer (Lowe 2012). Nonetheless, results offer a preliminary insight into feeding strategies of different fish species, keystone prey species and their distribution within the habitats.

5.2 Nursery role of seagrass habitats – shellfish

The small number of comparisons which could be drawn from the bivalve abundance data derived from this survey of seagrass habitats throughout New Zealand, does not support any definitive 'nursery role' of seagrass habitats in preference to bare sand habitats for the infaunal bivalve species, *Austrovenus stutchburyi* or *Nucula hartvigiana*. This is in part due to the nature of the sampling design undertaken, which was designed more specifically to investigate infaunal community composition, and did not cover a large enough sampling area to collect large number of bivalves. At present the evidence for an invertebrate nursery role in seagrass habitats seems to come consistently from warm subtropical latitudes, and to be less obvious in temperate and boreal latitudes (Williams & Heck Jr 2001).

5.3 Faunal biodiversity and secondary production associated with seagrass habitats

Numerous international studies have documented the high abundance, diversity, biomass and productivity of macroinvertebrate assemblages within seagrass compared to adjacent unvegetated habitats (e.g. Orth, 1973, Edgar et al. 1994, Heck Jr et al. 1995, Boström & Bonsdorff 1997, Edgar & Barrett 2002, Polte et al. 2005; see reviews by Orth et al. 1984, Hemminga & Duarte 2000, Gillanders 2006). Faunal abundance and diversity has also been shown to positively co-vary with seagrass biomass (i.e. density and blade length), (e.g. Stoner 1980; Summerson & Peterson 1984, Sogard et al. 1987, Lubbers et al. 1990, Edgar et al. 1994, Edgar & Shaw 1995, Heck et al. 1995, Boström & Bonsdorff 1997, Connolly 1997, Mattila et al. 1999, Edgar & Barret 2002). This has been attributed to increased resource availability (Connolly 1997), reduced competition and refuge from hydrodynamic forces (Murphey & Fonseca 1995, Boström & Mattila 1999) and predation (Heck & Thoman 1981, Orth et al. 1984, Stunz & Minello 2001). However, prior emphasis on the role of vegetation protecting macrofauna from predation is unclear, due to the ability of many highly mobile macrofaunal predator species to actively select more dense/complex seagrass habitat (Stoner 1980, Leber 1985, Bell & Westoby 1986, Howard et al. 1989, Edgar 1990b). In addition, if both prey and predator densities co-vary with increasing habitat complexity then each should counteract the other.

Univariate measures from the biogeographic survey of seagrass meadows across New Zealand identified that densities of infauna and epifauna were not significantly different within a particular seagrass habitat type (e.g. intertidal seagrass or subtidal seagrass habitats), across the different position/island combinations. Further, intertidal seagrass and subtidal seagrass habitats were not significantly different with respect to total densities of infauna or epifauna within a particular position/island combination (e.g. North Island upper or North Island lower etc). In terms of total densities found at seagrass versus bare sites, no consistent trends were apparent along a north to south gradient.

Infaunal and epifaunal species richness showed similar trends to those described for total density above for intertidal seagrass or subtidal seagrass, irrespective of which position within an island they were from. However, for North Island lower harbour sites, subtidal seagrass habitats had higher infaunal species richness than intertidal seagrass habitats (but this was not the case for epifaunal species richness, where intertidal and subtidal seagrass habitats were not significantly different). Interpretation of the dataset identified generally higher species richness along the eastern coast of the North Island (although not statistically significant) which is likely to be an effect of the East Auckland current supplying warm temperate/subtropical species to this region. South Island sites showed no significant differences across intertidal or subtidal seagrass sites for either infaunal or epifaunal species richness. For both the North and South Island lower harbour sites, both intertidal and subtidal seagrass sites had significantly greater infaunal and epifaunal species richness than their bare habitat counterparts. This same pattern was consistent for the South Island, upper harbour sites (for infaunal species richness) for the intertidal seagrass versus bare seagrass comparison.

An investigation of the infaunal biomass derived from each habitat type did not identify any significant differences for each seagrass habitat (intertidal or subtidal) irrespective of which island/position combination they were derived from. Within each island/position combination, intertidal and subtidal seagrass infaunal invertebrate biomass contributions were not significantly different.

Estuaries are known to contribute to coastal food webs via their high primary and secondary production (Beck et al. 2001, Kennish 2002). The contribution of the infaunal community found in each habitat type to overall secondary production was investigated and did not identify any significant differences within seagrass habitats (e.g. intertidal or subtidal) irrespective of which island/position combination they were from. Within each island/position combination, intertidal and subtidal seagrass faunal secondary production estimates were not significantly different. However, for the North Island upper harbours, subtidal seagrass sites did have significantly higher faunal invertebrate secondary production values when compared to their subtidal bare counterparts. This last result should be tempered by the fact that this comparison was only able to be made in Rangaunu Harbour (arguably one of the most pristine harbours left in mainland New Zealand) as this was the only location where upper harbour, subtidal seagrass was found. This may suggest that more pristine harbours are characterised by the presence of upper harbour subtidal seagrass sites, as this habitat has also been identified in another relative pristine location, Parengarenga Harbour (upper North Island, east coast) (M.L., pers. obs.). The estimates of faunal secondary production for seagrass habitats identified by this study are of a similar magnitude to those identified by other studies overseas (e.g. Fredette & Diaz 1990)

The lack of any consistent trends in these univariate measures, e.g. overall density/species richness/biomass or secondary production at these broader geographic scales, either across habitats and between different Island/position combinations or within a particular Island/position combination between intertidal and subtidal seagrass habitat, is in direct contrast to the conclusions drawn from previous studies of New Zealand seagrass habitats. These previous studies (conducted only in northern New Zealand) generally identified that lower faunal density/biomass/productivity was observed for intertidal relative to subtidal seagrass habitats (e.g. Ellis et al. 2004, van Houte-Howes et al. 2004, Alfaro 2006, Schwarz et al. 2006, Mills & Berkenbusch 2009).

However, multivariate analysis is often recognised as being more sensitive in detecting differences in community assemblage responses across known gradients. The species level analysis of both infaunal and epifaunal invertebrate community assemblages identified significant differences between various habitat types at all spatial scales investigated. From inspection of the numerous SIMPER analyses conducted on the basis of the PERMANOVA analyses (too numerous to report here), it becomes apparent that these differences in infaunal and epifaunal invertebrate community composition between habitat types (both seagrass and bare) are driven less by large changes in individual species, but rather by a multitude of small-scale changes in individual species densities. For example, the most that any individual species contributed to the overall community composition was around 5% dissimilarity.

This study has filled a significant gap in our scientific knowledge of seagrass/soft-shore community biodiversity across the various bioregions of New Zealand. Specifically, investigating the within-habitat distribution of associated seagrass fauna has identified the large amount of species heterogeneity inherent in these seagrass systems. The results of this broader geographic study of New Zealand seagrass habitats mirror those of Van Houte-Howes et al. (2004) which identified that macrofaunal (in this case faunal) softshore communities (seagrass and bare) are influenced by estuary wide effects, within estuary processes specific to the environment at each site, and to differences between seagrass and bare/sand sites. The main conclusion to be drawn here is that the role seagrass habitat plays on faunal softshore communities is complex and highly variable on a spatial scale. The presence of seagrass does not always equate to higher invertebrate abundance, species richness or secondary production when compared to local bare/sand habitats (although this relationship may vary even between sites across the same estuary).

5.4 Seagrass as a dominant ecosystem fuel

The most relevant environmental factors which help predict variability in seagrass $\delta^{13}\text{C}$ are in order of decreasing importance: carbon source, irradiance and temperature (Hemminga & Mateo 1996). The role that sediment derived inorganic carbon may have on the differences in $\delta^{13}\text{C}$ found between locations in this study cannot be quantified as sediment samples were not taken in tandem with the seagrass samples used. In estuarine and coastal areas where land-run off is accepted, considerably lower values of $\delta^{13}\text{C}$ can be expected. However, in this study there did not appear to be significantly higher $\delta^{13}\text{C}$ values in Rangaunu Harbour (a relatively pristine harbour) when compared to the Kaipara Harbour (with known anthropogenic impacts). Possible reasons for this are not known.

The relative role of seagrass as a food source for higher level consumers sampled in this study requires a more quantitative assessment of this dataset by newer software such as IsoSource.

5.5 Seagrass replication and connectivity

There was significant genetic differentiation among the seven regional populations of *Zostera muelleri* around New Zealand (Figure 41), with no shared composite genotypes among regions. This suggests that sexual reproduction rather than cloning dominates at these scales. There was no evidence for a simple isolation by distance model at the national level or within the east coast or North Island sites. The high level of regional genetic differentiation is indicative of limited gene flow, and that there is little long distance (over 100 km) dispersal of seeds or vegetative parts of plants between widely separated geographic regions, with each of the regions tested for this project representing isolated populations. However, there is a need to investigate genetic diversity at the intermediate geographic scale of 10–100 km level to determine if there is gene flow at medium distance spatial scales around the New Zealand coastline.

Extensive dispersal has been reported in *Zostera marina* with reproductive fragments and viable seeds found on shorelines up to 34 km from established meadows, while new patches of *Z. marina* have been established in Chesapeake Bay up to 100 km from source populations (Harwell & Orth 2002). Genetic studies of European populations of *Z. marina* have indicated that about 150 km was the limit for dispersal within metapopulations (Olsen et al. 2004), while genetic differentiation increased markedly among European populations of *Z. noltii* at distances over 100–150 km (Coyer et al. 2004). Populations of *Z. marina* in the North Sea showed weak and non-significant differentiation at the 12–42 km scale, and it was suggested that exchange of propagules occurred through strong tidal currents, but in the relatively low current Baltic Sea a significant fraction of the genetic variance was distributed among populations at the 15–35 km scale (Reusch et al. 2000). At the larger geographical scale (500–1000 km) most of the genetic differentiation in *Z. marina* was distributed among regions, and for European populations genetic distance was correlated with geographic distance (Reusch et al. 2000).

A recent study of RAPDs in *Z. muelleri* around New Zealand also reported high genetic variation among regions (Jones et al. 2008). Jones et al. (2008) reported a major genetic break between North Island and South Island populations of *Z. muelleri* which accounted for 46% of the total genetic variation, with Cook Strait acting as a barrier to dispersal. There was no evidence for a major genetic break between North and South Island populations in the present data set, although the Cook Strait region with the D'Urville, Southland, and Wairarapa coastal currents appears to be a barrier to gene flow in other coastal species such as snapper (Bernal-Ramirez et al. 2003) and some invertebrates (Apte & Gardner 2002, Ayers & Waters 2005, Goldstein et al. 2006).

Biogeographic clusters have been reported in *Z. noltii* in the Black Sea and off northern Europe (Coyer et al. 2004), and a division between northern and southern populations was reported off western Spain, maintained by oceanic circulation and unsuitable habitats between the northern and southern regions (Diekmann et al. 2005). It is possible that the open coastal environment around much of New

Zealand does not provide ideal habitat for *Z. muelleri* and may act as barriers to long distance dispersal among isolated populations in sheltered environments.

Given the regional genetic structure in *Zostera muelleri*, restoration projects should aim to utilise local material sourced within the same region (about 1 km scale) to avoid transfer of non-local genotypes. There is evidence that genetic diversity is positively associated with survival and recovery of seagrasses (Diaz-Almela 2007, Hughes et al. 2004, Reusch et al. 2005); consequently some genetic monitoring may be required to ensure maximum genetic diversity is captured in local transplants.

In *Z. muelleri*, individual sample sites were characterised by a limited number of shared composite genotypes, with three or more composite genotypes observed at 28 out of 29 sites. At around 45% of sites (13 out of 29) all plants had different composite genotypes. Finding two, or more, composite genotypes at each site indicates that these sites are not dominated by a single clone but are composed of genetically different individual plants. However, some composite genotypes were shared among sites within a region, and coupled with lack of isolation by distance at the local scale within regions, implies local dispersal of seeds and/or rafting of vegetative shoots. Samples with shared composite genotypes may represent single clones, especially within a site, and in the 1 and 10 m sites, but intuitively seem unlikely between the 100 and 1000 m sites. There may have been insufficient variation with this set of RAPD markers to distinguish all individuals. Jones et al. (2008) found limited evidence for clones in their RAPD data set on *Z. muelleri* in which most individuals had a unique composite genotype. Clonal diversity appears to be common in other seagrasses (Alberto et al. 2005, Coyer et al. 2004, Olsen et al. 2004). In the widely distributed *Zostera marina* duplicate genotypes had an average size of 2–4 m, but larger clones extended up to 50–75 m, and were reported in populations from the Baltic and Black Seas, and the California Channel Islands (Olsen et al. 2004). Likewise in *Z. noltii* clones were present in the majority of populations and most were contiguous and generally small (under 3 m²), although exceptions up to 50 m were reported in the Black Sea (Coyer et al. 2004). There were no shared clones among sites separated by about 800 m (Coyer et al. 2004). In *Cymodocea nodosa* the clonal range extended up to 35 m (Alberto et al. 2005).

RAPD markers provide a relatively quick and simple technique for screening genetic diversity when compared with microsatellite DNA markers that require the development of species-specific primer pairs (Reusch et al. 2000). Alternative, and more costly molecular methods, may need to be considered for further genetic studies on *Z. muelleri*. Microsatellite DNA has become the marker of choice in many population studies, including seagrasses (Coyer et al. 2004, Reusch et al. 2000). Genome scans provide a powerful tool to detect natural selection in wild populations and have recently been applied to populations of *Zostera marina*, from different habitat types (exposed and permanently submerged) in the North Frisian Wadden Sea (Oetjen & Reusch 2007). Nevertheless the current results have shown significant differentiation among seven regional populations.

6. RISK IDENTIFICATION AND APPRAISAL FRAMEWORK

6.1 Distribution

Seagrass within New Zealand is represented by a single species (*Zostera muelleri*). It forms extensive monospecific beds, or mosaics, of discrete patches surrounded by unvegetated sediments. Seagrass occurs predominantly intertidally, but also extends into the shallow subtidal of sheltered estuaries, and permanently submerged meadows of a small number of offshore islands (e.g. Slipper Island and Great Mercury Island off Coromandel Peninsula, and Urupukapuka Island in the Bay of Islands) where water clarity is greatest (maximum depth recorded is 7 m) (Turner & Schwarz 2006). Seagrass also occurs in association with sediment-filled crevices and tide pools on siltstone platform reefs in open coastal areas on the eastern coastline of both islands (e.g. Gisborne, and Kaikoura Peninsula, Figure 45), where biotic assemblages are more characteristic of rocky, intertidal assemblages (Woods & Schiel 1997, Inglis 2003).



Figure 45: (A) Collecting samples from seagrass on an intertidal, rocky reef, Gisborne; (B) Example of rocky reef intertidal platform with seagrass at Kaikoura.

Zostera occurs throughout the mainland coast of New Zealand, from Parengarenga Harbour in the north to Stewart Island in the south (Figure 46). Large seagrass meadows remain in estuaries and embayments, including east Northland (Parengarenga, Rangaunu and Kaipara harbours), on the west coast (Aotea and Kawhia harbours), and in the Bay of Plenty (Tauranga). In the South Island extensive meadows remain in Farewell Spit, Whanganui Inlet and further south in Bluff Harbour and Patterson Inlet (Stewart Island). Seagrass meadows also occur in numerous smaller estuaries (see table 1, Inglis, 2003) which are not well documented. Only about 50 out of some 300 estuaries have current seagrass survey information available (H Kettles, DoC pers. comm.). With only an estimated 44 km² of seagrass remaining in New Zealand (Spalding et al. 2003), most of which are located in the more remote ‘pristine’ areas of the country, it is a relatively uncommon habitat within New Zealand (Inglis 2003). However Spalding’s figure is probably an underestimate; e.g. Morrison et al 2014b mapped more than 20 km² of seagrass in the southern Kaipara Harbour in 2012).

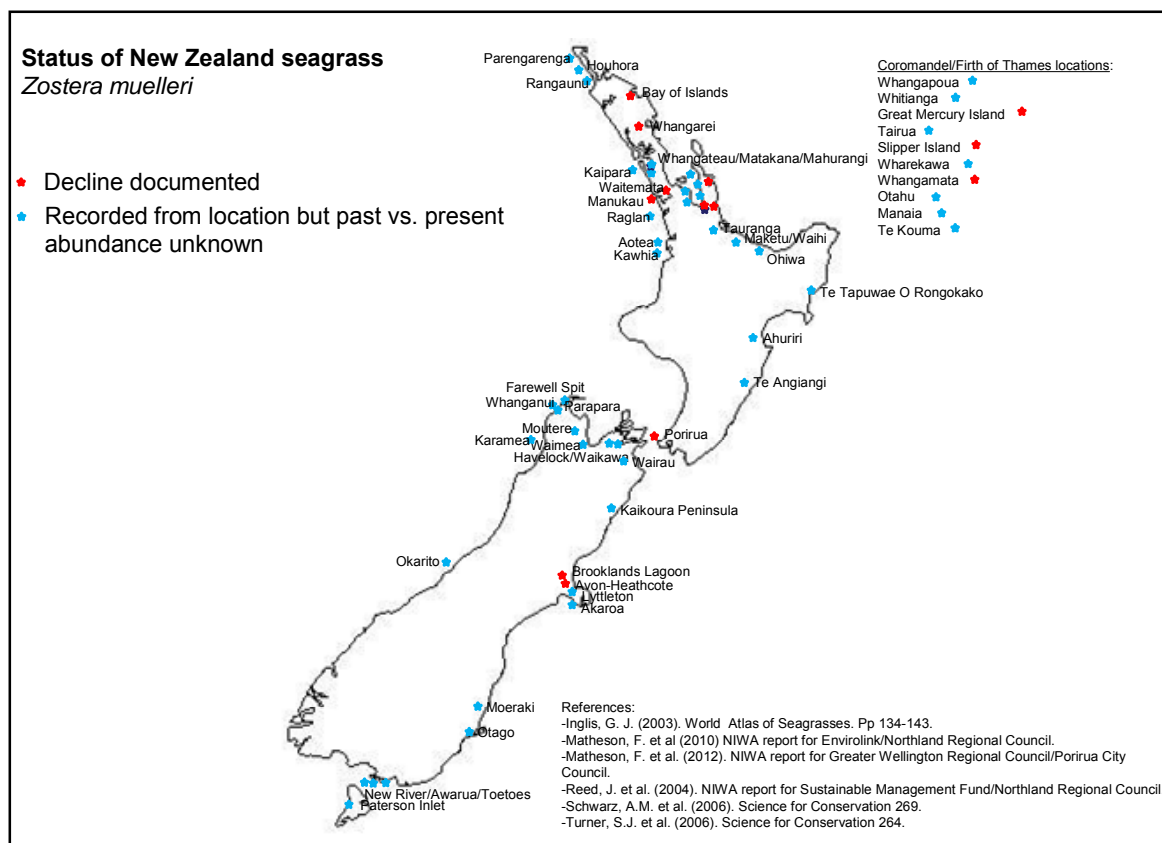


Figure 46: Known status of seagrass in New Zealand. Blue stars indicate documented locations, but the current status relative to its historical abundance is unknown for many of these sites. Red stars indicate documented cases of seagrass decline, with virtually all losses associated with human activities and development of these areas. The Department of Conservation has recently reclassified *Zostera muelleri*'s threatened species status, from stable to declining (Source: Matheson et al. 2011, Matheson & Wadhwa 2012).

6.2 Historical distribution

A paucity of detailed mapping and long-term studies of seagrass habitats in New Zealand makes it difficult to determine changes in its distribution, condition and spatial extent over time (Inglis 2003). Additionally, little information exists on natural changes between years, and evaluation of the contribution of different environmental factors and coastal processes to changes in seagrass distribution (Turner & Schwarz 2006). Few documented instances of seagrass loss in New Zealand are available, with analysis being limited by the availability of reliable photography and field data from the last 40–50 years (Turner & Schwarz 2004). However, historical accounts suggest that seagrass meadows were quite widespread at the end of the nineteenth century, where it was described by Leonard Cockayne (1855–1934) as “*extremely common in shallow estuaries*” (Inglis 2003). In the Auckland region, seagrass was reputedly once very abundant in Waitemata Harbour, but it had all but disappeared by 1931. Powell (1937) associated this loss with marked reduction in catches of snapper and other carnivorous fishes. Similarly, extensive meadows were present in areas around Auckland (e.g., Tamaki Estuary, Okahu Bay, Cheltenham Beach, and Manukau Harbour), but these had all but disappeared by the early 1980s (Inglis 2003). Other regions recording large scale losses (predominantly between 1930 and 1970) include Whangarei, Tauranga, Whangamata, eastern Bay of Islands, Porirua (Wellington) and Avon-Heathcote estuaries (Table 23, see also reviews by Inglis 2003, Morrison 2003, Morrison et al. 2009, 2014a, 2014b).

Table 23: Examples of seagrass (*Zostera muelleri*) loss within the North Island of New Zealand.

Location	Description of seagrass loss	Reference
Porirua Harbour (1960s–1980) Wellington	Loss of about 50% of seagrass (41 ha of about 92 ha). Linked to estuary eutrophication and marina development.	Matheson & Wadhwa (2012)
Bay of Islands (Eastern) (1961–2006)	Loss of 90% of subtidal seagrass from mainland bays. Probably linked with sediment and nutrient inputs.	Matheson et al. (2010)
Whangarei Harbour (late 1960s–1970)	1400 ha of seagrass (mostly subtidal) reduced to only remnant patches post–1970s. Linked to dumping of 5 million cubic tonnes of sediment ‘fines’ into harbour from port expansion/cement works. Note: significant expansion since 2008, now an estimated 3.5 km ² of sub-tidal seagrass (occurring as patch mosaic) (D. Parsons, NIWA, pers. comm.).	Reed et al. (2004), Morrison (2005), Morrison et al. (2009)
Whangamata (1965–1998)	Loss of 40.6% attributed to a reduction in suitable habitat, i.e., the expansion of mudflats.	Cawthron Institute (2000), cited in Turner & Schwarz (2004)
New Zealand wide (1960s)	Widespread die-back of seagrass attributed to ‘slime mould’	Armiger (1965), cited in Inglis (2003)

6.3 Threats and stressors

The causes of seagrass decline within New Zealand have been attributed to a range of anthropogenic activities and natural events which can act synergistically (Table 23, Figure 47) (Inglis 2003, Turner & Schwarz 2006, Matheson & Wadhwa 2012). A significant problem, especially for urban estuaries is nutrient enrichment from land based sources leading to the proliferation of phytoplankton, macroalgae or epiphytic algae on seagrass leaves and stems (eutrophication) (Inglis 2003, Morrison et al. 2009). Other factors include storms, pathogens, competition from invasive marine plants (e.g. the bryozoan - *Zoobotryon verticillatum*, now present in many Northland estuaries.) and overgrazing from waterfowl (Dos Santos et al. 2013). However, changes in sediment regimes associated with increased sedimentation rates, and associated turbidity (i.e., declining water clarity) and/or sediment textural characteristics have been identified as the most widespread and serious problem facing New Zealand's estuarine and coastal systems (Inglis 2003, Turner & Schwarz 2006, Matheson et al. 2009, Morrison et al. 2009). New Zealand's natural steep terrain, and relatively high annual rainfall in conjunction with increasing coastal development and intensifying agricultural practices has resulted in high loads of suspended sediments entering our coastal environs (contributing 1% of the worldwide total, Morrison et al. 2009). These factors, in conjunction with deforestation, including the harvesting of large areas of plantation forests currently underway in regional areas bordering on some of the most pristine areas of remaining seagrass (e.g. Parengarenga Harbour), are likely, unless well managed, to exacerbate the delivery of suspended sediments and promote the subsequent decline in seagrass meadows (Inglis 2003, M.L., pers. obs.).

Possible causes of seagrass decline

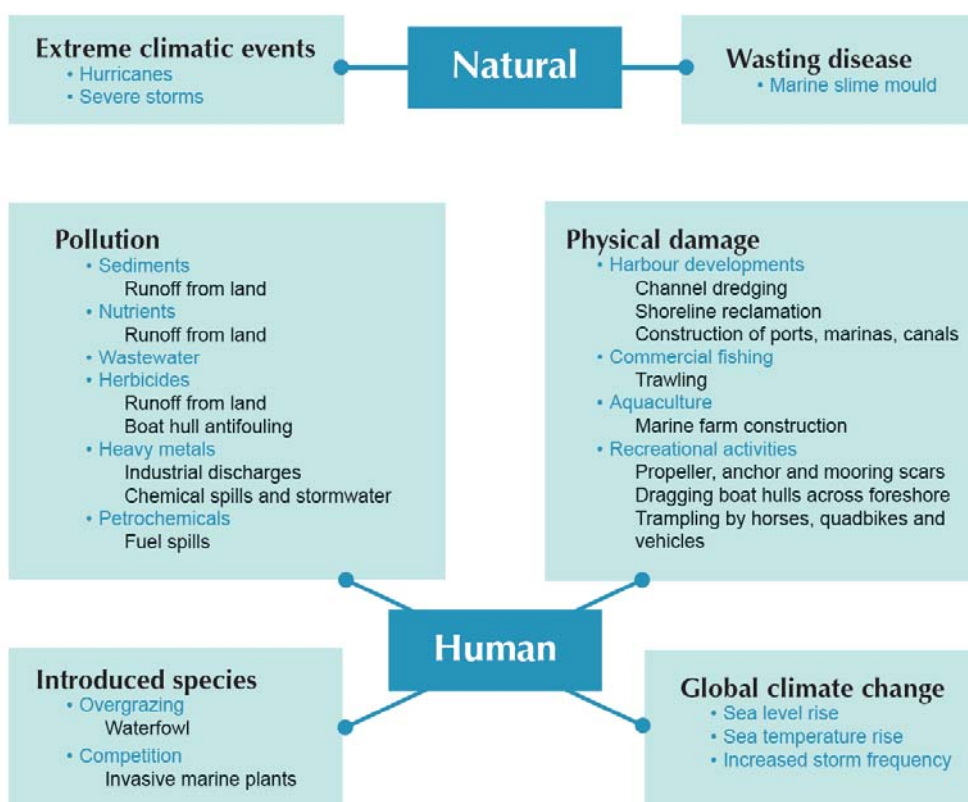
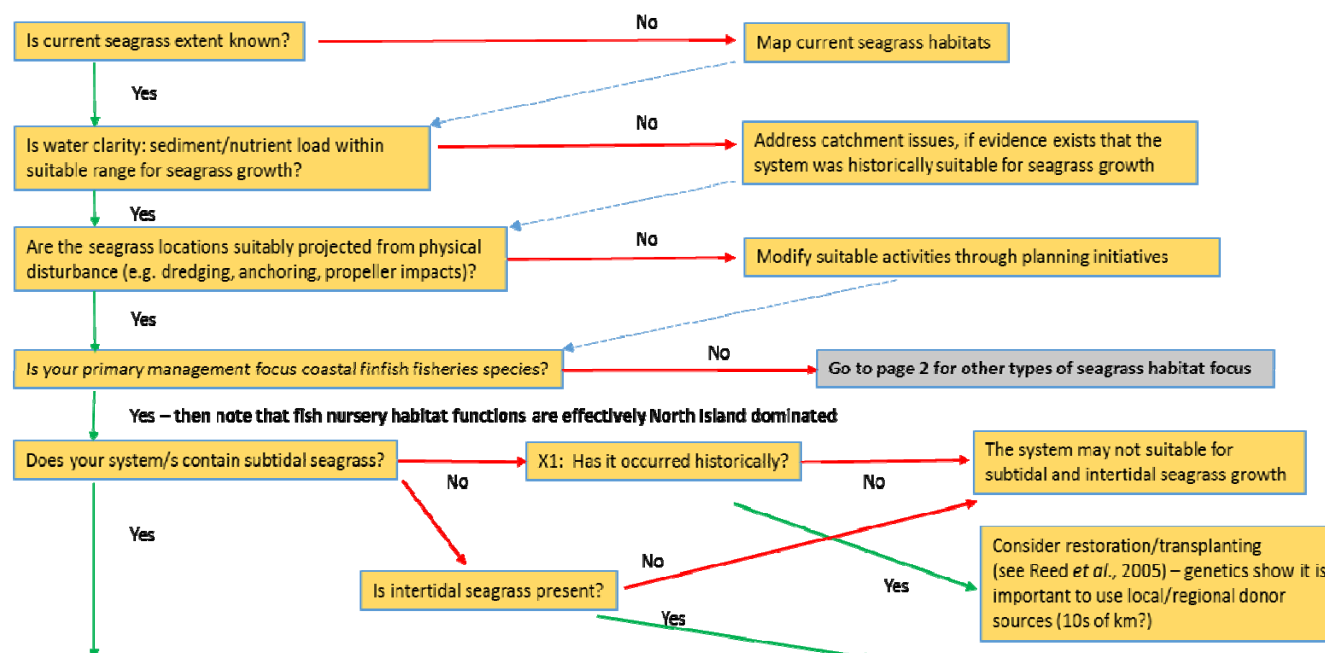


Figure 47: Possible causes of seagrass decline within New Zealand estuaries. (Source: Matheson & Wadhwa 2012).

Nevertheless, there have been reports of resurgence and re-establishment of seagrass meadows returning to some areas where improvements in water quality have been made (e.g. Whangarei Harbour 3.5 km² subtidal seagrass, and Avon-Heathcote Estuary) in addition to areas of the lower Kaipara Harbour, Snells Beach and St Heliers beach in the Auckland region (Morrison et al. 2007).

6.4 Ecological appraisal and decision matrix for New Zealand seagrass meadows

Using the existing literature on general seagrass habitat preferences and the main findings of this study with regard to biodiversity and production of seagrass associated fish and faunal communities, an ecological appraisal matrix was designed for resource managers as outlined below.



Is it of sufficient extent to hold sizeable juvenile fish populations? If it is presently small but was historically much greater (e.g. Tauranga Harbour) go to X1. If larger, then designate as high value in fisheries or other authority plans (e.g. Habitats of Significance, Significant Ecological Areas). Adopt appropriate catchment management to maintain or improve water and seafloor quality.

Implement suitable long term monitoring approach, incorporating ongoing mapping/ground truthing and measurement of appropriate 'driver' variables. Ideally this should be part of a broader coastal monitoring approach. Build fisheries values into improved coastal management.

Research needs:

- Consider local fish-habitat surveys if not done previously (e.g. as now underway for Parengarenga, Rangaunu, Kaipara seagrass systems as part of CCM CO1X0907), as fish assemblages vary considerably across locations
- Quantify what proportion of juvenile recruitment seagrass meadows contribute to fisheries stocks – is it significant? (expectation is yes for systems such as mentioned above – CCM East Northland work upcoming on snapper recruitment, including Parengarenga, Ranganunu, Bay of Islands, Whangarei seagrass habitats)
- Assess how changes in seagrass extent / configuration / landscape context (e.g. associated current speeds) affect juvenile fish production (e.g. as currently in progress for Kaipara Harbour, CCM)
- Assess how seagrass spatial context in the larger ecosystem landscape affects larval fish supply of specific species e.g. Tairua seagrass had high juvenile parore abundances but very few snapper – how does the presence of adjacent adult spawning populations affect larval fish supply? i.e. larval supply drives seagrass juvenile fish densities?

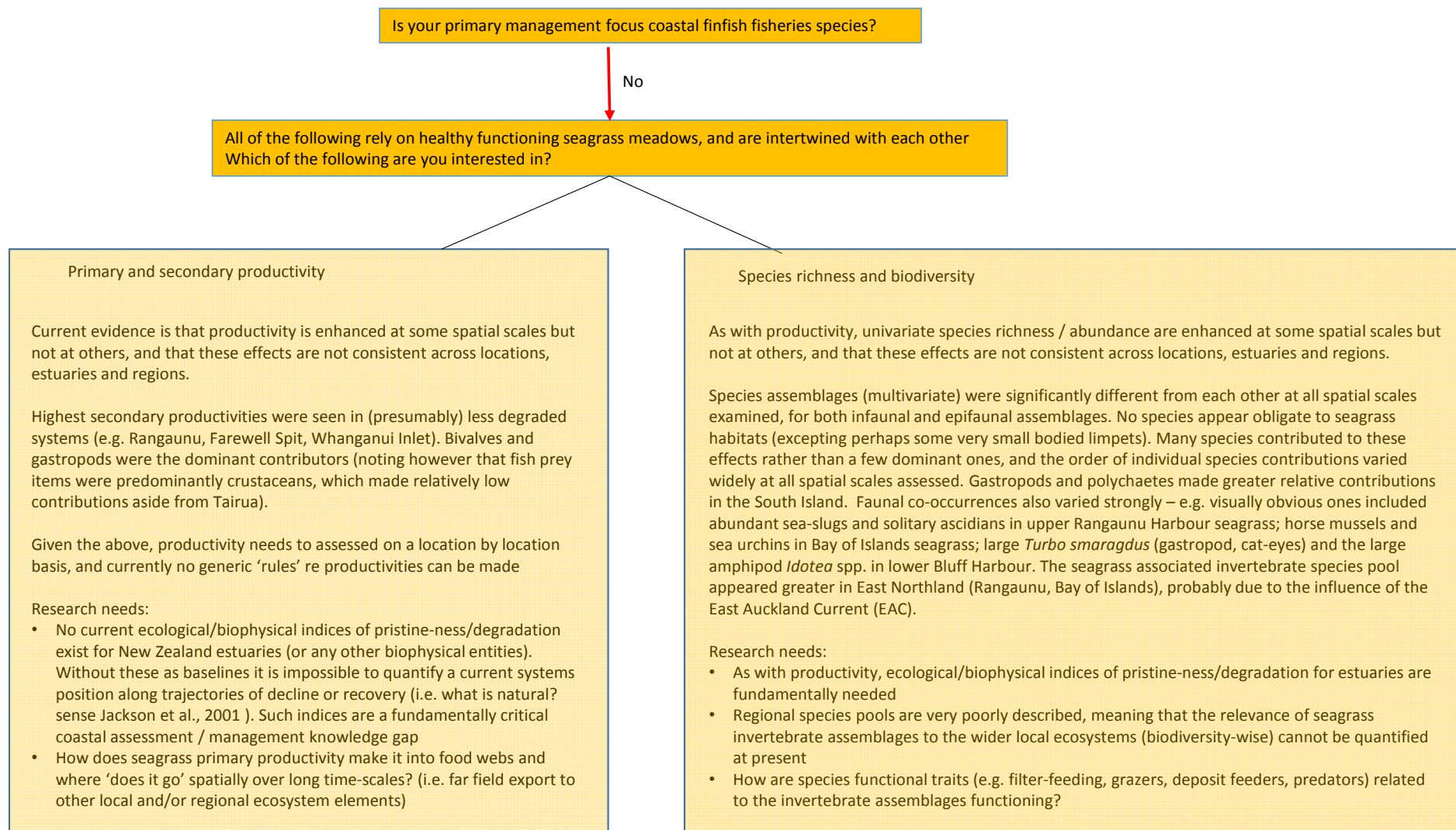
Current evidence is that intertidal seagrass does not contribute significantly to finfish nursery functions (though both direct and indirect trophic fuelling effects remain uncertain, re high tide foraging, and supporting far field food webs).

An exception is an intertidal seagrass association of very small juvenile grey mullet, trevally and kahawai in the Kaipara Harbour, and some evidence of settlement of very small snapper into intertidal beds that extend close to the low tide mark (Rangaunu Harbour) (this report).

Given the above, designation of these habitats as important to juvenile finfish fisheries production is currently not warranted based on available evidence.

Research needs:

- Quantify extent of tidal foraging movement of 'important juvenile fishes into intertidal seagrass meadows (e.g. snapper, trevally)
- Investigate whether these habitats might be useful initial settlement (suspected scale of weeks)
- sites as part of an ontogenetic chain of habitats. Quantify whether intertidal seagrass productivity is making its way through food chains into supporting juvenile fish diet.



7. CONCLUSIONS AND PRIORITIES FOR FUTURE RESEARCH

Results from this survey revealed that seagrass meadows within northern New Zealand are important nursery areas for juvenile fish, including several commercially important fish species (snapper, trevally). Key harbours identified include the southern Kaipara, Rangaunu and Parengarenga (not a study site, but identified independently, M.L., pers. obs.). However, values of seagrass meadows varied strongly spatially, dependent upon depth, coast, landscape setting and latitude. Southern seagrass meadows for example, were characterized by lower overall densities with little differentiation in fish assemblages between seagrass and bare habitats. This concurs with international studies showing that environmental context is important and suggests that universal generalisations are difficult given that each estuary possesses unique individual characteristics (Edgar et al. 2000). This suggests that resource managers need to incorporate this variability into their decision making. Examples might include: explicitly linking catchment sediment and nutrient loads to seagrass and other habitats health in key estuaries, with land-based activities having a management component designed to keep loads below some threshold of change value; or removing more localised stressors such as boat propeller scarring or recreational scallop dredging, by excluding boats or specific activities from selected key areas.

Seagrass meadows are sensitive bio indicators of water quality due to their need for high water clarity. It has been suggested that they be used as indicators of the biological health of estuarine ecosystems i.e. *sensu* ‘canaries in a coalmine’. Given that the major threats to seagrasses are largely terrestrially based, their nearshore coastal position makes them extremely vulnerable to anthropogenic impacts (increased sedimentation and eutrophication) (Grech et al. 2012, Morrison et al. 2009). The significant declines of *Zostera muelleri* documented within New Zealand, and the recent reclassification as a ‘declining species’ (e.g., Tauranga Harbour 90% loss of subtidal beds), highlights the need for integrated management with a focus on regional differences in vulnerability, linking both estuarine and coastal ecosystems to their catchments (e.g. better forestry/agricultural practices). Additionally, public awareness needs to be raised: first to the presence of seagrass, and second to its importance (Inglis 2003, Turner & Schwarz 2006). At present there is no national inventory of seagrass distribution and extent in New Zealand or how it is changing over time (Turner & Schwarz 2006), although DOC is currently in the process of assembling one using GIS (H. Kettles, pers. comm.).

Mitigating seagrass losses within New Zealand involving restoration of seagrass meadows, while successful (e.g. Whangarei Harbour) in trials (Matheson et al., in prep.), has been on a limited spatial scale, and is expensive and laborious. Overseas results have also been equivocal as to the return of full ecological functioning of seagrass habitats, even three years on from restoration (Meyer et al. 1993, cited in Turner et al. 1999). This emphasizes the need to protect and conserve the remaining areas of significance via improvement in water quality management and associated monitoring to quantify that seagrass meadows are responding positively.

Another area which warrents further investigation is seagrass genetic diversity at intermediate spatial scales of 10–100 km to determine if there is gene flow at medium distance spatial scales around the New Zealand coastline.

Implications for future research on fish nurseries

Ultimately, understanding of the relative contribution of seagrasses and other estuarine and coastal biogenic habitats (e.g. horse mussel beds, rhodolith beds, sponge gardens, green-lipped mussel beds) to recruitment to coastal fish populations will require information on spatio temporal variability in ontogenetic habitat use, including not only density estimates, but growth and survival rates during juvenile habitat utilization (Beck et al. 2003, Fodrie et al. 2009, Nunn et al. 2011, Morrison et al. 2014a–c) and subsequent emigration to adjacent coastal fisheries. Further research utilizing stable isotope analysis, in combination with traditional dietary analyses and estimates of prey availability (as undertaken in this survey) along with nutritional condition indices (using RNA-DNA ratio analysis; Nunn et al. 2011) and otolith microchemistry (e.g. Gillanders 2003), may allow better identification of

key habitats of all life stages/species. Work on the likely relative contributions of estuarine (especially subtidal seagrass meadows) versus coastal habitats, with a particular focus on juvenile snapper, is currently underway in upper East Northland (March–May 2014). Based on the information from this current report, Parengarenga and Rangaunu harbour seagrass meadows have been subsequently relatively intensely sampled using beach seines, as have adjacent coastal biogenic habitats using beam trawl and underwater cameras, in selected coastal segments including the eastern Bay of Islands (including additional subtidal seagrass areas), Sandy Bay coastline, Cavalli Islands to Whangapoua Harbour, Doubtless Bay, and Rangaunu Bay and Great Exhibition Bay (the latter two into which Rangaunu and Parengarenga harbours connect) (M.M. & M.L., unpubl. data). Initial data indications are that subtidal seagrass meadows are providing a significant proportion of overall snapper recruitment for East Northland. In stark contrast, subtidal seagrass meadows in the Hauraki Gulf are functionally (and almost physically) extinct, and juvenile snapper recruitment must be coming from other biogenic habitat types such as horse mussel beds, sponge gardens, and other seafloor structure (e.g. Battershill 1986, Kingett & Choat 1981, Morrison & Carbines 2006, Usmar 2009, Compton et al. 2012). What fish production was lost with the historical degradation and loss of habitats (e.g. subtidal seagrass, but also green-lipped mussel beds and others) remains unknown (Morrison et al. 2014c).

Research is also underway within the southern Kaipara, Rangaunu and Parengarenga harbours to quantify what specific components of seagrass meadows contribute the most as juvenile fish nurseries (e.g. blade densities, water depth, patch size, edge to interior ratios, distance from harbour entrance and so on) (NB: ongoing experimental work with artificial seagrass units is also being undertaken in Whangarei Harbour, having replaced Whangapoua Harbour due to logistical constraints; see Parsons et al. 2013, 2014). Satellite and aerial imagery of seagrass and other habitats has been used to drive the sampling design, with a strong correlation between pre-identified ‘prime’ habitats and their subsequent juvenile snapper densities. The value of remote sensing in mapping and assigning values to estuarine and coastal (fish) habitats is being assessed, with promising preliminary results (e.g. see Morrison et al. 2014b, for southern Kaipara intertidal and subtidal seagrass meadows). Use of such remote sensing techniques through time will allow better quantification of how seagrass meadows vary temporally, in response to direct anthropogenic land and marine based activities, as well as indirect impacts such as increasing frequency and intensity of storm events (and increased turbidities) associated with climate change, along with natural long term cycles (suspected to operate at decadal scales). DOC is also currently running a project which is assembling and digitizing/importing all available spatial and temporal material on seagrass distribution and abundance (H. Kettles, DOC, unpubl. data), which is a fundamental resource inventory that will be immensely valuable.

As part of a post-doctoral programme, work is likely to start in the near future on building a conceptual model of how juvenile fish and northern subtidal seagrass meadows interact and function, including the role of invertebrates, and how human stressors such as sedimentation and eutrophication impact on that functioning as their severity increases. That proposed model is also likely to include effects such as coastal setting, larval supply, and the increasing pressure of climate change (e.g. through land run-off, storminess, and impacts on zooplankton populations (fish prey)). As noted by Nunn et al. (2011), given that recruitment into adult fish stocks are, directly, or indirectly, limited by the quality and quantity of habitat and food available to larval and juvenile fishes, such information is a fundamental pre requisite for ecosystem-based management (Hinz et al. 2005, Nunn et al. 2011, De Raedemaeker et al. 2011).

More broadly, there is work proposed in that programme, integrated with the MBIE Coastal Conservation Management programme (C01X0907) on how changes in biogenic habitats, in particular subtidal seagrass, influence juvenile fish production over time, and how that translates into recruitment (in the fisheries sense of the word) to adult coastal stocks that support important commercial, recreational, and customary fisheries (see Morrison et al. 2009, 2014a–c). This information and data presented in this report form the foundation on which all of the subsequent work mentioned above is been built.

8. ACKNOWLEDGMENTS

This research was funded by the Ministry for Primary Industries, within project ZBD2004–08 and we are most grateful for Mary Livingston’s patience in seeing it through, as well as her and Richard Ford’s refereeing comments. We are very grateful to the many people involved who helped to complete this project, both in the field and laboratory. We thank Ken Becker and Jeremy Mckenzie for their facilitating role in the project. We also thank Ian Tuck for his much appreciated comment and Beverley Wilson for her patience in formatting the final report at short notice and Marianne Vignaux for providing appreciated editorial on the report.

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10. APPENDICES

10.1 Appendix 1 Stable Isotopes

Stable isotope accuracy and precision data for NIST standard analyses and DL-Leucine standards during batch analysis of Black-fronted tern samples.

Table A1.1: Comparison of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values analysed on the NIWA Thermo-Finnigan Deltaplus mass spectrometer compared to reported NIST values. The +/- values represent 1 standard deviation. The value in brackets are the number of samples used.

NIST standard	NIST $\delta^{15}\text{N}$ ‰ reported values (n=)	NIWA measured $\delta^{15}\text{N}$ ‰ values (n=)	NIST $\delta^{13}\text{C}$ ‰ reported values	NIWA $\delta^{13}\text{C}$ ‰ values measured (n=)
1577b Bovine Liver*	+7.78+/-0.22 (61)	+7.88 +/- 0.26 (8)	-	-
1547 Peach Leaves*	+2.08+/-0.18 (32)	+2.26 +/- 0.31 (8)	-	-
2685a Coal Sub-bituminous*	+2.79+/-0.74 (12)	+2.33 +/- 0.27 (3)	-	-
2704 BuffaloRiver Sediment*	+3.80+/-0.39 (59)	+3.88 +/- 0.47 (5)	-	-
2682a Coal Bituminous*	+3.38+/-0.75 (15)	+2.27 +/- 0.10 (3)	-	-
8547 N1 Ammonium sulphate	+0.40 +/- 0.20	+0.56+/-0.23 (17)	-	-
8548 N2 Ammonium sulphate	+20.3 +/- 0.20	+20.4+/-0.21 (17)	-	-
8549 N3 Potassium nitrate	+2 to +5	+4.61+/-0.51 (10)	-	-
8541 Graphite	-	-	-15.90 +/- 0.25	-15.48 +/- 0.11 (10)
8542 Sucrose	-	-	-10.47 +/- 0.13	-10.78 +/- 0.38 (10)

* reported values were co-ordinated by Environmental Isotope Laboratory, University of Waterloo

Table A1.2: Comparison of %N and %C values analysed on the NIWA Thermo-Finnigan Deltaplus mass spectrometer compared to reported NIST values. The +/- values represent 1 standard deviation.

NIST standard	NIST reported or calculated values (n=)	NIWA measured values (n=)	NIST reported or calculated values	NIWA measured values (n=)
1577b Bovine Liver*	10.2 +/- 0.29 (61)	9.76 +/- 0.47	-	-
1547 Peach Leaves*	2.83 +/- 0.11 (32)	2.63 +/- 0.09	-	-
2685a Coal Sub-bituminous*	0.96 +/- 0.04 (12)	0.88 +/- 0.04	-	-
2704 Buffalo River Sediment*	0.20 +/- 0.01 (59)	0.18 +/- 0.00	-	-
2682a Coal Bituminous*	1.11 +/- 0.06 (15)	0.83 +/- 0.11	-	-
8547 N1 Ammonium sulphate	21.21	20.83 +/- 0.66	-	-
8548 N2 Ammonium sulphate	21.21	21.01 +/- 0.18	-	-
8549 N3 Potassium nitrate	13.86	13.33 +/- 0.28	-	-
8541 Graphite	-	-	-	-
8542 Sucrose	-	-	42.11	43.84 +/- 0.61 (9)

* reported values were co-ordinated by Environmental Isotope Laboratory, University of Waterloo

Table A1.3: Precision data for repeat analysis of DL-Leucine standards during sample batch analyses. The +/- values represent 1 standard deviation.

Internal DL-Leucine Standard	Wt% N	$\delta^{15}\text{N}$	Wt % C	$\delta^{13}\text{C}$
Known value	10.57		54.38	
Measured value during batch analysis of Black-fronted tern samples	10.56 +/- 0.23 (n=28)	12.97 +/- 0.24 (n=44)	54.38 +/- 1.01 (n=28)	-30.22 +/- 0.17 (n=44)
Measured value during delta plus sample runs from Aug 06 – Mar 08	10.57 +/- 0.31 (n=128)	13.18 +/- 0.77 (n=219)	54.27 +/- 1.53 (n=128)	-30.100 +/- 0.23 (n=224)

10.2 Appendix 2: Operon 10-base oligonucleotide primers tested in *Z. muelleri*.

(<https://www.operon.com/stock/RAPD10mers.php>).

Primer Code No	Sequence 5'-3'	Primer Code No	Sequence 5'-3'
OPD-01	ACCGCGAAGG	OPH-11	CTTCCGCAGT
OPD-02	GGACCCAACC	OPH-12	ACGCGCATGT
OPD-03	GTCGCCGTCA	OPH-13	GACGCCACAC
OPD-04	TCTGGTGAGG	OPH-14	ACCAGGTTGG
OPD-05	TGAGCGGACA	OPH-15	AATGGCGCAG
OPD-06	ACCTGAACGG	OPH-16	TCTCAGCTGG
OPD-07	TTGGCACGGG	OPH-17	CACTCTCCTC
OPD-09	CTCTGGAGAC	OPH-18	GAATCGGCCA
OPD-10	GGTCTACACC	OPH-19	CTGACCAGCC
OPD-11	AGCGCCATTG	OPH-20	GGGAGACATC
OPD-12	CACCGTATCC	OPW-01	CTCAGTGTCC
OPD-13	GGGGTGACGA	OPW-02	ACCCCGCCAA
OPD-14	CTTCCCCAAG	OPW-03	GTCCGGAGTG
OPD-15	CATCCGTGCT	OPW-04	CAGAAGCGGA
OPD-16	AGGGCGTAAG	OPW-05	GGCGGATAAG
OPD-17	TTTCCACGG	OPW-06	AGGCCCGATG
OPD-18	GAGAGCCAAC	OPW-07	CTGGACGTCA
OPD-19	CTGGGGACTT	OPW-08	GACTGCCTCT
OPD-20	ACCCGGTCAC	OPW-09	GTGACCGAGT
OPH-01	GGTCGGAGAA	OPW-10	TCGCATCCCT
OPH-02	TCGGACGTGA	OPW-11	CTGATGCGTG
OPH-03	AGACGTCCAC	OPW-12	TGGGCAGAAG
OPH-04	GGAAGTCGCC	OPW-13	CACAGCGACA
OPH-05	AGTCGTCCCC	OPW-14	CTGCTGAGCA
OPH-06	ACGCATCGCA	OPW-15	ACACCGGAAC
OPH-07	CTGCATCGTG	OPW-16	CAGCCTACCA
OPH-08	GAAACACCCC	OPW-17	GTCCTGGGTT
OPH-09	TGTAGCTGGG	OPW-18	TTCAGGGCAC
OPH-10	CCTACGTCAG	OPW-19	CAAAGCGCTC
		OPW-20	TGTGGCAGCA

10.3 Appendix 3. Species list of infaunal invertebrates – New Zealand biogeographic survey of seagrass sites (mean density per core \pm s.e.)

North Island locations

Location	Rangauu Hbr						Bay of Islands				Kaipara Harbo				Tairua				Kawhia				Gisborne	
Position	Upper		Lower		Subtidal		Subtidal		Subtidal		Upper		Lower		Subtidal		Intertidal		Intertidal		Intertidal			
Site	Sybtdal		Intertidal		Seagrass		Seagrass		Seagrass		Seagrass		Seagrass		Seagrass		Seagrass		Seagrass		Seagrass			
Habitat	Seagrass		Bare		Seagrass		Bare		Seagrass		Bare		Seagrass		Bare		Seagrass		Bare		Seagrass			
Amphiura aster	-	-	-	0.50	0.29	-	-	2.00	1.41	-	-	-	-	-	-	-	-	-	-	-	-	-		
Amphiura rosea	-	-	-	-	-	-	-	0.75	0.48	-	-	-	-	-	-	-	-	-	-	-	-	-		
Anatides sp.	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Aplysia dactylomela	-	-	-	-	-	-	-	0.50	0.50	-	-	-	-	-	-	-	-	-	-	-	-	-		
Ascidian sp.	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Ball anemone	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Cylaspis thomsoni	-	1.00	0.58	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Cymothoidae sp.	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Duplicaria tristis	-	-	-	0.50	0.29	0.25	0.25	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Eteone sp.	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Eunicid sp.	-	-	-	-	-	-	-	0.75	0.75	-	-	-	-	-	-	-	-	-	-	-	-	-		
Hemigrapsis crenulatus	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Hippolyte bifidirostris	0.25	0.25	-	-	-	-	-	0.50	0.50	-	-	-	-	-	-	-	-	-	-	-	-	-		
Mactra ovata	-	-	-	-	-	-	-	0.75	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Marphysa	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Microcosmus kura	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Nereis pereneis	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Olividae sp. 2	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Paphies sp.	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Paranthura flagellata	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Phenatoma rosea	-	-	-	-	-	-	-	1.25	0.95	-	-	-	-	-	-	-	-	-	-	-	-	-		
Prionospio aucklandica	-	-	-	1.75	1.75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Spionid sp.	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Stylochoplana sp.	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Turbonilla zelandica	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Tharyx sp.	1.00	0.58	-	0.25	0.25	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Wandering sea anemone	-	-	-	-	-	-	-	3.75	1.65	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-		
Chaetopteridae	0.50	0.50	-	0.25	0.25	-	-	57.75	23.71	-	-	2.50	1.55	3.25	2.93	-	-	-	-	-	-	-		
Balanoglossus australiensis	-	-	-	-	-	2.00	0.91	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-		
Bulla quoyii	1.00	0.58	-	-	-	-	-	0.25	0.25	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-		
Branchiomma sp.	-	-	-	-	-	-	-	3.00	2.38	-	-	1.00	0.58	-	-	-	-	-	-	-	-	-		
Timarete anchylochaeta	1.75	1.44	0.75	0.48	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Marginella pygmaea	-	-	-	-	-	-	-	2.00	1.15	-	-	0.75	0.75	-	-	-	-	-	-	-	-	-		
Notomithrax sp.	-	-	-	-	-	-	-	0.50	0.50	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-		
Amalda mucronata	-	-	-	0.50	0.50	-	-	0.50	0.29	-	-	0.50	0.50	-	-	-	-	-	-	-	-	-		
Amalda australis	-	-	-	-	-	-	-	0.25	0.25	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-		
Pelogenia antipoda	-	-	-	-	-	-	-	0.25	0.25	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-		
Estea zosterophila	-	-	-	-	-	-	-	3.50	1.55	-	-	4.50	4.50	-	-	-	-	-	-	-	-	-		
Onuphis eremita	-	-	-	-	-	-	-	0.50	0.50	-	-	1.00	0.41	0.50	0.29	-	-	-	-	-	-	-		
Euclymene sp. B	-	-	-	-	-	-	-	1.75	1.75	-	-	1.50	1.50	-	-	-	-	-	-	-	-	-		
Barnacle cyprid	0.25	0.25	0.50	0.29	-	-	-	0.25	0.25	0.50	0.50	1.50	0.87	-	-	0.25	0.25	-	-	-	-	-		
Syllid sp.	-	-	-	-	-	0.25	0.25	-	-	-	-	1.00	0.58	-	-	-	-	-	-	-	-	-		
Palaemon affinis	0.25	0.25	-	-	-	-	-	3.25	3.25	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-		
Neanthes sp.	3.00	1.58	-	1.00	1.00	-	-	0.50	0.50	-	-	-	-	-	-	-	-	-	-	-	-	-		
Eatoniella limbata	-	-	-	0.25	0.25	-	-	-	-	-	-	75.50	41.28	-	-	-	-	-	-	-	-	-		
Barnea similis	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-		
Cirsotrema zelebori	-	-	-	-	-	-	-	0.50	0.50	-	-	-	-	-	-	-	-	-	-	-	-	-		
Dosinia sp.	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-		
Isodadus armatus	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Maoricolpus sp. A	-	-	-	-	-	-	-	16.00	5.40	-	-	-	-	-	-	-	-	-	-	-	-	-		
Nebalia sp.	-	-	-	-	-	-	-	0.50	0.29	-	-	-	-	-	-	-	-	-	-	-	-	-		
Neoguraleus sp.	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Neosabellaria kauparensis	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Nerita atramentosa	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Ovalipes catharus	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-		
Rissoina sp. A	-	-	-	-	-	-	-	11.50	4.13	-	-	-	-	-	-	-	-	-	-	-	-	-		
Rissoina sp. B	-	-	-	-	-	-	-	3.25	2.63	-	-	-	-	-	-	-	-	-	-	-	-	-		

North Island locations continued...

[illegible]

North Island locations continued...

Location	Rangaunu Hbr								Bay of Islands				Kaipara Harbo								Tairua				Kawhia				Gisborne						
Position	Upper				Lower								Upper				Lower								Intertidal				Intertidal				Intertidal		
Site	Subtidal				Intertidal				Subtidal				Subtidal				Subtidal				Subtidal				Seagrass		Bare		Seagrass		Bare		Seagrass		
Habitat	Seagrass		Bare		Seagrass		Bare		Seagrass		Bare		Seagrass		Bare		Seagrass		Bare		Seagrass		Bare		Seagrass		Bare		Seagrass		Bare		Seagrass		
Nereis falcaria	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.75	1.03	0.50	0.50	-	-	-	-	-	-		
Alpheus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	0.25	0.25	-	-		
Hiatalia siliquens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	
Scolecopleides benhami	1.00	0.41	8.50	7.23	0.75	0.48	0.75	0.75	6.00	4.08	2.75	1.80	-	-	-	-	0.25	0.25	-	-	1.75	1.44	-	-	-	-	-	-	-	-	1.75	1.03	-	-	
Magelona dakini	-	-	0.25	0.25	-	-	0.25	0.25	-	-	-	-	0.50	0.50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Macomona liliana	0.50	0.29	0.25	0.25	2.00	0.91	0.50	0.29	2.00	0.41	1.50	0.65	-	-	-	-	0.75	0.48	4.75	1.44	-	-	-	1.25	0.48	-	-	5.50	3.57	-	-	5.75	3.47		
Melagraphia aethiops	-	-	-	-	0.75	0.48	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	4.00	1.08	13.25	1.97	0.50	0.50	0.25	0.25	3.25	1.25	1.50	0.87	0.50	0.50	
Waitangi brevirostris	-	-	0.25	0.25	0.75	0.48	0.25	0.25	0.25	0.25	-	-	-	-	-	-	1.25	0.75	-	-	-	-	-	1.25	0.63	1.50	0.65	-	-	-	-	-	-		
Marginella sp.	-	-	-	-	-	-	-	-	0.50	0.50	0.25	0.25	-	-	-	-	3.25	1.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Trochodonta dendyi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Xymene plebeius	-	-	-	-	-	0.25	0.25	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	
Chamaesipho columna	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Perna canaliculus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Theora lubrica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Diloma substrata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Nemertean	1.75	1.11	0.75	0.75	-	-	0.25	0.25	5.50	2.33	1.25	0.75	-	-	-	-	1.25	0.25	1.00	0.58	1.00	0.71	-	-	-	-	-	-	-	-	-	-	0.50	0.29	
Nereid sp.	-	-	-	-	-	-	-	-	0.75	0.48	-	-	-	-	-	-	0.50	0.29	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Orbinia papillosa	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	1.75	1.18	0.25	0.25	-	-	-	-	-	-	-	-	-	
Ischnochiton maorianus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.50	0.29	1.25	0.75	1.00	0.58	-	-	-	-	-	
Peridimeneus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.75	0.48	
Rissoia chathamensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	
Upogebia hirtifrons	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.00	0.71	
Paracallioppe novaezealandiae	-	-	-	-	-	0.50	0.50	-	0.75	0.48	-	-	-	-	-	-	32.25	17.09	0.50	0.29	-	-	-	-	0.50	0.50	-	-	-	-	-	-	0.25	0.25	
Haminoea zelandiae	-	-	-	-	-	-	-	-	2.00	0.41	0.50	0.50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.50	1.85
Notoacmea helmsi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Nucula hartvigiana	1.50	0.96	4.50	2.18	27.25	5.31	0.75	0.25	44.75	12.74	1.50	0.65	-	-	-	-	15.75	7.65	2.50	1.50	-	-	-	1.50	1.50	1.00	0.58	3.25	1.60	-	-	-	-	5.00	1.87
Hesionidae sp.	0.25	0.25	-	-	-	-	-	-	2.25	0.85	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	0.25	0.25	
Notoacmea scapha	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	
Turbo smaragdus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.00	2.86	
Pectinaria australis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.50	0.29	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	1.00	0.58	
Edwardsia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.50	0.50	
Austrovenus stutchburyi	6.75	6.75	-	-	25.50	7.90	0.25	0.25	-	-	-	-	-	-	-	-	0.75	0.48	0.25	0.25	-	-	-	2.25	1.60	-	-	14.00	4.02	2.50	0.65	12.00	4.97		
Travisia olens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.50	0.50	-	-	-	-	0.50	0.50	-	-	-	-	-	-	1.50	1.50		
Cirratulid sp.	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Owenia fusiformis	-	-	-	-	0.25	0.25	-	-	4.75	1.97	0.25	0.25	-	-	-	-	0.75	0.75	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	
Cominella adpersa	-	-	-	-	-	0.25	0.25	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Ruditapes largillierii	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Divaricella huttoniana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Patiriella regularis	0.75	0.75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Colurostylis lemurum	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Aonides sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9.50	8.22	0.75	0.75	-	-	-	-	-	-	-	-	1.00	0.71	0.25	0.25	-	1.00	
Chiton glaucus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Exogonid sp.	0.25	0.25	-	-	-	-	-	-	0.25	0.25	0.50	0.29	-	-	-	-	-	-	-	-	-	-	-	0.50	0.50	-	-	-	-	-	-	-	-	0.50	0.50
Exosphaeroma 'thin uropods'	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Caraziella sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Cirolanidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Epitonium jukesiana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Hyboscolex sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Pseudopolydora #91 (modified 2)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Squilla armata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Xenostrobus pulex	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Elminius modestus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Paphies australis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7.00	5.74	
Phoxocephalidae	-	-	2.00	1.22	-	-	-	-	3.00	1.78	0.50	0.29	-	-	-	-	0.25	0.25	-	-	0.25	0.25	-	0.50	0.29	-	-	-	0.25	0.25	-	-	2.50	1.32	
Eatoniella sp.	-	-	3.25	2.93	-	-	-	-	0.75	0.75	-	-	-	-	-	-	36.50	19.78	12.50	12.50	-	-	-	-	-	-	-	-	-	-	-	-	-	2.75	0.85
Soletellina siliquens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Crab larvae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Platynereis australis	0.50	0.50	-	-	0.50	0.50	-	-	2.75	1.31	-																								

North Island locations continued...

[illegible]

South Island locations

Location	Farewell Spit				Whanganui In				Waikawa				Kaikoura				Bluff Harbour			
Position	Upper		Lower														Upper		Lower	
Site	Intertidal		Intertidal		Intertidal		Intertidal		Subtidal		Intertidal		Intertidal		Intertidal		Intertidal		Subtidal	
Habitat	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare
Amphiura aster	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amphiura rosea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anatides sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aplysia dactylomela	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ascidian sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ball anemone	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cylaspis thomsoni	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cymothoidae sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Duplicaria tristis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eteone sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eunicid sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hemigrapsis crenulatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hippolyte bifidirostris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mactra ovata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Marphysa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Microcosmus kura	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nereis pereneis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Olividae sp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paphies sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paranthura flagellata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phenatoma rosea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Prionospio aucklandica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spionid sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stylochopiana sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Turbonilla zelandica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tharyx sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Wandering sea anemone	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chaetopteridae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Balanoglossus australiensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bulla quoyii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Branchiomma sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Timarete anchylochaeta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Marginella pygmaea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Notomithrax sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amalda mucronata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amalda australis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pelogenia antipoda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Estea zosterophila	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Onuphis eremita	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euclymene sp. B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Barnacle cyprid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Syllid sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Palaemon affinis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Neanthes sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eatoniella limbata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Barnea similis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cirsotrema zelebori	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dosinia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Isocladus armatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maoricolpus sp. A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nebalia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Neoguraleus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Neosabellaria kauparensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nerita atramentosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ovalipes catharus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rissoina sp. A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rissoina sp. B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

South Island locations continued...

Location	Farewell Spit				Whanganui In				Waikawa				Kaikoura				Bluff Harbour			
Position	Upper		Lower		Intertidal		Subtidal		Intertidal		Subtidal		Intertidal		Subtidal		Upper		Lower	
Site	Intertidal		Intertidal		Intertidal		Subtidal		Intertidal		Subtidal		Intertidal		Subtidal		Intertidal		Subtidal	
Habitat	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare
Trochidae sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Zegalerus tenuis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Zegalerus tenuis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Zenatia acinaces	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paradexamine sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Asychis amphiglyptus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amphicteis-A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Myadora striata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cirolana aff woodjonesi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ophiuroid sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tubificidae sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pagurus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tanaid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caprellina longicollis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Armandia maculata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bursatella leachii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tenagomysis n.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Solemya parkinsoni	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Felaniella zelandica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maldanidae sp. A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Torridoharpinia hurleyi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bivalve sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maoricolpus roseus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-
Aora sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Egg case	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dendrostoma aeneum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Zethalia zelandica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spirorbis sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Musculista senhousia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scolecopsis antipoda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Erichthonius pugnax	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Callianassa filholi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Echinoidea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ozius truncatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paracorophium sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Perinereis novaehollandiae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phoronida	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Polydora sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sabellid sp. A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trochodota sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trochus viridus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Xymene ambiguous	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Corophium sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Halicarcinus whitei	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Peramphithoe aorangi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Boccardia syrtis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cossura consimilis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euclymene aucklandica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Glycera americana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Halicarcinus cooki	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Goniada emerita	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aonides oxycephala	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Notomastus tenuis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sipunculus maoricus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aora typica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

South Island locations continued...

Location	Farewell Spit								Whanganui In				Waikawa				Kaikoura				Bluff Harbour				Lower			
Position	Upper																				Upper				Subtidal			
Site	Intertidal								Intertidal				Subtidal				Intertidal				Intertidal							
Habitat	Seagrass		Bare		Seagrass		Bare		Seagrass		Bare		Seagrass		Bare		Seagrass		Bare		Seagrass		Bare		Seagrass		Bare	
Nereis falcaria	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alpheus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hiatula siliquens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scolecopides benhami	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.50	0.50	-	-	-	-	-	-	0.50	0.50	-	-
Magelona dakini	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.50	0.50	-	-	-	-	-	-	-	-	-	-
Macomona liliana	-	-	-	-	-	-	-	-	0.50	0.50	-	-	1.25	0.63	0.75	0.25	-	-	-	-	0.25	0.25	-	-	-	-	-	-
Melagraphia aethiops	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Waitangi brevirostris	-	-	0.75	0.48	0.50	0.50	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Marginella sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-
Trochodonta dendyl	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Xymene plebeius	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chamaesipho columna	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Perna canaliculus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Theora lubrica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diloma subrostrata	0.75	0.25	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nemertean	0.25	0.25	-	-	-	0.25	0.25	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	0.25	0.25	1.00	1.00	-	-	-	-
Nereid sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	0.25	0.25	-	-
Orbinia papillosa	-	-	-	-	-	-	-	-	1.50	0.96	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-
Ischnochiton maorianus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Periclimenaeus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rissonia chathamensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Upogebia hirtifrons	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paracallioppe novaezealandiae	17.50	6.33	-	-	4.50	1.66	10.50	6.40	3.75	2.25	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	1.00	0.71	-
Haminoea zelandiae	-	-	-	-	-	-	-	-	0.75	0.48	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Notoacmea helmsi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-
Nucula hartvigiana	0.50	0.29	-	-	16.25	3.47	24.75	9.96	31.25	9.58	2.25	1.31	0.75	0.48	-	-	0.25	0.25	-	-	-	-	-	-	-	1.00	1.00	-
Heslonidae sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.50	0.50	-	-	-	-	-	-	-	-	-
Notoacmea scapha	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-
Turbo smaragdus	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-
Pectinaria australis	-	-	-	-	-	-	-	-	0.25	0.25	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Edwardsia sp.	-	-	-	-	-	-	-	-	0.75	0.48	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Austrovenus stutchburyi	12.00	1.78	-	-	25.50	4.17	5.50	1.44	27.50	2.75	23.25	6.75	1.25	0.75	1.00	0.41	0.50	0.50	-	-	0.25	0.25	0.50	0.29	0.25	0.25	-	-
Travisia olens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.50	0.29	-	-	0.25	0.25	-
Cirratulid sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-
Owenia fusiformis	0.25	0.25	-	-	4.00	1.08	32.00	20.48	1.25	0.63	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cominella adpersa	-	-	-	-	-	0.25	0.25	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ruditapes largillierti	-	-	-	-	-	-	-	-	0.50	0.29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Divaricella huttoniana	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Patriella regularis	-	-	-	-	0.50	0.50	-	-	0.50	0.29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Colurostylis lemurum	8.25	2.29	-	-	-	-	13.75	10.50	-	-	0.50	0.50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aonides sp.	0.25	0.25	-	-	1.00	0.71	-	-	-	-	-	-	-	-	-	-	1.25	0.75	-	-	-	-	-	-	1.00	0.58	1.25	0.63
Chiton glaucus	-	-	-	-	0.75	0.48	0.25	0.25	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Exogonid sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-
Exosphaeroma 'thin uropods'	10.75	4.50	0.50	0.50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caraziella sp.	0.50	0.50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cirolanidae	-	-	0.50	0.50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epitonium jukesiana	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hyboscolex sp.	-	-	-	-	2.25	0.75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pseudopolydora #91 (modified 2r)	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Squilla armata	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Xenostrobus pulex	-	-	-	-	2.50	0.96	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Elminius modestus	-	-	-	-	4.25	3.07	-	-	-	12.50	7.77	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paphies australis	7.00	3.03	12.50	8.92	1.00	0.71	0.50	0.50	-	7.50	4.11	0.75	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phoxocephalidae	-	-	-	-	0.50	0.50	0.25	0.25	-	0.50	0.29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.00	1.35	-
Eatonella sp.	14.75	3.42	-	-	16.50	8.51	-	-	54.50	15.60	-	-	-	-	-	-	1.75	1.44	-	-	7.50	3.93	-	-	-	-	-	-
Soletellina siliquens	-	-	0.25	0.25	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Crab larvae	-	-	-	-	-	-	0.25	0.25	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Platynereis australis	-	-	-	-	-	-	0.25	0.25	-	-	-	-	4.25	1.03	0.75	0.48	-	-	-	-	0.75	0.48	-	-	-	0.25	0.25	-

South Island locations continued...

Location	Farewell Spit						Whanganui In				Waikawa				Kaikoura				Bluff Harbour			
Position	Upper			Lower																		
Site	Intertidal			Intertidal			Seagrass			Subtidal			Intertidal			Upper Intertidal			Lower Subtidal			
Habitat	Seagrass	Bare		Seagrass	Bare		Seagrass	Bare		Seagrass	Bare		Seagrass	Bare		Seagrass	Bare		Seagrass	Bare		
Sypharochiton pelliserpentis	-	-	-	-	-	-	0.50	0.50	-	-	-	-	-	-	-	-	-	-	0.50	0.50	-	
Arthrithica bifurca	-	-	-	1.75	1.18	-	10.75	4.85	-	1.25	0.75	0.50	0.50	-	-	-	-	0.50	0.50	-	-	
Macrophthalmus hirtipes	-	-	-	-	-	-	-	-	-	1.25	0.63	-	-	-	-	-	-	-	-	-	-	
Gammarid sp.	-	-	-	-	-	-	-	-	-	1.25	0.48	-	-	0.25	0.25	-	-	0.25	0.25	-	-	
Ceallana radians	1.00	0.71	-	1.00	0.71	-	-	-	-	1.00	0.58	-	0.25	0.25	2.25	1.44	-	0.50	0.29	-	1.75	
Ostracod	-	-	-	0.25	0.25	-	-	-	-	-	-	-	1.25	0.48	-	-	6.50	5.25	0.50	0.29	0.25	
Helice crassa	-	-	-	0.25	0.25	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	-	1.25	
Aquillaspio auklandica	-	-	-	14.50	9.13	11.25	7.93	9.25	4.09	-	-	35.25	11.80	1.25	0.95	0.75	0.48	-	-	-	0.50	
Glycera sp.	-	1.00	0.71	-	-	-	-	-	-	-	-	0.25	0.25	1.00	1.00	-	-	-	-	-	4.50	
Aglaophamus macrousa	-	-	-	-	-	-	-	-	-	-	-	1.50	0.50	0.75	0.75	-	-	0.50	0.29	-	0.25	
Cominella glandiformis	0.75	0.75	-	2.50	0.87	2.00	2.00	0.75	0.48	-	-	1.00	0.41	-	-	9.25	2.14	-	-	-	0.25	
Cominella maculosa	0.25	0.25	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	0.25	0.25	0.25	0.25	-	1.00	
Corophidae	16.00	13.08	-	-	-	-	-	-	-	-	-	-	-	-	-	0.75	0.75	13.00	11.70	-	0.25	
Perinereis nuntia	1.25	0.95	-	0.25	0.25	0.25	0.25	2.75	1.70	3.75	1.75	-	-	-	-	3.75	1.11	-	-	-	1.00	
Neanthes criognatha	0.75	0.75	-	-	-	-	-	3.25	1.97	-	-	-	-	-	-	-	-	-	-	-	1.00	
Heteromastus filiformis	0.25	0.25	0.25	0.25	0.75	0.75	1.25	1.25	0.75	0.75	0.25	0.25	11.75	2.63	9.50	0.96	2.25	1.93	1.50	1.50	1.75	
Isocladus armatus	3.50	3.50	-	6.00	2.68	-	-	-	-	-	-	-	-	-	-	0.50	0.50	-	-	-	1.11	
Unidentified Bivalve (no shell)	0.50	0.50	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	0.25	
Oligochaeta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	
Holothuroidea	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	
Paracalliopae sp.	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	
Exosphaeroma sp.	0.50	0.29	0.50	0.50	0.25	0.25	0.50	0.75	0.25	1.25	0.95	-	-	0.50	0.50	6.00	6.00	0.50	0.50	-	0.50	
Zeeumantius lutulentus	-	-	-	14.50	5.68	0.25	0.25	2.75	0.95	-	-	-	-	-	-	51.00	21.67	-	-	-	0.29	
Hallarcinus spp.	1.00	1.00	-	4.25	1.11	0.25	0.25	1.50	0.87	-	-	3.00	1.47	-	-	3.00	1.35	-	-	-	3.75	
Anthopleura aureoradiata	4.75	1.44	-	5.50	3.01	-	-	-	-	0.75	0.48	0.25	0.25	1.25	0.95	12.75	2.84	24.75	16.98	1.00	0.58	
Scoloplos cylindrifrer	-	-	-	-	-	-	-	-	-	-	-	1.00	0.71	-	-	14.75	2.39	2.25	1.31	-	0.63	
Lumbrineridae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.75	0.75	0.25	0.25	-	1.00	
Pontophilus australis	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	0.25	
Turbonilla sp.	-	-	-	-	-	-	0.25	0.25	-	-	-	-	0.25	0.25	-	-	1.50	0.65	0.25	0.25	0.25	
Aora maculata	-	-	-	-	-	-	0.25	0.25	-	-	-	4.00	1.68	0.50	0.29	10.00	6.84	-	-	0.25	0.25	
Macropdymenella stewartensis	-	-	-	-	-	-	-	-	1.00	0.58	-	2.00	1.68	1.25	0.63	-	-	0.50	0.50	-	3.25	
Capitella sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	1.25	0.75	-	2.02	
Abarenicola sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	1.25	0.75	-	0.75	
Amphiliuridae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.75	2.06	7.25	5.44	-	8.25	
Boccardia otakouica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	6.00	
Chaetozone sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	106.75	54.90	-	-	-	5.33	
Diloma zelandica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	
Insect larvae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.25	1.25	-	-	-	-	
Merelina sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.75	0.75	-	-	-	
Polydorid #3 (horned, 3rd chaetig	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	
Prototheca crassica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	
Terebellidae sp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.75	1.18	-	-	-	-	
Boccardia acus	0.50	0.50	-	2.00	1.41	-	0.50	0.29	0.25	0.25	0.25	2.50	1.89	3.50	3.18	107.00	52.07	19.00	6.75	4.25	4.50	
Micrelenehus tenebrosus	4.00	0.91	-	17.75	7.04	0.25	0.25	-	-	-	-	67.00	13.58	2.50	1.85	-	-	3.00	3.00	100.50	9.51	
Lysianassidae	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	6.00	3.24	-	-	1.25	
Terebellidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.63	
Anthuridae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	
Spionidae (Lindispio?)	-	-	-	-	-	-	0.50	0.50	-	-	-	0.50	0.29	-	-	0.25	0.25	-	-	-	1.25	
Paridotea unglata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	0.95	
Pycnogonida	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	0.25	0.25	
Thelepus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.50	0.50	0.50	0.50	-	-	
Notomastus sp.	-	-	-	-	-	-	1.25	0.75	-	-	-	-	-	-	-	-	-	-	-	1.00	5.50	
Nematoda	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-	-	1.00	2.10	
Aricidea sp.	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	-	-	-	-	-	-	1.75	0.48	
Hippolyte sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	
Lepidastheniella comma	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	11.00	5.21	3.00	1.35	
Nectocarcinus bennetti	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.25	0.48	-	-	-	1.00	
Nereis sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	
Odostomia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	
Ostrea chilensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.25	1.25	-	0.75	
Scolecipis sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.50	1.19	1.75	1.44	
Scoloplos ohlini	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.25	
Sigapattella novaezelandiae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.00	0.71	-	1.50	
Tawera spissa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	

10.4 Appendix 4: Infaunal invertebrate community composition – PERMANOVA pairwise test

Species Analysis

(A) Habitat variation between islands (by species)

Table A4.1: Results of pairwise tests for differences in infaunal invertebrate community composition (by species) for each specific habitat type, between the North and South Islands. P(perm) values which are significant are shown in bold.

Habitat	Position	Groups	<i>Zostera muelleri</i>	<i>Zostera muelleri</i>
SI	Upper	N, S	2.2319	0.006
BI	Upper	N, S	2.1136	0.004
SS	Lower	N, S	3.3537	0.001
BS	Lower	N, S	2.1358	0.001
SI	Lower	N, S	2.4579	0.001
BI	Lower	N, S	1.8681	0.001

(B) Habitat variation within islands (by species)

Table A4.2: Results of pairwise tests for differences in infaunal invertebrate community composition (by species), for each specific habitat type, within either the North or South Island. * denotes that Monte Carlo simulations were used to obtain more permutations where the original comparison returned fewer than 100 permutations. P(perm) values which are significant are shown in bold.

Island	Position	Groups	t	P(perm)
North	Upper	SS, BS	1.3058	0.168*
		SS, SI	1.9792	0.017*
		SS, BI	2.1556	0.008*
		BS, SI	1.8622	0.017*
		BS, BI	1.9636	0.023*
		SI, BI	1.8898	0.037*
North	Lower	SS, BS	1.8374	0.001
		SS, SI	2.4873	0.001
		SS, BI	2.6135	0.001
		BS, SI	2.0751	0.001
		BS, BI	1.8492	0.001
		SI, BI	1.7042	0.001
South	Upper	SI, BI	2.0246	0.001
South	Lower	SS, BS	1.5777	0.005
		SS, SI	2.8468	0.001
		SS, BI	2.4878	0.001
		BS, SI	2.4064	0.001
		BS, BI	1.7004	0.002
		SI, BI	1.8192	0.004

(C) Habitat variation across locations (by species)

Table A4.3: Results of pairwise tests for differences in infaunal invertebrate community composition (by species), for each specific habitat type, between all location combinations. * denotes that Monte Carlo simulations were used to obtain more permutations where the original comparison returned fewer than 100 permutations. P(perm) values which are significant are shown in bold.

Habitat	Position	Groups	t	P(perm)
SI	Upper	BLUF, FWSP	2.8692	0.004*
		BLUF, KAIP	2.7488	0.003*
		FWSP, KAIP	2.7003	0.002*
SS	Lower	BISL, BLUF	4.0574	0.001*
		BISL, KAIP	2.3997	0.006*
		BISL, RUNU	2.5099	0.009*
		BISL, WAKW	3.9538	0.001*
		BLUF, KAIP	3.0778	0.002*
		BLUF, RUNU	3.7315	0.002*
		BLUF, WAKW	2.7799	0.004*
		KAIP, RUNU	1.8472	0.020*
		KAIP, WAKW	3.0554	0.002*
		RUNU, WAKW	3.5968	0.001*
SI	Lower	FWSP, GISB	2.9400	0.006*
		FWSP, KAIK	3.1875	0.001*
		FWSP, KAIP	2.7762	0.004*
		FWSP, KAWH	2.6182	0.005*
		FWSP, RUNU	2.4200	0.004*
		FWSP, TAIR	3.5032	0.004*
		FWSP, WNUI	2.1379	0.011*
		GISB, KAIK	2.9465	0.004*
		GISB, KAIP	2.3677	0.006*
		GISB, KAWH	2.4307	0.006*
		GISB, RUNU	2.3253	0.009*
		GISB, TAIR	3.3987	0.001*
		GISB, WNUI	2.7289	0.002*
		KAIK, KAIP	2.7499	0.003*
		KAIK, KAWH	2.8901	0.003*
		KAIK, RUNU	2.7336	0.002*
		KAIK, TAIR	3.5462	0.001*
		KAIK, WNUI	3.3076	0.002*
		KAIP, KAWH	1.4831	0.078*
		KAIP, RUNU	1.9413	0.011*
		KAIP, TAIR	2.2637	0.006*
		KAIP, WNUI	2.4952	0.003*
		KAWH, RUNU	1.4819	0.068*
		KAWH, TAIR	1.7930	0.034*
		KAWH, WNUI	2.3305	0.009*
		RUNU, TAIR	2.0553	0.010*
		RUNU, WNUI	2.2091	0.005*
		TAIR, WNUI	3.0492	0.001*
BI	Upper	BLUF, FWSP	2.5850	0.004*
		BLUF, KAIP	2.7421	0.003*
		FWSP, KAIP	2.9991	0.002*

BS	Lower	BISL, BLUF	2.2239	0.007*
		BISL, KAIP	1.8424	0.015*
		BISL, RUNU	1.6711	0.053*
		BISL, WAKW	2.5433	0.003*
		BLUF, KAIP	2.0796	0.019*
		BLUF, RUNU	1.6604	0.037*
		BLUF, WAKW	1.6818	0.047*
		KAIP, RUNU	1.7233	0.042*
		KAIP, WAKW	2.1989	0.008*
		RUNU, WAKW	1.7670	0.034*
BI	Lower	FWSP, KAIK	3.1216	0.001*
		FWSP, KAIP	2.9931	0.003*
		FWSP, KAWH	1.8304	0.035*
		FWSP, RUNU	2.0692	0.011*
		FWSP, TAIR	2.6406	0.008*
		FWSP, WNUI	2.2983	0.009*
		KAIK, KAIP	2.7235	0.001*
		KAIK, KAWH	2.1630	0.015*
		KAIK, RUNU	2.0608	0.014*
		KAIK, TAIR	2.8094	0.003*
		KAIK, WNUI	2.3855	0.007*
		KAIP, KAWH	1.8217	0.036*
		KAIP, RUNU	1.6593	0.050*
		KAIP, TAIR	2.2580	0.012*
		KAIP, WNUI	2.5700	0.006*
		KAWH, RUNU	1.5537	0.069*
		KAWH, TAIR	1.6043	0.064*
		KAWH, WNUI	1.4208	0.127*
		RUNU, TAIR	1.9710	0.020*
		RUNU, WNUI	1.8890	0.025*
		TAIR, WNUI	1.9916	0.025*

(D) Habitat variation within locations (by species)

Table A4.4: Results of pairwise tests for differences in infaunal invertebrate community composition (by species), for each specific habitat type combination, within each location. * denotes that Monte Carlo simulations were used to obtain more permutations where the original comparison returned fewer than 100 permutations. P(perm) values which are significant are shown in bold.

Location	Position	Groups	t	P(perm)
Rangaunu	Upper	SS, BS	1.3058	0.152*
Rangaunu	Lower	SS, BS	1.7692	0.025*
		SS, SI	2.2291	0.008*
		SS, BI	2.0432	0.011*
		BS, SI	1.6449	0.041*
		BS, BI	1.0897	0.338*
		SI, BI	1.5901	0.058*
Bay of Islands	Lower	SS, BS	1.9916	0.020*
Kaipara	Upper	SI, BI	1.8898	0.023*
Kaipara	Lower	SS, BS	1.8668	0.025*
		SS, SI	1.9712	0.016*
		SS, BI	2.1580	0.007*
		BS, SI	1.8425	0.012*
		BS, BI	1.8849	0.031*
		SI, BI	1.7702	0.029*
Tairua	Lower	SI, BI	2.4333	0.002*
Kawhia	Lower	SI, BI	1.4880	0.093*
Farewell Spit	Upper	SI, BI	2.8107	0.002*
Farewell Spit	Lower	SI, BI	2.5711	0.006*
Whanganui Inlet	Lower	SI, BI	2.4558	0.007*
Kaikoura	Lower	SI, BI	2.2096	0.008*
Waikawa	Lower	SS, BS	1.7277	0.035*
Bluff	Upper	SI, BI	2.1234	0.012*
Bluff	Lower	SS, BS	1.8189	0.037*

Analysis by class group

(A) Habitat variation between islands (by class group)

Table A4.5: Results of pairwise tests for differences in infaunal invertebrate community composition (by class group) for each specific habitat type, between the North and South Islands. P(perm) values which are significant are shown in bold.

Habitat	Position	Groups	t	P(perm)
SI	Upper	N, S	1.7894	0.022
BI	Upper	N, S	1.8696	0.015
SS	Lower	N, S	2.9503	0.001
BS	Lower	N, S	1.2578	0.001
SI	Lower	N, S	2.8160	0.001
BI	Lower	N, S	1.9392	0.002

(B) Habitat variation within islands (by class group)

Table A4.6: Results of pairwise tests for differences in infaunal invertebrate community composition (by class group), for each specific habitat type, within either the North or South Island. * denotes that Monte Carlo simulations were used to obtain more permutations where the original comparison returned fewer than 100 permutations. P(permutation) values which are significant are shown in bold.

Island	Position	Groups	t	P(permutation)
North	Upper	SS, BS	1.0026	0.429*
		SS, SI	1.2814	0.183*
		SS, BI	1.7690	0.053*
		BS, SI	1.2238	0.246*
		BS, BI	1.4511	0.127*
		SI, BI	2.0929	0.030*
North	Lower	SS, BS	2.6163	0.001
		SS, SI	2.9618	0.001
		SS, BI	3.3527	0.001
		BS, SI	2.0642	0.003
		BS, BI	1.2456	0.177
		SI, BI	2.1336	0.002
South	Upper	SI, BI	2.6996	0.001
South	Lower	SS, BS	2.3312	0.001
		SS, SI	2.5482	0.001
		SS, BI	1.6077	0.042
		BS, SI	2.8086	0.001
		BS, BI	1.2290	0.220
		SI, BI	1.1122	0.297

(C) Habitat variation across locations (by class group)

Table A4.7: Results of pairwise tests for differences in infaunal invertebrate community composition (by class group), for each specific habitat type, between all location combinations. * denotes that Monte Carlo simulations were used to obtain more permutations where the original comparison returned fewer than 100 permutations. P(perm) values which are significant are shown in bold. Negative = a negative sum of squares, which means this value can't be reliably calculated.

Habitat	Position	Groups	t	P(perm)
SI	Upper	BLUF, FWSP	3.8801	0.002*
		BLUF, KAIP	2.4822	0.022*
		FWSP, KAIP	2.0161	0.031*
SS	Lower	BISL, BLUF	3.0594	0.005*
		BISL, KAIP	2.2518	0.016*
		BISL, RUNU	3.8371	0.003*
		BISL, WAKW	2.6668	0.013*
		BLUF, KAIP	3.2189	0.006*
		BLUF, RUNU	5.6593	0.002*
		BLUF, WAKW	2.5408	0.022*
		KAIP, RUNU	2.8321	0.003*
		KAIP, WAKW	2.7483	0.007*
		RUNU, WAKW	4.2995	0.001*
SI	Lower	FWSP, GISB	1.5769	0.112*
		FWSP, KAIK	2.3228	0.015*
		FWSP, KAIP	2.8459	0.004*
		FWSP, KAWH	1.9468	0.029*
		FWSP, RUNU	1.7839	0.040*
		FWSP, TAIR	2.4169	0.013*
		FWSP, WNUI	0.8858	0.487*
		GISB, KAIK	2.4474	0.018*
		GISB, KAIP	2.1011	0.018*
		GISB, KAWH	1.5556	0.086*
		GISB, RUNU	1.4759	0.145*
		GISB, TAIR	2.0969	0.026*
		GISB, WNUI	1.9526	0.035*
		KAIK, KAIP	3.7878	0.001*
		KAIK, KAWH	3.0223	0.006*
		KAIK, RUNU	2.8253	0.005*
		KAIK, TAIR	3.2869	0.001*
		KAIK, WNUI	3.5371	0.002*
		KAIP, KAWH	1.1714	0.235*
		KAIP, RUNU	1.9531	0.047*
		KAIP, TAIR	2.0268	0.021*
		KAIP, WNUI	2.8936	0.006*
		KAWH, RUNU	1.3993	0.047*
		KAWH, TAIR	1.3709	0.164*
		KAWH, WNUI	2.0028	0.012*
		RUNU, TAIR	1.9458	0.029*
		RUNU, WNUI	1.8005	0.040*
		TAIR, WNUI	2.7382	0.003*
BI	Upper	BLUF, FWSP	2.9503	0.005*
		BLUF, KAIP	2.3759	0.015*

		FWSP, KAIP	2.9503	0.005*
BS	Lower	BISL, BLUF	1.2266	0.266*
		BISL, KAIP	0.8946	0.494*
		BISL, RUNU	1.0758	0.356*
		BISL, WAKW	0.9161	0.495*
		BLUF, KAIP	1.3439	0.189*
		BLUF, RUNU	1.3636	0.175*
		BLUF, WAKW	0.8757	0.517*
		KAIP, RUNU	1.5965	1.010*
		KAIP, WAKW	1.2109	0.264*
		RUNU, WAKW	0.6546	0.728*
BI	Lower	FWSP, KAIK	2.6491	0.007*
		FWSP, KAIP	1.5479	0.084*
		FWSP, KAWH	1.3345	0.203*
		FWSP, RUNU	2.3987	0.020*
		FWSP, TAIR	2.1986	0.028*
		FWSP, WNUI	1.6016	0.102*
		KAIK, KAIP	3.5658	0.005*
		KAIK, KAWH	2.2433	0.013*
		KAIK, RUNU	2.9009	0.005*
		KAIK, TAIR	4.1311	0.002*
		KAIK, WNUI	3.0253	0.003*
		KAIP, KAWH	1.6856	0.087*
		KAIP, RUNU	2.5533	0.008*
		KAIP, TAIR	1.7325	0.059*
		KAIP, WNUI	2.0643	0.042*
		KAWH, RUNU	1.7079	0.070*
		KAWH, TAIR	2.0624	0.068*
		KAWH, WNUI	Negative	
		RUNU, TAIR	2.7742	0.011*
		RUNU, WNUI	2.1774	0.035*
		TAIR, WNUI	2.6625	0.020*

(D) Habitat variation within locations (by class group)

Table A4.8: Results of pairwise tests for differences in infaunal invertebrate community composition (by class group), for each specific habitat combination, within each location. * denotes that Monte Carlo simulations were used to obtain more permutations where the original comparison returned fewer than 100 permutations. P(perm) values which are significant are shown in bold.

Location	Position	Groups	t	P(perm)
Rangaunu	Upper	SS, BS	1.0026	0.41*
Rangaunu	Lower	SS, BS	3.0408	0.003*
		SS, SI	2.4247	0.005*
		SS, BI	4.0573	0.002*
		BS, SI	1.8587	0.038*
		BS, BI	1.6744	0.071*
		SI, BI	2.2702	0.013*
Bay of Islands	Lower	SS, BS	1.7754	0.074*
Kaipara	Upper	SI, BI	2.0929	0.025*
Kaipara	Lower	SS, BS	1.9663	0.056*
		SS, SI	1.6799	0.062*
		SS, BI	1.9141	0.053*
		BS, SI	2.0617	0.027*
		BS, BI	2.6811	0.009*
		SI, BI	1.1763	0.288*
Tairua	Lower	SI, BI	4.2858	0.002*
Kawhia	Lower	SI, BI	0.9518	0.442*
Farewell Spit	Upper	SI, BI	5.1160	0.003*
Farewell Spit	Lower	SI, BI	1.9287	0.034*
Whanganui Inlet	Lower	SI, BI	2.3750	0.015*
Kaikoura	Lower	SI, BI	1.4436	0.121*
Waikawa	Lower	SS, BS	1.8814	0.057*
Bluff	Upper	SI, BI	2.4916	0.025*
Bluff	Lower	SS, BS	1.8616	0.065*

10.5 Appendix 5: Species list of epifaunal invertebrates – New Zealand biogeographic seagrass survey (mean density per core ± s.e.).

North Island locations

Location	Rangauu Hbr								Bay of Islands				Kaipara Harbo								Tairua				Kawhia				Gisborne			
Position	Upper				Lower								Upper				Lower								Intertidal				Intertidal			
Site	Subtidal				Intertidal				Subtidal				Intertidal				Subtidal				Intertidal				Seagrass				Seagrass			
Habitat	Seagrass		Bare		Seagrass		Bare	Seagrass		Bare	Seagrass		Bare	Seagrass		Bare	Seagrass		Bare	Seagrass		Bare	Seagrass		Bare	Seagrass		Bare	Seagrass		Bare	
Styela sp.	145.00	18.48	21.67	19.17	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Petrolisthes novaezelandiae	-	-	-	-	-	1.25	1.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Astropecten polyacanthus	-	-	-	-	-	-	-	-	-	-	2.50	1.77	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Atrina zelandica	-	-	-	-	-	-	-	-	-	-	26.25	5.54	18.13	1.20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Cliona cellata	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Gastro 19	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Ovalipes catharus	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Pecten novaezelandiae	-	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Pinnotheres atrinocola	-	-	-	-	-	-	-	-	-	-	1.25	1.25	2.50	1.77	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Pupa affinis	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Wandering sea anemone	-	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Evechinus chloroticus	-	-	-	-	-	-	-	-	-	-	38.13	14.84	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.25	1.25	
Hydrozoa spp	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Ascidacea spp.	655.84	288.49	1.67	1.67	1.25	1.25	-	161.25	21.76	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coscinasterias muricata	18.75	5.54	-	-	0.63	0.63	6.25	1.25	0.72	-	7.50	1.77	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Myadora striata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Amalda australis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Musculista senhousia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Palaemon affinis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Paramithrax minor	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Pinnotheres spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	
Pyromaila tuberculata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Zethalia zelandica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.63	0.63	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	
Unknown Decapoda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Philine sp	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Notomithrax sp.	-	-	-	-	-	3.13	3.13	10.00	5.40	-	2.50	1.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cominella quoyana	-	-	-	-	-	-	-	8.13	4.72	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Peronaea gaimardi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Chamaesipho columna	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Pinnotheres novaezelandiae	-	-	-	-	-	-	-	-	-	-	0.63	0.63	3.75	3.75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Diloma sp	-	-	-	-	91.27	78.08	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Patriella regularis	21.25	2.39	15.00	6.61	13.75	7.25	15.63	21.88	11.79	3.13	0.63	11.25	11.25	13.13	6.95	1.25	0.72	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Haminoea zelandiae	-	-	-	-	7.50	4.45	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Helice crassa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hemigrapsus edwardsi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gastro 20	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Halicarcinus whitei	-	-	-	-	2.50	2.50	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cominella glandiformis	-	-	-	-	313.13	128.90	-	-	-	-	-	-	-	-	-	-	43.13	15.19	29.38	13.71	37.50	6.85	18.13	5.98	-	-	-	-	-	-	-	-
Cominella adspersa	1.25	1.25	11.67	7.95	8.75	2.39	0.63	101.88	11.34	-	3.13	2.37	-	-	-	0.63	0.63	-	-	0.63	0.63	1.88	1.20	2.50	-	6.25	2.39	-	-	-	-	-
Pagurus spp.	1.25	1.25	1.67	0.83	1.25	1.25	-	23.13	7.73	3.13	1.20	28.13	13.01	6.25	5.45	-	-	-	-	-	0.63	0.63	3.75	2.17	13.75	4.15	-	-	-	-	-	-
Ischnochiton maorianus	-	-	-	-	-	-	-	-	-	-	-	3.75	1.61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Zeacumantus lutulentus	-	-	-	-	11.88	9.43	-	-	-	0.63	0.63	-	-	-	-	-	4.38	2.13	38.75	10.83	60.63	21.25	53.75	11.20	-	-	-	-	-	-	-	-
Xymene plebeius	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-	-	4.38	1.88	0.63	0.63	0.63	0.63	-	-	-	-	-	-
Xenostrobus pulex	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anthopleura aureoradiata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nucula hartvigiana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-

North Islands locations continued...

Location	Rangaunu Hbr								Bay of Islands				Kaipara Harbo								Tairua				Kawhia				Gisborne			
Position	Upper				Lower								Upper				Lower															
Site	Subtidal				Intertidal				Subtidal				Intertidal				Intertidal				Intertidal				Intertidal				Intertidal			
Habitat	Seagrass				Bare				Seagrass				Seagrass				Seagrass				Seagrass				Seagrass				Seagrass			
Unident blob	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.88	1.20
Maoricrypta monoxyla	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.38	2.95
Austrominius modestus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Haliclona sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chiton glaucus	-	-	-	-	25.63	21.66	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Limpet sp 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Perna canaliculus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Epopella plicata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Haustorium haustorium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unident slug	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Notoacmaea spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Neogastropoda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leptochiton inquinatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Paphies australis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Porifera spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cominella maculosa	-	-	-	-	1.25	0.72	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hemigrapsus crenulatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dosina zelandica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Micrelenchus huttonii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Zeacumantus subcarinatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Petrolisthes elongatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Halicarcinus cookii	2.50	2.50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acanthochitona zelandica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lunella smaragdus	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Melagraphia aethiops	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cellana denticulata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cellana flava	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cellana radians	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sypharochiton pelliserpantis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Siphonaria australis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Halicarcinus varius	-	-	-	-	2.50	2.50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sigapatella novaezelandiae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Macropthalmus hirtipes	-	-	-	-	1.25	1.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maoricolpus roseus	1.25	1.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Saccostrea cucullata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ostrea chilensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chitonida	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Colonial ascidian	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nectocarcinus antarcticus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pontophilus australis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
UNI Cyanobacteria 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Xymene ambiguus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

South Island locations

Location	Farewell Spit					Whanganui Inl				Kaikoura				Waikawa				Bluff Harbour				Bluff Harbour			
Position	Upper		Lower			Intertidal				Intertidal				Subtidal				Upper		Lower					
Site	Intertidal		Intertidal			Seagrass		Bare		Seagrass		Bare		Seagrass		Bare		Intertidal		Subtidal		Bare			
Habitat	Seagrass		Seagrass			Seagrass		Bare		Seagrass		Bare		Seagrass		Bare		Seagrass		Seagrass		Bare			
Styela sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Petrolisthes novaezelandiae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Astropecten polycanthus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Atrina zelandica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Cliona cellata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Gastro 19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Ovalipes catharus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Pecten novaezelandiae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Pinnotheres atrinocola	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Pupa affinis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Wandering sea anemone	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Evechinus chloroticus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Hydrozoa spp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Ascidacea spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Coccinasterias muricata	-	-	-	-	-	1.25	0.72	-	-	-	-	-	-	-	-	-	-	21.25	18.83	-	-	-			
Myadora striata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Amalda australis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Musculista senhousia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Palaemon affinis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Paramithrax minor	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Pinnotheres spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Pyromaila tuberculata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Zethalia zelandica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Unknown Decapoda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Philine sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Notomithrax sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Cominella quoyana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-			
Peronaea gaimardi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Chamaesipho columna	-	-	-	-	26.88	26.88	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Pinnotheres novaezelandiae	1.25	1.25	0.63	0.63	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Diloma sp	0.63	0.63	6.88	5.24	0.63	0.63	0.63	0.63	178.07	51.81	-	-	7.50	-	8.13	6.49	26.88	13.13	16.88	7.39	63.75	25.85	-		
Patriella regularis	8.75	3.31	2.50	1.77	0.63	0.63	0.63	0.63	5.63	5.63	-	-	-	-	-	-	-	-	-	-	-	0.63			
Haminoea zelandiae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Helice crassa	0.63	0.63	1.25	0.72	-	-	-	-	3.13	2.37	3.13	1.57	-	-	-	-	-	-	-	-	-	-			
Hemigrapsus edwardsi	0.63	0.63	-	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	0.63	0.63	-	-			
Gastro 20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Halicarcinus whitei	-	-	0.63	0.63	-	-	-	-	-	1.88	0.63	-	-	-	-	-	0.63	0.63	-	-	-	-			
Cominella glandiformis	67.50	33.99	397.50	20.51	376.88	37.44	22.50	11.59	51.25	41.40	-	-	15.00	-	30.00	10.41	0.63	0.63	31.88	18.86	-	-			
Cominella adspersa	4.38	2.58	6.88	1.88	0.63	0.63	3.75	1.61	21.25	9.60	2.50	2.50	-	-	-	-	-	-	-	-	-	-			
Pagurus spp.	0.63	0.63	-	-	-	-	27.50	17.68	1.88	1.20	-	-	-	-	-	-	-	-	-	-	2.50	1.44			
Ischnochiton maorianus	-	-	0.63	0.63	1.88	1.20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.88	1.20			
Zeacumantus lutulentus	115.68	115.68	453.13	70.74	569.99	234.48	5.00	3.54	1.25	1.25	45.00	38.62	-	-	-	-	-	-	-	4.38	2.95	-			
Xymene plebeius	2.50	2.50	1.25	0.72	1.25	1.25	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-			
Xenostrobus pulex	456.78	429.52	15.00	11.04	5.00	2.70	-	-	12.50	5.10	-	-	-	-	-	-	-	-	-	-	-	-			
Anthopleura aureoradiata	5.00	2.89	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-			
Nucula hartvigiana	0.63	0.63	-	-	2.50	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Unident blob	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Maoricrypta monoxyla	-	-	-	-	-	-	5.63	5.63	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Austrominius modestus	13.75	12.93	33.75	31.30	7.50	4.45	-	-	1169.42	181.87	-	-	-	-	-	-	-	-	-	-	-	-			
Haliclona sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Chiton glaucus	5.63	4.00	53.75	11.66	4.38	0.63	18.13	4.83	1.88	1.88	0.63	0.63	-	-	-	0.63	0.63	-	5.00	2.70	5.00	0.63			
Limpet sp 4	-	-	-	-	-	-	-	-	58.75	40.12	-	-	-	-	-	-	-	-	-	1.88	1.88	-			
Perna canaliculus	5.00	2.04	3.75	2.17	11.25	4.84	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Epopella plicata	120.76	120.76	-	-	171.05	171.05	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Haustrum haustrorium	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-			
Unident slug	1.25	1.25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Notoacmaea spp.	-	-	-	-	-	-	-	-	53.13	34.06	3.75	3.75	-	-	-	-	4.38	2.77	-	-	-	-			
Neogastropoda	-	-	-	-	-	-	-	-	-	-	-	-	-	1.25	1.25	-	-	-	-	-	-	-			
Leptochiton inquinatus	-	-	-	-	-	-	6.88	3.29	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Paphies australis	-	-	-	-	-	-	-	-	1.88	1.88	-	-	-	-	-	-	-	-	-	-	-	-			
Porifera spp.	0.63	0.63	2.50	1.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.25	0.72	5.00	1.02			
Cominella maculosa	-	-	-	-	-	-	4.38	2.58	-	-	1.88	1.88	20.00	-	-	-	-	-	-	-	-	-			
Hemigrapsus crenulatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.25	1.25	-	-			
Dosina zelandica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Micrelenchus huttonii	55.63	22.18	40.63	16.28	0.63	0.63	-	-	25.00	8.48	-	-	-	-	466.67	60.27	493.04	78.60	454.30	230.86	11.25	6.50			
Zeacumantus subcarinatus	-	-	-	-	-	-	-	-	-	-	-	-	255.00	-	-	-	-	-	-	-	61.25	16.02			
Petrolisthes elongatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.63	0.63	4.38			
Halicarcinus cookii	2.50	1.02	3.75	1.61	1.88	1.88	-	-	-	-	-	-	-	-	5.00	2.28	7.50	5.86	-	-	-	2.95			
Acanthochitona zelandica	1.25	1.25	4.38	2.58	-	-	6.88	3.44	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-	1.77			
Lunella smaragdus	-	-	53.13	21.17	2.50	1.02	-	-	1.25	0.72	1.88	1.20	7.50	-	-	-	-	-	13.13	10.77	280.63	36.32			
Melagraphia aethiops	-	-	-	-	-	-	-	-	-	-	216.88	51.88	-	-	-	-	-	-	-	-	-	8.68			
Cellana denticulata	-	-	-	-	-	-	-	-	-	-	195.37	144.73	-	-	-	-	-	-	-	3.13	2.37	-			
Cellana flava	-	-	-	-	-	-	-	-	-	-	1.88	1.88	-	-	-	-	-	-	-	-	-	-			
Cellana radians	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-			
Sypharochiton pelliserpentis	-	-	-	-	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-			
Siphonaria australis	-	-	-	-	-	-	-	-	-	-	109.38	29.23	-	-	-	-	-	-	-	0.63	0.63	-			
Halicarcinus varius	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	1.88	1.20	0.63	0.63	5.00	2.28	-	6.88			
Sigapatella novaezelandiae	-	-	-	-	-	-	3.75	2.17	-	-	-	-	-	-	-	-	-	-	-	13.75	9.44	1.25			
Macrophthalmus hirtipes	-	-	1.25	0.72	-	-	-	-	-	-	-	-	-	-	0.63	0.63	1.88	1.20	5.00	2.04	-	48.13			
Maoricolpus roseus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.25	3.89	0.63	0.63			
Saccostrea cucullata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.25	1.25	-	-	0.63	0.63	146.88	34.38			
Ostrea chilensis	-	-	-	-	-	-	0.63	0.63	-	-	-	-	-	-	-	-	-	-	14.38	8.13	170.63	146.69			
Chitonida	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18.75			
Colonial ascidian	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8.75			
Nectocarc																									

10.6 Appendix 6: Epifaunal invertebrate community composition – PERMANOVA analysis

(A) Habitat variation between islands

Table A6.1: Results of pairwise tests for differences in infaunal invertebrate community composition (by species) for each specific habitat type, between the North and South islands. P(perm) values which are significant are shown in bold.

Habitat	Position	Groups	t	P(perm)
SI	Upper	N, S	1.3411	0.112
BI	Upper	N, S	2.1629	0.013*
SS	Lower	N, S	3.3243	0.001
BS	Lower	N, S	3.2338	0.001
SI	Lower	N, S	2.3071	0.001
BI	Lower	N, S	1.7362	0.007

(B) Habitat variation within islands

Table A6.2: Results of pairwise tests for differences in epifaunal invertebrate community composition (by species), for each specific habitat type, within either the North or South Island. * denotes that Monte Carlo simulations were used to obtain more permutations where the original comparison returned fewer than 100 permutations. P(perm) values which are significant are shown in bold.

Island	Position	Groups	t	P(perm)
North	Upper	SS, BS	3.9525	0.005*
		SS, SI	6.6764	0.001*
		SS, BI	10.6130	0.001*
		BS, SI	4.8287	0.003*
		BS, BI	7.2623	0.001*
		SI, BI	3.9549	0.003*
North	Lower	SS, BS	2.4229	0.001
		SS, SI	4.1862	0.001
		SS, BI	2.3566	0.001
		BS, SI	4.0427	0.001
		BS, BI	2.0243	0.002
		SI, BI	2.0456	0.002
South	Upper	SI, BI	1.8572	0.004
South	Lower	SS, BS	1.2387	0.192
		SS, SI	2.4081	0.001
		SS, BI	2.5884	0.001
		BS, SI	2.4015	0.001
		BS, BI	2.3940	0.001
		SI, BI	1.6762	0.005

(C) Habitat variation across locations

Table A6.3: Results of pairwise tests for differences in epifaunal invertebrate community composition (by species), for each specific habitat type, between all Location combinations. * denotes that Monte Carlo simulations were used to obtain more permutations where the original comparison returned fewer than 100 permutations. P(perm) values which are significant are shown in bold.

Habitat	Position	Groups	t	P(perm)
SI	Upper	BLUF, FWSP	2.4684	0.007*
		BLUF, KAIP	2.3828	0.004*
		FWSP, KAIP	1.9149	0.014*
SS	Lower	BISL, BLUF	4.7464	0.001*
		BISL, KAIP	2.4307	0.007*
		BISL, RUNU	3.5512	0.004*
		BISL, WAKW	4.7483	0.001*
		BLUF, KAIP	3.7673	0.002*
		BLUF, RUNU	5.6656	0.001*
		BLUF, WAKW	5.1293	0.002*
		KAIP, RUNU	2.5090	0.009*
		KAIP, WAKW	3.9007	0.002*
		RUNU, WAKW	5.4603	0.002*
SI	Lower	FWSP, GISB	2.6302	0.011*
		FWSP, KAIK	3.3012	0.019*
		FWSP, KAIP	3.4116	0.002*
		FWSP, KAWH	2.7432	0.005*
		FWSP, RUNU	1.9981	0.029*
		FWSP, TAIR	3.0106	0.003*
		FWSP, WNUI	2.6610	0.005*
		GISB, KAIK	1.2906	0.250*
		GISB, KAIP	3.0838	0.001*
		GISB, KAWH	3.1196	0.003*
		GISB, RUNU	1.8227	0.034*
		GISB, TAIR	3.0190	0.004*
		GISB, WNUI	2.0746	0.014*
		KAIK, KAIP	3.0711	0.013*
		KAIK, KAWH	3.2139	0.014*
		KAIK, RUNU	1.3845	0.209*
		KAIK, TAIR	2.4507	0.031*
		KAIK, WNUI	1.7557	0.102*
		KAIP, KAWH	2.5253	0.001*
		KAIP, RUNU	2.1841	0.018*
		KAIP, TAIR	3.0729	0.003*
		KAIP, WNUI	2.9878	0.002*
		KAWH, RUNU	2.1733	0.024*
		KAWH, TAIR	2.9918	0.005*
		KAWH, WNUI	2.8978	0.003*
		RUNU, TAIR	2.2186	0.016*
		RUNU, WNUI	1.5680	0.080*
		TAIR, WNUI	3.1152	0.006*
BI	Upper	BLUF, KAIP	2.1629	0.029*
BS	Lower	BISL, BLUF	3.7320	0.003*
		BISL, KAIP	2.8223	0.008*

		BISL, RUNU	2.7411	0.029*
		BISL, WAKW	4.0872	0.002*
		BLUF, KAIP	3.8009	0.001*
		BLUF, RUNU	4.3205	0.002*
		BLUF, WAKW	4.0026	0.002*
		KAIP, RUNU	2.6016	0.003*
		KAIP, WAKW	4.3267	0.001*
		RUNU, WAKW	4.9656	0.001*
BI	Lower	FWSP, KAIK	3.8851	0.002*
		FWSP, KAIP	2.9835	0.006*
		FWSP, KAWH	3.0498	0.007*
		FWSP, RUNU	3.0178	0.003*
		FWSP, TAIR	1.6521	0.083*
		FWSP, WNUI	3.8813	0.001*
		KAIK, KAIP	3.0957	0.003*
		KAIK, KAWH	3.7711	0.002*
		KAIK, RUNU	2.7533	0.004*
		KAIK, TAIR	2.3019	0.011*
		KAIK, WNUI	4.4567	0.001*
		KAIP, KAWH	3.1060	0.007*
		KAIP, RUNU	2.5098	0.009*
		KAIP, TAIR	0.9859	0.446*
		KAIP, WNUI	3.6573	0.001*
		KAWH, RUNU	2.5727	0.007*
		KAWH, TAIR	1.8810	0.035*
		KAWH, WNUI	2.1021	0.034*
		RUNU, TAIR	1.9235	0.030*
		RUNU, WNUI	3.0826	0.006*
		TAIR, WNUI	2.2489	0.021*
		RUNU, GISB	1.9735	0.026*
		KAIP, GISB	3.0588	0.002
		TAIR, GISB	2.1951	0.012
		KAWH, GISB	2.5818	0.005
		FWSP, GISB	3.3719	0.003
		WNUI, GISB	3.3352	0.004
		KAIK, GISB	2.6660	0.005

(D) Habitat variation within locations

Table A6.4: Results of pairwise tests for differences in epifaunal invertebrate community composition (by species), for each specific habitat combination, within each location. * denotes that Monte Carlo simulations were used to obtain more permutations where the original comparison returned fewer than 100 permutations. P(perm) values which are significant are shown in bold.

Location	Position	Groups	t	P(perm)
Rangaunu	Upper	SS, BS	3.9525	0.002*
Rangaunu	Lower	SS, BS	4.0017	0.003*
		SS, SI	2.5578	0.006*
		SS, BI	2.4057	0.009*
		BS, SI	2.5324	0.015*
		BS, BI	1.6747	0.091*
		SI, BI	1.7423	0.058*
Bay of Islands	Lower	SS, BS	2.4480	0.006*
Kaipara	Upper	SI, BI	3.9549	0.005*
Kaipara	Lower	SS, BS	1.9918	0.021*
		SS, SI	4.0274	0.001*
		SS, BI	3.4271	0.001*
		BS, SI	3.3772	0.001*
		BS, BI	1.8849	0.031*
		SI, BI	1.6833	0.077*
Tairua	Lower	SI, BI	1.1250	0.325*
Kawhia	Lower	SI, BI	2.8724	0.002*
Gisborne	Lower	SI, BI	1.4716	0.1080
Farewell Spit	Upper	SI, BI	No comparison possible	
Farewell Spit	Lower	SI, BI	1.9947	0.019*
Whanganui Inlet	Lower	SI, BI	3.1157	0.006*
Kaikoura	Lower	SI, BI	2.4047	0.038*
Waikawa	Lower	SS, BS	1.5554	0.110*
Bluff	Upper	SI, BI	1.8989	0.034*
Bluff	Lower	SS, BS	2.8332	0.009*