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RESEARCH ARTICLE

Mussel reefs on soft sediments: a severely reduced but important habitat for macroinvertebrates and fishes in New Zealand

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Green-lipped mussels (*Perna canaliculus*) formed extensive reefs on soft sediments in sheltered embayments around northern New Zealand until overfishing and/or increased sediment input caused their virtual disappearance by 1980. To determine the role of mussel reefs as habitat for other animals, we located remnant soft-sediment reefs in five locations and compared the density, biomass, productivity and composition of mobile macroinvertebrate communities, and the density of small fishes associated with mussels, with fauna in the surrounding soft sediments. The mussel reefs had a distinct assemblage of macroinvertebrates, which had 3.5 times the density, 3.4 times the biomass and 3.5 times the productivity of surrounding areas. The density of small fishes was 13.7 times higher than in surrounding areas. These results show that soft-sediment mussel reefs support an abundant and productive fauna, highlighting the probable large loss of productivity associated with the historical decline in mussel habitat and the consequent desirability of restoration efforts.

Keywords: biogenic habitat; bivalve reef; ecosystem engineer; mussel; New Zealand; *Perna canaliculus*; sediment

Introduction

Reefs composed of dense aggregations of bivalves such as oysters and mussels are widespread in temperate waters. Bivalve reefs serve an important role as ecosystem engineers through their influence on nutrient cycling, water filtration, habitat structure, biodiversity and food web dynamics (Jackson et al. 2001; Grabowski & Peterson 2007). These bivalve reefs are inhabited by a diverse and abundant community of invertebrates and fishes that utilise the structural complexity of the reefs as a refuge from predation and environmental stresses (Coen et al. 2007; Commito et al. 2008). The effects of the provision of structural complexity are particularly

evident where bivalve reefs occur on soft sediments, as the reefs comprise islands of hard surfaces in a sea of sand or mud, so greatly increase habitat diversity. Once considered near inexhaustible, many bivalve reefs have declined precipitously, some to commercial extinction (Dare et al. 2004; Beck et al. 2011). For example, in a recent review of oyster reefs worldwide, Beck et al. (2011) estimated that 85% of oyster reefs have been lost globally and most of the remaining reefs were in poor condition. Bivalve reef declines are due to overfishing and an overall decline in the condition of coastal waters through impacts such as sedimentation, habitat disturbance and eutrophication (Cook et al.

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2000; Edgar & Samson 2004; Kirby 2004). Because of these declines there is an urgent need to understand the consequences of bivalve reef habitat loss and thus the potential benefits that restoration could bring.

In New Zealand, the green-lipped mussel *Perna canaliculus* forms aggregations on hard and soft surfaces that can reach 50 cm above the substratum (I. McLeod, Leigh Marine Laboratory, pers. obs. 2008). The historical extent of mussel reefs on areas of soft sediment has been poorly documented; however, Greenway (1969) described 'dense beds' (reefs) across tens of km² on subtidal soft sediments in the Firth of Thames, southeast of Auckland City. Soft-sediment mussel reefs supported dredge fisheries in the Firth of Thames and in Golden Bay, Tasman Bay, and the Marlborough Sounds in the northern South Island of New Zealand. These reefs were almost completely destroyed by dredging and/or sedimentation by 1980 (Paul 2012) and have not since recovered (McLeod et al. 2012; Paul 2012). Little is known about the former role of these reefs in shallow coastal ecosystems.

The aim of this paper is to estimate the value of soft-sediment *P. canaliculus* reefs as habitat for fish and mobile macroinvertebrates. To achieve this, we compared the fauna of mussel reefs with that of adjacent bare sediment areas at five sites in northeastern New Zealand.

Methods

Study sites

We sampled five soft-sediment mussel reefs located in sheltered embayments in northeastern New Zealand (Fig. 1). The Waimangō Point site (5 m depth below mean low water spring, sampled February 2008, August 2008, October 2008 and January 2009) and Man of War Passage (20 m depth, sampled February 2008) were adjacent to mussel farms, and the Ohiwa Harbour (2 m depth, sampled July 2008), Okiwi Estuary (0.5 m depth, sampled October 2008) and Weiti River (0.5 m depth, sampled September 2008) sites were in the channels of shallow estuaries. For logistical reasons the

sites could not all be sampled during the same season. The mussel reef at Waimangō Point was sampled repeatedly over a year to determine whether differences in invertebrate assemblages between mussel-associated habitats and adjacent bare sediments were consistent through time.

Mobile invertebrates

At each site mobile invertebrates were sampled from three locations among the mussels and adjacent bare soft sediments: 1) the mussel-associated habitat including the mussels themselves and their associated byssus/shell matrix (hereafter 'mussel matrix'); 2) the under-mussel habitat including the top 100 mm of sediment below mussel aggregations; 3) the adjacent bare soft-sediment habitat consisting of the surface and the top 100 mm of sediment within the general area of the mussel reefs but > 3 m away from live mussels. The net impact of mussels on the density, biomass and productivity of fauna was assumed to equal 1 + 2 – 3.

To sample the mobile invertebrates associated with mussel reefs, under mussel reefs, and in bare soft sediments, two methods were used. The mussel matrix was sampled using a 200 × 200 mm steel frame with a heavy-duty plastic bag wrapped around the edges. The frame was pushed through the mussel/byssus matrix and the mussels and any associated organisms were slid into the bag. The under-mussel and adjacent bare soft-sediment habitats were sampled using a circular 130 mm internal diameter corer that was forced 100 mm deep into the substrate. Samples were preserved in 70% isopropanol alcohol. Five samples were taken during each sampling occasion, except at Man of War Passage where four samples were taken from each habitat and the Waimangō Point site in July when four under-mussel and two adjacent bare area samples were taken.

To estimate the density, biomass and productivity of the mobile invertebrates associated with the three habitats, samples were washed through a series of sieves (8, 5.6, 4, 2.8, 2, 1.4, 1,

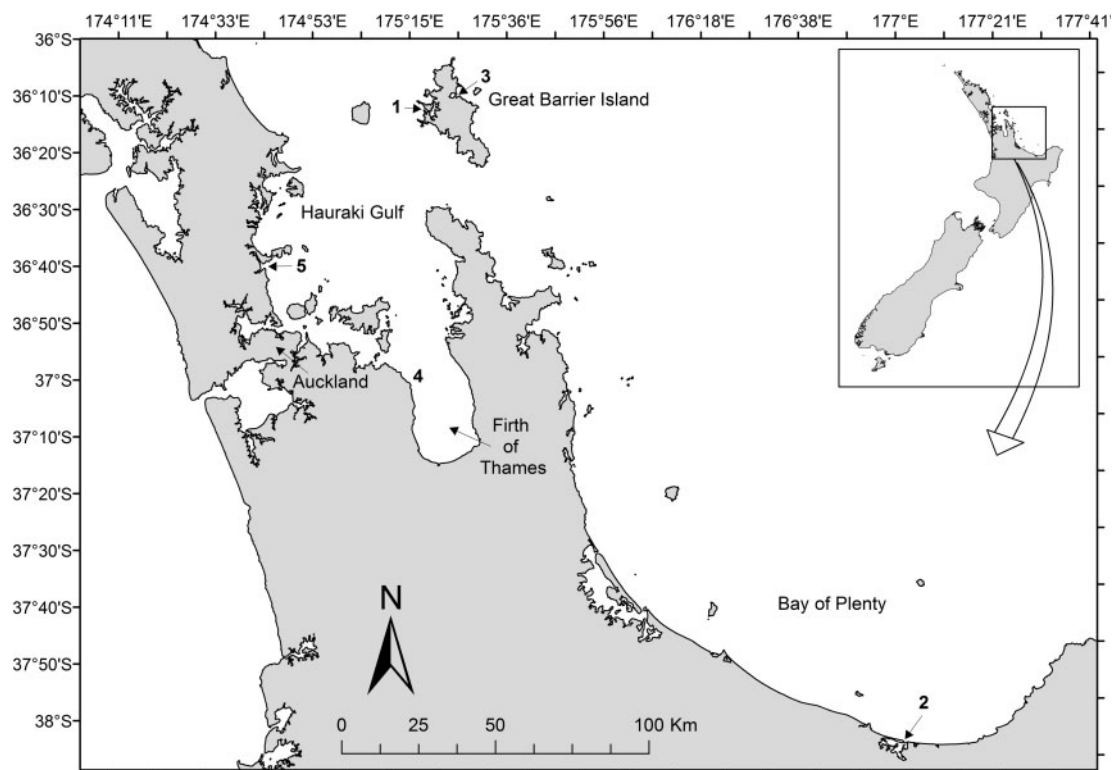


Figure 1 Sites in northeastern New Zealand at which soft-sediment reefs of the mussel *Perna canaliculus* were sampled. 1, Man of War Passage; 2, Ohiwa Harbour; 3, Okiwi Estuary; 4, Waimangō Point; 5, Weiti River.

0.71 and 0.5 mm mesh sizes) to size-fractionate the animals (Edgar 1990). Material present in the 1.4, 1, 0.71 and 0.5 mm sieves was sub-sampled by halving the sample up to five times using a Folsom plankton splitter. Invertebrates retained on the sieve sizes 0.5–5.6 mm were identified to coarse taxonomic levels and counted. Mobile invertebrates retained on the 8 mm sieve were put into sieve-size categories 8, 11.2, 16, 22.4 and >22.4 mm by passing them through the appropriately sized sieve and identified to species level, except polychaete worms, which were identified to family, and Nemertea (ribbon worms), which were identified to phylum. The two size categories 0.5–5.6 mm and 8.0–22.4 mm were analysed both together and separately. Sessile organisms were noted but were not included in the analysis. Biomass and productivity of mobile invertebrates (both expressed as ash-free dry

weight [AFDW]) were estimated using the general equations of Edgar (1990), which predict individual biomass as a function of sieve mesh size, and production as a function of individual biomass and water temperature. Water temperature was measured using a Suunto EOS dive computer during sample collection.

Fish

The small and cryptic fish associated with mussel reefs were sampled once in Ohiwa Harbour (October 2008), Okiwi Estuary (October 2008) and Waimangō Point (May 2008) using a circular net. The outer margin of the net accommodated a 9 mm diameter lead-lined rope that could be pulled tight like a noose. During sampling two scuba divers spread the net out underwater to make a 1 m² area before placing it over the

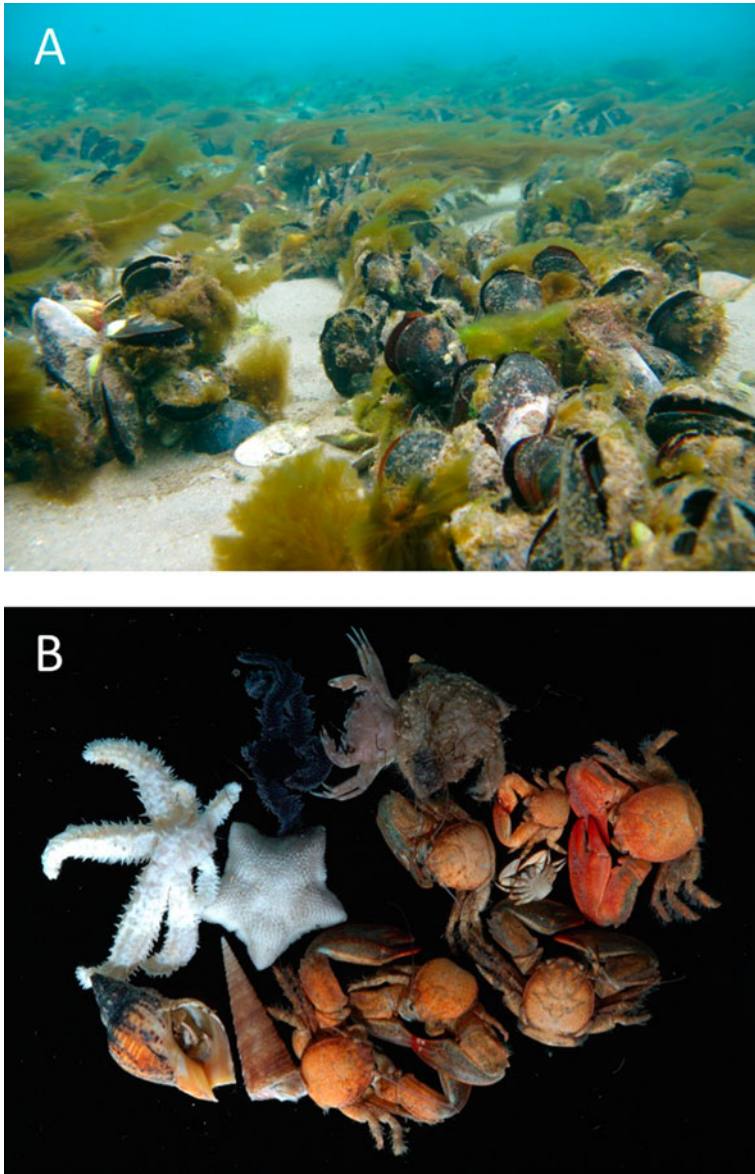


Figure 2 Photos of mussel reef habitat and species. **A**, Mussel reef in Okiwi Estuary, Great Barrier Island, New Zealand. **B**, A sample of mobile invertebrate species commonly found associated with mussel reefs.

mussels (or substrate in adjacent areas). The divers held down the sides of the net while working it under the mussels (or along the substrate) and tightening the rope. Five samples were taken at each location. All fish caught were identified to species level.

Data analysis

Significant differences in the densities, biomasses and productivities of mobile invertebrates between sites and habitats were tested for using independent sample *T*-tests. Only the spring 2008 samples at Waimangō Point were included in

the analysis of abundance, biomass, productivity and species assemblage among sites. This was because the water temperature during the spring sampling was the most similar to the mean temperature among other sites. An independent-samples Mann-Whitney U Test was used to test for between-habitat differences in fish density because the fish density data violated the assumptions of homogeneity of variances and normal distribution. The above statistical analysis was done using the software package SPSS v 20.

Differences in mobile invertebrate assemblages among sites and habitats were identified using analysis of similarities (ANOSIM). Principal component analysis (PCA) was used to visualise species' assemblages across different sites and habitats, and to identify the main species driving differences between these assemblages (Field 1982). Analysis was run on fourth-root transformed density data for taxa. All multivariate analyses were completed using the software package Primer v 6.1.6.

Results

Density, biomass, and productivity of mobile invertebrates

Combining the mobile invertebrates found in the mussel matrix and under-mussels habitats (hereafter mussel matrix+under mussels=mussel-associated) showed that mussel-associated assemblages had consistently higher densities, biomasses and productivities of mobile macroinvertebrates than adjacent bare sediment areas across sites and size classes (Figs. 3A–F). Densities of mobile invertebrates 0.5–22.4 mm in the mussel-associated habitat were 3.5 times higher ($11,100 \pm 7740$ SEM ind.m⁻²) than in surrounding bare soft sediments (3140 ± 2620 ind.m⁻²) ($t_{46} = 4.78$, $P < 0.001$). Mobile invertebrates in the 0.5–5.6 mm size class made up 95.4% of the total density (Figs. 3A, 3B). The average biomass of mobile invertebrates 0.5–22.4 mm in the mussel-associated habitat (98.2 ± 79.4 g AFDW m⁻²) was 3.4 times higher than in surrounding areas (28.9 ± 34.9 g AFDW m⁻²) ($t_{46} = 3.92$, $P = 0.001$). Most of the biomass

(92.1%) was made up of individuals from the 8.0–22.4 mm size class (Figs. 3C, 3D). Average productivity of mobile invertebrates 0.5–22.4 mm in the mussel-associated habitat was 3.5 times higher (0.46 ± 0.42 g AFDW m⁻² d⁻¹) than in surrounding areas (0.013 ± 0.142 g AFDW m⁻² d⁻¹) ($t_{46} = 3.87$, $P = 0.001$). Most of the productivity (78.1%) was made up of individuals in the 8.0–22.4 mm size class (Figs. 3E, 3F).

Species composition of small mobile invertebrates

In the 0.5–5.6 mm size class, 19 taxa were present in the mussel matrix, compared with 11 taxa under mussels and nine in adjacent bare sediment areas (Figs. 4A–C). Gastropods were the numerically dominant taxa in the mussel matrix accounting for 49.6% of all individuals in this size class. Gammarid amphipods (12.5%), bivalves (10%) and polychaetes (7.7%) were also common in the mussel matrix (Fig. 4A). Three taxa made up 95.3% of all the macroinvertebrates under mussels; polychaetes (54.6%), bivalves (31.6%) and gastropods (9.1%) (Fig. 4B). Four taxa made up 93.1% of the mobile invertebrates in the adjacent bare sediment areas; bivalves (40.0%), polychaetes (28.9%), gastropods (17.6%) and ostracods (8.6%) (Fig. 4C). Caridean shrimps, cumaceans, harpacticoid copepods, mysid shrimps, ophiuroids (brittle stars), hermit crabs, porcelain crabs, pycnogonids (sea spiders) and tanaids were found in the mussel matrix or under mussels, but were never present in adjacent bare sediment areas (Figs. 4A–C).

In the 8.0–22.4 mm size class, 38 taxa were identified in the mussel matrix, compared to 25 taxa under mussels and 16 in adjacent bare sediment areas (Figs. 5A–C). The porcelain crab *Petrolisthes elongatus* was the numerically dominant taxa in the mussel matrix accounting for 42.4% of all individuals in this size class (Fig. 5B). Nemertean (12.5%) and two families of polychaetes (Maldanidae; 12.5%) and Oweniidae (7.5%) were the most common taxa under mussels (Fig. 1). Of the four most common

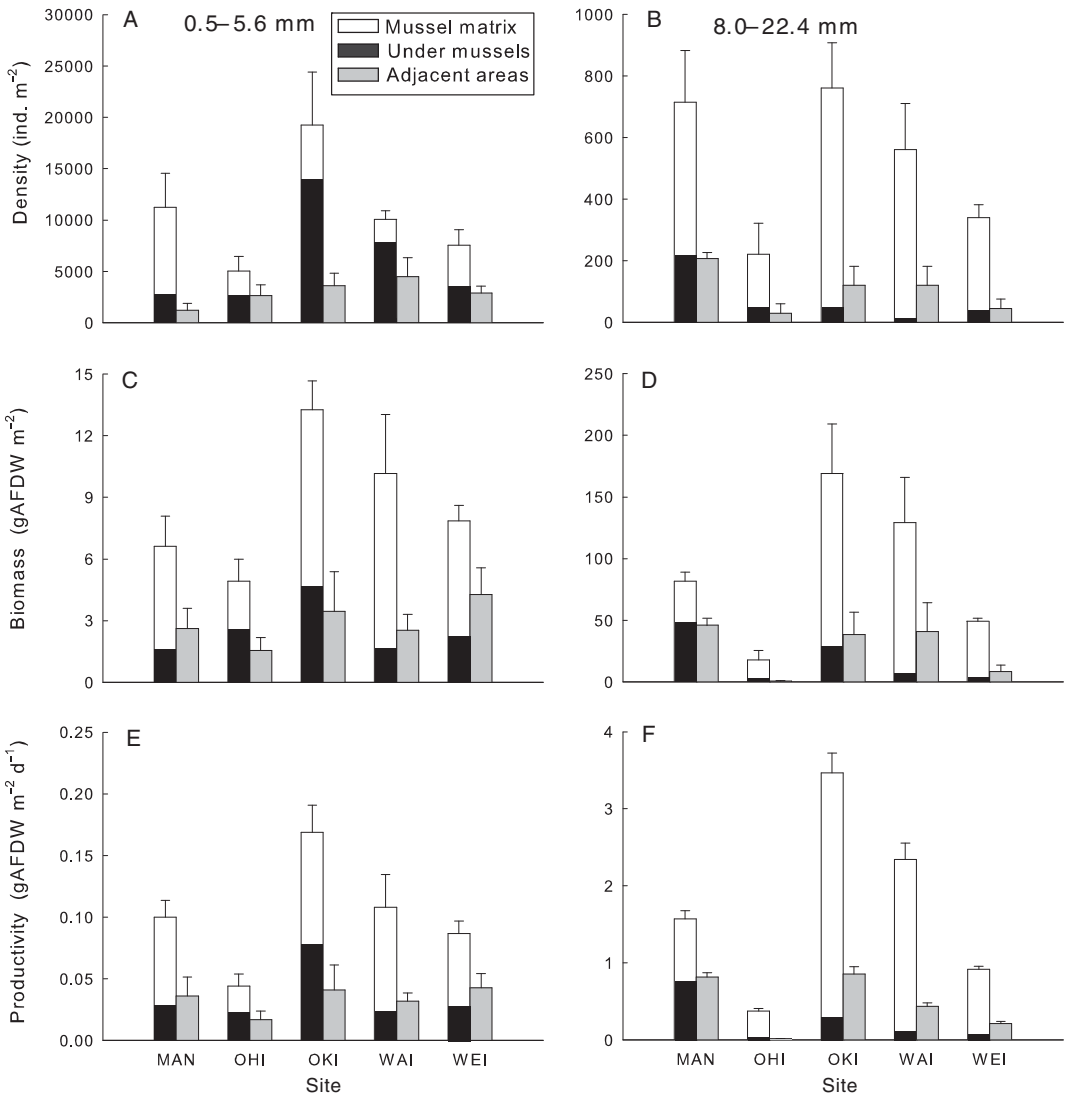


Figure 3 Densities, biomasses and productivities in and under soft-sediment reefs of the mussel *Perna canaliculus* and in adjacent bare sediment habitats. **A–B**, Mean densities (ind.m⁻²) of mobile invertebrates. **C–D**, Mean biomasses (g AFDW m⁻²) of mobile invertebrates. **E–F**, Mean productivities (g AFDW m⁻² d⁻¹) of mobile invertebrates. The white (mussel matrix) and black (under mussels) bands show the mussel reef habitat and the grey bands show the adjacent bare sediment areas. MAN, Man of War Passage; OKI, Okiwi Estuary; OHI, Ohiwa Harbour; WAI, Waimangō Point; WEI, Weiti River. Means \pm SEM are shown.

species found in adjacent bare sediment areas, three were bivalves: *Paphies australis* (17.2%), *Austrovenus stutchburyi* (10.3%), and *Dosinia lambata* (10.3%).

PCA of densities of taxa 0.5–5.6 mm revealed that the mussel matrix had a different

mobile invertebrate assemblage to the under-mussel (ANOSIM Global $R=0.64$, $P=0.008$) and adjacent bare sediment habitats (ANOSIM Global $R=0.4$, $P=0.002$) (Fig. 6A). The assemblages of mobile invertebrates were more similar among mussel reefs, even those hundreds

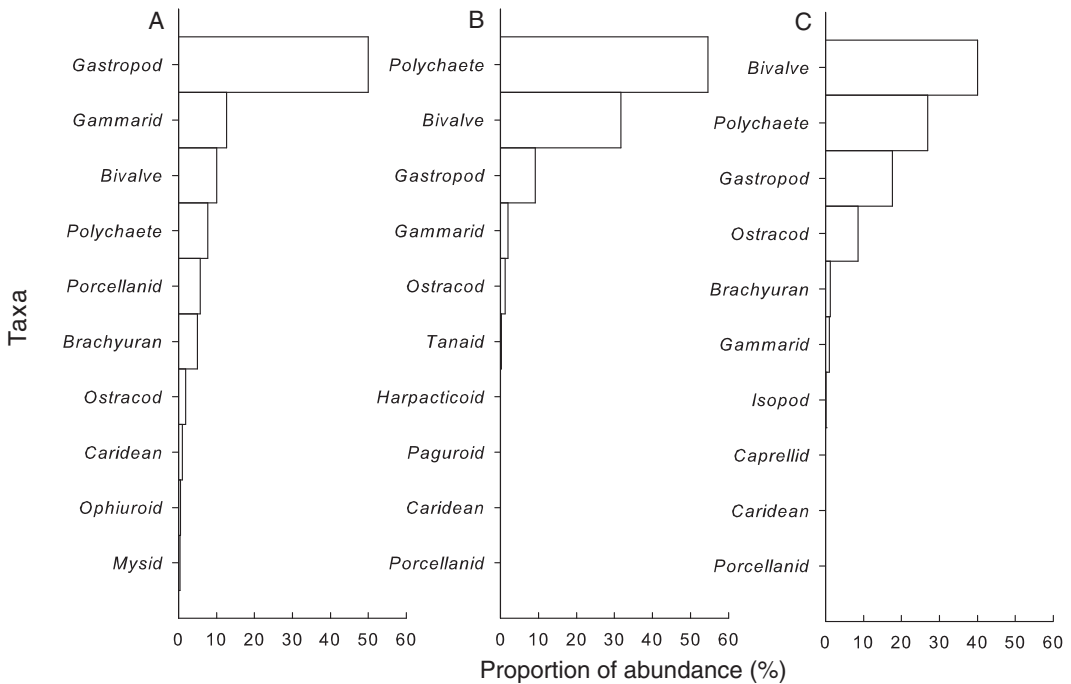


Figure 4 Rank abundance of the 10 most common mobile invertebrate taxa 0.5–5.6 mm across sites. **A**, Mussel associated. **B**, Under mussels. **C**, Adjacent bare sediment areas.

of km away, than to under-mussel or adjacent bare sediment habitats at the same site. There was no significant difference between the under-mussel and bare sediment area assemblages or between sites. Brachyuran crabs, caridean shrimps, gammarid amphipods, gastropods and porcelain crabs were the main taxa driving the differences between the mussel matrix and other habitat types (Fig. 6). There was no significant difference in the 8.0–22.4 mm mobile invertebrate assemblage (ANOSIM Global $R=0.106$, $P=0.15$) (Fig. 6) between habitats. The eight most important taxa in the 0.5–5.6 mm size class and the 11 most important species for the 8.0–22.4 mm size class as identified using principal component 1 and 2 are shown in Figures 6A and 6B respectively.

Seasonal variation in density, biomass and productivity of small mobile invertebrates

The mussel matrix had consistently higher densities, biomasses and productivities of mobile

invertebrates 0.5–5.6 mm and 8.0–22.4 mm than adjacent bare sediment areas across seasons at Waimangō Point (Figs. 7A–F). Notably, there was an increase in the density, biomass and productivity of mobile invertebrates 8.0–22.4 mm in February 2009 driven by an increase in the most numerous species *Petrolisthes elongatus*.

Fish

Mean total fish density in the mussel-associated habitat was 13.7 times higher than in adjacent bare sediment areas ($u=10$, $z=-4.399$, $P=0.001$). A total of five fish species were present (Fig. 8). Two species, the clingfish *Tracheloichismus melobesia* and the labrid *Notolabrus celidotus*, were only found associated with mussels. Two species, the invasive goby *Acentrogobius pfaumii* and the turbot *Colistium nudipinnis*, were found only in adjacent bare sediment areas. One species, the triplefin *Grahamina capito*, was present in both habitats.

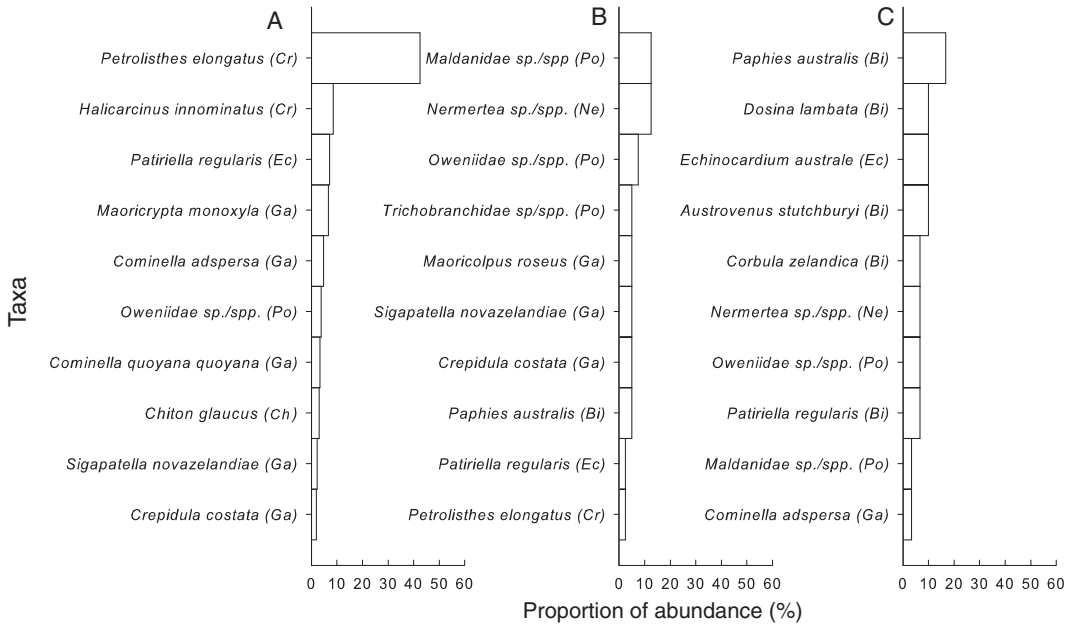


Figure 5 Rank abundance of the 10 most common mobile invertebrate taxa 8.0–22.4 mm across sites. **A**, Mussel associated. **B**, Under mussels. **C**, Adjacent bare sediment areas. Bi, bivalve; Ch, chitron; Cr, crab; Ec, echinoderm; Ga, gastropod; Ne, nemertean; Po, polychaete.

Discussion

Marine bivalves are common in many benthic soft-sediment environments and have major impacts on their local ecosystems (Meadows et al. 2011). Mussel reefs have usually been considered ‘hot spots’ of biodiversity (Asmus 1987; Crooks 1998; Ragnarsson & Raffaelli 1999, but see Buschbaum et al. 2009). Our study has shown that soft sediment mussel reefs of *Perna canaliculus* host a diverse assemblage of mobile invertebrates with higher densities, biomasses and productivities than found in adjacent bare sediments.

As expected for a habitat spread across a wide range of sites with different environmental conditions, the species assemblages were different at each site. However, for the 0.5–5.6 mm size class mussel-matrix associated mobile invertebrate assemblages were more similar to each other than nearby bare sediments, even when sites were hundreds of km apart. Although the statistical tests found no significant difference, it appeared that the 8.0–22.4 mm mussel-matrix

assemblages were more similar to each other than the under-mussel and adjacent bare sediment assemblages. Crustaceans, gastropods and polychaetes dominated the mussel-matrix mobile invertebrate assemblages and the dominant species in terms of biomass was the porcelain crab *Petrolisthes elongatus*.

High densities and productivities of communities of benthic invertebrates are often associated with structurally complex habitats (e.g. Coull & Wells 1983) and high inputs of detrital organic matter (e.g. Vetter 1995). Mobile invertebrates inhabiting structurally complex habitats may be less vulnerable to predation than those associated with a more homogeneous structure (Heck & Thoman 1981; Coull & Wells 1983). In addition, mussels offer a hard surface for algae or sessile invertebrates to attach to. These algae and sessile invertebrates may offer further habitat and food for mobile invertebrates. Mussels may also provide a food source through being preyed upon directly, being scavenged when they die, or providing food for

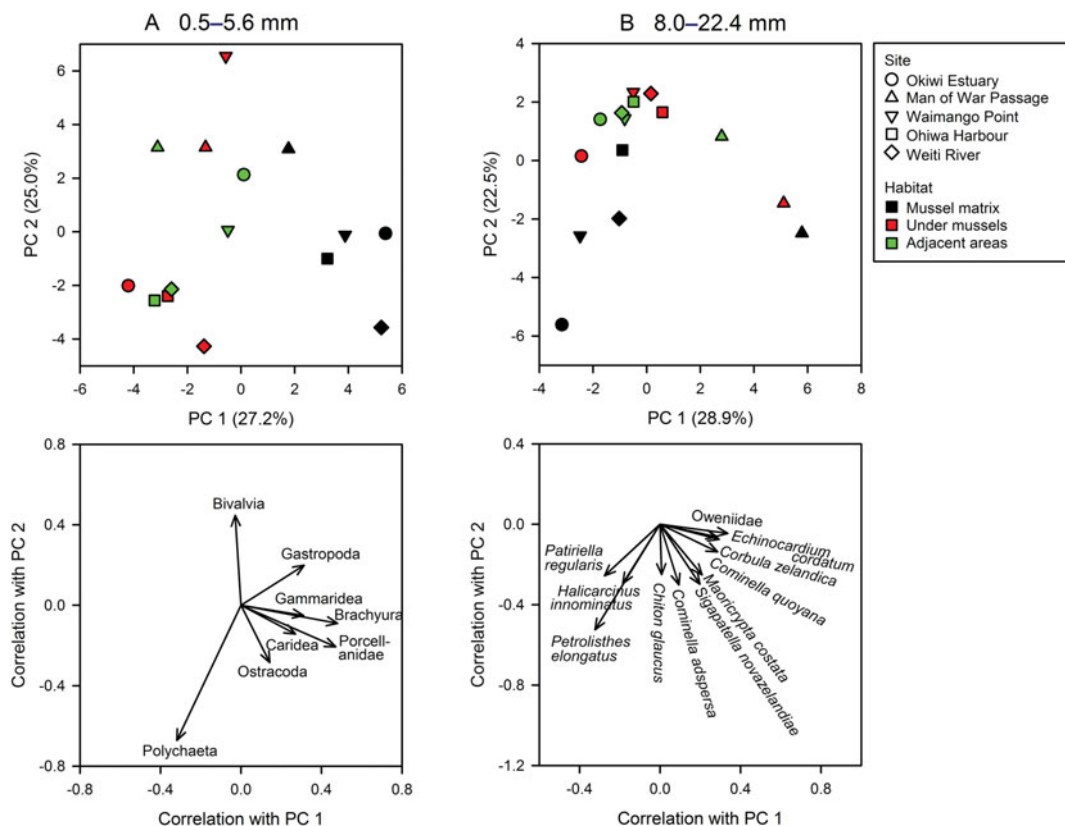


Figure 6 Principal component analysis of the density of species of mobile macroinvertebrates across three habitats and five sites in northeastern New Zealand. The black lines show the eight most important taxa as defined by principal component 1 and 2. Percentages associated with each principal component refer to the proportion of variation accounted for by that principal component. **A**, Mobile invertebrates 0.5–5.6 mm. **B**, Mobile invertebrates 8.0–22.4 mm.

detritus-feeding species through their production of biodeposits. For example, the biodeposits of the related blue mussel (*Mytilus edulis*) supplied up to 31% of the energy demands of an associated macroinvertebrate community on the west coast of Sweden (Norling & Kautsky 2007).

It has been hypothesised that bivalve aggregations may negatively affect infaunal communities through the build up of an anoxic layer of biodeposits (Creese et al. 1997) or through the predation of infaunal larvae via filter feeding (Commuto & Boncavage 1989). We found no evidence of a reduction in infaunal density, biomass or productivity under mussels compared to adjacent bare sediment areas. However,

the taxa present under mussels differed from those in adjacent bare sediment areas, indicating that mussels facilitate the presence of some macroinvertebrate species and inhibit others.

Total densities of small fishes were over 10 times higher in mussel-associated habitats than in adjacent bare sediment areas. Mussel reefs may provide shelter, nesting sites and a food supply for fish. For example, the mobile invertebrates associated with mussel reefs may represent an important food source for fish. Crustaceans >1 mm are the primary food source for fish weighing 0.1–100 g (Edgar & Shaw 1995). Crustaceans within this size range dominated the biomasses and productivities of

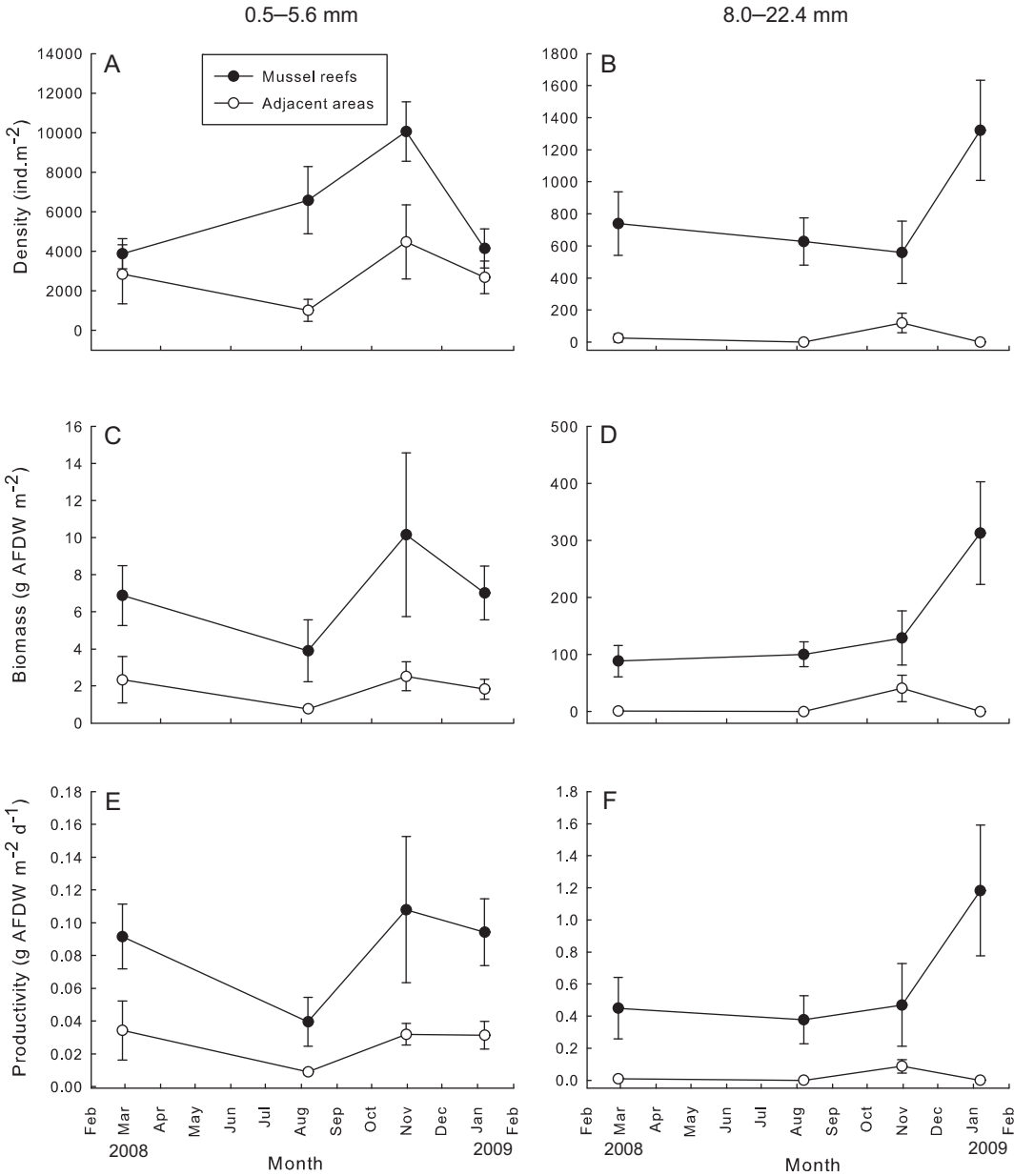


Figure 7 Densities, biomasses and productivities in the mussel-associated habitat (mussel matrix+under mussels) and in adjacent bare sediment habitats over time at Waimangō Point. **A**, Densities of mobile invertebrates 0.5–5.6 mm. **B**, Densities of mobile invertebrates 8.0–22.4 mm. **C**, Biomasses (g AFDW m⁻²) of mobile invertebrates 0.5–5.6 mm. **D**, Biomasses (g AFDW m⁻²) of mobile invertebrates 8– 22.4 mm. **E**, Productivities (g AFDW m⁻² d⁻¹) of mobile invertebrates 0.5–5.6 mm. **F**, Productivities (g AFDW m⁻² d⁻¹) of mobile invertebrates 8.0–22.4 mm. Means \pm SEM are shown.

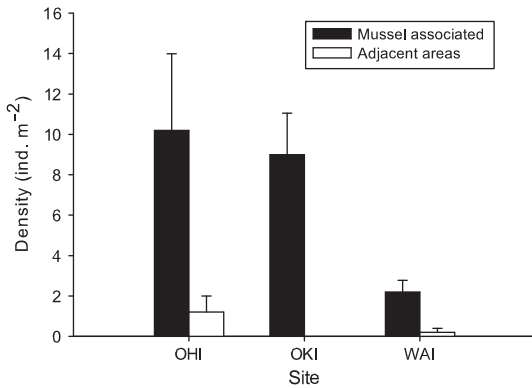


Figure 8 Total densities (ind.m⁻²) of fish in the mussel-associated habitat (black bars) and in adjacent bare sediment areas (white bars) across three sites in northeastern New Zealand. OHI, Ohiwa Harbour; OKI, Okiwi Estuary; WAI, Waimangō Point. Means \pm SEM are shown.

mussel reef assemblages, but were uncommon in adjacent bare sediment areas.

In summary, mussel reefs enhance coastal biodiversity by increasing habitat heterogeneity. The reefs support an abundant and productive assemblage of mobile animals that would otherwise not occur on soft sediments. The reduction in macroinvertebrate productivity due to mussel reef destruction is difficult to quantify due to uncertainty about the former extent of the reefs, but it is likely to be large, and the removal of reefs is also likely to have had important consequences for fish communities that utilise mussel reefs as a source of food and/or shelter. Mussel reef restoration may be possible through reintroductions to their former range (McLeod et al. 2012), and this would help to restore an important habitat for macroinvertebrates and fishes.

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