

Change in the benthic assemblages of the Waitemata Harbour:

Invasion risk as a function of community structure

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1. Abstract

The Waitemata Harbour is a large tidal estuary adjacent to New Zealand's largest and fastest growing city. The harbour is highly valued and is used for numerous recreational and commercial purposes. A potentially important stressor in the Waitemata Harbour has been the establishment and spread of non-indigenous species (NIS); with more than 66 marine NIS having been recorded. However, the ecological consequences of NIS invasions in the Waitemata Harbour have not been fully explored. It is important to investigate the role of native biodiversity in promoting invasion resistance, and the likelihood of "invasional meltdown" in the Waitemata Harbour.

The purpose of this investigation was to determine whether invasions in soft-sediment habitats of the Waitemata Harbour have affected key ecosystem functions to the extent that (1) resistance to new invasions has been compromised, and (2) ecosystem services have been affected. The work was structured around three study objectives:

1. To characterise faunal changes that have occurred in the Waitemata Harbour since the 1930's by reviewing published research and any other available data.
2. To develop a conceptual model of the effects of NIS and other stressors on the benthic assemblages of Waitemata Harbour.
3. To undertake field studies to ground truth the model and to investigate the impact of faunal changes at higher trophic levels (particularly snapper).

This study of marine soft-sediment habitats was divided into two separate parts: intertidal and subtidal. The intertidal work involved a re-analysis of previously existing data, while the subtidal work involved the development and empirical evaluation of a conceptual model.

To assess the status of NIS in intertidal habitats of the Waitemata Harbour, species and environmental data were collated from 62 intertidal sites spread throughout the Harbour. GIS mapping and regression-based techniques were used to analyse the relationships between NIS abundance/occurrence/richness and various biotic and abiotic variables.

To assess the status of NIS in subtidal habitats, we reviewed existing literature on benthic communities, with particular emphasis on the landmark studies of Powell (1937) and Hayward et al. (1997). A conceptual model was constructed using five main benthic species—three NIS and two native species—that had expanded or contracted markedly between the 1930s and 1990s. As there was great interest in knowing the potential flow on effects of NIS to commercially and culturally valued species, snapper were also included in the model as generalist predators. Five subtidal sites in the Waitemata Harbour were then sampled in order to challenge the model with empirical data.

The intertidal flats in the Waitemata Harbour had a relatively low abundance and occurrence of NIS, with the NIS predominantly distributed in the Upper Harbour (far from the Port of Auckland). The species tended to occur in muddy habitats that had low numbers of native individuals and taxa.

In contrast to the intertidal sites, subtidal habitats in the Waitemata Harbour were highly invaded, with the invasive Asian bivalves *Musculista senhousia* and *Theora lubrica* predominant. Snapper, known for their broad diets, were found to have high numbers of non-indigenous prey in their guts. Although several NIS co-occurred at subtidal sites in the outer Harbour, we found no evidence of positive interactions among pairs or sets of NIS (e.g., densities of *M. senhousia* and *T. lubrica* were negatively correlated). Nevertheless, we were able to confirm several of the interactions defined in our conceptual model, and we suggest that anthropogenic perturbations to the Waitemata Harbour ecosystem may have influenced invasion resistance by altering the densities of large native bivalves and other functionally important benthic species.

Keywords: Non-indigenous species, Invasion, benthic community structure, ecological interactions, Waitemata Harbour, snapper, *Musculista senhousia*, *Theora lubrica*, *Limaria orientalis*.

2. Introduction

The Waitemata Harbour is a large tidal estuary in the Auckland Region and a quintessential part of New Zealand's largest and fastest growing city. The harbour is highly valued, as it is used for all manner of recreational and commercial purposes: it is the site of New Zealand's busiest commercial port, it is home to tens of thousands of private yachts and launches, it is a place of recreational and commercial fishing, it contains a bird sanctuary and diverse shellfish beds, it has intrinsic value as well as aesthetic, educational, spiritual and cultural significance. However, some of the anthropogenic activities in and around the Harbour have the potential to affect the health and biodiversity of the system, creating negative feedbacks that may impact upon the delivery of ecosystem services both now and in the future.

One potentially important stressor in the Waitemata Harbour has been the establishment and spread of non-indigenous species (NIS). The Waitemata Harbour has been invaded by as many as 66 marine NIS (Hayward 1997, Cranfield et al. 1998, Inglis et al. 2005a,b). The majority of NIS introductions to the Harbour probably occurred in conjunction with international trade and vessel traffic through the Port of Auckland and the movements of private boats both nationally and internationally. Adult and juvenile life-stages, larvae, eggs and cysts can be transported in ships ballast water or as components of hull fouling communities on vessels of all types.

Although the arrival of NIS in the Waitemata Harbour is clearly a necessary pre-condition for invasion, post-introduction invasion success likely depends on many factors, including the health and diversity of the recipient ecological system (Landis 2004). Ecosystems containing healthy and diverse assemblages may be more able to repel invaders, a concept known as "invasion resistance" (Elton 1958, McGrady-Steed et al. 1997, Naeem et al. 1999). The chance of invasion is reduced by predators, competitors or other key species in the native community that are able to eat, disturb, or otherwise interfere with the NIS and prevent establishment. However, others suggest the opposite, that factors promoting native diversity may also provide favourable conditions that facilitate the establishment and spread of new species (Stohlgren et al. 1999). Both native and invasive diversity can be promoted and regulated by dominant species (Emery and Gross 2006). Furthermore, theoretical arguments suggest that high diversity is unstable (May 1973) and can thus provide opportunity for invasion if native species are locally transient (Emery and Gross 2006).

The composition and health of native communities is not necessarily static. There have been significant changes in the Auckland region during the last 50-70 years that may have affected the health and diversity of ecological communities in the Waitemata Harbour (Hayward et al. 1997). Thus, along with increases in global shipping and other sources of invasive propagules, there may have been concomitant decreases in the Harbour's ecological resistance to invasion. An accelerating rate of new invasions in the estuary would support this hypothesis (see Cohen and Carlton 1998).

An increasing rate of invasion may also indicate "invasional meltdown" (Simberloff and Von Holle 1999). The term "meltdown" is vernacular for a process that accelerates beyond control and causes system-wide failure. Simberloff and Von Holle (1999) argue that accumulations of NIS facilitate one another's survival and accelerate the rate of new invasions. The hypothesis includes the possibility of multiplicative impacts, i.e., that the combined effects of two or more NIS can be greater than the sum of their individual impacts. With >60 NIS now present in the Waitemata Harbour, including several recent invasions (Inglis et al. 2005a,b, Smith et al. 2003, Read 2006), the chances of positive interactions among NIS leading to invasional meltdown are elevated.

Given the potential for NIS to be driving considerable ecological change, it is increasingly important to examine ecological interactions involving NIS and native communities to elucidate the factors affecting invasion resistance. The purpose of this investigation was to determine whether invasions in soft-sediment habitats of the Waitemata Harbour have affected key ecosystem functions to the extent that (1) resistance to new invasions has been compromised, and (2) ecosystem services have been affected. The work was structured around three study objectives:

1. To characterise faunal changes that have occurred in the Waitemata Harbour since the 1930's by reviewing published research and any other available data.
2. To develop a conceptual model of the effects of NIS and other stressors on the benthic assemblages of the Waitemata Harbour.
3. To undertake field studies to ground truth the model and to investigate the impact of faunal changes at higher trophic levels (particularly snapper).

2.1 BACKGROUND

In one of the first analyses of benthic soft-sediment communities in the Waitemata Harbour, Powell (1937) presented a map of the seabed that included the distributions of several broad groupings of animals. These “associations” were differentiated intuitively (rather than quantitatively), although they did reflect the dominance of large, abundant creatures living in the sediments of the harbour. Powell's associations were based largely on molluscs, but also provided information on dominant echinoderms, crustaceans and polychaetes.

Hayward et al. (1997) revisited many of Powell's sampling stations and re-examined Powell's “associations”, employing the same methods. Hayward et al. (1997) described new faunal associations and documented changes occurring during the 60 year sampling interval. Importantly, many of Hayward's associations of the late 1990's included non-indigenous species that are likely to have been introduced to the Waitemata Harbour after Powell's studies. Three non-indigenous bivalves from Asia had emerged as dominants in areas of subtidal soft-sediment seabed: *Musculista senhousia*, *Theora lubrica* and *Limaria orientalis*. A fourth Asian bivalve, the Pacific oyster *Crassostrea gigas*, was dominating areas of the intertidal shoreline (Hayward 1997). Along with the dominant invaders, various other NIS including algae, invertebrates and fishes were recorded in the Waitemata in the late 1990's and early 2000's (Hayward 1997, Nelson 1999, Willis et al. 1999, Francis et al. 2003, Francis et al. 2004, Inglis et al. 2005a,b).

The Powell (1937) and Hayward et al. (1997) studies provide a springboard for further studies of invasions in the Waitemata Harbour. Both studies were, however, snap-shots of the distribution and structure of limited components of the benthic assemblage. Understanding the impacts of invasions requires knowledge of spatial and temporal variability in these assemblages and of the functional roles played by both native and non-indigenous species. The historical descriptions of Powell (1937) and Hayward et al. (1997) can be augmented by other datasets that are (i) more quantitative, (ii) have better taxonomic resolution and information on functional roles, (iii) incorporate spatial and temporal variability, (iv) have well-defined methods, (v) have GPS-derived latitude and longitude coordinates, meta-data and sediment quality information.

2.2 APPROACH

Datasets held by the Auckland Regional Council on intertidal assemblages within the Waitemata Harbour fit all of the criteria listed above. We received permission to query these data sets to investigate changes occurring in the decade post 1997. Importantly, the quality of the data was sufficient to allow us to address many questions about invasion success in the central and upper Waitemata. The questions were mainly related to the status of NIS. For example, how many NIS are present in intertidal soft-sediment habitats of the Waitemata Harbour? Are NIS dominant relative to native species in intertidal soft-sediment habitats? Are the NIS clustered at sites close to the Port of Auckland? Are there more NIS at contaminated sites? Are there fewer NIS at sites with high native species richness? Does the presence of one NIS affect the likelihood of occurrence of another?

Although the intertidal data sets can be used to address important questions of NIS status, direct comparisons with the subtidal studies of Powell (1937) and Hayward et al. (1997) were not possible. Therefore, a new subtidal sampling scheme was specifically designed so that recent changes in the subtidal realm could be characterised, relative to the historical situation. By sampling in subtidal

habitats, we were also able to search for NIS that were not well represented in the ARC data sets (e.g., *Styela clava*, *Charybdis japonica*, *Acentrogobius pflaumii*, *Limaria orientalis*, *Chaetopterus* sp.). The subtidal sampling scheme was designed with the express aim of testing and refining a conceptual model, which was the third component of our investigation.

The conceptual model was constructed around five main benthic species—two native and three NIS—and one predatory fish (snapper). The inclusion of snapper added trophic complexity to the model. Furthermore, snapper represent a commercially and recreationally valued species in the Auckland Region. There is great interest in knowing the potential flow on effects of NIS to valued species such as snapper, and the flow on effects outlined in the model were tested by means of fish sampling and gut content analysis.

The rationale for including the five main benthic species in the model was derived directly from the papers of Powell (1937) and Hayward et al. (1997). These species had dominated subtidal habitats in the Waitemata Harbour during the time of either Powell (1937) or Hayward et al. (1997) and had undergone dramatic shifts in abundance or extent in the 70 years between the studies. For example, Hayward suggested that one of Powell's major assemblage types—the “*Echinocardium* association”—had declined, whereas an “*Atrina zelandica* association” had emerged. Powell recognised the importance of both of these species to higher trophic levels, particularly as they were top components of snapper diets in a sample of 3515 fish. The *Echinocardium cordatum* formation constituted “a considerable proportion of the snapper's diet throughout the year”, with *E. cordatum* (8.10%) and *A. zelandica* (7.25%) ranking as the most important individual food items of this formation (Powell 1937). The locations of occurrence of these species were reported by Hayward et al. (1997), enabling us to select the most suitable sites for the subtidal sampling scheme.

The inclusion of *A. zelandica* and *E. cordatum* in the model was also dictated by their key functional roles in New Zealand soft-sediment habitats (Norkko et al. 2001, 2006, Lohrer et al. 2004, 2005; Hewitt et al. 2006). Both *A. zelandica* and *E. cordatum* are native species that have the potential to affect invasion resistance. Invasions by *Theora lubrica*, *Musculista senhousia*, and *Limaria orientalis* (all infaunal bivalves from Asia) were modelled in light of changes in the distribution of *A. zelandica* and *E. cordatum* and according to the particular natural histories of the sets of interacting species.

3. Methods

3.1 INTERTIDAL SURVEY

Data used in the intertidal meta-analysis were selected from four separate datasets, encompassing information from a total of 62 sites. The data set incorporated a wide spatial extent of the Greater Waitemata Harbour, including the Central and Upper sections of the Waitemata Harbour, the Tamaki Estuary and an intertidal site on Waiheke Island. The central section of the Waitemata Harbour spanned from the Whau River west to the Purewa Creek. The Upper Harbour section spanned from Hobsonville north to Lucas Creek (See Figure 1). Forty of the sites were from the Auckland Regional Council (ARC) contaminants dataset, which was collected in order to examine the effects of sediment contamination on intertidal macrofaunal communities. For these forty sites, all macrofaunal data were accompanied by heavy metal concentration data. A further 18 sites were chosen from ARC monitoring datasets: 5 from the Central Waitemata Harbour monitoring programme and 13 from the newly initiated Upper Waitemata Harbour monitoring programme. The remaining 4 sites were collected as part of a NIWA-run project, with two of the sites positioned inside marine reserves. Although the four data sets were compiled for different reasons, standard methods were used at all 62 sites and NIWA staff were involved in the collection and processing of all samples. Ten macrofauna samples per site, plus available environmental data (including biotic and environmental indices we calculated), were used in the meta-analysis.

Sample methodologies have been described in detail in ARC reports (Halliday and Hewitt 2006; Hewitt et al. 2006). To summarise, all macrofauna were collected using sediment cores (13 cm internal diameter, 15 cm deep), with samples sieved through a 500 μm mesh screen. All material retained on the sieve was preserved in 70% isopropyl alcohol and stained with Rose Bengal. Samples were sorted, and macrofauna were identified to the lowest taxonomic level practicable (usually species level). For the meta-analysis, abundance data from 10 replicate cores were averaged, providing one representative value for each species per site. In addition to the average abundance data for individual species, several summary variables were calculated. These are listed as follows:

- **Community indices.** The total number of individuals, the total number of native individuals, and the total number of NIS individuals were tabulated using PRIMER version 6 software (Clarke and Gorley 2006). Also using PRIMER, measures of species richness, community evenness (Margalef's d) and species diversity (Shannon-Wiener H' , Simpsons) were calculated for all species, native species and NIS.
- **Bioturbation Index.** The degree of bioturbation at each site was estimated using a per capita index of bioturbation (Swales et al. 2007; Lohrer et al. *in prep.*). The bioturbation index ranked different benthic species in relation to three categories important in sediment reworking: burrowing behaviour, mobility and size. At each site, the bioturbation potential of each species present was multiplied by its abundance. Bioturbation values were then summed across all species to give an estimate of bioturbation at the site.

At each site, sediment characteristics were sampled in order to quantify grain size, organic matter and chlorophyll a content. At six locations within each site, two small sediment cores (2 cm deep, 2 cm diameter) were collected, one to determine grain size and organic matter content, and the other for chlorophyll a analysis. The six individual cores per site were pooled prior to analysis, yielding one representative value per site. For sediment metal concentrations, samples were collected with deeper cores (15 cm deep, 5 cm diameter, $n=3$ per site). All samples were kept frozen in the dark prior to being analysed. Sediment analyses were performed as follows:

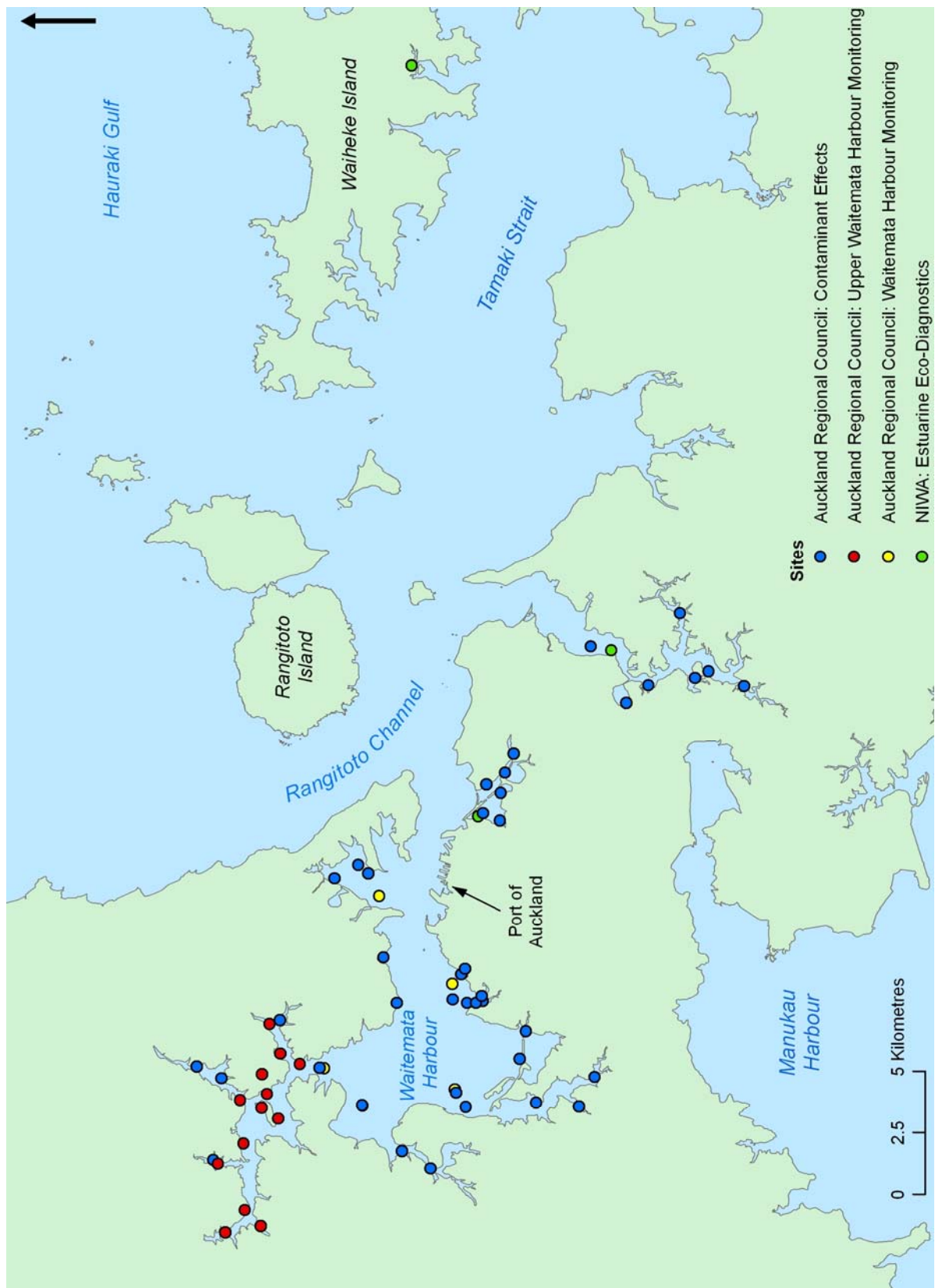


Figure 1: Locations of 62 intertidal sites used in the Waitemata Harbour NIS meta-analysis.

- **Grain size.** Samples were homogenised and a subsample of approximately 5 g of sediment taken. The subsample was digested in ~9% hydrogen peroxide until frothing ceased. The sediment sample was then wet sieved through 2000 µm, 500 µm, 250 µm and 63 µm mesh sieves. All fractions were then dried at 60°C until a constant weight was achieved (fractions were weighed at ~40 h and then again at 48 h). The results of the analysis were calculated as percentage weight of coarse (>500 µm), sand (500–62.5 µm) and mud (<62.5 µm).
- **Organic matter content.** Approximately 5 g of sediment was placed in a dry, pre-weighed tray. The sample was then dried at 60°C until a constant weight was achieved (the sample was weighed after ~40 h and then again after 48 h). The sample was then combusted at 400°C for 5.5 h (Mook and Hoskin 1982) and then reweighed. Organic matter content was calculated as percent loss on ignition (%LOI).
- **Chlorophyll *a*.** Due to chlorophyll *a* degradation over time, chlorophyll *a* samples were analysed within 1 month of collection. Prior to analysis, samples were freeze dried (to standardise water content), weighed, then homogenised. A subsample (~0.5 g) was taken for analysis. Chlorophyll *a* was extracted by boiling the sediment in 90% ethanol, and the extract processed using a spectrophotometer. An acidification step was used to separate degradation products from chlorophyll *a*.
- **Heavy Metals.** Concentrations of copper, lead and zinc were determined using strong acid digestion of freeze dried <500 µm surface sediment in aqua regia (HCl/HNO₃) at 100–110 °C. Metal concentrations were determined for each of the three cores and then averaged per site.
- **Distance from Port.** As the port was a possible source of NIS propagules (due to hull fouling and discharge of NIS from ship ballast water), the distance from the main port to all 62 intertidal sampling sites was calculated for use in the meta-analysis. An arbitrary but central location in the Port of Auckland (36° 50' 30" S, 174° 46' 23" E) was selected. Distance was calculated using Garmin MapSource software, using a direct route over water from each site to the port.

3.2 STATISTICAL METHODS FOR THE INTERTIDAL META-ANALYSIS

Multiple regression models were used to analyse the relationships between species abundance and variables of interest. Non-linearities in the data were incorporated by utilising log transformations and including polynomial terms and splines (GAMs). Due to the high incidence of zeros in species abundance data (i.e., the dependent variables), Poisson error structures and log-link functions were sometimes required. When data were over dispersed, quasi-likelihood estimators were used. Logistic regressions, where the presence or absence of a variable is modelled, were appropriate for determining factors associated with the presence/absence of NIS at particular sites. A backwards elimination method—starting with a full model with all independent variables included—was used to select the best possible final model (based on criteria including sums of squares, r^2 and AIC values).

Variables used as dependent variables in the meta-analysis included the number of NIS individuals and species, and the number of individuals of the most common NIS species (*Theora lubrica* and *Polydora cornuta*). As independent (predictor) variables, the number of native individuals and taxa, native evenness (Margelef's) and diversity indices (Shannon-Weiner and Simpsons) were used. Indices of bioturbation and native functional richness were also used, as were the numbers of individuals of two important native species (the tellinid bivalve *Macomona liliana* and the venerid bivalve *Austrovenus stutchburyi*). When analysing *T. lubrica* and *P. cornuta*, total native bivalve abundance and total native spionid abundance (tube worms *Boccardia syrtis*) were used as predictors, respectively. For some analyses (depending on the question), NIS individuals, *T. lubrica* individuals and *P. cornuta* individuals were used as independent variables.

Contaminant data were available from the majority of sites and were used to determine whether or not contamination (a form of stress/disturbance) was related to invasion success. Copper, zinc and lead were highly correlated with each other in our data set (Table 1). There was also some correlation between mud and metals (and mud and other variables), but these were not strong. Due to the high correlation of the three metals, and because we were interested in the overall effect of stormwater contamination (rather than a specific metal), a variable representing overall metal contamination was derived following Anderson et al. (2006). Briefly, a principle component analysis (PCA) on $\log_e(x + 1)$ transformed metal data was run using the PRIMER version 6 software (Clarke and Gorley 2006) with the first axis used (representing 98.7% of the variability). The PCA was carried out on raw rather than normalized data, as all three log metal concentration variables were measured in the same units on the same scale. This approach was also attempted to condense sediment grain sizes into a single variable. However, this was unsuccessful due to both positive and negative correlations amongst different size classes and so was not used in the analysis.

Table 1: Pearson’s correlation coefficients between environmental variables. Copper, lead and zinc are measured as total extracted from <0.5 mm sediment fraction and given as mg kg⁻¹. Sediment grain sizes are measured in % weight of size fraction.

	Medium sand	Mud	Distance	Copper	Lead	Zinc
Coarse sand (> 500µm)	0.38	-0.44	0.00	-0.27	-0.17	-0.13
Medium sand (500 – 63µm)		-1.00	-0.42	-0.66	-0.39	-0.39
Mud (< 63µm)			0.41	0.66	0.39	0.38
Distance (km)				0.37	0.05	0.16
Copper					0.86	0.85
Lead						0.92

Interactions between environmental variables were investigated in two ways: as categorical variables and as multiplicative effects between continuous variables. In the categorical analysis, the sediment particle size variables were converted to sediment type classes (e.g., mud, muddy sand, see Table 2). As many of the relationships between NIS variables and distance from port exhibited a unimodal distribution, distance was also converted to a class variable (near < 8 km, mid >8 km <16 km, far > 16 km). Sediment type and distance were then included in the regression analysis as class variables along with their interaction term, the contaminant variable and the biological variables of interest. In the categorical analysis, all first-order interactions (pairs of variables multiplied together) were included in initial models. As not all sites had information on sediment organic matter or chlorophyll *a* content, these variables were incorporated at the end of the analysis, into the end model. We had intended, if they proved important and replaced other variables, to use patch analysis to investigate their correlations with the replaced variables. However, this was not necessary as chlorophyll *a* and organic matter content had low explanatory power and did not replace other variables.

Table 2: Categorical classification of sediment types based on their percentage mud content. Sediment varied between sites from very muddy to sandy and included sites with a mixture of shelly sand and mud.

Category	Description	Site representation
Very muddy	Mud content > 70%	18
Mud	Mud content 30 - 70%	8
Muddy sand	Mud content 3 - 10%, coarse sand < 4%	5
Sandy mud	Mud content 10 - 30%	8
Sandy	Sand content > 90%	7
Coarse sand and mud	Mud content > 5%, coarse sand > 4%	4
Muddy, shelly sand	Mud content 3 - 10%, coarse sand > 4%	8

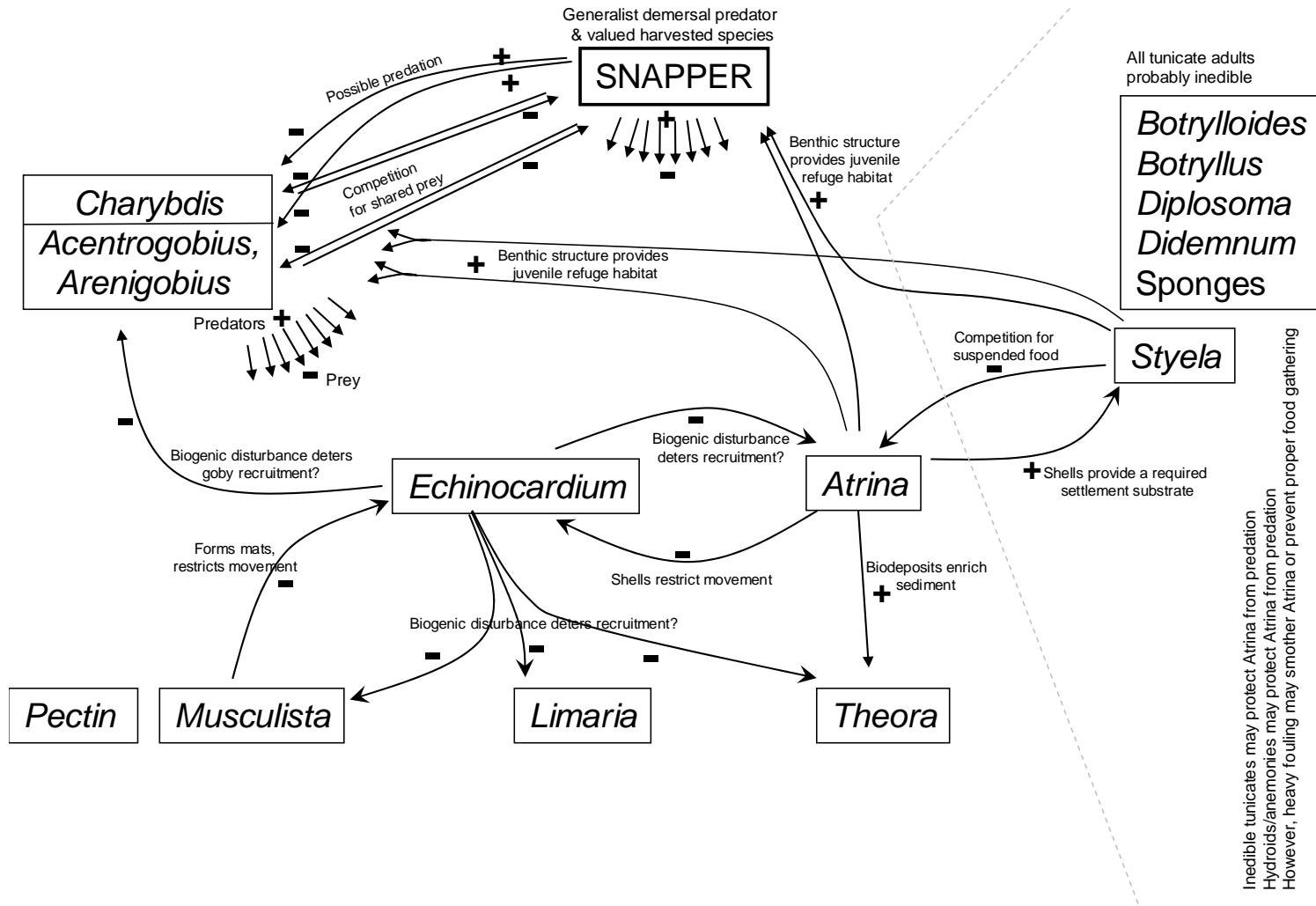


Figure 2: The conceptual model of species interactions in the Waitemata Harbour. Model structure adapted from Duffy (2006). Species listed are a small subset of total diversity.

3.3 MODELLING APPROACH

A preliminary conceptual model was created (Figure 2) in a format similar to Duffy's Figure 2 (Duffy 2006). The preliminary model mapped out relationships between a selection of species of interest: a predatory demersal fish that is a valued harvested species (native snapper *Pagrus auratus*), invasive benthic predators (invasive paddle crabs *Charybdis japonica* and invasive gobiid fishes *Acentrogobius pflaumi* and *Arenigobius bifrenatus*), key native benthic species (the heart urchin *Echinocardium cordatum* and the horse mussel *Atrina zelandica*), invasive infaunal bivalves (the Asian semelid *Theora lubrica*, the file shell *Limaria orientalis*, the Asian date mussel *Musculista senhousia*), a native epifaunal bivalve (the edible scallop *Pecten novaezealandiae*), and several epifaunal invaders (mainly tunicates of the Styelidae family). The species explicitly listed in the model were a small subset of total benthic biodiversity.

Each box in the model was connected with signed (+ or -) digraph arrows, representing positive or negative interactions. Unlike Duffy (2006), functional interactions (biogenic disturbance, provision of hard substrate, organic enrichment) as well as possible trophic interactions were included in the model. Some of the interactions made explicit in the model are as follows:

- **Role of snapper.** Snapper are generalist predators that consume primarily large (>4mm) invertebrates from both soft and rocky substrates (Babcock et al. 1999). It is well recognised that snapper have a broad feeding niche in benthic habitats (Godfriaux 1969, Coleman 1972). Their generalist feeding strategy has resulted in many studies reporting different and broad diets (Powell 1937, Graham 1939, McKenzie 1960, Coleman 1972, Russell 1983), with the dominant food source varying according to local sedimentary conditions and the availability of suitably sized food. Godfriaux (1969) lists nearly one hundred species or higher taxonomic groups of organisms that formed part of the diet, including crustaceans (44%), polychaetes (11%), echinoderms (9.6%), molluscs and other fish. Powell (1937) stated that animals of the soft-bottom "*Echinocardium* formation" accounted for almost one-third of the varied diet of snapper, and he noted *Atrina zelandica* in the guts of snapper also. Large snapper have sizable teeth (Paulin 1990) capable of crushing thick-shelled benthic organisms, which implies that non-indigenous bivalves such as *L. orientalis* and *M. senhousia* are not immune to predation by snapper. Furthermore, snapper are known to alternate among food sources depending on their availability (Godfriaux 1969), suggesting that snapper will utilise NIS species as a food resource if NIS become abundant in the system. Therefore, snapper were modelled as having a general negative effect on all benthic taxa. Conversely, we predicted no significant negative effects of invasive species on snapper, with the possible exception of the paddle crab, *Charybdis japonica*, which could potentially compete with snapper by feeding on the same types of prey (e.g., benthic bivalves such as *M. senhousia*, *L. orientalis* and *T. lubrica*).
- **Role of *Atrina zelandica*.** *Atrina zelandica* is a large immobile bivalve whose shells protrude 5 to 15 cm above the sediment-water interface. The shells provide hard substrate above the soft-sediment surface, facilitating the colonisation of diverse encrusting and epifaunal life. Importantly, the protrusion of *A. zelandica* shells out of the sediment increases the vertical relief of soft-sediment habitats, particularly when the shells are covered with epibionts. Young-of-the-year juvenile snapper often associate with structured microhabitats, presumably as a refuge from predation (Thrush et al. 2002, M. Morrison, unpubl. data). Thus, *A. zelandica* was predicted to have general positive effects on snapper. *A. zelandica* is also known to promote the abundance and richness of infauna in sediments near its shells by producing organic-rich biodeposits (Norkko et al. 2001, 2006, Hewitt et al. 2006). The enhancement of diversity by *A. zelandica* may apply to native and invasive species alike. We know, for example, that *A. zelandica* shells can be colonised by non-indigenous ascidians (e.g., *Styela clava*) and cryptogenic parchment worms (*Chaetopterus* sp.) (Plate 1).

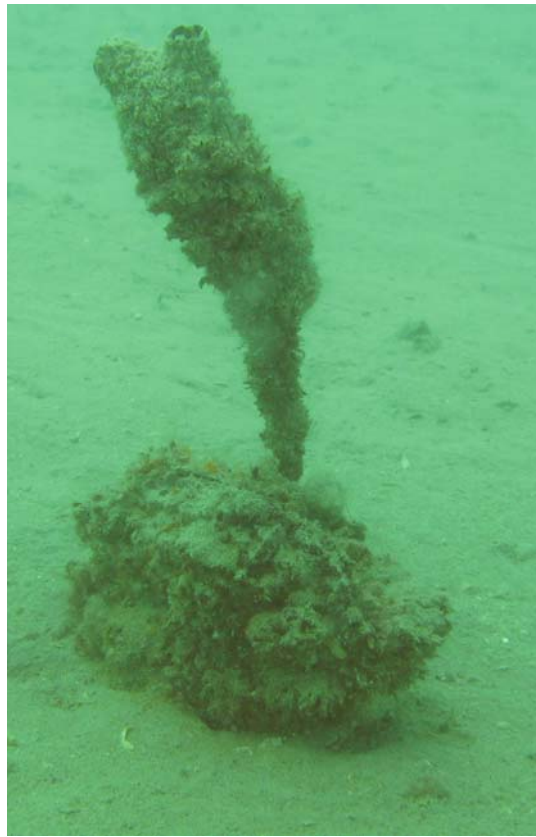


Plate 1: A specimen of *Styela clava* attached to *Atrina zelandica*. Photo taken in Kawau Bay, D. Lohrer (NIWA).

- Atrina zelandica*-*Theora lubrica* interactions.** *Theora lubrica* is a small semelid bivalve from Asia that has been present in New Zealand for 30-40 years (Climo 1976). It is an opportunistic species with fast growth and high reproduction (taking just 8 to 12 weeks to reach a reproductive size of 5-6 mm), though it is likely that it has low survivorship/competitive ability (very thin fragile shells) (Kikuchi and Tanaka 1976). In its native range, *Theora lubrica* is associated with muddy, organically enriched sediments (Yokoyama and Ishihi 2003). Several investigations (Cummings et al. 1998, 2001; Norkko et al. 2001, 2006; Hewitt et al. 2006) have demonstrated how *A. zelandica* facilitates certain types of macrofauna in the vicinity of its shells, due to the local enrichment of sediments via biodeposition. Positive effects of *A. zelandica* on *T. lubrica* are likely, given the life-history strategy and habitat preferences of *T. lubrica*. Furthermore, controlled manipulative experiments at three sites in the Mahurangi Harbour (North Island, New Zealand) demonstrated strong positive effects of *A. zelandica* on *T. lubrica* (Lohrer et al. 2008b). Therefore, a positive interaction between *A. zelandica* and *T. lubrica* was made explicit in the conceptual model. Similar enhancement effects could be true for the other non-indigenous bivalves in the Waitemata Harbour (e.g., *L. orientalis* and *M. senhousia*), but there was not enough information to warrant model arrows at the time of model development.
- Echinocardium cordatum*-*Theora lubrica* interactions.** *Echinocardium cordatum* is a burrowing heart urchin that is widely distributed in estuarine and coastal sediments around New Zealand. It can reach densities of ~80 individuals m⁻². Biogenic disturbance by *E. cordatum* is substantial in terms of the volume of sediment reworked (sometimes exceeding 20,000 cm³ m⁻² d⁻¹) as the urchins continually bulldoze through the upper 5 cm of sediment (Lohrer et al. 2005). Bioturbators often deter colonists by destabilising surface sediments (Rhoads and Young 1970, Woodin 1976, Thrush 1988, Wilson 1991, Tamaki 1994, Widdicombe and Austen 1999, Norkko et al. 2006, Pillay et al. 2007). In this way, bioturbators may contribute to an increased capacity to resist invaders. *T. lubrica* fits the

description of a species likely to be affected: it is a small bivalve with limited free movement that feeds from the sediment surface using a short siphon. Bioturbation by *E. cordatum* (with its constant lateral movements) would interfere with *T. lubrica* and most other small species that use vertical tubes or maintain burrow openings in order to gain access to the sediment surface and oxic water. *M. senhousia* and *L. orientalis* recruits may be affected in a similar way.

- **Role of *Musculista senhousia*.** *M. senhousia* is another small bivalve from Asia (32 mm maximum reported size) that has become prominent in Auckland area estuaries including the Waitemata Harbour (Hayward et al. 1997), the Tamaki Estuary (Creese et al. 1997), and the Manukau Harbour (Plate 2). *M. senhousia* can achieve sexual maturity and a size of 25 mm in one year (Crooks 1996). The impact of the species is generally linked to its role as an ecosystem engineer: *M. senhousia* individuals create cocoons using their byssal threads and, at moderate-to-high densities, populations of *M. senhousia* create thick byssal mats that alter the nature of the habitat (Crooks 1996). The mat structure has been shown to facilitate some types of intertidal organisms (Creese et al. 1997, Crooks 1998, Crooks and Khim 1999), but other larger organisms—such as bivalves and *E. cordatum*—may be negatively impacted by the mussel mats (Crooks 2001). Although high densities of *E. cordatum* may prevent the establishment of high density *M. senhousia* mats (see above), *E. cordatum* may not survive well in locations where *M. senhousia* mats are already established. Thus, *M. senhousia* and *E. cordatum* were linked by reciprocal negative interactions (- -) in the conceptual model.

We acknowledge that the veracity of the model is difficult to ascertain without explicit experimental tests of the modelled interactions. Nevertheless, the aim of the field work was to search and sample for species in the conceptual model at each of the five subtidal study locations. Based on positive or negative correlations in the densities of these species (plus field observations, literature, and general background knowledge), we sought to confirm the sign of the digraph arrows and to apply arrow weights, signifying the directions and strengths of key interactions between native and non-indigenous species. The ultimate goal was to better understand processes affecting invasion success and the potential flow-on consequences of established invaders in the Waitemata Harbour (Landis 2004).



Plate 2: *Musculista senhousia* mat from the Manukau Harbour. Photo C. Lundquist (NIWA)

3.4 SUBTIDAL SAMPLING

Five sites (Figure 3) were selected for quantitative sampling based on the species distributions reported in Hayward et al. (1997). Each of the sites had previously been shown to be dominated by a species of interest with respect to the modelling approach, including: (1) invasive *Limaria orientalis*, (2) native *Echinocardium cordatum*, (3) native *Atrina zelandica*, (4) invasive *Musculista senhousia*, (5) invasive *Theora lubrica*.

At each site, divers laid out a 20 m transect with 5 randomly determined sampling positions labelled along the length with pegs. To sample small benthic infauna, cores of sediment (10 cm internal diameter x 13 cm deep) were collected near each of the five marked sampling positions along the length of the transect. Five additional cores were collected away from the transect, often next to structures of interest that were present at the site (e.g., *A. zelandica* shells). After collection, all samples were sieved across a 0.5 mm mesh screen, preserved, sorted and identified (as described above; section 3.1). To quantify larger infauna that may not have been well represented in the core samples, five 0.25 m² quadrats were sampled per site (one quadrat at each of the five transect positions). Sediments within each quadrat were excavated and placed into a 5 mm plastic mesh bag. Large-sized animals (i.e., >5 mm longest axis) present in these samples were preserved in 70% IPA for later identification at the laboratory.

The entire length of the transect was videoed twice: once with the camera lens approximately 40 cm above the seabed and once with the camera lens 70 cm above the bed. Any notable species or features within the general vicinity of the transect (large tunicates, chaetopterids and tubes, epibionts on *Atrina zelandica*, scallops, etc) were also filmed when possible.

3.5 SNAPPER SAMPLING

To sample small juvenile fish and other mobile organisms living near the seafloor, opera house fish traps (Thrush et al. 2002, Inglis et al. 2005b) were deployed to Sites 1, 2, 3 and 5. Three traps on a single line (5 m apart) were baited with two pilchards and soaked overnight. All fish, crabs and starfish present in the traps the next day (minimum 12 hours soak time) were collected, identified and measured. All native organisms caught in the traps were released live after enumeration.

To sample snapper abundance and diet (to investigate the reliance of snapper on benthic food resources in particular), long-lines were used to catch snapper at each study site. For each of the sites, spatial coordinates for a 200 x 200 metre box were generated, centred on the mid-point of the diver-surveyed transect. A commercial long-line vessel, was used to set as many hooks as practical within the confines of these boxes, using either a V or Z shape set, depending on the area available. At some sites the full extent could not be fished, due to very shallow waters, rocks and tidal currents, and/or the presence of moored recreational yachts. Sets were made after 9 am in the morning. Recent work (M. Morrison pers. obs.) has demonstrated that while setting before or at dawn returns the highest snapper catch rates (and is standard commercial practise), stomach contents from these fish are effectively empty, and of little use for dietary studies. A range of 120 to 200 hooks were fished in each block per set, baited with squid and pilchard, and left to fish for 1 to 2 hours. Additional sets were made at several sites in an effort to boost sample sizes.

On retrieval, all fish were placed in an ice-seawater slurry, with onion sacks used to keep fish from different sites separate. Both live and dead (gut-hooked) snapper were kept, as well as all by-catch. On the completion of fishing, fish were packed into standard iki fish bins with ice, landed at the wharf, and immediately transported to a NIWA laboratory. At the laboratory, the following were collected from each fish – fork length down to the nearest mm, sex, both otoliths, the foregut/stomach, and the hind gut. Guts were fixed in 10% formalin buffered in salt water and later transferred to 70% IPA. The foreguts were dissected and rinsed to remove all ingested organisms which were identified under a microscope (x120 magnification). Counts were based on whole organisms or readily identifiable fragments of whole individuals (using a conservative approach to avoid overestimation of food item counts).

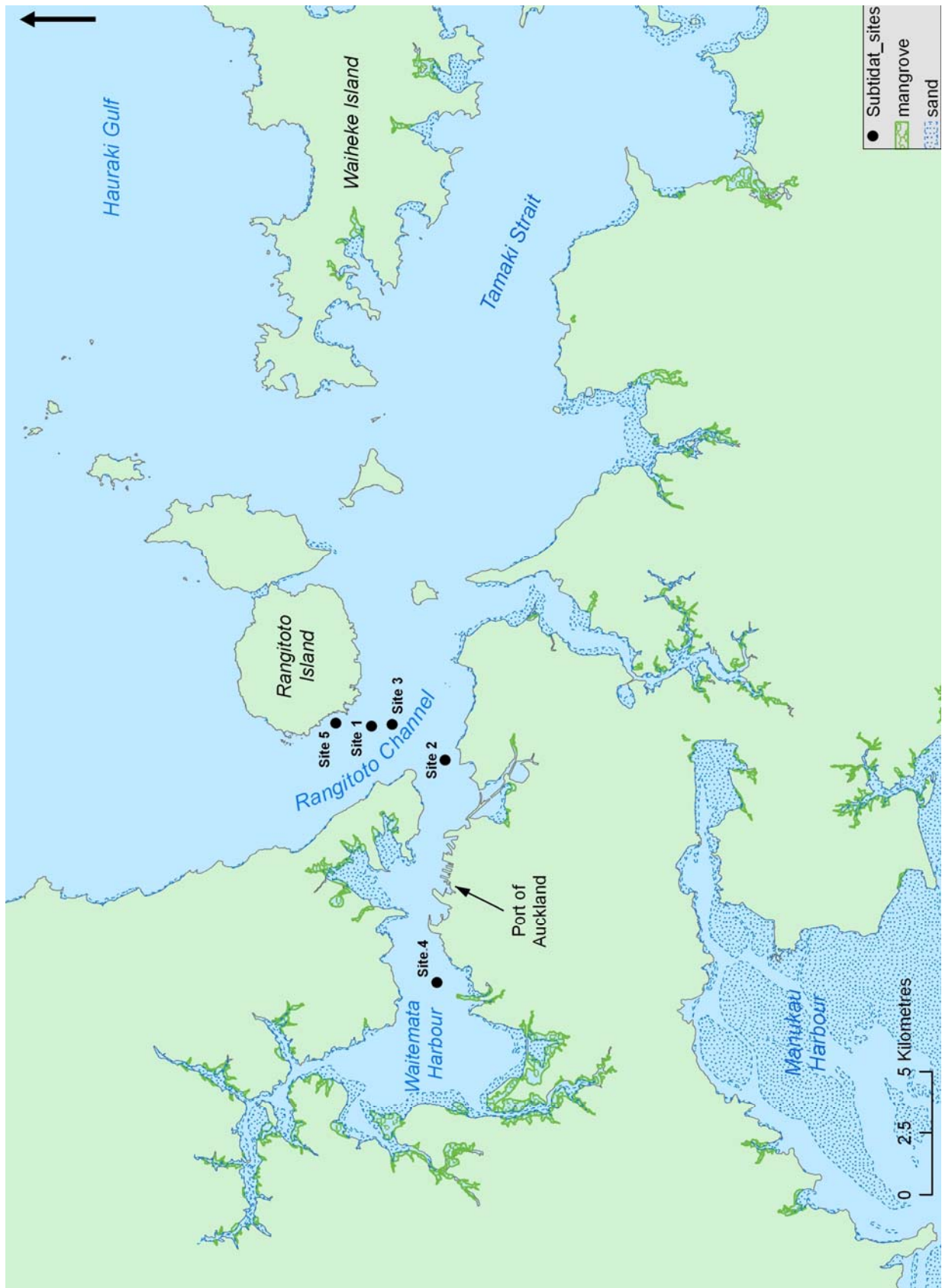


Figure 3: Map of five subtidal study locations in Waitemata Harbour that were sampled as part of this investigation. Previous data from these locations, which formed the basis of the conceptual model shown in Fig. 2, was given in Powell (1937) and Hayward et al. (1997).

4. Results

4.1 INVASION OF INTERTIDAL SOFT-SEDIMENTS

Two NIS that can be readily observed in intertidal estuarine habitats of the Auckland Region are Pacific oysters (*Crassostrea gigas*) and Asian date mussels (*Musculista senhousia*). There are other NIS that may occur in these intertidal habitats (Appendix 1), but the majority of these species are tiny, infaunal and most seem to be rare. When present at low densities, even *Musculista senhousia* can be considered a “cryptic NIS”, as it cannot be observed or easily quantified without collecting and processing sediment samples. In the data available for the meta-analysis, the most prevalent of the “cryptic NIS” were *Musculista senhousia*, *Theora lubrica*, and *Polydora cornuta*. In our analysis of cryptic NIS, we focused on the total number of non-indigenous individuals (NIS abundance), the number of non-indigenous taxa (NIS richness), and abundance of *T. lubrica* and *P. cornuta*. *M. senhousia* and the invasive corophid *Corophium acutum* were not analysed as they only occurred at a few sites (i.e., the data set was dominated by 0’s).

Distribution maps of native and invasive species richness and the abundances of *M. senhousia*, *T. lubrica* and *P. cornuta* were constructed using Arcview software (Figures 4 to 8). Figure 4 shows that the numbers of native taxa were generally high, although lower numbers were recorded in the upper creeks. In comparison with native richness, NIS richness was often an order of magnitude lower, with no site containing more than 3 non-indigenous species (Figure 5). Also in contrast to the native taxa, NIS richness was higher in the upper tidal creeks, relative to the rest of the harbour (Figure 5).

The abundances and distributions of *T. lubrica* and *P. cornuta* followed the general pattern for invasive taxa, with higher abundances in the upper tidal creeks than the lower estuarine sections (Figures 6 and 7). *T. lubrica* was distributed throughout the Waitemata Harbour and in the Tamaki estuary. *P. cornuta* was found to occur in the central and outer harbour sections, although in much lower abundances. *M. senhousia* was less common than *T. lubrica* and was only found at a few sites within the Central and Upper Waitemata Harbour (Figure 8). Where *M. senhousia* occurred, it was generally of low abundance, typically containing between 1-16 individuals per 13cm diameter core (75-1205 individuals m⁻²). Higher densities of *M. senhousia* (46-75 individuals per core) were recorded at only two sites near the Whau and Lucas Creeks.

The multiple regression analysis found NIS abundance, *T. lubrica* abundance and *P. cornuta* abundance to be explained by several model variables (57, 66 and 66 % explained respectively, Table 3). The abundance of NIS was positively related to mud content, the bioturbation index, and the density of *M. liliiana*. NIS richness was not well explained by any of the independent variables (<15%), although there were indications of a positive relationship with mud content and the density of *M. liliiana*.

The abundances of individual invasive species were influenced by multiple model parameters. *P. cornuta* abundance was positively related to mud content and the density of *M. liliiana*, and negatively related to the density of native individuals. *P. cornuta* was also negatively influenced by stormwater contaminants (i.e., the “pcm” variable). Both *P. cornuta* and *T. lubrica* abundances were positively related to the bioturbation index. *T. lubrica* abundance was also found to be negatively affected by the density of native cockles (*Austrovenus stutchburyi*). Interestingly, *T. lubrica* abundance was negatively influenced by *P. cornuta* abundance (and vice versa). It is not possible to tell from the analysis whether one species is controlling the other, or whether there is a mutual antagonistic interaction. However, analysis based on presence/absence data (Table 4) suggests that it is *P. cornuta* that influences the presence of *T. lubrica*.

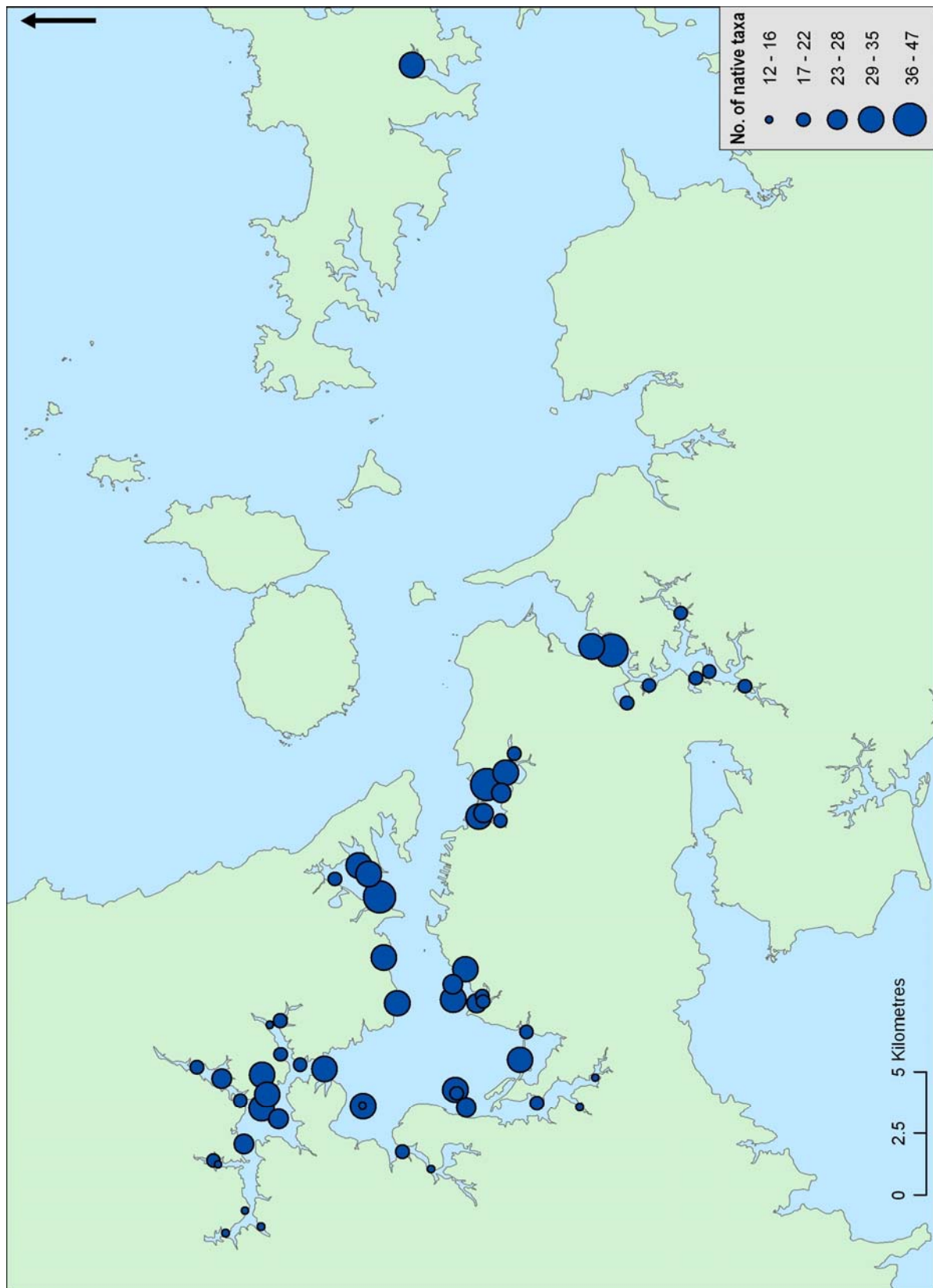


Figure 4: Map showing the spatial distribution of native richness (No. of native taxa per 13 cm dia. core) in the Waitemata Harbour. Sites with large dots had more native taxa (see legend on figure).

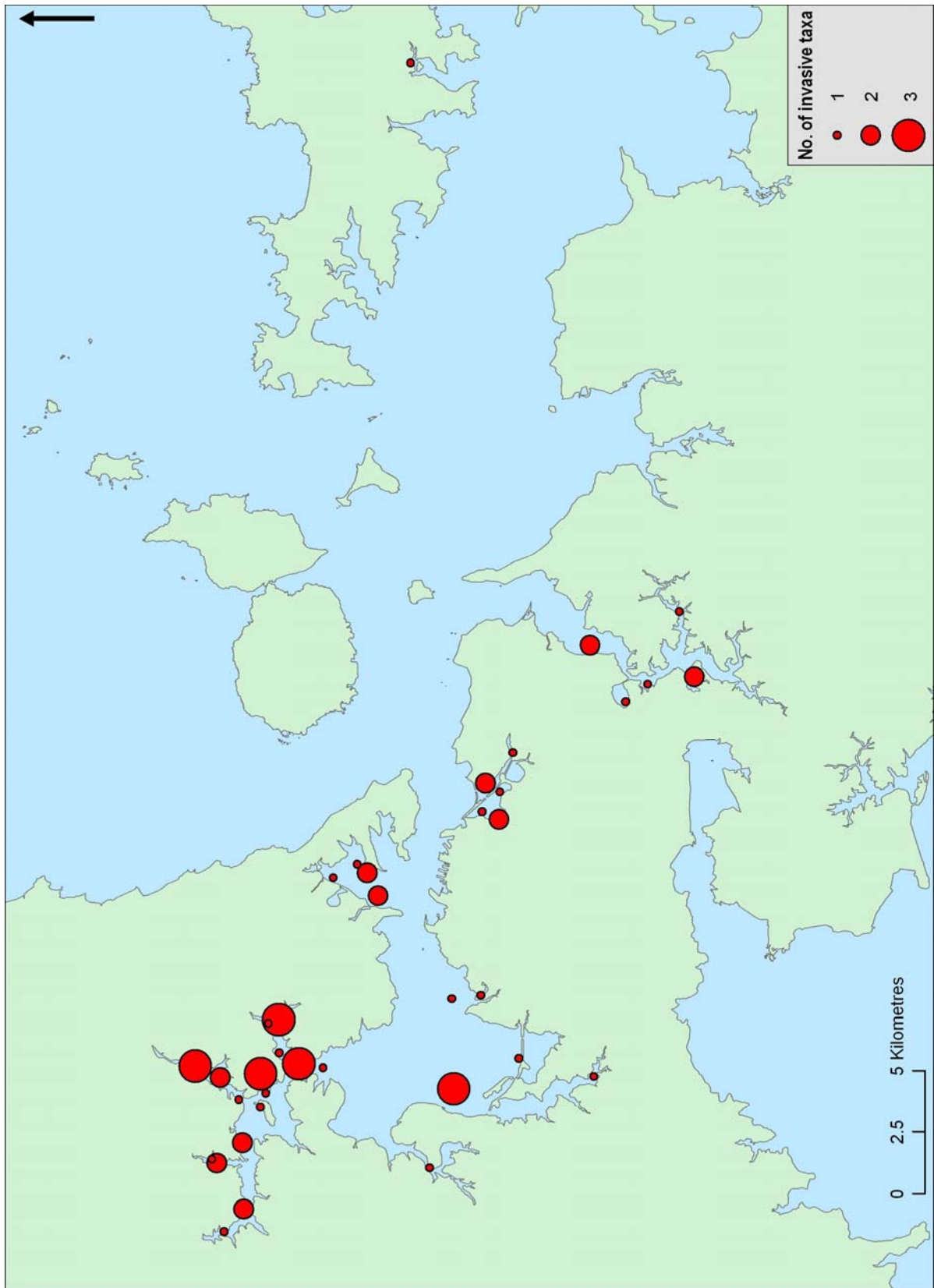


Figure 5: Map showing the spatial distribution of NIS richness (No. of NIS taxa per 13 cm dia. core) in the Waitemata Harbour. Sites with large dots had more non-indigenous taxa (see legend on figure).

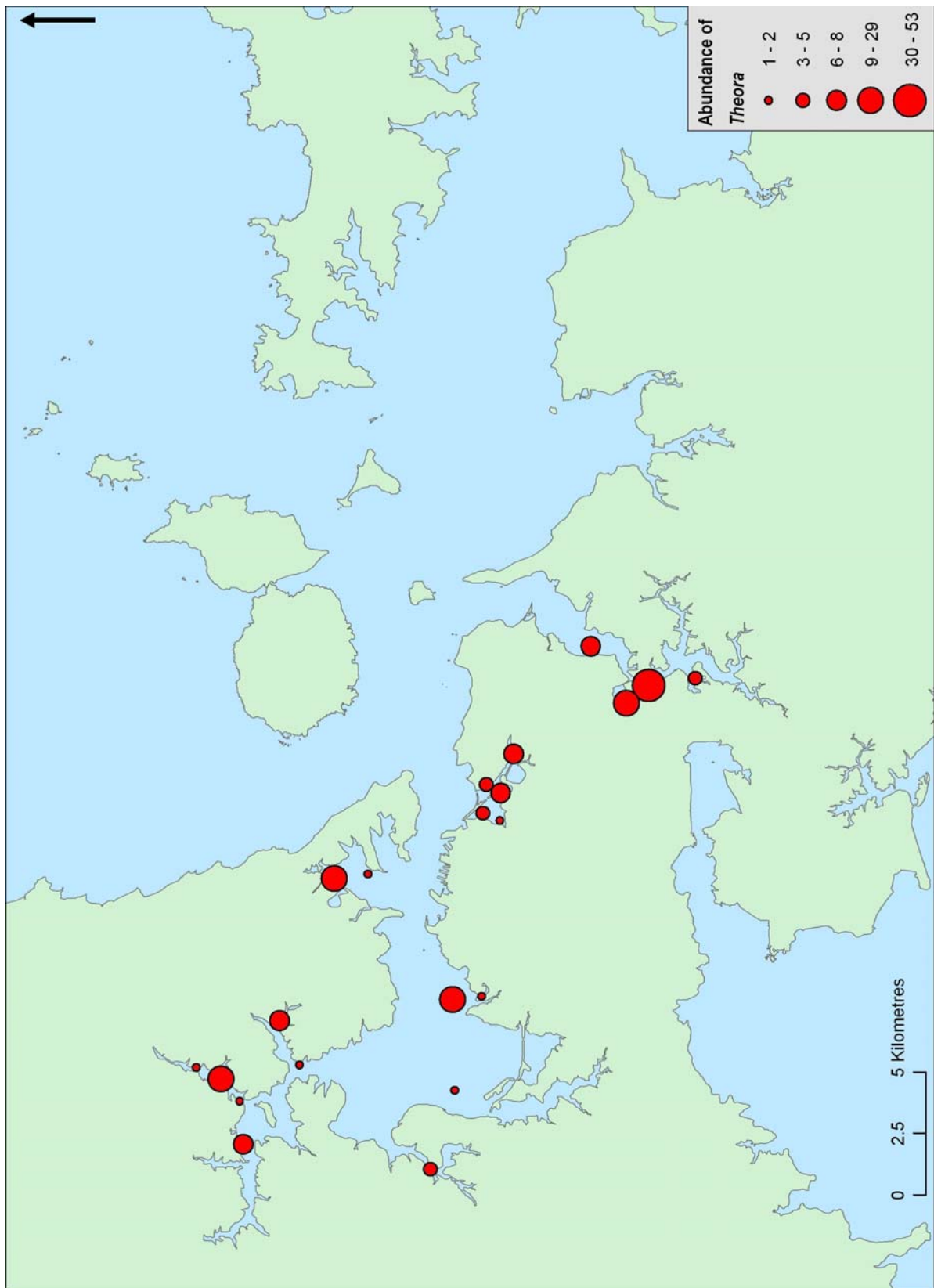


Figure 6: Map showing the spatial distribution of *Theora lubrica* abundance (No. per 13 cm dia. core) in the Waitemata Harbour. Sites with large dots had more *T. lubrica* (see legend on figure).

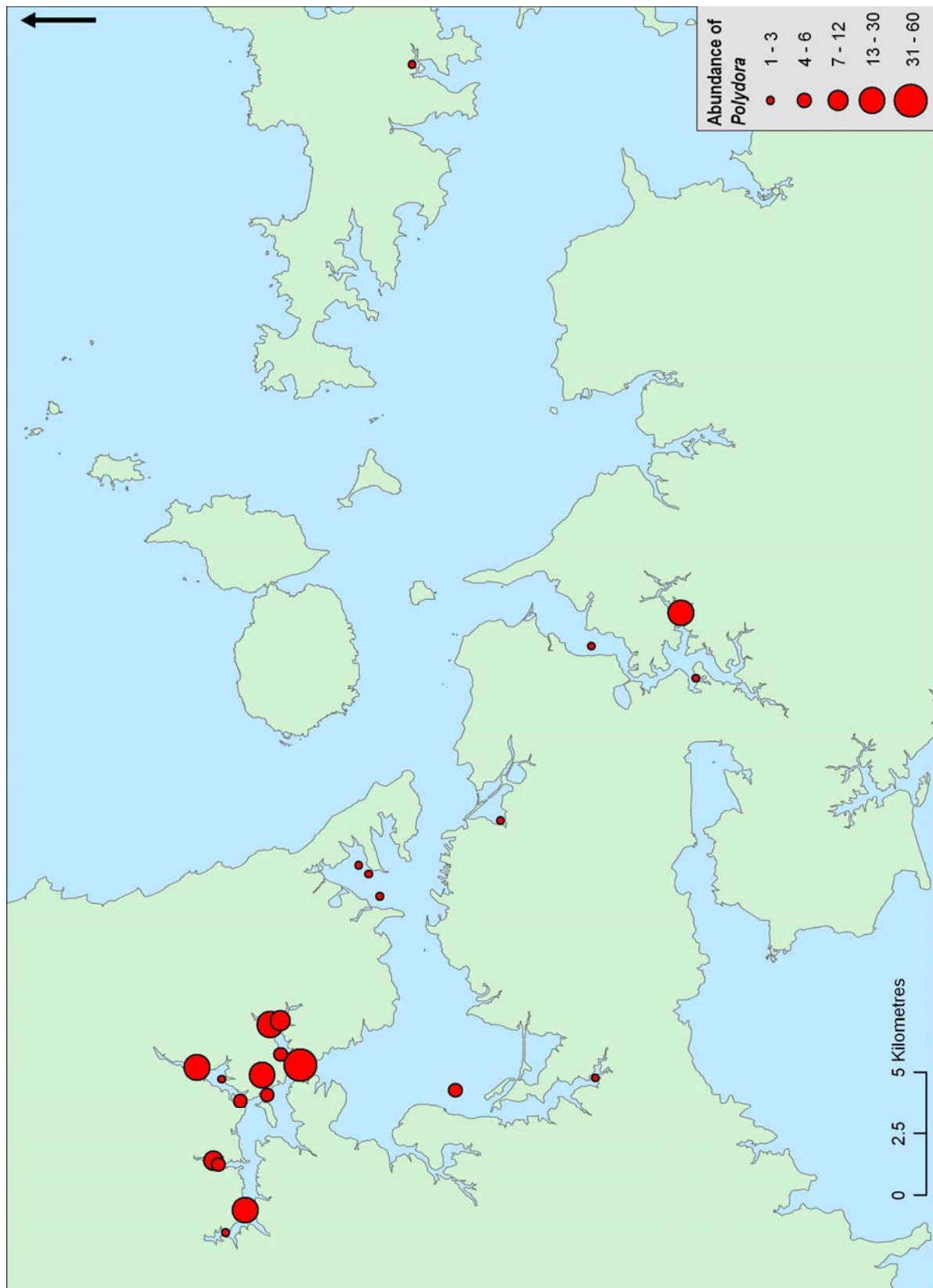


Figure 7: Map showing the spatial distribution of *Polydora cornuta* (No. per 13 cm dia. core) abundance in the Waitemata Harbour. Sites with large dots had more *P. cornuta* (see legend on figure).

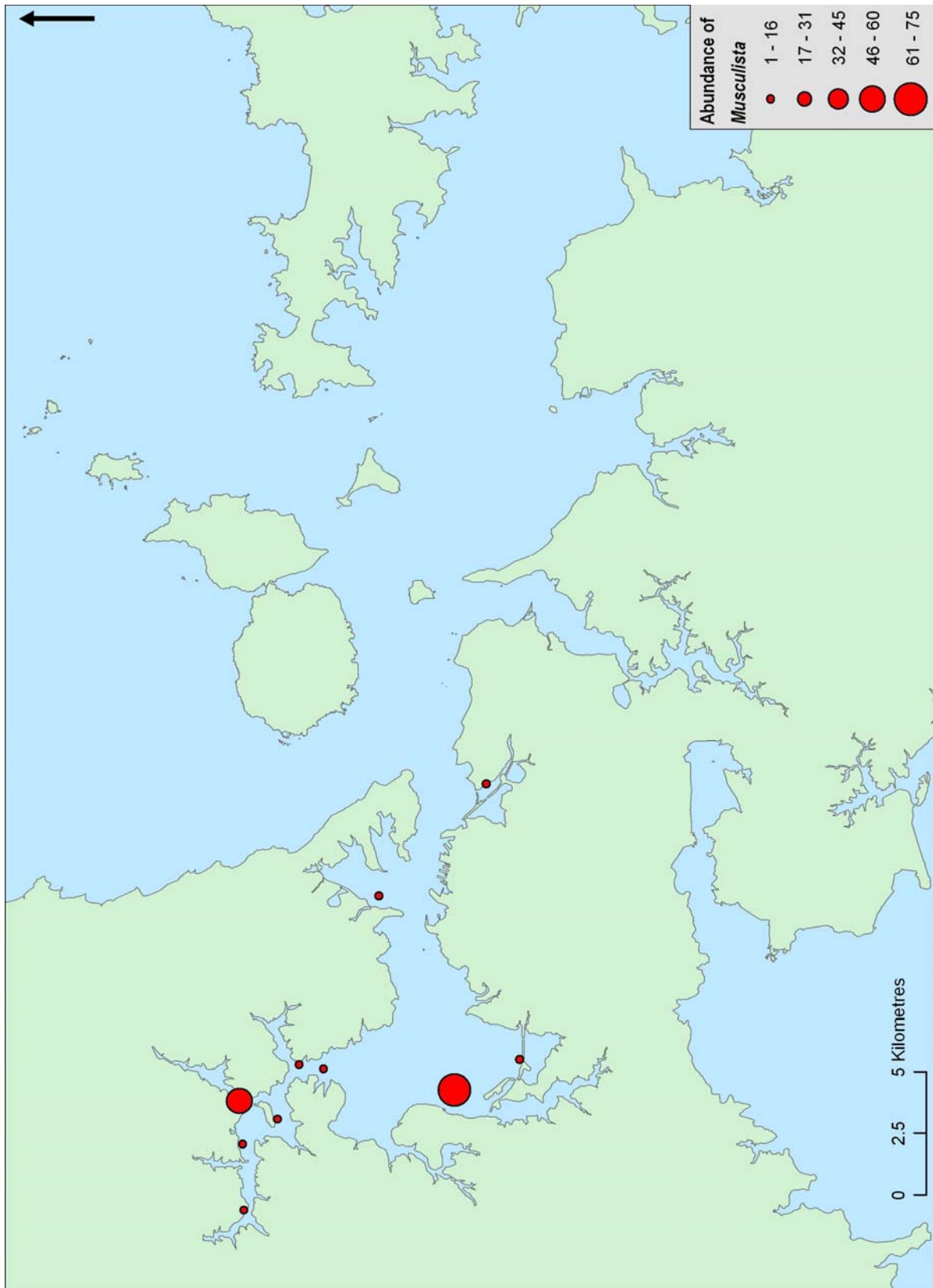


Figure 8: Map showing the spatial distribution of *Musculista senhousia* (No. per 13 cm dia. core) abundance in the Waitemata Harbour. Sites with large dots had more *M. senhousia* (see legend on figure).

Table 3: Results of modelling the abundance of NIS in Waitemata. Total degrees of freedom is 57 for all models, all results were obtained using quasi-likelihood estimators for a Poisson variance with a log link function, except that for the Number of non-indigenous species. The percent explained by the model is given after the dependent variable name. Nnind=total density of natives, bioturb = Bioturbation index, mud = sediment mud content, *Macomona* = density of *M. liliana*, *Austrovenus* = density of *A. stutchburyi*, *Polydora* = density of *P. cornuta*, *Theora* = density of *T. lubrica*, pcm = contamination index from PCA.

Number of non-indigenous individuals (NIS abundance) (56.6%)							
	SS or Deviance	F-value	p-value	Estimate	SE	Chi-square value	p-value
Model	684.33						
Error	524.23						
Intercept				-0.2577	0.468	0.30	0.5819
Nnind				-0.0015	0.0007	4.40	0.0359
Bioturb				0.0001	0	19.49	<.0001
Mud				0.0224	0.0056	15.96	<.0001
<i>Macomona</i>				0.0513	0.008	41.53	<.0001
Number of non-indigenous species (NIS richness) (12.5%)							
Model	7.83	7.83	0.02				
Error	54.84	54.84					
Intercept				-0.7263	0.3064	5.62	0.0177
Mud				0.0113	0.0044	6.65	0.0099
<i>Macomona</i>				0.0207	0.0085	5.87	0.0154
<i>Theora</i> abundance (65.9%)							
Model	427.46						
Error	223.29						
Intercept				-1.4605	0.4736	9.51	0.002
<i>Polydora</i>				-0.0847	0.0242	12.30	0.0005
Bioturb				0.0001	0	81.96	<.0001
<i>Austrovenus</i>				-0.0085	0.0026	10.59	0.0011
<i>Polydora</i> abundance (66.3%)							
Model	485.93						
Error	246.74						
Intercept				3.258	1.9317	2.84	0.0917
Bioturb				0.0001	0	22.01	<.0001
Mud				0.0407	0.0078	27.26	<.0001
Pcm				-4.9021	2.1757	5.08	0.0243
Nnind				-0.0032	0.0011	8.80	0.003
<i>Theora</i>				-0.0861	0.0414	4.33	0.0374

Table 4: Results of modelling the presence/absence of NIS in Waitemata. Total degrees of freedom is 57 for all models, all results were obtained using binary functions with a logit link. The percent concordance of the model is given after the dependent variable name. NB 50% is equivalent to random. Nnind=total density of natives, bioturb = Bioturbation index, mud = sediment mud content, *Austrovenus* = density of *A. stutchburyi*, *Polydora* = density of *P. cornuta*, pcm = contamination index from PCA.

Parameter	Estimate	SE	Chi-square value	p-value
<i>Polydora</i> (74.4%)				
Intercept	-1.5764	0.8328	3.58	0.0584
Mud	0.0204	0.0095	4.61	0.0318
Nnind	-0.00159	0.00139	1.29	0.2553
Bioturb	0.000029	0.000033	0.81	0.3668
<i>Theora</i> (73.6%)				
Intercept	-2.8466	0.9017	9.97	0.0016
<i>Polydora</i>	-0.1153	0.0654	3.11	0.0779
<i>Austrovenus</i>	-0.00668	0.00403	2.74	0.0977
Bioturb	0.000094	0.000035	7.24	0.0071
Non-indigenous species (68.0%)				
Intercept	0.7716	2.3993	0.10	0.7478
Mud	0.0257	0.0124	4.30	0.0381
Pcm	-3.2245	2.8103	1.32	0.2512

Most of the analyses based on presence/absence data (Table 4) show similar results to the analyses based on abundance data, although the density of *M. liliانا* is no longer important (suggesting that *M. liliانا* affects NIS abundance, but does not determine occurrence of NIS species at a site). Similarly, the degree of contamination is important for the abundance of *P. cornuta*, but not for its occurrence. Interestingly, stormwater contaminants were important in predicting the overall presence/absence of NIS, with increased contamination decreasing the likelihood of NIS occurrence.

Variables that were not selected by the model as important for prediction included native evenness, Shannon-Weiner index and Simpsons index and the total density of native bivalves. While the sediment mud content was important, overall sediment type (a descriptor that included the amount of fine sand and coarse shell particles) wasn't; neither as a categorical or continuous variable. There was also no apparent relationship between NIS and distance to the port, which may not be surprising given the length of time most of these cryptic invaders have been in New Zealand, and the fact that they prefer the muddier sediments located in upper estuaries.

4.2 INVASION OF SUBTIDAL SOFT-SEDIMENTS: SURVEY OF 5 SITES

4.2.1 Macrofauna

Using macrofauna data collected at our five subtidal sampling sites, we were able to differentiate three distinctive benthic community types (Figure 9). The community types were determined primarily by the densities of *M. senhousia* and *T. lubrica*. The first community type was dominated by high densities of *M. senhousia* (averaging >148 inds core⁻¹). The second community type had high *T. lubrica* density (>13 inds core⁻¹) in combination with low *M. senhousia* density (<1 individual per core). The third community type had low densities of both invaders (<4 inds core⁻¹).

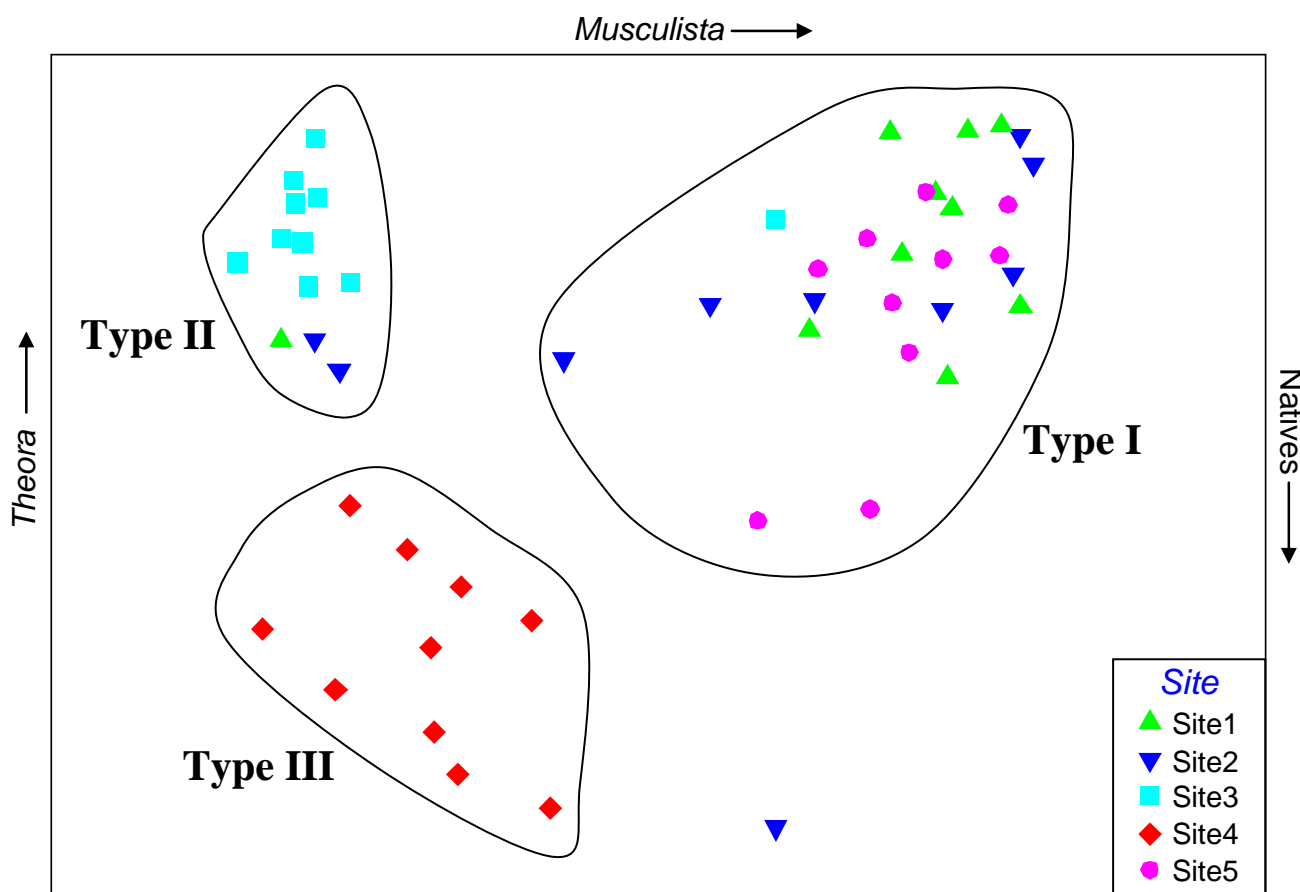


Figure 9. Nonmetric multidimensional scaling (MDS) ordination plot depicting similarities in macrofaunal community structure. Untransformed data from $n=10$ cores, collected at 5 subtidal sites in the Waitemata Harbour, are presented. Data points that are close together in ordination space have similar macrofaunal community composition (based on Bray-Curtis similarities). Stress = 0.12. The three clusters of points are separated primarily by the densities of two non-indigenous species, *Musculista senhousia* and *Theora lubrica*.

The different community types reflected differences among our sampling sites. For example, extensive *M. senhousia* mats dominated the seafloor at Sites 1, 2 and 5, and macrofauna collected at these three sites generally clustered together as community type I (Figure 9). Site 3 was *T. lubrica* - dominated (community type II), whilst Site 4 had moderately low proportions of both invaders (community type III). Nevertheless, at all five study sites, non-indigenous bivalves constituted more than 20% of the total macrofaunal abundance quantified using sediment cores. NIS comprised more than 85% of the total individuals at Sites 1 and 5, about 65% at Site 2, and 45% at Site 3. Apart from NIS, differences in macrofaunal community structure among sites were subtle (Figure 10).

Site 1, with the greatest abundance of NIS individuals (Figure 11), had low abundance and low richness of native macrofauna. However, despite wide variation in NIS abundance at Sites 2-5, the number of native individuals did not differ significantly among these sites (Figure 11). Site 3 had relatively few invaders, but also a low native species richness (Figure 11).

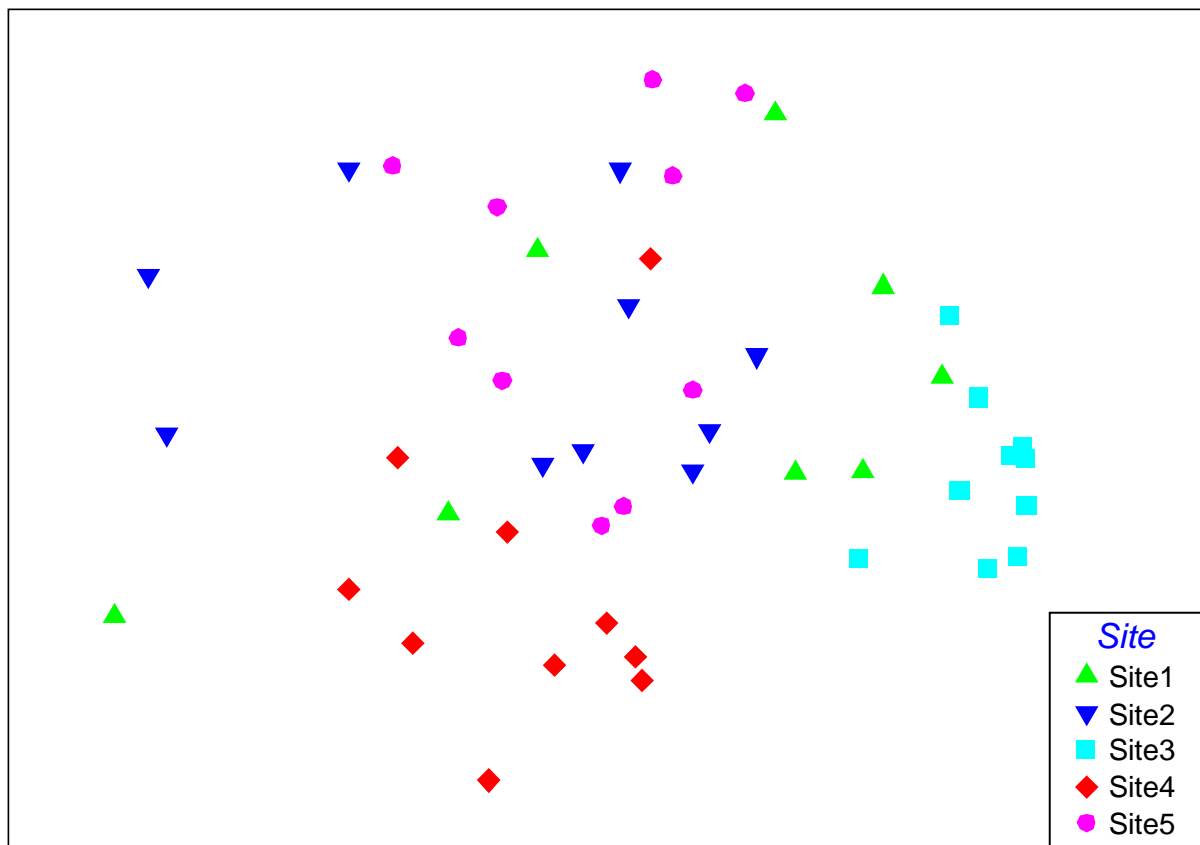


Figure 10. Nonmetric multidimensional scaling (MDS) ordination plot depicting similarities in macrofaunal community structure after removing NIS from the data set. Untransformed data from $n=10$ cores, collected at 5 subtidal sites in the Waitemata Harbour, are presented. Data points that are close together in ordination space have similar macrofaunal community composition (based on Bray-Curtis similarities). Stress = 0.22.

The dominance of *M. senhousia* at sites in the Waitemata Harbour was not unexpected, given the findings of Hayward et al. (1997). However, Hayward's maps indicated that Site 4 was dominated by *M. senhousia* in the mid-1990s, and that *M. senhousia* was absent at Sites 1, 2 and 5 in the mid-1990s (Table 5). Therefore, our results from 2008 (Figure 10) document the collapse of *M. senhousia* populations at Site 4 in the central Harbour¹, with massive new recruitment of *M. senhousia* at Sites 1, 2 and 5 in the outer Harbour. At the outer Harbour sites, dense mats of *M. senhousia* covered 50-90% of the sediment surface over vast tracts of seafloor (at least 250 m² in spatial extent), with maximum densities exceeding 350 inds core⁻¹ (45,000 mussels m²).

Hayward et al. (1997) documented the presence of *Theora lubrica* in practically all parts of the Waitemata Harbour during the mid-1990s. According to Hayward's maps, Sites 2, 3 and 5 were occupied by high densities of *T. lubrica* during the mid-1990s (>250 inds m⁻²), while Sites 1 and 4 had fewer *T. lubrica* (5 to 50 inds m⁻²) (Table 5). In our 2008 investigation, high densities of *T. lubrica* were present at all study sites (averaging 3.9 inds core⁻¹ at Site 4 to 12.4 inds core⁻¹ at Site 3; Figure 11). This translates to densities >250 inds m⁻² at all five locations (Table 5), with densities commonly exceeding 1000 inds m⁻². Therefore, *T. lubrica* seems to have remained a dominant component of the macrofaunal community at Sites 2, 3 and 5 since the time of Hayward, and it has increased its dominance at Sites 1 and 4. We surmise that *T. lubrica* continues to be widespread in subtidal sediments in the Waitemata Harbour.

¹ The presence of *M. senhousia* in the guts of snapper caught at Site 4 (see below) may indicate its presence in the general area. *M. senhousia* is present at low densities in intertidal habitats of the Central Waitemata and densities of *M. senhousia* seem to have increased slightly in 2008.

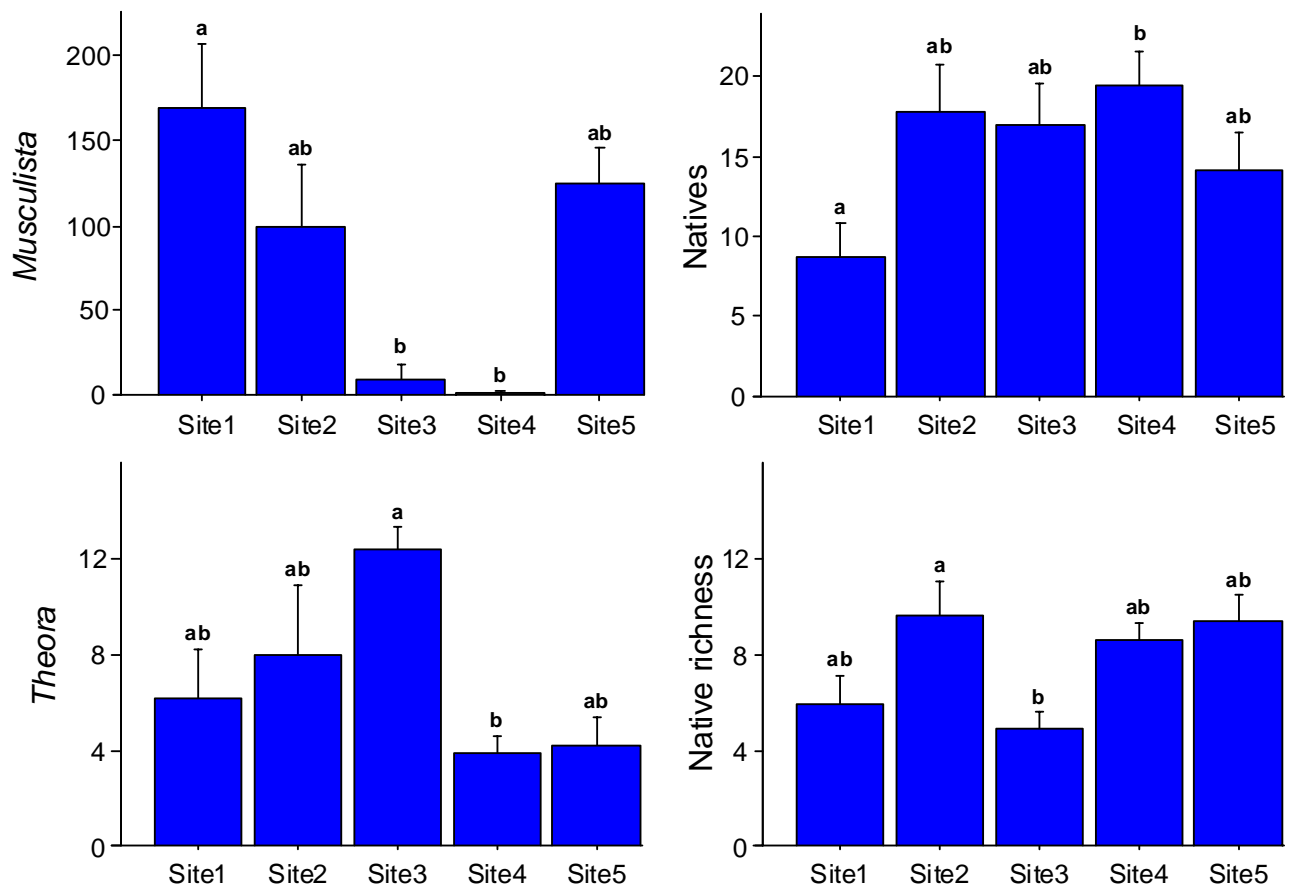


Figure 11. Panels on the left show the abundance (mean No. per 10 cm dia core) of two dominant NIS (*Musculista senhousia* and *Theora lubrica*) at five subtidal sites in the Waitemata Harbour. Upper right panel; gives the average number of individuals per core from all native species collected; lower right panel gives the total number of native taxa collected per core. Data are means + 1 SE. Letters above bars indicate results of Tukey-Kramer pairwise comparisons following ANOVA; bars that share a letter are not significantly different from one another ($\alpha = 0.05$).

According to Hayward et al. (1997), *Limaria orientalis* dominated a shallow area southwest of Rangitoto Island in addition to several deep channels in the Waitemata Harbour. We selected a site within the shallower area near Rangitoto Island (Site 1), which Hayward had described as “*Limaria* association”² in the mid-1990s. The Hayward sampling in the mid-1990s indicated densities of 50-125 *L. orientalis* m⁻² at this site.³ However, during our sampling in 2008, *L. orientalis* was a very minor component of the soft-sediment community at Site 1. No *L. orientalis* were collected in n=10 macrofaunal core samples, and just two *L. orientalis* were collected from n=5 quadrats (total area quantified using cores and quadrats = 1.58 m²).

Limaria orientalis was also rare or absent at Sites 2 – 5 in 2008 (Table 5; Figure 12). Although sampling indicated the average density of live *L. orientalis* to be less than one individual per m² at all five study sites during our survey, divers observed empty shells at several of the sampling sites, and empty shells were found in several core and quadrat samples. Nevertheless, in 2008, none of our five study sites had sufficient densities of *L. orientalis* to warrant the label “*Limaria* association” or “*Limaria*-dominated”.

² Association “N3” in Figure 3 of Hayward et al. 1997, discussed on page 8 of Hayward et al. 1997

³ Other benthic sampling nearby in 2003 (n = 3 Smith-McIntyre grabs station¹) revealed patches of *L. orientalis* with densities of 370 - 570 inds m⁻² in Motiuhu Channel, 18 - 55 inds m⁻² in Ponui Channel, 0-36 inds m⁻² in Tamaki Strait (M. Morrison, unpubl. data).

Table 5. Estimation of temporal changes in macrobenthic species at 5 sites in the Waitemata Harbour, based on information reported in a.) Hayward et al. (1997) and b.) data collected during the current study (2008). All data are numbers are of individuals m⁻².

a.)

Site	Name of 1930 Powell Association	Name of 1997 Hayward Association	1997 <i>T. lubrica</i> Inds m ⁻²	1997 <i>L. orientalis</i> Inds m ⁻²	1997 <i>A. zelandica</i> Inds m ⁻²
1	<i>Maoricolpus</i>	<i>L. orientalis</i>	5-50	55-125	0
2	<i>E. cordatum</i>	<i>T. lubrica</i>	250+	0-5	0-1
3	<i>E. cordatum</i>	<i>A. zelandica</i>	250+	5-50	125-250
4	No data	<i>M. senhousia</i>	5-50	0	0
5	<i>Amalda</i>	<i>T. lubrica</i>	250+	0-5	0-2

b.)

Site	Name of 1930 Powell Association	Name of 1997 Hayward Association	2008 <i>T. lubrica</i> Inds m ⁻²	2008 <i>L. orientalis</i> Inds m ⁻²	2008 <i>A. zelandica</i> Inds m ⁻²	2008 <i>M. senhousia</i> Inds m ⁻²	2008 <i>E. cordatum</i> Inds m ⁻²
1	<i>Maoricolpus</i>	<i>L. orientalis</i>	500-1000	0-2	0.05	15000-25000	0-8
2	<i>E. cordatum</i>	<i>T. lubrica</i>	600-1400	0-2	0.15	8000-17000	0
3	<i>E. cordatum</i>	<i>A. zelandica</i>	1400-1700	0	0.15	0-1200	0
4	No data	<i>M. senhousia</i>	400-600	0	0	0-250	0
5	<i>Amalda</i>	<i>T. lubrica</i>	300-700	0-5	0.45	12000-19000	4-16

Hayward et al. (1997) also discussed the presence of a dense *A. zelandica* bed southwest of Rangitoto Island, the “*Atrina* association”⁴. The maps suggest that this *Atrina* association contained 125-250 inds m⁻² in some places, with the *A. zelandica* bed being “richest and most extensive on the outside of the bend of the main harbour channel”. This was the location of our Site 3. During the mid-1990s, according to Hayward et al. (1997), this area also contained *E. cordatum*, high densities of *T. lubrica*, and moderately high densities of *L. orientalis*. Hayward et al. (1997) does not state whether adult or small juvenile *A. zelandica* were collected. We suggest that either (1) the high *A. zelandica* densities were composed of relatively small-sized individuals, or (2) the *A. zelandica* densities were overestimated to some degree and were likely in the 50-80 inds m⁻² range. Otherwise, it would be difficult for *T. lubrica*, *L. orientalis* and particularly *E. cordatum* to maintain moderate-to-high densities. However, regardless of the actual density of *A. zelandica* in the mid-1990s, it was largely absent in 2008 (Table 5), with only three shells found during extensive searching at Site 3 (Figure 12).

⁴ Association “N5” in Figure 3 of Hayward et al. 1997, discussed on page 8 of Hayward et al. 1997

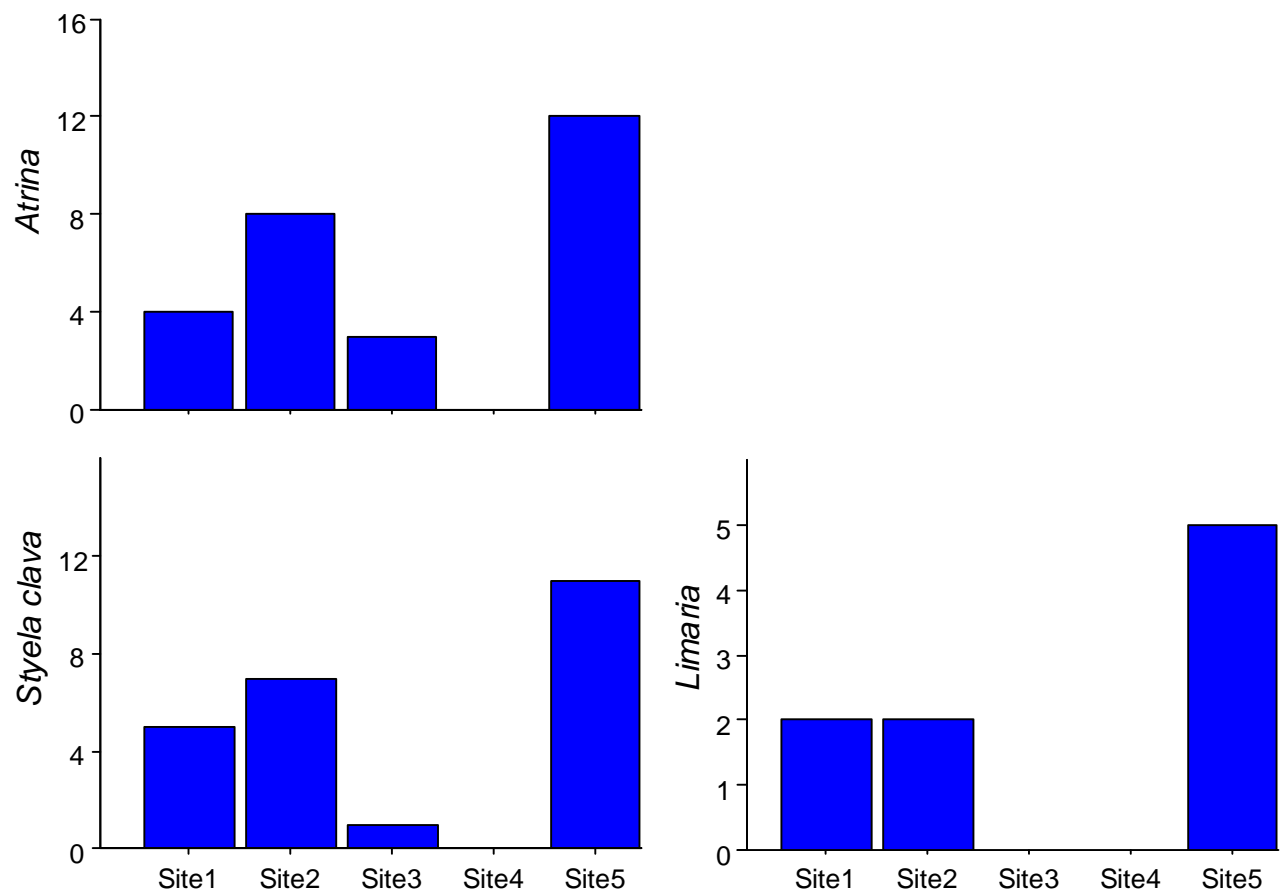


Figure 12. Total number of *Atrina zelandica*, *Styela clava* and *Limaria orientalis* individuals observed at the five sampling sites in the Waitemata Harbour, 2008. *A. zelandica* and *S. clava* were quantified from video footage collected at each site (namely, the 20 m length x 1 m width video transect, plus an additional 20 m of footage at the site, for a total video area of ~40 m²). *L. orientalis* abundance was calculated as the total number of individuals collected in cores and quadrats at each site (total area = 1.58 m²).

Quantitative sampling at Site 3 also indicated an absence of *E. cordatum*. Hayward remarked⁵ that Powell's (1937) *Echinocardium* association was "not as readily recognised in the study area as it may have been in the 1930s". However, Hayward suggested that the lack of a distinctive *Echinocardium* association in the mid-1990s may have been more related to the emergence of *A. zelandica* and *T. lubrica*, than due to declines of *E. cordatum* (Hayward et al. 1997,⁴). This is difficult to explore, as neither Powell nor Hayward provided data on *E. cordatum* densities. Nevertheless, in a location where Hayward found *E. cordatum* in the mid-1990s (i.e., Site 3, which Hayward considered "*Atrina*-*Theora*-*Echinocardium* association"), no *E. cordatum* were found in 2008 (Figure 13).

⁵ Hayward et al. 1997, middle section of page 13

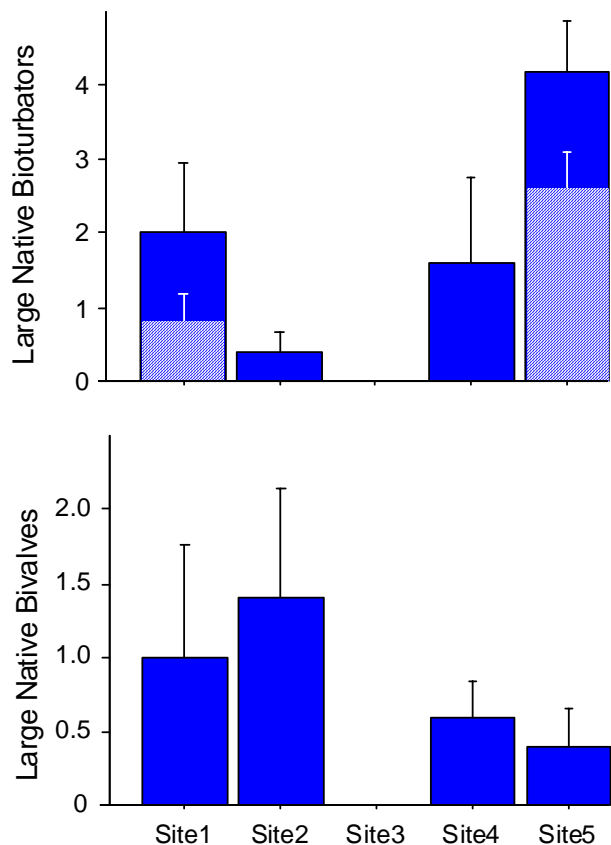


Figure 13. Density of large native taxa (individuals per 0.25 m² quadrat) at the five subtidal sites in the Waitemata Harbour. Data are means + 1 SE. The density of large native bioturbators was calculated as the sum total of burrowing crabs (*Macrophthalmus hirtipes*), brittle stars (*Amphiura rosea*) and spatangoid urchins (*Echinocardium cordatum*). *E. cordatum* densities are shown explicitly with the hatched pattern. Bottom panel shows another composite variable, large native bivalves. The density (individuals per 0.25 m² quadrat) included all large native bivalve species found in the quadrats including *Dosinia subrosea*, *Dosinia zelandica* and *Solemya parkinsonii*.

There were at least three other NIS that were positively identified at our study sites: the Asian club tunicate *Styela clava*, the Asian goby *Acentrogobius pflaumii*, and Asian paddle crab *Charybdis japonica*:

- *Styela clava* was most common at Sites 5, 2 and 1 (in order of abundance, Figure 12). *S. clava* individuals were usually associated with live or standing dead *A. zelandica* shells, with an average of approximately one *S. clava* recorded for every *A. zelandica* recorded. However, *S. clava* were occasionally found attached to small pieces of shell present in the upper sediment column (specimens attached to shell hash were collected in quadrats at Site 1 and Site 2).
- Divers observed small benthic fishes (blennies, gobies and triplefins) at all the subtidal sampling sites, though it was impractical to capture and quantify them. The Asian goby, *Acentrogobius pflaumii*, seemed to be rare relative to the native estuarine triple fin, *Grahamina nigripenne*, though the two species (and other co-occurring fishes) had similar behaviours and appeared to utilise the soft-sediment habitats in the same manner. The small fishes were observed to rest on their pectoral fins on the sediment surface, but would quickly dart into any large holes and burrows present when startled. They also took refuge next to live *A. zelandica* and inside empty *A. zelandica* shells. Thus, biogenic structures created by *A. zelandica* and burrowing crustaceans (e.g., the crab *Macrophthalmus hirtipes*) probably enhanced densities of small benthic fishes including native and invasive gobies, blennies and triple fins.

- Although baited opera house traps were deployed overnight at the four outer Harbour sites (Sites 1, 2, 3, 5), no *Charybdis japonica* were collected in the traps. However, one *Charybdis japonica* was observed *in situ* during the sampling at Site 5. The crab, a mature gravid female, was found nestled next to an *A. zelandica* shell. It was collected and later preserved in isopropyl alcohol. The same divers collected 3 specimens of *Charybdis japonica* in Mahurangi Harbour later in the same season (March 2008). In each case, the *C. japonica* specimens were found nestled next to *A. zelandica* (Plate 3).

The cryptogenic species *Styela plicata* and *Chaetopterus* sp. were also detected on video or during dives at our field sites. *Styela plicata* is a solitary ascidian similar to its congener, *Styela clava*, though it is more bulky and without a noticeable stalk. *Chaetopterus* sp. is a large tube-building “parchment worm” that became abundant in northern New Zealand during the late 1990s. Although *Chaetopterus* was present at the outer Harbour sites, the density of live worms in this region of the Waitemata was relatively low. Worm tubes were seen attached to living and dead *A. zelandica* shells and sometimes standing alone in bare sediment, but never as dense mats⁶. Chaetopterid tube debris was also apparent and occasionally collected in quadrat samples.



Plate 3: A specimen of *Charybdis japonica* nestled between *A. zelandica* shells. Photo L. Chiaroni (NIWA).

4.2.2 Fish

Snapper were caught at all five sites using long lines and at all four sites sampled with opera house traps. Both sampling methods suggested highest snapper density at Site 3 (juveniles and adults). Sites 4 and 5, in contrast, had relatively few snapper (Figure 14).

Food items found in snapper foreguts reflected, to a degree, the dominant benthic species present at the site of collection. For example, guts from snapper collected at Site 1 were full of *M. senhousia* (Figure 15), and Site 1 had the highest density of *M. senhousia* (Figure 11). Snapper collected at Site 3 had very few *M. senhousia* in their guts, reflecting the low density of *M. senhousia* at Site 3. At Site 2, however, snapper diet did not reflect the benthic habitat well. For example, numerous *L. orientalis* individuals were present in Site 2 snapper guts (despite low abundance of *L. orientalis* at the site), and

⁶ Dense mats of *Chaetopterus* sp. were observed in Martin’s Bay (Auckland Region coordinates 36° 29.862’, 174° 44.565’) as recently as 2007 (D. Lohrer, personal observations).

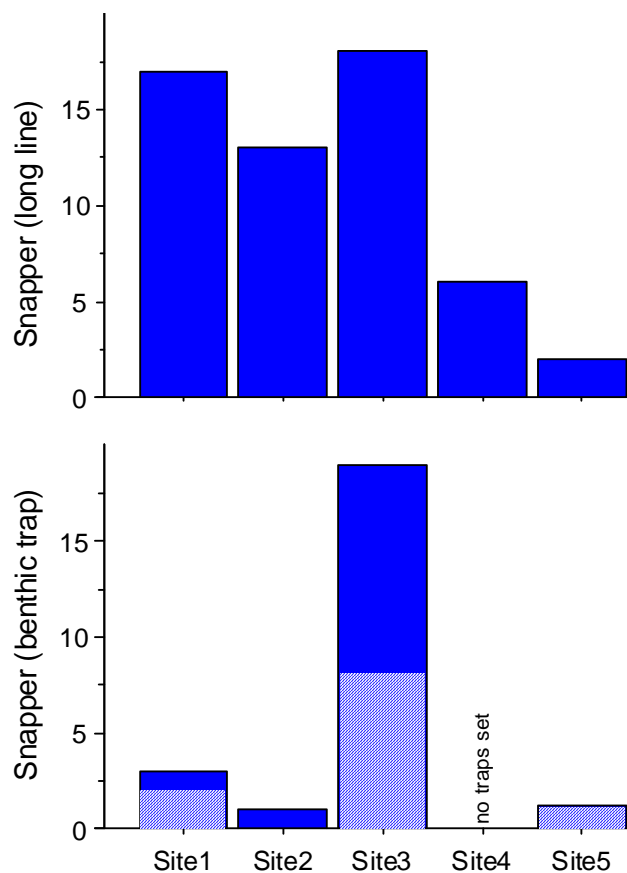


Figure 14. Abundance of fish caught at the 5 sampling sites in the Waitemata Harbour. Top panel shows fish caught by long line (see methods); lower panel shows fish caught in opera house traps, which were deployed to the seabed at each site. Hatched pattern in the lower panel shows the number of juvenile fish trapped, relative to total (<10 cm vs. >10 cm).

few *M. senhousia* were present in Site 2 snapper guts (despite the moderately high abundance of *M. senhousia* at Site 2).

Invasive species (specifically *M. senhousia* and *L. orientalis*) made up the largest proportion of foods in the snapper guts we sampled (46 fish) (Figure 15). Although *Theora lubrica* was common at all five study sites and is thought to be widespread throughout the Harbour, no *T. lubrica* individuals were recorded in the snapper guts we sampled.

Other items observed in snapper guts included native molluscs, crustaceans, worms, and juvenile conspecifics (indicating cannibalism by adult snapper on juveniles). In contrast to the findings of Powell (1937), *E. cordatum* was not a major food item for snapper in 2008. However, *E. cordatum* density in the Waitemata Harbour was apparently much greater during the 1930s. Powell also noted *A. zelandica* (probably newly recruited juveniles) in the guts of snapper in the 1930s⁷. We saw no juvenile *A. zelandica* individuals at any of the Waitemata sites we surveyed⁸, and no *A. zelandica* or *A. zelandica* fragments were recorded in the snapper guts we sampled.

⁷ Powell had a sample size of 3515 fish, relative to ours of 46.

⁸ We have not observed significant recruitment of *Atrina* in any Auckland area estuaries during this decade. *Atrina* recruitment may be extremely sporadic.

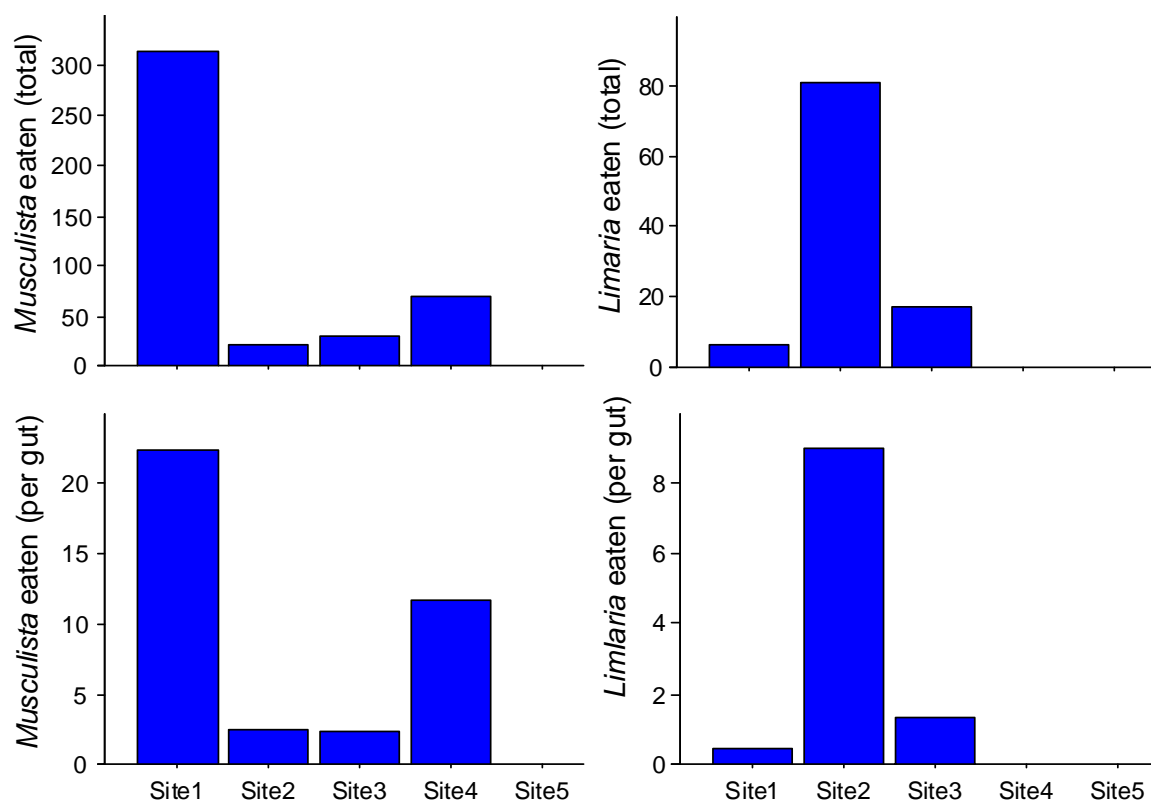


Figure 15. Prey items found in the foreguts of snapper that were caught at 5 sites in the Waitemata Harbour. All data come from snapper caught on long line. The two dominant prey species (*Musculista senhousia* and *Limaria orientalis*) are displayed. Upper panels show the total numbers of *M. senhousia* and *L. orientalis* found in snapper foreguts per site. Lower panels show per capita consumption of *M. senhousia* and *Limaria* (fish with empty guts excluded).

4.2.3 Species interactions

Correlation strengths among variables in our data set were useful in assessing the veracity of our conceptual model as well as more general concepts in invasion ecology. For example, there is significant interest in knowing whether native species promote resistance to invasion, and whether established NIS promote the success of new invaders. In addition, when monitoring impacts of NIS, it is common to examine their effects on the abundance and diversity of native species. In all such cases, correlation analyses can be informative, though interpretive caution is warranted in the absence of explicit testing of cause and effect relationships. In other words, significant correlations may be due to active species interactions (e.g., facilitation, competition, interference, predation), or may simply reflect the convergent/divergent responses of different species to the same sets of environmental conditions. Table 6 summarises the correlation analyses we performed, and the particular questions those correlations addressed.

In our data set (50 macrofaunal cores, $n=10 \times 5$ sites), NIS abundance was negatively correlated with the abundance of native individuals (Figure 16) (Table 6). The variable “NIS abundance” was the sum total of all *M. senhousia*, *T. lubrica*, and *L. orientalis* individuals, whereas “native abundance” was the sum of all other macrofauna. Because *M. senhousia* was by far the most abundant of the three non-indigenous bivalves, the variables “NIS abundance” and “*M. senhousia* abundance” behaved similarly in all analyses.

At sites where *M. senhousia* abundance was high, macrofaunal diversity was low (Figure 16). This was due to the dominance of total macrofaunal abundance by *M. senhousia* individuals, which resulted in low evenness and low Shannon-Weiner diversity index values. Therefore, as an additional step, we

re-calculated Shannon-Weiner diversity after removing NIS from the data set in order to generate values of “native diversity”. Native diversity was not correlated with *M. senhousia* abundance or *T. lubrica* abundance, and neither was native richness (Figure 17, Table 6).

Table 6: Correlation statistics between variables of interest. Bold values indicate significant correlations. See Appendix 2 for further explanation of why variables were compared, i.e., what specific questions they addressed.

Variable 1	Variable 2	Correlation (r-value)	P-value	Appendix 2 questions addressed
Native abund. (inds core ⁻¹)	NIS / <i>M. senhousia</i> (inds core⁻¹)	-.339	.0155 Negative	1, 5
Native abund. (inds core ⁻¹)	<i>T. lubrica</i> (inds core⁻¹)	.269	.0592 Positive	1,5
Native richness (taxa core ⁻¹)	NIS / <i>M. senhousia</i> (inds core ⁻¹)	-.042	.7717	2,6
Native richness (taxa core ⁻¹)	<i>T. lubrica</i> (inds core ⁻¹)	.042	.7725	2,6
Native diversity	NIS / <i>M. senhousia</i> (inds core ⁻¹)	-.042	.7717	3,7
Native diversity	<i>T. lubrica</i> (inds core ⁻¹)	.042	.7725	3,7
Total diversity	NIS / <i>M. senhousia</i> (inds core⁻¹)	-.736	<.0001 Negative	4
Total diversity	<i>T. lubrica</i> (inds core ⁻¹)	.205	.1545	4
<i>M. senhousia</i> (inds core⁻¹)	<i>T. lubrica</i> (inds core⁻¹)	-.291	.0403 Negative	8
Bioturbators (ave inds site ⁻¹)	NIS / <i>M. senhousia</i> (ave inds site ⁻¹)	.465	.4762	9
Bioturbators (ave inds site ⁻¹)	<i>T. lubrica</i> (ave inds site ⁻¹)	-.760	.1592	9
Native bivalves (ave inds site ⁻¹)	NIS / <i>M. senhousia</i> (ave inds site ⁻¹)	.572	.4071	10
Native bivalves (ave inds site ⁻¹)	<i>T. lubrica</i> (ave inds site ⁻¹)	-.290	.6729	10
Total <i>A. zelandica</i> per site	Total <i>S. clava</i> per site	.970	.0031 Positive	11
Total <i>A. zelandica</i> per site	NIS / <i>M. senhousia</i> (ave inds site ⁻¹)	.592	.3352	11
Total <i>A. zelandica</i> per site	<i>T. lubrica</i> (ave inds site ⁻¹)	-.169	.8090	11

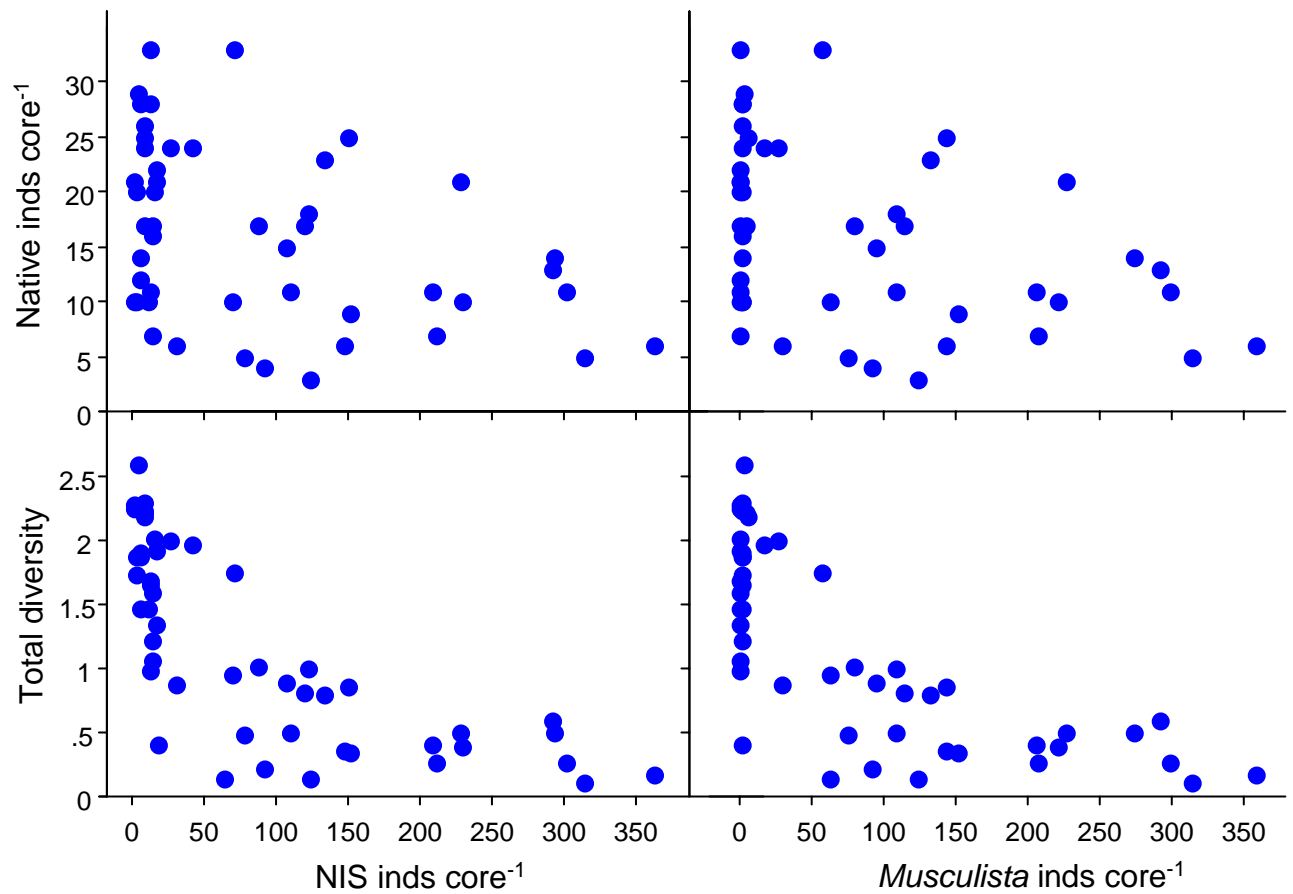


Figure 16. Relationships between macrofaunal variables. Data are from $n=10$ cores collected at 5 subtidal sites in the Waitemata Harbour (50 data points). The number of NIS individuals per core is the sum of *Musculista senhousia*, *Theora lubrica* and *Limaria orientalis* abundances. The number of native individuals is basically everything else (excluding one small unidentified crustacean sp.). *M. senhousia* was by far the most abundant of any species collected. Total diversity is the Shannon-Wiener H' value, with NIS included in the data set.

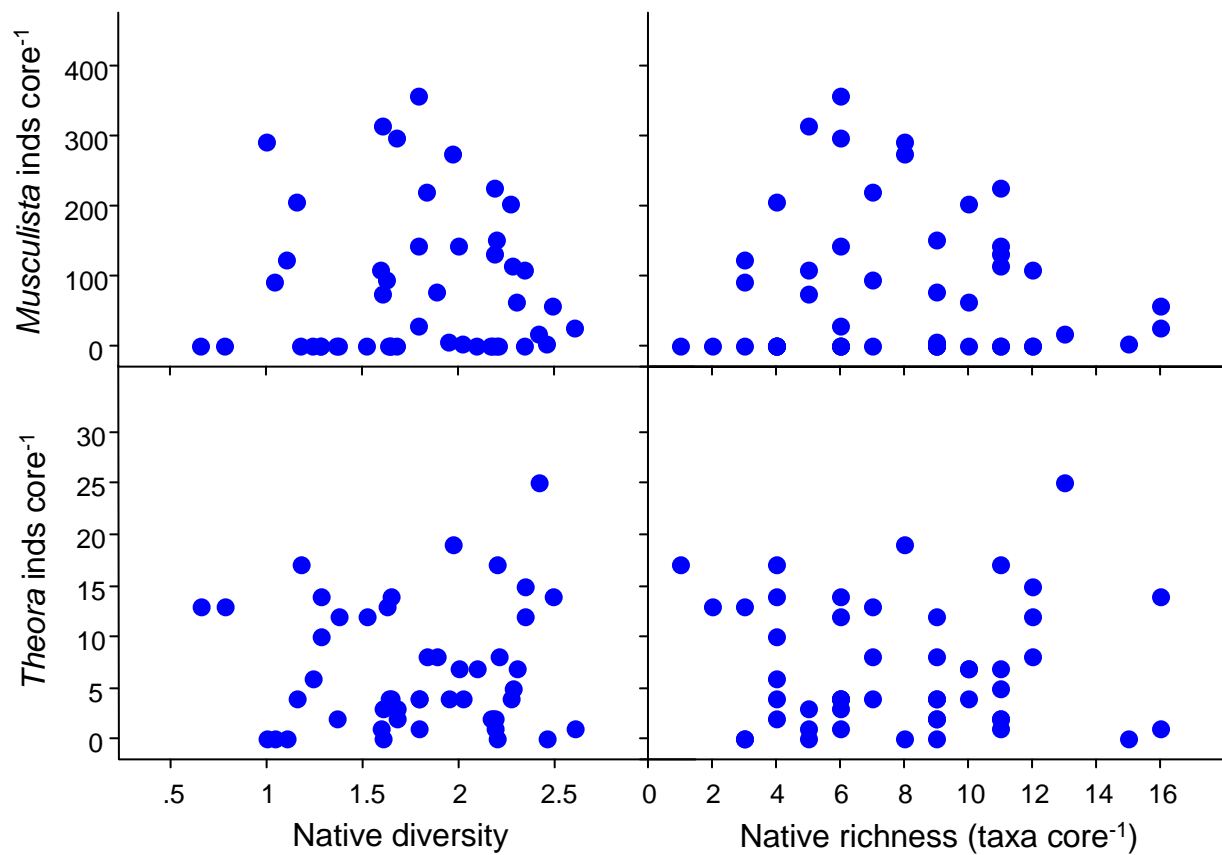


Figure 17. Relationships between native diversity and native richness, and *Musculista senhousia* and *Theora lubrica*. Data are from n=10 cores collected at 5 subtidal sites in Waitemata Harbour (50 data points). Native diversity is the Shannon-Wiener H' value, with NIS excluded from the data set.

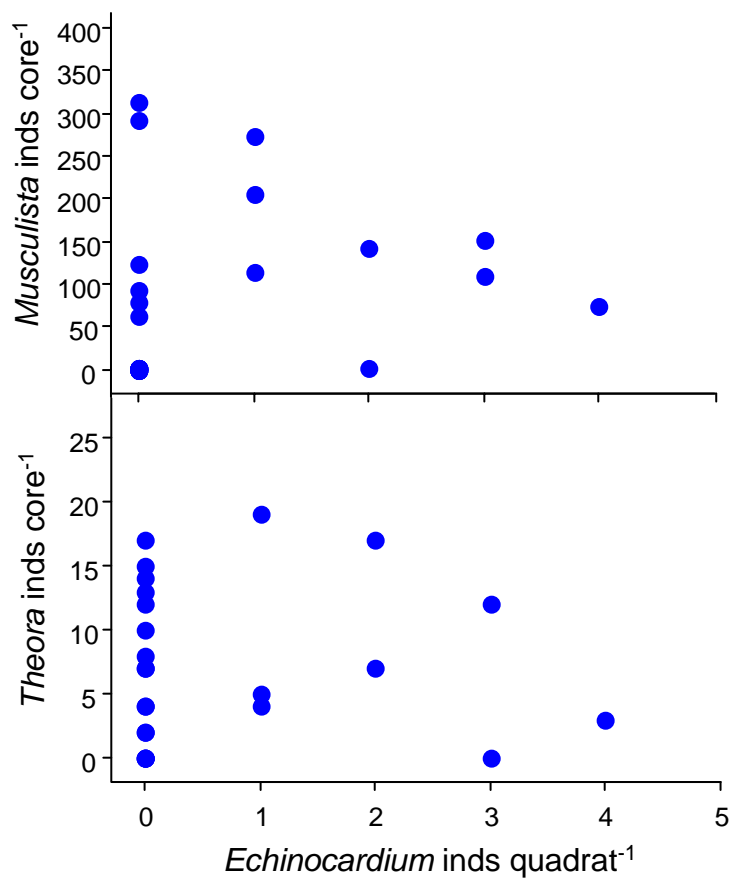


Figure 18. Relationship between the number of *Echinocardium cordatum* collected per 0.25 m² quadrat, and the abundance of *Musculista senhousia* and *Theora lubrica* collected in sediment cores nearby.

5. Discussion

5.1 INTERTIDAL

The Waitemata Harbour has been invaded by many NIS species (Cranfield et al. 1998, Inglis et al. 2005a,b, Halliday and Hewitt 2006). Two conspicuous NIS in the intertidal environment are *Crassostrea gigas* and *Musculista senhousia*, both of which can occur in high density patches: oyster reefs and mussel mats, respectively. There are places in the Tamaki Estuary and the Manukau Harbour where extensive oyster reefs and mussel mats have been observed (Plate 2), though neither species seems to dominate large areas of intertidal habitat in the central or upper Waitemata Harbour. Small oyster reefs that are present at Henderson Creek and Meola Reef (Central Waitemata) have remained stable in size for at least 8 years (C. Lundquist, pers. comm.). *C. gigas* reefs tend to be persistent (as oysters recruit to living and dead shells on the existing reef) whereas *M. senhousia* populations often crash after achieving astoundingly high densities (mortality of individuals in dense mussel mats is extremely high; Crooks 1996). However, analysis of data from 62 intertidal soft-sediment habitats spread throughout the Harbour showed relatively low levels of NIS occurrence. On average, the number of native taxa exceeded the number of invasive taxa by an order of magnitude (e.g., 30 taxa vs 3). Even *Musculista senhousia*, which occurs at high densities elsewhere, was relatively rare in intertidal habitats of the Waitemata Harbour.

Intertidal sites near the Port of Auckland were no more invaded than distant ones. In fact, most of the NIS were concentrated in tidal creeks in the Upper Waitemata, with fewer present near the port in the Central Waitemata. There may be two (or more) interacting factors that contribute to explain this spatial pattern. First, sites in the Upper Waitemata tend to be very muddy, and the three most common NIS in the data set (*Theora lubrica*, *Polydora cornuta*, and *Musculista senhousia*) are known to be mud-tolerant species. Second, sites in the Upper Harbour tended to have fewer native individuals, including key species like cockles (*Austrovenus stutchburyi*), a factor that could have affected invasion resistance.

Although a relatively small number of NIS were present in intertidal soft-sediment habitats, the analysis indicated that anthropogenic activities can influence invasion risk. For example, catchment activities that increase the delivery of fine sediments to estuaries (e.g., construction, logging) could benefit mud-tolerant NIS. In addition, urban contaminants (e.g., copper, lead, zinc) are known to affect functionally important species such as *Austrovenus stutchburyi* and *Macomona liliiana* (Thrush et al. in press). Both of these native bivalves were found to have significant effects on the abundance and/or occurrence of NIS. Thus, management activities that maximise overall system health may also reduce the likelihood of NIS impacts.

The meta-analysis revealed negative effects of native individuals on the total abundance of NIS. The number of native individuals was also negatively correlated with numbers of *P. cornuta* (a deposit feeding polychaete similar to the native spionid *Boccardia syrtis*). Another example of natives deterring NIS was cockles (*A. stutchburyi*): cockles were negatively correlated with *T. lubrica* abundance. As a counter example, native *M. liliiana* had positive effects on *P. cornuta*. This result may be explained by the behaviour of *M. liliiana* in the sediment environment. *M. liliiana* is a large deposit feeding bivalve that feeds by vacuuming the sediment surface. Its feeding activities seem to disturb smaller co-occurring species, resulting in a negative relationship between densities of *M. liliiana* and many other native species (Thrush et al. 1996, Thrush et al. 2000, Thrush et al. 2006), which could potentially facilitate establishment of invasive species. In previous studies, *A. stutchburyi* has proved, unlike *M. liliiana*, to have a positive influence on some native species (Whitlatch et al. 1997, Thrush et al. 2006). Thus, the negative effects of *A. stutchburyi* and density of native individuals, together with the positive influence of *M. liliiana*, suggest that (1) NIS individuals are more tolerant of disturbance than our native species, and/or (2) high densities of native species impart a measure of invasion resistance. However, these relationships are likely to be further complicated by the strong negative relationship between *M. liliiana* density and sediment mud content (Thrush et al. 2005).

The meta-analysis also revealed a positive relationship between the bioturbation index and the abundance of NIS, *T. lubrica* and *P. cornuta*. This was unexpected, given the known negative effects of bioturbation on *T. lubrica* and other small surface feeders (e.g. by *E. cordatum*, Lohrer et al. 2008a,b). However, most of the bioturbators in this intertidal system are themselves small, with the exception of *M. liliana* and *A. stutchburyi*, whose effects were assessed separately. It is likely that the small bioturbators, working mainly within the top 2 cm of the sediment surface, do not disrupt *T. lubrica* to the same extent that *E. cordatum* does.

In addition to interactions with environmental stimuli and native organisms, *T. lubrica* and *P. cornuta* were found to have a negative influence on the abundance of each other. The data (Table 4) suggested that it is *P. cornuta* that influences the presence of *T. lubrica*. This could be because *P. cornuta* can form a dense mat or tubes, inhibiting successful settlement by larval and juvenile *T. lubrica*, similar to the relationship of *Boccardia syrtis* and juvenile *M. liliana* (Cummings et al. 1996). The negative effect of invasive species upon each other does not support, and is contrary to, an ‘invasion meltdown’ scenario.

5.2 SUBTIDAL

In contrast to the intertidal sites, NIS were dominant at the five subtidal habitats sampled during this investigation. *Musculista senhousia* was extremely abundant (up to 45,000 inds m⁻²) and tended to occur as consolidated mats of mussels, joined together by copious byssal threads. These mats were observed to cover >50% of the seafloor at three of the five sites we sampled. *M. senhousia* mats can trap fine particles, increasing the mud content of the sediment and preventing the penetration of oxygen to underlying sediments. Thus, increases in *M. senhousia* are likely to have a negative impact on the abundance of other macrofauna, by means of smothering and habitat modification. The significant negative correlation between *M. senhousia* and native individuals supports this idea (Figure 16). The increased abundance of *M. senhousia* at several sites represents significant, although possibly short-term, alterations of soft-sediment habitats in the outer Waitemata Harbour. These effects may result in the alteration of benthic-pelagic coupling and trophic dynamics involving predatory demersal fishes such as snapper.

Theora lubrica was also present at several sites in high densities (up to 1000 inds m⁻²), and several other invasive species were also recorded: solitary ascidians *Styela clava*, gobiid fishes *Acentrogobius pfaumii*, file shells *Limaria orientalis*, paddle crabs *Charybdis japonica*, and parchment worms *Chaetopterus* sp. Thus, NIS were common and conspicuous components of subtidal soft-sediment habitats in the Waitemata Harbour, where they can co-occur and interact. That being said, our data did not reveal any overt facilitation or positive interactions among the NIS. In fact, there was a significant negative correlation between the two most abundant NIS, *M. senhousia* and *T. lubrica*.

The simultaneous disappearance of two large long-lived native species at Site 3 (*A. zelandica* and *E. cordatum*), in addition to the presence of copious *A. zelandica* shell fragments in the sediment, is suggestive of major physical disturbance at the site. Possible sources of anthropogenic disturbance are fishing (the dragging of scallop dredges and other fish trawling gear across the seabed) and channel dredging activities (dumps and removals of sediments from the nearby Rangitoto channel). Storm-driven swells capable of disturbing the bed are probably infrequent on the south western side of Rangitoto Island. *T. lubrica*, which occupies the site now, is an opportunistic species (high annual recruitment, fast growth, short life span) that may have colonised after the last major disturbance event.

Negative interactions between *E. cordatum* and non-indigenous bivalves were predicted in our conceptual model (see section 3.3). Our hypothesis was that the recruitment of non-indigenous bivalves would be significantly reduced at sites with high rates of biogenic sediment disturbance (e.g., sites averaging 10 to 60 *E. cordatum* per m²). Due to the low density of *E. cordatum* at all 5 sites, having declined since Hayward et al. (1997), correlations between *E. cordatum* and NIS were not significant (Figure 18). However, the low densities of *E. cordatum* at the outer Harbour sites during the last 2-3 years may have created a window of opportunity for *M. senhousia* to establish massive

populations. Once established, thick *M. senhousia* mats may pre-empt *E. cordatum* by restricting urchin recruitment, movement, and feeding. The few *E. cordatum* observed at Site 5 were generally associated with small gaps in the mussel mats (bare patches <500 cm²).

Manipulative field experiments performed in a separate estuary (Mahurangi Harbour, 2005-2008,⁹) provide clear evidence of the negative impacts of *E. cordatum* on *T. lubrica*. Weak negative trends observed in the present study (Figure 18), despite low numbers of *E. cordatum*, are consistent with our predication of *E. cordatum*-*T. lubrica* interactions and the experimental results from Mahurangi. The relatively high abundance of *T. lubrica* at subtidal sites in the Waitemata Harbour may be partially explained by the relatively low densities of *E. cordatum* at those sites.

Experiments in the Mahurangi Harbour also showed significant positive effects of *A. zelandica* on *T. lubrica* (Lohrer et al. 2008b). However, the positive effects of *A. zelandica* on *T. lubrica* are localised (generally occurring within 10 cm of the sessile *A. zelandica* shells). Positive effects at the site scale, given the sparse distribution of *A. zelandica* at the sites we studied, were not likely to be observed (Cummings et al. 2001). Thus, as expected, site-scale correlations between *A. zelandica* and *T. lubrica* were not significant.

As *A. zelandica* shells provide the only hard substrate in vast areas of soft-sediment habitat, the shells are attractive habitat for various encrusting organisms (soft-corals, hydroids, ascidians, bryozoans) as well as thigmotactic mobile organisms (e.g., sea cumpers, star fish, crabs) that preferentially remain in contact with hard surfaces. Although the diversity of epifauna living on *A. zelandica* shells potentially includes some NIS and cryptogenic taxa (e.g., *Botrylloides leachii*, *Bugula neritina*, *Schizoporella errata*, *Haliclona heterofibrosa*, *Hydroides elegans*, *Zoobotryon verticillatum*; Inglis et al. 2005a,b), we did not quantify encrusting taxa. The exception was the large stalked ascidian, *Styela clava* (Asian sea squirt), which was quantified from video footage captured at each site. *S. clava* abundance was linearly related to *A. zelandica* abundance, with approximately one *S. clava* counted per *A. zelandica* shell.

Our results confirmed that snapper take NIS as prey items in the Waitemata Harbour. At Sites 1 and 3, snapper diets reflected benthic prey composition relatively well, though this was not the case for Site 2 (recall there were numerous *L. orientalis* present in snapper guts at Site 2, despite low abundance of *L. orientalis* recorded in benthic samples). There are several possible explanations for the Site 2 observations. First, the 200 m long line at Site 2 may have spanned a greater range of benthic habitat types than the 20 m transect sampled by divers, with some of the habitats containing high concentrations of *L. orientalis*. Second, snapper caught at Site 2 could have fed in a different part of the Harbour (i.e., where *L. orientalis* was abundant) prior to their capture. Third, selective feeding by snapper at Site 2 could have produced an over-representation of *L. orientalis* in the snapper guts (relative to the abundance of *L. orientalis* at the site). Snapper may selectively target *L. orientalis* as it is a large, fleshy, easily-seen species that lives on the sediment surface.

The absence of *T. lubrica* in snapper guts was puzzling, considering the widespread distribution of this species in the Waitemata Harbour and its relatively high abundance at all five of the subtidal sampling sites. However, it is difficult to know definitively whether or not snapper eat *T. lubrica*, as the fragile shells of *T. lubrica* are likely to be thoroughly crushed (and unidentifiable) by the time they reach the foregut.

5.3 MODELLING

Although it is difficult to know what contributed to the dominance of NIS at the outer Harbour sites, the studies of Powell (1937) and Hayward et al. (1997) provided some general insights. Importantly, there appeared to have been changes to the densities of functionally important native organisms (*E. cordatum* and *A. zelandica*) that coincided with the invasions by three non-indigenous bivalves from Asia (*T. lubrica*, *M. senhousia*, and *L. orientalis*). The ecological roles of *E. cordatum* and *A.*

⁹ Ministry of Fisheries Project ZBD200419. Results presented in draft NZ Aquatic Environment and Biodiversity Report by Lohrer et al. (2008b) titled "Interactive effects of two key species on ecosystem function and trophic linkages in New Zealand soft-sediment habitats"

zelandica are now relatively well understood, and effects of these species on invasion success can be predicted with reasonable confidence (Norkko et al. 2001, 2006, Lohrer et al. 2004, 2005, 2008a,b, Hewitt et al. 2006). This knowledge was incorporated into a conceptual model, which was evaluated using all available information (including new quantitative data).

One key hypothesis in the model was the link between burrowing urchins (*Echinocardium cordatum*) and invasion resistance. According to Hayward et al. (1997), invaders such as *T. lubrica* and *L. orientalis* increased in parts of the harbour where *E. cordatum* had declined. *E. cordatum* and *T. lubrica* were negatively correlated during this investigation also, despite having data from just five sites (and a small gradient in *E. cordatum* density). Manipulative experiments in the Mahurangi Harbour further elucidated this interaction, providing clear cause-and-effect evidence of the negative impacts of *E. cordatum* on *T. lubrica* (Lohrer et al. 2008a,b). Thus the presence and sign (-) of the interaction between *E. cordatum* and *T. lubrica* has been confirmed in our conceptual model (Figure 19).

Other model relationships that the subtidal sampling confirmed were *Atrina-Theora* (+), *Atrina-Styela* (+), and *Atrina-Charybdis* (+) interactions (Figure 19). The positive effects of *A. zelandica* on *T. lubrica* were due to increased organic enrichment of surrounding sediments (faeces/pseudofaeces production by *A. zelandica*) and increased sediment stability in *A. zelandica* beds. The positive effects on *S. clava* and *C. japonica* were due to habitat provisioning (i.e., primary settlement substrates and refuge habitats created by these structure-forming pinnid bivalves).

Although *A. zelandica* may facilitate NIS, all the invaders listed in the model can be abundant in areas where *A. zelandica* do not exist. For example, *S. clava* and *C. japonica* will readily utilise *A. zelandica* as an essential habitat element, but other natural and artificial structures within the Waitemata provide suitable habitat as well. (Densities of *S. clava* are actually much higher on marina pier pilings and floating docks; Kluza et al. 2006). Another factor to consider is timing. The abundance of *A. zelandica* decreased in the Waitemata Harbour sometime after 1997 (Site 3, Table 5), whereas *S. clava* and *C. japonica* were first reported in New Zealand in 2005 and 2000, respectively. Thus, it would be incorrect to fully attribute the success of these invaders to the presence and abundance of *A. zelandica*. Furthermore, in our opinion, losses of *A. zelandica* may well indicate ecological damage to the Harbour system, which may be more important to overall invasion risk.

The model acknowledges several other possible interactions, including a negative feedback of *S. clava* on *A. zelandica*, and interactions between *E. cordatum* and *A. zelandica*. *S. clava* could potentially reduce the feeding efficiency of *A. zelandica* by modifying flow and by pre-filtering the seawater that *A. zelandica* uses for nutrition. The increased drag on *A. zelandica* shells caused by fouling organisms like *S. clava* could also increase losses of *A. zelandica* during storms. Dense beds of *A. zelandica* likely limit the abundance of *E. cordatum* by restricting its movement and altering sediment characteristics. These more complicated interactions were not tested or confirmed here, but they remain in the model as possibilities.

Charybdis japonica may feed upon non-indigenous bivalves such as *T. lubrica*, *M. senhousia* and *L. orientalis* (Figure 19). If true, *C. japonica* would benefit from the high densities of NIS prey that we have documented in the Waitemata Harbour. Thus it is conceivable that the established non-indigenous bivalves facilitated the post-introduction establishment of *C. japonica*. The idea of established NIS improving the likelihood of additional NIS invasions is certainly consistent with the hypothesis of invasional meltdown (Simberloff and Von Holle 1999). However, predator-prey interactions are negative from the prey's perspective, and expansion of *C. japonica* populations could potentially limit NIS prey populations. Thus, it is difficult to fully evaluate the invasional meltdown hypothesis and the various alternatives in this case, as the feeding habits of *C. japonica* are not yet well understood. Empirical testing and knowledge of its feeding preferences when given a range of prey items is needed to better understand the impact of *C. japonica* on both native and NIS prey. Such work would also prove useful in predicting the risks and impacts of other invasive predators that may arrive in New Zealand in the future, particularly the portunid crab *Carcinus maenas* and the sea star *Asterias amurensis*. Each of these species is listed as an unwanted organism not yet present in New Zealand (<http://www.biosecurity.govt.nz/pest-and-disease-response/pests-and-diseases-watchlist>).

Conceptual model:

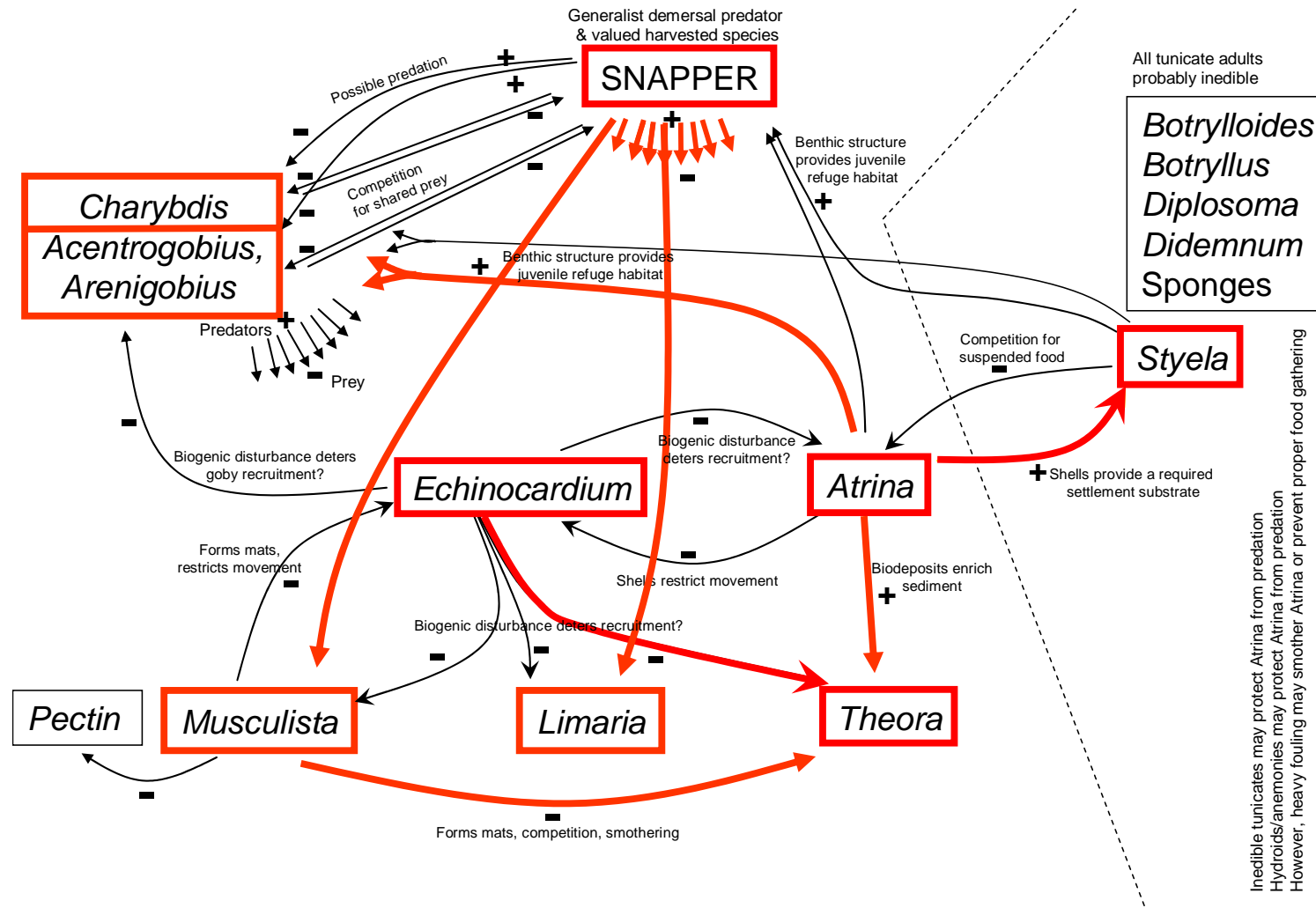


Figure 19: The revised (based on subtidal sampling) conceptual model of species interactions in the Waitemata Harbour. Red/Bold arrows indicate species interactions that were confirmed from subtidal observations and data.

A negative impact of *C. japonica* on the three non-indigenous bivalves (*M. senhousia*, *T. lubrica*, *L. orientalis*) would counteract any slight positive effects of *A. zelandica* on the bivalves. Alternatively, *C. japonica* may reduce *E. cordatum* survival, to the benefit of the NIS bivalve prey. There are multiple possibilities for direct and indirect interactions involving native species and NIS in our conceptual model; more basic ecological work is needed to tease apart this interaction web and better predict the individual and combined impacts of NIS in the Waitemata Harbour. Examples from the literature about the effects of non-indigenous predators are instructive (Lohrer and Whitlatch 2002a,b, Grosholz 2005, Rodriguez 2006, Salo et al. 2007), but targeted studies of the interacting species in the Waitemata Harbour will be the most useful.

To gauge the impacts of NIS invasions on upper trophic levels and valued resources within the Waitemata Harbour (ecosystem services), the feeding habits of snapper were sampled at the five subtidal sampling sites. *Musculista senhousia* and *Limaria orientalis* were the two most common items found in the guts of snapper. It appears that snapper have recognised these NIS as suitable prey. The presence of *M. senhousia* in snapper guts was not entirely surprising, as *M. senhousia* was extremely abundant at 3 of the 5 study sites, with mats covering large areas of seafloor. *L. orientalis*, however, may be a specific target of snapper, as it was over-represented in snapper guts relative to its abundance at the sites. We conclude, as has been previously reported, that snapper are generalist feeders that will switch among prey items in accordance with their relative abundance. As NIS have become dominant in the Harbour, they seem to have become a major component of snapper diet. We suggest that future invasions by non-indigenous benthic species may not have direct negative impacts on snapper, unless the particular NIS are inedible¹⁰ or dramatically reduce the abundance of higher quality prey. Furthermore, there is some evidence to suggest that snapper may benefit from the NIS now present in the Waitemata Harbour, judging from the dominance of NIS in their diet relative to native species. Powell (1937) indicated that the native “*Echinocardium* formation” made up a considerable portion of the snapper diet in the Waitemata. However, Godfriaux (1969) cites Thorson (1957) who demonstrated that echinoderms have low percentages of dry organic matter relative to other benthic invertebrates. In contrast to echinoderms, both *L. orientalis* and *M. senhousia* are predicted to have higher nutritional content. *L. orientalis* has a thin shell (hence a greater proportion of flesh contributing to total weight) and a thick mantle of tentacles which permanently protrude from the shell. *M. senhousia* also has a thin shell and, with extremely high densities, can achieve large biomass per unit area. Thus, moving from a native, nutritionally poor benthic formation to one dominated by fleshy invasive bivalves may actually constitute a net benefit for higher trophic levels.

Although NIS dominated several subtidal habitats in the Waitemata Harbour during this investigation, there was limited support for the invasional meltdown hypothesis. In fact, no positive interactions between invaders were detected, only negative ones. As a specific example, increased densities of *M. senhousia* were correlated with reductions in *T. lubrica*. Furthermore, meltdown is a community level process, and evidence of facilitation alone is not enough to accurately ascribe this label (Simberloff 2006¹¹). Nevertheless, more than 60 NIS have invaded the Waitemata Harbour, and NIS seem to continue to invade (e.g., the *Styela clava* and *Charybdis japonica* invasions of this decade), which makes co-occurrence and interactions among invaders increasingly likely. Thus, although we did not document invasional meltdown in the Waitemata Harbour, neither did we rule it out. Invasions by NIS continue to be a major threat that needs to be taken seriously to preserve the valuable goods and services associated with the Waitemata Harbour ecosystem.

Once NIS become established, impacts can reverberate through the ecosystem via multiple interaction pathways. Thus, the introduction of NIS is a form of “ecological roulette” (Carton and Geller 1993); the majority of invaders may be relatively benign, but some can cause sweeping and irreversible changes to ecosystems, with high economic and ecological costs. Pre-border controls that prevent the transfers of NIS are clearly an important step in avoiding invasive outbreaks. However, the

¹⁰ Adult-sized Asian sea squirts (*Styela clava*) do not seem to have many predators, perhaps due to low palatability (e.g., noxious chemical compounds and a tough leathery tunic; R. Whitlatch personal communication). However, tiny week-old recruits are taken by micro-predators in the eastern USA (gastropods *Mitrella lunata*, *Anachis avara*, *A. lafresnayi*; Osman et al 1992, Osman and Whitlatch 1995).

¹¹ The author of Simberloff 2006 was one of the original proponents of the invasional meltdown hypothesis, which appeared in Simberloff and Von Holle 1999.

maintenance of healthy and diverse ecosystems should also be a part of any integrated pest management plan, as diverse systems and certain native species are known to promote invasion resistance. Environmental damage can open windows of opportunity for invaders, and increased disturbance levels will tend to favour opportunistic species with fast growth and high reproductive capacity. These life-history traits are characteristic of many NIS (Lockwood et al 2007), including *M. senhousia* and *T. lubrica*. Hayward et al. (1997) suggests that 14 molluscs have declined or disappeared in the last 60 years due to various anthropogenic impacts, and *E. cordatum*—a species known to reduce *T. lubrica* success—declined during the period as well. *E. cordatum* is known to be affected by trawling and dredging, pollutants, anoxia, terrigenous sediments and invasive predators (Ross et al. 2002, Lohrer et al. 2005 and references therein). We conclude that the losses of large native bivalves and *E. cordatum* from Outer Harbour sites may have contributed to the invasions of *M. senhousia* and *T. lubrica*. Now firmly established and widespread in the Waitemata Harbour, these NIS are likely to persist and affect the ecology of the system, both benthic and pelagic.

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8. Appendices

Appendix 1: Table of invasive species identified in the Waitemata, from Halliday and Hewitt (2006).

Taxon	Species	Family	Probable native range
Algae	<i>Codium fragile</i> ssp. <i>tomentosoides</i>	Codiaceae	Northwest Pacific (adventive in Africa, the northeastern and northwestern Atlantic, North and South America, the Mediterranean, eastern Pacific, Australia)
Algae	<i>Colpomenia durvilleae</i>	Scytosiphonaceae	Northern Pacific N. Japan – central California
Algae	<i>Cutleria multifida</i>	Cutleriaceae	Cosmopolitan in temperate seas
Algae	<i>Hydroclathrus clathratus</i>	Scytosiphonaceae	Cosmopolitan temperate & tropical seas
Algae	unidentified species	Solieriaceae	Probably Southeast Asia
Algae	<i>Undaria pinnatifida</i>	Alariaceae	Japan, Korea, parts of China
Amphipoda	<i>Chelura terebrans</i>	Cheluridae	Cosmopolitan
Amphipoda	<i>Corophium acutum</i>	Corophiidae	Coasts of Europe; now circumglobal
Amphipoda	<i>Erichthonius pugnax</i>	Ischyroceridae	South East Asia (adventive in Australia)
Angiospermae	<i>Spartina alterniflora</i>	Poaceae	Eastern USA
Angiospermae	<i>Spartina anglica</i>	Poaceae	Britain
Angiospermae	<i>Spartina x townsendi</i>	Poaceae	Britain
Asciacea	<i>Asterocarpa cerea</i>	Styelidae	South Australia & Sub-Antarctica
Asciacea	<i>Botrylloides magnicoecum</i>	Styelidae	Southern African coasts (now adventive on coasts of Australia, New Zealand, and the Mediterranean)
Asciacea	<i>Botryllus schlosseri</i>	Styelidae	Atlantic
Asciacea	<i>Ciona intestinalis</i>	Cionidae	Europe?
Asciacea	<i>Corella eumyota</i>	Rhodosmatidae	Southern & western Australia
Asciacea	<i>Cystodytes dellechiaiei</i>	Polycitoridae	Warm water cosmopolitan
Asciacea	<i>Didemnum "candidum"</i>	Didemnidae	Now cosmopolitan
Asciacea	<i>Diplosoma listerianum</i>	Didemnidae	South Africa, now cosmopolitan
Asciacea	<i>Styela plicata</i>	Styelidae	Cosmopolitan
Asciacea	<i>Styela clava</i>	Styelidae	Japan, Korea, northern China, (adventive in NW Europe, California, Eastern USA, southern Australia)
Asciacea	<i>Aplidium phortax</i>	Polyclinidae	Northeastern Australia, Solomon Islands
Asciacea	<i>Botrylloides leachii</i>	Styelidae	English Channel
Cirripedia	<i>Balanus amphitrite</i>	Balanidae	Cosmopolitan warm temperate & tropical seas
Cirripedia	<i>Balanus trigonus</i>	Balanidae	Cosmopolitan warm temperate & tropical seas
Cirripedia	<i>Balanus variegatus</i>	Balanidae	Indo-Malaysia to Australia
Cnidaria	<i>Coryne pusilla</i>	Corynidae	All European coasts, Mediterranean; now also South Africa, East Asia
Cnidaria	<i>Diadumene lineata</i> (<i>Sagartia luciae</i>)	Diadumenidae	Cosmopolitan
Cnidaria	<i>Ectopleura crocea</i>	Tubulariidae	NE USA, Europe Japan, NE Pacific
Cnidaria	<i>Eudendrium ritchiei</i>	Eudendriidae	South Africa
Cnidaria	<i>Hoplania durotrix</i>	Caryophylliidae	NE Atlantic
Cnidaria	<i>Pennaria disticha</i>	Pennariidae	Europe; now circum- global in warm water
Cnidaria	<i>Tethocyathus cylindraceus</i>	Caryophylliidae	W. Atlantic
Cnidaria	<i>Bougainvillia muscus</i>	Bougainvillidae	North Atlantic
Cnidaria	<i>Clytia hemisphaerica</i>	Campanulariidae	Atlantic
Cnidaria	<i>Obelia bidentata</i>	Campanulariidae	North Atlantic
Decapoda	<i>Charybdis japonica</i>	Portunidae	Japan, Korea, Northern China, Malaysia
Decapoda	<i>Merocryptus lambriformis</i>	Leucosidae	Southern Australia (adventive Japan)

Taxon	Species	Family	Probable native range
Decapoda	<i>Pilumnopus serratifrons</i>	Xanthidae	South Australia
Decapoda	<i>Plagusia chabrus</i>	Grapsidae	West Indo-Pacific
Decapoda	<i>Pyromaia tuberculata</i>	Majidae	West coast North America (adventive Japan)
Entoprocta	<i>Amathia distans</i>	Vesiculariidae	Atlantic coast of America, North Carolina to Brazil
Entoprocta	<i>Anguinella palmata</i>	Nolellidae	Southern Europe
Entoprocta	<i>Bowerbankia gracilis</i>	Vesiculariidae	Eastern North America
Entoprocta	<i>Bugula flabellata</i>	Bugulidae	Probably European waters
Entoprocta	<i>Bugula neritina</i>	Bugulidae	Mediterranean and southern Europe
Entoprocta	<i>Bugula stolonifera</i>	Bugulidae	Europe
Entoprocta	<i>Buskia nitens</i>	Buskiidae	European seas
Entoprocta	<i>Celloporaria</i> sp. 1	Lepaliellidae	?
Entoprocta	<i>Conopeum seurati</i>	Electridae	Caspian Sea, Sea of Azov, Mediterranean, North Africa
Entoprocta	<i>Cryptosula pallasiana</i>	Cryptosulidae	Cosmopolitan
Entoprocta	<i>Electra tenella</i>	Electridae	Atlantic coast of Florida, Puerto Rico, Brazil
Entoprocta	<i>Tricellaria porteri</i>	Candidae	Southern Australia or Japan, now cosmopolitan
Entoprocta	<i>Watersipora arcuata</i>	Watersiporidae	California to Galapagos Islands
Entoprocta	<i>Watersipora subtorquata</i>	Watersiporidae	Brazil, Bermuda, Cape Verde Islands
Entoprocta	<i>Zoobotryon verticillatum</i>	Vesiculariidae	Mediterranean
Isopoda	<i>Limnoria tripunctata</i>	Limnoriidae	Cosmopolitan warm to tropical waters
Mollusca	<i>Crassostrea gigas</i>	Ostreidae	Japan, Korea and vicinity (adventive: Pacific & Atlantic coast of North America, Hawaii, Okinawa, New South Wales)
Mollusca	<i>Cuthona alpha</i>	Tergipediidae	Japan (adventive: Pacific coast North America)
Mollusca	<i>Cuthona beta</i>	Tergipediidae	Japan
Mollusca	<i>Eubbranchus agrius</i>	Eubbranchidae	Chile
Mollusca	<i>Limaria orientalis</i>	Limidae	Japan, Philippines & widely distributed in Indo Pacific
Mollusca	<i>Lyrodus mediolobatus</i>	Teredinidae	Tropical cosmopolitan
Mollusca	<i>Lyrodus pedicellatus</i>	Teredinidae	Tropical to temperate seas, cosmopolitan
Mollusca	<i>Microtralia</i> sp.= <i>M. insularis</i>	Ellobiidae	Unknown
Mollusca	<i>Musculista senhousia</i>	Mytilidae	Eastern Asia from Singapore to Siberia
Mollusca	<i>Okenia pellucida</i>	Goniodorididae	Australia
Mollusca	<i>Okenia plana</i>	Goniodorididae	Cosmopolitan
Mollusca	<i>Polycera hedgpethi</i>	Polyceridae	Unknown, now almost cosmopolitan
Mollusca	<i>Thecacera pennigera</i>	Polyceridae	Unknown; temperate cosmopolitan (perhaps originally temperate latitude of eastern South America)
Mollusca	<i>Theora lubrica</i>	Semelidae	Japan, the tropical Pacific, Indonesia, Thailand, China Philippines and Australia
Polychaeta	<i>Ficopomatus enigmaticus</i>	Serpulidae	Obscure, European coastal waters
Polychaeta	<i>Hydroides elegans</i>	Serpulidae	Unknown, now cosmopolitan
Polychaeta	<i>Hydroides ezoensis</i>	Serpulidae	Japan (adventive in northeast Atlantic, Australia)
Polychaeta	<i>Polydora cornuta</i>	Spionidae	Atlantic Coast North America European coastal waters
Polychaeta	<i>Polydora haswelli</i>	Spionidae	Australia
Polychaeta	<i>Pseudopolydora corniculata</i>	Spionidae	Taiwan
Polychaeta	<i>Chaetopterus</i> sp. A	Chaetopteridae	Unknown
Porifera	<i>Clathrina coriacea</i>	Clathrinidae	North Atlantic, Mediterranean, Japan Indian Ocean, Arctic, Antarctic
Porifera	<i>Cliona celata</i>	Clionidae	Arctic, Atlantic coasts of Europe & North America, West Indies, Indian Ocean, Red Sea,

Taxon	Species	Family	Probable native range
			Malaysia, Australia, New Guinea
Porifera	Dendya poterium	Clathrinidae	Europe, circumglobal
Porifera	Halichondria panicea	Halichondriidae	Europe, cosmopolitan
Porifera	Halisarca dujardini	Halisarcidae	Europe, cosmopolitan
Porifera	Hymeniacidon perleve	Hymeniacidonidae	Europe, cosmopolitan
Porifera	Tethya aurantium	Tethyidae	California
Porifera	Haliclona heterofibrosa	Haliclonidae	North-eastern Atlantic
Porifera	Plakina monolopha	Plakinidae	Mediterranean
Protozoa	Siphogenerina raphanus	Siphogenerinoididae	Cosmopolitan
Teleostei	Acentrogobius pflaumii	Gobiidae	Japan, Korea, Taiwan, Philippines (adventive in Australia)
Teleostei	Arenigobius bifrenatus	Gobiidae	Southern Australia
Teleostei	Omobranchus anolius	Blenniidae	Southern Australia

Appendix 2: List of questions that were the motivation for correlation analyses. Question numbers are listed in Table X.X of the main body text.

1. Does abundance of natives affect invasion success by NIS?
Correlate: Native inds with NIS inds, *Musculista* inds, *Theora* inds
2. Does the richness of native taxa affect invasion success by NIS?
Correlate: Native taxa with NIS inds, *Musculista* inds, *Theora* inds
3. Does the diversity of native assemblages affect invasion success by NIS?
Correlate: Native diversity with NIS inds, *Musculista* inds, *Theora* inds
4. Does invader abundance affect the diversity of the soft-sediment macrofaunal assemblage?
Correlate: NIS inds, *Musculista* inds, *Theora* inds with Total diversity
5. Does invader abundance affect the abundance of native taxa?
Correlate: NIS inds, *Musculista* inds, *Theora* inds with Native inds
6. Does invader abundance affect the richness of native taxa?
Correlate: NIS inds, *Musculista* inds, *Theora* inds with Native taxa
7. Does invader abundance affect the diversity of native assemblages?
Correlate: NIS inds, *Musculista* inds, *Theora* inds with Native diversity
8. Does the abundance of one NIS affect the invasion success of another NIS (positive effects would support invasional meltdown hypothesis)?
Correlate: *Musculista* with *Theora* inds
9. Does bioturbation by large native taxa affect the invasion success of NIS (negative effect would suggest biogenic disturbance hypothesis)?
Correlate: *Echinocardium*, Native bioturbators with NIS inds, *Musculista* inds, *Theora* inds
10. Does the abundance of large native bivalves affect invasion success of NIS bivalves?
Correlate: Large native bivalves with NIS inds, *Musculista* inds, *Theora* inds
11. Does the abundance of *Atrina* affect invasion success by NIS?
Correlate: *Atrina* with *Styela*, NIS inds, *Musculista* inds, *Theora* inds,
12. Does the abundance of *Atrina* at a site affect snapper abundance?
Correlate: *Atrina* with Snapper