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Faunal changes in Waitemata Harbour sediments, 1930s-1990s

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Faunal changes in Waitemata Harbour sediments, 1930s–1990s

Bruce W. Hayward*, A. Brett Stephenson*, Margaret Morley*, Jenny L. Riley*, Hugh R. Grenfell*

A resurvey of Powell's classic study of subtidal, soft-bottom communities in the Waitemata Harbour, Auckland, was undertaken to determine the nature of faunal changes between the 1930s and 1990s. Samples were dredged and associations were intuitively deduced largely on the basis of molluscs and echinoderms, in a similar fashion to Powell's 1930s study.

Away from the wharves and marinas the soft-bottom fauna is still remarkably rich and diverse, and retains a similar gross pattern to the 1930s. Fourteen mollusc species (dominantly carnivorous gastropods) appear to have disappeared or suffered major reductions in abundance within the harbour. This has resulted in the disappearance of two of Powell's associations (*Tawera-Tucetona, Amalda*) from the outer harbour. There has also been an apparent reduction in the abundance and range of the turritellid *Maoricolpus roseus* and a number of associated species of the shelly channel sediments in the centre of the harbour.

Since the 1930s at least nine New Zealand mollusc species (mostly deposit- and suspension-feeders) and one crab appear to have colonised the harbour, and nine others seem to have increased in abundance. The establishment of extensive horse mussel (*Atrina*) beds north-east of North Head is the most significant of these changes. Three exotic bivalves (*Limaria orientalis, Theora lubrica, Musculista senhousia*) introduced in the 1960s and 1970s have become so abundant in the harbour that they are now codominant characterising species of six of the eight associations recognised in the 1990s.

The exact causes of many of these observed changes will never be determinable. Some may be natural (e.g., spread of *Atrina*), but many are attributable to human activities associated with New Zealand's largest city (e.g., TBT poisoning, closure of sewage outfalls, increased sediment, fresh water and pollutants, ballast water introductions, dredging).

Keywords: Auckland; Waitemata Harbour; marine soft-bottom associations; benthos; Mollusca; *Atrina; Limaria; Theora; Musculista*

INTRODUCTION

Mitigation of the ever-growing impact of human activities on the world's natural environment and ecosystems is the major challenge of this generation. Before we can address the issues of how to reduce or eliminate these impacts and move towards more sustainable use, we need to determine their nature. Monitoring programmes started in the 1990s have problems assessing the extent of historical impacts and will take many years before long-term effects can be documented and separated out from background natural changes. Investigations of long-term (>50 year) natural changes and the effect of human impacts require reliable historical documentation and/or samples of the biota and possibly its substrate (e.g., sediment or soil) that are suitable for comparison with present-day studies.

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Historical (pre–1950s) studies on subtidal marine ecosystems in New Zealand are very limited. The most significant and extensive documentation of any area of subtidal soft-bottom marine biota in this country during this period was the pioneering study of the Waitemata Harbour by Powell (1937).

This paper reports on a 1990s restudy of part of the Waitemata Harbour using similar methods of sampling and analysis to Powell, in an attempt to determine what changes have occurred between the 1930s and 1990s in the sea floor biota of New Zealand's most used harbour, surrounded by its largest city.

Our 1990s restudy was restricted to the Waitemata Harbour in its strict sense, extending seaward from its upper reaches out as far as Bean Rock in the east and Rangitoto Beacon in the north (Fig. 1). This equates to Powell's (1937) survey areas A, B, and most of E. It encompasses the commercial wharves and main pleasure boat marinas and the area of assumed greatest human impact and pollution in the harbour.

Information on the physical characteristics of the Waitemata Harbour are presented in Hounsell (1935), Slinn (1968), and Gregory et al. (1994).

POWELL'S 1930s WAITEMATA HARBOUR SURVEY

Field methods

Between 1926 and 1936 the late Dr A. W. B. (Baden) Powell, then Curator of Mollusca at Auckland Institute and Museum, dredged bottom samples from 148 stations in the Waitemata and, to a smaller extent, Manukau harbours (Fig. 1). Most sampling was undertaken during the latter five years of this period. Samples were hand-hauled from a motor launch using either a small naturalist's dredge or a conical dredge, each taking 10–15 litres of sediment per haul. At some stations Powell took several hauls, which were used to help define the boundaries of his faunal associations.

Powell does not record how his samples were processed nor what was the smallest size of live organism that he identified. His records of numerous micromolluscs suggest that he probably washed some samples over a sieve with about 1 mm openings.

Basic data

Powell (1937) undertook crude grain size analyses on some of his samples using the early non-standard grading method of Allen (1899). The full unpublished data has been found for a few of the samples, but its grain size divisions and method of separating fine sand from mud are incapable of being directly compared with modern results. Information on tides, sea temperatures, salinity, and pH was obtained from Hounsell (1935).

Powell identified—and in some instances counted—all the live molluscs, echinoderms, and crabs in his samples. He had a selection of polychaetes identified by Prof. W.B. Benham. E.W. Bennett assisted with crab identifications and later included these Waitemata collections in his review of New Zealand crabs (Bennett 1964). Amphipods, isopods, and a miscellany of other groups of organisms were beyond the scope of his study.

Powell sampled 52 subtidal stations within our Waitemata Harbour restudy area, but no results have been found or published for 13 of these, and a further 9 have very limited identifications available (fewer than 3 taxa). Effectively for purposes of comparison we have reliable presence/absence data on macromolluscs, most echinoderms, and most crabs for 30 stations.

Polychaete data is more patchy, with apparently many unidentified specimens. Powell's polychaete list of 43 taxa is much harder to compare with our modern polychaete list of 105 taxa. For these reasons we do not believe that a comparison of the polychaete faunas would produce any meaningful results.

A selection of preserved specimens, dead shells, and sieved dry bulk samples are held in the Auckland Museum collections. Some of Powell's original notes, observations, identifications, and counts are also available but provide little more information than that published by Powell (1937).

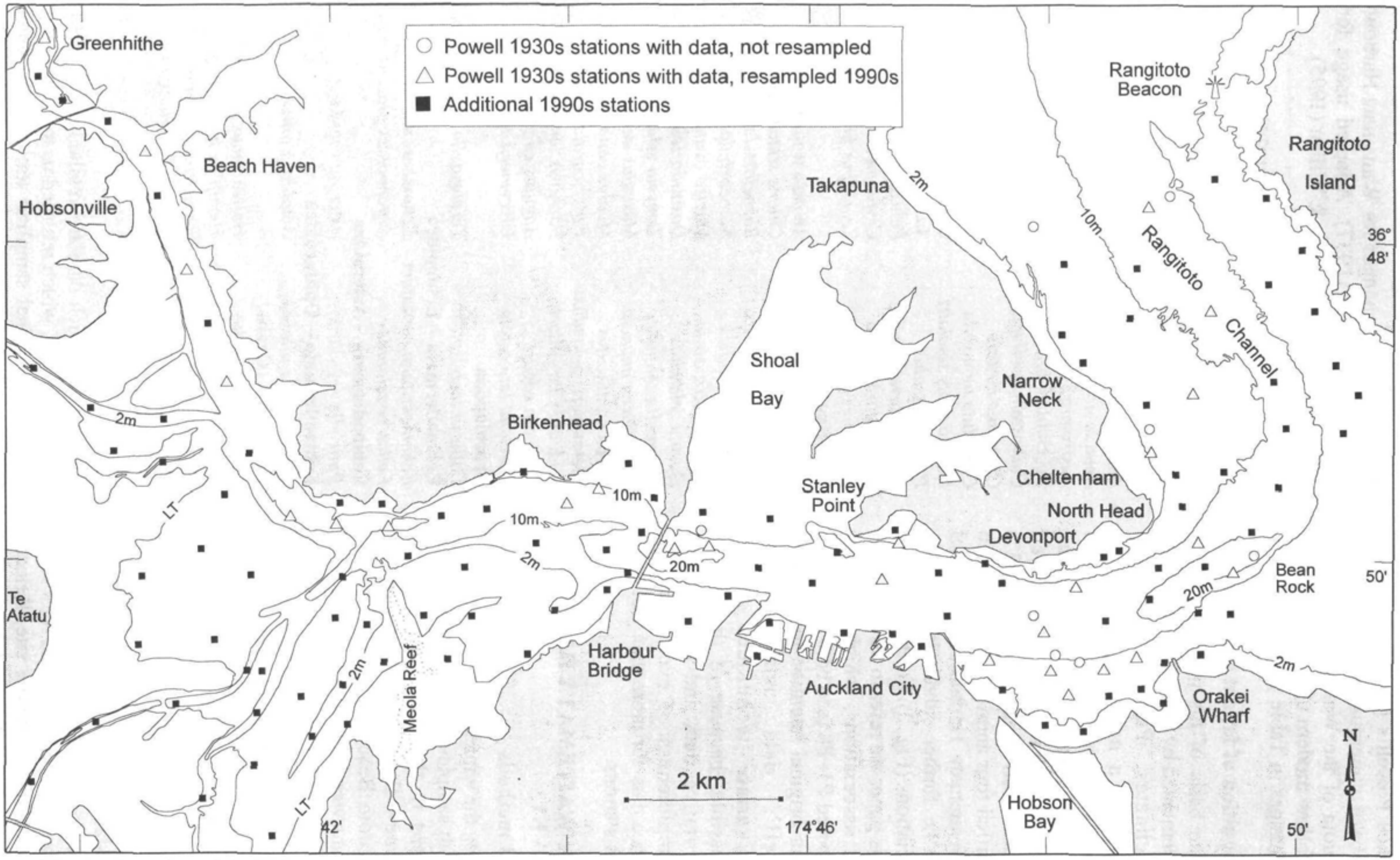

Fig. 1 Location of the Waitemata Harbour study area, Auckland, New Zealand. The 1930s sampling stations of Powell (1937) and the 1990s stations of this study are shown.

Since Powell's (1937) study there have been numerous name changes for the biota of the Waitemata Harbour. We follow modern usage, but also list the changes in Table 1.

Recognition of faunal associations

On the basis of his molluscan data, supplemented by the echinoderms and polychaetes, Powell intuitively recognised a number of recurring animal communities, which he named after the larger and more dominant members that he considered characterised them. Powell (1937) identified four animal "formations" in the Waitemata Harbour, and two of these he further subdivided into six associations (Fig. 2). For the purposes of this paper we refer to all of these as eight associations, which we have numbered P1–P8 (see below).

Our original intention to reanalyse Powell's data using modern multivariate techniques proved impossible, because of the lack of quantitative data and the apparent incompleteness of even presence/absence data for more than just a few of his stations.

Table 1 Name changes for Waitemata Harbour biota since Powell (1937). Adopted usage for molluscs is that of Spencer & Willan (1995).

Present name	Powell (1937) name
Mollusca – Polyplacophora	
Leptochiton inquinatus	*Terenochiton inquinatus*
Mollusca – Gastropoda	
Amalda australis	*Baryspira australis*
Amalda mucronata	*Baryspira mucronata*
Amalda novaezelandiae	*Baryspira novaezelandiae*
Austromitra rubiginosa	*Austromitra rubiradix*
Buccinulum linea	*Buccinulum multilineum*
Calliostoma pellucidum	*Maurea pellucida*
Crepidula costata	*Maoricrypta costata*
Crepidula monoxyla	*Maoricrypta monoxyla*
Neoguraleus sinclairi	*Guraleus sinclairi*
Penion sulcatus	*Austrosipho adusta*
Struthiolaria vermis	*Pelicaria vermis*
Tomopleura albula	*Cryptomella albula*
Zeacolpus pagoda	*Zeacolpus fulminatus*
Mollusca – Bivalvia	
Anomia trigonopsis	*Anomia walteri*
Austrovenus stutchburyi	*Chione stutchburyi*
Borniola reniformis	*Rochefortula reniformis*
Corbula zelandica	*Notocorbula zelandica*
Cyclomactra ovata	*Mactra ovata*
Dosina zelandica	*Dosinula zelandica*
Felaniella zelandica	*Zemysia zelandica*
Modiolarca impacta	*Musculus impactus*
Perna canaliculus	*Mytilus canaliculus*
Pleuromeris zelandica	*Venericardia lutea*
Ruditapes largillierti	*Paphirus largillierti*
Tellinota edgari	*Angulus edgari*
Tucetona laticostata	*Glycymeris laticostata*
Brachiopoda	
Calloria inconspicua	*Terebratella inconspicua*
Echinodermata – Echinoidea	
Echinocardium cordatum	*Echinocardium australe*
Fellaster zelandiae	*Arachnoides placenta*
Echinodermata – Asteroidea	
Patiriella regularis	*Asterina regularis*
Echinodermata – Ophiuroidea	
Amphiocnida pilosa	*Amphiura pilosa*
Crustacea – Crabs	
Halicarcinus varius	*Halicarcinus planatus*
Macrophthalmus hirtipes	*Hemiplax hirtipes*
Notomithrax minor	*Paramithrax minor*
Petrolisthes novaezelandiae	*Petrolisthes elongatus*

1990s WAITEMATA HARBOUR SURVEY

Field methods

During the winter (June, July) of 1993, bottom samples were dredged from 72 stations in the Waitemata Harbour, between the harbour bridge and Rangitoto Beacon (Fig. 1). These 72 stations were resampled in the summer (January, February) of 1994. During the summer (November–January) of 1994–95 a further 78 stations were sampled in the upper Waitemata Harbour above the harbour bridge (Fig. 1).

Station locations were selected to give broad coverage of the whole subtidal area of the harbour and to coincide with most of the Powell station localities for which data are available. The 1990s stations were recorded and relocated using a portable GPS, which returned us to within 10 m of the earlier sampling site. Relocation of Powell's original sampling stations, for which there is a description and depth, was less accurate.

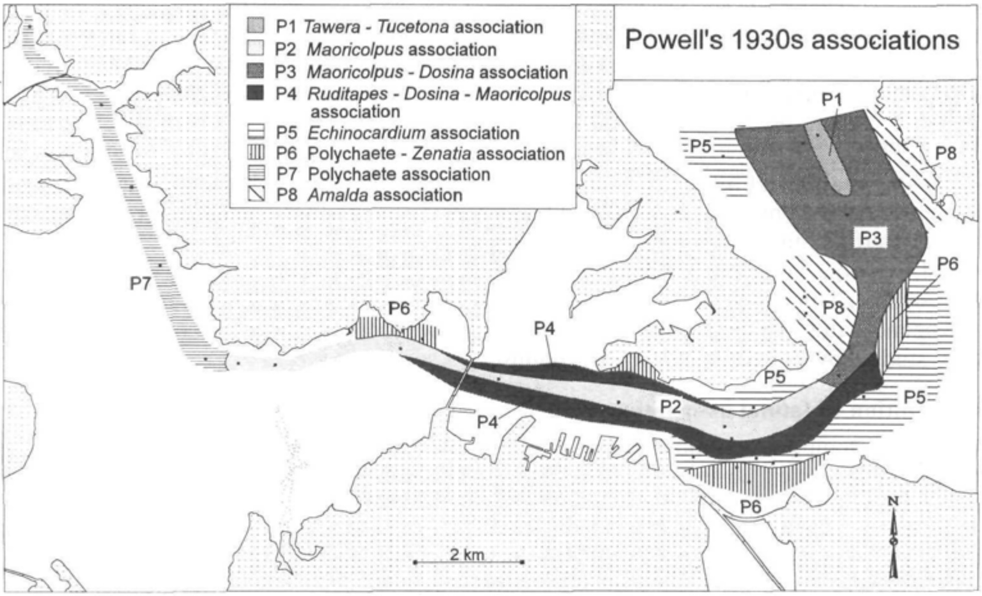

Fig. 2 Distribution of Powell's 1930s subtidal soft-bottom associations, redrawn from Powell (1937, diagram 4).

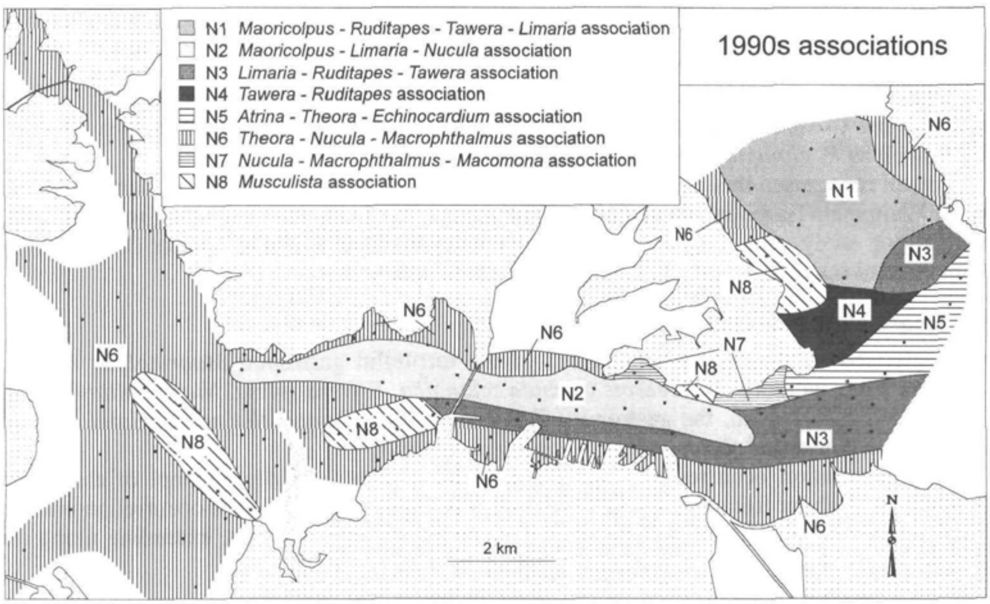

Fig. 3 Distribution of the 1990s subtidal soft-bottom associations derived from a combination of summer and winter sampling, using similar intuitive qualitative methods to Powell (1937).

Samples were hand-hauled from a 4 m dinghy powered by a small outboard motor. A naturalist's dredge with 10 litre capacity was used, for compatibility with Powell's data. Depending on substrate type, the dredge sampled 6–10 cm into the seafloor sediment and in every instance came up 90–110% full. In most instances the dredge bit deeply into the relatively soft substrate and needed to be dragged less than several metres across the sea floor in order to be filled. Powell (1937) made the same observation for his dredge hauls. After removal of a 200 ml split for sediment grain size analysis, each sample was washed over a 1 mm sieve to remove mud and sand, and the residue was fixed with preservative.

Basic data

Grain size analyses of bulk sediment splits were undertaken for each station using standard sieve sizes at one phi intervals (Folk 1968). Unfortunately it is not possible to compare these with Powell's limited, non-standard grain size data.

All live organisms that had been preserved in the residues were hand picked, identified, and counted. This produced a data set of over 20 000 specimens in 300 different taxa which will be more fully reported elsewhere. In this paper we focus on the groups of organisms that were studied by Powell, primarily the molluscs.

Recognition of faunal associations

We have attempted to follow Powell's (1937) intuitive approach to recognise recurring animal communities, largely on the basis of macromolluscs, supplemented by echinoderms and to a smaller extent by crabs. We identify eight faunal associations, N1–N8 (Fig. 3).

Multivariate analysis techniques have been used to identify a set of somewhat different faunal associations based on our total quantitative data for all taxa, and this will be published elsewhere—together, we hope, with the complete data set.

1930s FAUNAL ASSOCIATIONS

Station numbers quoted in this section are those of Powell.

P1 *Tawera – Tucetona* association

Characterised by the bivalves *Tawera spissa* and *Tucetona laticostata,* the gastropods *Trochus tiaratus* and *Cominella quoyana,* and the crabs *Petrolisthes novaezealandiae* (misidentified by Powell as *P. elongatus*) and *Notomithrax minor.*

Powell recognised this association in clean, coarse substrates in the main channels of the outer Waitemata Harbour. His mapping of this association in the centre of Rangitoto Channel, within our study area, appears to be based on data from a single station (E.3), which contained two live and a number of dead *Tucetona laticostata.*

P2 *Maoricolpus* association

Characterised by the "great abundance" of the turritellid gastropod *Maoricolpus roseus.* Subdominants included the bivalves *Corbula zelandica, Tawera spissa, Nucula nitidula,* and *Venericardia purpurata,* the gastropods *Zegalerus tenuis, Sigapatella novaezelandiae,* and *Buccinulum linea,* and the chiton *Leptochiton inquinatus.*

This association occurred as a narrow belt in the centre of the channel of the inner Waitemata Harbour from near the end of Meola Reef to off North Head. It occurred in muddy shell gravel and was based on data from a minimum of eight stations, extending along its length.

P3 *Maoricolpus – Dosina* association

Dominated by six molluscs—*Maoricolpus roseus, Dosina zelandica, Ruditapes largillierti, Corbula zelandica, Trochus tiaratus,* and *Cominella quoyana.*

Powell recognised this as transitional between the *Maoricolpus* association of the inner harbour channel and the *Tawera-Tucetona* association of Rangitoto Channel. It bordered this latter association on either side of Rangitoto Channel, and was based on data from three stations within our 1990s study area (B.24, E.17, E.18).

P4 *Ruditapes – Dosina – Maoricolpus* association

Characterised by common *Ruditapes largillierti*, and *Dosina zelandica* with a few *Maoricolpus roseus*.

This association occurred on the sides of the channel in the inner Waitemata Harbour bordering the typical *Maoricolpus* association, where Powell recorded the substrate as shelly mud. It appears to have been based on data from five widely spaced stations (B.28, B.36, B.37, B.38, B.41) between Northcote and Bean Rock.

P5 *Echinocardium* association

Characterised by the heart urchin *Echinocardium cordatum*, the bivalve *Dosinia lambata*, and the brittle star *Amphiura rosea*. Subdominants included a number of polychaetes and the molluscs *Cominella adspersa*, *Neilo australis*, *Tellinota edgari*, and *Zenatia acinaces*.

This association was present in fine sand and mud over a large area of sea floor east of the present study. Within our 1990s study area it occurred in the northwest off Takapuna Beach (E.12), in the east between Bean Rock and Rangitoto Island (C.10), and in narrow bands on the channel slopes on either side of the entrance to the inner harbour, offshore from Devonport (B.34) and Hobson Bay (B.17, B.18, B.21, B.22).

P6 Polychaete – *Zenatia* association

Characterised by its low diversity of molluscs, dominated by *Zenatia acinaces*, and an abundance of polychaetes. Subdominants included the polychaete *Pectinaria australis*, the crab *Macrophthalmus hirtipes*, and the molluscs *Cominella adspersa*, *Leptomya retiaria*, and *Nucula nitidula*.

This association was recognised in the fine sand and mud in the shallows on either side of the inner harbour channel, from Devonport to Birkenhead on the north side and in Hobson Bay on the south shore. An area was also mapped in deeper water near Bean Rock.

P7 Polychaete association

Dominated by polychaetes, only a few of which were identified, and having the lowest diversity and density of live animals. This upper harbour estuarine association was recognised in the harbour channel from Meola Reef to Greenhithe.

P8 *Amalda* association

Characteristed by the carnivorous olive shell *Amalda australis*, and the whelk *Cominella adspersa*. This association was found on clean fine sand from low tide to about 8 m depth off outer harbour beaches of Rangitoto and Cheltenham. In our 1990s study area it was based on sparse data from three stations (E.5, E.13, E.14).

1990s FAUNAL ASSOCIATIONS

N1 *Maoricolpus – Ruditapes – Tawera – Limaria* association

Characterised by the presence of numerous turret shells *Maoricolpus roseus*, and bivalves *Ruditapes largillierti*, *Tawera spissa*, and *Limaria orientalis*. Other common organisms are the small chiton *Leptochiton inquinatus*, the gastropods *Cominella quoyana*, *Sigapatella novaezelandiae*, and *Zegalerus tenuis*, the bivalves *Corbula zelandica* and *Gari stangeri*, the crabs *Halicarcinus varius* and *Paguristes pilosus*, and the small brittle stars *Amphiocnida pilosa* and *Amphiopolis squamata*.

This association occurs in muddy, shelly, fine sand over a wide area of Rangitoto Channel (Fig. 3, 4).

N2 *Maoricolpus – Limaria – Nucula* association

Dominated by abundant live turret shells, *Maoricolpus roseus* (Fig. 5), and numerous bivalves *Limaria orientalis* and *Nucula nitidula*. Also common are *Leptochiton inquinatus*, *Tawera spissa*, *Paguristes pilosus*, *Amphiocnida pilosus*, and *Amphiopolis squamata*.

The association occurs in muddy, shelly, fine sand and shell gravel in the channel of the inner harbour from Meola Reef in the west to Devonport wharf in the east (Fig. 3).

N3 *Limaria – Ruditapes – Tawera* association

Similar to the *Maoricolpus-Ruditapes-Tawera-Limaria* association, differing largely in the greatly reduced incidence (often absence) of live *Maoricolpus roseus* (Fig. 5). Also absent or rare are *Gari stangeri*, *Paguristes pilosus*, *Halicarcinus varius*, *Amphiocnida pilosa*, and *Amphiopolis squamata*. The bivalves *Pleuromeris zelandica* and *Dosina zelandica* are most abundant in this association.

The association occurs in muddy, shelly, fine sand and very fine sand in the southeastern part of Rangitoto Channel, in the entrance to the inner harbour channel between Devonport and Orakei, and along the south side of the inner harbour channel seaward of the wharves (Fig. 3).

N4 *Tawera – Ruditapes* association

Having the greatest abundance of *Tawera spissa* (Fig. 5), although not as abundant as in the *Tawera* shellbeds found elsewhere around northern New Zealand (e.g., Grace & Hayward 1980). Also common are *Ruditapes largillierti* and *Gari stangeri*. Differs from similar associations (above) in the general absence of *Maoricolpus roseus*, *Limaria orientalis*, *Dosina zelandica*, and *Paguristes pilosus*. The association occurs in clean fine sand at 0–10 m depth off shore from Cheltenham Beach (Fig. 3, 4).

N5 *Atrina – Theora – Echinocardium* association

Characterised by numerous live horse mussels *Atrina pectinata zelandica*, together with the heart urchin *Echinocardium cordatum* and many small, thin-shelled *Theora lubrica*. *Tawera spissa*, *Ruditapes largillierti*, and *Halicarcinus varius* are present in low numbers, but most of the organisms characteristic of other associations are absent or rare.

The association occurs in muddy fine to very fine sand in a triangle between south Rangitoto, Bean Rock, and Devonport (Fig. 4). The *Atrina* bed is richest and most extensive on the outside of the bend of the main harbour channel, but extends up into the shallows of Torpedo Bay, between Devonport and North Head (Fig. 5). Small beds of *Atrina* have also been found in less than 5 m of water off the west coast of Rangitoto, north of Narrow Neck Beach, and near Orakei Wharf.

N6 *Theora – Nucula – Macrophthalmus* association

Characterised by the abundance of small *Theora lubrica* and, to a slightly smaller degree, *Nucula hartvigiana* and *N. nitidula*. Also frequently present are the small burrowing mud crab *Macrophthalmus hirtipes* and a number of polychaetes. Diversity is much lower than in the preceding associations, and most of their characterising species are lacking.

The association inhabits most of the subtidal upper Waitemata Harbour above the bridge, and most of the shallow subtidal muddy fine sand areas on either side of the main channel from the bridge out to Rangitoto Beacon. It does not occur in the cleaner fine sand in the shallows on the north side of the inner harbour channel between Stanley Point and North Head.

N7 *Nucula – Macrophthalmus – Macomona* association

Similar to N6 in the abundance of the two species of small nut shell *Nucula*, the crab *Macrophthalmus hirtipes*, and polychaete worms, but differing in the absence of the mud-loving *Theora lubrica* and the greater frequency of the wedge shell *Macomona liliana*.

This association occurs in the clean fine sand in the shallows on the north side of the main harbour channel between Stanley Point and North Head.

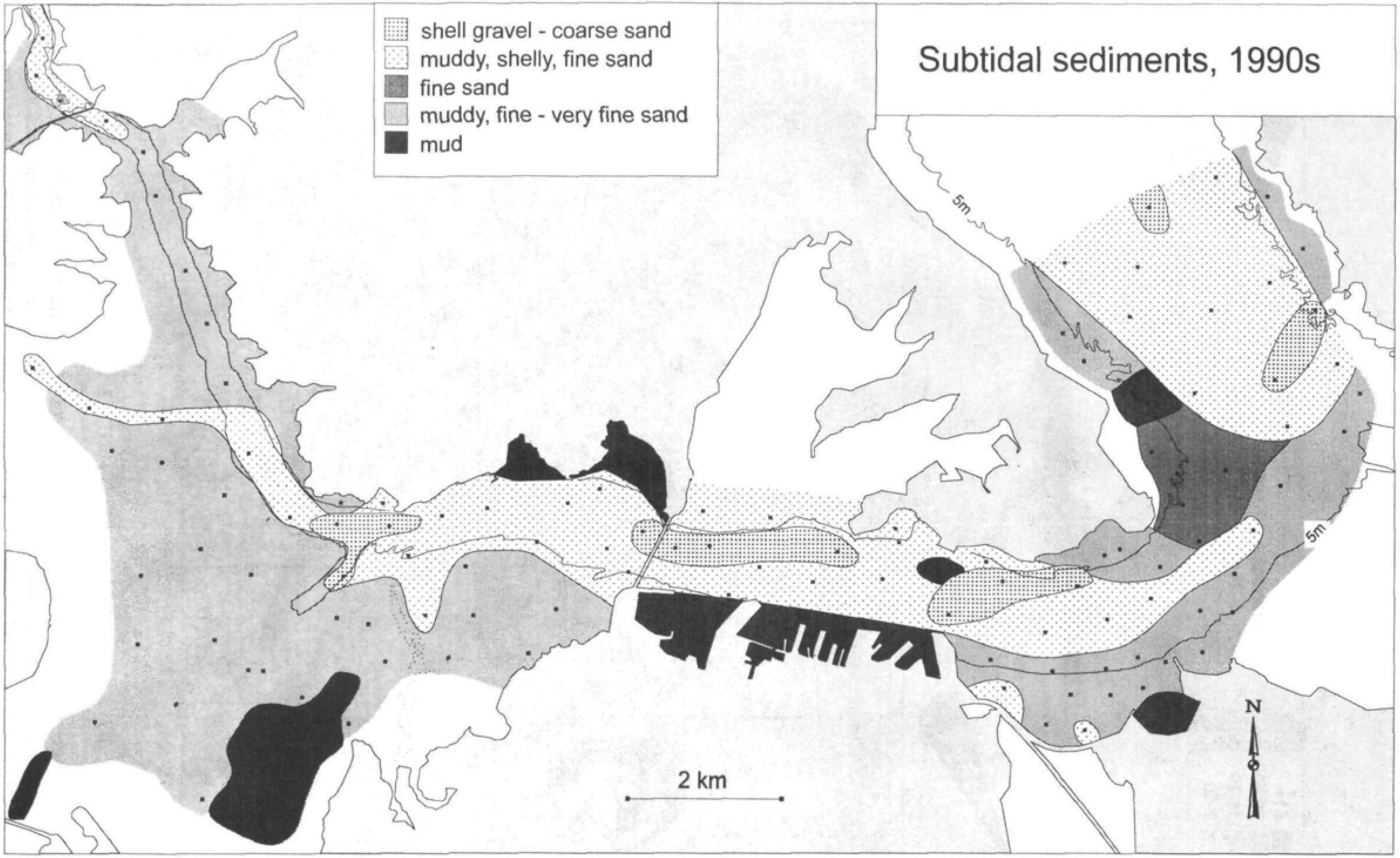

Fig. 4 Subtidal seafloor sediment distribution in the Waitemata Harbour, derived from analysis of this study's 1990s samples.

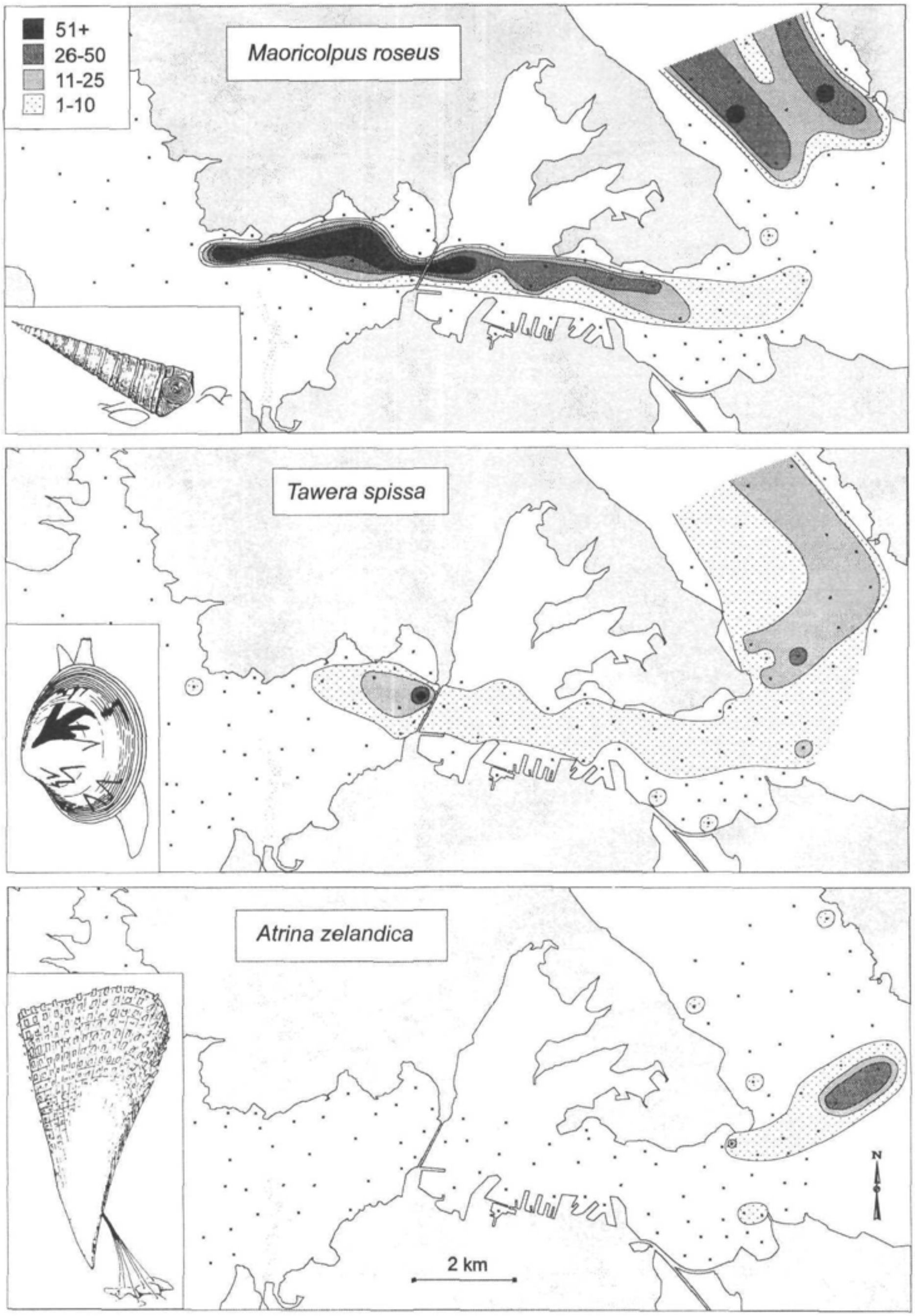

Fig. 5 Contoured distribution and abundance maps in Waitemata Harbour for *Maoricolpus roseus, Tawera spissa* and *Atrina pectinata zelandica* from our 1990s survey. Data combines summer and winter samplings and is standardised as number of live organisms per 20 litres of sediment (approx. per 0.2 m^2 of seafloor).

N8 *Musculista* association

Characterised by abundant live individuals of the small introduced Asian mussel *Musculista senhousia,* their byssal threads forming a thick mat over the seafloor which accumulates mud. The subordinate fauna is largely that of the *Theora-Nucula-Macrophthalmus* association.

The association occurs as patches within the range of the *Theora-Nucula-Macrophthalmus* association. Our studies found three dense patches of live *Musculista* in the winter of 1993 (off Narrow Neck, Cheltenham, and Devonport), but all had died off and virtually disappeared apart from dead shells 6 months later. The unpredictable seasonal nature of *Musculista* beds intertidally has been noted around other parts of the Waitemata Harbour (M. Morley, pers. obs.) and in Japanese waters (Kikuchi & Tanaka 1978). The largest extent of this association appears to be in 0–3 m of water on either side of Meola Reef in the upper harbour, which was sampled in 1994 (Fig. 3).

CHANGES TO THE FAUNAL ASSOCIATIONS, 1930s–1990s

P1 *Tawera-Tucetona* association

No live specimens of *Tucetona laticostata* were recovered during our 1990s survey, so this association may no longer be present in the study area. However, the basis of Powell's area of P1 mapped in the Rangitoto Channel was confined to just two live *Tucetona* and a number of dead shells recovered from a single dredge station, so the absence of live *Tucetona* in the 1990s may not be significant. It should be noted, though, that neither were any dead shells of *Tucetona* recovered from anywhere in the study area in the 1990s (Appendix 1).

The perceived loss of this association might be purely an artifact of fortuitous sampling of a small patch of *Tucetona* present in Rangitoto Channel in the 1930s. Otherwise its loss could be a natural process resulting from poor years of settlement and recolonisation, or it might be a result of the extensive dredging that has occurred in Rangitoto Channel in recent decades to deepen it for shipping.

Living *Tucetona* have been found in the 1990s just outside the study area, in gravels close to Rangitoto Beacon (R. Roberts, pers. comm.). It is also reported to be still living in other areas mapped by Powell east of the study area in Motuihe Channel and near the Noises (M. Miller and J. Morton, pers. comm.).

P2 *Maoricolpus*, P3 *Maoricolpus – Dosina*, and P4 *Ruditapes – Dosina – Maoricolpus* associations

These three associations are mostly still present in the coarser sediment of the channels in which they were found in the 1930s, although there have been some changes in composition and extent.

In the 1930s Powell mapped these associations as a continuous belt in the channel from Birkenhead out to Rangitoto Beacon. In the 1990s there is a distinct gap in the middle of this belt, both in the sediment type and in the faunal associations of the coarse shelly substrate. This gap of about 2 km forms a triangle between North Head, Bean Rock, and southwest Rangitoto Island and is occupied by muddy, fine to very fine sand inhabited by association N5.

Whether the continuous belt of the 1930s was a true representation is questionable. In the area of the 1990s gap, Powell has only one sample with data (B24 – *Maoricolpus* association) and it is close to the southern edge of the gap. There does, however, appear to be sufficient data to indicate that the total range of *Maoricolpus* has contracted since the 1930s. It occurs in very low densities in the channel between Devonport wharf and Bean Rock, and is virtually absent over a 2–2.5 km length of the channel in the central part of the harbour around North Head (Fig. 5). The same 2 km gap is apparent in the distribution pattern of a number of other characteristic species of these three 1930s associations (e.g., *Dosina zelandica, Corbula zelandica, Venericardia purpurata, Leptochiton inquinatus, Cominella quoyana,* and *Trochus tiaratus).*

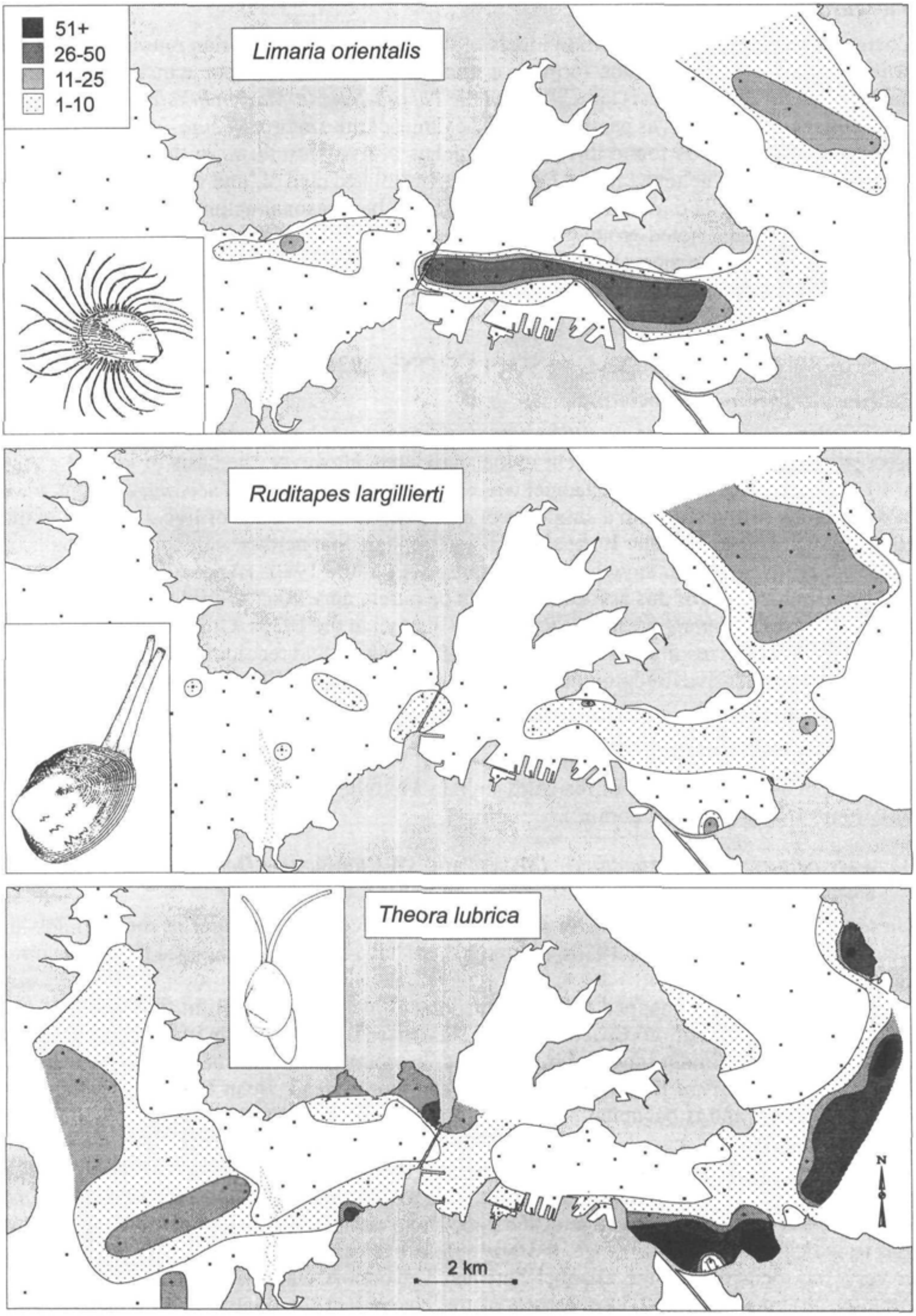

Fig. 6 Contoured distribution and abundance maps in Waitemata Harbour for *Limaria orientalis, Ruditapes largillierti* and *Theora lubrica* from our 1990s survey. Data combines summer and winter samplings and is standardised as number of live organisms per 20 litres of sediment (approx. per 0.2 m^2 of seafloor).

Apart from the above-mentioned gap, Powell's associations P2, P3, and P4 equate with our 1990s associations N2, N1, and N3 respectively. The major differences are the addition of the introduced Asian bivalve *Limaria orientalis,* which is now one of the most abundant and characterising species of these associations (Fig. 6). This species suddenly appeared around the Hauraki Gulf in 1972 (Powell 1974).

In our 1990s surveys *Dosina zelandica* is still present in all three of these associations but is neither common nor persistent enough to justify being called a characterising species. Powell considered *D. zelandica* to be sufficiently abundant to be one of the dominant molluscs in Rangitoto Channel and the sides of the inner harbour channel (P3, P4). Live *Dosina* may have considerably decreased in abundance since the 1930s. In the 1990s *Ruditapes largillierti* and *Tawera spissa* (Fig. 5, 6) have distribution patterns similar to those recorded in the 1930s.

P5 *Echinocardium* association

Powell's *Echinocardium* association is not as readily recognised in the study area as it may have been in the 1930s. This is probably due to the arrival and proliferation of the New Zealand horse mussel *Atrina pectinata zelandica* and the small Asian bivalve *Theora lubrica,* neither of which was present in the harbour in the 1930s. For example, the area north of Bean Rock mapped as P5 by Powell is now inhabited by our *Atrina-Theora-Echinocardium* association (N5), wherein *Echinocardium* may still be at similar densities to the 1930s but has been joined by abundant *Atrina* and *Theora* (Fig. 5, 6). The mapped extent of N5 does not equate with P5, however, as it extends right across the harbour channel to North Head. As mentioned earlier, this pattern equates with a change in sediment type and might be explained by the paucity of Powell's sampling in this critical area. Otherwise there has been a considerable accumulation of fine sediment in this area of the channel bend since the 1930s.

In the 1930s Powell's *Echinocardium* association was also mapped in a strip across the entrance of Hobson Bay. In the 1990s there is little perceptible difference between the fauna of this area and further into the bay, and all is inhabited by the *Theora-Nucula-Macrophthalmus* association with a fauna of low diversity. Rare *Echinocardium* are still present in this strip, but the greater abundance and significance now of the introduced *Theora* place it in N6.

Two of the characterising species of Powell's *Echinocardium* association – *Dosinia lambata* and *Neilo australis* – have not been found alive in the 1990s, and may have decreased in abundance or extent. There are, however, numerous dead shells of *D. lambata* throughout the harbour and, not surprisingly, very few of the more fragile shells of *Neilo* (Appendix 1). Powell also records the brittlestar *Amphiura roseus* as a characteristic species of P5, and it is still present today in low numbers in the same areas of the harbour (N5, N6), although another brittlestar, *Amphiocnida pilosa,* appears to be even more abundant and certainly more widespread.

P6 Polychaete – *Zenatia* and P7 Polychaete associations

The areas occupied by these associations in the 1930s are still characterised by the least diverse faunas, with only a few mollusc taxa and a number of polychaetes. In the 1990s, however, the small, thin-shelled, introduced bivalve *Theora lubrica* is the most abundant, widespread, and persistent organism living in the fine-grained sediment in the shallows of the Waitemata Harbour (Fig. 6). First reported from New Zealand in 1972 (Powell 1974), *Theora* was already a major element in the soft sediments of the upper Waitemata Harbour by the early 1980s (Bioresearches Ltd 1981, Grange 1982). Today most of the upper harbour and the shallows on either side of the inner harbour and on the south-west side of Rangitoto Island are occupied by the *Theora-Nucula-Macrophthalmus* association.

The small, burrowing mud crab *Macrophthalmus hirtipes* was a characterising species in Powell's P6, and probably occurs at similar densities and in similar areas today as in the 1930s. The small nut shells *Nucula hartvigiana* and *N. nitidula* were found in these associations in the 1930s, but Powell's records suggest that they were not particularly common or abundant, in contrast to the 1990s. This difference might be explained if Powell used a coarser sieve for many of his samples than we did.

The northern shore of the inner harbour around Devonport, mapped as P6 in the 1930s, has few *Theora* in the 1990s and is now placed in the *Nucula-Macrophthalmus-Macomona* association, which may differ from what Powell found only in the smaller sieve mesh used and the greater number of shallower stations sampled in the 1990s.

Several other areas that would undoubtedly have been placed in P6 or P7 had they been sampled in the 1930s were occupied in the 1990s by the *Musculista* association (N8), overwhelmingly dominated by this small introduced mussel. *M. senhousia* was first reported from the Waitemata Harbour in 1980 (Willan 1985). In the early 1980s none were found in the upper harbour between Te Atatu and Pt Chevalier (Grange 1982), an area now rich in this species.

P8 *Amalda* association

This association is no longer recognised in the study area, as no live *Amalda* were found in our 1990s survey. Powell recorded live specimens of three species of *Amalda* from at least five stations in the 1930s, and thus their disappearance—or at least significantly reduced density—is likely to be real. Numerous dead *Amalda* shells were recovered from many parts of the harbour in the 1990s, indicating their abundance in fairly recent times.

As recently as the 1970s *A. australis* was exceedingly abundant in low tide sand of Cheltenham Beach (Margaret Morley & Noel Gardner, pers.comm.), just inshore from where Powell mapped his *Amalda* association. In the 1990s live *A. australis* are still present at Cheltenham Beach, but in numbers greatly reduced from a decade or so ago. In the early 1980s single live specimens of *A. australis* were dredged in the upper Waitemata Harbour, between Te Atatu and Pt Chevalier (Grange 1982) and near Herald Island (Bioresearches Ltd 1981).

The greatly reduced number of *Amalda* living in Waitemata Harbour may be a result of poisoning by tributyl tin (TBT) from anti-foulant paints, which has been shown to induce imposex (resulting in the inability to breed) in a selection of marine neogastropods including *Amalda* (Stewart et al. 1992, Scott 1993).

CHANGES TO SPECIES DISTRIBUTION PATTERNS, 1930s–1990s

Introductions of exotic species

Four species in our 1990s subtidal dredge survey of the Waitemata Harbour are definite introductions from overseas since the 1930s (Dromgoole & Foster 1983). These are the bivalves *Limaria orientalis* (Grange 1974), *Theora lubrica* (Climo 1976), and *Musculista senhousia* (Willan 1985, 1987, Morley 1988), and the Californian crab *Pyromaia tuberculata* (Webber & Wear 1981).

Species increases

Nine New Zealand mollusc and one crab species appear to have colonised or recolonised parts of the harbour since the 1930s, or at least dramatically increased in abundance, as they were not recorded living in the study area by Powell. These are the chiton *Pseudotonicia cuneata,* the gastropod *Crepidula costata,* and the bivalves *Atrina pectinata zelandica, Dosinia maoriana, D. subrosea, Gari stangeri, G. lineolata, Hiatella arctica,* and *Scalpomactra scalpellum.* The pea crab *Pinnotheres atrinocola* has not surprisingly appeared in considerable numbers considering the enormous flush of its host, the horse mussel *Atrina pectinata zelandica.*

Species present in both surveys but with an apparent significant increase in abundance and range since the 1930s include the molluscs *Sigapatella novaezelandiae, Zegalerus tenuis, Felaniella zelandica, Nucula hartvigiana, N. nitidula,* and *Pleuromeris zelandica,* the echinoderms *Amphiocnida pilosa* and *Patiriella regularis,* and the pillbox crab *Halicarcinus* *varius*. Most of this latter group are moderately small organisms, and the apparent increase may be explained if Powell used a larger sieve size for many of his samples. He records micromolluscs for his associations, so obviously he did look at some finer fractions.

Deposit- and suspension-feeders are the main groups that appear to have increased in abundance since the 1930s, followed by herbivores.

Species declines

Six mollusc species appear to have disappeared or at least greatly declined in abundance since the 1930s, as they were recorded quite commonly alive by Powell but were not found living in the 1990s. These are the gastropods *Amalda australis* and *A. novaezelandiae,* and the bivalves *Tucetona laticostata, Neilo australis, Dosinia lambata,* and *Tellinota edgari.*

The range of the turret shell *Maoricolpus roseus* appears to have become more restricted, or at least its abundance around the bend of the channel has decreased considerably. Other species with apparent reductions in abundance include *Cominella quoyana, Penion sulcatus, Proxiuber australis, Taron dubius, Trochus tiaratus,* and *Dosina zelandica.*

Skilled amateur shell collectors who have been walking the harbour beaches for the past 50 years report a major decline in the carnivorous sand- and mud-dwelling gastropod *Alcithoe arabica,* formerly frequently seen alive at low tide (Noel Gardner, pers. comm.). They were not recorded alive in either the 1930s or 1990s subtidal surveys.

Carnivorous gastropods (7 species) are the dominant group to have suffered major declines, followed by deposit-feeders (4 species), suspension-feeding bivalves (2 species), and a herbivore.

Comparison with shell debris

The dead shells of *Zeacolpus pagoda, Anomia trigonopsis,* and *Austrovenus stutchburyi* are abundant throughout the harbour in our sampling, but were found alive hardly at all in the 1930s or 1990s surveys. This is partly explained by their robust shells, which survive longer on the sea floor after the animal has died.

The cockle, *A. stutchburyi,* is the most abundant bivalve intertidally around the harbour and its shells are clearly being washed and floated out into deeper water (Hayward & Stillwell 1995).

The golden oyster, *A. trigonopsis,* commonly lives attached by a calcareous byssal plug to low tidal and subtidal rocks around the harbour, and these areas were specifically avoided when dredging, so no live animals were encountered. Their abundance in the dead shell component throughout the harbour is an indication of their probable numbers living in suitable habitats around the Waitemata Harbour.

The small turret shell, *Z. pagoda,* is a subtidal species that has been recorded living in high densities in association with *Zegalerus tenuis* in clean fine to shelly sand at 2–30 m depth around the Cavalli Islands and the Bay of Islands (Grace & Hayward 1980, Hayward et al. 1981). The abundance of their shells throughout the harbour and the absence of live specimens in any of our 1990s stations is rather puzzling. Are there dense populations within the study area that we failed to sample? Are there dense populations just outside the study area from which they could have been transported in? Or were there large populations living in the study area in the past that have subsequently disappeared? It is not possible to be sure of the answer.

POSSIBLE CAUSES OF FAUNAL CHANGES

The cause of each of the observed changes in the biota in the Waitemata Harbour sediments between the 1930s and 1990s may never be determinable. Some of the changes may be natural (e.g., spread of *Atrina*), but most are probably attributable to the concentration of human activities within New Zealand's largest city.

Some of the known physical, chemical, and biological changes to the Waitemata Harbour between the 1930s and 1990s are as follows.

Closure of sewage outfalls. In the 1930s, 15 million gallons of sewage per day was discharged into the study area, mainly from the Orakei wharf area but also from Northcote Point and North Head (Hounsell 1935). Almost all of this discharge was eliminated in the 1950s and 1960s. This has undoubtedly resulted in lower nutrient levels and presumably less fine sediment accumulation in some areas of the harbour, and may have impacted on the numbers of certain detritus feeders (e.g. *Maoricolpus roseus, Zeacolpus pagoda, Tellinota edgari*) that were previously more abundant in the harbour.

Dredging. The area in and around Auckland's wharves has been dredged on numerous occasions in the past 60 years as mud accumulates in the sheltered waters. The Rangitoto Channel has also been deepened by dredging since the 1930s, to allow larger ships to use the harbour. This could be expected to have had a major impact on the biota and sediment of this part of the harbour.

Sediment and freshwater runoff. Clearance of the natural forests in the harbour catchment, starting in pre-European times, will have greatly increased sediment discharge into the harbour, especially the upper harbour, and may have contributed to the largely muddy substrate. Earthworks associated with extensive subdivision in west Auckland and the North Shore since the 1930s may have also increased the quantities of clay and mud entering the harbour.

The vast increase in urbanisation in the harbour catchment in the past 60 years would have greatly increased freshwater, sediment, and pollution run-off into the harbour at times of heavy rain (van Roon 1983). This is reflected in heavy metal concentrations in the harbour sediments and possibly in salinities periodically lower than would have been the natural range.

Reclamations and erosion retardation structures. Since the 1930s there has been a considerable increase in reclamations around the shores of the study area, particularly around the wharves and the northern and northwestern motorways (Dromgoole & Foster 1983, fig. 1). These and additional erosion retardation structures will have had local inshore effects, and will have reduced the supply of sediment derived from coastal erosion.

Tributyl tin (TBT) pollution. TBT has been widely used as the active biocide in anti-foulant paint for the hulls of ships and pleasure craft for several decades. In 1989 New Zealand legislation banned its use on smaller craft, although it is still used on larger commercial vessels. Research overseas and in New Zealand has shown that TBT induces imposex, which in severe cases prevents reproduction, particularly in neogastropods (Ellis & Pattisina 1990, Stewart et al. 1992). Recent studies have shown dramatic impacts throughout most of the Waitemata Harbour on intertidal and shallow subtidal neogastropods such as *Lepsiella scobina, Haustrum haustorium, Dicathais orbita, Xymene plebeius, Murexsul octogonus, Amalda, Buccinulum,* and *Cominella* (Jones 1992, Scott 1993). TBT has been shown to accumulate in the seafloor sediments in particularly high concentrations in areas of runoff from boat wash-down areas and under marinas and wharves (Scott 1993).

Exotic introductions. Periodic natural introductions of warm-water organisms have been recorded from the east coast of Northland (Powell 1976). Very few are known to have established viable breeding populations, and none are known to have spread down into the Waitemata Harbour. Exotic organisms are also known to have been brought into New Zealand waters as fouling on barges and drilling platforms (Foster & Willan 1979). Vast volumes of ballast water are discharged into the Hauraki Gulf and Waitemata Harbour by overseas shipping. Studies overseas have shown that many different organisms can be transferred around the world in ballast water, and this has been implicated as the probable mechanism of introduction for the three exotic bivalves now so prevalent subtidally in the Waitemata (Willan 1985). It is believed that the Pacific oyster (*Crassostrea gigas*), now abundant around New Zealand's northern coasts, may have been introduced deliberately (Dromgoole & Foster 1983).

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APPENDIX 1

Qualitative abundance of macromolluscs, crabs and echinoderms recorded from the study area in Powell's 1930s associations (prefixed by P), this study's 1990s associations (prefixed by N) and the dead shell content of our 1990s associations (prefixed by D). Qualitative abundance scale: a = abundant, c = common, p = present, r = rare.

Association	P1	P2	P3	P4	P5	P6	P7	P8	N1	N2	N3	N4	N5	N6	N7	N8	D1	D2	D3	D4	D5	D6	D7	D8
Number of stations	1	8	3	5	7	5	5	3	9	19	13	5	8	65	2	11	9	10	12	4	8	22	2	3
Mollusca – Polyplacophora																								
Acanthochitona mariae							r																	
Chiton glaucus									r															
Ischnochiton maorianus			r						r															
Leptochiton inquinatus	p	c	c				r		c	c	c	p		r		r								
Pseudotonicia cuneata									r	r	r													
Rhyssoplax stangeri			p						r	r														
Mollusca – Gastropoda																								
Alcithoe arabica																	r					r		
Amalda australis								c											r					
Amalda mucronata					r																			
Amalda novaezelandiae			r		r													r	p	r	p	r		r
Austromitra rubiginosa	r		r						r								r			r				r
Buccinulum linea	p	p	r						r								r		r			r		
Buccinulum vittatum			r																					
Calliostoma pellucidum		r																	r					
Cirsotrema zelebori			p																r					
Cominella adspersa		p			p	p		r			p		r			r	r	r	p	r	r	p		
Cominella quoyana	c	p	c						r	r							r	r	p		r	p		r
Crepidula costata									r	r							r	r	r	p	r	r		r
Crepidula monoxyla		r	r																					
Epitonium minora			r											r		r								
Maoricolpus roseus		a	a	p					a	a	p	r					a	a	a	c	p	c	r	p
Murexsul octogonus		r							r															
Neoguraleus murdochi					r				r								r	r	p		r	r		
Neoguraleus sinclairi						r																		
Penion sulcatus	p	r	r						r									r	r			r		
Proxiuber australis		p	r														r		r					
Sigapatella novaezelandiae			p						p	p	p	p	r			r	c	p	p	c	p	p		r
Struthiolaria vermis			r		r	p			r				r					r	r	r		r		
Taron dubius	p																							
Trichosirius inornatus		r															r	p	r	r	r	r	r	

Association	P1	P2	P3	P4	P5	P6	P7	P8	N1	N2	N3	N4	N5	N6	N7	N8	D1	D2	D3	D4	D5	D6	D7	D8
Number of stations	1	8	3	5	7	5	5	3	9	19	13	5	8	65	2	11	9	10	12	4	8	22	2	3
Tomopleura albula			p														r	r			r			
Trochus tiaratus	c	p	c						r	r							r	p	r	r		r		r
Xymene pusillus	r								r	r							r				r			
Xymene plebeius		r									r			r	r		r	r	p	r	r	r	r	r
Zeacolpus pagoda																	p	c	c	p	p	c	p	p
Zegalerus tenuis		c	p						p	p	p	p	r		r	r	c	c	c	p	r	p		r
Mollusca – Bivalvia																								
Anomia trigonopsis		r															c	c	c	c	p	p	r	c
Atrina pectinata zelandica												r	a	r			r	r	r	c	c	r	r	r
Austrovenus stutchburyi														r	r		r	c	c	r		c	p	r
Bassina yatei											r													
Borniola reniformis		p							r	r	r									r				
Chlamys zelandiae	r	p	r							r	r		r				p	c	c	p	p	p	r	p
Corbula zelandica	p	c	c					r	c	p	c	p		r		r	c	c	c	p	r	r		p
Cyclomactra ovata					r							r		r				r	p		r	r	r	
Diplodonta striatula									r	r							r		r					
Divaricella huttoniana												r												
Dosina zelandica		p	c	c					p	p	p					r	p	c	p	p		p		
Dosinia greyi					r	r					r		r	r			r	r	r	r	r	r		r
Dosinia lambata					p									r			p	r	r	p	p	p	r	r
Dosinia maoriana										r				r	r				r					
Dosinia subrosea														r					r	r	r	r		r
Felaniella zelandica		p	r						c	p	p	c	r	r		p	p	p	p	p	r	r		r
Gari lineolata												r					r			r	r	r		
Gari stangeri									c	r	r	c					p	p	r	r				r
Hiatella arctica									p	r	r		r	r			r	r						
Irus reflexus									r								r	r	r	r	r			
Leptomya retiaria		p	r		r	p			c	c	c	p	r	p	p	p	c	p	p	r	p	p		p
Limaria orientalis									c	c	a	r	r			r	a	c	c	p	r	r		p
Macomona liliana														r	c			r		r		r	c	
Modiolarca impacta	r		r								r									r				
Maorimactra ordinaria												r					r	r	r	r	p	r		
Musculista senhousia													r			a		r		r		r	r	a
Myadora striata												r					r		r	p	r	r		r
Neilo australis					r	r																		
Nucula hartvigiana		p					r		p	p	p	p	r	c	a	r	p	c	p			p	p	r
Nucula nitidula		c			r	p			c	a	c	p	p	c	a	p	c	c	c	p	r	p	r	p
Periploma angasi													p											
Paphies australis											r					r		r		r				r
Pecten novaezelandiae									r								c	p	p	p	r	p		r
Perna canaliculus		p					r					p	p	r			r	r	p	p	r	r		r
Pleuromeris zelandica				r					p	r	p	p	p	p	r	r	p	p	c	r	p	p	r	p
Ruditapes largillierti	r	p	p	c					a	p	c	p	r	r		p	c	a	a	p	r	p		r
Scalpomactra scalpellum												p							r	p		r		
Serratina charlottae																	p		r	r	r	r		
Soletellina nitida														r								r		
Tawera spissa		p	p		r	r	r		c	p	c	a	p	r		r	a	c	a	a	c	p	r	p
Tellinota edgari					r	p																		
Theora lubrica									r	r	p	r	a	a		p								
Tiostrea chilensis lutaria											r						r	p	p	p	p	p		p
Tucetona laticostata	p																							
Varinucula gallinacea									r										r					
Venericardia purpurata		p	p	r					c	p	p	r					c	p	c	p		r		r
Zelithophaga truncata	r		r								r						r							
Zenatia acinaces					p	c					r	r	p	r			r	r	r	p	r	r		

Association	P1	P2	P3	P4	P5	P6	P7	P8	N1	N2	N3	N4	N5	N6	N7	N8	D1	D2	D3	D4	D5	D6	D7	D8
Number of stations	1	8	3	5	7	5	5	3	9	19	13	5	8	65	2	11	9	10	12	4	8	22	2	3
Brachiopoda																								
Calloria inconspicua	r	r							r	r	r						r		r					
Echinodermata – Echinoidea																								
Echinocardium cordatum					c						r	p	c	p							r			
Fellaster zelandiae					p										p		r		r	p	r	r		
Echinodermata – Asteroidea																								
Allostichaster polyplax									r		r	r												
Coscinasterias calamaria	p	r							r	r	r	r												
Patiriella regularis								r	r	r	r			r										
Stegnaster inflatus									r	r														
Echinodermata – Ophiuroidea																								
Amphiocnida pilosa					r				c	p	p	p	p	r		r								
Amphiopolis squamata									p	c	c	r		r										
Amphiura alba	r																							
Amphiura rosea					p	r	r		r		r		r	r										
Ophiactis resiliens									p	p	r		r											
Ophionephthys ?perplexa									r		r	p	r	r		r								
Crustacea – Crabs																								
Australeremus sp.									r	r	r													
Halicarcinus varius			r						p	p		r	p	r		r								
Helice crassa							r																	
Liocarcinus corrugatus	r																							
Macrophthalmus hirtipes		r			r	c			r	r	p	r	p	a	c	c								
Nectocarcinus antarcticus	r								r															
Notomithrax minor	c	p	p			p			p	r	p	p	p	r		r								
Paguristes pilosus									p	c	p		r	r										
Pagurus spp.									r	p	r			r		r								
Petrolisthes novaezelandiae	c	c	p	r	r				p	c	c		r			r								
Pilumnus novaezelandiae	p	p	r						r	r	r													
Pinnotheres atrinocoloa													c	r	r									
Pyromaia tuberculata											r	r												