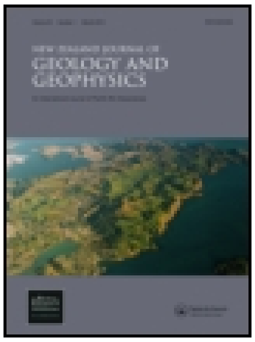

New Zealand Journal of Geology and Geophysics

ISSN: 0028-8306 (Print) 1175-8791 (Online) Journal homepage: https://www.tandfonline.com/loi/tnzg20

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To cite this article: Bruce W. Hayward , Hugh R. Grenfell & David B. Scott (1999) Tidal range of marsh foraminifera for determining former sea-level heights in New Zealand, New Zealand Journal of Geology and Geophysics, 42:3, 395-413, DOI: 10.1080/00288306.1999.9514853

To link to this article: https://doi.org/10.1080/00288306.1999.9514853

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New Zealand Journal of Geology & Geophysics, 1999, Vol. 42: 395–413 395
0028–8306/99/4203–0395 $7.00/0 © The Royal Society of New Zealand 1999

Tidal range of marsh foraminifera for determining former sea-level heights in New Zealand

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Abstract Quantitative study of live and total foraminiferal faunas in samples from six transects through marsh environments at Kaipara Harbour, Miranda, and Pauatahanui Inlet, New Zealand (two transects each), show the presence of a distinctive high tidal species association that has potential for the recognition of former sea-level heights from late Quaternary deposits.

Seven species associations are recognised by R-mode cluster analysis of total (live plus dead) foraminiferal faunal data. Mangrove forest and salt meadow below MHWS (mean high water spring level), in near normal salinity marshes (Kaipara, Miranda), are dominated by an *Ammonia* association with subsidiary *Elphidium excavatum, Haplophragmoides-Miliammina fusca,* and *Helenina* associations. In less saline marshes (Pauatahanui), the salt meadow and rush marsh below MHWS, are dominated by a *Haplophragmoides-Miliammina fusca* association. In all transects, the narrow zone between MHWS and EHWS (extreme high water spring level) is dominated (>90% relative abundance) by a *Trochammina* association (*T. inflata, T. macrescens, Miliammina obliqua*). A palimpsest, *Ammonia*-dominated, exposed beach fauna on the penultimate chenier interferes with the recognition of this high tidal *Trochammina* zone in one Miranda transect. Dependent upon their proximity to exposed sea conditions and fast-flowing tidal channels, there are variable numbers of introduced foraminiferal tests (*Cornuspira* association) in the marshes at all levels. At Pauatahanui, a monospecific fauna of *T. macrescens* is present just at EHWS (upper 0.1 m of tidal range). This has been recognised previously only in northeast America and may provide the most accurate paleo-sea level marker known.

There appear to be no significant tide-related trends in diversity, but in all transects there is a marked abundance peak between MHWS and EHWS levels, which if recognised in fossil faunas could also be useful in determining previous sea-level heights.

G98028
Received 17 August 1998; accepted 29 March 1999.

Keywords New Zealand; Kaipara Harbour; Miranda; Pauatahanui Inlet; marsh foraminifera; former sea levels; tidal range

INTRODUCTION

Prediction and mitigation of the effects of sea-level rise along New Zealand's coasts caused by climate warming, storm surges, tsunamis or earthquakes require an understanding of late Quaternary, and particularly Holocene, sea-level changes (Isla 1989; Tooley & Jelgersma 1993). If eustatic sea-level curves and amounts and rates of vertical tectonic movements or gravity-induced coastal subsidence are to be fully documented, then methods of more accurately determining former sea-level heights are required.

One method is through the recognition of fossil faunas that live within a narrow tidal range in quiet coastal environments (e.g., marshes) where reworking and displacement are less likely to destroy or blur the signal. Potentially one of the most useful groups of fossilisable marsh inhabitants are benthic foraminifera, as they are: relatively abundant; generally large enough not to be transported around by gentle current and tidal action; and their shells are readily preserved as fossils in marsh sediments (e.g., Guibault et al. 1996).

An understanding of the relationship of modern marsh foraminiferal assemblages to tide levels is a prerequisite for interpreting sea-level changes from fossil faunas. A number of overseas studies on modern foraminiferal assemblages along transects through intertidal marshes have shown that some assemblages have a narrow elevational range with respect to tide levels (e.g., Scott & Medioli 1986; Scott & Leckie 1990; Jennings et al. 1995). Where assemblages with narrow tidal ranges are identifiable in fossil deposits, former sea levels can be precisely located (Scott & Medioli 1980; Guilbault et al. 1996).

Around the coast of New Zealand a few studies have been undertaken in an attempt to reconstruct a Holocene sea-level curve for the region (e.g., Schofield 1960, 1973; Gibb 1986), but none have been based on foraminiferal assemblages. Some studies have also looked at the late Quaternary history of earthquake uplifts along sections of the coast (e.g., Ota et al. 1995; McSaveney 1997), again without any foraminiferal assistance.

This study was designed to investigate and calibrate previously recognised New Zealand high tidal marsh assemblages dominated by the agglutinated foraminifera *Trochammina inflata*, *T. macrescens* and *Miliammina obliqua* (Hayward & Hollis 1994; Hayward et al. 1996, 1997a).

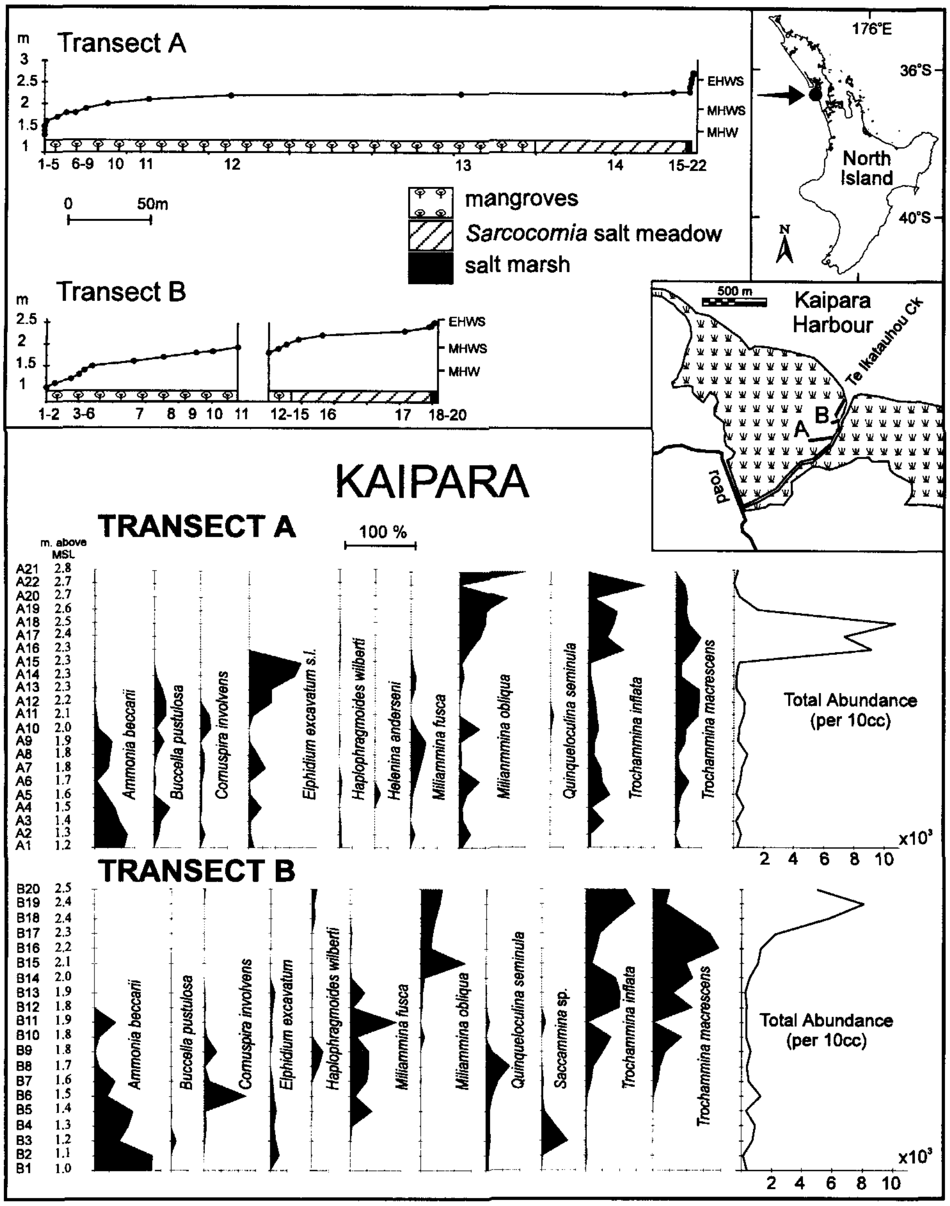


Fig. 1 Location, profiles, and vegetation cover of transects A and B, Kaipara Harbour, and distribution graphs of the relative abundance of species in their total (live plus dead) foraminiferal faunas.

Previous work on New Zealand marsh foraminifera

The first study of Recent marsh foraminifera in New Zealand was a reconnaissance survey of a limited number of samples collected from nine sites around the northern half of the North Island (Phleger 1970). Phleger concluded that in terms of composition and zonation, the New Zealand marsh faunas had considerable similarity to other parts of the world.

Gregory (1973) documented typical agglutinated marsh faunas from mangrove forest on Great Barrier Island and later supervised two theses on marsh foraminiferal distributions, by Topping (1973) in the Puhoi Estuary, on Auckland's east coast, and by Adams (1979) in Rangaunu Harbour, in northern Northland.

More recently there have been a number of studies on the ecological distribution of brackish and marsh foraminiferal associations in northern (Hayward 1993; Hollis et al. 1995; Hayward et al. 1997a), central (Hayward & Triggs 1994) and southern New Zealand (Hayward et al. 1996). The results of these studies and others have been summarised, together with discussion of the taxonomy and biogeography, by Hayward & Hollis (1994) and Hayward et al. (1999). Scott et al. (1996) discussed these New Zealand results in the context of other Pacific Rim marsh faunas. The present study is the first to accurately relate the distribution of foraminiferal associations and species to measured sea-level heights in New Zealand.

Tidal range terminology

In this paper the standard New Zealand tidal range terminology is used:

EHWS = extreme high water spring level
MHWS = mean high water spring level
MHW = mean high water level
MSL = mean sea level (mid tide)

Study sites

Kaipara Harbour, Auckland (Fig. 1)

The chosen study site (36°32.5′S 174°19′E) was in the largest area of remaining salt marsh on the western shore of the

Fig. 2 Part of transect B (site B16), Kaipara Harbour, where it passes through *Sarcocornia* salt meadow and up into *Juncus* salt marsh.

southern Kaipara Harbour, at the mouth of Te Ikatauhou Creek near Waioneke, 6 km northwest of Shelly Beach (Fig. 1). The tidal range here is c. 5.2 m. The marsh is situated well away from any major river or stream mouth and is normally bathed in water of only slightly reduced salinity (c. >30, measured values 32–34), similar to that in the middle stretches of the harbour. A small stream drains through a tidal channel adjacent to the site but its freshwater contribution would be minimal except after major rainfall events.

Transect A extended from the mud bank of the tidal stream channel (A1–A6) across a gently sloping mudflat clothed in scattered low (0.2–0.5 m high) mangrove (*Avicennia marina*) forest (A7–A13) and glasswort (*Sarcocornia australis*) salt meadow (A14–A15) to an abandoned, steep-sided shell ridge clothed in a mix of *Sarcocornia* and *Plagianthus* (A16–A19), *Juncus maritimus* and pasture grasses (A18–A21). A22 was taken from moss-covered soil beneath a ngaio (*Myaporum laetum*) tree on the crest of the ridge.

Transect B (Fig. 2) extended from the seaward edge of the mangrove forest across gently sloping mudflat beneath mature mangroves (2–3 m high, B1–B9), low mangroves (0.5–1 m high, B10–B14), *Sarcocornia* salt meadow with sea primrose, *Samolus repens* (B15–B19) to the top of a low shell ridge clothed in salt marsh (*Stipa stipoides* and *Plagianthus*, B20). The transect was sampled in two segments with a gap of 50 m between B11 and B12 to avoid a high intervening, vegetated shell ridge.

Miranda, Auckland (Fig. 3)

Miranda is on the west coast of the Firth of Thames in an area many kilometres from major river mouths. Normally these coastal marshes are bathed in water of near normal to only slightly reduced salinity (c. >30, measured values 31–36), except after extreme rainfall events when the small creeks running past the two transects would be swollen with fresh water. The tidal range here is c. 3.6 m. The two chosen transect sites are 3.5 km apart.

Transect C (37°10.5′S 175°19′E, Fig. 4) was located at Access Bay, 0.5 km southeast of the Miranda Naturalist Trust headquarters. It extended from mud beneath a patch of mangroves beside a tidal channel (C1–C4) up the gentle slope of the penultimate shell beach ridge (chenier) clothed in *Sarcocornia* salt meadow (C5–C7) and mixed salt meadow/pasture of *Parapholis strigosa, Plantago coronopus* and *Melilotus indicus* (C8–C11) to grass pasture on the crest (C12). Three stations (C13–C15) were sampled in a *Sarcocornia* salt meadow pool, 50 m to the north.

Transect D (37°12.5′S 175°19.5′E) was located seaward of a stop bank and small pumping station, 2 km south of Miranda and 1 km north of Miranda hot springs. It extended from the steep mud bank of a tidal channel beneath mature mangroves (D1–D5) across a gently rising, sandy mudflat clothed in low mangroves (D6) and *Sarcocornia* (D7) and *Sellieria* salt meadow (D8) to grassy pasture on the slopes of the stopbank (D9–D11).

Pauatahanui Inlet, Wellington (Fig. 5)

The chosen study site (41°07′S 174°55′E) was in the largest area of salt marsh around the head of the inlet adjacent to Pauatahanui settlement. Flowing through this marsh in tidal channels are Pauatahanui and Ration Streams which contribute over 40% of the surface runoff into the inlet (Healy 1980). The inlet has a narrow entrance and is otherwise completely enclosed and hence has a slightly reduced background salinity. Salinity in the salt marsh would be further reduced (c. 0–20) by the outflow from the streams, particularly after times of heavy rainfall. The tidal range here is c. 2.4 m. Thus, these two transects are from lower salinity environments than Kaipara and Miranda. Foraminiferal associations in Pauatahanui Inlet have been documented by Hayward & Triggs (1994).

Transect E was located on the north side of the Pauatahanui Stream mouth running approximately north-south. It extended from the mud bank edge of a small channel (E1) through a salt marsh/salt meadow dominated by the rush, *Juncus maritimus*, with variable amounts of *Samolus*

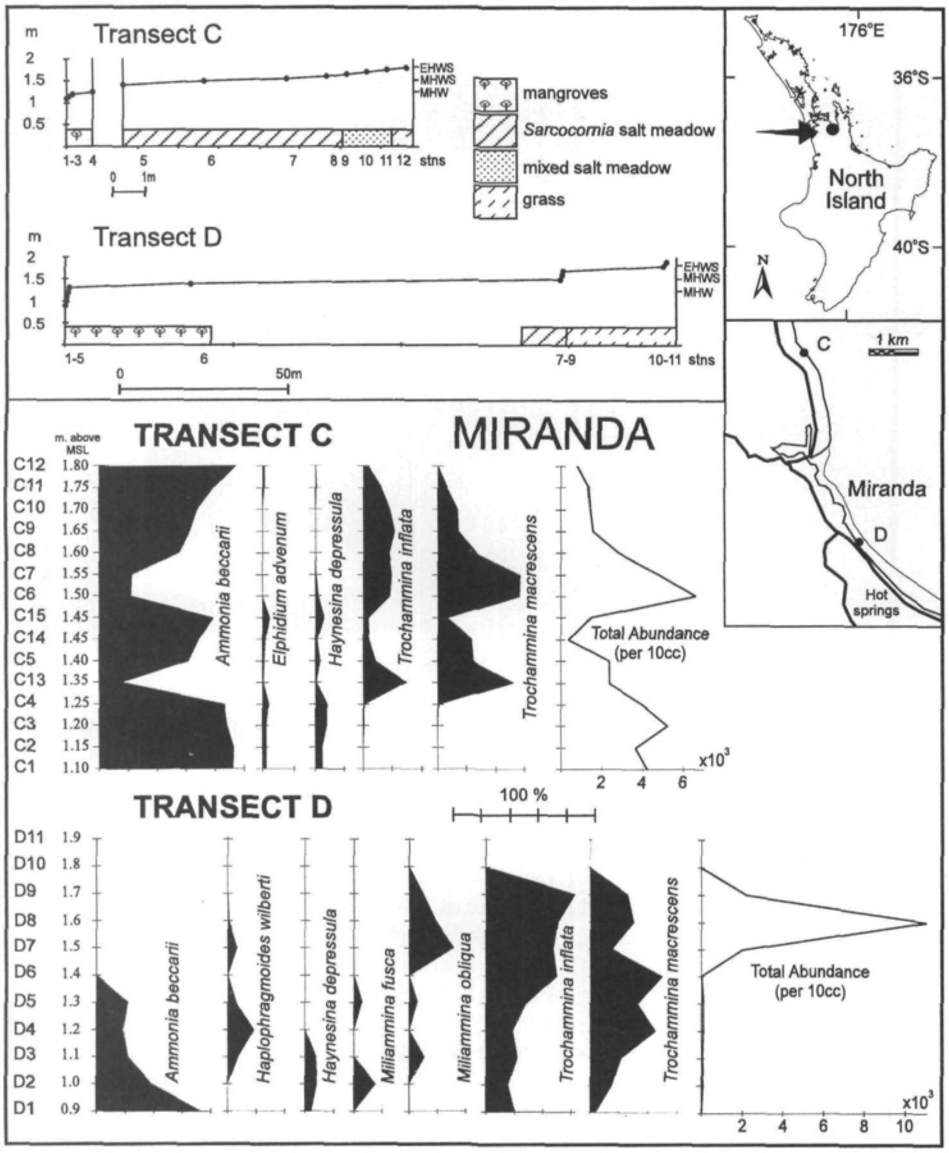


Fig. 3 Location, profiles, and vegetation cover of transects C and D, Miranda, and distribution graphs of the relative abundance of species in their total (live plus dead) foraminiferal faunas.

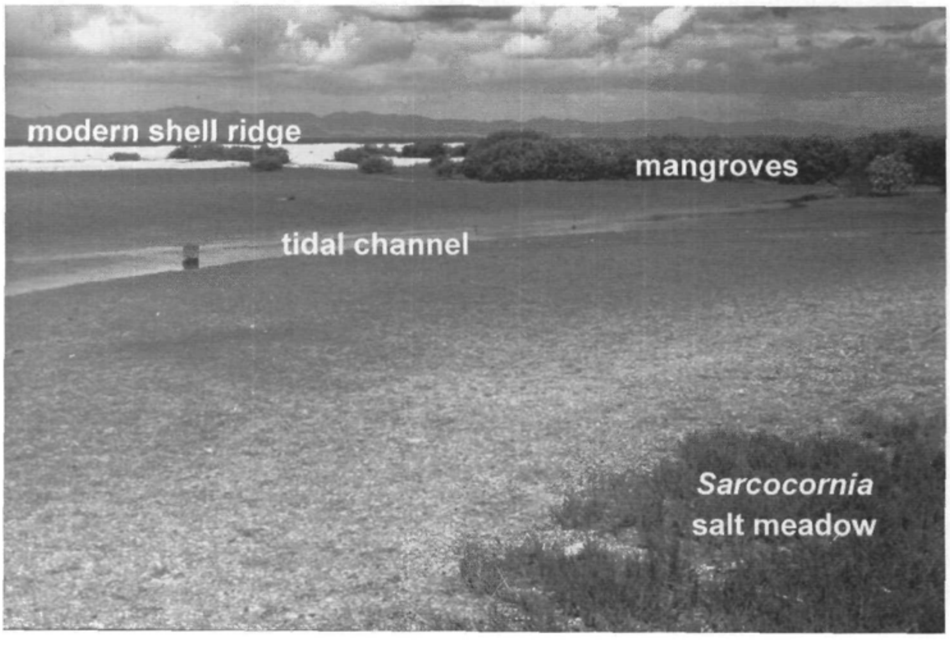


Fig. 4 Location of transect C, Miranda, where it passes from intertidal mud beside a tidal channel and up into *Sarcocornia* salt meadow (bottom right). In the background, the white present-day beach-front shell ridge (chenier) separates the site from the open sea.

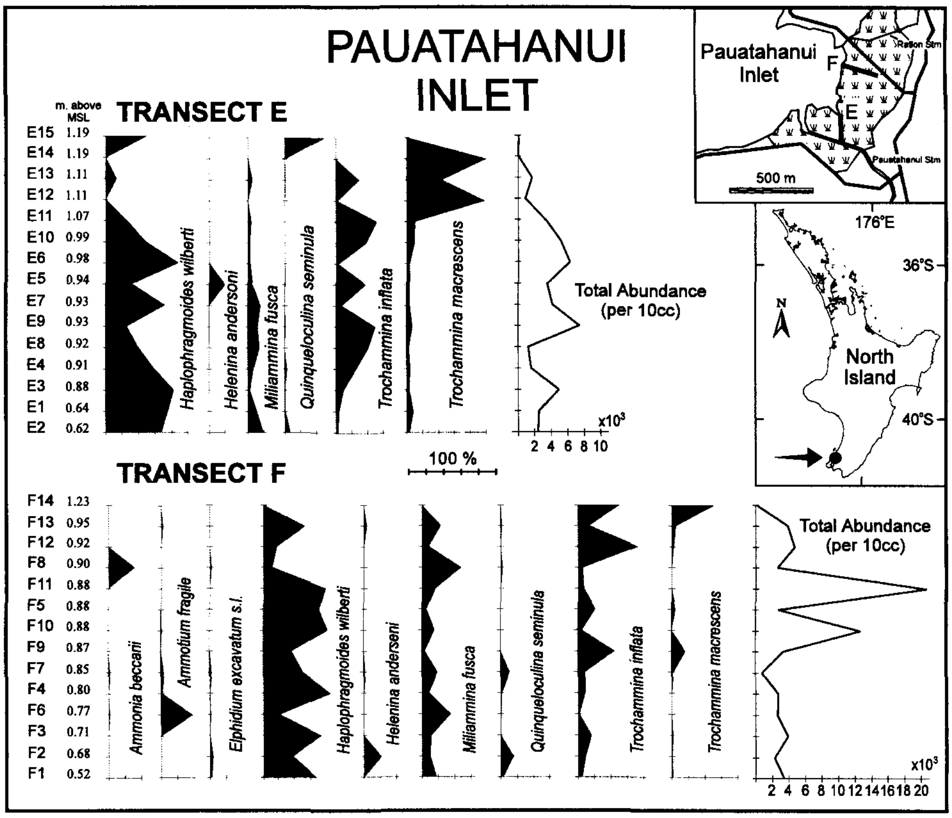


Fig. 5 Location and distribution graphs of the relative abundance of species in the total (live plus dead) foraminiferal faunas of transects E and F, Pauatahanui Inlet.

repens, *Sarcocornia* and *Selliera* (E2–E11) to grassy pasture (E12–E15). Spot salinities along the transect ranged between 7 and 20.

Transect F was located c. 100 m south of and nearly parallel to the road between Pauatahanui and Plimmerton (Fig. 5). It was c.150 m long and crossed a gently sloping partially vegetated tidal flat with occasional low shell ridges, and was more exposed to wave action than transect E. It extended from the upper edge of the unvegetated tidal mud flats (F1) through *Juncus*-dominated marsh (F2–F5, F7, F10–F11) with sporadic patches of *Samolus repens* (F6, F8–F9, F13) and *Selliera radicans* (F12) into pasture grasses (F14). Elevations between 0.95 and 1.23 m were not sampled as they coincided with a steep rocky bank with F14 in grass at the top. Spot salinities along this transect ranged between 0 and 20.

Pauatahanui Inlet lacks mangrove forest as it lies south of their southern climatic limit.

METHODS

Field

Samples were collected along transects oriented normal to the tide line and consistently down slope (preferably with no rises), through representative suites of tidally zoned vegetation. A 10 cm^3 sample was obtained from the top 10 mm of sediment from each station using a short length of PVC pipe (36 mm inside diameter) with a sharpened lip. The pipe was pushed into the sediment to take a short core, which after extraction from the ground was extruded so that the top 10 mm could be sliced off and kept. This method permits comparison with a number of overseas studies (e.g., Scott et al. 1990, 1996).

Two transects were sampled at each of three study sites. Samples in the Kaipara and Miranda transects were mostly taken at vertical intervals of 100 mm, measured using a graduated staff on a rising spring tide. Samples at Pauatahanui were taken at qualitatively selected intervals and the tidal height was later surveyed and tied into a nearby benchmark. Tidal levels have been calculated and extrapolated from observed heights and tidal charts.

During sampling, spot salinities were measured with an American optical, temperature-compensated, refractometer. No other salinity values are available, and it is recognised that salinities vary enormously with rainfall and tidal fluctuations (e.g., Scott & Medioli 1980).

Laboratory

Within 48 h of collection, samples were wet sieved through 0.5 mm and 0.063 mm sieves. Coarse and fine fractions were discarded and the medium fraction was fixed in a solution of buffered formalin and Rose Bengal and allowed to stand for 24 h. The samples were then washed and preserved in ethanol until required (Scott & Medioli 1980).

Large samples were split using a wet microsplitter (Scott & Hermelin 1993) to a subsample containing 100–300 benthic foraminiferal tests. These were identified and counted under water, thus making the tests transparent to facilitate detection of Rose Bengal stained protoplasm (= detection of live specimens). Live and total (live plus dead) tests were scored separately (Appendix 1). The number of live and total tests per 10 cm^3 was calculated (Appendix 1).

Statistical analysis

The data used for statistical analyses consisted of census counts of the total (live plus dead) foraminiferal species in the samples from all six transects together. The data matrix was standardised by converting counts to percentages of sample totals (as in Appendix 1).

Unweighted pair group R-mode cluster analysis using arithmetic averages of a distance matrix produced using Horn's (1966) modified version of Morista's (1959) index for proportions was used to produce a dendrogram classification of the abundant species (>3% in at least one sample) from which seven species associations were selected. Mathematical definition of the modified Morista coefficients is given in Rohlf (1989). This index down-weights the more abundant species and produces a more realistic clustering of species that commonly occur together. Cluster analyses were computed using the "NTSYS" statistical package (Rohlf 1989).

Species diversity

Three measures of species diversity were calculated for each foraminiferal fauna (Appendix 1).

1. Number of species, S
2. Shannon-Wiener Information Function: $H_{(S)} = -\Sigma P_i \log_e P_i$. where P_i is the proportion of the ith species (MacArthur & MacArthur 1961; Gibson & Buzas 1973). The value of H depends on a combination of the evenness of species counts together, to a lesser extent, with the number of species present.
3. Evenness, $E = e^H/S$, where S = number of species present. This is a measure solely of evenness of species counts within a fauna, irrespective of the number of species present (Buzas & Gibson 1969).

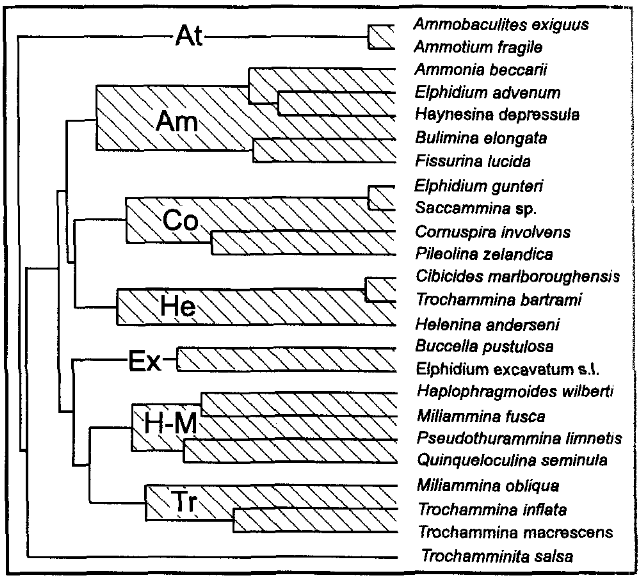


Fig. 6 Dendrogram classification of the New Zealand marsh species produced by cluster analysis using modified Morista distance (Rohlf 1989). The seven species associations were selected by the authors after inspection of the dendrogram. At = *Ammotium* association, Am = *Ammonia* association, Co = *Cornuspira* association, He = *Helenina* association, Ex = *Elphidium excavatum* association, H-M = *Haplophragmoides - Miliammina* association, Tr = *Trochammina* association.

SPECIES ASSOCIATIONS

The following four major and three minor species associations were selected by inspection from the R-mode cluster analysis dendrogram run on the total assemblage data (Fig. 6). Four relatively rare species were ungrouped. The relative abundance of the major species associations is graphed against the transects in Fig. 7.

Major associations

Ammonia association

DOMINANT SPECIES: *Ammonia beccarii.*

OTHER CONSTITUENT SPECIES: *Haynesina depressula, Elphidium advenum, Fissurina lucida, Bulimina elongata.* The last species occurs only as dead specimens and is inferred to have been swept into the marsh.

STUDY SITES: Mostly Kaipara and Miranda.

HABITAT: In Kaipara transects A and B and Miranda transect D, the *Ammonia* association is largely confined to the mud beneath taller mangrove forest. In Miranda transect C this association is the dominant element in the total assemblage throughout most of its length. Live specimens are dominant only beneath the mangrove forest and only occur in low numbers higher on the shore, where they are inferred to be palimpsest, derived from the original shelly beach ridge substrate. The association is absent from Pauatahanui transect E and only present in low numbers in low marsh in transect F.

TIDAL RANGE: It comprises >50% of the total fauna below MHW in the Kaipara and Miranda transects and decreases in abundance with increasing elevation, generally disappearing midway between MHW and MHWS (except for the palimpsest faunas in transect C).

NEW ZEALAND DISTRIBUTION: The association is widespread intertidally throughout New Zealand where it occurs most commonly in sand and mud flats in the slightly brackish upper parts of harbours and tidal inlets and at the seaward ends of estuaries (Hayward & Hollis 1994; Hayward et al. 1999). In some more detailed studies the association is split into two mappable associations—a slightly higher, less saline *Ammonia* association and a slightly lower or subtidal, more saline *Elphidium-Haynesina* association (Hayward et al. 1996, 1999.).

Elphidium excavatum association

DOMINANT SPECIES: *Elphidium excavatum.*

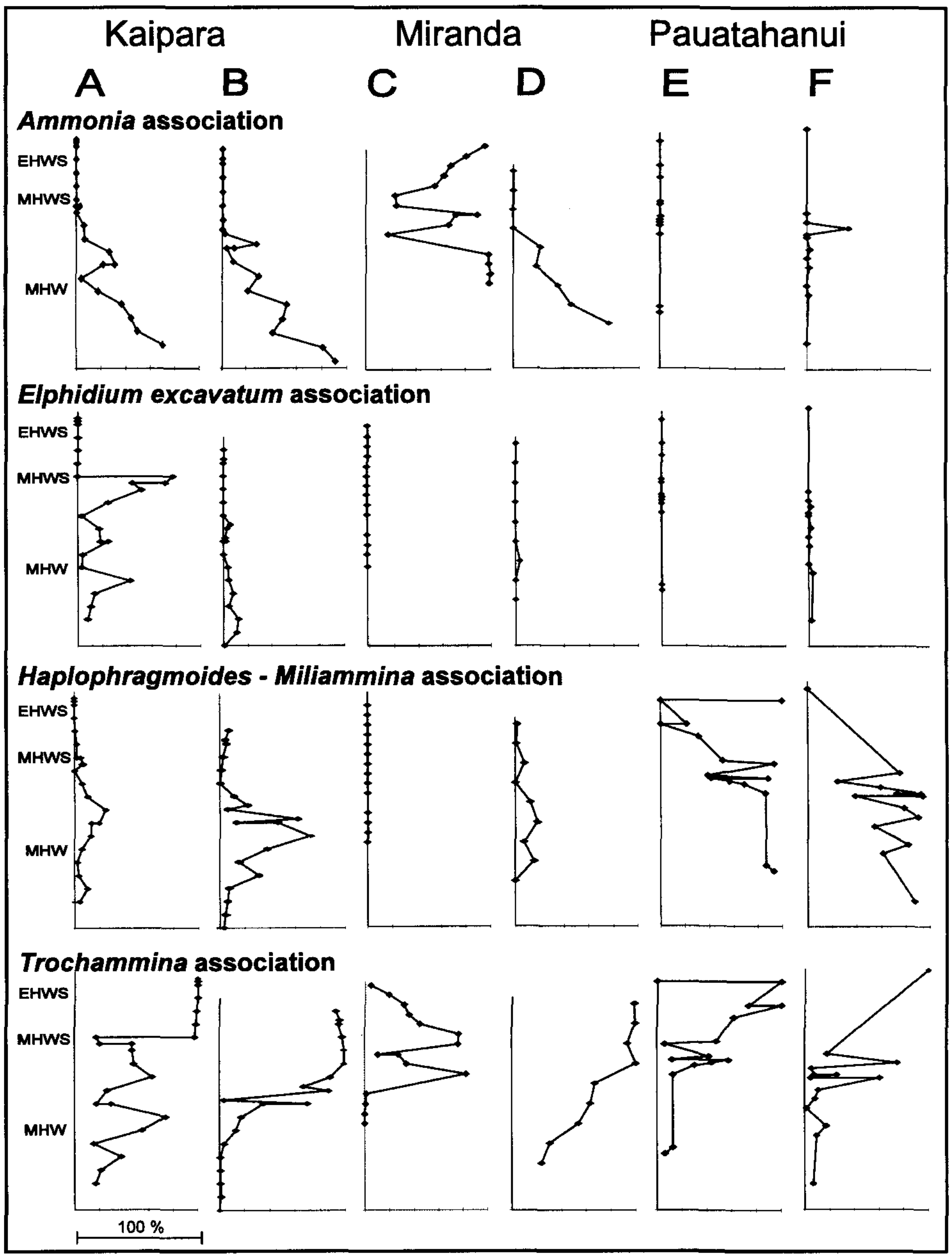
OTHER CONSTITUENT SPECIES: *Buccella pustulosa.*

STUDY SITES: Kaipara, less abundant at Miranda and Pauatahanui.

HABITAT: In the Kaipara transects the association occurs throughout most of the mangrove forest and extends into the *Sarcocornia* salt meadow in transect A. The greatest relative abundance of total and live faunas is in the *Sarcocornia* salt meadow and beneath low mangroves.

TIDAL RANGE: The association is sporadically present below MHWS, with its greatest abundance (>50%) in salt meadow just below MHWS in transect A.

Fig. 7 Distribution of the relative abundance of *the Ammonia, Trochammina, Haplophragmoides-Miliammina* and *Elphidium excavatum* associations in the total foraminiferal faunas with increasing sea level in each transect. Transects have been scaled to a standard tidal range between EHWS and MSL.



NEW ZEALAND DISTRIBUTION: The association is widespread intertidally (between MLW and MHWS) throughout New Zealand, mostly in unvegetated tidal sand and mudflats and in mangrove forests around the heads of inlets and harbours of normal marine to only slightly brackish salinity (Hayward & Hollis 1994; Hayward et al. 1997b, 1999).

Haplophragmoides-Miliammina association

DOMINANT SPECIES: *Haplophragmoides wilberti, Miliammina fusca.*

OTHER CONSTITUENT SPECIES: *Quinqueloculina seminula, Pseudothurammina limnetis.*

STUDY SITES: Pauatahanui, Kaipara and less abundant at Miranda.

HABITAT: The *Haplophragmoides-Miliammina* association is largely restricted to the mud beneath mangroves in the Kaipara and Miranda transects. In the absence of mangroves at Pauatahanui, the association is abundant throughout most of the rush salt marsh and salt meadow areas.

TIDAL RANGE: The association is most abundant in the less saline Pauatahanui transects where it comprises >50% of the total and live faunas from the lowest samples up to c. MHWS above which it is largely replaced in a narrow zone by the *Trochammina* association. In the more saline Kaipara transects the *Haplophragmoides* association (mostly *Miliammina fusca*) has its greatest relative abundances (>30%) close to MHW level and is almost absent at other levels.

NEW ZEALAND DISTRIBUTION: Separate *Haplophragmoides* and *Miliammina* associations are recognised throughout New Zealand (Hayward & Hollis 1994; Hayward et al. 1999.), mostly in salt marshes and meadows around the heads of harbours and middle reaches of estuaries, usually in lower salinity than the *Trochammina* association. The *Miliammina* association occurs below MHW whereas the *Haplophragmoides* association predominantly occurs above MHW (Hayward et al. 1996, 1999).

DISCUSSION: *Haplophragmoides wilberti, Miliammina fusca* and *Pseudothurammina limnetis* are well documented as obligate brackish water inhabitants around New Zealand (Hayward & Hollis 1994) but *Quinqueloculina seminula* is best known as a dominant species in normal salinity, inner shelf environments (e.g., Hayward et al. 1999; Murray 1991).

The widespread occurrence of live *Q. seminula* throughout the intertidal range at Kaipara and Pauatahanui and absence from Miranda and many other New Zealand marshes is perplexing. Overseas, *Q. seminula* is known to occur in irregular patterns, sometimes with great abundance, in marshes of high salinity (Scott 1976a) and also of low salinity and low temperature (Scott & Medioli 1980). We see two possible explanations for these *Quinqueloculina*. They are either living and reproducing in marshes of highly variable salinity and in a wide range of elevations extending up to EHWS or they are being transported in from offshore (see later discussion on displaced foraminifera). Whatever the situation, it is clear that the thin *Quinqueloculina* tests dissolve soon after death and are seldom preserved fossil.

Trochammina association

DOMINANT SPECIES: *Trochammina inflata, Trochammina macrescens, Miliammina obliqua.*

STUDY SITES: Kaipara, Miranda, and Pauatahanui.

HABITAT: The *Trochammina* association, including live specimens, generally occurs throughout the full length of all transects in mangroves, salt marsh, salt meadow, and pasture. Sometimes live specimens are absent from the lowest or highest stations. The association is more abundant in low (stunted) mangrove forest, salt meadow, and salt marsh with its greatest relative abundance (>95%) in the highest salt marsh and pasture grasses.

TIDAL RANGE: The association shows a strong trend of increasing abundance up the shore. It generally comprises <30% of the total faunas below MHW, increasing to 90%+ by MHWS, and comprising >95% of the total and live fauna between MHWS and EHWS. Relative abundances are somewhat less below MHWS in the less saline Pauatahanui transects because of the presence of *Haplophragmoides* association.

A fauna composed entirely of *T. macrescens* occurs c. EHWS at Pauatahanui (E12, E14). Before this study, such a fauna had previously been identified only from northeastern North America where it occurs at the same extreme high tidal level (Gehrels 1994), showing that they really are universally distributed in terms of elevation.

NEW ZEALAND DISTRIBUTION: The association is widespread throughout New Zealand above high tide level in slightly brackish salt meadows and marshes around the fringes of harbours and tidal inlets (Hayward & Hollis 1994; Hayward et al. 1999). In some more detailed studies the association is split into two separate associations—a *Trochammina inflata* and a *Trochammina macrescens (=Jadammina)* association (Hayward et al. 1996, 1997a), with the *T. inflata* association occurring in higher salinities (Scott & Medioli 1980).

Minor associations

Helenina association

DOMINANT SPECIES: *Helenina anderseni.*

OTHER CONSTITUENT SPECIES: *Trochammina bartrami, Cibicides marlboroughensis*—neither has been recorded live and are both assumed to have been transported into the marsh in low numbers to Kaipara transect A, where fortuitously they occur together with *Helenina anderseni.*

STUDY SITES: Kaipara and Pauatahanui.

HABITAT: The association occurs in patches beneath mangrove forest at Kaipara and in rush salt marsh and salt meadow at Pauatahanui.

TIDAL RANGE: Patchily between MSL and MHW.

DISCUSSION: *Helenina anderseni* occurs sporadically in a rather random pattern seemingly unrelated to other species in a wide range of intertidal brackish environments around the North Island (Hayward & Hollis 1994; Hayward et al. 1999). This patchiness is also observed worldwide (Scott & Medioli 1980).

Ammotium association

CONSTITUENT SPECIES: *Ammotium fragile, Ammobaculites exiguus.*

STUDY SITES: Pauatahanui.

HABITAT: In this study, the *Ammotium* association is mostly recorded from rush salt marsh and from a patch of *Samolus* salt meadow (F6), although it also occurs beneath mangroves and in unvegetated tidal mud flats elsewhere (Hayward et al. 1997a).

TIDAL RANGE: Patchily below MHW.

DISCUSSION: Both species are regarded as obligate brackish water foraminifera in New Zealand (Hayward & Hollis 1994) although only *Ammotium fragile* is recorded live in this study. In New Zealand, *A. exiguus* is usually recorded alive and in greatest numbers in low tidal and subtidal environments. Its occurrence in low numbers in the Pauatahanui marsh is inferred to reflect transport in by waves or currents. Elsewhere in the world these species are regarded as low marsh species (Scott & Medioli 1980).

Cornuspira association

CONSTITUENT SPECIES: *Cornuspira involvens, Saccammina* sp., *Pileolina zealandica, Elphidium gunteri.*

STUDY SITES: Kaipara.

HABITAT: The association is confined to mud beneath mangrove forest.

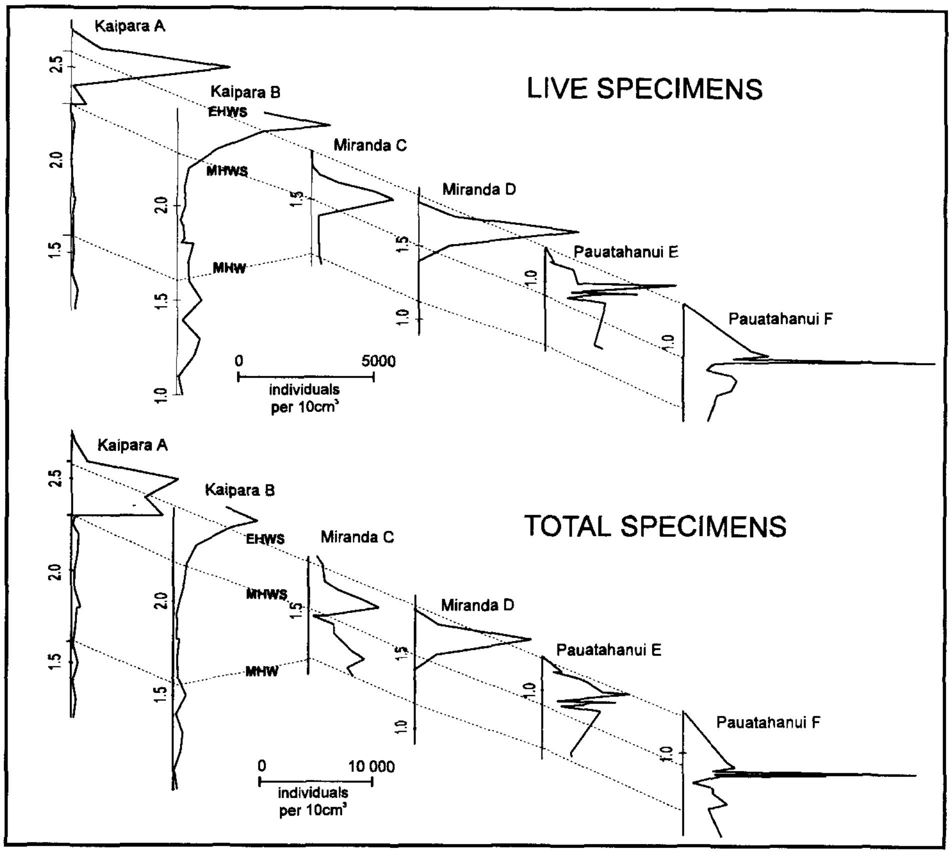


Fig. 8 Distribution of the abundance of live and total (dead plus live) foraminifera per 10 cm^3 through all transects.

TIDAL RANGE: Between the lowest stations and half-way between MHW and MHWS, with greatest abundances around MHW ± 0.5 m.

DISCUSSION: Three of these species (*C. involvens*, *Saccammina* sp., *P. zealandica*) are recorded live in this study. *Saccammina* is probably reproducing here because of its local abundance, but *P. zealandica* and *C. involvens* are more usually found as common members of normal salinity inner shelf faunas (Hayward et al. 1999) and may have been swept into the marsh where they survive but do not reproduce.

Ungrouped species

Trochamminita salsa—this species characterises a monospecific association that is widespread around New Zealand at the extremes of saltwater incursion at the heads of tidal estuaries in low salinity tidal and subtidal environments (Hayward & Hollis 1994). The species occurs only rarely in this study.

TOTAL LIVE SPECIMENS (Fig. 8, Appendix 1)

All six transects show a similar pattern with a relatively low, erratic abundance of live foraminifera (mostly >1000 per 10 cm^3) below MHWS level and a sharp peak abundance (4000–7000 per 10 cm^3) between MHWS and EHWS. There are no live specimens above 50–100 mm below EHWS, except in transect E where the few recorded live *Q. seminula* are inferred to be transported exotics.

The position of the peak absolute abundance of live foraminiferal specimens between MHWS and EHWS at a level inundated by the tide for less than 2 hours on fewer than 10 occasions per year is unexpected. A partial explanation may be the higher sedimentation rates lower on the shore, but this is unlikely to account for the order of magnitude difference documented. These peak abundances are a result of the combined abundances of just four agglutinated species—*Haplophragmoides wilberti*, *Miliammina obliqua*, *Trochammina inflata*, and *T. macrescens*.

TOTAL SPECIMENS (Fig. 8, Appendix 1)

All stations, except D11 above EHWS, contain foraminiferal tests. In each transect there is a sharp abundance peak (6000–20000 per 10 cm^3) of total tests (dead plus live) coinciding with the live peak between MHWS and EHWS. The abundance drops away dramatically approaching EHWS and at higher elevations.

Between MHW and MHWS, total test abundance is considerably lower than the peak but in highly variable and somewhat erratic numbers. Lowest total abundances occur in transect D at Miranda (20–40 per 10 cm^3), with intermediate levels in the Kaipara transects (100–1000 per 10 cm^3) and the highest abundances in Pauatahanui and Miranda transect C (1–5000 per 10 cm^3).

The peak abundances of total tests reflect the peak live abundances at this level on the shore which may be partially ascribed to lower sedimentation rates. In any one station the percentage of the total fauna that was live ranges between 0 and 90% with most within the range 5–30%. This range generally applies to both peak and low abundance values.

The consistently lowest live percentages occur in transect C at Miranda (av. c. 5%), which also has the highest total abundances of tests outside the MHWS-EHWS peak. These support the inference that this transect has abundant palimpsest tests from when it was the exposed face of a shelly beach.

SPECIES DIVERSITY (Appendix 1)

The two Kaipara transects show strong trends of decreasing species diversity (*S*) moving up the shore in both the total and live faunas. Similar but much weaker trends are discernible in the two Pauatahanui transects. The two Miranda transects have similar numbers of species in the total faunas all the way up the shore. This is also true of the live fauna in transect C but the number of species in the live fauna in transect D increases shorewards. This reversed trend appears to be due to the lower number of species (and specimens) low on the shore in transect D than elsewhere.

Values for the Shannon-Wiener Information Function (*H*) show no consistent trends through a majority of transects. Transects B to F have highly variable values of *H* with no discernible trends. Only Kaipara transect A shows a shorewards trend of decreasing diversity values.

FACTORS INFLUENCING MARSH FORAMINIFERAL DISTRIBUTION

The overall distribution of foraminifera in New Zealand salt marshes is influenced by salinity, tidal level (exposure), and by susceptibility to contamination by transported or palimpsest foraminifera (Hayward & Hollis 1994; Hayward et al. 1996).

Salinity (Fig. 9)

The two study sites with only slightly reduced salinity (Kaipara and Miranda) have a similar suite of foraminiferal associations dominated by *Ammonia* and *Trochammina* associations and in places by subdominant *Elphidium excavatum* and *Cornuspira* associations. The lower salinity Pauatahanui study site is dominated by the *Haplophragmoides-Miliammina* and to a lesser extent the *Trochammina* associations. Elsewhere in New Zealand, a *Trochamminita* association is present only in the lowest salinity brackish conditions (Hayward et al. 1997a).

Tidal level (Fig. 9)

In the more saline transects that lack significant introduced exotic specimens (transects A, B, D), the foraminifera show a clear zonation with tidal level (Fig. 7). The *Ammonia* association is dominant throughout the lower marsh up to a level midway between MHW and MHWS where it is replaced gradationally by the *Trochammina* association. Between MHWS and EHWS the *Trochammina* association generally comprises >90% of the total and live faunas. The *Elphidium excavatum, Haplophragmoides, Cornuspira*, and *Helenina* associations also occur patchily (sometimes comprising >50% of the fauna) below MHWS in these transects.

In the less saline transects (E, F) the marsh occupied a smaller tidal range but two foraminiferal zones related to tidal level are recognisable (Fig. 7). Below about MHWS the faunas are dominated by *Haplophragmoides-Miliammina* association with relatively low background levels of *Trochammina* association. Occurring patchily within this zone are *Ammonia, Ammotium, Helenina*, and *Cornuspira* associations (sometimes >20% of the fauna). A narrow zone around the top of the marsh between MHWS and EHWS is dominated by *Trochammina* association.

Displaced foraminifera

The presence of dead, and in places also live, tests of species that usually occur in more saline low tidal or subtidal environments suggests that some transects (A, B, and C) have a significant proportion of displaced foraminifera that have been transported in from outside.

Studies in the United Kingdom (Murray et al. 1982; Wang & Murray 1983; Murray 1991; Wang 1992) show that numerous, particularly small and low density foraminiferal tests are lifted into suspension by storm waves off the coast, transported shorewards and often swept into estuaries where they are deposited in quieter water. A similar process is envisaged here for Pauatahanui Inlet, with suspended tests of small size and low density (e.g., *Cornuspira involvens*, possibly *Quinqueloculina seminula*) being swept by strong tidal currents into the inlet and carried into the marsh at its head by the tide.

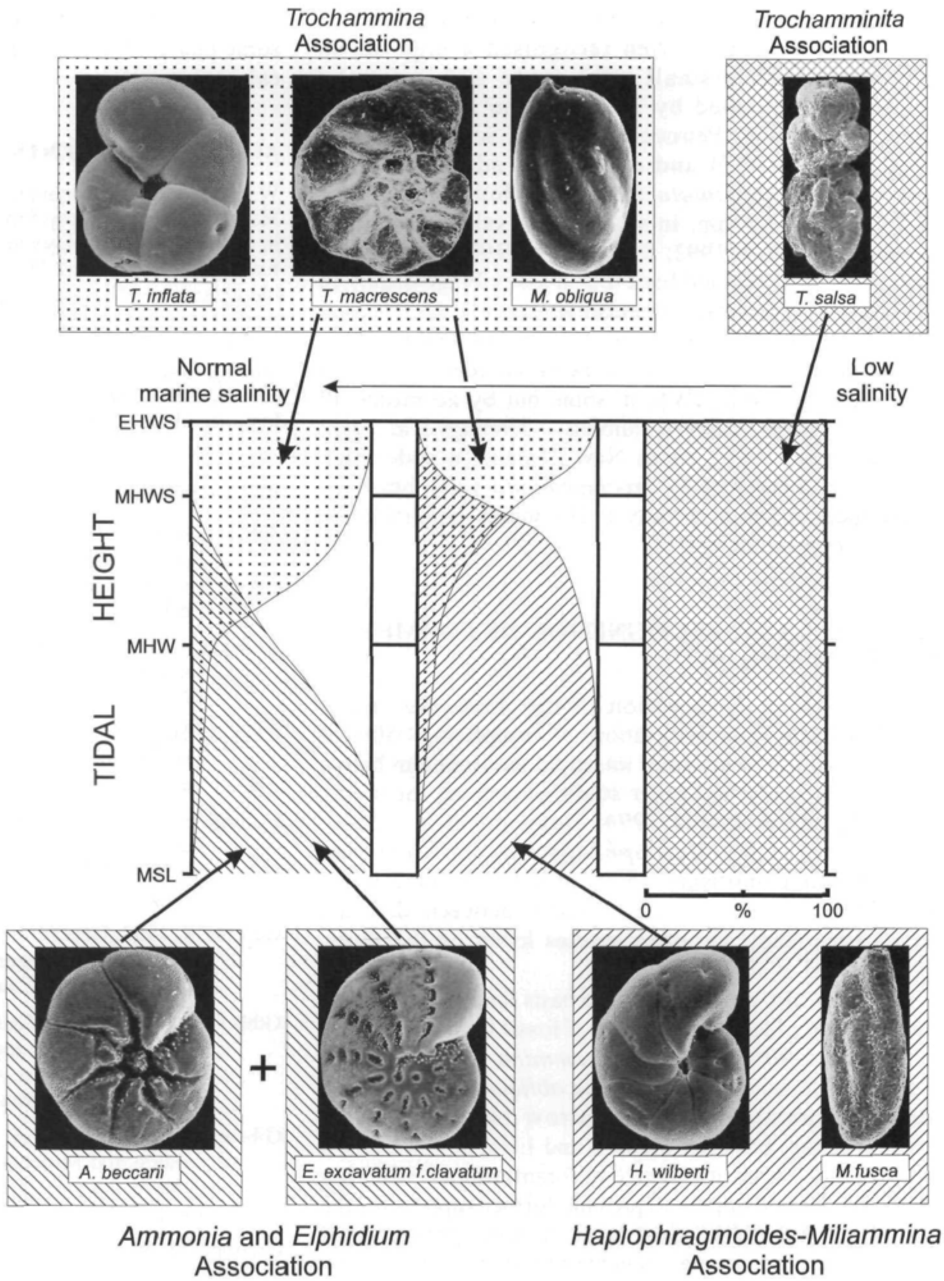
At Kaipara we envisage onshore waves within the large, shallow harbour, or off the exposed coast outside the harbour, lifting smaller and lighter subtidal foraminifera (e.g., *Bolivina neocompacta, Bulimina* spp., *Cassidulina carinata, Cornuspira involvens, Nonionellina flemingi, Pileolina zealandica, Spiroloxostoma glabra, Trochammina sorosa, Zeaflorilus parri*, and possibly *Quinqueloculina seminula*) into suspension to be transported by the incoming tide into the marsh. All these species are prominent members of normal salinity, inner shelf associations around New Zealand (Hayward et al. 1999). Small, transparent specimens of *Cassidulina carinata, Cornuspira involvens*, and *Quinqueloculina seminula* are commonly found transported into marshes in other places (e.g., Hayward et al. 1997a) and we attribute this to their lightweight tests that allow them to be carried in suspension for longer. Often the greatest concentration of these exotic tests is around MHW where they are deposited as the tide turns.

Transect D at Miranda appears to have the lowest proportion of displaced tests. We suspect that tidal currents are of insufficient strength to carry many suspended tests through the 200 m wide belt of mangrove forest that separates the transect from the sea.

Palimpsest foraminifera

Transect C, at Miranda, is located on the face of the penultimate shell ridge, now sheltered from the sea by the modern shell ridge (Fig. 4), which grew across in front of it less than 50 years ago. Mud has accumulated in the depression between the two ridges (stns. C1–4) but only a thin veneer (1–2 mm) of sediment has subsequently accumulated over the former beach face (stns. C5–12). Hence, our 10 mm deep samples contain a high proportion of beach face sediment.

Fig. 9 Generalised, salinity-influenced, tidal zonation of New Zealand marsh foraminifera, based on this and previous studies (Hayward et al. 1999). EHWS = extreme high water spring level; MHWS = mean high water spring level; MHW = mean high water level; MSL = mean sea level (mid tide).



Over 90% of the foraminiferal fauna on the beach on the outer slope of the modern Miranda shell ridge is *Ammonia beccarii*; thus, it is not surprising that the recognisably palimpsest fauna (from when this was the beach) in the upper part of transect C is dominated by this species. Many of these specimens are large, abraded and quite dense and thus distinguishable from most exotic tests transported in suspension. Recognising palimpsest foraminifera is important in studies of ancient chenier plain deposits.

COMPARISON WITH FORAMINIFERA FROM OTHER TEMPERATE MARSHES

None of these marsh-inhabiting foraminifera are endemic to New Zealand, although several of the allochthonous species are (e.g., *Nonionellina flemingi, Pileolina zealandica, Zeaflorilus parri*). All, except two of the New Zealand marsh-inhabiting foraminiferal species, have a cosmopolitan distribution—*Trochamminita salsa* is known to be common elsewhere only in Chile (Jennings et al. 1995) with sporadic records from Australia, British Columbia, and the Caribbean; *Miliammina obliqua* is largely restricted to Southern Hemisphere shores (Hayward et al. 1999). Several species (e.g., *Haplophragmoides manilaensis*, *Tiphotrocha comprimata, Discorinopsis aquayoi*) common in temperate and subtropical marshes elsewhere are absent from New Zealand.

The tidal flat and low marsh assemblages dominated in New Zealand by *Ammonia beccarii, Elphidium excavatum, Miliammina fusca*, and *Haplophragmoides wilberti* appear to have similar compositions and tidal and salinity ranges to those found in temperate marshes around North America, South America, Europe, and Australia (e.g., Scott et al. 1990; Patterson 1990; Ozarko et al. 1997).

Detailed transect studies on the coasts of North America and Europe have also often recognised a high marsh assemblage with a small tidal range and increased abundance, dominated by *Trochammina inflata* and *T. macrescens* s.l. (e.g., Petrucci et al. 1983; Scott et al. 1990; Ozarko et al. 1997) and sometimes additionally by *Tiphotrocha comprimata* (Scott & Medioli 1980) or *Haplophragmoides* spp. in slightly less saline conditions (Jennings & Nelson 1992; Collins et al. 1995; Scott et al. 1996). The New Zealand high marsh assemblage differs in the additional sporadically abundant presence of *Miliammina obliqua*. A relatively narrow zone of foraminiferal test (live and total) concentrations has also been recorded in the high marsh, at or above MHWS, in some but by no means all studies (e.g., Chile, British Columbia — Jennings et al. 1995; Guilbault et al. 1996). As in New Zealand, a wider high marsh zone dominated by *Trochamminita salsa* has been documented in lower salinity (<10) marsh conditions in Chile (Jennings et al. 1995).

POTENTIAL FOR RECOGNITION OF FORMER SEA LEVELS (Fig. 9)

In New Zealand, recognition of the *Ammonia* and/or *Elphidium excavatum* associations as comprising >50% of a fossil fauna infers a former intertidal environment below MHWS (this study and other studies lower on the shore, e.g., Hayward & Hollis 1994; Hayward et al. 1999). Recognition of the *Haplophragmoides-Miliammina* association as comprising >50% of a fossil fauna infers reduced salinity in a marsh environment, between MSL and MHWS (this study and other studies lower on the shore, e.g., Hayward et al. 1999).

This study also provides a sound basis for a more accurate determination of former sea levels if fossil faunas are found that contain >90% of the *Trochammina* association (*T. inflata, T. macrescens, Miliammina obliqua*). These would indicate accumulation in the narrow zone (0.1–0.3 m elevation range) between MHWS and EHWS. If the fossil fauna also has a high abundance of foraminifera (>6000 per 10 cm^3) this would appear to provide further support for the inferred MHWS-EHWS tidal level. A monospecific fossil fauna of *T. macrescens* may indicate an elevation even closer to EHWS (0.05–0.1 m elevation range, depending on tidal range).

Previous studies indicate that in areas of greatly reduced salinity (through ground-water seepage or stream discharge) the *Trochammina* assemblage at MHWS-EHWS is replaced by a *Trochamminita salsa* assemblage (Hayward et al. 1996).

Recognition of a diagnostic high marsh assemblage in fossil deposits is beginning to be used overseas in determining former sea levels and in documenting earthquake-related vertical movements (Guilbault et al. 1996) or eustatic sea-level curves (Scott et al. 1995). Fossil marsh foraminiferal faunas have not yet been documented from New Zealand but are known to exist in a number of late Quaternary coastal deposits (B. Hayward unpubl. data). Selective taphonomic loss of marsh foraminiferal species could interfere with paleo-sea level and paleo-salinity assessments and require more study. Overseas work indicates that all the main New Zealand marsh species can be preserved in fossil deposits (e.g., Guilbault et al. 1996), but it is also known that low pH conditions found typically in some marsh sediments promote the selective destruction of calcareous tests.

ACKNOWLEDGMENTS

We thank Kelvin Berryman, Murray Gregory, Kathryn Hayward Margaret Morley, Percy Strong, and George Scott for assistance in the field. Kathryn Hayward assisted with figure preparation and Ewen Cameron and Doug Rogan helped with the plant identification. The manuscript has benefited from the critical appraisal of George Scott, Murray Gregory, and referees Alberto Albani and Tim Patterson. This research was undertaken with funding from the Foundation for Research Science and Technology (BWH, HRG). DBS's stay in New Zealand was funded by the Institute of Geological and Nuclear Sciences Ltd, Lower Hutt

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APPENDIX 1

Species diversity of total benthic foraminiferal faunas (*S*, *H*, *E*) and total foraminiferal abundance (no. of specimens per 10 cm^3) in six salt marsh transects in New Zealand. Percentage relative frequency of species in live and total foraminiferal faunas. L = living specimens (stained protoplasm in tests); T = total specimens (living plus dead); x = less than 1% relative frequency.

KAIPARA TRANSECT A		A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	A11	A12	A13	A14	A15	A16	A17	A18	A19	A20	A21	A22
Height above MSL (m)		1–2	1–3	1–4	1–5	1–6	1–7	1–8	1–8	1–9	2–0	2–1	2–2	2–25	2–25	2–3	2–3	2–4	2–5	2–6	2–7	2–8	2–7
						MHW										MHWS				EHWS			
Total no. of species, *S*	T	8	8	8	9	10	11	8	20	10	8	11	6	7	6	6	6	4	5	3	3	1	2
H		1–8	1–6	1–7	1–8	2–0	1–8	1–9	2–3	1–9	1–8	1–9	1–4	1–6	1–1	0–8	1–1	1–2	1–1	1–0	0–8	0–0	0–4
E		0–82	0–76	0–83	0–83	0–84	0–79	0–89	0–79	0–81	0–88	0–79	0–76	0–80	0–63	0–47	0–61	0–84	0–79	0–93	0–69	0	0–59
No. of specimens per	L	120	180	30	90	42	54	126	78	24	6	18	78	27	0	12	396	56	4212	792	0	0	0
10 cm^3	T	264	504	174	684	198	420	540	918	312	342	654	750	201	162	378	9144	7308	10764	1584	396	18	252
BENTHIC FORAMINIFERA																							
Ammonia beccarii s.l.	L	40	30	20	40	–	11	14	8	50	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	45	50	38	32	18	4	22	24	27	7	5	1	3	–	–	–	–	–	–	–	–	–
Bolivina neocompacta	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Buccella pustulosa	L	–	–	–	–	–	11	–	–	50	–	–	8	–	–	–	–	–	–	–	–	–	–
	T	–	7	10	24	–	3	–	5	15	4	18	18	12	4	–	–	–	–	–	–	–	–
Bulimina elongata	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Cassidulina carinata	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cibicides marlboroughensis	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cornuspira involvens	L	–	20	–	–	–	–	–	23	–	–	67	–	–	–	–	–	–	–	–	–	–	–
	T	–	7	–	3	3	3	7	7	–	16	14	1	–	–	–	–	–	–	–	–	–	–
Elphidium advenum s.l.	L	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Elphidium charlottense	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Elphidium excavatum s.l.	L	–	10	–	20	–	–	43	31	–	–	33	85	89	–	100	–	–	–	–	–	–	–
	T	8	4	3	18	3	1	25	14	2	–	6	34	33	68	78	–	–	–	–	–	–	–
Fissurina lucida	L	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	5	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Haplophragmoides wilberti	L	–	–	20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
	T	5	4	3	–	3	4	–	–	2	–	–	–	–	–	2	2	2	1	–	–	–	–
Haynesina depressula	L	30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	13	–	7	5	–	–	–	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Helenina anderseni	L	–	–	–	–	14	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Miliammina fusca	L	–	20	–	–	–	22	14	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	7	–	3	3	9	13	19	23	9	1	–	6	7	3	x	–	–	–	–	–	–
Miliammina obliqua	L	10	10	20	20	29	33	–	31	–	100	–	–	11	–	–	9	96	35	36	–	–	–
	T	5	18	7	5	12	31	3	4	2	32	2	–	3	7	5	17	32	39	41	73	100	–
Nonionellina flemingi	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nonionoides turgida	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pileolina zelandica	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pseudothurammina limnetis	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Quinqueloculina seminula	L	–	–	–	–	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	1	–	2	6	–	–	–	–	–	–	–	–	–	–	–
Scherochorella moniliforme	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Spiroloxostoma glabra	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Textularia earlandi	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Trochammina bartrami	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	3	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Trochammina inflata	L	–	10	20	20	57	11	14	–	–	–	–	–	–	–	–	73	–	44	36	–	–	–
	T	5	4	24	5	33	21	20	9	10	16	13	11	7	4	3	54	29	39	43	9	–	86
Trochammina macrescens	L	–	–	20	–	–	11	14	–	–	–	–	8	–	–	–	18	4	19	27	–	–	–
	T	8	–	7	5	9	21	7	5	15	16	34	35	36	10	10	27	38	21	16	18		14
Trochammina sorosa	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–
Zeaflorilus parri	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–
ARCELLACEANS																							
Difflugia capreolata	L	–	–	–	–	–	–	–	–	–	1	3	2	3	–	9	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	x	–	x	–	1	1	1	1	4	–	18	–	–	–	–	–
PLANKTIC FORAMINIFERA																							
Globigerina falconensis	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Globigerina quinqueloba	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–

(continued)

APPENDIX 1 (*continued*)

KAIPARA TRANSECT B		B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13	B14	B15	B16	B17	B18	B19	B20
Height above MSL (m)		1–0	1–1	1 2	1–3	1–4	1–5	1–6	1–7	1–8	1–8	1–9	1–8	1–9	2–0	2–1	2–2	2–3	2–4	2–43	2–5
								MHW										MHWS			
Total no. of species, *S*	T	9	7	17	18	13	17	18	9	10	9	10	13	10	7	4	4	5	6	5	6
H		1–1	1–0	2 0	2–0	1–6	1–8	2–2	1–9	2–0	1–3	1–6	1–8	1–3	1–2	0–9	0–8	0–9	1–3	1–1	1–3
E		0 49	0–50	0–72	0–68	0–61	0–61	0–76	0–87	0–86	0 59	0–68	0–71	0–56	0–63	0–66	0–55	0–58	0–68	0–69	0–71
No. of specimens per	L	165	54	426	588	132	657	325	303	426	190	72	106	164	249	186	288	1017	2268	4050	2304
10 cm³	T	366	114	741	945	296	1254	460	393	588	324	274	324	360	573	1080	1296	2232	5742	8082	5004
BENTHIC FORAMINIFERA																					
Ammonia beccarii s.l.	L	55	59	23	44	22	16	29	11	3	24	–	8	–	–	–	–	–	–	–	–
	T	66	70	32	42	47	18	27	8	3	27	–	8	2	–	–	–	–	–	–	–
Bolivina neocompacta	L	–	–	1	1	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	1	–	1	1	1	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bucella pustulosa	L	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	6	x	1	x	x	–	–	–	–	–	–	–	–	–	–	–	–	–
Bulimina marginata	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cassidulina carinata	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cornuspira involvens	L	–	–	1	3	3	53	7	2	18	2	3	9	4	–	–	–	–	–	–	1
	T	–	–	1	3	2	49	7	2	15	1	1	4	2	–	–	–	–	–	–	–
Cribrostomoides jeffreysi	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Elphidium advenum s.l.	L	7	11	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
	T	6	5	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Elphidium excavatum s.l.	L	2	19	5	3	5	2	2	–	–	2	19	8	2	–	–	–	–	–	–	–
	T	1	11	7	4	7	5	3	–	–	1	6	3	3	–	–	–	–	–	–	–
Elphidium gunteri	L	–	–	4	4	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	5	4	1	1	x	–	–	–	–	–	–	–	–	–	–	–	–	–
Fissurina lucida	L	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gaudryina sp.	L	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	1	–	x	x	–	–	–	–	–	–	–	–	–	–	–	–	–
Haplophragmoides wilberti	L	–	–	–	–	–	1	–	6	17	1	–	–	–	–	–	–	–	8	2	9
	T	–	–	–	–	1	1	x	8	14	1	1	1	–	1	–	–	–	4	3	6
Haynesina depressula	L	16	–	4	2	–	1	2	–	–	–	–	4	–	–	–	–	–	–	–	–
	T	14	2	10	6	4	3	2	–	–	–	–	1	–	–	–	–	–	–	–	–
Helenina anderseni	L	7	4	5	11	-	2	2	–	–	–	–	2	–	–	–	–	–	–	–	–
	T	3	2	4	8	2	2	1	–	–	–	–	1	–	–	–	–	–	–	–	–
Miliammina fusca	L	–	–	–	3	26	6	15	17	18	56	8	2	–	–	–	–	1	–	–	–
	T	–	–	1	2	26	6	20	22	22	54	18	8	4	2	–	1	2	–	–	–
Miliammina obliqua	L	–	–	–	–	–	–	–	–	–	–	–	2	–	5	81	17	15	19	25	19
	T	–	–	–	–	–	–	–	–	–	–	2	5	2	5	53	12	14	18	23	26
Nonionellina flemingi	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	x	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pileolina zelandica	L	2	–	–	2	1	2	5	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	1	–	–	2	1	3	5	–	–	–	–	1	1	–	–	–	–	–	–	–
Polysaccammina ipohalina	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	1	–	2	1	–	–	1	–	–	–	–	–
Pseudothurammina limnetis	L	–	–	–	–	–	–	4	14	5	3	11	4	1	13	–	–	–	1	2	–
	T	–	–	–	–	–	–	4	14	5	2	3	4	1	8	–	–	x	1	2	–
Quinqueloculina seminula	L	2	–	6	2	7	11	18	33	9	6	–	–	1	–	–	–	–	–	–	2
	T	3	4	5	5	5	8	14	28	7	4	1	–	1	–	–	–	–	–	–	1
Rosalina sp.	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Saccammina sp.	L	2	4	49	27	8	1	2	1	–	3	–	–	–	–	–	–	–	–	–	–
	T	1	2	31	18	4	1	3	1	–	5	–	–	–	–	–	–	–	–	–	–
Scherochorella moniliforme	L	–	-	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	x	–	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–
Trochammina inflata	L	–	4	1	–	1	3	6	9	18	2	31	25	40	40	6	13	14	44	64	53
	T	–	2	x	1	1	2	7	9	20	2	41	30	39	36	7	12	17	35	58	47
Trochammina macrescens	L	–	–	–	–	–	2	4	8	13	2	28	37	51	41	13	71	70	11	7	17
	T	–	–	–	–	–	1	6	8	15	1	24	35	47	48	39	77	67	42	15	20
Trochammina sorosa	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	x	–	–	x	x	–	1	–	1	–	–	–	–	–	–	–	–	–
ARCELLACEANS																					
Centropyxis aculeata	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–
PLANKTIC FORAMINIFERA		1	4	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

(*continued*)

APPENDIX 1 (*continued*)

MIRANDA TRANSECT C

		C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	C15
Height above MSL (m)		1–1	1–15	1–2 MHW	1–25	1–4	1–5 MHWS	1–55	1–6	1–65	1–7	1–75	1–8	1–35	1–45	1–45
Total no. of species, *S*	T	4	3	6	6	6	7	5	4	5	4	5	5	7	6	7
H		0–3	0–3	0–5	0–5	1–0	1–1	1–0	1–0	1–0	0–9	0–7	0–3	1–1	0–9	0–8
E		0–24	0–28	0–28	0–31	0–57	0–58	0–63	0–73	0–60	0–63	0–41	0–18	0–57	0–50	0–45
No. of specimens per	L	270	216	216	180	180	2214	1692	720	207	27	0	0	954	80	114
10 cm^3	T	4230	3672	5256	4014	2376	6624	4878	2808	1566	1458	1368	810	2376	400	1494
BENTHIC FORAMINIFERA																
Ammonia beccarii s.l.	L	93	92	75	60	27	–	–	3	4	–	–	–	–	10	37
	T	92	93	88	86	62	22	23	55	63	68	79	94	16	69	79
Elphidium advenum s.l.	L	–	8	–	10	–	–	–	–	–	–	–	–	–	–	–
	T	3	3	3	4	1	x	–	–	–	–	1	1	x	2	4
Elphidium excavatum s.l.	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	1	x	–	–	–	–	–	–	–	–	–	–	–
Elphidium gunteri	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Haynesina depressula	L	7	–	17	20	7	5	–	–	–	–	–	–	–	–	–
	T	5	4	8	8	3	2	x	–	–	–	1	–	1	2	6
Miliammina obliqua	L	–	–	–	–	–	2	–	–	–	–	–	–	2	–	–
	T	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–
Notorotalia sp.	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Polysaccammina ipohalina	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x
	T	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Trochammina inflata	L	–	–	8	–	33	24	32	45	65	100	–	–	50	8	16
	T	–	–	1	1	9	19	20	18	22	19	13	3	30	4	4
Trochammina macrescens	L	–	–	–	10	33	68	68	52	30	–	–	–	48	83	47
	T	–	–	x	x	25	57	57	27	14	14	7	1	53	24	7
ARCELLACEANS																
Centropyxis aculeata	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–

MIRANDA TRANSECT D

		D1	D2	D3	D4	D5	D6	D7	D8	D9	D10	D11
Height above MSL (m)		0–9	1–0	1–1	1–2 MHW	1–3	1–4	1–5 MHWS	1–6	1–7 EHWS	1–8	1–9
Total no. of species, *S*	T	3	6	9	4	6	2	4	4	4	0	0
H		0–8	1–6	2–0	1–3	1–6	0–7	1–1	1–1	0–9	–	–
E		0–59	0–91	0–89	0–93	0–87	1–0	0–66	0–77	0–68	–	–
No. of specimens per	L	1	0	3	6	3	0	924	4788	1080	0	0
10 cm^3	T	24	39	28	33	42	6	2016	11016	2196	0	0
BENTHIC FORAMINIFERA												
Ammonia beccarii s.l.	L	100	–	33	–	–	–	–	–	–	–	–
	T	72	38	21	18	21	–	–	–	–	–	–
Bulimina elongata	L	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	4	–	–	–	–	–	–	–	–
Elphidium excavatum s.l.	L	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	4	–	–	–	–	–	–	–	–
Fissurina lucida	L	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	4	–	–	–	–	–	–	–	–
Haplophragmoides wilberti	L	–	–	–	100	–	–	10	1	–	–	–
	T	–	–	8	18	6	–	6	1	23	–	–
Haynesina depressula	L	–	–	–	–	–	–	–	–	–	–	–
	T	4	8	7	–	–	–	–	–	–	–	–
Miliammina fusca	L	–	–	–	–	–	–	1	–	–	–	–
	T	–	15	–	–	6	–	1	–	–	–	–
Miliammina obliqua	L	–	–	–	–	–	–	20	22	3	–	–
	T	–	–	11	–	6	–	29	18	10	–	–
Pseudothurammina limnetis	L	–	–	–	–	–	–	–	–	3	–	–
	T	–	–	–	–	–	–	–	–	2	–	–
Spiroloxostoma glabra	L	–	–	–	–	–	–	–	–	–	–	–
	T	–	8	–	–	–	–	–	–	–	–	–
Trochammina inflata	L	–	–	33	–	–	–	62	47	71	–	–
	T	20	15	21	18	28	50	58	51	62	–	–
Trochammina macrescens	L	–	–	33	–	100	–	7	29	23	–	–
	T	4	15	21	45	33	50	6	30	26	–	–
ARCELLACEANS												
Centropyxis aculeata	L	–	–	–	–	–	–	36	–	–	–	–
	T	1	–	–	–	–	–	–	–	–	–	–
PLANKTIC FORAMINIFERA												
Globigerina quinqueloba	L	–	–	1	–	–	–	–	–	–	–	–
	T	–	–	1	–	–	–	–	–	–	–	–

(*continued*)

APPENDIX 1 (*continued*)

PAUATAHANUI TRANSECT E

		E1	E2	E3	E4	E5	E6	E7	E8	E9	E10	E11	E12	E13	E14	E15
Height above MSL (m)		0–64	0–62	0–88	0–91	0–94	0–98	0–93	0–92	0–93	0–99	1–07	1–11	1–11	1–19	1–19
Organic carbon %		4–9	3–6	5–4	6–3	9–2	9–6	39–5	35	32–9	39–2	–	37–1	–	40–5	–
Total no. of species, *S*	T	5	7	7	6	7	6	8	5	5	5	6	2	6	1	2
H		0–8	1–0	0–6	1–1	1–4	0–5	1–3	1–2	0–9	1–1	1–3	0–1	1–4	0–0	0–7
E		0–52	0–51	0–33	0–63	0–72	0–26	0–65	0–73	0–54	0–65	0–72	0–13	0–73	0–00	1–00
No. of specimens per	L	1448	1700	1792	640	784	3880	1808	1088	2736	976	840	144	264	24	12
10 cm^3	T	2428	2548	4944	1600	1240	7440	4144	3552	6256	5136	3300	880	1692	80	228
BENTHIC FORAMINIFERA																
Ammotium fragile	L	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
	T	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–
Cornuspira involvens	L	–	x	–	3	–	–	–	–	–	–	–	–	–	–	–
	T	–	x	–	1	–	–	–	–	–	–	–	–	–	–	–
Elphidium excavatum s.l.	L	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	x	–	–	–	–	–	–	–	–
Haplophragmoides wilberti	L	82	70	85	63	24	91	13	16	79	34	27	–	14	–	–
	T	76	67	83	60	32	88	26	40	72	49	26	–	13	–	5
Haynesina depressula	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Helenina anderseni	L	–	–	x	–	28	–	1	–	–	–	–	–	–	–	–
	T	–	–	x	–	20	–	x	–	–	–	–	–	–	–	–
Miliammina fusca	L	8	19	5	13	5	–	13	22	8	3	–	–	5	–	–
	T	11	19	3	7	6	3	12	14	16	2	4	–	6	–	–
Polysaccammina ipohalina	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	x	–	–	–	–	–
Pseudothurammina limnetis	L	–	–	–	–	–	–	6	3	1	–	–	–	2	–	–
	T	–	–	–	–	–	–	3	2	x	–	1	–	2	–	–
Quinqueloculina seminula	L	1	9	1	6	1	–	3	–	–	–	–	–	2	–	100
	T	1	6	x	3	1	–	1	–	–	–	–	–	x	–	5
Trochammina inflata	L	3	1	6	13	38	4	54	57	8	56	53	–	30	–	–
	T	4	3	10	26	38	3	50	41	8	39	52	2	29	–	–
Trochammina macrescens	L	7	1	2	4	3	1	9	2	5	7	4	100	48	100	–
	T	9	3	3	5	4	4	8	3	4	10	10	98	43	100	–
Trochamminita salsa	L	–	–	2	–	–	–	–	–	–	–	11	–	–	–	–
	T	–	–	1	–	–	–	–	–	–	–	7	–	5	–	–
ARCELLACEANS																
Centropyxis aculeata	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	x	–	–	2	–	79
Centropyxis constricta	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5
Difflugia globulus	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5

PAUATAHANUI TRANSECT F

		F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12	F13	F14
Height above MSL (m)		0–52	0–68	0–71	0–80	0–88	0–77	0–85	0–9	0–87	0–88	0–88	0–92	0–95	1–23
Organic carbon %		18–5	7–7	10	27–1	16–9	7–6	4–5	2–4	6–4	24–6	25–8	27	8–7	57–9
Total no. of species, *S*	T	9	10	5	6	5	11	9	5	5	6	7	6	8	2
H		1–2	1–8	0–9	0–7	0–9	1–4	1–6	1–3	1–2	0–7	0–8	0–9	1–4	0–7
E		0–55	0–76	0–56	0–40	0–59	0–60	0–71	0–68	0–74	0–41	0–40	0–48	0–68	1–00
No. of specimens per	L	720	984	1424	1424	1552	1568	688	1456	912	6208	7296	2480	1936	16
10 cm^3	T	3456	2274	3904	2704	2736	2640	832	2640	3360	12704	20704	4688	3920	192
BENTHIC FORAMINIFERA															
Ammobaculites exiguus	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	3	–	–	–	–	–	–	–	–
Ammonia beccarii s.l.	L	–	–	–	–	–	2	–	2	–	–	–	–	–	–
	T	–	–	–	–	–	1	2	32	–	–	–	–	–	–
Ammotium fragile	L	–	–	–	–	–	43	5	–	–	1	–	–	3	–
	T	–	–	–	1	–	39	4	–	–	1	–	–	2	–
Cornuspira involvens	L	10	5	–	–	–	–	–	–	–	–	–	–	–	–
	T	2	3	–	–	–	–	–	–	–	–	–	–	–	–
Elphidium advenum s.l.	L	–	–	–	–	–	1	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Elphidium excavatum s.l.	L	8	2	–	–	–	1	–	–	–	–	–	–	–	–
	T	2	3	–	–	–	1	2	2	–	–	–	–	–	–
Haplophragmoides wilberti	L	33	9	64	81	65	21	51	12	47	85	70	6	47	–
	T	65	36	70	81	67	19	48	10	34	78	75	16	51	–
Haynesina depressula	L	–	1	–	–	–	–	–	1	–	–	–	–	–	–
	T	–	1	–	–	–	–	–	2	–	–	–	–	–	–
Helenina anderseni	L	8	45	–	–	–	–	2	–	–	–	–	–	5	–
	T	2	21	–	–	–	–	2	–	–	–	–	–	4	–
Miliammina fusca	L	30	6	9	5	6	32	21	77	9	9	15	12	27	–
	T	18	10	12	8	6	36	19	47	4	15	16	8	23	–
Polysaccammina ipohalina	L	–	–	–	–	1	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	1	–	–	–	–	–	–	x	–	–
Pseudothurammina limnetis	L	–	–	–	1	–	–	–	–	2	1	1	1	–	–
	T	2	–	1	1	–	–	–	–	1	1	1	1	–	–
Quinqueloculina seminula	L	13	27	–	2	–	1	14	3	–	–	1	–	3	–
	T	3	16	–	1	–	1	12	2	–	–	x	–	2	–
Textularia earlandi	L	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	T	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Trochammina inflata	L	–	4	24	11	24	1	5	4	37	4	12	77	14	–
	T	5	9	16	8	22	1	10	5	45	5	7	72	14	8
Trochammina macrescens	L	–	1	3	–	4	–	2	–	7	1	–	2	1	–
	T	2	1	1	–	4	–	2	–	17	x	x	2	4	8
Trochamminita salsa	L	–	–	–	–	–	–	–	–	–	–	x	–	–	–
	T	–	–	–	–	–	–	–	–	–	–	x	–	1	–
ARCELLACEANS															
Centropyxis aculeata	L	–	–	–	–	–	–	–	–	–	–	–	–	–	100
	T	–	–	–	–	–	–	–	–	–	–	–	–	–	75
Centropyxis constricta	L	–	–	–	–	–	–	–	–	–	–	–	1	–	–
	T	–	–	–	–	–	–	–	–	–	–	–	1	–	–

APPENDIX 2

List of identified foraminifera and references to published figures that portray their features.

Benthic species

Suborder Textulariina

Ammobaculites exiguus Cushman & Brönnimann. Hayward & Hollis 1994, pl.1, figs.17–19.
Ammotium fragile Warren. Hayward & Hollis 1994, pl.2, figs.1–3.
Cribrostomoides jeffreysi (Williamson). Haynes 1973, pl.2, figs.5,6, pl.8, fig.9, pl.29, fig.10, text-fig.5.
Gaudryina sp.
Haplophragmoides wilberti Andersen. Hayward & Hollis 1994, pl.2, figs.4–6.
Miliammina fusca (Brady). Hayward & Hollis 1994, pl.3, figs.5–8.
Miliammina obliqua Heron-Allen & Earland. Hayward & Hollis 1994, pl.3, figs.9,10.
Polysaccammina ipohalina Scott 1976b, text fig. 4a-c.
Pseudothurammina limnetis (Scott & Medioli). Hayward & Hollis 1994, pl.1, figs.1–3.
Saccammina sp.
Scherochorella moniliforme (Siddall). Hayward & Hollis 1994, pl.1, figs.11–16.
Textularia earlandi Parker. Hayward & Hollis 1994, pl.3, figs.1–4.
Trochammina bartrami Hedley et al. 1967, pl.1, figs.10,11.
Trochammina inflata (Montagu). Hayward & Hollis 1994, pl.2, figs.10,11.
Trochammina macrescens Brady. Hayward & Hollis 1994, pl.2, figs.7–9.
Trochammina sorosa (Parr). Hayward & Triggs 1994, pl.1, figs.12,13.
Trochamminita salsa (Cushman & Brönnimann). Hayward & Hollis 1994, pl.2, figs.12–14.

Suborder Miliolina

Cornuspira involvens (Reuss). Hedley et al. 1967, text-fig.16.
Quinqueloculina seminula (Linnaeus). Hayward & Triggs 1994, pl.1, fig.16.

Suborder Lagenina

Fissurina lucida (Williamson). Hayward & Triggs 1994, fig. 3, no.17.

Suborder Rotaliina

Ammonia beccarii (Linnaeus) s.l. Hayward & Hollis 1994, pl.4, figs.1–6.
Bolivina neocompacta McCulloch 1981, pl.45, figs.3,7.
Buccella pustulosa Albani. Hayward & Hollis 1994, pl.3, figs.11–13 (as *B. frigida*).
Bulimina elongata d'Orbigny. Jones 1994, pl.51, figs.1,2.
Bulimina marginata d'Orbigny s.l. Hayward & Grenfell 1994, fig.16.
Cassidulina carinata Silvestri. Hayward 1982, fig.6l.
Cibicides marlboroughensis Vella. Hayward 1982, figs.5r,s.
Elphidium advenum (Cushman) s.l. Hayward et al. 1997b, pl.2, figs.9–18, pl.3, figs.9–17, pl.4, figs.11–16.
Elphidium charlottense (Vella). Hayward et al. 1997b, pl.6, figs.13–16, pl.7, figs.1,2.
Elphidium excavatum (Terquem) s.l. Hayward & Hollis 1994, pl.5, figs.1–12.
Elphidium gunteri Cole s.l. Hayward & Hollis 1994, pl.4, figs.10–12.
Haynesina depressula (Walker & Jacob). Hayward & Hollis 1994, pl.5, figs.13–16.
Helenina anderseni (Warren). Hayward & Hollis 1994, pl.3, figs.14–16.
Nonionellina flemingi (Vella 1957), pl.9, figs.183,184 (as *Nonion*).
Nonionoides turgida (Williamson). Jones 1994, pl.109, figs.17–19 (as *Nonionella*).
Notorotalia sp.
Pileolina zealandica Vella. Hayward 1982, figs.5l,m.
Rosalina sp.
Spiroloxostoma glabra (Millett). Hayward & Triggs 1994, fig.4, no.3.
Zeaflorilus parri (Cushman). Hayward et al. 1996, pl.2, figs.14,15,19.

Arcellaceans

Centropyxis aculeata (Ehrenberg). Scott et al. 1991, pl.1, figs.7–9.
Centropyxis constricta (Ehrenberg). Scott et al. 1991, pl.1, fig.4.
Difflugia capreolata Penard. Scott et al. 1980, pl.1, figs.4–7.
Difflugia globulus (Ehrenberg). Cash & Hopkinson 1909, pl.21, figs.5–9.

Planktic species

Globigerina falconensis Blow. Hayward 1983, figs.2I–K.
Globigerina quinqueloba Natland. Hayward 1983, figs.2O–Q.