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Biogeography and ecological distribution of shallow-water benthic foraminifera from the Auckland and Campbell Islands, subantarctic southwest Pacific

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ABSTRACT – One hundred and forty-eight species of benthic foraminifera are recorded from depths shallower than 80 m around the subantarctic Auckland (130 spp.) and Campbell (71 spp.) Islands, southwest Pacific. Comparisons with other circum-polar, subantarctic island groups suggest that they all have relatively low diversity, shallow-water benthic, foraminiferal faunas, with their sheltered harbours dominated by species of *Elphidium*, *Notorotalia*, *Cassidulina*, *Haynesina* and *Nonionella-Nonionellina*. More exposed environments are dominated by a small number of species of *Cibicides*, *Miliolinella*, *Rosalina*, *Quinqueloculina* and Glabratellidae. The extremely low species richness (three species) in high-tidal grass-dominated salt marsh on Campbell Island is similar to that reported from Tierra del Fuego at a similar latitude. The faunas of Auckland and Campbell Islands have their strongest affinities (70–75% species in common) with New Zealand's three main islands, 460–700 km away. Ten percent of their fauna has not been recorded from mainland New Zealand, reflecting one endemic species and a small element of apparently subantarctic and bipolar-restricted species. Since there have been no shallow-water (<500 m) links to other lands since these two Miocene volcanic islands were formed, it is concluded that most benthic foraminiferal species have arrived in suspension in eddies of surface water, many since the peak of the Last Glacial. *J. Micropalaeontol*. **26**(2): 127–143, October 2007.

KEYWORDS: *subantarctic islands, Auckland Islands, Campbell Island, shallow-water benthic foraminifera, biogeography*

INTRODUCTION

Location and setting

The uninhabited Auckland (50° 45′ S, 166° E) and Campbell (52° 30′ S, 169° E) Islands are the southern-most land areas within New Zealand's Exclusive Economic Zone in the southern SW Pacific Ocean (Fig. 1). Auckland Islands (626 km^2) and Campbell Island (113 km^2) are separated from New Zealand's South Island by 460 km and 700 km, respectively (Peat, 2003). Both are the partly eroded remnants of Miocene basalt shield volcanoes sitting on uplifted basement and oceanic sedimentary rocks (Cook, 1981) that form seamounts sitting above the 500 m background average depth of the Campbell Plateau.

During the Pleistocene, glaciers flowed down radiating stream valleys on both island groups and eroded out wide 'U-shaped' profiles. Most of these valleys were flooded by rising sea-level during each interglacial, forming long, deep (up to 70 m) inlets and harbours (Fig. 1). The Auckland Islands have a coastal fringe of low rata (*Metrosideros*) forest that passes upwards into dense scrub. Campbell Island has *Dracophyllum* scrub and grassland extending down to the shore (Peat, 2003). The average rainfall on both islands is 1000–1500 cm, with precipitation averaging 325 days each year on Campbell Island (Peat, 2003). Much of this rain soaks into the peaty soil beneath the forest or scrub and flows out through the intertidal zone as acidic, tannin-stained seepage.

Mean annual sea surface temperature range is 7–11 °C at the Auckland Islands and 1.5–2 °C cooler at Campbell Island. Both island groups are today surrounded by Subantarctic Surface Water within weaker parts of the northeast-flowing Subantarctic Current (Fig. 1), between the Subtropical Front and Subantarctic Front (Carter *et al*., 1998).

Previous work and source of samples studied

The Auckland and Campbell Islands groups were first discovered by Europeans (fur sealers) in 1806 and 1810, respectively (McNab, 1909) and, since then, many scientific expeditions have visited them and collected shallow-marine biological samples (summarized in Chilton, 1909; Hayward & Morley, 2005). From the late 1870s until the early twentieth century, New Zealand government steamers made regular visits to both island groups to check for castaways. Natural scientists sometimes joined these trips and their collections and observations added to knowledge of the subantarctic biota (e.g. Hutton, 1879). On one of these trips in 1897, several samples of seafloor sediment were dredged from depths shallower than 20 m near Enderby Island (Auckland Islands) and Campbell Island. These samples were washed and floated by New Zealand amateur microscopist R. L. Mestayer, who made numerous slides of qualitative picks of foraminifera (F201105, F201106, F201107, F201108), mostly unilocular forms (now held in the collections of the Institute of Geological and Nuclear Sciences, Lower Hutt).

The only previous work devoted entirely to the foraminifera of New Zealand's Subantarctic Islands has been by Australian micropalaeontologist, Frederick Chapman (1909). He provided extensive documentation of the species' composition (168 taxa) of five sediment samples dredged during the 1907 scientific expedition by the Philosophical Institute of Canterbury (Chilton, 1909). Four of the samples were from outer-shelf depths (100–170 m) offshore from Auckland, Enderby, Snares and Bounty Islands and one sample was from sheltered harbour waters (16 m, Perseverance Harbour, Campbell Island). Chapman described and named six new species or varieties (Table 1), all of which came from the deeper samples off Enderby and the Snares Islands. He also identified ten species in the shallow-water sample from Campbell Island (Table 2).

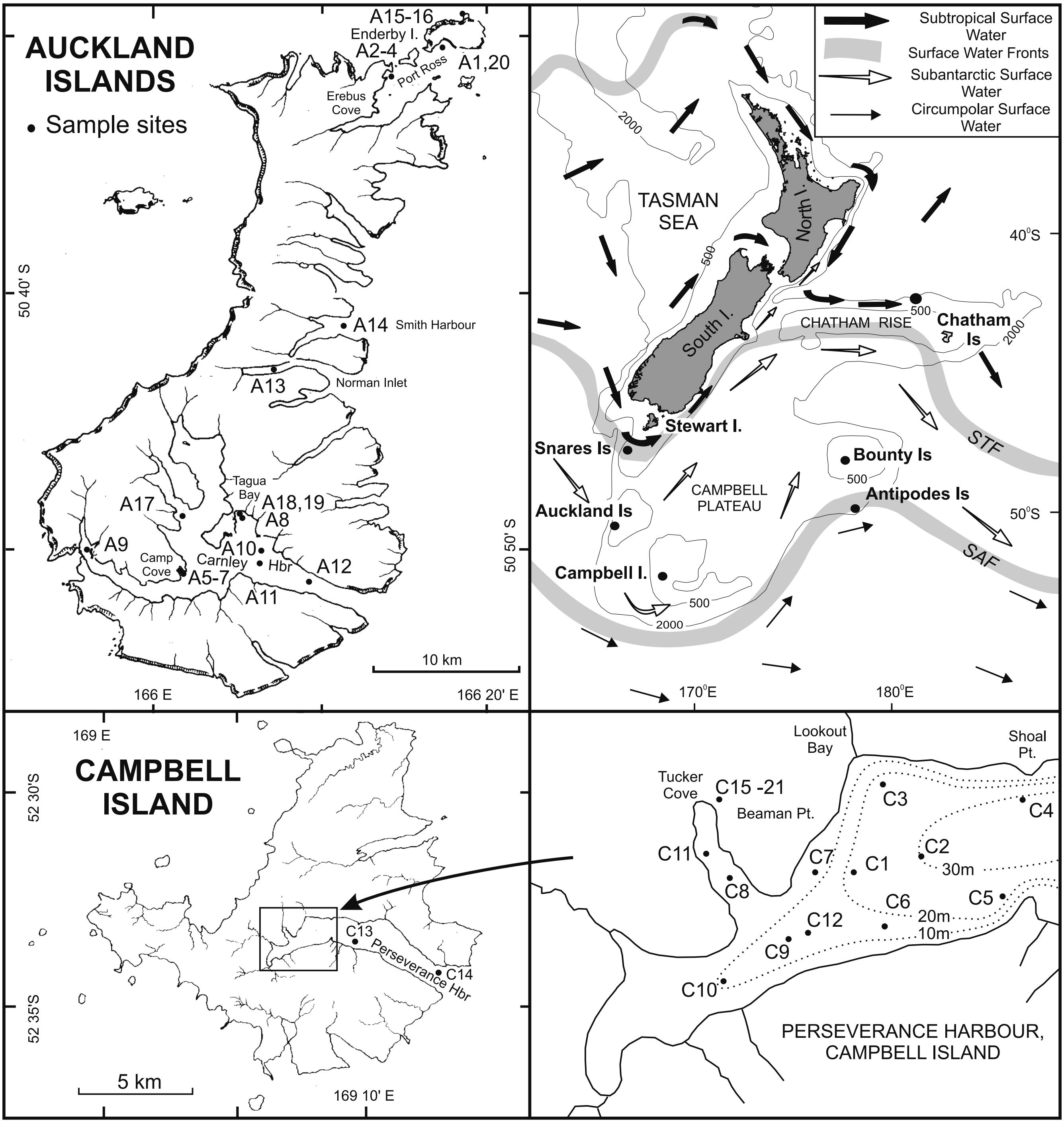

Fig. 1. Location of the Auckland and Campbell Islands southeast of New Zealand, also showing surface current directions and oceanic fronts. Sample locations around Auckland and Campbell Islands. SAF, Subantarctic Front; STF, Subtropical Front.

Marjorie (M. K.) Mestayer, conchologist at the Dominion Museum (Wellington), obtained sediment from *c.* 50 m depth at the Auckland Islands in the 1910s and donated some with its molluscs to Baden (A. W. B.) Powell at Auckland Museum (L13513, F201015). In the 1940s, several natural scientists were stationed on the Auckland Islands to watch for enemy warships (Peat, 2003) and, during their time there, Charles (C. A.) Fleming, Bill (W. H.) Dawbin and Jack (J. H.) Sorenson all took small dredge samples of sediment from Carnley Harbour. These samples, and slides of foraminifera picked from them, were deposited in the collections of the New Zealand Geological Survey (where Fleming was employed as a palaeontologist; F201102, F201162) and Auckland Museum (L6184, L13574). In his study of New Zealand ostracods (including the Auckland Islands), Norcott Hornibrook (1953) used M. K. Mestayer, Fleming and Sorenson material (above), and Paul Vella (1957)

Original name	Author, year	Type location	Name accepted in this study
Miliolina chrysostoma	Chapman, 1909	off Enderby Island, Auckland Islands	*Triloculina chrysostoma*
Planispirinina antarctica	Chapman, 1909	off Enderby Island, Auckland Islands	
Lagena lagenoides var. *nuda*	Chapman, 1909	off Enderby Island, Auckland Islands	
Lagena quadrata var. *carinata*	Chapman, 1909	off Snares Islands	
Lagena enderbiensis	Chapman, 1909	off Enderby Island, Auckland Islands	
Spirillina novaezealandiae	Chapman, 1909	off Snares Islands	*Spirillina novaezealandiae*
Notorotalia aucklandica	Vella, 1957	Carnley Harbour, Auckland Islands	*Notorotalia aucklandica*
Nonion flemingi	Vella, 1957	Carnley Harbour, Auckland Islands	*Nonionellina flemingi*
Elphidiononion simplex aoteanum	Vella, 1957	Carnley Harbour, Auckland Islands	*Haynesina depressula*
Siphotextularia mestayerae	Vella, 1957	Auckland Islands	*Siphotextularia mestayerae*
Textularia subantarctica	Vella, 1957	Auckland Islands	*Textularia subantarctica*

Table 1. Species of foraminifera described as new from material collected around New Zealand's Subantarctic Islands.

Original name and authority	Recorded by	Location	Name accepted in this study
Rhizammina indivisa	Chapman, 1909	Campbell Island	*Rhizammina algaeformis*
Reophax scorpiurus	Chapman, 1909	Campbell Island	*Reophax subfusiformis*
Reophax nodulosa	Chapman, 1909	Campbell Island	*Reophax nodulosa*
Uvigerina angulosa	Chapman, 1909	Campbell Island	*Trifarina angulosa*
Sphaeroidina bulloides	Chapman, 1909	Campbell Island	*Sphaeroidina bulloides*
Truncatulina variabilis	Chapman, 1909	Campbell Island	*Cibicides dispars*
Anomalina coronata	Chapman, 1909	Campbell Island	*Discanomalina coronata*
Rotalia clathrata	Chapman, 1909	Campbell Island	*Notorotalia aucklandica*
Nonionina boueana	Chapman, 1909	Campbell Island	*Nonionellina flemingi*
Polystomella macella	Chapman, 1909	Campbell Island	*Elphidium advenum limbatum*

Table 2. Species of foraminifera previously recorded from inner shelf depths (0–50 m) around the Auckland and Campbell Islands.

described five new species of foraminifera from the Fleming and M. K. Mestayer samples (Table 1). Many of the old qualitative foraminiferal slides from R. L. Mestayer, M. K. Mestayer, Fleming and Dawbin have been examined during this study, with additional taxa, especially unilocular, being added to the species list (Appendix A).

Recently, the deep-water foraminiferal faunas (deeper than 50 m) have been described and mapped for the Campbell Plateau and surrounding region, including mid- and outer-shelf depths (>50 m) around Auckland and Campbell Islands (Hayward *et al*., 2007).

Objectives

The main objective of this study is to document more fully the foraminiferal biodiversity of these distant subantarctic islands, compare their faunal composition with that of mainland New Zealand (Hayward *et al*., 1999) and other islands in the subantarctic zone around the world (e.g. Heron-Allen & Earland, 1932; Earland, 1933, 1935; Parr, 1950). From these studies it is hoped to provide a better idea of foraminiferal biogeography in the SW Pacific and Southern Ocean and infer modes of dispersal.

Unilocular species

One complicating factor in this study is the highly variable richness and diversity of unilocular lagenid species that sometimes occur in huge numbers in shallow-water subantarctic samples. It is suspected that many of these small, low density species may have been winnowed out of deeper-water sediments and transported into the shallows in suspension (e.g. Murray *et al*., 1982) and thus do not accurately represent the true living biodiversity near the islands. Because of this, the unilocular records have been removed from species lists before making comparisons between regions.

MATERIAL AND METHODS

Samples

Most sediment samples used in this study (Fig. 1, Appendix B) were taken by BWH during a visit to the two island groups in March, 2004. Subtidal seafloor samples were taken by a hand-hauled surficial grab or small box dredge, which tended to sample the upper 5–7 cm of surface sediment. Intertidally a 10 cm^3 sample of the upper 1 cm of surface sediment was taken with a plastic tube. This set of samples was supplemented by older samples held in the collections of the Auckland War Memorial Museum, and the Institute of Geological and Nuclear Sciences, Lower Hutt (above). Some of these samples consisted entirely of a rich qualitative pick of foraminifera, but, where washed bulk sediment was also present, a new quantitative pick of the foraminiferal fauna was made to produce the total species list (Appendix A). There was no opportunity to distinguish living from dead shells through staining.

Faunal slides (Appendix B) are housed in the collections of the University of Auckland, Auckland War Memorial Museum and Institute of Geological and Nuclear Sciences, Lower Hutt (prefixed by AU, L, and F20, respectively). Census data are available digitally as Appendix C (available online at http://www.geolsoc.org.uk/SUP18275. A hard copy can be obtained from the Geological Society Library).

Laboratory processing

Samples were washed gently over a 63 µm sieve, and the sand residue dried and microsplit down to an amount containing approximately 200 benthic specimens. All benthic foraminifera were picked from the microsplit, mounted on faunal slides, identified and counted (Appendix C). All taxa were identified to species level. Specimens of planktic foraminifera were counted during picking. Some of the samples from the harbours that were rich in small (63–150 µm) specimens which may have been transported in, were dry sieved over a 150 µm sieve and additional picks of this coarse fraction were made (samples with 'c' suffix).

Statistical analyses and diversity measures

Quantitative samples (>63 µm) selected for statistical analysis comprised 16 from Auckland Islands and 21 from Campbell Island – seven Campbell and two Auckland Islands samples were intertidal. Three Auckland and 12 Campbell Islands coarse samples (>150 µm) were also included. Thus the quantitative faunal data consist of census counts of 93 foraminiferal species from 52 samples. The data matrix was transformed by converting counts to percentages of sample totals. A Q-mode cluster analysis dendrogram classification was produced using a Chord dissimilarity coefficient matrix. The mathematical definition of this coefficient is given in Sneath & Sokal (1973).

Detrended canonical correspondence analysis (DCCA, Ter Braak, 1985) was used to summarize the percentage faunal data in a two-dimensional ordination plot and relate them to a set of measured environmental and diversity factors (Appendix B). Three indices of benthic foraminiferal species diversity (Appendix B) were determined (Hayek & Buzas, 1997): (1) Fisher Alpha Index, α (number of species standardized by number of individuals counted); (2) Information Function, H (a combination of the number of species present and, to a lesser extent, the evenness of species counts); and (3) Evenness, E (a measure of dominance versus evenness of species counts).

TAXONOMIC COMPOSITION OF THE SUBANTARCTIC FAUNA

Species richness

A total of 148 species of benthic foraminifera, including unilocular species, are recorded here from the Auckland (130 spp.) and Campbell (71 spp.) Islands (Fig. 2). If unilocular species are excluded, there are 113 species from these two groups (Auckland – 96 spp., Campbell – 64 spp.). This number of species (without uniloculars) is of a similar order to the 53 spp. recorded from around Snares Islands (Hayward *et al.*, 1999) and the 102 spp. from the Chatham Islands (Fig. 2; Hayward & Grenfell, 1999).

As happens elsewhere in the world (Gibson & Buzas, 1973; Murray, 1991) there is a decrease in total benthic foraminiferal species richness in shallow water, from warm to cool through the 18° of latitude of the New Zealand region (Fig. 2).

Comparisons between Auckland and Campbell Islands

The main difference between their benthic foraminifera is the greater diversity recorded from Auckland Islands (130 spp.) compared with Campbell Island (71 spp.), partly as a result of the greater variety of habitats sampled and partly because of the

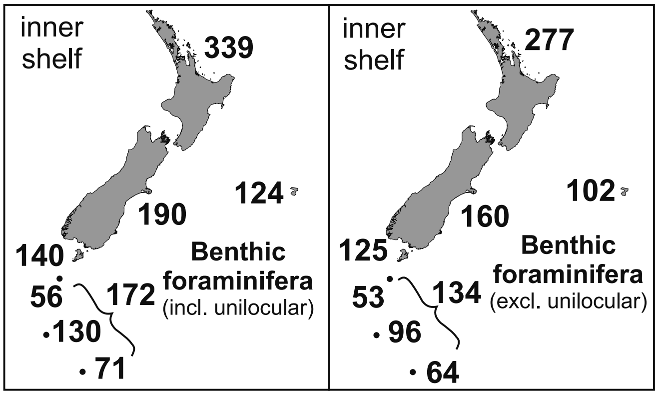

Fig. 2. Number of species of shallow-water (<100 m) benthic foraminifera (with and without unilocular taxa) from around northeast North, South, Stewart, Chatham, Snares, Auckland and Campbell Islands.

rich unilocular fauna present in several historic collections (unilocular species from Auckland Islands=31; from Campbell Island=7). Among the more common New Zealand-wide species that are present at Auckland Islands but absent from the more distant Campbell Island are *Scherochorella moniliforme*, *Trochammina inflata*, *Patellina corrugata*, *Rosalina vitrevoluta* and four species of *Quinqueloculina*. Within the harbours the most noteworthy difference is the abundance of *Nonionellina flemingi* and, to a lesser degree, *Haynesina depressula* at Auckland Islands, and their near absence from Campbell Island. The harbours in both groups have almost identical diversity, with 61–63 species each in the quantitative samples and, apart from the two species already mentioned, they share the same suite of dominant species. Lack of sampling of salt marsh or brackish environments in the Auckland Islands prevents comparisons between the agglutinated faunas, and the lack of sampling of high energy, shallow-water environments at Campbell Island prevents comparison between faunas characteristic of these.

Taxa restricted to the Subantarctic in the New Zealand region

Here we record fourteen species (other than unilocular) that have not previously been recorded from elsewhere in the New Zealand region – eight from the Auckland Islands, two from Campbell Island and four from both. There are several additional species (*Discanomalina coronata*, *Lagenammina difflugiformis*, *Rhizammina algaeformis*, *Siphogenerina dimorpha*) that have been recorded occasionally from bathyal and abyssal depths elsewhere in the region but are here recorded from shallower than 80 m at both island groups. A similar phenomenon is known from the shelf around Antarctica, where a number of species occur that are restricted to deeper water in lower latitudes (Mikhalevich, 2004).

Haplophragmoides manilaensis – this large agglutinated species with inflated chambers (Pl. 1, figs 1–2) occurs widely in salt marshes around the world. It was described from subtropical conditions in the Gulf of Mexico, but has also been recorded from subantarctic marshes as far south as Tierra del Fuego (Scott *et al.*, 1990).

Labrospira spiculolega –This distinctive species (Pl. 1, figs 3–4) was described from 120–160 m depth, south of Tasmania (Parr, 1950) and is here recorded from inner-shelf depths at

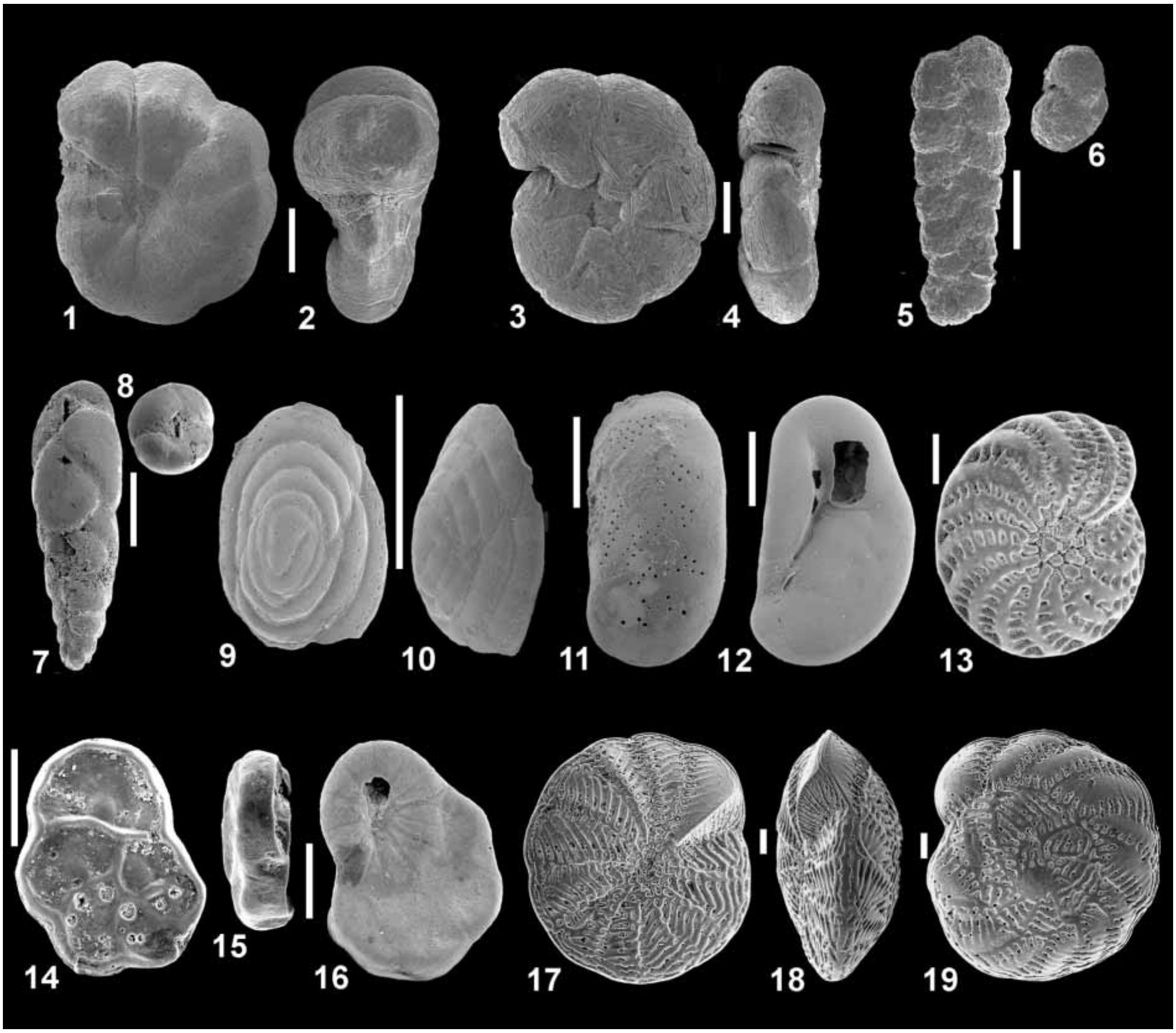

Plate 1.

Explanation of Plate 1. Some common and distinctive benthic foraminifera from southwest Pacific subantarctic islands. Scale bar 0.1 mm. **figs 1–2.** *Haplophragmoides manilaensis* Andersen, 1953. BWH163/24, AU18127, Campbell Island intertidal MHWN. **figs 3–4.** *Labrospira spiculolega* (Parr, 1950). BWH 169/11, F201106, Auckland Islands 12 m. **figs 5–6.** *Spiroplectammina biformis* (Parker & Jones, 1865). BWH 168/14, AU18124, Campbell Island intertidal MHW. Apertural view is slightly oblique. **figs 7–8.** *Verneuilinulla advena* (Cushman, 1922). BWH168/22, F201106, Auckland Islands 12 m. **figs 9–10.** *Patellinoides conica* Heron-Allen & Earland, 1932. BWH169/12, F202511, Auckland Islands 80 m. Peripheral view is slightly oblique. **fig. 11.** *Cerobertina tenuis* (Chapman & Parr, 1937). BWH 169/15, F201106, Auckland Islands 12 m. **fig. 12.** *Cerobertina tenuis* (Chapman & Parr, 1937). BWH 169/16, F201106, Auckland Islands 12 m. **fig. 13.** *Elphidium advenum* f. *limbatum* (Chapman, 1907). FP4320, F201106, Auckland Islands 12 m. **fig. 14.** *Heronallenia lingulata* (Burrows & Holland, 1895). BWH 125/17, F202072, Snares Islands 100 m. **figs 15–16.** *Heronallenia lingulata* (Burrows & Holland, 1895). BWH 125/16, F202072, Snares Islands 100 m. **fig. 17.** *Notorotalia aucklandica* Vella, 1957. Topotype BWH 131/8, F201002, Auckland Islands 12 m. **figs 18–19.** *Notorotalia aucklandica* Vella, 1957. Topotype BWH 131/8, F201002, Auckland Islands 12 m.

the Auckland Islands. It may be endemic to shelf depths in the subantarctic region of the SW Pacific.

Spiroplectammina biformis (Pl. 1, figs 5–6) – appears to be a widespread, shallow-water, higher-latitude, Northern Hemisphere species (Murray, 1991) with a few rare records from higher latitudes in the Southern Hemisphere. Its type locality is in 100 m of water off Greenland (Parker & Jones, 1865) and it is widespread around the Gulf of St Lawrence (e.g. Schafer & Cole, 1982) and in Scandinavian fiords (e.g. Alve & Nagy, 1986; Hanslik & Nordberg, 2006). It also occurs in higher latitudes in the North Pacific (Murray, 1991) and at King George Island, South Shetland Islands (Gaździcki & Majewski, 2003; Majewski, 2005) in the Southern Hemisphere.

Verneuilinulla advena (Pl. 1, figs 7–8) – this small agglutinated species appears to occur in shallow sheltered environments at high latitudes in both hemispheres, with its types from 10–40 m in Hudson Bay, Canada (Cushman, 1922). It has been recorded from abyssal depths at low latitudes (Loeblich & Tappan, 1994).

Spirillina obconica – this uncommon species has been recorded from off northern Europe and Florida in the Northern

Hemisphere and from 100–300 m depth off the subantarctic Prince Edward and Kerguelen Islands (Brady, 1884).

Laryngosigma williamsoni – this species was described from off the coast of the UK (Terquem, 1878) and has been recorded from a number of European localities.

Neolingulina viejoensis – this rare, distinctive species has been recorded previously from 40–50 m depth off Peru and Korea (McCulloch, 1977). It probably is more widespread and under-reported.

Pseudolingulina bradii – an uncommon but distinctive species, described from Indonesia, and also recorded from Hawaii, and 80–1000 m in the South Atlantic (Brady, 1884).

Cerobertina tenuis (Pl. 1, figs 11–12) – this appears to be a southern, high-latitude species, with its type locality in upper abyssal depths (2600 m) between Australia and the Auckland Islands (Chapman & Parr, 1937).

Bolivina translucens – this is a cosmopolitan species that is often identified under several other names.

Fursenkoina cf. *riggi* – this small distinctive and uncommon species may be restricted to the subantarctic, having been described from the Gulf of San Gorge, southern Argentina (Boltovskoy, 1954) and recorded from Isla de los Estados (Thompson, 1978).

Notorotalia aucklandica (Pl. 1, figs 17–19) – appears to be endemic to the Auckland and Campbell Islands. It is morphologically most similar to several New Zealand species of *Notorotalia* from which it presumably evolved (Vella, 1957).

Patellinoides conica (Pl. 1, figs 9–10) – this species occurs in mid- to high latitudes in the North and South Atlantic, and was described from the subantarctic region, near the Falkland Islands (e.g. Heron-Allen & Earland, 1932).

Heronallenia lingulata – around New Zealand, this small species (Pl. 1, figs 14–16) is restricted to subantarctic Auckland and Campbell Islands plus the Snares Islands. It appears to have a scattered cosmopolitan distribution in deeper water, but occurs in relatively shallow water of higher latitudes in the SW Pacific and southern Australia (e.g. Brady, 1884). A similar distribution is displayed by *H. unguiculata* which occurs in shallow water at the Auckland and Campbell Islands but at depths >200 m off northern New Zealand (Heron-Allen & Earland, 1922) and northeast Australia (Sidebottom, 1918).

New Zealand taxa absent from the subantarctic. Notable by their absence from New Zealand's subantarctic islands are a number of species that are common or abundant in shallow water around mainland New Zealand (Hayward *et al*., 1999). These include a number of the brackish and high tidal agglutinated species (e.g. *Ammobaculites exiguus*, *Ammoscalaria tenuimargo*, *Ammotium fragile*, *Jadammina macrescens*, *Miliammina obliqua*, *Trochamminita salsa*), with 13–14 species occurring around the two main islands and a combined total of nine at the subantarctic islands (Fig. 3). The abundant shallow-water genus *Elphidium* is represented by only one species at Auckland and Campbell Islands and two additional species at the Snares, whereas nine species are present at the South Island and 11 off northeast North Island (Fig. 3). In the related genus *Notorotalia*, five species occur around the main islands, but only two in the subantarctic (including the subantarctic endemic *N. aucklandica*). Similarly, nine species of Glabratellidae occur off northeast North Island but only four occur in the subantarctic (Fig. 3) – mostly absent are species of *Pileolina*. The same pattern also occurs in the shallow-water Rosalinidae and the genus *Quinqueloculina* (Fig. 3). Other notable absences from the subantarctic are New Zealand's most common foraminiferal genus in sheltered harbour settings (Hayward *et al*., 1999), *Ammonia*, and several of the most abundant open-marine species, *Gaudryina convexa*, *Patellinella inconspicua* and *Trochulina dimidiatus*.

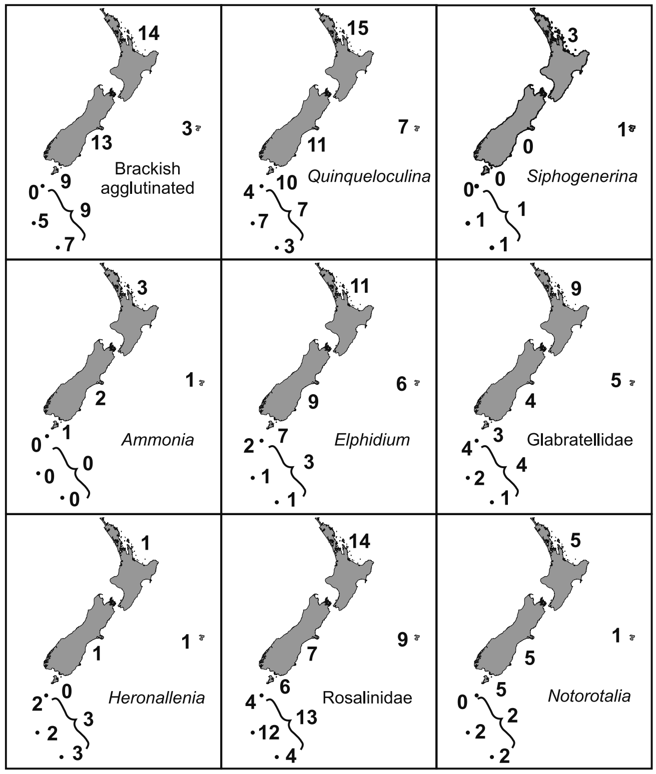

Fig. 3. Number of species in selected genera and families of shallow-water (<100 m) benthic foraminifera from around northeast North, South, Stewart, Chatham, Snares, Auckland and Campbell Islands.

A different pattern emerges in the shallow-water members of the Rosalinidae, with similar levels of species richness (13–14 spp.) off northeast North Island and in the subantarctic (Fig. 3).

Affinities with shallow-water foraminifera of the New Zealand region

Auckland and Campbell Islands have 68–76% of their benthic foraminifera (excluding uniloculars) in common with the South Island and northeast North Island (Table 3). In contrast, a smaller percentage (52–59%) live around the nearer, but smaller, Chatham and Stewart Islands and just 31–32% have been recorded around the Snares Islands (Table 3). An explanation for the low levels of co-occurrence with the Snares is probably the lack of sheltered, harbour or brackish environments there. Explanations for the lower level of co-occurrence with Stewart and Chatham Islands are more difficult. It may reflect the lower number of samples and environments examined around these two island groups.

Of most significance is the observation that 94–98% of the Snares fauna co-occurs around the South and North Islands.

	Campbell Island	Auckland Islands	Snares Islands	Stewart Island	Chatham Islands	South Island	NE North Island	Total no. of spp.
Campbell Island	100	73	32	59	57	68	71	64
Auckland Islands	47	100	31	55	52	74	76	96
Snares Islands	38	55	100	75	74	94	98	53
Subantarctic Islands	47	71	40	53	49	74	77	134

Table 3. Percentage of the benthic foraminiferal fauna (excluding unilocular spp.) of subantarctic Campbell, Auckland and Snares Islands (separately and jointly) in common with other parts of the New Zealand region.

This reflects the fact that only one Snares species (*Heronallenia lingulata*) is restricted to the subantarctic islands, whereas the more distant Auckland and Campbell Islands have 13 species not found further north in the New Zealand region.

FAUNAL ASSOCIATIONS

From the cluster analysis dendrogram we identified 10 faunal associations (Fig. 4, Table 4). Five associations (1–3, 5, 8) are from Campbell Island and six from the Auckland Islands (4, 6–10), with only one association (8) occurring in both places (Fig. 5). With three exceptions, the clustering separated the coarse faunas (>150 µm) from the total sand range faunas (>63 µm), with the coarse faunas from Auckland Islands (assoc. 6) separated from the Campbell Island ones (assoc. 5). The two total faunas (A3, C11) that cluster with the coarse faunas have minimal fine fraction specimens present, and the same is true for the two total faunas (A5, A8) that cluster with the coarse fauna (A6c) forming association 4.

Agglutinated benthic foraminiferal associations

The first-order subdivision in the dendrogram separates faunas that are dominated by agglutinated species and live in Tucker Cove, Campbell Island (assocs 1–3), from all the remaining faunas, which are dominated by calcareous species. Two of the three agglutinated associations (1, 2) occur in high tidal salt meadow composed entirely of the salt-tolerant grass *Isolepis cernua*. The *Haplophragmoides*-dominated association (2) occurs in a 20 cm wide (tidal elevation) zone around extreme high water spring (EHWS) with the *Miliammina fusca*-dominated association (1) present between EHWS and mean high tide level. These two high tidal associations have the lowest diversity (α=0.5–0.6, H=0.2–0.9) but highest level of evenness (E=0.5–0.8) of all associations.

The third agglutinated association (3) is dominated by *Eggerelloides scaber* and *Textularia earlandi*, with secondary *Paratrochammina bartrami* and *Spiroplectammina biformis* (Fig. 6). This also occurs in Tucker Cove (Fig. 5), but in anoxic organic-rich mud at 4 m depth in the middle of the narrow bay. It has moderate levels of species diversity and evenness (Table 4).

Calcareous benthic foraminiferal associations

A second-order subdivision within the calcareous faunas separates associations 4–8 from 9–10 (Fig. 4). The first of these two groups of associations is restricted in occurrence to the muddy sand and sandy mud on the floor of the relatively sheltered, elongate harbours of Campbell (Perseverance Harbour) and Auckland Islands (Carnley, Norman, Smith Harbours, Port Ross). These associations are dominated by varying combinations and abundances of four species. Association 4 (*Nonionellina flemingi*) occurs in muddy sand at 17–42 m depth in Tagua Bay and Camp Cove (Figs 1, 5) in the cleaner, shallower parts of Carnley Harbour, Auckland Islands. Association 7 (*Cassidulina carinata–Nonionellina flemingi*) is most widespread inside the sheltered deeper (42–80 m), muddier parts of the long Carnley,

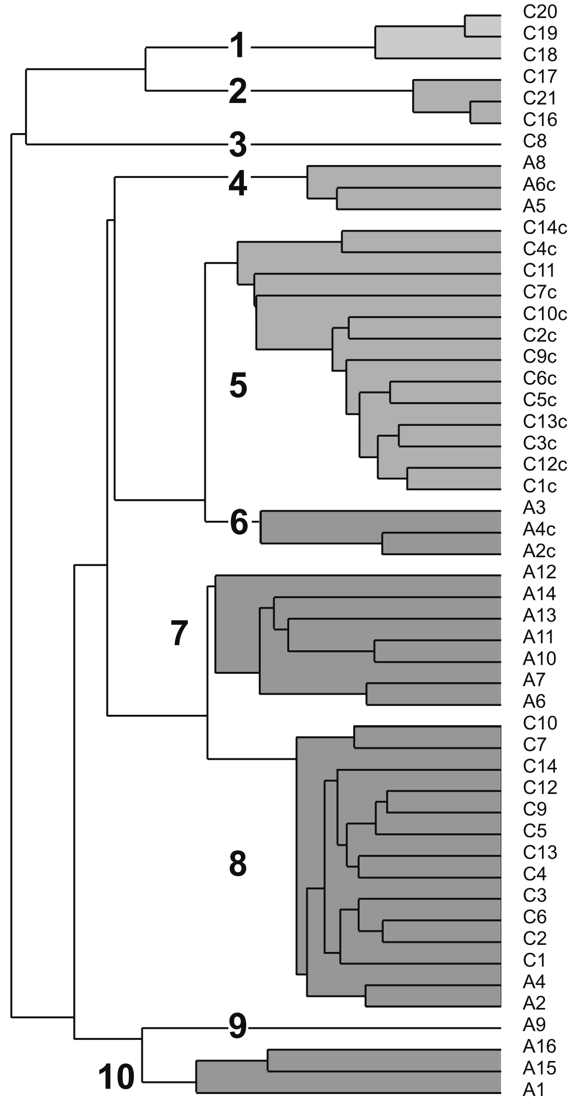

Fig. 4. Dendrogram classifications of shallow-marine foraminiferal sample associations produced by cluster analysis using Chord distance. Associations 1–10 were selected by inspection of the dendrogram.

Ass	Dominant species	Depth (m)	*n*	α	H	E	Islands
1	*Miliammina fusca*	EHWS	3	0.5	0.2	0.50	Campbell
2	*Haplophragmoides manilaensis*, *H. wilberti*	EHWS	3	0.6	0.9	0.80	Campbell
3	*Eggerelloides scaber*, *Textularia earlandi*	4	1	2.3	1.5	0.49	Campbell
4	*Nonionellina flemingi*, *Notorotalia aucklandica*	17–42	3	1.9	1.2	0.40	Auckland
5	*Elphidium advenum*	MT–40	13	2.4	1.0	0.36	Campbell
6	*Notorotalia aucklandica*, *Elphidium advenum*	10–17	3	2.9	1.6	0.44	Auckland
7	*Cassidulina carinata*, *Nonionellina flemingi*	42–80	7	6.9	2.3	0.44	Auckland
8	*Cassidulina carinata*	4–40	14	4.1	1.5	0.29	Auckland, Campbell
9	*Pileolina radiata*	9	1	2.5	1.0	0.24	Auckland
10	*Rosalina irregularis*	0–8	3	4.4	2.0	0.48	Auckland

α, Fisher Alpha Index (number of species standardized by number of individuals counted); H, Information Function (a combination of the number of species present and, to a lesser extent, the evenness of species counts); E, Evenness (a measure of dominance versus evenness of species counts); EHWS, extreme high water spring; MT, mid-tide.

Table 4. Dominant species, depth range, number of stations (*n*), mean of diversity indices (α, H, E) and island distribution of foraminiferal sample associations (Ass).

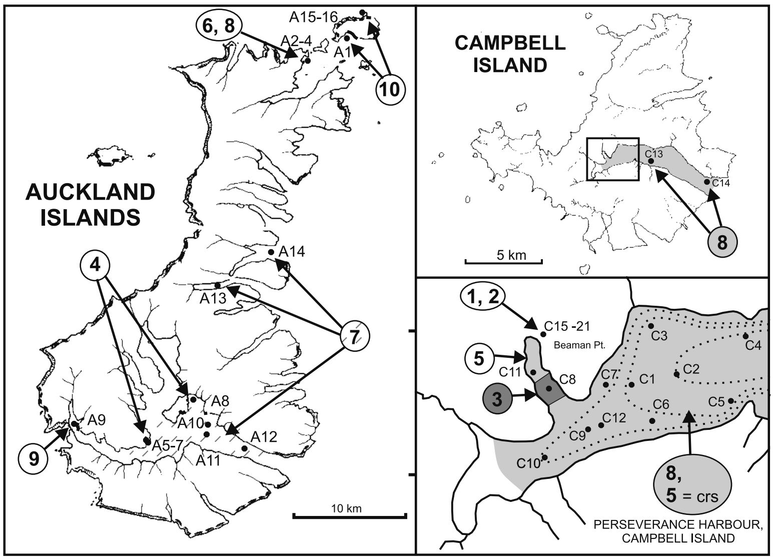

Fig. 5. Distribution of faunal associations produced by cluster analysis (1–10, Fig. 2) in the shallow water around Auckland and Campbell Islands.

Norman and Smith Harbours in the Auckland Islands. This association has subdominant *Sigmoilopsis elliptica*, *Trifarina angulosa* and *Eilohedra vitrea* and has the highest species diversity in the study (α=6.9, H=2.3). Association 6 (*Notorotalia aucklandica*) is limited to the slightly more exposed, shallower (10–17 m) Port Ross, in the northern Auckland Islands.

Association 5 (*Elphidium advenum*) is restricted to Campbell Island and consists of all the coarse faunas throughout Perseverance Harbour, at depths of 4–40 m, plus the total fauna (C11) from mid-tidal level on the muddy sand beach in Tucker Cove (Fig. 5). Association 8 (*Cassidulina carinata*) contains all the total faunas (>63 μm) from the same samples as association 5, plus the total faunas from two samples (A2, A4) at 10–18 m depth in Port Ross, Auckland Islands. The main difference between these two associations is in the relative abundance of small *Cassidulina*, which comprises 40–70% of the total faunas and less than 2% of the coarse faunas and, to a lesser extent, the greater abundance of small *Eilohedra vitrea* in the total faunas.

The second of the two calcareous groups occurs in cleaner sands from more exposed, wave- or current-swept locations around the Auckland Islands. Association 9 (*Pileolina radiata*) is known from one sample at 9 m deep from just inside the western entrance to Carnley Harbour (Fig. 5) where big swells and strong currents sweep over the seafloor. Subdominant are *Quinqueloculina suborbicularis* and *Notorotalia aucklandica.* It has relatively low species diversity and the lowest evenness of all the associations (E=0.24) as a result of the strong dominance by *P. radiata*. Association 10 (*Rosalina irregularis*) occurs in three samples at 0–8 m depth from either side of Enderby Island (Fig. 5). The samples from the north side (A15–A16) are not *in situ* and comprise sand washed up onto the rocks by storms, but are considered representative of the fauna in the shallow subtidal just offshore. Subdominant in this association are *P. radiata*, *Miliolinella subrotundata* and *Quinqueloculina incisa* (Fig. 6).

DISCUSSION

Distribution of benthic foraminiferal associations (Fig. 5)

The DCCA ordination (Fig. 7) shows that there are four separate groups of associations.

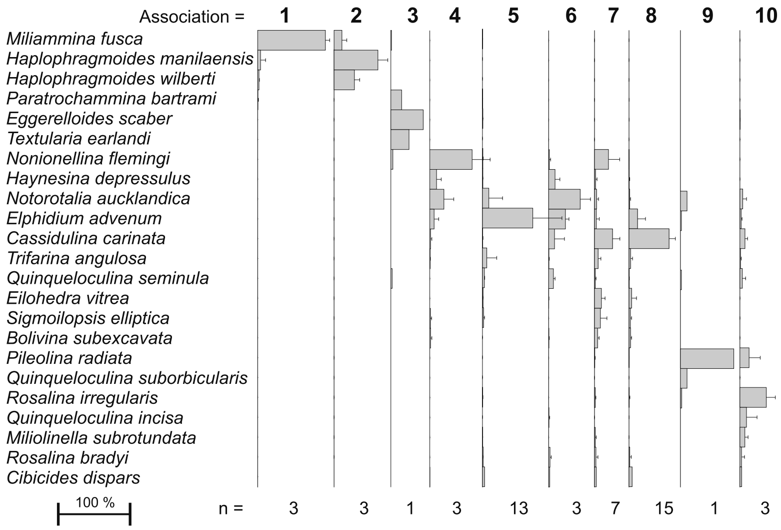

Fig. 6. Mean relative abundance and standard deviation of the characterizing benthic foraminifera (>4% in at least one association) in each faunal association.

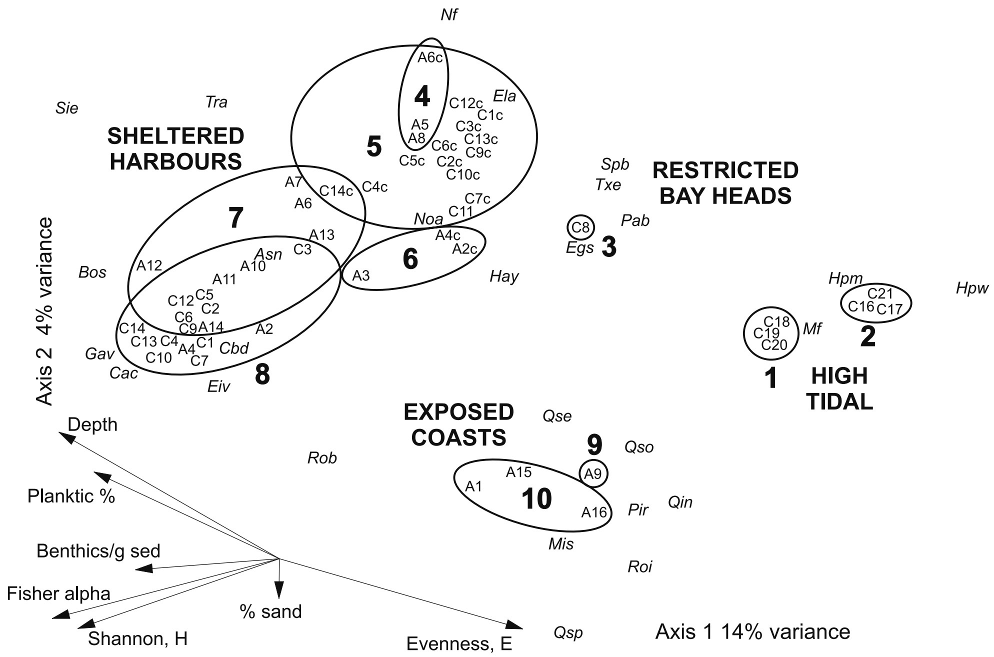

Fig. 7. Two-dimensional ordination of benthic foraminiferal faunal samples from the Auckland (prefixed by A) and Campbell (prefixed by C) islands, produced by Detrended Canonical Correspondence Analysis using the census data of species with >5% relative abundance in at least one sample. The common species (>5% in at least one sample, three-letter abbreviations) are plotted. Vector axes (arrows) show the correlation of faunal distribution patterns with some environmental and diversity factors. The sample associations (1–10) are those identified from the cluster analysis (Fig. 2). Species abbreviations: *Asn*, *Astrononion novozealandicum*; *Bos*, *Bolivina subexcavata*; *Cac*, *Cassidulina carinata*; *Cbd*, *Cibicides bradyi*; *Egs*, *Eggerelloides scaber*; *Eiv*, *Eilohedra vitrea*; *Ela*, *Elphidium advenum*; *Gav*, *Gavelinopsis praegeri*; *Hay*, *Haynesina depressula*; *Hpm*, *Haplophragmoides manilaensis*; *Hpw*, *Haplophragmoides wilberti*; *Mis*, *Miliolinella subrotundata*; *Nf*, *Nonionellina flemingi*; *Noa*, *Notorotalia aucklandica*; *Pab*, *Paratrochammina bartrami*; *Pir*, *Pileolina radita*; *Qin*, *Quinqueloculina incise*; *Qse*, *Quinqueloculina seminula*; *Qso*, *Quinqueloculina suborbicularis*; *Qsp*, *Quinqueloculina subpolygona*; *Rob*, *Rosalina bradyi*; *Roi*, *Rosalina irregularis*; *Sie*, *Sigmoilopsis elliptica*; *Spb*, *Spiroplectammina biformis*; *Tra*, *Trifarina angulosa*; *Txe*, *Textularia earlandi*.

1. High tidal. In common with other tropical–subpolar regions, high tidal salt marsh and salt meadow environments are dominated by agglutinated foraminiferal associations (1, 2), whereas most other shelf and bathyal environments have calcareous-dominated faunas (e.g. Murray, 1991; Hayward *et al*., 1999). Although agglutinated associations are recorded here only from the head of Perseverance Harbour, Campbell Island, similar high tidal environments were not sampled on the Auckland Islands and they will undoubtedly be present there.
2. Restricted bay head. This shallow subtidal association (3) is unusual and unique in the New Zealand region, where

subtidal substrates dominated by agglutinated foraminifera (usually *M. fusca* and *Trochamminita salsa*) are restricted to low salinity environments at the head of estuaries (Hayward *et al*., 1999). Here in Tucker Cove at the head of Perseverance Harbour there is sometimes a thin low salinity surface layer, but subtidally salinity is only slightly lower than normal marine values. Here the water is commonly tannin-coloured from all the freshwater seepage from the peat soils and the sediment on the subtidal floor of the cove is chocolate brown and anaerobic. Anaerobic, acidic conditions are inferred, which might favour this agglutinated assemblage and dissolve the shells of any calcareous taxa. Partly dissolved shells are frequently encountered in other samples in Perseverance Harbour.

3. Exposed coasts. The two associations (9–10) which occur in relatively shallow, wave- and current-swept, sandy environments around the Auckland Islands have distinctively different faunal compositions than the other associations (Figs. 6, 7). Although not recorded from Campbell Island, they may be present there as no samples were available for study from similar environments around this island.
4. Sheltered harbours. Five calcareous-dominated associations (4–8) occur within the glacially incised harbours of the two island groups. All share in common the presence of *Elphidium advenum* and *Notorotalia aucklandica*, but the common co-occurrence of *Nonionellina flemingi* separates out associations 4 and 7, which are confined to the more sheltered southern and central harbours of the Auckland Islands at depths of 17–80 m. The faunas in muddy sand at 0–40 m depth in Perseverance Harbour, Campbell Island (associations 5, 8) differ from those in similar environments in the Auckland Islands by the abundance of *Cassidulina carinata* (faunas >63 μm) or *E. advenum* (>150 μm). In the relatively shallow depths (10–17 m) near the more exposed mouth of Port Ross, northern Auckland Islands, *N. aucklandica* reaches its greatest relative abundance and characterizes the separate association 6 (Fig. 6).

The vectors on the DCCA ordination (Fig. 7) indicate a strong correlation of the distribution of faunal assemblages and species with depth (long vector arrow), with depth increasing from bottom right to top left. This trend parallels the expected increase in planktic foraminiferal percentage with increasing distance from shore (Hayward *et al*., 1999) and also an unusual trend of decreasing evenness (E) in faunal structure. Both species richness and absolute abundance of benthic foraminifera (specimens g^{-1} sediment) show an increasing trend with increasing water depth (Fig. 7). The short vector for sand percentage indicates that grain size has little influence on faunal composition.

In situ versus transported specimens

Most faunas picked from the coarser fraction (>150 μm) cluster separately (assocs 5, 6) from the faunas from the total sand fraction (>63 μm). The coarse fraction faunas have lower species richness (mean α=2.4–2.9) than the total faunas (mean α=4.1–6.9) but all have a similar range of dominance and evenness (Table 4). Thus, the main difference between the two size fractions is the additional presence in the total faunas of numerous small, low density shells of *C. carinata*, *E. vitrea*, *S. elliptica*, *Bolivina* and a diversity of unilocular species. Do these small specimens live *in situ* in these sheltered harbour settings, or have they been winnowed out of seafloor sediment by strong currents or large Southern Ocean swells outside the harbour and transported into the harbours in suspension with the incoming tide or onshore winds? This latter method of displacement has been documented in the English Channel (Murray *et al*., 1982) and elsewhere around New Zealand (Reid & Hayward, 1997).

The strongest hint that at least some of these small lightweight specimens have been transported in, comes from the size range of *C. carinata*. *In situ* populations contain a mix of juveniles and adults (up to 400 μm), but in these harbour samples (particularly from Campbell Island), only populations of juveniles (<150 μm) are present. The other common species (above) represented only by small specimens do not have large adults and thus could be *in situ* or displaced. It is strongly suspected that most *E. vitrea*, *S. elliptica* and many of the unilocular specimens have also been transported in from mid-outer shelf depths offshore, where they are relatively abundant (Hayward *et al*., 2007). Thus, the coarse fraction faunal compositions (dominated by *E. advenum*, *N. flemingi*, *N. aucklandica* and *Haynesina depressula*) are considered to reflect more correctly the *in situ* fauna of the sheltered harbours.

Biogeographical affinities with other subantarctic island groups

It is not possible to make detailed comparisons of the faunal composition with other subantarctic island groups beyond the SW Pacific, because the taxonomic concepts and names used in earlier studies (e.g. Chapman, 1909; Heron-Allen & Earland, 1932; Earland, 1933, 1935) are incompatible with this study. A full and consistent review of the fauna from all islands is required for detailed biogeographical analysis and this is well beyond the scope of this study. It is possible, however, to make some general comparisons.

In terms of species richness, the relatively low diversity of the inner-mid shelf (<80 m) benthic foraminiferal fauna (including uniloculars) of the Auckland Islands, 51° S (130 spp.) and Campbell Island, 52° S (71 spp.) is of a similar order to that recorded from the same depth range around South Georgia, 54° S (60 spp. from three samples; Earland, 1933), Tierra del Fuego, 53° S (75 spp. from one sample; Heron-Allen & Earland, 1932) and Isla de los Estados, 54° S (76 spp. from 36 samples; Thompson, 1978). The Auckland and Campbell Islands have a significantly higher species richness from that recorded around Macquarie Island, 54° S (19 spp. from one sample; Parr, 1950), Kerguelen Islands, 50° S (33 spp. from 13 samples; Parr, 1950) and Falkland Islands, 52° S (33 spp. from ten samples; Brady, 1884; Pearcy, 1914; Cushman & Parker, 1931; Heron-Allen & Earland, 1932). The species lists for all these islands are undoubtedly incomplete and would be expanded with more exhaustive sampling. The main conclusion that can be drawn, however, is that species richness at inner-shelf depths around the subantarctic islands is relatively low, akin to that around the shores of Antarctica (e.g. Stockton, 1973; Delaca & Lipps, 1976; Gaździcki & Majewski, 2003; Majewski, 2005), but considerably lower than around southern temperate, subtropical and tropical islands (e.g. Murray, 1991; Hayward *et al*., 1999).

The larger subantarctic islands (Auckland, Campbell, Kerguelen, South Georgia, Falklands, Estados, Fig. 8) all have

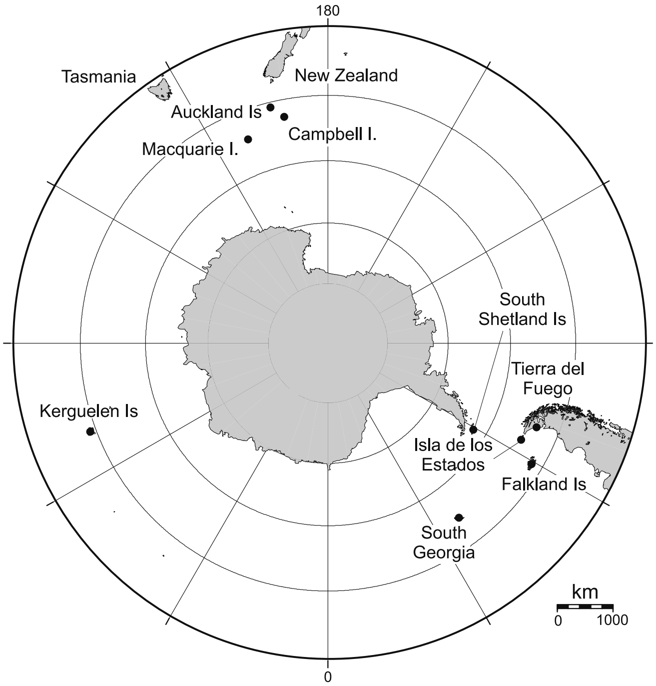

Fig. 8. Major island groups in the subantarctic zone of the Southern Ocean.

similar nearshore topography, with a mix of exposed rocky coasts and more sheltered, glacially carved harbours. At the generic level their shallow-water foraminiferal faunas have considerable commonality (Heron-Allen & Earland, 1932; Earland, 1933; Parr, 1950; Thompson, 1978; this study). The more sheltered harbours have a dominance of *Elphidium*, *Cassidulina*, *Haynesina depressula*, *Nonionella-Nonionellina* and the Southern Hemisphere-endemic genus *Notorotalia.* In all places, *Trifarina angulosa* becomes common in deeper parts of the inner shelf (>30 m). In sandier, more exposed locations the faunas are usually dominated by *Cibicides*, *Rosalina*, *Quinqueloculina*, *Pileolina–Glabratella* and *Miliolinella subrotunda*. Numerous, small, unilocular foraminifera have been recorded from the shallows around all these island groups. A number of rarer species appears to be common to all of the larger subantarctic islands, e.g. *Patellina corrugata*, *Cornuspira involvens*, *Tubinella funalis*. *Ammonia* and *Pyrgo* appear to be absent from all except South Georgia (Heron-Allen & Earland, 1932) and Isla de los Estados (Thompson, 1978).

High-tidal marsh faunas have not been reported from most other subantarctic islands. The marsh fauna from Campbell Island, 52° S, 3 spp. (associations 1, 2), is of similar low diversity to that recorded from salt marshes on Tierra del Fuego, 52° S, 5 spp. (Scott *et al*., 1990). They have two species in common (*H. manilaensis*, *M. fusca*) although the dominants differ *(Trochammina inflata*, *Jadammina macrescens* at Tierra del Fuego).

Dispersal and geological history

The Campbell Plateau has been submerged continuously since at least the Eocene, 35 million years ago, well before the eruption and formation of the volcanic Auckland and Campbell Islands (Adams *et al*., 1979; Adams, 1983; Cook *et al*., 1999). Therefore, there has never been a shallow-water connection (<500 m) between the islands or across to mainland New Zealand that would have aided progressive dispersal of shallow-water benthic foraminifera. Thus, all the intertidal and shallow-marine foraminifera that now live around the Auckland and Campbell Islands must have arrived by dispersal across the Southern Ocean. Only one species (*Notorotalia aucklandica*) has inhabited these island shores for sufficiently long to have evolved into a distinct endemic species. Some species that do not occur around mainland New Zealand, may have reached these islands after long journeys in the Subantarctic Current from far distant lands, such as Kerguelen Islands or even South America.

The majority of species (*c*. 70–75%) share their geographical distribution with mainland New Zealand and show that this is by far the most usual dispersal route (possibly in both directions). The route from mainland New Zealand to the Auckland and Campbell Islands is contrary to the main net surface current direction of the Subantarctic Current (SW to NE). Surface currents commonly have large mobile eddies that at certain times could sweep larval stages, juveniles or even floating logs from southern New Zealand down to the islands, or the reverse. The best evidence that this happens comes from the shared distribution patterns themselves. The most likely source for many of the dispersed foraminifera is the southwest coast of the South and Stewart Islands, where currents associated with the Subtropical Front sweep southeastwards in the direction of the Auckland Islands before swinging northeast in the vicinity of the Snares Islands (Fig. 1). This would have been particularly emphasized during glacial periods when sea-level was *c*. 100 m lower than present.

During the last 2–3 million years, sea surface temperatures around the Auckland and Campbell Islands have seldom, if ever, been any warmer than they are today. During the many glacial periods, sea surface temperatures could have been 2–5° C colder than today (e.g. Weaver *et al*., 1998) and could potentially have killed-off island populations of some intertidal and shallow-marine species. A further contributor to a hypothesized lower diversity foraminiferal fauna during glacials, could have been the much lower sea-levels, when there is unlikely to have been many sheltered shallow-water environments similar to the present fiord-like harbours. Thus, it is suggested that a sizeable proportion of the present shallow-water benthic foraminiferal fauna of the islands has probably arrived by dispersal from mainland New Zealand and recolonized their shores only since the Last Glacial peak, 18 000 years ago.

ACKNOWLEDGEMENTS

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APPENDIX A: Foraminiferal list

Appendix A provides a taxonomic list of all foraminifera recorded here from the Auckland (A), Campbell (C) and Snares (S) Islands, shallower than 100 m, with references to easily accessible published figures that best portray the species as interpreted by us. Generic classification largely follows Loeblich & Tappan (1987), with the ordinal classification after Loeblich & Tappan (1992). The original descriptions of these species can be found in the Ellis & Messina world catalogue of foraminiferal species on www.micropress.org.

APPENDIX A.1: Benthic foraminifera

Order **Astrorhizida**
Lagenammina difflugiformis (Brady, 1879); Jones, 1994, pl. 30, figs 1–3. A, C
Rhizammina algaeformis Brady, 1879; Jones, 1994, pl. 28, figs 1–11. C

Order **Lituolida**
Cribrostomoides jeffreysi (Williamson, 1858); Hayward *et al*., 1999, pl. 1, figs 23–24. A, C
Glomospira cf. *fijiensis* Brönnimann, Whittaker & Zaninetti, 1992; Hayward *et al*., 1999, pl. 1, figs 3–4. C
Haplophragmoides manilaensis Andersen, 1953; Edwards *et al*., 2004, pl. 1, figs 5–6. C
Haplophragmoides wilberti Andersen, 1953; Hayward *et al*., 1999, pl. 1, figs 25–26. A, C
Labrospira spiculolega (Parr, 1950); Parr, 1950, pl. 5, figs 8–10 (as *Trochammina*). A
Miliammina fusca (Brady); Hayward *et al*., 1999, pl. 1, figs 5–6. C
Reophax nodulosus Brady, 1879; Jones, 1994, pl. 31, figs 6–9. C
Reophax subfusiformis Earland, 1933; Hayward *et al*., 1999, pl. 1, figs 15–16. C
Scherochorella moniliforme (Siddall, 1886); Hayward *et al*., 1999, pl. 1, figs 13–14. A
Spiroplectammina biformis (Parker & Jones, 1865); Jones, 1994, pl. 45, figs 25–27. C

Order **Trochamminida**
Paratrochammina bartrami (Hedley *et al.*, 1967); Hayward *et al*., 1999, pl. 2, figs 1–3. A, C, S
Portatrochammina sorosa (Parr, 1950); Hayward *et al*., 1999, pl. 2, figs 4–5. A, C
Rotaliammina ochracea (Williamson, 1858); Thomas *et al*., 1990, pl. 1, fig. 10 (as *Trochammina*). A
Trochammina inflata (Montagu, 1808); Hayward *et al*., 1999, pl. 2, figs 6–8. A

Order **Textulariida**
Eggerelloides scaber (Williamson, 1858); Jones, 1994, pl. 47, fig. 15–17. A, C
Textularia earlandi Parker, 1952; Hayward *et al*., 1999, pl. 2, figs 22–23. C
Verneuilinulla advena (Cushman, 1922); Loeblich & Tappan, 1994, pl. 19, figs 8–9. A

Order **Spirillinida**
Patellina corrugata Williamson, 1858; Hayward *et al*., 1999, pl. 3, figs 11–13. A, S
Patellinoides conica Heron-Allen & Earland, 1932, pl. 13, figs 26–29. A
Spirillina obconica Brady, 1879; Jones, 1994, pl. 85, figs 6–7. A
Spirillina vivipara Ehrenberg, 1843; Hayward *et al*., 1999, pl. 3, fig. 7. A, S

Order **Miliolida**
Cornuspira involvens (Reuss, 1850); Hayward *et al*., 1999, pl. 3, fig. 16. A, C
Miliolinella subrotunda (Montagu, 1808); Hayward *et al*., 1999, pl. 3, fig. 25. A, C
Quinqueloculina bicostoides Vella, 1957; Hayward *et al*., 1999, pl. 4, figs 15–17. A, C
Quinqueloculina delicatula Vella, 1957; Hayward *et al*., 1999, pl. 4, figs 23–24. A
Quinqueloculina incisa Vella, 1957; Hayward *et al*., 1999, pl. 4, figs 25–26. A
Quinqueloculina oblonga (Montagu); Yassini & Jones, 1995 (as *Triloculina*), figs 188–192, 196–197. A, S
Quinqueloculina seminula (Linnaeus); Hayward *et al*., 1999, pl. 5, figs 9–10. A, C, S
Quinqueloculina suborbicularis d'Orbigny, 1826; Hayward *et al*., 1999, pl. 5, figs 6–8. A, S
Quinqueloculina subpolygona Parr, 1945; Hayward *et al*., 1999, pl. 5, figs 11–13. A, S
Sigmoilopsis elliptica (Galloway & Wissler, 1927); Hayward *et al*., 1999, pl. 5, figs 16–18. A, C
Tubinella funalis (Brady, 1884); Jones, 1994, pl. 13, fig. 6–11. A

Order **Lagenida**
Amphicoryne separans (Brady, 1884); Loeblich & Tappan, 1994, pl. 127, fig. 1–18. A
Astacolus crepidulus (Fichtel & Moll, 1798); Hayward *et al*., 1999, pl. 6, figs 28–29. A
Astacolus insolutus (Schwager, 1866); Hayward *et al*., 1999, pl. 6, fig. 30. A
Astacolus vellai Saidova, 1975, pl. 50, fig. 10. A
Favulina hexagona (Williamson, 1848); Hayward *et al*., 1999, pl. 8, fig. 2 (as *Oolina hexagona*). A, C
Favulina punctatiformis (McCulloch, 1977); McCulloch, 1977, pl. 54, fig. 18 (as *Lagena*). A
Fissurina baccata (Heron-Allen & Earland, 1922); Hayward *et al*., 1999, pl. 7, fig. 15. A

Fissurina crucifera McCulloch, 1977, pl. 58, fig. 2. A
Fissurina evoluta McCulloch; Hayward & Grace, 1981, p. 50, fig. 5e. A
Fissurina evolutiquetra McCulloch, 1977, pl. 58, figs 21, 24, 25, 27. A
Fissurina lucida (Williamson, 1848); Hayward *et al*., 1999, pl. 7, figs 20–21. A, C
Fissurina marginata (Montagu, 1803); Hayward *et al*., 1999, pl. 7, figs 22–23. A
Fissurina marginatoperforata (Seguenza, 1880); Yassini & Jones, 1995, figs 411, 413–5. A, C
Fissurina staphyllearia Schwager, 1866; Sidebottom, 1912, pl. 17, fig. 20. A
Galwayella trigonomarginata (Balkwill & Millett, 1884); Jones, 1994, pl. 61, figs 12–13. A
Grigelis orectus Loeblich & Tappan, 1994; Hayward *et al*., 1999, pl. 6, figs 14–15.
Guttulina irregularis (d'Orbigny, 1846); Hayward *et al*., 1999, pl. 7, figs 10–11. A
Guttulina yabei Cushman & Ozawa, 1929; Hayward *et al*., 1999, pl. 7, fig. 12. A, S
Homalohedra liratiformis (McCulloch, 1977); McCulloch, 1977, pl. 53, figs 25, 32. A
Laevidentalina neugeboreni (Schwager, 1866); Hayward *et al*., 1999, pl. 6, figs 16–17 (as *L. bradyensis*). A
Lagena crenata Parker & Jones, 1865; Jones, 1994, pl. 57, figs 15, 21. A
Lagena hispida Reuss, 1858; Hayward *et al*., 1999, pl. 7, figs 1–2. C
Lagena laevicostatiformis McCulloch, 1981; Hayward *et al*., 1999, pl. 7, fig. 3. A, C
Lagena lyellii (Seguenza, 1862); Cushman, 1923, pl. 6, fig. 3. A
Lagena spicata Cushman & McCulloch; Jones, 1994, pl. 58, figs 4, 5–6. A
Lagena spiratiformis McCulloch, 1981; Hayward *et al*., 1999, pl. 7, figs 6–7. A
Lagena sulcata (Walker & Jacob, 1798); Jones, 1994, pl. 57, figs 23, 25–27, 33, 34. A
Lagenosolenia confossa McCulloch, 1977; Hayward *et al*., 1999, pl. 7, figs 27–28. A
Lagenosolenia laciniosa Loeblich & Tappan, 1994, pl. 161, figs 11–15. A
Lagenosolenia neosigmoidella McCulloch, 1977, pl. 51, fig. 9. A
Lagenosolenia rara McCulloch, 1977, pl. 52, fig. 3. A
Lagenosolenia strigimarginata Loeblich & Tappan, 1994, pl. 161, figs 9–10. A
Lagnea sp. A
Laryngosigma hyalascidia Loeblich & Tappan, 1953, pl. 15, figs 6–8. A
Laryngosigma williamsoni (Terquem, 1878); Yi & Jones, 1995, figs 661–663. A
Lenticulina australis Parr, 1950; Hayward *et al*., 1999, pl. 6, figs 31–32. A, C, S
Neolingulina viejoensis McCulloch, 1977, pl. 49, fig. 8. A
Nodosaria nebulosa (Ishizaki, 1943); Ishizaki, 1943, pl. 10, figs 5, 7–8 (as *Lagenonodosaria*). A
Oolina borealis Loeblich & Tappan, 1954; Hayward *et al*., 1999, pl. 8, fig. 1. A, C, S
Oolina globosa (Montagu); Yassini & Jones, 1995, p. 112, figs 369–370. A
Oolina lineata (Williamson); Jones, 1994, pl. 57, fig. 13. A
Oolina melo d'Orbigny, 1839; Hayward *et al*., 1999, pl. 8, fig. 3. A, C, S
Parafissurina basispinata McCulloch, 1977, pl. 72, figs 1–3. A
Parafissurina scaphaeformis Parr, 1950, pl. 10, figs 1–3. A
Parafissurina unguis (Heron-Allen & Earland, 1913); Heron-Allen & Earland, 1913, pl. 7, figs 1–3. A
Procerolagena meridonalis (Wiesner, 1931); Jones, 1994, pl. 58, fig. 19. A
Procerolagena multilatera (McCulloch, 1977); McCulloch, 1977, pl. 50, fig. 5 (as *Lagena*). A
Pseudolingulina bradii (Silvestri, 1903); Jones, 1994, pl. 65, fig. 16 (as *Frondicularia*). A
Pseudosolenia wiesneri (Barker, 1960); Jones, 1994, pl. 59, fig. 23. A
Pyramidulina n. sp. Hayward *et al*., 1999, pl. 6, figs 25–26 (as *Pyramidulina perversa*). A
Sigmoidella pacifica Cushman & Ozawa, 1928; Loeblich & Tappan, 1994, pl. 149, figs 1–9. A

Order **Robertinida**
Cerobertina tenuis (Chapman & Parr, 1937); Finlay, 1938, pl. 11, figs 4–5. A

Order **Buliminida**
Abditodentrix pseudothalmanni (Boltovskoy & Guissani de Kahn, 1981); Loeblich & Tappan, 1994, pl. 218, figs 1–2. A, C
Bolivina cacozela Vella, 1957; Hayward *et al*., 1999, pl. 8, figs 8–9. A, C
Bolivina compacta Sidebottom, 1905; Hayward *et al*., 1999, pl. 8, figs 10–11. A, C
Bolivina neocompacta McCulloch, 1981; Hayward *et al*., 1999, pl. 8, figs 12–13. A, C
Bolivina pygmaea (Brady, 1881); Jones, 1994, pl. 53, figs 5–6 (as *Brizalina*). A, C
Bolivina robusta Brady; Jones, 1994, pl. 53, figs 7–9. C
Bolivina spathulata (Williamson, 1858); Hayward *et al*., 1999, pl. 8, fig. 17. A, C, S
Bolivina subexcavata Cushman & Wickenden, 1929; Hayward *et al*., 1999, pl. 8, fig. 22. A, C, S
Bolivina translucens Phleger & Parker, 1951; Loeblich & Tappan, 1994, pl. 213, figs 9–14. A, C
Bulimina elongata d'Orbigny, 1826; Hayward *et al*., 1999, pl. 9, figs 6–7. A, C

Bulimina marginata acanthia Costa, 1856; Hayward *et al.*, 1999, pl. 9, figs 16–17. A, C
Bulimina marginata marginata d'Orbigny, 1826; Hayward *et al.*, 1999, pl. 9, figs 13–15. A, C, S
Buliminella elegantissima (d'Orbigny, 1839); Hayward *et al.*, 1999, pl. 9, figs 18–19. A, C
Cassidulina carinata Silvestri, 1896; Hayward *et al.*, 1999, pl. 8, figs 23–24. A, C, S
Cassidulina norvangi Thalmann, 1952; Nomura, 1983, figs 45–46, pl. 4, figs 12a–c, 13. C
Evolvocassidulina orientalis (Cushman, 1922); Hayward *et al.*, 1999, pl. 8, fig. 28. A
Fursenkoina cf. *riggii* (Boltovskoy, 1954); Boltovskoy *et al.*, 1980, pl. 34, figs 19–22. A, C
Globocassidulina canalisuturata Eade, 1967; Hayward *et al.*, 1999, pl. 8, figs 29–30. A, S
Globocassidulina elegans (Sidebottom, 1910); Loeblich & Tappan, 1994, pl. 223, figs 1–6. A
Globocassidulina subglobosa (Brady, 1881); Jones, 1994, pl. 54, figs 17a–c. C
Rutherfordoides rotundata (Parr, 1950); Jones, 1994, pl. 52, figs 10–11 (as *Fursenkoina*). A
Siphogenerina dimorpha (Parker & Jones); Yassini & Jones, 1995, fig. 623 (as *Rectobolivina dimorpha pacifica*). A, C
Trifarina angulosa (Williamson, 1858) *sensu lato*; Hayward *et al.*, 1999, pl. 9, figs 23–24. A, C, S
Uvigerina peregrina Cushman, 1923; s.l. Jones, 1994, pl. 74, figs 24–26 (as *U. bradyana*). A

Suborder **Rotaliina**
Anomalinoides spherica (Finlay, 1940); Hayward *et al.*, 1999, pl. 15, figs 27–29. A, S
Anomalinoides tasmanica (Parr, 1950); Parr, 1950, pl. 15, figs 4a–c. C
Astrononion novozealandicum Cushman & Edwards, 1937; Hayward *et al.*, 1999, pl. 15, figs 8–9. A, C, S
Cibicides corticatus Earland, 1934; Hayward *et al.*, 1999, pl. 14, figs 19–21. A
Cibicides dispars (d'Orbigny, 1839); Hayward *et al.*, 1999, pl. 14, figs 22–24. A, C, S
Cibicides pachyderma (Rzehak, 1886); van Morkhoven *et al.*, 1986, pl. 22. A
Cibicidoides bradyi (Trauth, 1918); van Morkhoven *et al.*, 1986, pl. 30. A, C
Cymbaloporetta bradyi (Cushman, 1915); Hayward *et al.*, 1999, pl. 14, figs 28–29. A
Discanomalina coronata (Parker & Jones, 1857); Jones, 1994, pl. 97, figs 1–2. C
Discorbinella bertheloti (d'Orbigny, 1839); Hayward *et al.*, 1999, pl. 14, figs 1–3. A, C, S
Discorbinella complanata (Sidebottom, 1918); Hayward *et al.*, 1999, pl. 14, figs 4–6. A, C, S
Discorbinella deflata (Finlay, 1940); Hayward *et al.*, 1999, pl. 14, figs 7–9. A
Discorbinella subcomplanata (Parr, 1950); Hayward *et al.*, 1999, pl. 14, figs 10–12. A
Discorbinella timida Hornibrook, 1961, p. 116, pl. 14, figs 288, 293, 297. A, C
Discorbinella vitrevoluta (Hornibrook, 1961); Hayward *et al.*, 1999, pl. 14, figs 16–18. A
Dyocibicides sp. A, C
Eilohedra vitrea (Parker, 1953); Hayward *et al.*, 1999, pl. 13, figs 14–16. A, C
Elphidium advenum f. *limbatum* (Chapman, 1907); Hayward *et al.*, 1999, pl. 17, figs 1–2. A, C
Eponides repandus (Fichtel & Moll, 1798); Jones, 1994, pl. 104, fig. 19. C, S
Gavelinopsis praegeri (Heron-Allen & Earland, 1913); Hayward *et al.*, 1999, pl. 10, figs 15–17. A, C, S
Haynesina depressula (Walker & Jacob, 1798); Hayward *et al.*, 1999, pl. 15, figs 10–11. A, C
Heronallenia lingulata (Burrows & Holland, 1895); Jones, 1994, pl. 91, fig. 3. A, C, S
Heronallenia pulvinulinoides (Cushman, 1915); Hayward *et al.*, 1999, pl. 13, figs 7–9. C, S
Heronallenia unguiculata (Sidebottom, 1918); Sidebottom, 1918, pl. 6, figs 12–14.
Neoconorbina terquemi (Rzehak, 1888); Jones, 1994, pl. 88, figs 5–8. A
Nonionellina flemingi (Vella, 1957); Hayward *et al.*, 1999, pl. 15, figs 14–15. A, C
Nonionoides turgida (Williamson, 1858); Hayward *et al.*, 1999, pl. 15, figs 16–17. A
Notorotalia aucklandica Vella, 1957; Hayward *et al.*, 1999, pl. 16, figs 13–15. A, C
Notorotalia depressa Vella, 1957; Hayward *et al.*, 1999, pl. 16, figs 16–18. C
Oriodorsalis umbonatus (Reuss, 1851); Hayward *et al.*, 1999, pl. 15, figs 24–26. C, S
Pileolina radiata Vella, 1957; Hayward *et al.*, 1999, pl. 12, figs 13–15. A, S
Planodiscorbis rarescens (Brady, 1884); Jones, 1994, pl. 90, figs 2, 3. A
Planoglabratella opercularis (d'Orbigny, 1826); Hayward *et al.*, 1999, pl. 13, figs 1–3. A, C, S
Rosalina bradyi (Cushman, 1915); Hayward *et al.*, 1999, pl. 11, figs 1–3. A, C, S
Rosalina irregularis (Rhumbler, 1906); Hayward *et al.*, 1999, pl. 11, figs 4–5. A, C
Rosalina paupereques Vella, 1957; Hayward *et al.*, 1999, pl. 11, figs 6–8. A, S
Rosalina vitrizea Hornibrook, 1961; Hayward *et al.*, 1999, pl. 11, figs 9–11. A
Sphaeroidina bulloides d'Orbigny, 1826; Hayward *et al.*, 1999, pl. 11, figs 15–16. A, C, S
Stomatorbina concentrica (Parker & Jones, 1864); Hayward *et al.*, 1999, pl. 10, figs 7–8. A, S

APPENDIX B: Auckland and Campbell Islands station data

Table B1 provides the data from the Auckland and Campbell Islands stations. Note that samples with a 'c' suffix represent faunal picks of the >150 μm fraction only.

No.	Station No.	Cat No.	Latitude (° ′ S)	Longitude (° ′ E)	Water depth (m)	Plank %	Alpha >63 µm	H >63 µm	E >63 µm
Auckland Islands									
A1		AU18098	50 30.2	166 17.0	8	16	6.7	2.5	0.54
A2		AU18099	50 31.3	166 13.6	10	19	5.8	2.0	0.35
A3		AU18100	50 31.3	166 13.7	13.5	7	3.5	1.9	0.46
A4		AU18101	50 31.3	166 13.8	16.5	27	4.7	1.5	0.25
A5		AU18102	50 50.8	166 00.9	22	2	2.3	1.4	0.40
A6		AU18103	50 50.9	166 00.9	4	13	5.2	2.1	0.42
A7		AU18104	50 51.0	166 01.0	51	11	4.8	1.8	0.35
A8		AU18105	50 48.8	166 04.6	17.5	1	2.5	1.6	0.43
A9	L12457	AU18455	50 49.8	165 55.7	9	0	2.5	1.0	0.24
A10	J531	AU18456	50 51.0	166 06.0	46	12	6.4	2.4	0.51
A11	J526	AU18457	50 50.89	166 06.0	59	23	7.1	2.3	0.40
A12	J522	F202511	50 52.5	166 09.2	80	22	6.9	2.4	0.43
A13	J515	AU18458	50 42.85	166 07.3	54	9	10.4	2.8	0.52
A14	J512	AU18459	50 41.3	166 11.5	59	28	7.2	2.4	0.47
A15	L12454a	AU18460	50 29.1	166 18.2	H.T.	0	3.8	1.9	0.45
A16	L12454w	AU18461	50 29.1	166 18.2	H.T.	4	2.7	1.5	0.44
A17		F201002	50 49	166 04	12				
A18		F201162	50 49	166 04	18				
A19	L6184	L6184	50 48.7	166 04.3	3				
A20		F201106–7	50 30.5	166 17	12				
Campbell Island									
C1		AU18107	52 33.1	166 09.3	21	45	4.8	1.4	0.23
C2		AU18108	52 33.1	166 09.8	30	42	3.1	1.4	0.32
C3		AU18109	52 32.8	166 09.5	22	5	2.9	1.3	0.30
C4		AU18110	52 32.9	166 10.3	31	55	4.9	1.6	0.28
C5		AU18111	52 33.2	166 10.1	28	38	4.1	1.5	0.29
C6		AU18112	52 33.3	166 09.5	17	50	2.2	1.1	0.31
C7		AU18113	52 33.1	166 09.1	4	56	3.7	1.4	0.30
C8		AU18114	52 33.2	166 08.8	4	45	2.3	1.5	0.49
C9		AU18115	52 33.3	166 09.0	12	59	2.8	1.2	0.29
C10		AU18116	52 33.5	166 08.6	10	64	4.5	1.5	0.26
C11		AU18120	52 33.1	166 08.7	M.T.	1	1.8	1.1	0.43
C12	B189	AU18462	52 33.3	166 09.2	19	45	3.2	1.5	0.34
C13	D29	AU18463	52 33.3	166 10.8	18	62	6.0	1.7	0.25
C14	D30	AU18464	52 33.5	166 14.0	40	47	4.8	1.5	0.24
C15		AU18121	52 33.0	166 08.7	MHWS	0	2.6	0.6	0.94
C16		AU18122	52 33.0	166 08.7	EHWS	0	0.6	0.8	0.77
C17		AU18123	52 33.0	166 08.7	MHWS	0	0.6	1.0	0.94
C18		AU18124	52 33.0	166 08.7	MHW	0	0.6	0.4	0.41
C19		AU18125	52 33.0	166 08.7	MHW	0	0.6	0.2	0.39
C20		AU18126	52 33.0	166 08.7	MHWN	0	0.4	0.1	0.56
C21		AU18127	52 33.0	166 08.7	MHWN	0	0.6	0.7	0.70

Alpha is the Fisher Alpha Index (number of species standardized by number of individuals counted). H is the Information Function (a combination of the number of species present and, to a lesser extent, the evenness of species counts). E is the Evenness (a measure of dominance versus evenness of species counts). EHWS, Extreme high water spring level; MHW, mean high water; MHWN, mean high water neap; MHWS, mean high water spring level; M.T., mid-tide level

Table B1. Data from the Auckland and Campbell Islands stations

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