



Changes in the landsnail fauna of Lady Alice Island, northeastern New Zealand

F. J. Brook

To cite this article: F. J. Brook (1999) Changes in the landsnail fauna of Lady Alice Island, northeastern New Zealand, Journal of the Royal Society of New Zealand, 29:2, 135-157, DOI: [10.1080/03014223.1999.9517588](https://doi.org/10.1080/03014223.1999.9517588)

To link to this article: <http://dx.doi.org/10.1080/03014223.1999.9517588>



Published online: 30 Mar 2010.



Submit your article to this journal [↗](#)



Article views: 99



View related articles [↗](#)



Citing articles: 19 View citing articles [↗](#)

Changes in the landsnail fauna of Lady Alice Island, northeastern New Zealand

F. J. Brook*

A small coastal dunefield on Lady Alice Island off northern New Zealand incorporates a stratigraphic record of the historic period and much if not all of the period of prehistoric Maori occupation of the island. Fossil landsnail faunas from the dunefield are closely comparable with those from present-day dune shrubland habitats and differ from contiguous hillslope forest and shrubland faunas. Three of the landsnail species are no longer extant on Lady Alice Island. Two are large species (*Amborhytida tarangensis*, *Placostylus hongii*) that are inferred to have become extinct following the introduction of kiore (*Rattus exulans*) to the island. Failure to find any snail shells with breakages characteristic of rat predation suggests that kiore may not have established on the island until the early 19th century. The other, smaller species of landsnail (*Phrixgnathus paralaomiformis*) probably became extinct in the late 19th or early 20th century as a result of habitat disturbance from fires and cattle.

Keywords landsnails; coastal dunes; islands; Holocene; prehistoric; extinction; *Rattus exulans*

INTRODUCTION

The biotas of all of the larger offshore islands of northern New Zealand have been significantly modified by human activity, through the clearance and modification of vegetation, and by the introduction of exotic plant and animal species (Hayward 1986). One introduced species that is present on a number of islands and which has been implicated in the local extinction or permanent reduction of some native species is the kiore or Polynesian rat (*Rattus exulans*). The kiore is thought to have been brought to New Zealand by Polynesians, but whether it was originally introduced at the time of Polynesian settlement of New Zealand (i.e., AD 1100 or later: Anderson 1991, 1995; McFadgen et al. 1994; Higham & Hogg 1997), or during earlier visits as much as 2000 years ago, is presently the subject of some debate (Anderson 1996; Holdaway 1996). Whichever is the case, archaeological evidence indicates that the kiore has been widely distributed on mainland New Zealand for at least 700 years. The timing of introduction of kiore to northern offshore islands has not been documented systematically, but is widely assumed to have been during the prehistoric period (e.g., Hayward 1986; Davidson 1990). Kiore were used by Maori for food and some authors (e.g., Stead 1937) have suggested that they may have been deliberately introduced to offshore islands to supplement existing food sources. However, the irregular distribution of kiore among islands settled by prehistoric Maori, and in particular their absence from the Three Kings and Poor Knights groups, has been cited as evidence that island introductions may have been accidental rather than purposeful (Atkinson 1986).

*Department of Conservation, P.O. Box 842, Whangarei, New Zealand

Studies of the diet of kiore in New Zealand indicate that the species is omnivorous, feeding on seeds, fruit, stems, leaves and roots, as well as on a variety of animals including insects, spiders, centipedes, isopods, amphipods, false scorpions, worms, snails, slugs, lizards, bird eggs and chicks (Atkinson & Moller 1990; Newman & McFadden 1990; Ussher 1995; Booth et al 1996).

The arguments for linking the presence of kiore on offshore islands with local extinctions and population reductions of some native plant and animal species are largely circumstantial, based on studies of contemporary disjunct distributions of island species (Whitaker 1973, 1978; Atkinson 1986; Watt 1986; Atkinson & Moller 1990), comparisons of the abundance of particular native species, and of the age structure of populations on rat-free islands and islands where kiore is the only rodent species present (Crook 1973; Whitaker 1973; Atkinson 1978; Campbell 1978; Towns 1992; Cree et al. 1995). However, there is also a historically-documented instance of the local extinction of possibly as many as three lizard species and a large, flightless beetle following kiore invasion of a previously rodent-free islet in the Mokohinau group (McCallum 1986; Watt 1986).

Craig (1986) noted that the hypothesis attributing present-day disjunct native species distributions to local kiore-induced extinctions does not take account of other potentially confounding ecological factors, and argued that previous anthropogenic habitat disturbance on islands may be an equally or more important determinant of present-day distributions of many native species.

The relative effects on native biotas of kiore predation and prehistoric-historic habitat modification will probably never be disentangled for most of the northern offshore islands occupied by kiore, but paleoenvironmental studies of late Holocene sedimentary sequences in coastal dunefields, caves and under rock overhangs have the potential to contribute information on the biotic histories of at least some of these islands.

The present study is focused on a small dunefield on Lady Alice Island, Hen and Chickens group (Fig. 1), that incorporates a stratigraphic sequence spanning the historic period and much if not all of the period of prehistoric Maori occupation of the island. The sequence contains rich fossil landsnail faunas that provide a record of environmental change on the dunefield from prehistoric time. Three of the fossil landsnail species are no longer extant on Lady Alice Island. Kiore were present on the island up until 1994, when they were eradicated by the Department of Conservation.

The aims of the study were: to describe the recent history of environmental change on the West Bay dunefield as determined primarily from landsnail faunas; to determine the stratigraphic distribution of the locally extinct landsnail species; and to attempt to identify causes of their extinctions from ecological correlates.

Physical setting

Lady Alice Island (35°53.5'S 174°43'E) is c. 138 ha in area with a broadly rounded central ridge system at c. 100–158 m elevation, and a series of short, deeply incised valleys containing ephemeral streams draining to the western, southern and eastern coasts (Fig. 1). Most of the coastline is bounded by cliffs and rock platforms, but there are pocket sand beaches at South Cove and West Bay. The island is formed of Torlesse Terrane indurated alternating sandstone and mudstone (hereafter referred to as greywacke) of possible Jurassic age, cut by andesitic dikes of early Miocene age (Moore 1984; Isaac 1996). Hillslopes typically have leached clay soils with common rock outcrops and granule to pebble size, weathered colluvial gravel.

Cemented gravelly sandstone beach rock underlying modern beach sand in West Bay, and narrow relict wave-cut notches in greywacke at about 1.5 m above mean high water mark at the northern end of West Bay, probably formed during the last interglacial period (120–125 ka ago) when sea level was up to about 3 m higher than at present.

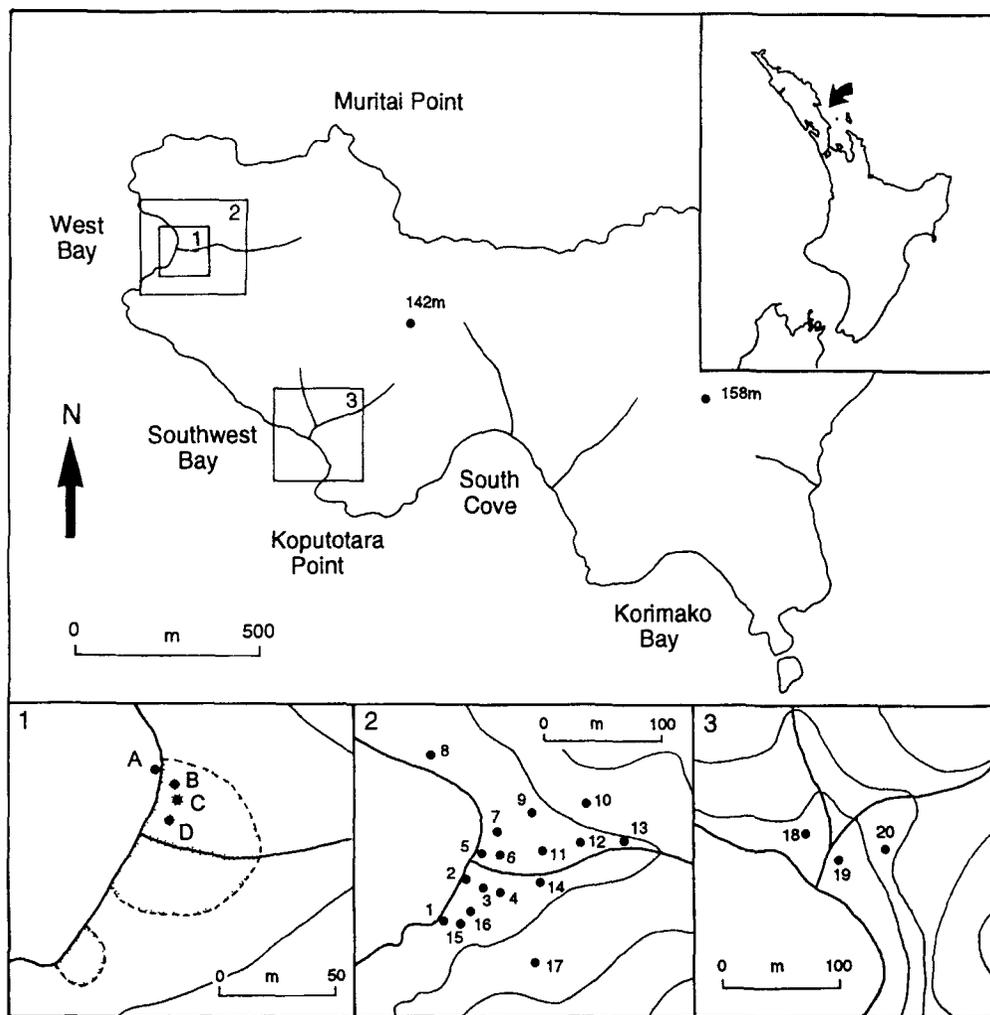


Fig. 1 Lady Alice Island, Hen and Chickens group, with insets showing location of dunefield (stippled) and stratigraphic sections (A-D) in West Bay, and present-day landsnail faunal sites in West Bay (1-17) and South West Bay (18-20). Contours on inset maps are at 20 m intervals.

The Holocene dunefield in West Bay on which this study is based occupies a valley mouth. It unconformably overlies greywacke and probably also late Pleistocene-Holocene beach and alluvial sediments. Like other Holocene coastal dune areas in New Zealand it probably formed following the post-glacial transgression and attainment of modern sea level about 6500 years B.P. (Gibb 1986).

West Bay is sheltered from unrefracted oceanic swells from the easterly and northerly quarters, but is directly exposed to westerly wind waves with a fetch of up to 22 km.

Human history and vegetation changes

The remains of prehistoric Maori settlement of Lady Alice Island include three ridge-top pa (ranging in defensive area from 1800 to 5000 m²) as well as shell midden, terrace and pit sites on spurs behind South Cove, South West Bay and West Bay, and an occupation site on dunes

and lower hillslopes behind West Bay (Prickett 1984). According to Prickett (1984), neither Lady Alice Island nor any of the other Chicken Islands supported large permanent populations, and archaeological evidence suggests that Maori occupation on Lady Alice was largely of a transient nature. The timing of the first settlement of the Chicken Islands is unknown, but they were apparently finally abandoned by Maori around 1820 (G. Graham pers. comm. in Cranwell & Moore 1935).

In 1880 Reischek (1881: 274) observed that the larger of the Chicken Islands, including Lady Alice Island, were "covered in bush, with the exception of a few abandoned Maori plantations now overgrown with flax and scrub". Reischek (1930: 97) also recorded finding on the larger islands "the remains of Maori settlements and cooking middens in which I dug out burnt stone, mussels, snail shells, the bones of seals and of rats, the remains of birds and fishes, firestone knives and other things". Subsequently, in the later part of the 19th century, Lady Alice Island was periodically occupied by Nova Scotian fishermen from Waipu who are variously recorded as having been based at South Cove (Percy 1956) or West Bay (Skegg 1965). At that time also flax was commercially harvested on the Chicken Islands and barged to a mill at Whangarei, and parts of Lady Alice Island, particularly areas behind West Bay and South Cove, were fired (Percy 1956).

In the early 20th century, Lady Alice Island was reportedly again swept by fire, and only isolated pockets of forest in gullies avoided destruction. In 1908 the last fire observed this century burnt an area behind West Bay (Bellingham 1956; Percy 1956). Soon after that cattle were released on the island and remained there in "fairly large numbers" until 1924–25 (Atkinson 1956; Percy 1956: 3). There has been very little human disturbance of Lady Alice Island since cattle were removed, and the island group has had reserve status since 1928 (Hayward & McCallum 1984).

The first detailed vegetation descriptions of Lady Alice Island were made by Atkinson (1956), Bellingham (1956), Percy (1956) and Pook (1956), based on surveys carried out in 1955. At that time, the main ridgetops on Lady Alice Island supported kanuka (*Kunzea ericoides*) forest and shrubland, locally with common manuka (*Leptospermum scoparium*), mapou (*Myrsine australis*) and five-finger (*Pseudopanax arboreus*) as associated canopy species, whereas valleys on the southern and eastern sides of the island showed a fairly uniform transition from flax (*Phormium tenax*) and broadleaf shrubland at the mouth, through kohekohe (*Dysoxylum spectabile*)-puriri (*Vitex lucens*) forest to pohutukawa (*Metrosideros excelsa*)-kohekohe-puriri forest in the upper reaches. However, the vegetation behind West Bay differed markedly from that general pattern in having an extensive area of stunted manuka-kanuka shrubland on the north-facing valley slopes, mixed broadleaf shrubland on valley floors and extending over the south-facing valley slopes, and flaxland at the valley mouth (Percy 1956). The relative youthfulness of the vegetation behind West Bay compared with much of the rest of the island was attributed to a legacy of the combined effects of extensive firing and cattle damage earlier in the 20th century (Percy 1956).

In 1982 a forest vegetation survey on Lady Alice Island (Bellingham 1984) found substantial changes in forest communities compared with 1955, most notably the expansion of broadleaf-dominated forest at the expense of broadleaf shrubland and kanuka forest, and the virtual disappearance of manuka from all but exposed coastal communities. The Bellingham (1984) study also recorded widespread regeneration of karaka (*Corynocarpus laevigatus*) and kohekohe, and more localised regeneration of other canopy tree species including coastal maire (*Nestegis apetala*), haekaro (*Pittosporum umbellatum*), houhere (*Hoheria populnea*), kowhai (*Sophora microphylla*), parapara (*Pisonia brunoniana*), pigeonwood (*Hedycarya arborea*), pukanui (*Meryta sinclairii*), taraire (*Beilschmiedia tarairi*), tawa (*Beilschmiedia tawa*) and tawapou (*Pouteria costata*). No information was provided on vegetation in the

West Bay area, but a contemporary study by Cameron (1984) provided the first record of the presence of sandfield vegetation including spinifex (*Spinifex sericeus*), pingao (*Desmoschoenus spiralis*), shore bindweed (*Calystegia soldanella*) and *Carex pumila* on the dunes there.

METHODS

Holocene stratigraphy and fossil faunas

The stratigraphy of the West Bay dune sequence was determined from a wave-eroded exposure in the foredune at the northern end of the dune field and from sections exposed in three holes dug immediately inland of the present-day foredune crest north of the stream (Fig. 1). Stratigraphic and sedimentologic descriptions were compiled for each of the four sections, with particular attention being paid to the stratigraphic distribution of cultural material, paleosols and pumice clasts. Scattered clasts of Loiseles pumice (Wellman 1962) were present in all four sections, but no primary deposits were found. Following McFadgen (1982, 1994), horizons containing Loiseles pumice were considered to be no older than 660–510 calendar years B.P. A single radiocarbon age was determined from fossil shells of *Placostylus hongii*. Dating was carried out by the University of Waikato Radiocarbon Laboratory (sample no. WK 5486).

The species composition of fossil landsnail faunas within a number of stratigraphic horizons exposed in the four sections was determined both from on-site collection of shells and from off-site examination of bulk sediment samples of approximately two litres each. Snail shells in the bulk samples were separated and concentrated by sieving, flotation in water and hand-sorting under a binocular microscope.

Present-day habitats and faunas

A total of 20 coastal and near-coastal shrubland and forest sites were sampled for landsnail faunas between January and May 1997, covering a representative selection of the vegetation and physical habitat types present on western Lady Alice Island. Seven of those sites were located on the West Bay dune field (sites 1–7) and a further ten sites were on clay and gravelly colluvial soils on nearby hillslopes (sites 8–17). For a comparison with the West Bay landsnail faunas, a single coastal shrubland site and two forest sites were also sampled on hillslopes in South West Bay (sites 18–20).

Lists of landsnail species present at each site were compiled from searches made on site by eye, and from bulk collections of leaf litter, humus and soil that were taken off-site and sorted for landsnails under a binocular microscope. The sampling regime was aimed at qualitatively covering as great a variety of microhabitats at each site as possible. The area sampled at each site ranged between 10 and 100 m². Site vegetation descriptions are held by the author.

Classification of snail faunas

Similarities in species composition among present-day and fossil landsnail faunas were examined by cluster analysis of a presence/absence data matrix comprising a total of 22 species from the 20 present-day and 23 fossil faunas. The cluster analysis was computed using the NTSYS statistical package of Rohlf (1989). Similarity of the initial data matrix was calculated using the Jaccard coefficient, and clustering was done by the unweighted pair group method.

Patterns of diversity within the main groupings of fossil and present-day landsnail faunas identified by the cluster analysis were measured in terms of the total number of species per group, range and mean number of species per site for each group, and mean number of sites per species for each group.

Paleoenvironmental history and extinctions

Patterns of stratigraphic change in species diversity and composition among the dunefield landsnail faunas are described, and the stratigraphic range of locally extinct species determined. A paleoenvironmental history for the dunefield is given based on analogy with present-day snail faunas. The range of locally extinct landsnail species is examined within the context of that history in order to assess whether their last appearances can be correlated with inferred changes in habitat types.

Predation on large landsnails by kiore has been documented from a number of New Zealand islands (Campbell et al. 1984; Meads et al. 1984; Parrish & Sherley 1993). In this study the role of kiore as a predator of the large landsnail species *Amborhytida tarangensis* and *Placostylus hongii* on Lady Alice Island is assessed on the basis of taphonomic evidence from the West Bay populations and by comparison with other Northland *Amborhytida* and *Placostylus* populations, both at sites without any rats and also at sites with kiore as the only rat species present.

Attacks on landsnails by kiore and other rat species produce characteristic shell damage. *Amborhytida* shells preyed on by rats typically have the periphery or base of the body whorl bitten back from the outer lip, leaving the edges of the broken area jagged and irregular (Fig. 2). Juvenile *Placostylus* shells are also typically bitten back from the outer lip around the whorl periphery, but adult *Placostylus* shells have a thickened varix around the outer lip which evidently affords them some degree of protection from rat predation (pers. obs.). In the case of modern *Placostylus* populations coexisting with kiore (see below) there is clear evidence, from repaired lip breakages on the spire whorls of some adult snails, that not all attacks by kiore on juvenile snails are fatal (Fig. 2). Recognition of repaired damage in fossil shells is particularly useful. It provides unambiguous evidence of the co-existence of snails and rats, because such damage clearly cannot be attributed to taphonomic processes operating after death of the snail. Further, the percentage of adults with repaired juvenile shell damage within a population can be easily determined, and provides a relative measure of the prevalence of kiore attacks on snails.

For this study all *Amborhytida* and adult *Placostylus* collected from the West Bay dune sequence were examined for the presence of repaired lip breakages characteristic of rat damage. The proportion of damaged shells within each population was determined and compared with values obtained from an identical analysis of collections of *Amborhytida* and *Placostylus* shells from sites elsewhere in Northland (Table 1). That study included comparisons with samples from rat-free islands (Poor Knights group, Motukokako), islands where kiore was the only rodent present (Coppermine, Hen, Motuopao), and one mainland prehistoric site in a dune sequence at Te Ruatahi near Mimiwhangata (Q06/f61, radiocarbon age of 466–273 calendar years BP at two sigma limits: Brook & Goulstone 1999).

Landsnail taxonomy and collection data

Landsnail identifications were based on comparison with reference material in the collections of the Auckland War Memorial Museum. The present-day and fossil faunas contain four punctid species that have not been formally described but which are also known from elsewhere in New Zealand and are recognised among New Zealand malacologists as distinct at the species level. The two punctid species with number suffixes have previously been listed and figured in other publications (e.g., Solem et al. 1981; Solem & Climo 1985; Goulstone 1990; Goulstone et al. 1993). Nomenclature of *Phrixgnathus* sp. cf. *P. moellendorfi* and *Phrixgnathus* sp. "marshalli" follows Brook & Goulstone (1999).

Fossil faunal sites are allocated sheet numbers of the New Zealand Fossil Record File (with prefix R07/f), and the collections of fossil and modern landsnails made during the study have been deposited in the Auckland Museum and the Museum of New Zealand, Wellington.

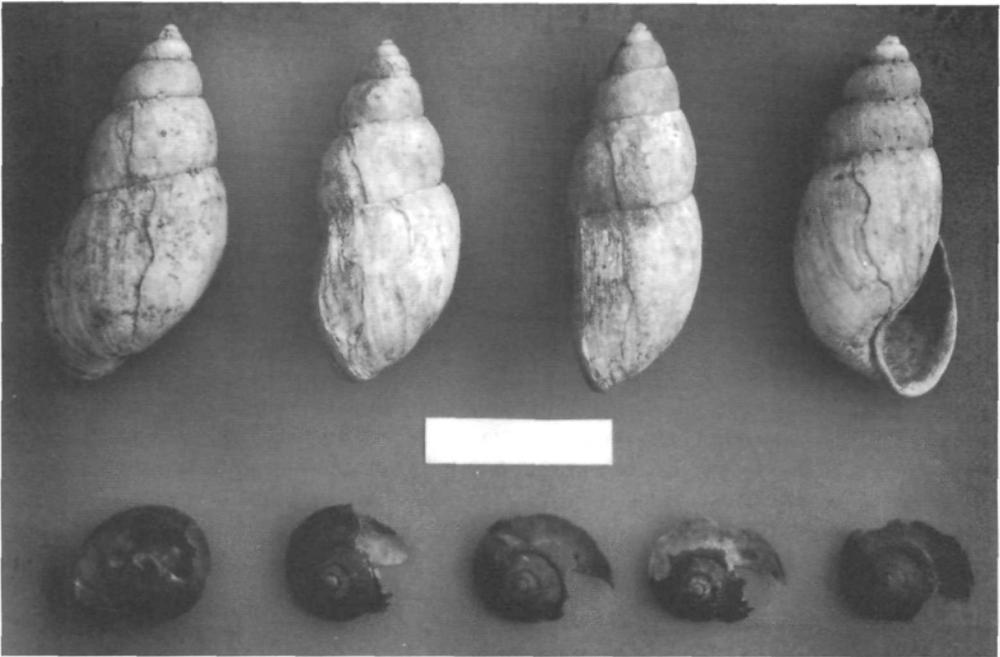


Fig. 2 Examples of shells damaged by predators. Repaired lip breakages characteristic of rat damage in *Placostylus hongii* from Coppermine Island. Lip breakages in *Amborhytida tarangensis* from Hen Island. Scale bar 4 cm in length.

Table 1 Site data for *Amborhytida* and *Placostylus* shell collections used for comparative assessment of relative incidence of predation.

	Species	Location	NZMS 260 Grid Ref.	Collection date/sample age	Coexistence with kiore
<i>Amborhytida</i>	<i>A. tarangensis</i>	Hen I., coastal flat	R08/649798	1995	yes
	<i>A. tarangensis</i>	Hen I., ridge crest	R07/654804	1995	yes
	<i>A. pycrofti</i>	Aorangi I.	R06/689343	1995	no
	<i>A. pycrofti</i>	Tawhiti Rahi I.	R06/685359	1995	no
	<i>A. sp.</i>	Motukokako	Q05/329697	1995	no
<i>Placostylus</i>	<i>P. hongii</i>	Coppermine I. ¹	R07/701884	1971, 1996, 1997	yes
	<i>P. hongii</i>	Te Ruatahi dune ²	Q06/407370	466–273 years B.P.	yes
	<i>P. hongii</i>	Tawhiti Rahi I.	R06/683379	1997	no
	<i>P. hongii</i>	Aorangi I.	R06/685347	1997	no
	<i>P. hongii</i>	Archway I.	R06/687329	1997	no
	<i>P. hongii</i>	Aorangaia I.	R06/692333	1997	no
	<i>P. ambagiosus</i>	Motuopao I. ³	M02/777476	ca. 1895–1934	yes

¹Includes Auckland Museum and Museum of New Zealand collections (AK 53618, M138220, M138230).

²Shells from fossil fauna Q06/f61, Brook & Goulstone (1999).

³Includes Auckland Museum and Museum of New Zealand collections (AK10507, AK25010, AK25016, AK25021, AK25023, AK25032, AK61896, AK80775, AK92480, AK133773, M23006).

RESULTS

Dunefield geomorphology and stratigraphy

The Holocene dunefield in West Bay comprises (1), a larger northern part that extends up to 50 m inland and covers an area of approximately 2600 m², and (2), a smaller dune area of approximately 200 m² at the southern end of the bay (Fig. 1). The two are separated by a rocky spur.

The northern dunefield is bisected by the main stream draining into West Bay, and is bounded on its southern side by a watercourse that is dry except during periods of heavy rain. A foredune on the seaward margin of the dunefield has a crest that ranges in height from c. 3 m above high water mark north of the stream to c. 2 m above high water mark south of the stream. The seaward face of the foredune is steep where it is cut back by storm waves, but elsewhere has a slope of about 35°. Behind the foredune crest the dunefield mostly has a hummocked surface that slopes gently upwards inland, but on the south side of the stream the landward part of the dunefield mantles the toe of a rocky spur. The foredune face and seaward part of the dunefield south of the stream are mantled by unweathered sand, but elsewhere a weakly developed soil profile caps the dune sequence (below). Weathered greywacke clasts of colluvial origin are common on the dunefield surface adjacent to hillslopes.

The smaller dune area comprises unweathered sand and admixed colluvial gravel abutting a rocky coastal hillslope. There is no foredune, and instead the dune surface slopes at 30–35° up to approximately 6 m above high water mark.

Four stratigraphic sections were examined to the north of the stream in the northern dunefield. The location of sections is shown in Fig. 1, and stratigraphic columns in Fig. 3.

In the two northern sections (A, B) Holocene sediments unconformably overlie Torlesse Terrane greywacke, but in the two southern sections (C, D) the basal part of the Holocene sequence was not exposed. Four main stratigraphic units, numbered 1–4 below, are represented in the Holocene sections examined.

Unit 1: This is the lowest stratigraphic unit, exposed only at the base of section A where it comprises a 35 cm thick paleosol of moderately consolidated, dark brown, slightly muddy, gravelly coarse sand containing landsnails (R07/f51). The gravel component includes well-rounded pebbles and granules of unweathered greywacke probably of beach origin, as well as subangular colluvial pebbles of weathered greywacke.

Unit 2: This comprises a laterally variable sequence of cm–dm thick, weakly developed sand paleosols and intercalated cm-thick lenses of unweathered bioclastic-lithic dune sand. Unit 2 was exposed in sections A, C and D, but the basal contact was visible only in section A. At that site it disconformably overlies the gravelly sand paleosol of Unit 1, and comprises four main horizons with a combined thickness of 95 cm. The lowest is a 5 cm thick lens of weakly consolidated, dark grey coarse sand. It is overlain by a 30 cm thick paleosol of moderately consolidated, brown, slightly muddy medium–coarse sand containing landsnails, common Loiseles pumice and abundant subangular colluvial granules and pebbles of weathered greywacke (R07/f50). That paleosol is overlain by 15 cm of weakly consolidated, dark grey medium–coarse sand, which is in turn overlain by a 45 cm thick composite paleosol of moderately consolidated, moderately humic-stained, brown medium–coarse sand containing landsnails and scattered charcoal fragments (R07/f48, f49). Colluvial weathered greywacke clasts are scattered throughout that paleosol unit and concentrated in a cm-thick lens within it.

The lower 80 cm of section C and lower 40 cm of section D are also included in Unit 2. The lowest exposed horizon in section C is a moderately consolidated, strongly humic-stained, dark brown-black, medium–coarse sandy paleosol containing abundant colluvial

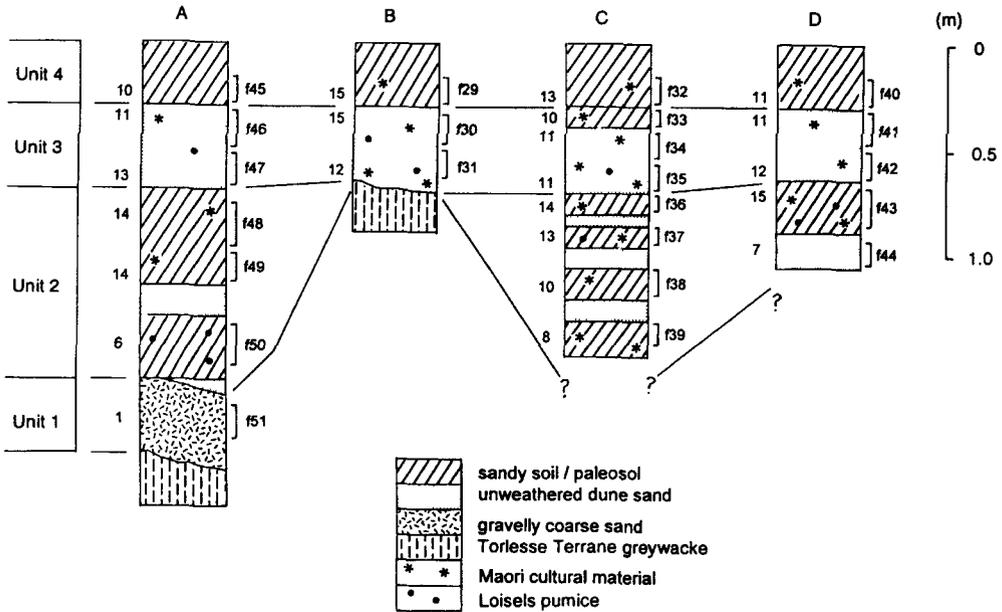


Fig. 3 Stratigraphy of West Bay dunefield showing location of faunal samples (f prefix, right side of columns) and species diversities of fossil landsnail faunas (left side of columns).

weathered greywacke clasts, landsnails and *in-situ* cultural material including fire-blackened stones, marine shell and fishbone (R07/f39). Above that is a series of three paleosols (R07/f36–38), each 10–15 cm thick, with intercalated lenses of moderately consolidated, dark grey medium-coarse sand.

The paleosols comprise moderately consolidated, moderately humic-stained, brown, medium-coarse sand. They contain landsnails and a variety of *in situ* cultural material including marine shell, fishbone, charcoal and obsidian flakes.

The Unit 2 sequence in section D includes a 25 cm thick paleosol (R07/f43) and underlying weakly consolidated dark grey medium-coarse sand (R07/f44). The paleosol comprises moderately consolidated, moderately humic-stained, brown, medium-coarse sand with scattered Loiseles pumice, common landsnails and *in situ* cultural material including marine shell, fishbone, charcoal and fire-blackened stones.

Unit 3: This stratigraphic unit was exposed in all four sections. It conformably overlies Unit 2 in sections A, C and D, and unconformably overlies greywacke bedrock in section B. Unit 3 is 35–50 cm thick and comprises weakly to moderately consolidated, dark grey, medium-coarse sand containing scattered colluvial weathered rock fragments, Loiseles pumice, *in situ* cultural material (including marine shell, fishbone, charcoal, fire-blackened stones, obsidian flakes) and common landsnails (R07/f30, f31, f34, f35, f41, f42, f46, f47). In section C this unit is capped by a 10 cm-thick lens of black-dark brown medium sand containing abundant finely comminuted charcoal (R07/f33).

Unit 4: This includes the present-day soil exposed in sections A-D (R07/f29, f32, f40, f45). The soil is 30 cm thick and comprises a colour A horizon of weakly consolidated, moderately humic-stained, dark brown, medium-coarse sand that contains common landsnails and charcoal fragments, and which is densely invaded by roots of the present-day shrub vegetation

cover (see below). Colluvial subangular weathered greywacke clasts are locally abundant within the soil, and the locally scattered cultural material (including marine shell and fishbone), is also apparently of colluvial (i.e., slopewash) origin.

Key stratigraphic points from the above are, firstly, that the lowest stratigraphic occurrence of Loiseles pumice is at the base of Unit 2 (R07/f50, section A); secondly, that the lowest stratigraphic occurrence of Maori cultural material is also in Unit 2 (R07/f39, section C); and thirdly, that the top of Unit 3 apparently marks the upper stratigraphic limit of in-situ Maori cultural material. If McFadgen's (1982, 1994) dates for the initial washup of Loiseles pumice in New Zealand are correct, it follows that Unit 2 accumulated in the prehistoric period sometime after AD 1300, and that Maori occupation of the dunefield began after that date. The age of Unit 1 is unknown, although the absence of Loiseles pumice suggests that it could be older than AD 1300. Shells of the landsnail *Placostylus hongii* from Unit 3 gave a 'modern' radiocarbon age of <200 years B.P. (WK 5486), indicating that at least the upper part of that unit accumulated after AD 1750. From the presence of *in situ* Maori cultural material, coupled with historical records of the timing of the cessation of Maori occupation of the Chickens Islands (see above), I conclude that deposition of Unit 3 is unlikely to have continued later than the first two decades of the 19th century. If that is correct, it follows that Unit 4 formed over the last 180 or so years.

Burrows of various seabird species, including flesh-footed shearwater (*Puffinus carneipes*), little shearwater (*Puffinus assimilis haurakiensis*), grey-faced petrel (*Pterodroma macroptera*), Pycroft's petrel (*Pterodroma pycrofti*) and northern blue penguin (*Eudyptula minor*), some cohabited by tuatara (*Sphenodon punctatus*), are present in the West Bay dunefield, extending as deep as 0.5 m below the present ground surface (R. J. Pierce pers. comm. 1998). Existing burrows on the dunefield are widely spaced. However, it is clear that such burrowing activity by seabirds and tuatara, if formerly more extensive, could have largely obliterated primary depositional and weathering features in near-surface sediments, and caused mixing of material from surface and subsurface horizons. The internal layered stratigraphy of Unit 2 suggests that at least this part of the sequence has not been so disrupted. The distinction between stratigraphic units 3 and 4 indicates that if bioturbation has modified the upper part of the sequence in the sections examined, its effects must have been largely confined within those respective stratigraphic units.

Present-day vegetation

West Bay dunefield: Dune areas at the southern end of West Bay and to the north and south of the main stream all had different vegetation sequences.

The seaward part of the small dune area at the southern end of the bay had spinifex and shore bindweed, backed by prostrate to low (2 m) shrubland dominated by ngaio (*Myoporum laetum*) with taupata (*Coprosma repens*) in the seaward part, and *Coprosma macrocarpa*, flax, houpara (*Pseudopanax lessonii*) kawakawa (*Macropiper excelsum*), *Melicytus novaezelandiae*, trailing *Muehlenbeckia complexa* and shore bindweed to landward (site 1).

The seaward face of the foredune of the main dunefield south of the stream had sandfield vegetation dominated by spinifex and shore bindweed with rare pingao near the strandline, and common *M. complexa* on the upper slope. Prostrate shrubland dominated by *M. complexa* covered the foredune crest, extending inland for approximately 14 m, with scattered *C. macrocarpa* and taupata along with spinifex, bracken (*Pteridium esculentum*), knobby clubbrush (*Isolepis nodosa*) and shore bindweed (site 2). Between that and the foot of a spur to landwards was a mosaic of 1–2 m tall shrub thickets dominated by *C. macrocarpa* and *M. novaezelandiae*, plus less common kawakawa and ngaio, interspersed with open areas of bracken, flax, knobby clubbrush, *M. complexa*, renga lily (*Arthropodium cirratum*), shore

bindweed and scattered shrubs (site 3). Dune sand also extended up onto the spur where the vegetation cover consisted of 2–4 m tall shrubland dominated by *Streblus banksii* with common *C. macrocarpa*, hangehange (*Geniostoma rupestre*), kawakawa, karaka, mapou, *M. novaezelandiae*, trailing *M. complexa* and scattered groundcover plants of *Phymatosorus pustulatus* and renga lily (site 4).

The sequence north of the stream started with sandfield vegetation dominated by spinifex with common shore bindweed and minor knobby clubbrush and *M. complexa* on the lower seaward foredune slope, grading up into windshorn, prostrate *M. complexa* shrubland with shore bindweed and minor spinifex on the midslope (site 5). Above that was windshorn shrubland of *C. macrocarpa*, houpara, *M. novaezelandiae*, ngaio, trailing *M. complexa* and shore bindweed with minor flax and karaka, ranging in height from approximately 0.6 m at its seaward edge to 1.5 m at the foredune crest. Immediately behind the foredune crest was 3 m tall shrubland dominated by *C. macrocarpa*, houpara and kawakawa with scattered karaka, mahoe (*Melicytus ramiflorus*), *M. novaezelandiae*, ngaio and trailing *M. complexa*, shore bindweed and *Sicyos australis*. Inland of that and extending to the landward margin of the dunefield was 3–3.5 m tall shrubland dominated by *C. macrocarpa*, hangehange and kawakawa with scattered karaka, mahoe, *M. novaezelandiae*, mapou, whau (*Entelea arborescens*), sedges and *Asplenium oblongifolium* groundferns (sites 6, 7).

West Bay hillsides and valley: The vegetation cover consisted of a mosaic of flaxland-shrubland, broadleaf forest and kanuka shrubland and forest.

Areas of flaxland and 1–2 m tall broadleaf shrubland were present on coastal slopes at the northwestern and southern ends of West Bay, and immediately inland of the dunefield shrubland to the north of the stream (sites 8, 11, 15, 16). Characteristic canopy species included flax, *C. macrocarpa*, five-finger, hangehange, *Hebe bollonsii*, karaka, kawakawa, mapou, cabbage tree (*Cordyline australis*), ngaio and tawapou with less common coastal maire, mahoe, pukanui, *Streblus banksii*, whau and wharangi (*Melicope ternata*).

Broadleaf forest was present along the floor of the main stream valley and on south-facing hillslopes to the north of the stream. In the latter area it consisted of pohutukawa emergent over a 6–8 m tall canopy dominated by kohekohe with associated cabbage tree, houhere, kanuka, karaka, mahoe, mapou and pukanui (sites 9, 10). Forest along the valley floor had a 4–7 m tall canopy of cabbage tree, kohekohe, kowhai, mahoe and wharangi with patchily distributed *Carmichaelia australis*, five-finger, karaka, mapou, parapara, tawapou and whau (sites 12–14).

The vegetation cover of north-facing hillslopes on the south side of the stream was predominantly kanuka forest with an understorey including common *Carmichaelia australis*, *Coprosma macrocarpa*, *Coprosma rhamnoides*, fivefinger, flax, hangehange, *Hebe parviflora*, kawakawa, mahoe, mapou and *Pittosporum umbellatum* (site 17).

South West Bay: In this area coastal flaxland-broadleaf shrubland comparable with that described above for the West Bay area, albeit with locally common pohutukawa (site 19), passed landwards into broadleaf forest with emergent pohutukawa over a canopy of coastal maire, karaka, karo (*Pittosporum crassifolium*), kohekohe, mahoe, pukanui, tawapou and wharangi (sites 18, 20).

Classification of snail faunas

A total of 22 landsnail species is recorded here from West and South West bays, comprising 19 fossil species from the West Bay dune sequence and 19 species from present-day habitats (Appendix). Three landsnail species were recorded only as fossils (*Phrixgnathus paralaomiformis*, *Amborhytida tarangensis*, *Placostylus hongii*), and another three species were collected only from present-day habitats (*Liarea egea*, *Cavellia buccinella*, *Flammulina perdita*).

All of the landsnail species recorded from present-day habitats were terrestrial, in leaf litter, humus (where present), and under stones and groundcover plants, but two species (*Tornatellides subperforata*, *Tornatellinops novoseelandica*) were also arboreal. The majority of the snail species present were small, with maximum shell dimensions of 5 mm or less (18 species, 82% of fauna), and two species (*Liarea egea*, *Thalassohelix zelandiae*) had maximum shell dimensions of between 5 mm and 10 mm. Two of the fossil species, *Amborhytida tarangensis* and *Placostylus hongii*, were large, with maximum shell dimensions of up to 33 mm and 78 mm respectively.

Shells of a hydrobiid snail ("*Potamopyrgus*" sp.) were present in several horizons in the dune sequence (see Appendix). The species is extant on Lady Alice Island, but restricted to freshwater seeps (G. R. Parrish pers. comm. 1998). It was not found in any of the shrubland and forest habitats sampled during this study.

A classification of the 43 fossil and present-day faunas produced by cluster analysis of species presence/absence data (excluding "*Potamopyrgus*" sp.) is illustrated as a dendrogram in Fig. 4. The analysis divided faunas into three main groups, labelled A-C on the dendrogram, with one fauna remaining ungrouped. Various diversity measures of faunas in the three groups are listed in Table 2 and frequency distribution curves for sites per species in groups B and C are shown in Fig. 5. Characteristics of the groups are as follows:

Association A (sites 1, 2, f50)

Species diversity per site ranged from 5–6, and the maximum and mean site diversity was close to the total species diversity for the association. The mean of sites per species, 2.1 ± 0.8 SD, has relatively low variance. Three species (*Tornatellinops novoseelandica*, *Thalassohelix zelandiae*, *Paralaoma caputspinulae*) were present at all three sites, and a further three species (*Cytora torquilla*, *Tornatellides subperforata*, *Phrixgnathus* sp. "marshalli") were present at two out of three sites.

Association B (sites 3–7, 9, 15, f29–49)

Species diversity per site ranged from 7–15, with a mean of 11.4 ± 2.4 SD. The maximum site diversity and the mean are three-quarters and just above half of the total species diversity respectively. The mean of sites per species, 15.9 ± 9.7 SD, is low and has relatively high variance. As shown in Fig. 5, 35% of species were found at > 80% of sites. The most widely distributed species were *Tornatellinops novoseelandica*, *Thalassohelix zelandiae*, *Paralaoma caputspinulae* and *Phrixgnathus* sp. "marshalli" (28 sites each), *Delos coresia* (26 sites), *Taguahelix powelli* (25 sites), *Fectola unidentata* (24 sites), *Tornatellides subperforata* (22 sites) and *Phrixgnathus paralaomiformis* (21 sites – i.e., all of the fossil sites). Nine species (45%) were found at fewer than half of the sites, and four species (*Cavellia buccinella*, *Charopa parva*, *Phenacohelix pilula*, *Phrixgnathus* sp. cf. *P. moellendorfi*) were found only at between one and four sites each. Two species (*Phrixgnathus paralaomiformis*, *Placostylus hongii*) are restricted to this association.

Association C (sites 8, 10–14, 16–20)

Species diversity per site ranged from 7–13, with a mean of 10.2 ± 2.0 SD. The values of maximum site diversity and mean relative to total species diversity are very similar in associations B and C (Table 2). Approximately 33% of species were found at > 80% of sites, with the most widely distributed species being *Tornatellinops novoseelandica*, *Thalassohelix zelandiae*, punctid sp. 55 and *Delos coresia* (11 sites each) and *Phrixgnathus* sp. cf. *P. moellendorfi* and punctid sp. 29 (10 sites each). Ten species (56%) were found at fewer than half of the sites, and two species (*Charopa parva*, *Paralaoma caputspinulae*) from single

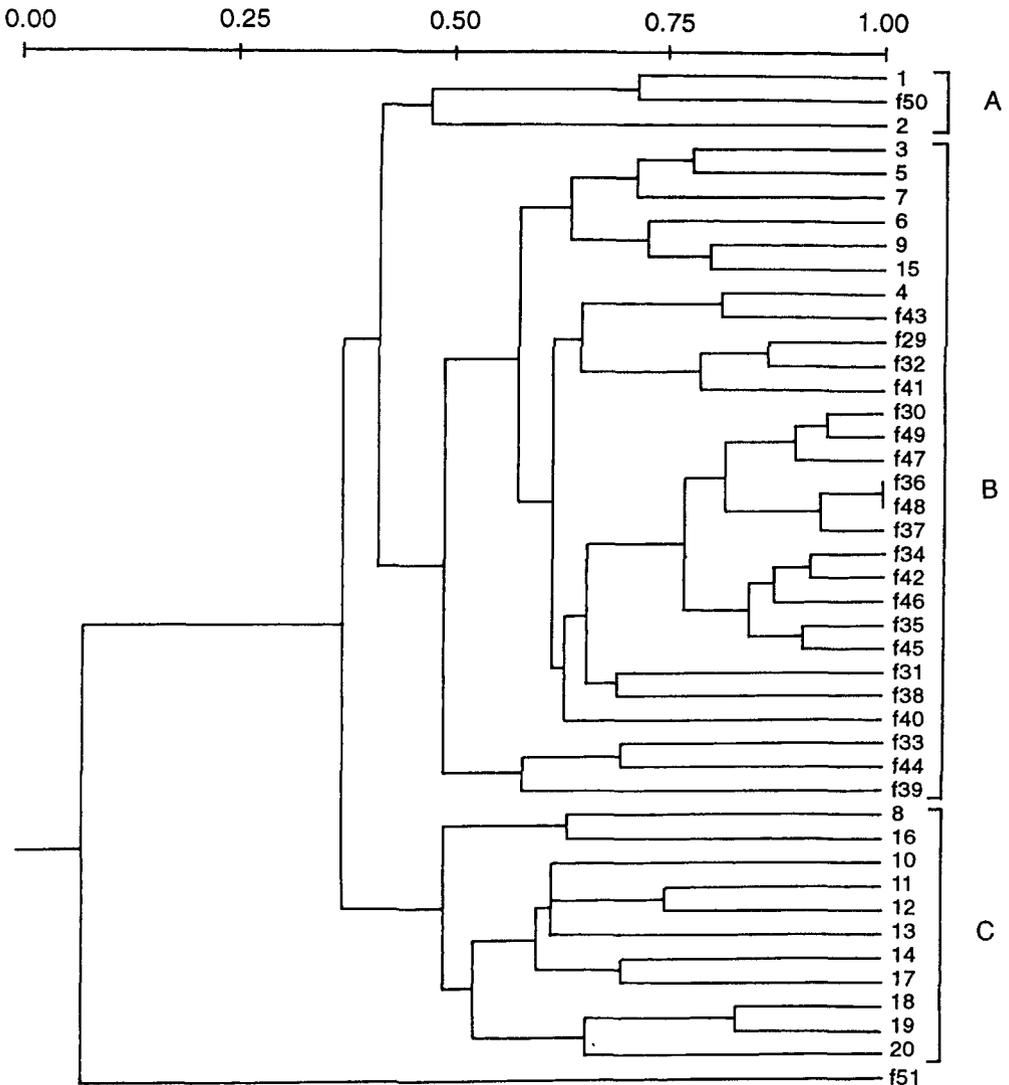


Fig. 4 Dendrogram classification of present-day and fossil landsnail faunas by cluster analysis of species presence/absence data. For descriptions of associations A, B and C see text.

sites each. A further two species (*Liarea egea*, *Flammulina perditia*) are restricted to this association.

The fossil fauna that was ungrouped in the cluster analysis (R07/f51) contained only a single species (*Paralaoma caputspinulae*).

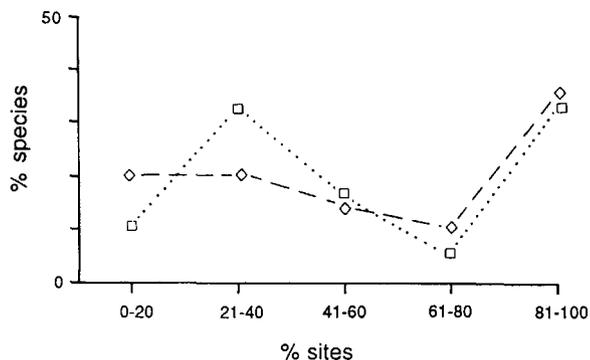
Summarising the species distribution information: *Tornatellinops novoseelandica* and *Thalassohelix zelandiae* were widely distributed across all three associations; *Paralaoma caputspinulae* and *Phrixgnathus* sp. “marshalli” in associations A and B; *Delos coresia* in associations B and C; *Fectola unidentata*, *Taguahelix powelli*, *Tornatellides subperforata* and *Phrixgnathus paralaomiformis* in association B; and *Phrixgnathus* sp. cf. *P. moellendorfi*, punctid sp. 29 and punctid sp. 55 in association C.

Associations A and B were more closely related to each other than either was to association C (Fig. 4). Association A comprised solely low diversity dunefield sites; association B incorporated the majority of fossil and present-day dunefield sites as well as two present-day sites on hillslopes peripheral to dune areas (i.e., sites 9, 15); association C included all other present-day sites on hillslopes. The cluster analysis thus indicates a clear differentiation between dunefield snail faunas and those from clay and gravel colluvium substrata on greywacke hillslopes, albeit with a limited overlap of association B faunas onto hillslopes adjacent to sand dunes. It also indicates the relatively close affinities within associations A and B between fossil and present-day dunefield faunas, despite the fact that three of the fossil species (*Phrixgnathus paralaomiformis*, *Amborhytida tarangensis*, *Placostylus hongii*) were not represented in any of the present-day faunas, and conversely, *Cavellia buccinella* was not found in fossil faunas (Appendix).

Landsnail faunal groupings identified by the cluster analysis show no obvious correlation with vegetation type. The two present-day association A faunas were from tall and prostrate shrubland habitats respectively, and present-day association B faunas were also from a variety of tall and prostrate shrubland plant associations. Association C faunas occupied an even greater range of vegetation types, including flax-shrubland, pohutukawa-kohekohe forest, mixed broadleaf forest lacking pohutukawa, and kanuka forest.

From a stratigraphic perspective the cluster analysis identified a three-fold subdivision of dunefield faunas comprising:

- (i) the monospecific fauna of stratigraphic Unit 1 in section A (R07/f51);
- (ii) a low diversity fauna from the disconformably overlying basal paleosol of stratigraphic Unit 2 in the same section (R07/f50); and



Key:

- ◇ --- ◇ Association B (28 sites, 20 species)
- □ Association C (11 sites, 18 species)

Fig. 5 Frequency distribution curves of sites per species for association B and association C faunas.

Table 2 Measures of diversity within the faunal groupings identified by cluster analysis.

Association	Number of sites	Total number of species	Species per site		Sites per species
			Range	Mean \pm SD	Mean \pm SD
A	3	8	5-6	5.7 \pm 0.6	2.1 \pm 0.8
B	28	20	7-15	11.4 \pm 2.4	15.9 \pm 9.7
C	11	18	7-13	10.2 \pm 2.0	6.2 \pm 3.6
Ungrouped fauna	1	1			

(iii) all of the other fossil faunas in stratigraphic Units 2–4

No correlation was found between faunal composition or diversity and the degree of paleosol development within the dune sequence. Section A showed an upwards increase in snail species diversity over the lower part of the Holocene sequence, which is possibly mirrored in the basal part of sections C and D, but there were no consistent diversity trends in the upper parts of the sequence (Fig. 3)

Paleoenvironmental history

The similarity between the fossil and present-day dunefield faunas within associations A and B suggests that the fossil faunas accumulated in habitats broadly analogous to those still found on the West Bay dunefield today. The species composition and diversity of the association B fossil faunas are comparable with those of present-day snail faunas from prostrate to tall broadleaf shrubland habitats (e.g., sites 3–7), and the fossil fauna in association A (R07/f50) is also very similar to some present-day broadleaf shrubland faunas from the seaward margin of the West Bay dunefield (e.g., sites 1, 2). No present-day analogues of the monospecific *Paralaoma caputspinulae* fauna (R07/f51) were sampled on Lady Alice Island, but identical faunas are widespread in spinifex-dominated sandfield habitats on dunes elsewhere in northern New Zealand (pers. obs). It follows that the faunal succession in the lower part of section A (Fig. 3), marked by an upwards increase in species diversity and a change in species composition from the ungrouped fauna (R07/f51) in Unit 1, to the Association A fauna (R07/f50) at the base of Unit 2, to Association B faunas (R07/f48, f49) higher up in Unit 2, is evidence of a temporal succession in dune vegetation at that site, from sandfield to broadleaf shrubland. That vertical faunal change quite likely represents a seaward shift in dune vegetation ‘zones’ consequent upon coastal progradation, consistent with the change from coarse sand containing wave-rounded pebbles in Unit 1 to a finer-grained sand fraction and absence of rounded pebbles in Unit 2 (above).

It is not clear whether increases in landsnail diversity within the lowest parts of sections C and D (Fig. 3) reflect a comparable succession of shrubland vegetation in those more landward parts of the dunefield, or have some other origin. No consistent faunal trends were observed in the upper parts of the dune sequence, rather, some sections showed an upwards decrease in snail species diversity and others showed an increase (Fig. 3). That variation in species diversity, along with the stratigraphic interfingering of sandy paleosols and unweathered dune sand horizons, presumably reflects a history of spatial and temporal variation in sand accretion and dunefield ecology throughout the period of deposition of Units 3, 4 and the upper part of Unit 2.

The stratigraphic distribution of the three fossil landsnail species that are apparently extinct on Lady Alice Island (*Phrixgnathus paralaomiformis*, *Amborhytida tarangensis*, *Placostylus hongu*) is shown in Fig. 6. The last appearance of *in situ* shells of the two large species is at the top of Unit 3 (i.e., R07/30, f34, f46), at approximately the upper stratigraphic limit of *in situ* Maori cultural material. A radiocarbon age on *Placostylus hongu* shells and historical records indicate that the upper part of Unit 3 accumulated between AD 1750 and about AD 1820 (above). It therefore follows that *Amborhytida tarangensis* and *Placostylus hongu* probably became extinct in the West Bay area in the early 19th century, close to the time when Maori occupation of the Chickens Islands ceased. The last record of *Phrixgnathus paralaomiformis* lies within the lower part of Unit 4 (i.e., R07/f27, f32, f40, f45), indicating that the local extinction of that species probably followed some time after the extinction of *Amborhytida tarangensis* and *Placostylus hongu*, possibly during the period of European occupation and modification of Lady Alice Island in the late 19th century and early part of the 20th century (above).

There is no correlated sedimentologic or faunal evidence to suggest that any of the landsnail extinctions can be attributed to major changes on the dunefield, in habitat type in general or in vegetation type in particular. Landsnail faunal successions spanning the last stratigraphic appearances of the three extinct species are, taken at face value, evidence of the persistence of a broadleaf shrubland vegetation cover on at least the northern part of the dunefield over that time interval. In particular, there was no clear paleoenvironmental evidence in Unit 4 indicating burn-off of dunefield vegetation, although charcoal fragments were common, and historical records indicate that the West Bay area was fired more than once between the late 1880s and 1908 (above). There is a possibility that the northern part of the dunefield escaped firing, and that the charcoal within Unit 4 is entirely of colluvial origin. However, it is more likely that the shrubland vegetation cover was in fact burnt off, but that it and the associated landsnail faunas subsequently re-established fairly rapidly. The apparent absence of any faunal and sedimentological discontinuity within Unit 4 may well be the result of mixing of primary stratigraphy by bioturbation.

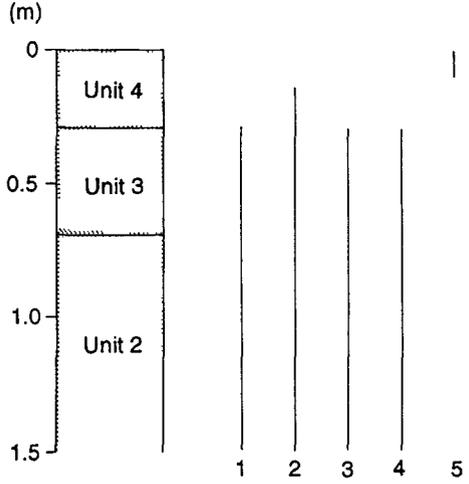


Fig. 6 Stratigraphic distribution in the upper part of the West Bay dune sequence of: (1), in-situ Maori cultural material; (2), *Phrixgnathus paralaomiformis*; (3), *Amborhytida tarangensis*; (4), *Placostylus hongu*; and (5), *Cavellia buccinella*.

Landsnail predation

Tables 3 and 4 give the comparative data on the incidence of repaired lip breakages characteristic of rat predation in collections of adult *Placostylus* shells, and the incidence of lip breakages characteristic of rat predation in collections of juvenile and adult *Amborhytida* shells.

Table 3 Incidence of repaired juvenile lip breakage in collections of adult *Placostylus* shells from rat-free sites compared with sites where kiore was the only rodent present

	Location	No. of shells in sample	No. of shells with breakages	% damaged shells	Kiore present
<i>P. hongu</i>	Lady Alice I. (Fossil, West Bay)	46	0	0	—
	Coppermine I.	28	17	61	yes
	Te Ruatahi dune	43	29	67	yes
	Tawhiti Rahi I.	58	0	0	no
	Aorangi I.	87	0	0	no
	Archway I.	78	0	0	no
	Aorangaia I.	59	0	0	no
<i>P. ambagiosus</i>	Motuopao I.	67	49	73	yes

The *Placostylus* collections from sites where kiore was the only rodent species present all contain a high proportion (61–73%) of shells with repaired lip breakages characteristic of rat predation, whereas no comparably damaged shells were seen in any of the *Placostylus* collections from rat-free islands. The data clearly show, firstly, that this particular type of shell damage is a good indicator of the coexistence of landsnails and kiore, and secondly, that at sites where kiore and *Placostylus* did coexist there was typically a high incidence of attacks by kiore on juvenile *Placostylus* snails. Further, the data provide only a minimum value for the incidence of rat attacks, given that the proportion of juvenile snails actually killed by rats is not considered.

The data on proportions of *Amborhytida* shells with broken lips in collections from rat-free sites and from sites where kiore was the only rodent present indicate that this particular type of shell damage is not caused exclusively by rats, but it is substantially more frequent at sites where rats are present. Thus although kiore are clearly implicated as having a significant impact on the Hen Island *Amborhytida* population, other predators – presumably lizards and birds – also attack snails by breaking the shell lip back in a similar fashion to rats. One noteworthy feature of the Hen Island data is that the proportion of damaged juvenile *Amborhytida* shells is approximately twice that of damaged adult shells. The actual proportion of juveniles killed by predators is probably even higher, given that the weakly calcified shells of small juvenile snails would be largely destroyed during predation, so would be under-represented in shell collections.

Amborhytida was uncommon in the West Bay dune sections examined during this study. A total of eight adults and 28 juveniles was seen. All of the adults were unbroken, and although some of the juveniles had their outer lip broken back, only one shell showed damage comparable with that caused by rat predation (Table 4). The very low incidence of this kind of damage in the West Bay population compares closely with that from two of the rat-free sites (i.e., Aorangī, Motukokako). That observation, and the fact that none of the 46 adult *Placostylus* shells examined from the West Bay dune sequence had repaired lip breakages characteristic of rat predation (Table 3), indicates that kiore were absent from Lady Alice Island during the time period represented by the known stratigraphic occurrence of the two large landsnail species (i.e., within Units 2 and 3, Fig. 6).

Table 4 Incidence of lip breakage in collections of *Amborhytida* from rat-free sites compared with sites where kiore was the only rodent present

	Location	No of shells in sample		% of shells with broken lip		Com- bined	Kiore present
		Adult	Juvenile	Adult	Juvenile		
<i>A. tarangensis</i>	Lady Alice I (Fossil, West Bay)	8	28	0	4	3	–
	Hen I, coastal flat	51	38	20	45	30	yes
	Hen I, ridge crest	57	90	32	67	53	yes
<i>A. pycrofti</i>	Aorangī I	107	11	4	0	4	no
	Tawhiti Rahi I	43	16	14	19	15	no
<i>Amborhytida</i> sp	Motukokako	155	22	1	5	2	no

DISCUSSION

Landsnail biogeography

The total number of landsnail species recorded in the study area, and the maximum number of species per site (22 and 15 respectively), are both relatively low compared with some other coastal areas in north-eastern New Zealand (e.g., Brook & Goulstone 1999). Species previously found on Lady Alice Island that were not recorded during the present study include the slug *Athoracophorus bitentaculatus* (Quoy & Gaimard), semi-slug *Otoconcha dimidiata* (Pfeiffer) and punctid *Paralaoma lateumbilicata* (Suter) (Milligan 1956; Auckland Museum colln.), giving a total known landsnail fauna of 25 species for the island.

The Lady Alice Island landsnail fauna is dominated by species that are widely distributed in Northland, of which 21 (84 %) have a distribution extending to south of Auckland. Of the remainder, two species (*Taguahelix powelli*, *Placostylus hongii*) are restricted to eastern Northland and Auckland regions and a further two species (*Phrixgnathus paralaomiformis*, *Amborhytida tarangensis*) are eastern Northland endemics. Lady Alice Island marks the southern distribution limit of *Phrixgnathus paralaomiformis* (G. R. Parrish pers. comm. 1997), and *Amborhytida tarangensis* is otherwise known only from Hen Island, 7 km to the south of Lady Alice Island (pers. obs.).

It has been suggested previously that *Placostylus* on the Chickens Islands and other Hauraki Gulf islands could have originated from accidental or intentional introductions by prehistoric Maori (Powell 1938; Hayward & Brook 1981; Hayward 1986). The present study documents the coexistence of *Placostylus* and Maori on the West Bay dunefield over a time period of unknown duration (i.e., spanning the deposition of Unit 3 and much of Unit 2, Fig. 6), but unfortunately did not establish whether the stratigraphic range of *Placostylus* extends below the lowest appearance of Maori cultural material or vice versa. That could be determined only by further examination of the lower part of the dunefield sequence.

The study identified a differentiation between landsnail faunas of dunefields (associations A, B) and hillslopes (association C) that parallels a faunistic distinction between prehistoric dunefield and present-day coastal hill forest landsnail faunas on the north-eastern Northland mainland coast between Whananaki and Whangamumu (Brook & Goulstone 1999). Because there was no apparent correlation with vegetation type among the Lady Alice Island landsnail faunal groupings, I suggest that the differentiation of landsnail faunas there results primarily from differences in the physical environment, especially the soil types, between the hillslopes with clay soils formed from weathered greywacke and the sandy dunefield soils with higher porosity, high bioclastic CaCO₃ content and, presumably, consequent higher pH.

The Lady Alice Island dunefield faunas share a number of species with the mainland fossil dune faunas referred to above, including *Cytora torquilla*, *Tornatellides subperforata*, *Tornatellinops novoseelandica*, *Mocella eta*, *Thalassohelix zelandiae*, *Therasiella tamora*, *Paralaoma caputspinulae*, *Phrixgnathus* sp. "marshalli", *Taguahelix powelli*, punctid sp. 29, punctid sp. 55, *Delos coresia* and *Placostylus hongii*. Two other species that were common in the West Bay dunefield, namely *Fectola unidentata* and *Phrixgnathus paralaomiformis*, had a very restricted distribution on the mainland coast, and conversely, *Cavellia buccinella* was widely distributed among the mainland fossil faunas but had very restricted distribution in the West Bay dunefield. The other main difference between the two areas was the absence of a number of widely distributed mainland dunefield species (e.g., *Georissa purchasi*, *Succinea archeyi*, *Huonodon hectori*, *Phenacohelix giveni*, *Phenacharopa novoseelandica*, *Kokikora angulata*) from the West Bay faunas.

The West Bay dunefield habitat is of particular conservation importance in that it contains the only remaining extant landsnail faunas of associations A- and B-type, and also the only sequence of sandfield-dune broadleaf shrubland-coastal hill forest left in Northland. The

faunistically similar mainland prehistoric dune landsnail faunas commented on above are inferred to have lived in broadleaf shrubland-forest habitats comparable with those in West Bay, and to have become extinct as a result of widespread clearance and continued modification of dunefield vegetation during the historic period (Brook & Goulstone 1999). Historic accounts of fires and cattle grazing on Lady Alice Island in the late 19th and early 20th centuries (above) suggest that the vegetation cover on the West Bay dunefield must also have been modified at that time, but unlike on mainland dunefields, native vegetation at West Bay was subsequently able to re-establish without further disruption by human activities.

Landsnail extinctions and kiore

Of the three locally extinct species from the West Bay dune sequence, the two larger species (*Amborhytida tarangensis*, *Placostylus hongii*) apparently died out in the early 19th century close to the time when Maori occupation of the islands ended, whereas the smaller *Phrixgnathus paraalomiformis* (maximum shell dimension of 3 mm) probably died out some time later. The time of extinction of the last-named species cannot be determined precisely from stratigraphy, but there is a strong probability that it was during the period of human impact on vegetation by firing and cattle grazing during the late 19th century and early 20th century (above). The fact that *Phrixgnathus paraalomiformis* disappeared, whereas all of the other small fossil dunefield species persisted, indicates a greater susceptibility to environmental disturbance, and/or that it may originally have had a very restricted distribution on Lady Alice Island. There is no taphonomic or other circumstantial evidence to suggest that kiore played a key role in the extinction of *Phrixgnathus paraalomiformis*. Studies of the diet of kiore on Lady Alice Island in the early 1980s and 1990s showed that although invertebrates smaller than 3 mm were eaten, they constituted only a small minority (<1%) of the total number of invertebrates taken, and the extant small landsnail species formed only a very minor component of the contemporary diet of kiore on the island (Newman & McFadden 1990; Ussher 1995). The invertebrate component of the modern kiore diet probably did not represent that in the period immediately following the arrival of the species on Lady Alice Island, but the predominant selection of prey items larger than 3 mm in the modern diet suggests that *Phrixgnathus paraalomiformis* and other small landsnail species are unlikely to have been preferentially preyed on by kiore.

How long have kiore been on Lady Alice Island? The absence of taphonomic evidence of rat predation on *Placostylus* and *Amborhytida* shells from stratigraphic Units 2 and 3 (i.e., coincident with Maori occupation) suggests that kiore were not present over that time period. It follows that kiore probably did not arrive on the island until the early part of the 19th century, at about the time Maori occupation ended. Such a relatively late arrival indicates that the introduction was probably accidental rather than purposeful. Interestingly, McCallum et al. (1984) had previously postulated that kiore did not reach Lady Alice Island until the 19th century. Their view was based on historical evidence of the high numbers of little shearwater breeding on the island in 1880 (Reischek 1885). McCallum et al. (1984) noted that little shearwaters are sensitive to rodent predation and generally survive only in low numbers on rat-inhabited islands (see also Booth et al. 1996).

The present study did not find any direct evidence to indicate whether kiore arrived on Lady Alice Island after or immediately before the extinction of *Amborhytida* and *Placostylus*. Such evidence could only be obtained from a more thorough excavation of the upper part of the dune sequence in West Bay. However, two lines of circumstantial evidence strongly implicate kiore as the agent of extinction for the two larger landsnail species.

The first is a lack of any correlated sedimentologic or faunal evidence to indicate that the extinctions could have been caused by habitat change. Rather, fossil landsnail faunal

successions indicate persistence of a broadleaf shrubland vegetation cover on the West Bay dunefield over the time interval that *Amborhytida* and *Placostylus* became extinct. In any case, *Placostylus* was not restricted to the West Bay area; shells have also been collected from a ridge above South Cove (Milligan 1956; Prickett 1984), and *Amborhytida*, which is widely distributed in forest on Hen Island, presumably also lived elsewhere on Lady Alice Island. If loss of habitat was the cause, only widespread vegetation clearance could have led to the extinction of both species. However, Reischek's (1881) description of the vegetation cover of Lady Alice Island in 1880 as comprising mostly forest, with second-growth flax and shrubland restricted to former Maori plantations, suggests that vegetation clearance by Maori earlier in the 19th century was localised and of only limited extent.

The second line of evidence is that kiore are known predators of large landsnails elsewhere. Data presented above clearly show that, at sites where kiore and *Amborhytida* coexist, a high proportion of the local population of snails is attacked and killed by the rats. Similarly, where kiore and *Placostylus* coexisted, the incidence of rat attacks was high, and in the case of the *Placostylus* populations on Motuopao and Coppermine islands, the overall abundance and density of snails was also extremely low compared with *Placostylus* populations at rat-free sites (pers. obs.).

If the kiore was responsible for the extinctions, why were the Lady Alice Island *Amborhytida* and *Placostylus* populations killed off when conspecific and congeneric populations have persisted elsewhere at sites with kiore? Obviously any attempt to answer that could only be speculative, but likely reasons include the influence of between-site differences in rat population dynamics and behaviour and/or the influence of macro- and micro-habitats on snail abundance, recruitment and susceptibility to rat attacks. For instance, most *Amborhytida tarangensis* snails on Hen Island live in stony areas and amongst piles of fallen fronds of mature nikau palms (*Rhopalostylis sapida*). Such complex three-dimensional microhabitat types, which presumably afford landsnails some degree of protection from rat attacks, are scarce on Lady Alice Island.

Whatever the particular environmental circumstances leading to the extinction of *Amborhytida* and *Placostylus* on Lady Alice Island, the fact that *Amborhytida tarangensis* is now a relictual endemic, confined to Hen Island and heavily preyed on by kiore, is of concern from a conservation perspective. Although *Amborhytida tarangensis* has evidently coexisted with kiore on Hen Island for a period of at least 100 years (Stead 1937) and possibly since the prehistoric Maori occupation of the island, the present high level of rat predation provides a compelling reason for eradicating kiore from Hen Island as a precaution against the total extinction of this landsnail taxon.

ACKNOWLEDGMENTS

I am grateful to Barbara Lyford for typing the manuscript, Loraine Wells for drafting the figures, Richard Parrish for providing information on landsnail species distribution, and Ian Atkinson, Keith Hawkins, Kim King, Ray Pierce and M. J. Shepherd for suggesting improvements to the text.

REFERENCES

- Anderson, A. J. 1991: The chronology of colonisation in New Zealand. *Antiquity* 65: 767–795.
- Anderson, A. J. 1995: Current approaches in East Polynesian colonisation research. *Journal of the Polynesian Society* 104: 110–132.
- Anderson, A. J. 1996: Was *Rattus exulans* in New Zealand 2000 years ago? AMS radiocarbon ages from Shag Rivermouth. *Archaeology in Oceania* 31: 178–184.
- Atkinson, I. A. E. 1956: An account of *Meryta sinclairii* (pukanui) on Marotiri Island. *Tane* 7: 16–22.
- Atkinson, I. A. E. 1978: Evidence for effects of rodents on the vertebrate wildlife of New Zealand islands. In: Dingwall, P. R.; Atkinson, I. A. E.; Hay, C. ed. *The ecology and control of rodents in New Zealand nature reserves. Department of Lands and Survey Information Series 4*: 7–30.

- Atkinson, I A E 1986 Rodents on New Zealand's northern offshore islands: distribution, effects and precautions against further spread. In Wright, A E, Beever, R E ed *The offshore islands of northern New Zealand Department of Lands and Survey Information Series 16* 13–40
- Atkinson, I A E, Moller, H 1990 Kiore, Polynesian rat. In King, C M ed *The handbook of New Zealand mammals Oxford University Press, Auckland* Pp 175–192
- Bellingham, N O 1956 Some *Leptospermum* communities on Marotiri Island *Tane* 7 23–28
- Bellingham, P J 1984 Forest regeneration on Lady Alice Island, Hen and Chickens group *Tane* 30 31–42
- Booth, A M, Minot, E O, Fordham, R A, Innes, J G 1996 Kiore (*Rattus exulans*) predation on the eggs of the Little Shearwater (*Puffinus assimilis haurakiensis*) *Notornis* 43 147–153
- Brook, F J, Goulstone, J F 1999 Prehistoric and present-day coastal landsnail faunas between Whananaki and Whangamumu, north-eastern New Zealand, and implications for vegetation history following human colonisation *Journal of The Royal Society of New Zealand* 29 107–134
- Cameron, E K 1984 Vascular plants of the three largest Chickens (Marotere) Islands: Lady Alice, Whatupuke, Coppermine north-east New Zealand *Tane* 30 53–75
- Campbell, D J 1978 The effects of rats on vegetation. In Dingwall, P R, Atkinson, I A E, Hay, C ed *The ecology and control of rodents in New Zealand nature reserves Department of Lands and Survey Information Series 4* 99–120
- Campbell, D J, Moller, H, Ramsay, G W, Watt, J C 1984 Observations on foods of kiore (*Rattus exulans*) found in husking stations on northern offshore islands of New Zealand *New Zealand Journal of Ecology* 7 131–138
- Craig, J L 1986 The effects of kiore on other fauna. In Wright, A E, Beever, R E ed *The offshore islands of northern New Zealand Department of Lands and Survey Information Series 16* 75–83
- Cranwell, L M, Moore, L B 1935 Botanical notes on the Hen and Chickens Islands *Records of the Auckland Institute and Museum* 5 215–232
- Cree, A, Daugherty, C H, Hay, J M 1995 Reproduction of a rare New Zealand reptile, the tuatara *Sphenodon punctatus*, on rat-free and rat-infested islands *Conservation Biology* 9 373–383
- Crook, I 1973 The tuatara, *Sphenodon punctatus* Gray, on islands with and without populations of the Polynesian rat, *Rattus exulans* (Peale) *Proceedings of the New Zealand Ecological Society* 20 115–120
- Davidson, J 1990 Key archaeological features of the offshore islands of New Zealand. In Towns, D R, Daugherty, C H, Atkinson, I A E ed *Ecological restoration of New Zealand islands Conservation Sciences Publication 2* 150–155
- Gibb, J G 1986 A New Zealand regional Holocene eustatic sea-level curve and its application to determination of vertical tectonic movements *Royal Society of New Zealand Bulletin* 24 377–395
- Goulstone, J F 1990 Landsnails from South Auckland *Poirieria* 16 2–44
- Goulstone, J F, Mayhill, P C, Parrish, G R 1993 An illustrated guide to the land mollusca of the Te Paki ecological region, Northland New Zealand *Tane* 34 1–32
- Hayward, B W 1986 Prehistoric man on the offshore islands of northern New Zealand and his impact on the biota. In Wright, A E, Beever, R E ed *The offshore islands of northern New Zealand Department of Lands and Survey Information Series 16* 139–152
- Hayward, B W, Brook, F J 1981 Exploitation and redistribution of flax snail (*Placostylus*) by the prehistoric Maori *New Zealand Journal of Ecology* 4 33–36
- Hayward, B W, McCallum J 1984 Offshore Islands Research Group trip to the Chickens (Marotere) Islands, north-east New Zealand, new year 1981–1982 *Tane* 30 12–22
- Higham, T F G, Hogg, A G 1997 Evidence for late Polynesian colonisation of New Zealand: University of Waikato radiocarbon measurements *Radiocarbon* 39 149–192
- Holdaway, R N 1996 Arrival of rats in New Zealand *Nature* 384 225–226
- Isaac, M J 1996 Geology of the Kaitiaki area. Institute of Geological and Nuclear Sciences 1:250 000 geological map 1 Lower Hutt, New Zealand. Institute of Geological and Nuclear Sciences Ltd
- McCallum, J 1986 Evidence of predation by kiore upon lizards from the Mokohinau Islands *New Zealand Journal of Ecology* 9 83–87
- McCallum, J, Bellingham, P J, Hay, J R, Hitchmough, R A 1984 The birds of the Chickens Islands, northern New Zealand *Tane* 30 105–124
- McFadgen, B F 1982 Dating New Zealand archaeology by radiocarbon *New Zealand Journal of Science* 25 379–392
- McFadgen, B F 1994 Archaeology and Holocene sand dune stratigraphy on Chatham Island *Journal of the Royal Society of New Zealand* 24 17–44

- McFadgen, B.G.; Knox, F.B.; Cole, T.R.L. 1994: Radiocarbon calibration curve variations and their implications for the interpretation of New Zealand prehistory. *Radiocarbon* 36: 221–236.
- Meads, M. J.; Walker, K. J.; Elliot, G. P. 1984: Status, conservation and management of the landsnails of the genus *Powelliphanta* (Mollusca: Pulmonata). *New Zealand Journal of Zoology* 11: 277–306.
- Milligan, E. N. 1956: Land Mollusca of some offshore islands. *Tane* 7: 56–57.
- Moore, P. R. 1984: Sedimentary and structural features of greywacke basement on the Chickens Islands. *Tane* 30: 23–29.
- Newman, D. G.; McFadden, I. 1990: Seasonal fluctuations of numbers, breeding, and food of kiore (*Rattus exulans*) on Lady Alice Island (Hen and Chickens group), with a consideration of kiore: tuatara (*Sphenodon punctatus*) relationships in New Zealand. *New Zealand Journal of Zoology* 17: 55–63.
- Parrish, G. R.; Sherley, G. 1993: Invertebrates of Motuopao Island. *Tane* 34: 45–52.
- Percy, C. A. 1956: A primary survey of the vegetation of Marotiri Island. *Tane* 7: 3–6.
- Pook, E. W. 1956: The coastal communities of Marotiri Island. *Tane* 7: 7–11.
- Powell, A. W. B. 1938: The Paryphantidae of New Zealand 4, and the genus *Placostylus* in New Zealand. *Records of the Auckland Institute and Museum* 2: 133–150.
- Prickett, N. 1984: An archaeological survey of the Chickens Islands (Marotere), New Zealand. *Tane* 30: 177–197.
- Reischek, A. 1881: Notes on zoological researches made on the Chickens Islands, east coast of the North Island. *Transactions and Proceedings of the New Zealand Institute* 14: 274–277.
- Reischek, A. 1885: Observations on *Puffinus assimilus* (Gould), Totorore, their habits and habitats. *Transactions and Proceedings of the New Zealand Institute* 18: 95–96.
- Reischek, A. 1930: Yesterdays in Maoriland: New Zealand in the eighties. London, Jonathon Cape, 309 p.
- Rohlf, F. J. 1989: NTSYS-pc. Numerical taxonomy and multivariate analysis system. Exeter Software.
- Skegg, P. D. G. 1965: Historical notes on the offshore islands recently visited by Auckland University Field Club. *Tane* 11: 93–98.
- Solem, A.; Climo, F. M.; Roscoe, D. J. 1981: Sympatric species diversity of New Zealand landsnails. *New Zealand Journal of Zoology* 8: 453–485.
- Solem, A.; Climo, F. M. 1985: Structure and habitat correlations of sympatric New Zealand landsnail species. *Malacologia* 26: 1–30.
- Stead, E. F. 1937: The Maori rat. *Transactions of the Royal Society of New Zealand* 66: 178–181.
- Towns, D. 1992: Response of lizard assemblages in the Mercury Islands, New Zealand, to removal of an introduced rodent: the kiore. *Journal of the Royal Society of New Zealand* 21: 199–136.
- Ussher, G. 1995: Feeding ecology and dietary interactions of tuatara and kiore on the Chickens Islands. Unpublished Msc thesis, University of Auckland.
- Watt, J. C. 1986: Beetles (Coleoptera) of the offshore islands of northern New Zealand. In: Wright, A. E.; Beever, R. E. ed. The offshore islands of northern New Zealand. *Department of Lands and Survey Information Series* 16: 221–228.
- Wellman, H. W. 1962: Holocene of the North Island of New Zealand: a coastal reconnaissance. *Transactions of the Royal Society of New Zealand (Geology)* 1: 29–99.
- Whitaker, A. H. 1973: Lizard populations on islands with and without Polynesian rats, *Rattus exulans* Peale. *Proceedings of the New Zealand Ecological Society* 20: 121–130.
- Whitaker, A. H. 1978: The effect of rodents on reptiles and amphibians. In: Dingwall, P. R.; Atkinson, I. A. E.; Hay, C. ed. The ecology and control of rodents in New Zealand nature reserves. *Department of Lands and Survey Information Series* 4: 75–86.

R98017 Received 12 June 1998, accepted 27 October 1998

APPENDIX

Distribution of snail species among surveyed sites on Lady Alice Island.

Numbers 1–20 are sites at which modern faunas were collected, and numbers with an f prefix denote fossil sites.

LIAREIDAE

Cytora torquilla (Suter)

1, 4, 11, 13, 14, 17–20; f34–37, f40, f42, f43, f45–50

Liarea egea (Gray)

13, 18–20

HYDROBIIDAE

“*Potamopyrgus*” sp.

f29, f35, f38, f40–43, f50

ACHATINELLIDAE

- Tornatellides subperforata* (Suter) 1–9, 15, 16, 18–20; f29, f30, f32, f34–37, f40–43, f45, f47–49
Tornatellinops novoseelandica (Pfeiffer) 1–20; f29–f50

CHAROPIDAE

- Cavellia buccinella* (Reeve) 4, 6, 19
Charopa parva (Suter) 20; f43
Fectola unidentata Climo 2–8, 11, 13, 15; f29–32, f34–38, f40–43, f45–49
Flammulina perdita (Hutton) 13, 14, 18, 19
Mocella eta (Pfeiffer) 4, 7, 10–13, 16, 20, f29, f33, f36, f37, f43, f44, f48
Phenacohelix pilula (Reeve) 8, 11, 12, 16; f29, f32, f33, f41
Thalassohelix zelandiae (Gray) 1–20; f29–50
Therasiella tamora (Hutton) 4, 7, 10, 13, 20; f29–31, f35, f36, f42, f43, f46, f48, f49

PUNCTIDAE

- Paralaoma caputspinulae* (Reeve) 1–7, 9, 15, 16; f29–f51
Phrixgnathus sp. cf. *P. moellendorfi* (Suter) 3, 8, 10–14, 17–20; f29, f32, f40
Phrixgnathus paralaomiformis (Climo) f29–49
Phrixgnathus sp. “marshalli” 1, 3–7, 9, 11, 14, 15, 18–20; f29–50
Taguahelix powelli (Climo) 3–7, 9, 11–14; f29–38, f40–43, f45–49
 punctid sp. 29 4, 8–18, 20; f29–32, f41, f43
 punctid sp. 55 4, 6, 8–20; f29–33, f38, f40, f43, f47, f49

RHYTIDIDAE

- Amborhyuda tarangensis* (Powell) f30, f31, f36, f37, f39, f47–50
Delos coresia (Gray) 3, 4, 6–20; f29–39, f41–49

BULIMULIDAE

- Placostylus hongu* (Lesson) f30, f34, f36–39, f42, f46–49