MINISTRY OF FISHERIES
Te Tautiaki i nga tini a Tangaroa

ISSN 1175-771X

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Published by Ministry of Fisheries
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Citation:
Battley, P.F.; Melville, D.S.; Schuckard, R.; Ballance, P.F. (2005).
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EXECUTIVE SUMMARY

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Farewell Spit and the adjacent intertidal flats (10 000 ha) have been designated as a wetland of international importance under the Ramsar Convention, especially because of the numbers of shorebirds present. Monitoring of shorebird numbers has revealed a reduction of about 75% in numbers of red knots (*Calidris canutus*) between 1961 and 2001, whereas other species have remained stable or increased. The reason(s) for this are unknown, but may relate to changes in food supply and/or availability; however, information on the macrozoobenthos of the tidal flats is limited. This project aimed to collect baseline information on the distribution and abundance of intertidal macro-benthic organisms, with particular reference to prey species for shorebirds.

The tidal flats were surveyed over a spring tide period in March 2003 using a regular 500 x 1000 m grid. A total of 192 sampling stations was visited on the tidal flats. Information was also obtained on eelgrass (*Zostera*) occurrence and sediment characteristics. Supplementary samples were taken at eight sites along the exposed ocean beach.

The tidal flats are composed predominantly of medium-sized sand (0.18–0.50 mm). Coarser sediments (over 0.5 mm) are mostly found on the southern and western edge of the central flats. *Zostera* is widespread, occurring across a 15 km stretch of the central flats, particularly in the mid- to lower-level flats, but surface area coverage varies considerably.

A total of 12 839 specimens of 91 taxa was recorded. Six taxa dominated the samples numerically, accounting for almost 70% of individuals recorded: the cockle (*Astrovenus stutchburyi*) spionid polychaetes, pipi (*Paphies australis*), amphipods, a barnacle (*Eliminius modestus*), and isopods. Most taxa were quite widely distributed and there was evidence of an increase in species diversity with increasing *Zostera* cover. There is some evidence that numbers of shorebirds at high tide roosts may be related to the amount of potential prey present in adjacent intertidal areas.

Sampling was done at a time when shorebird numbers are at an annual maximum, and thus prey stocks may have been depleted. There is a need to assess seasonal changes in prey availability. This survey has laid the groundwork for the development of a long-term monitoring programme, which is needed to meet requirements under the Ramsar Convention, especially in the face of increasing environmental pressures in adjacent areas.

1. INTRODUCTION

Farewell Spit (40°31´S, 172°45´E to 40°35´S 173°04´E) is a long curving sandspit that encloses the northwest part of Golden Bay, Northwest Nelson (Figure 1). Notorious as a shipping hazard, it is equally famous for its populations of migratory shorebirds (Suborder Charadrii). Large numbers of Arctic-breeding migrants as well as New Zealand breeders spend their non-breeding season on the spit and its associated tidal flats. Farewell Spit was designated a Flora and Fauna Reserve, and 9360 ha of tidal flats were set aside as a Sanctuary for the Preservation of Wildlife in 1938 (Cromarty & Scott 1996). It was listed as a Ramsar site (a wetland of international importance for birds) in 1976, and its official status was upgraded to that of a Nature Reserve in 1980. It was declared an East Asian-Australasian Flyway Shorebird Network Site in 2000.

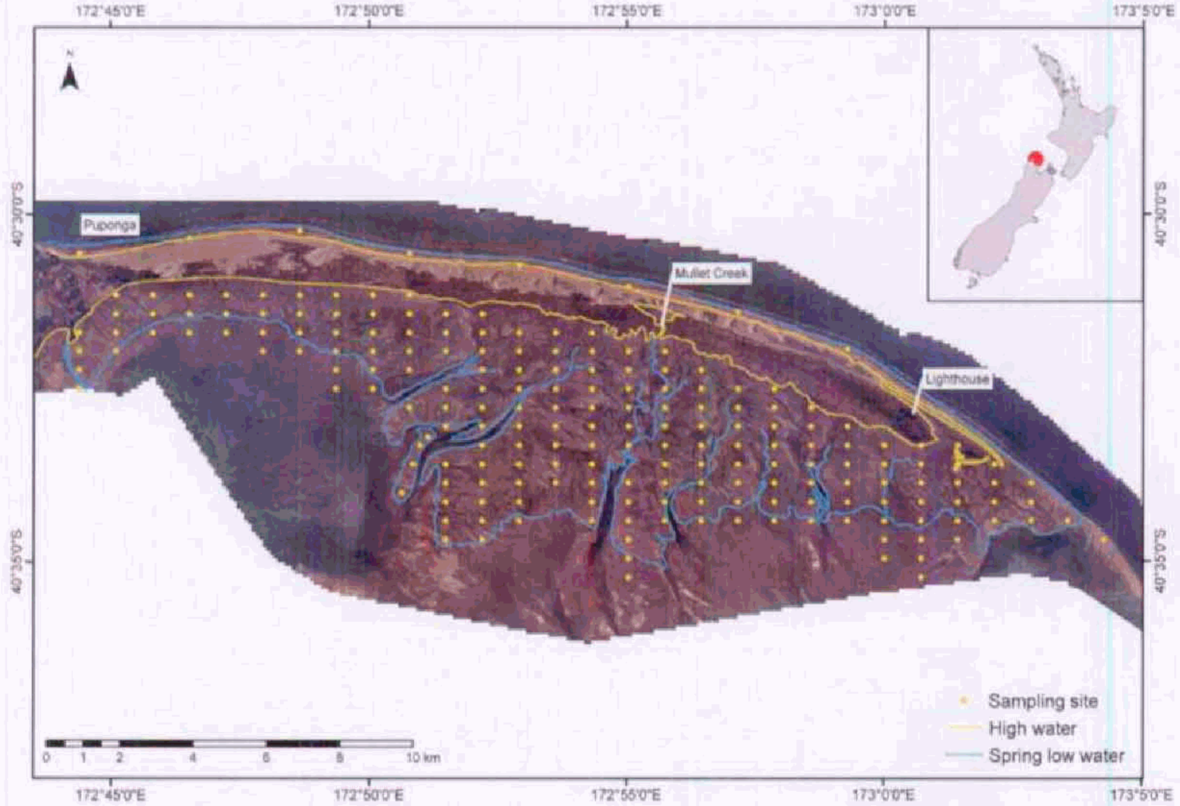

Figure 1: **Map and location of Farewell Spit. The blue line marks the approximate spring low tide edge of the tidal flats and the yellow line shows the 'dry' land part of the spit. Major landmarks are named. The yellow grid marks the sampling sites (Section 2).**

The Ornithological Society of New Zealand (OSNZ) has had a long association with Farewell Spit, the first bird counts being made in 1961 (Schuckard 2002). Since 1984, twice-yearly censuses have been made, which demonstrate the importance of Farewell Spit as a habitat for shorebirds. In summer (November-December) national OSNZ censuses from 1984 to 2001, Farewell Spit held on average 28 900 birds (17.7% of the national total of 163 000). Numbers present in later summer were even higher (39 400), reflecting continued arrivals of northern hemisphere migrants and the return of New Zealand-breeding birds from South Island breeding grounds.

The dominant shorebirds on Farewell Spit are the bar-tailed godwit (*Limosa lapponica*), red knot (*Calidris canutus*), and South Island pied oystercatcher (*Haematopus finschii*). The first two are Arctic migrants, breeding in Alaska and eastern Siberia respectively, whereas the oystercatcher breeds on riverbeds and farmland of the eastern and southern parts of the South Island. The three species show different population trends on Farewell Spit (Figure 2). Bar-tailed godwit numbers varied annually (ranging from 7500 to 23 000) over the 40 years of investigation covered by Schuckard (2002), but numbers appear stable at around 13 000–15 000 birds each year. Red knots, in contrast, have declined significantly from 26 000–27 000 in the 1960s to around 7000 by the early 2000s. This decline was not mirrored at other sites in New Zealand, implicating local effects as the cause. Pied oystercatchers have doubled in number on Farewell Spit since the early 1960s, in tandem with an increase in the national population (Sagar et al. 1999), but nearby populations in Golden Bay and Tasman Bay apparently have declined over the same period. It is not known what has caused these changes in bird populations.

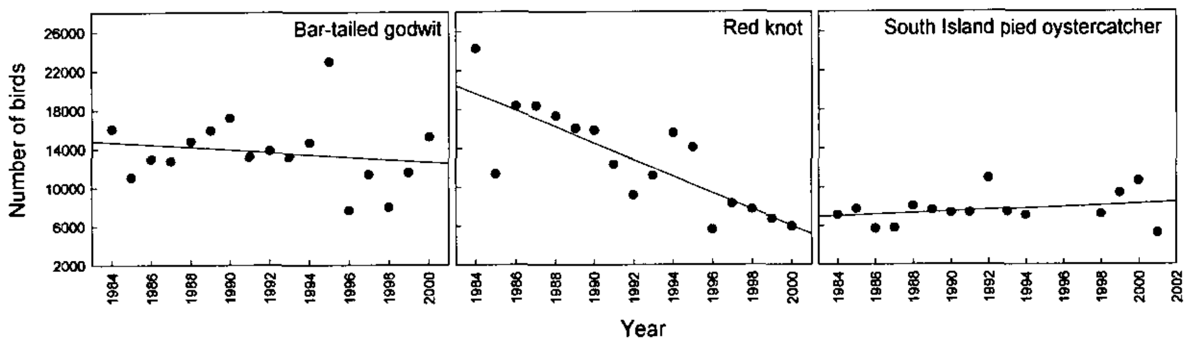

Figure 2: Changes in bird numbers on Farewell Spit from 1984 to 2002, based on OSNZ censuses in summer (November/December) for bar-tailed godwits and red knots, and winter (May/June) for South Island pied oystercatchers.

Formal scientific research on the ecosystems of Farewell Spit has been limited. Before the 1990s, the only investigations on the spit were short visits by the University of Auckland Zoology Department and the University of Auckland Field Club in the mid-late 1970s (Anon 1975, Wright 1978), who conducted single transect surveys across the tidal flats 8 km along the spit (Anon 1975, Anderson et al. 1978), and vegetation surveys of the spit by Bartlett (1985). From 1992 to 1995, Battley (1996) studied the food supply and diet of shorebirds on the tidal flats of the outer spit near the lighthouse compound. Using observations and faecal analyses he described the diets of bar-tailed godwits, red knots, and South Island pied oystercatchers, and made the first measurements of changes in prey quality and availability through the year. Some findings were probably quite robust and applicable to the tidal flats of Farewell Spit as a whole. Red knots were shown to predominantly feed on small molluscs, particularly bivalves (pipi (*Paphies australis*), cockle (*Austrovenus stutchburyi*) and nutshell *Nucula hartvigiana*)), 2–15 mm long. Oystercatchers showed what was probably individual prey specialisation, with many birds feeding on cockles, a few on mussels (*Xenostrobus pulex*), and others on polychaete worms (deeply buried species, fed on by probing, and the shallow stout scalibregmatid *Travisia olens*[1], fed on by 'sewing'). Bar-tailed godwits fed mostly on polychaetes, following the tide-line out to take advantage of the presumed higher availability of worms in wet sediment.

The benthos of four 1-ha quadrats (and an additional area of upper-beach 'pan' flooded only on spring tides) was sampled in detail to give information on the relative abundance and quality of different prey types in areas where birds regularly fed. There were large differences in the composition of the communities at each site, though cockles and worms dominated the biomass of 'offshore' sites while small Crustacea (especially amphipods) provided most of the biomass at a site close to the shore. There was huge variation in the biomass relevant to the different bird species between sites and also between sampling periods: for godwits, polychaete biomass ranged from 0.75 to 2.75 g m^{-2} ash-free dry mass (AFDM); for knots, biomass of small bivalves, Crustacea, and insect larvae (the last only on the sandy pan) ranged from 0.075 to 2.15 g m^{-2} AFDM; for oystercatchers, biomass of polychaetes and large cockles and pipi ranged from 1 to 11 g m^{-2} AFDM. Much of the variation in biomass was a result

[1] Following Read (2004), we treat *Travisia olens* as being a member of the Scalibregmatidae rather than the Orbiniidae.

of changes in flesh content of individuals, with an almost two-fold range in biomass calculated for 35 mm cockles in the year of study. Although the scale of study was appropriate for the project, it allowed strong inference about only a limited area and time. To determine how representative the invertebrate densities are, and to assess whether the apparent low numbers of small bivalves suitable for knots is a feature of the spit as a whole, a much larger-scale sampling effort was required.

This project was therefore stimulated by a desire to gather baseline data on the distribution of potential food resources for shorebirds across the entire tidal flat area of Farewell Spit. This was clearly beyond the abilities of a small team of researchers. The spit stretches almost 30 km in length, and best estimates of the size of the tidal flats are that they extend up to 7–8 km offshore in places, and cover about 9900 ha (Walker 1987). There is no high-tide vehicle access along the spit, and the only buildings are at either end of it. However, we were encouraged by the success of a recent large-scale benthic survey of Roebuck Bay in Northwest Australia (Pepping et al. 1999). In this survey, large numbers of volunteers and logistical acrobatics enabled a grid of 200 x 500 m to be sampled across an area of 45 km^2, and sorted on site. We based our sampling effort on this approach, albeit at a less ambitious scale. Calculations of the fieldwork effort required for initial plans to sample the spit on a 500 x 500 m grid made it clear that this intensity of sampling was impractical. Instead, transects every kilometre were planned with sample sites every 500 m. With the help of volunteers from the Nelson-Marlborough Institute of Technology and OSNZ, we completed the large-scale grid survey of the entire tidal flat area in less than 2 weeks. The overall and specific objectives for the project were as follows.

Overall objective
To provide baseline information on the distribution and abundance of intertidal macrobenthic organisms, with particular reference to prey species for shorebirds.

Specific objectives
1. To undertake a baseline survey of intertidal macrobenthic organisms at Farewell Spit Nature Reserve and adjacent flats.

2. To undertake an initial field survey of *Zostera* distribution at Farewell Spit Nature Reserve and adjacent intertidal flats.

3. To undertake a preliminary survey of sediment characteristics of the intertidal flats at Farewell Spit Nature Reserve and adjacent flats.

2. METHODS

2.1 Survey area and design

2.1.1 Study area

The study area (Figure 1) comprised the contiguous tidal flats on the south side of Farewell Spit from Triangle Flat, Puponga (40°30′30″ S, 172°44′25″ E) to the tip of the spit (40°34′41″ S, 173°04′16″ E), an area of about 10 000 ha. This includes areas both within and outside the declared Sanctuary for the Preservation of Wildlife.

2.1.2 Timing

The survey was undertaken between 15 and 28 March 2003 over a spring tide series, the greatest predicted tide range for Collingwood being 5.2–0.0 m on 20 March. The timing of the survey was determined largely by the availability of personnel and equipment, but also took into account expected weather conditions.

2.1.3 Survey design

A pilot survey in February 2002 to determine the feasibility of the project confirmed that the tidal area could be safely traversed on foot, and that adequate surface water was available for the sieving of benthos samples in situ. It became apparent during this survey that the surface cover of the eelgrass, *Zostera muelleri*[2], or lack of it, did not necessarily relate to conditions below the surface. In particular, some areas without *Zostera* cover had dense peaty deposits of dead material, including *Zostera* remains, below the surface, whereas other areas were more or less pure sand. This, together with the lack of full aerial image cover of the intertidal area, meant that the development of a stratified random sampling programme was inappropriate. Instead, we decided to use a regular grid pattern for sampling across the tidal flats.

The large study area, limited personnel, and the survey being undertaken over one spring tide period placed constraints on the sampling programme. We decided to use transects running south from the spit at 1 km spacing, with sample stations at 500 m intervals along transect lines from the edge of the saltmarsh to the lowest point which could be reached on low spring tides. Sample sites were identified by eastings and northings on the New Zealand Map Grid Projection.

Based on the area of 'sand and mud' shown on the 1:50 000 New Zealand Topographical Map (Sheets NZMS 260: M24, N24, N25) our initial estimate of potential sample sites was 279 (Appendix 1). The topographical map accurately located the major channels through the tidal flats, but determining the extent of saltmarsh on the upper tidal area and the lower tidal limits of the sandflats was difficult. Eight-seven proposed sites could not be sampled because they occurred in saltmarsh (12) or were subtidal even on spring tides or were in channels (75). One site on the mainland tidal flats could not be visited due to difficulty of access and safety considerations. Three sample sites on offshore banks could not be visited. An additional four sites were accessed on the southeastern and western intertidal area, and eight more along the ocean beach on the north shore of the spit. A total of 192 sites was sampled on the tidal flats (Figure 1, Appendix 1).

[2] Nomenclature of *Zostera* in New Zealand has been unclear to date. Two species were historically recognised (*Z. novazelandica* and *Z. capricornia*), but recent work has shown the two to be conspecific (Les et al. 2002). Although *capricornia* is the name currently in use (Inglis 2003), *Z. muelleri* in fact has precedence and was inadvertently not used by Les et al. (2002) (D.H. Les, Department of Ecology and Evolutionary Biology, University of Connecticut, USA, pers. comm., May 2004).

Practical considerations determined the choice of three cores per sample station – an increase in the number of cores could only have been accommodated through a reduction in sample sites: 615 cores were taken in total.

Although 0.5 mm sieves are commonly used in benthic community studies (Robertson et al. 2002), a 1 mm mesh sieve is usually used for studies of potential shorebird prey species and for community studies of sandy beaches (Howes & Bakewell 1989, Rafaelli & Hawkins 1996, Pepping et al. 1999) and was used in this study. Previous work on the spit (Battley 1996) found that a 0.565 mm sieve retained large amounts of sand at some sites near the spit tip, so a 1 mm sieve was deemed more practical than a smaller sieve size.

As an adjunct to this project, OSNZ coordinated an aerial survey of the Farewell Spit tidal flats, funded jointly by the Department of Conservation and the Tasman District Council. Unfortunately, this could not be done before fieldwork began, but it has allowed us to examine our field data in relation to a current map image.

2.2 Field and laboratory methods

The fieldwork was undertaken by volunteers from the OSNZ and Conservation Ranger students from the Nelson-Marlborough Institute of Technology. One day was spent introducing the field techniques and safety procedures to participants, all of whom were already experienced in the use of GPS.

The location of sample stations was determined in the field using GPS set to the New Zealand Map Grid, with an accuracy of usually +/- 5 m. Field teams operated from a boat for the outermost stations, the other sites being reached on foot across the flats from the spit. The daily programme was determined to maximise time on the tidal flats according to the varying tidal conditions.

2.2.1 Macrobenthos invertebrate survey

At each sample point, three cores (100 mm diameter) were taken to a maximum depth of 250 mm. Samples were sieved in situ over a 1 mm mesh, and material retained was stored in labelled plastic bags for sorting and processing. Sample material was taken to the laboratory and sorted in seawater in white plastic trays. Samples were then fixed in 5% formalin made with seawater and archived in labelled bottles.

Invertebrates were identified to the lowest possible taxon. Reference works used included: Day (1967), Morton & Miller (1973), Powell (1976), Hurley & Jansen (1977), Powell (1979), Jones (1983), McClay (1988), Winterbourn & Gregson (1989), Beesley et al. (1998), Crowe (1999), Beesley et al. (2000), Parkinson (2000), and Rouse & Pleijel (2001). A reference collection of named specimens was built on that collected by Battley (1996) and taxonomic assistance was provided by Rod Asher (Cawthron Institute, Nelson).

Specimens were measured to the nearest millimetre using vernier callipers or by placing the specimen over 1 mm graph paper. Size measurements were body length for most taxa (including partial specimens), apart from gastropods (shell length), bivalves (shell width), crabs (carapace width), barnacles (width), and anemones (width of the pedal disc). For each organism (or part thereof) we recorded whether it was whole or not, and if not, whether (for polychaetes) it represented a head, tail, or other body part. We additionally recorded whether the body part represented a new individual (e.g., all heads, tails only in the absence of head sections, or body parts of such different sizes that they could not have come from the same individual). In analyses, size distributions were calculated only from complete specimens, whereas density estimates were calculated from all whole or part specimens that could be identified as representing an individual. If larger polychaetes are more prone to breaking than smaller ones, then length distributions will be biased downwards. When selecting data on the basis of body size (Section 6), polychaetes will inevitably be underrepresented as broken worms will be recorded as shorter than they really were.

Hinge height and shell width were measured in a subset of *Nucula hartvigiana* to allow reconstruction of shell length from hinge remains, according to the methods of Battley (1996) (see Appendix 2). Relationships for *Austrovenus stutchburyi* and *Paphies australis* had already been determined and used in determining the diet of red knots (Battley 1996).

Ten percent of the samples collected were randomly selected and submitted to the Cawthron Institute for auditing of sorting and taxonomic determination. This proportion followed the Quality Control Protocol recommended for stream macroinvertebrates (Stark et al. 2001), as there is no accepted QCP for marine macrobenthos.

2.2.2 *Zostera* distribution and coverage

At each benthos sampling station a 0.25 m^2 quadrat was placed on the substrate and the percent cover of *Zostera* estimated with reference to a standard set of photographs, this being the recommended method of the SeagrassNet project (Short et al. 2001) (Figure 3). A six-category scale was used, based on the Braun-Blanquet scale (Mueller-Dombois & Ellenberg 1974). The 1–6 scale recorded in the field corresponded roughly with *Zostera* cover of 0%, 1–5%, 6–25%, 26–50%, 51–75%, and 75–100%. Observations were made at low tide, when the plants were lying flat.

Any live *Zostera* taken with the benthos cores was sorted in the laboratory. Initially it was planned to gently dry samples with absorbent paper and then weigh them to the nearest 0.5 g to provide an indication of *Zostera* biomass. In some samples it proved difficult to separate 'live' *Zostera* rhizomes from 'dead' material and the separation became somewhat subjective. Furthermore, the use of absorbent paper proved difficult and so samples were squeezed 'dry' and then weighed. This change in the method is not considered to be significant because the results are intended only to provide an index of *Zostera* biomass to compare with the visual cover estimates.

2.2.3 Sediment characteristics

At each benthos sampling station a core (25 mm diameter) 100 mm deep was taken for sediment grain size analysis. The sample was placed in a labelled plastic bag at the time of collection and returned to the laboratory for storage or analysis. In addition to samples from the tidal flats, samples were also collected from the ocean beach and the sand dunes.

The whole sample was washed (with seawater) through a kitchen sieve (mesh size about 1.5 mm) into a jar to remove shells, *Zostera*/algae, and any pebbles. A 25 ml subsample of washed sand was then washed through a set of five nested sieves using a domestic garden pressure-spray bottle. The sieve mesh sizes were: very coarse (over 1 mm), coarse (0.5–1 mm), medium (0.25–0.5 mm), fine (0.125–0.25 mm), and very fine (0.063–0.125 mm). These are the whole-phi divisions 0 to +4 of the Wentworth size scale, thus encompassing all of the sand particle-size divisions (2.0 mm to 0.063 mm). Sieves were removed from the top down, when it was considered that separation had been completed on each sieve. Starting with the coarsest mesh size, sieve contents were washed into a 25 ml measuring cylinder, graduated in 0.5 ml divisions, standing inside a jar in the bucket. As the contents of each sieve were washed into the cylinder, the cumulative volume of sand was measured to the nearest 0.5 ml (i.e., ±2%), after tapping the cylinder to ensure settlement of the sand. The final volume present in the cylinder was taken as the 100% figure for calculating grain size proportions. Any apparent silt fractions (which remain suspended in water) were noted (this was a very small component, if present at all, at most sites). There were some concerns about how reliably the wet-sieving method separated the sediment sizes, and turbulence where the funnel tip was guiding sand into the 25 ml measuring cylinder caused some loss of sand, particularly finer sand, with the water run-over from the cylinder. For analyses of the field-sieved samples, sediments have been grouped into three categories: fine sand (over 0.25 mm), medium sand (0.25–0.5 mm) and coarse sand (over 0.5 mm). As initial field-sieving suggested there was little variation between samples, and the processing proved to be relatively time-consuming (about 0.5 hours per sample), not all samples were analysed at the time. On some transects only every second sample was analysed, so that 145 samples were analysed fully. The coarse sand fraction was subsequently measured on 42 of the remaining sites. Duplicate samples from some sites were analysed with a laboratory dry-sieving method at the Geology Department, University of Auckland, with twice the frequency of sieve sizes (half-phi units).

The depth of the redox potential discontinuity (or depth of the anoxic layer, as it is sometimes referred to) was measured with a scaled rule in the field at the time of sample collection. At times this proved difficult, especially with very wet cores.

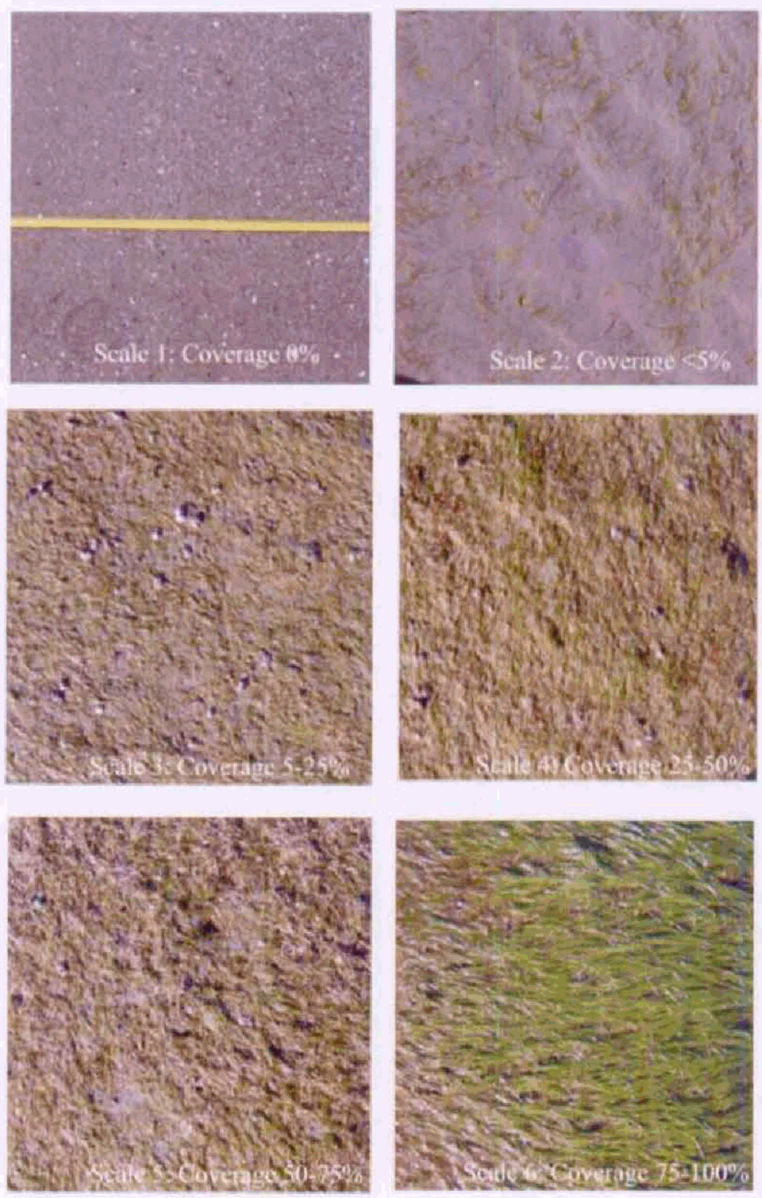

Figure 3: **The *Zostera* scale used for reference in the field.**

3. SEDIMENT COMPOSITION AND EELGRASS

3.1 Sand grain size

Laboratory analyses (dry-sieving) of seven tidal flat sediments found that they were composed predominantly of medium-sized sand grains (0.18–0.50 mm), with some variation between sites (towards both fine and coarse grains: Table 1). Sediments were well sorted and were mostly skewed in their grain size distributions.

Table 1: Grain size analysis (percent per size class) of sediments at seven tidal flat sites.

	Grain size range (mm)								Graphic mean[1]	Sorting[2]	Skewness[3]
Site	>1	0.5–1.0	0.36–0.50	0.25–0.36	0.18–0.25	0.125–0.18	0.09–0.125	0.063–0.09	(Ø)	(Ø)	(Ø)
FF6073500	0.0	0.4	2.9	21.9	47.7	25.4	1.4	0.2	2.03	0.45	-0.06
H6071000	0.0	0.6	10.4	40.7	39.3	8.6	0.3	0.0	1.73	0.46	+0.07
HH6071500	0.0	2.5	21.8	46.8	23.5	5.3	0.1	0.0	1.53	0.48	+0.10
II6073500	0.0	0.3	4.0	36.4	43.4	14.4	1.4	0.2	1.83	0.43	+0.15
LL6069500	0.0	2.5	14.8	39.1	33.9	9.4	0.2	0.0	1.65	0.48	0.00
N6070500	0.0	9.0	26.1	38.9	20.3	5.6	0.2	0.0	1.43	0.55	-0.04
O607000	0.0	7.7	46.9	38.6	5.1	1.2	0.0	0.0	1.20	0.41	+0.06

[1] 1 to 2Ø, medium sand; 2 to 3Ø, fine sand
[2] Inclusive graphic standard deviation: <0.35Ø, very well sorted; 0.35 to 0.5Ø, well sorted; 0.5 to 0.71Ø, moderately well sorted
[3] Inclusive graphic skewness: +0.3 to +0.1, fine skewed; +0.1 to -0.1, near symmetrical; 0.0, symmetrical; -0.1 to -0.3, coarse skewed

Less detailed analyses were done on most of the samples, which were processed with the field-friendly wet-sieving method. Apparent variation between samples and/or processors meant that we decided to combine the sand size-data into three categories: fine (under 0.25 mm), medium (0.25–0.5 mm) and coarse (over 0.5 mm). The resulting sand-size compositions are shown in Figure 4. Fine sand was present at most sites, and coarse sand had a more heterogeneous distribution on a large scale. The differences are more visible in the plots of these two categories on their own (Figures 5 and 6). Large proportions of fine sand were found only on one central transect and at the eastern end of the spit. The easternmost of those sites was adjacent to a sandy pan behind shellbanks that is flooded only on spring tides. This pan probably provides suitable conditions for settlement of fine sand, which may then wash out onto the nearby flats. The central sites with fine sand were either adjacent to the saltmarsh or in areas with moderate to high eelgrass cover.

Coarse sand was found mostly on the southern and western edges of the central flats, near the spring low tide edge (Figure 6). In contrast, almost all of the large central tidal flats had minimal quantities of coarse sand (under 10%). Comparison of grain sizes on selected tidal flat sites and sites on the large sand dunes of the spit itself indicated that the dunes are composed of finer sand than the tidal flats (OSNZ, unpublished data). This implies that sand blown from the dunes onto the tidal flats may be a source of medium- and fine-grained sediments, but coarse sand must be arriving by another mechanism.

The sediment analyses (both laboratory and field) confirm that the tidal flats of Farewell Spit are unequivocally sand flats. There were virtually no traces of truly fine sediment (which remain suspended in water during sieving), which accords with the findings of Sevon (1966) and Gregory et al. (1979). Traces that were present could as easily have been decomposing eelgrass as silt.

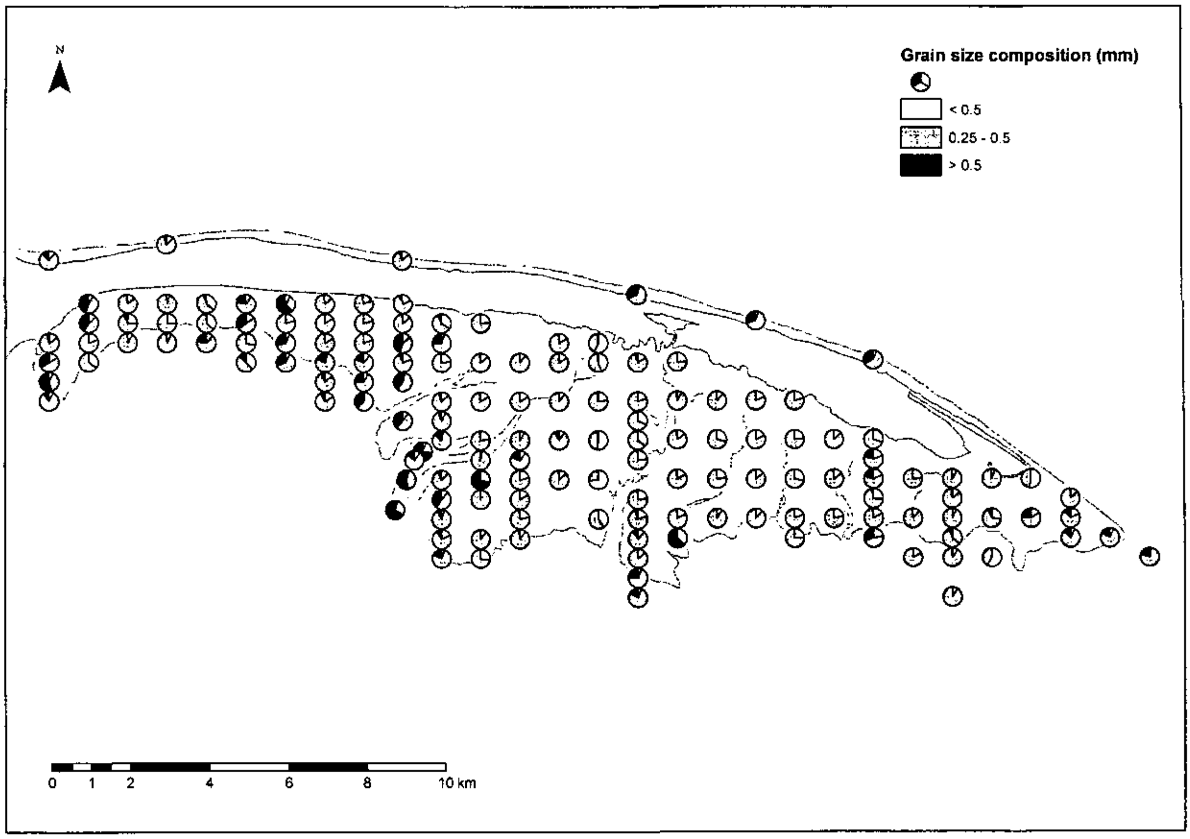

Figure 4: **Sediment grain size composition across the Farewell Spit tidal flats. Pie charts show the proportion of each grain size class at each site.**

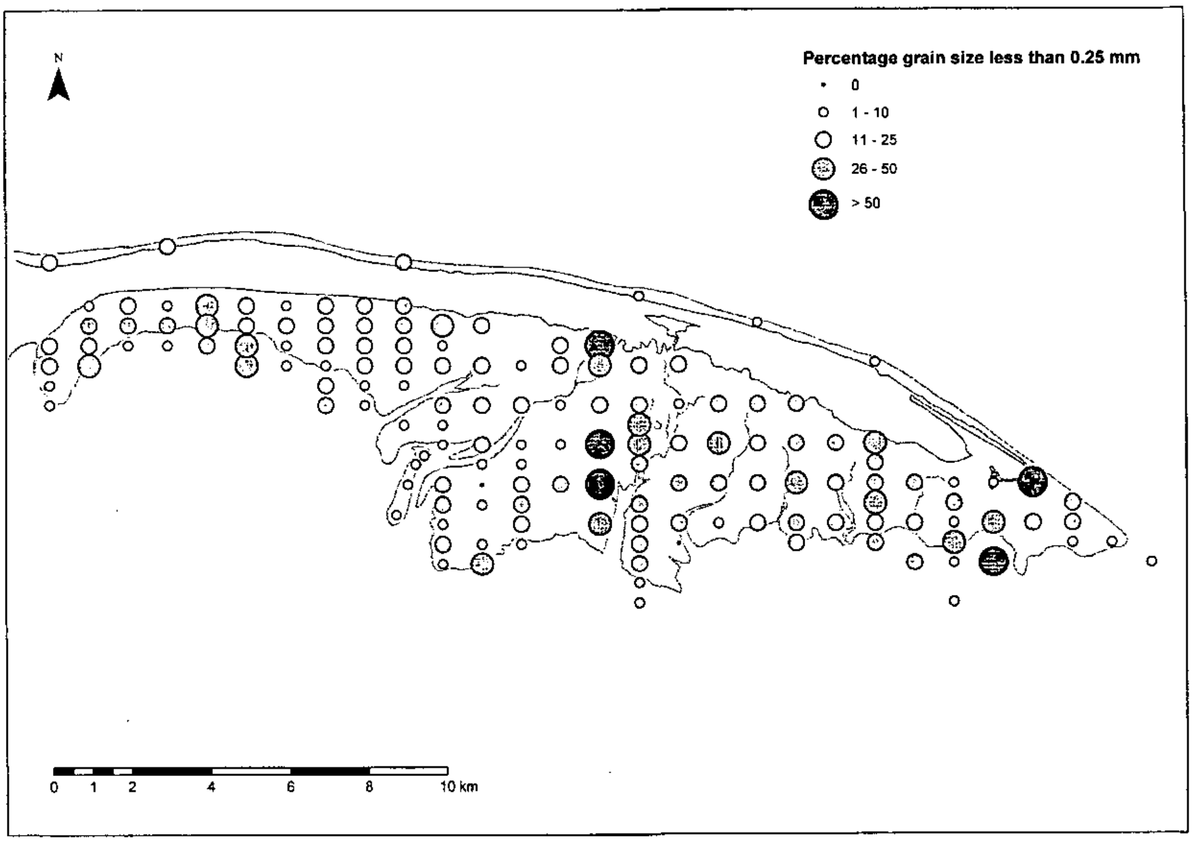

Figure 5: **Distribution of fine sediments (grain size <0.25 mm) across the Farewell Spit tidal flats.**

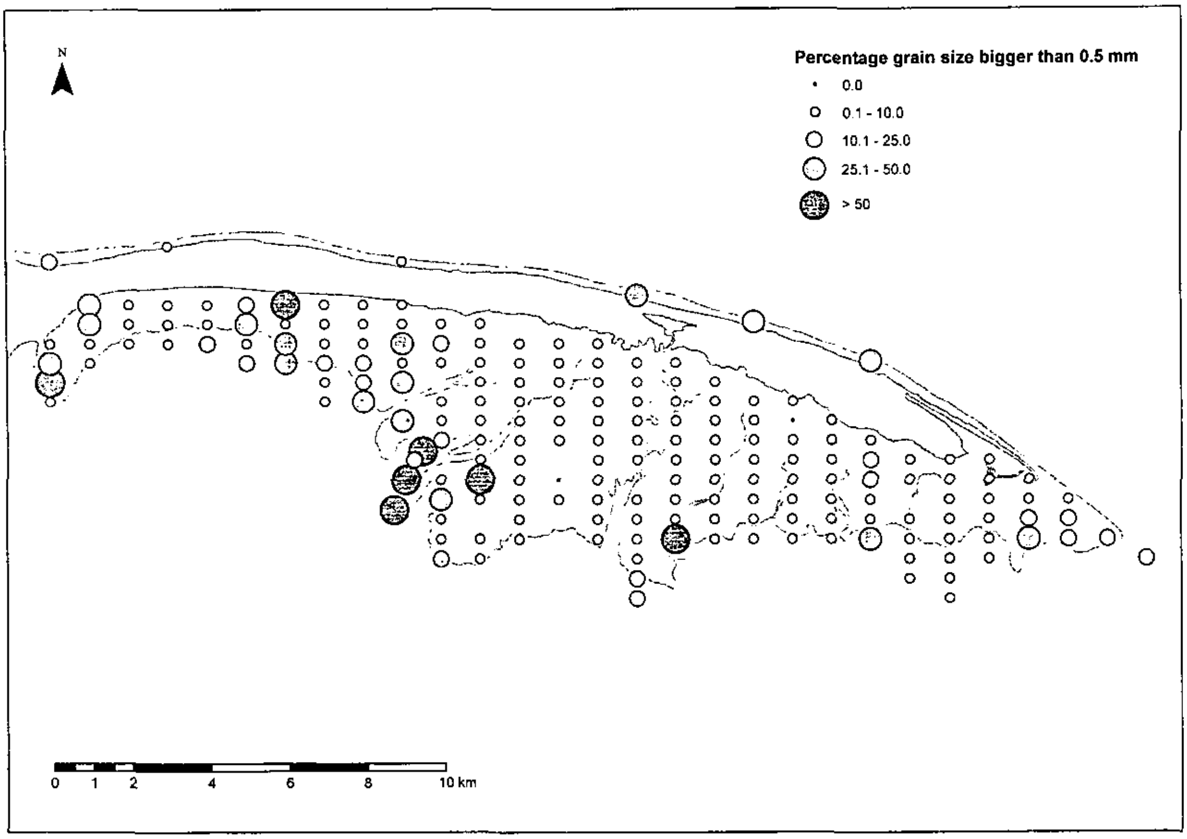

Figure 6: **Distribution of coarse sediments (grain size >0.5 mm) across the Farewell Spit tidal flats.**

3.2 Eelgrass (*Zostera muelleri*) cover

The eelgrass *Zostera muelleri* was present at 120 of the 192 sample sites on the tidal flats. Visual density estimates (using the 1–6 scale) recorded 55 sites with an eelgrass cover score of 2 (equating to about 1–5% cover), 33 with a score of 3 (6–25% cover), 14 with a score of 4 (26–50% cover), 13 with a score of 5 (51–75% cover), and five with a score of 6 (over 76% cover). Eelgrass was therefore mostly light in cover, with few sites having dense beds. Given the low intensity of sampling (transects every kilometre, sites every 500 m), these proportions nevertheless translate into extremely large eelgrass beds. The areas of moderate to high eelgrass cover occurred adjacent to Puponga at the base of the spit, and across a 15 km stretch of the central tidal flats of the spit, particularly in the mid- to lower-level flats (Figure 7).

All core-sampled eelgrass rhizome and leaf matter was squeeze-dried and weighed, so for most sites we have a surface cover estimate and an index of the mass of plant matter. *Zostera* mass was well correlated with the surface cover estimate (Figure 8; ANOVA, $F_{5,184}=80.721$, $P<0.0001$, $R^2=0.685$), with all but categories 5 and 6 having significantly different *Zostera* masses (Bonferroni post-hoc test). The map for *Zostera* mass (Figure 9) is therefore very similar to that for surface cover.

However, it is apparent that there is substantial variation in the amount of eelgrass cored for a given surface cover score. Part of this may reflect the fact that only a single cover estimate was made whereas three cores were taken from the immediate area (which could vary in eelgrass cover over that scale). Another influence could be the age of the eelgrass bed, as long-established beds may have denser root matter than recently established beds, despite their similarity on the surface. The presence of 1–18 g of eelgrass in areas without any eelgrass apparent on the surface could also reflect sampling errors; alternatively, light eelgrass will be more easily covered in sand and overlooked, or the material

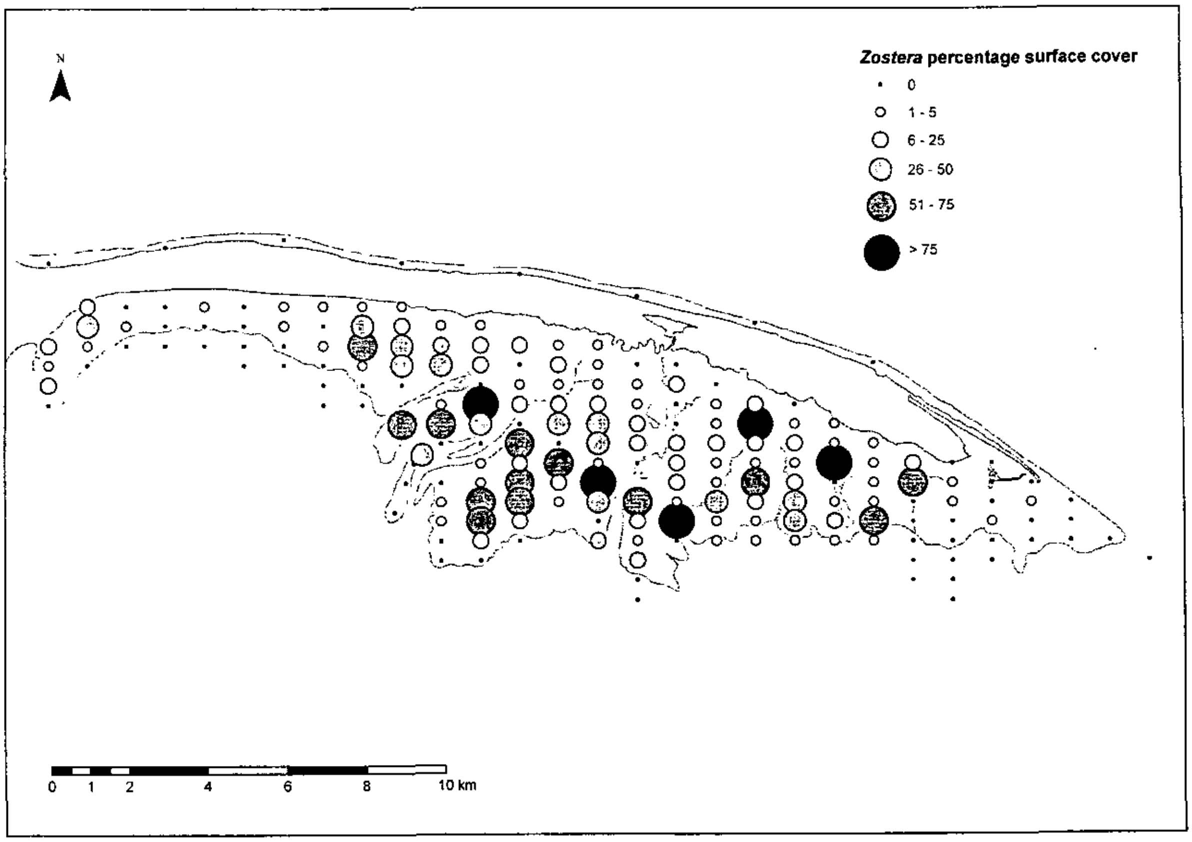

Figure 7: *Zostera* surface cover on the Farewell Spit tidal flats. Percentage surface cover is based on a visual assessment with reference to standard photographs.

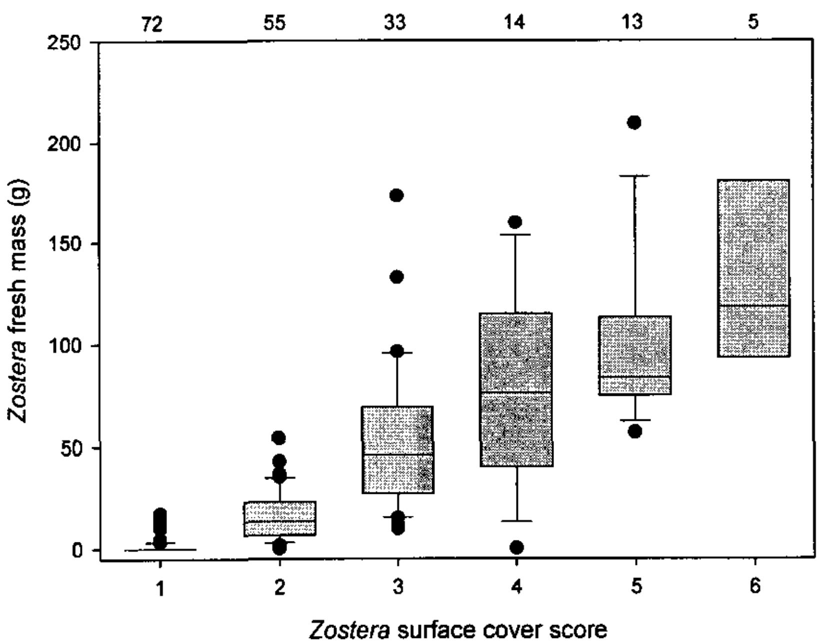

Figure 8: *Zostera* mass in relation to *Zostera* surface cover on the Farewell Spit tidal flats. *Zostera* surface cover score is based on a visual assessment with reference to standard photographs. *Zostera* mass is the fresh (squeeze-dried) mass of plant matter sampled in three core samples. Numbers above the boxes give the sample size per category.

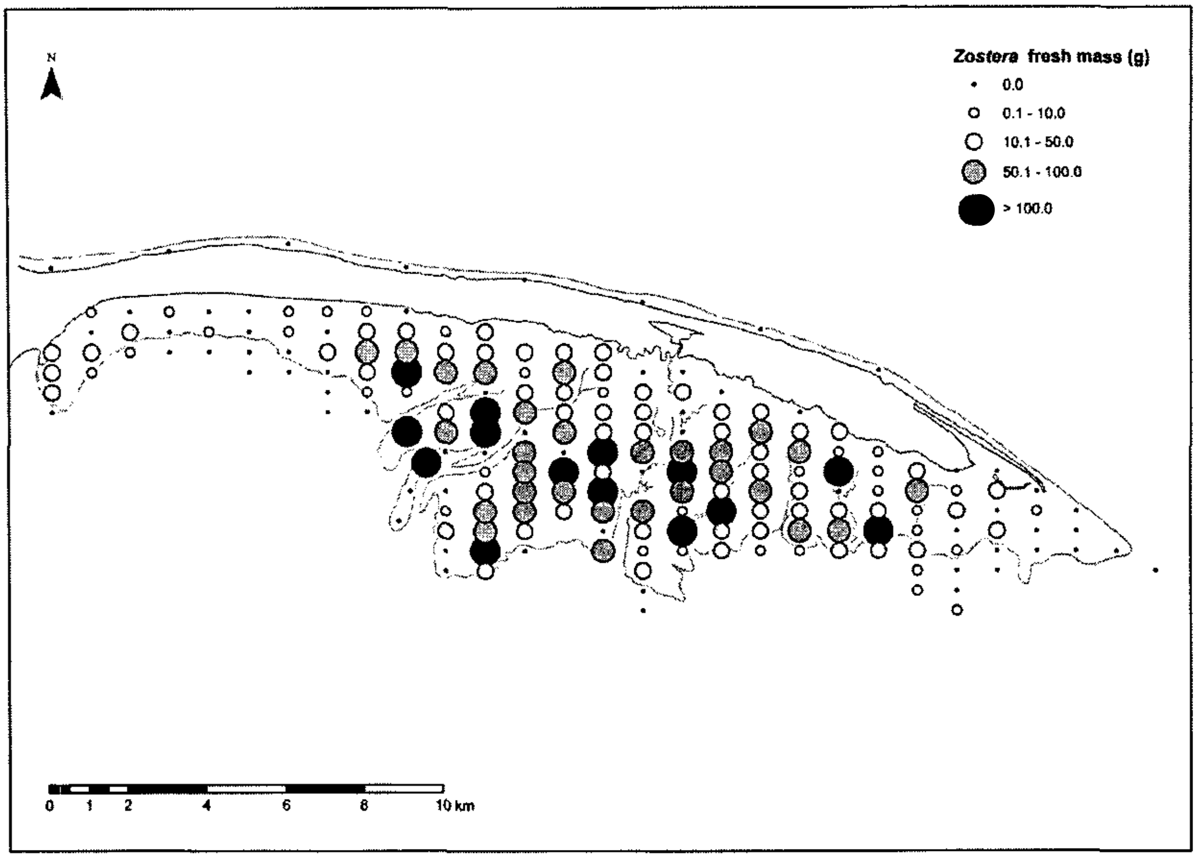

Figure 9: **Fresh mass of *Zostera* present in the three core samples per site on the Farewell Spit tidal flats.**

present could have been subsurface rhizome matter. Eelgrass beds tend to accumulate fine-particle sediments because of decreased water velocities, production of organic matter, and different infauna to unvegetated areas (Heiss et al. 2000, Little 2000). For the 189 sites for which we had coarse sand (particle size 0.5 mm and above) data, although there appeared to be a reduction in the coarse sediment component with an increase in *Zostera* surface cover (Figure 10), the large variation in sediment values in meant that no difference was discernable statistically (ANOVA, arcsine-transformed sediment proportions, $F_{5,183}=1.287$, P=0.272).

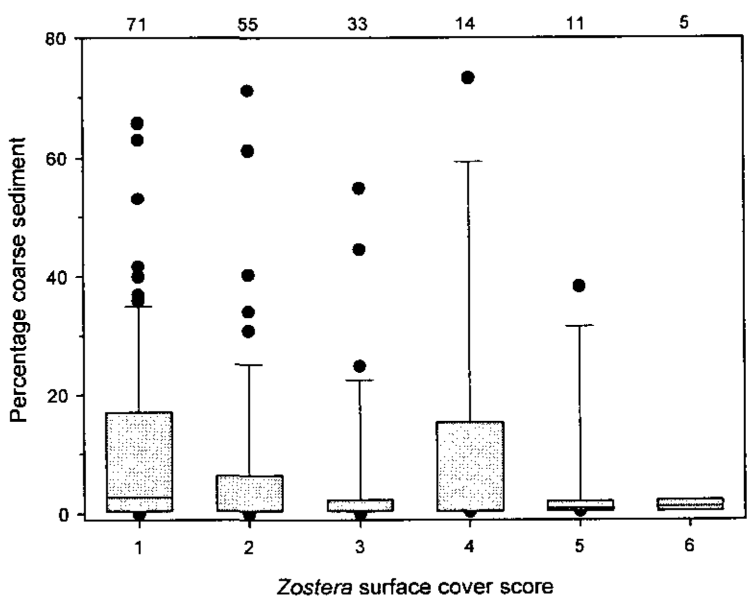

Figure 10: **Coarse sediment (>0.5 mm) in relation to *Zostera* surface cover.**

More complete sediment data (fine, medium, and coarse) are available for 144 sites (see Figure 4). Analysis of the sediment composition in relation to *Zostera* surface cover scores of this subset gave equivocal results. A significant effect of *Zostera* score on fine sediments was detected (ANOVA, arcsine-transformed sediment proportions, $F_{5,138}$=2.514, P=0.033, R^2=0.083), with an apparent increase in fine sediments at a *Zostera* score of 6, but this was due to a single site with *Zostera* cover of 6 and a high fine sediment component (73% c.f. 15% and 17% for the two remaining score 6 sites). Likewise, although the proportion of medium-sized sediments varied statistically with *Zostera* score ($F_{5,138}$=2.348, P=0.044, R^2=0.078), this was because sites with a *Zostera* score of 4 had a slightly lower percentage than the average, while score 5 sites had slightly higher. There was no consistent pattern between *Zostera* categories.

In summary, the sediment data indicate little effect of *Zostera* cover on the surrounding sediments, but this may reflect the limitations of the sampling and processing as much as any absence of an effect. The fairly general sediment categories we used may have been insensitive to subtle effects of eelgrass (e.g., any silt fraction that was not registered), and we have not investigated whether small-scale variation in sediment composition and *Zostera* presence may obscure any large-scale patterns. In general, however, broad patterns in the distribution of *Zostera* and coarse sediments are apparent (see Figures 6 and 7), with coarse sediments occurring towards the low tide edge and mainly on the western side of the central flats, while *Zostera* mainly occurs on the mid-lower parts of the central flats.

3.3 Redox potential discontinuity

At each site an attempt was made to measure the depth of the redox potential discontinuity (RPD) below the surface, but this was not always possible. In wet sand the sediment core could not be measured properly, and at others no change in sediment colour was discernable. The data suggest that the RPD was deeper at the highly exposed far eastern end of the spit, where wave action is high, and near major channels on the central flats (Figure 11).

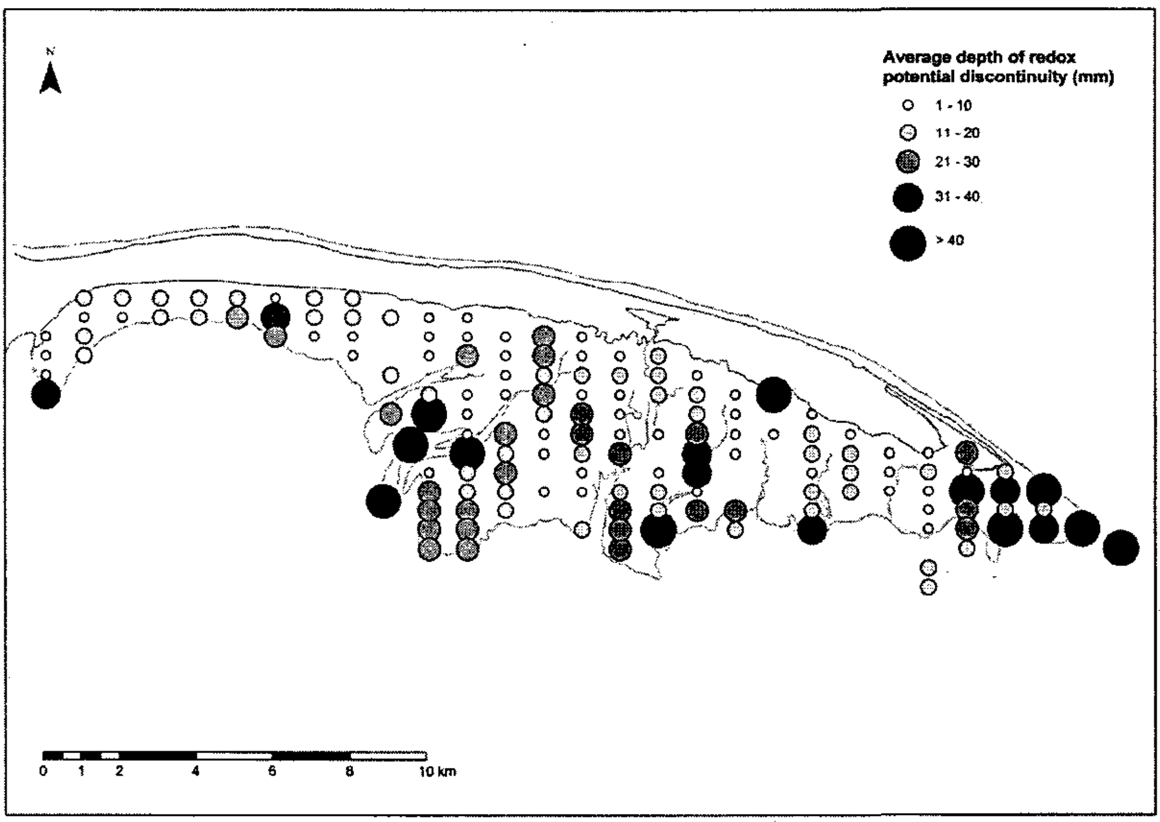

Figure 11: Average depth of the redox potential discontinuity on the Farewell Spit tidal flats.

4. DISTRIBUTION OF MAJOR INVERTEBRATE GROUPS ON THE FAREWELL SPIT TIDAL FLATS

4.1 Overall diversity

4.1.1 Taxa recorded

Ninety-one taxa or taxonomic groups were recorded during the survey, with another eight species recorded in earlier work (Table 2). Taxonomic levels used vary between species groups, but in general molluscs were identified to species or genus level, polychaetes to family, and small Crustacea to family.

Table 2: Taxonomic list for the Farewell Spit tidal flats. Species marked with an asterisk were not recorded in the 2003 survey but are known from previous work (P.F. Battley and OSNZ, unpublished data), and those with two asterisks were recorded by Auckland University (Anon 1975).

Phylum	Class	Order/Family	Genus/species	Common name
Cnidaria	Anthozoa	Actinaria	*Anthopleura aureoradiata* *Edwardsia tricolor*	anemone
Nemertea				nemertean/proboscis worm
Annelida	Polychaeta	Ampharetidae		
		Amphinomidae		
		Arenicolidae	*Abarenicola assimilis*	lug worm
		Capitellidae	*Capitella capitata* *Heteromastus filiformis*	
		Cirratulidae		
		Glyceridae	*Hemipodus* sp.	
		Lumbrineridae		
		Magelonidae	*Magelona* sp.	shovel-headed worm
		Maldanidae	*Axiothella quadrimaculata*** *Clymenella* sp. *Macroclymene* sp.	bamboo worm
		Nephtyidae	*Aglaophamus* sp. *Nephtys* sp.	cat worms
		Nereididae		rag worms
		Opheliidae	*Armandia maculata* *Ophelia* sp.	
		Orbiniidae	*Orbinia papillosa*	
		Oweniidae	*Owenia fusiformis*	
		Paraonidae		
		Pectinariidae	*Pectinaria australis*	gold comb worm
		Phyllodocidae		paddle worm
		Sabellidae		peacock worm
		Scalibregmatidae	*Travisia olens** unidentified species	
		Serpulidae	*Pomatoceros caeruleus*	

Phylum	Class	Order/Family	Genus/species	Common name
		Spionidae	*Aonides* sp. *Laonice* sp. *Polydora/Boccardia* sp. *Prionospio* sp. *Scolecolepides benhami*	
		Syllidae		
		Terebellidae		
Mollusca	Bivalvia	Galeommatidae	*Divariscintilla maori*	
		Lasaeidae	*Arthritica bifurca*	
		Lucinidae	*Divaricella huttoniana*	lace cockle
		Mactridae	*Mactra discors* *Zenatia acinaces*	large trough shell otter shell
		Mesodesmatidae	*Amphidesma subtriangulatum* *Paphies australis*	tuatua pipi
		Mytilidae	*Perna canaliculus* *Xenostrobus pulex*	green mussel small black mussel
		Nuculidae	*Nucula hartvigiana*	nut shell
		Psammobiidae	*Soletellina nitida**	golden sunset shell
		Solemyidae	*Solemya parkinsonii*	razor mussel
		Tellinidae	*Macomona liliana*	large wedge shell
		Veneridae	*Austrovenus stutchburyi* *Tawera spissa* *Venerupis largillerti*	tuangi, cockle morning star oblong venus shell
	Gastropoda	Amphibolidae	*Amphibola crenata***	mud snail
		Batillariidae	*Zeacumantus lutulensis* *Zeacumantus subcarinatus*	mudflat creeper southern creeper
		Buccinidae	*Cominella adspersa** *Cominella glandiformis*	speckled whelk mud whelk
		Eatoniellidae	*Eatoniella* cf. *lambata*	
		Haminoeidae	*Haminoea zelandiae*	bubble shell
		Littorinidae	*Risellopsis varia**	
		Lottiidae	*Notoacmea helmsi*	limpet
		Muricidae	*Xymene* sp.	boring whelk
		Olividae	*Amalda* sp.	olive shell
		Pyramidellidae	*Turbonilla* sp.	
		Rissoidae	*Rissoina* sp.	
		Trochidae	*Dioloma bicanaliculata* *Diloma zeylandica* *Micrelenchus tenebrosus*	knobbed top shell top shell
		Turbinidae	*Turbo smaragdus*	common catseye
	Polyplacophora	Acanthochitonidae Chitonidae	*Acanthochiton zelandicus* *Chiton glaucus*	 Green chiton
Arthropoda	Maxillopoda	Cirripedia, Balanidae	*Elminius modestus*	estuarine barnacle
	Maxillipoda	Copepoda		copepod

Phylum	Class	Order/Family	Genus/species	Common name
	Ostracoda			mussel shrimp
	Malacostraca	Amphipoda		sand hopper
		Caprellidae		skeleton shrimp
		Cumacea		cumacean
		Isopoda		
		Flabellifera	*Isocladus spicatus*	pill lice
		Valvifera	*Euidotea*	
		Lophogastrida (Mysidacea)		opossum shrimp
		Stomatopoda	*Lyiosquilla spinosa***	mantis shrimp
		Squillidae	*Squilla armata*	
		Decapoda		
		Callianassidae	*Callianassa filholi**	ghost shrimp
		Crangonidae	*Pontophilus* cf. *australis*	sand shrimp
		Grapsidae	*Cyclograpsus lavauxi*	smooth shore crab
			Helice crassa	tunnelling mud crab
		Hymenosomatidae	*Hemigrapsus crenulatus*	hairy-handed crab
		Ocypodidae	*Halicarcinus cookii*	pill-box crab
			Halicarcinus whitei	
		Pinotheridae	*Macrophthalmus hirtipes*	stalk-eyed mud crab
			*Pinotheres novaezeelandiae**	pea crab
	Insecta	Diptera		
		Empipidae		dance fly
		Ephydridae	*Neoscatella* sp.	shore fly
		Tipulidae	*Hexatomini* sp.	crane fly
		Trichoptera		
		Chathamiidae	*Philanisus plebeius*	caddis fly
Echinodermata	Echinoidea		*Fellaster zelandiae*	sand dollar
	Holothuroidea	Apodida	*Trochidota dendyi*	sea cucumber
	Stelleroidea	Asteroidea	*Coscinasterias calamaria*	eleven-armed seastar
			Patiriella regularis	cushion star
		Ophiuroidea		brittle star

4.1.2 Species abundance

In total, 12 839 individuals were recorded in samples, but six taxa dominated the samples numerically (*Austrovenus stutchburyi*, spionid polychaete worms, *Paphies australis*, amphipods, the barnacle *Eliminius modestus* and isopods). These six accounted for almost 70% of the individuals recorded (Figure 12), so the cumulative rank-abundance plot of 'species' abundance shows an abrupt change in slope at the seventh taxon (Figure 13). In biomass terms, cockles completely dominate the samples.

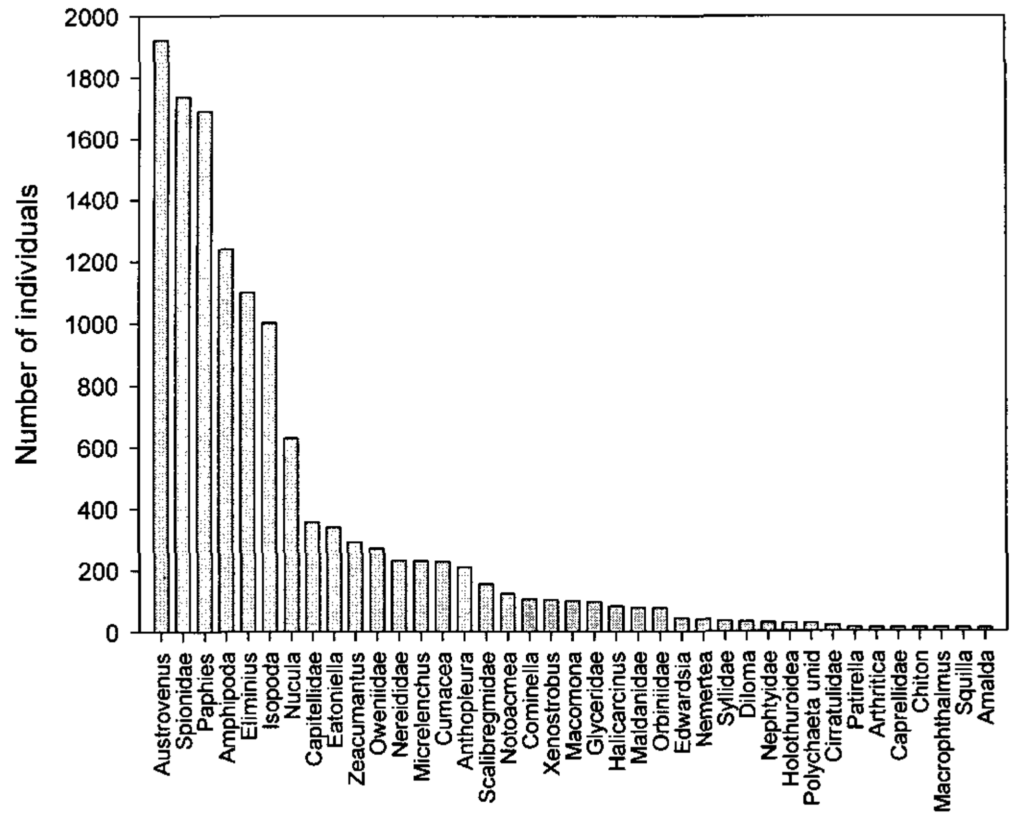

Figure 12: **Ranked abundances for taxa of which 10 or more individuals were found.**

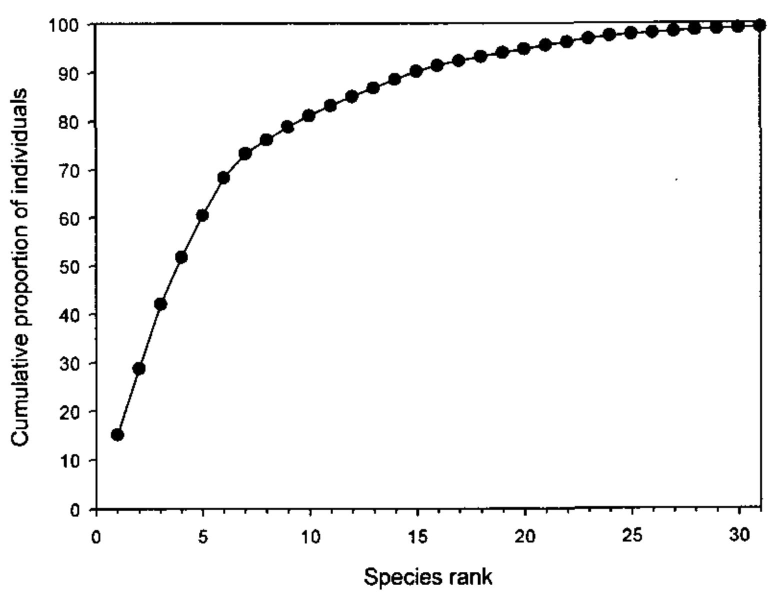

Figure 13: **Cumulative rank-abundance plot for taxa of which 10 or more individuals were recorded.**

4.1.3 Species diversity across the tidal flats

Only one of the 192 sampling sites had no macrofauna present (Figure 14). Most sites had from 2 to 14 taxa, with the mode of 7 being close to the median of 8 taxa. The most diverse site had 31 taxa.

The plot of the cumulative proportion of sites in relation to diversity (Figure 15) shows a near-linear increase of sites as diversity increases up to about 14 taxa, after which it levels off quite suddenly.

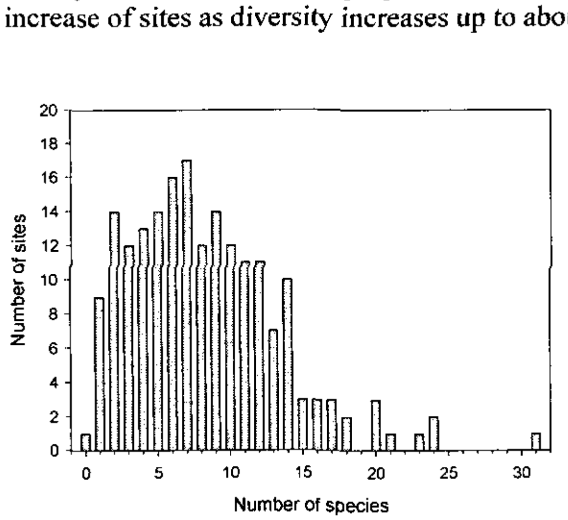

Figure 14: Frequency distribution of the number of taxa recorded at the 192 sampling sites.

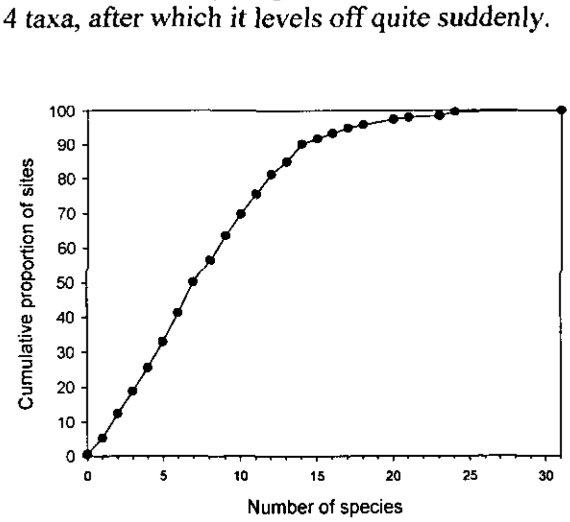

Figure 15: Cumulative proportion of sites that had a certain number of taxa recorded.

Spatially, the most diverse sites were those of the large central flats, with the least diverse areas being those on the fairly narrow tidal flats along the inner part of the spit and those on outer areas on the extreme eastward end of the spit (Figure 16). This partly reflects the extent of *Zostera* on the central flats, as the number of species at a site increased with surface cover of *Zostera* (Figure 17).

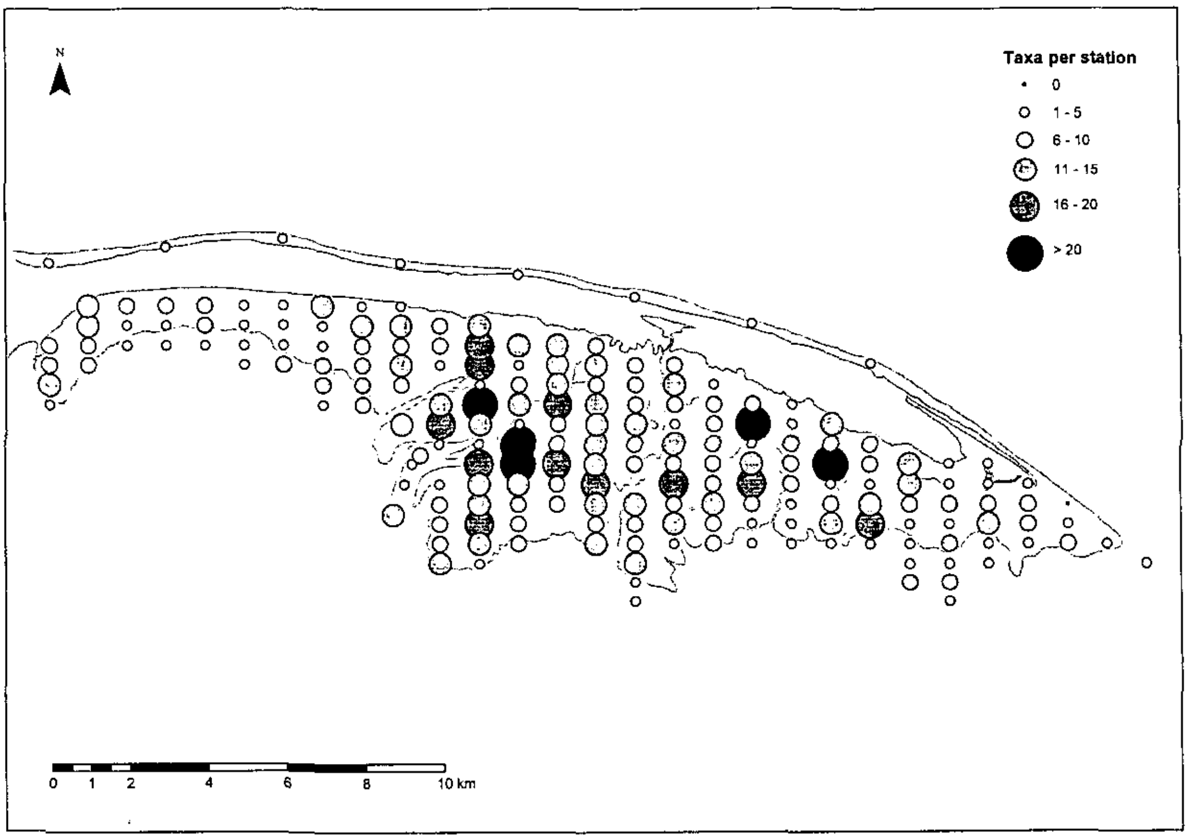

Figure 16: Map of species diversity along Farewell Spit.

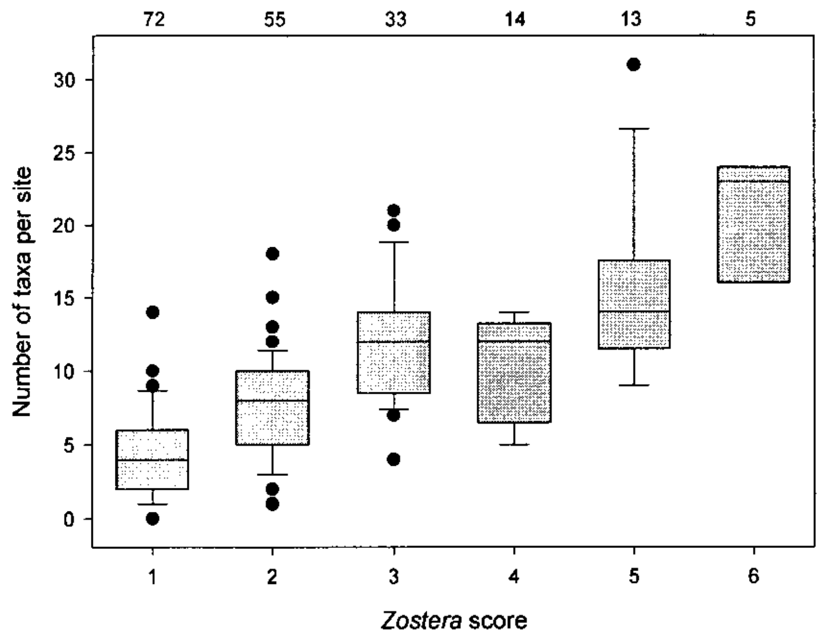

Figure 17: **Number of taxa per site in relation to surface cover of *Zostera*. Boxes enclose the median, with 25 to 75 percentiles, whiskers show the 10^{th} and 90^{th} percentiles, and outliers are shown as dots.**

4.2 Arthropoda: Crustacea

4.2.1 Amphipoda

Amphipods were the most widespread taxon recorded, occurring at almost two-thirds of the 192 sample sites (Table 3). Although occurring at extremely high densities at some sites, most sites had fewer than 1000 individuals per square metre (Table 3; Figures 18 and 19). Highest densities were typically towards the upper shore of the tidal flats, though densities of over 2000 individuals per square metre were also recorded about 2.5 km and 6.5 km offshore (Figure 18). The size distribution was unimodal and comparatively normal; most individuals were less than 5 mm long (Figure 20; Table 3).

Table 3: **Characteristics of sampled amphipod populations on the Farewell Spit tidal flats.**

Characteristic	Value
occurrence and density	
number of sample sites recorded at	115
total number of individuals sampled	1 246
average density all sites (no. per m^2)	257
average density where present (no. per m^2)	445
median density where present (no. per m^2)	127
maximum density (no. per m^2)	12 101
length	
number measured	1 245
average length (mm)	3.2
standard deviation	1.1
range	1–14

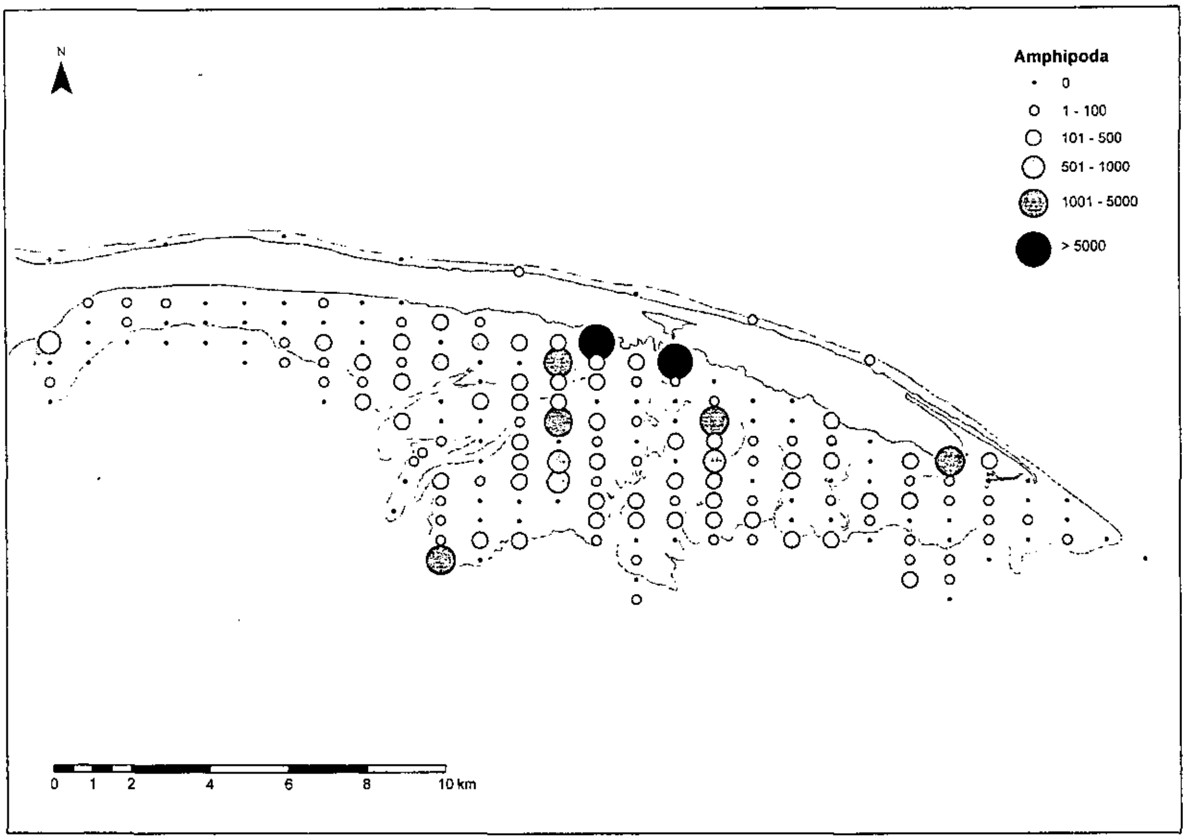

Figure 18: **Distribution of Amphipoda on the Farewell Spit tidal flats.**

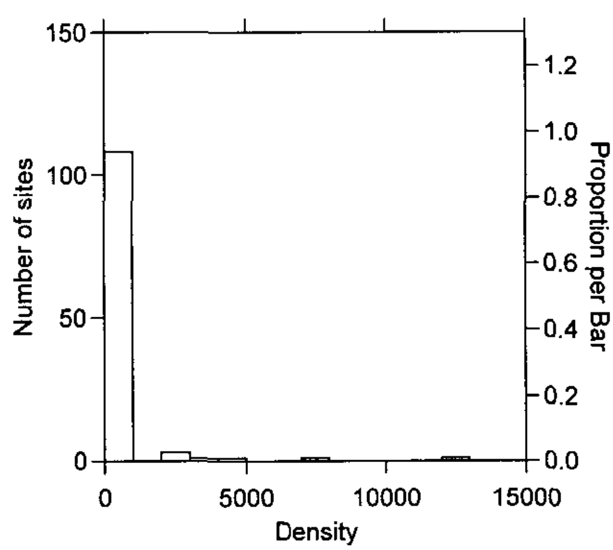

Figure 19: **Frequency distribution of amphipod densities (no. per m^2) at the 118 sample sites where they were recorded. The right-hand x-axis expresses the data as proportions of the total number recorded.**

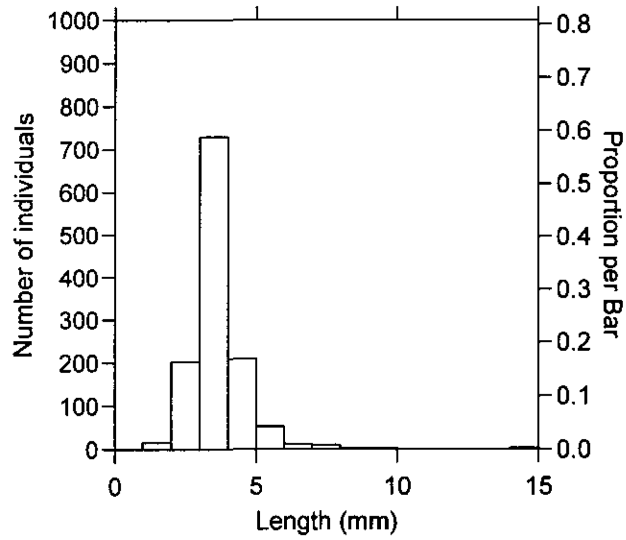

Figure 20: **Length distribution of amphipods on Farewell Spit. N = 1245 specimens.**

4.2.2 Cumacea

Cumacea were recorded at just under a third of the sites sampled (Table 4). Densities were lower than those of amphipods, generally occurring at fewer than 200 individuals per square metre (Table 4; Figure 21). Most cumaceans were recorded on the large 'central' tidal flats, where they were found from the upper tidal flats out towards the spring low tide edge (though generally not to the furthest extent of the flats; Figure 22). The size distribution was unimodal and comparatively normal; most individuals were less than 5 mm long (Figure 23; Table 4).

Table 4: **Characteristics of sampled cumacean populations on the Farewell Spit tidal flats.**

Characteristic	Value
occurrence and density	
number of sample sites recorded at	62
total number of individuals sampled	227
average density all sites (no. per m^2)	46
average density where present (no. per m^2)	152
median density where present (no. per m^2)	117
maximum density (no. per m^2)	722
length	
number measured	226
average length (mm)	4.1
standard deviation	0.7
range	2–6

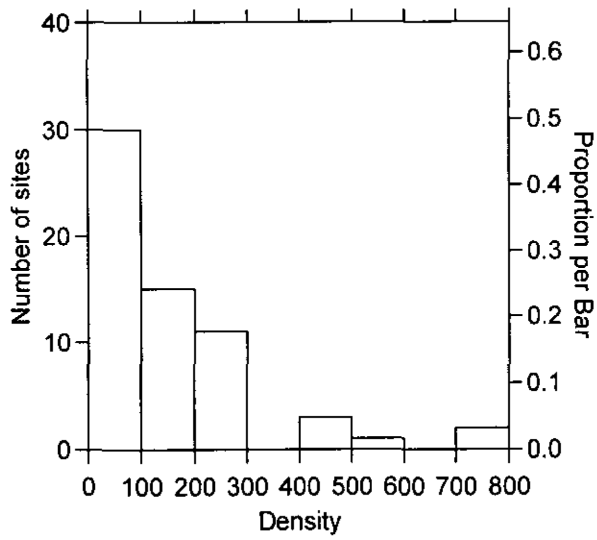

Figure 21: **Frequency distribution of cumacean densities (no. per m²) at the 62 sample sites where they were recorded.**

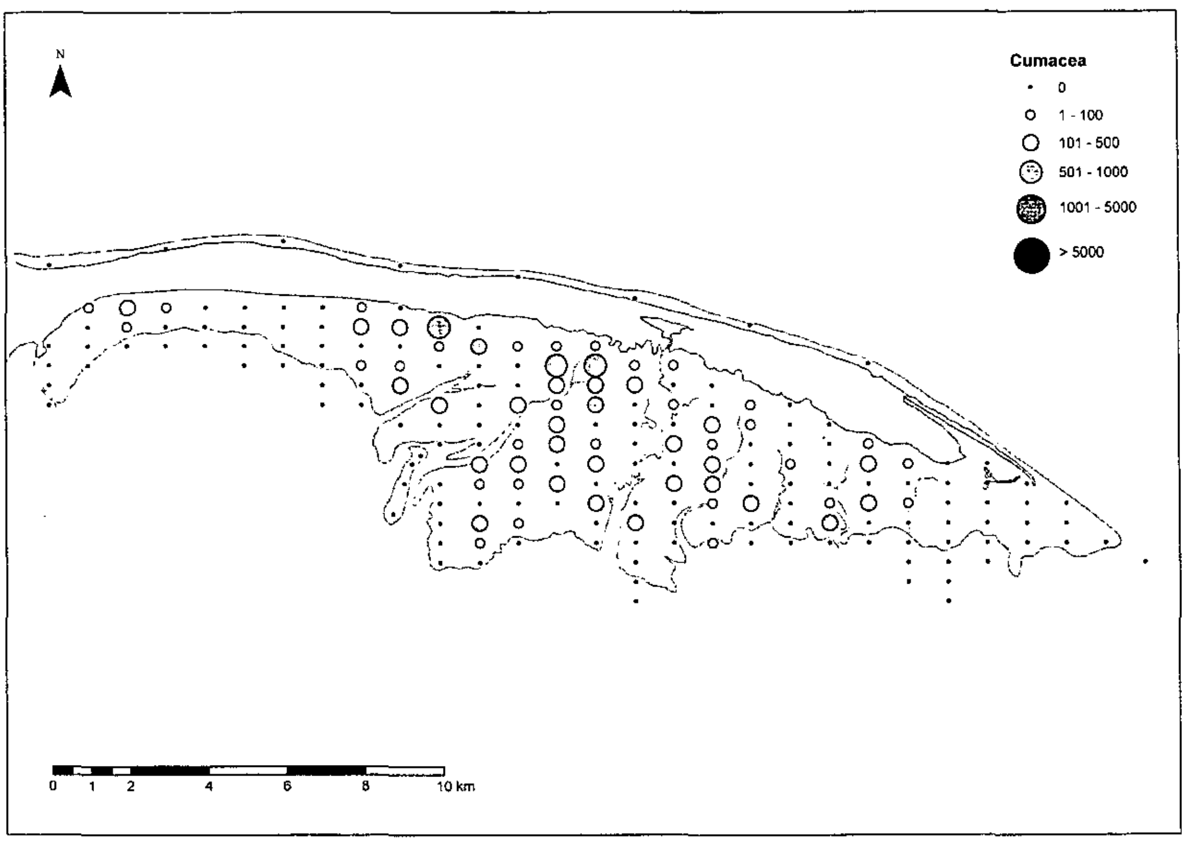

Figure 22: **Distribution of Cumacea on the Farewell Spit tidal flats.**

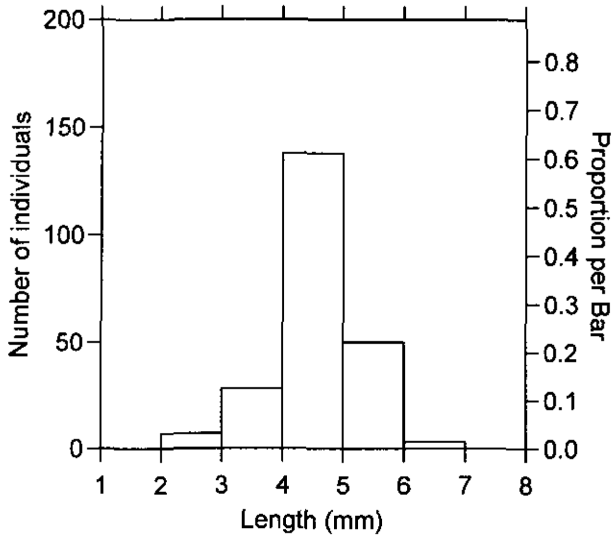

Figure 23: Length distribution of Cumacea on Farewell Spit. N = 226 specimens.

4.2.3 Isopoda: *Flabellifera*

Isopods (all analysed here were from the family Flabellifera) were recorded at over half the sites sampled (Table 5). Densities were lower than those of amphipods, generally occurring at fewer than 300 individuals per square metre (Table 5; Figure 24). Most isopods were recorded on the large 'central' tidal flats, where they were found from the upper tidal flats out towards the spring low tide edge (though generally not to the furthest extent of the flats, Figure 25). The size distribution was more skewed than those of Amphipoda and Cumacea; most individuals were less than 5 mm long (Figure 26; Table 5).

Table 5: Characteristics of sampled isopod populations on the Farewell Spit tidal flats.

Characteristic	Value
occurrence and density	
number of sample sites recorded at	108
total number of individuals sampled	1 002
average density all sites (no. per m^2)	211
average density where present (no. per m^2)	394
median density where present (no. per m^2)	212
maximum density (no. per m^2)	3 227
length	
number measured	998
average length (mm)	3.1
standard deviation	1.4
range	1–12

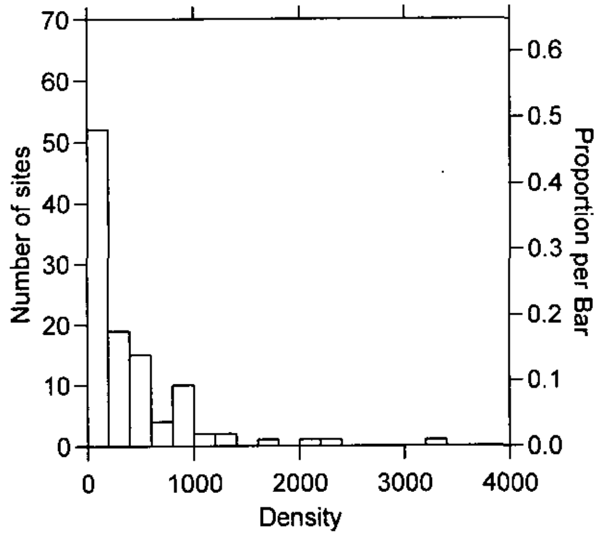

Figure 24: **Frequency distribution of isopod densities (no. per m²) at the 108 sample sites where they were recorded.**

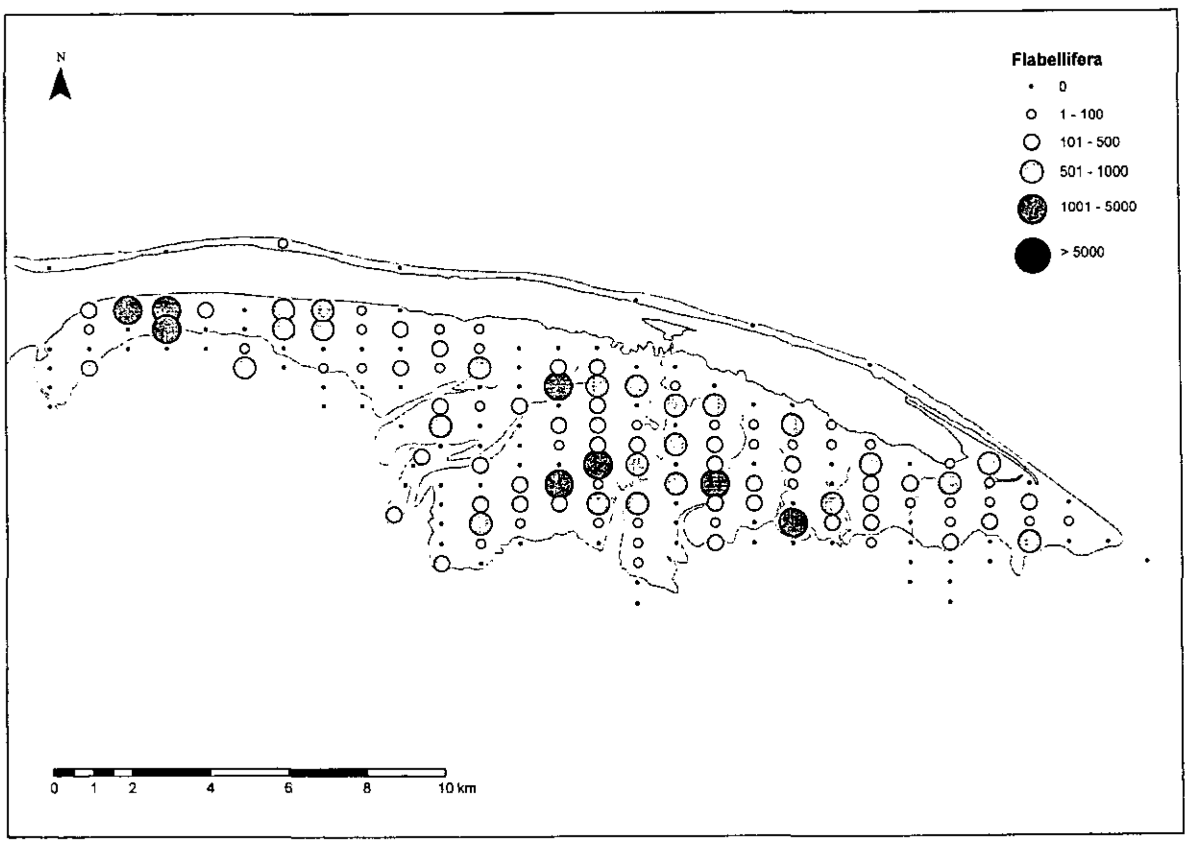

Figure 25: **Distribution of Isopoda on the Farewell Spit tidal flats.**

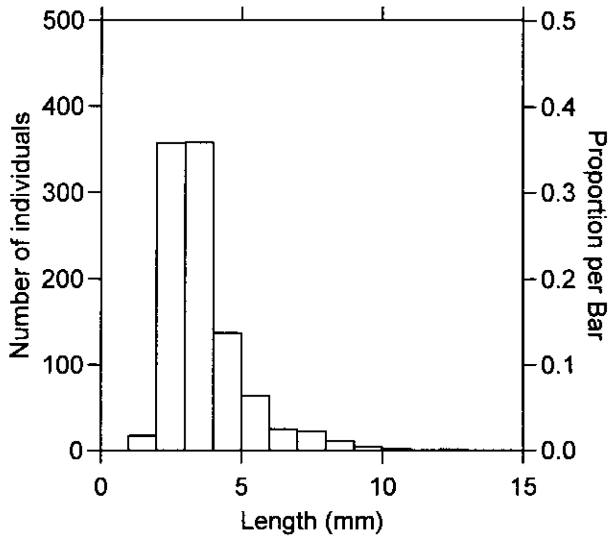

Figure 26: **Length distribution of isopods on Farewell Spit. N = 998 specimens.**

4.2.4 *Halicarcinus* spp.

The pill-box crabs, *Halicarcinus* spp., were not routinely identified to species, although both *H. cookii* and *H. whitei* were present in samples. They were found at generally low densities (less than 100 individuals per square metre) across the central flats, and also adjacent to Puponga at the base of the spit (Figures 27 and 28; Table 6). Their size distribution was unimodal, with most individuals being 2–8 mm wide (Figure 29; Table 6)

Table 6: **Characteristics of sampled *Halicarcinus* spp. populations on the Farewell Spit tidal flats.**

Characteristic	Value
occurrence and density	
number of sample sites recorded at	42
total number of individuals sampled	82
average density all sites (no. per m^2)	17
average density where present (no. per m^2)	82
median density where present (no. per m^2)	42
maximum density (no. per m^2)	340
length	
number measured	82
average carapace width (mm)	4.5
standard deviation	2.1
range	1–11

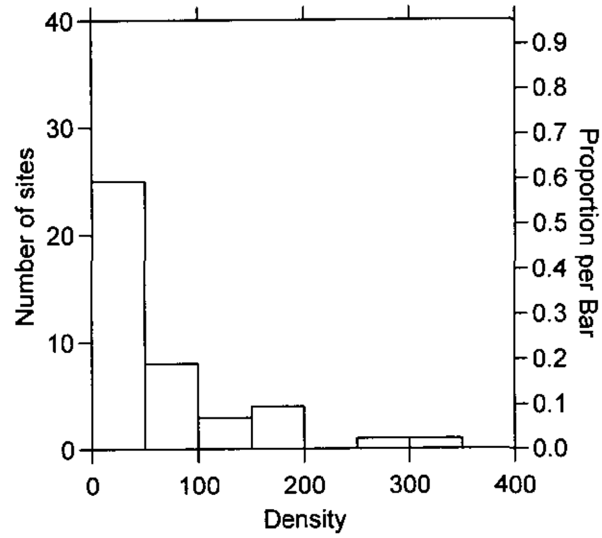

Figure 27: **Frequency distribution of *Halicarcinus* spp. densities (no. per m^2) at the 42 sample sites where they were recorded.**

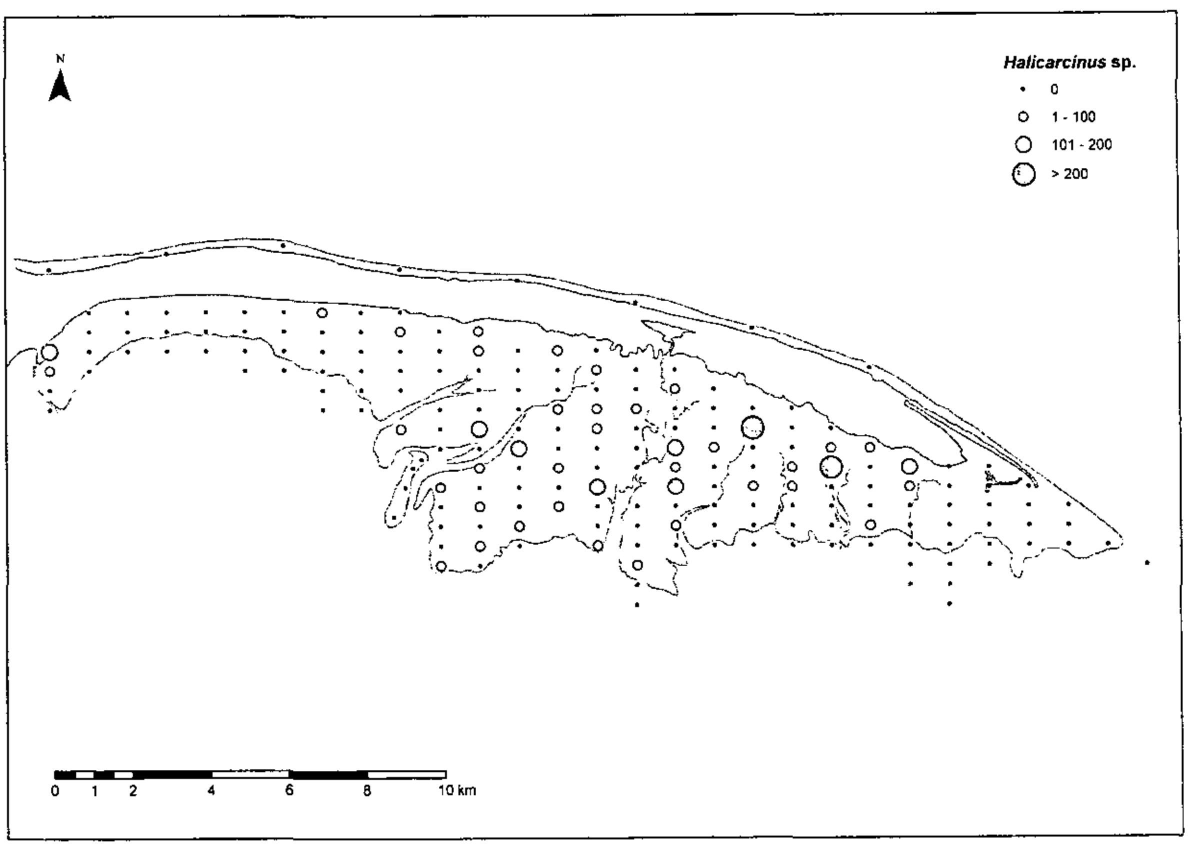

Figure 28: **Distribution of *Halicarcinus* spp. on the Farewell Spit tidal flats.**

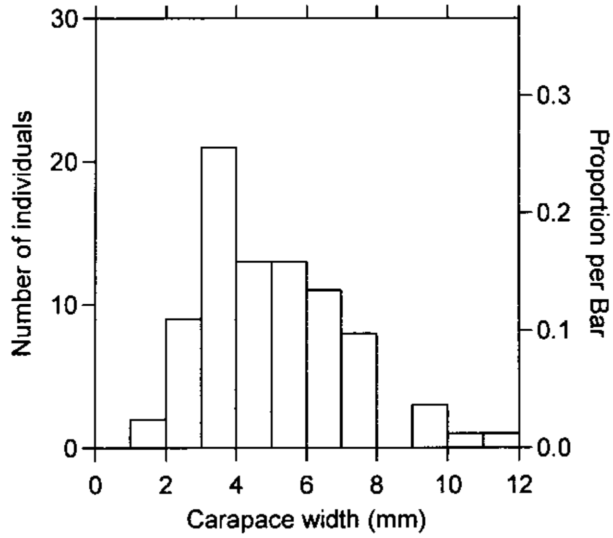

Figure 29: **Carapace width distribution of *Halicarcinus* spp. on Farewell Spit. N = 82 specimens.**

4.2.5 *Eliminius modestus*

The barnacle *Eliminius modestus* was encountered at reasonably high densities (Table 7; Figure 30) at 29 sites on the lower tidal flats, particularly near to channels on the central flats (Figure 31). Their distribution overlapped with that of 21–20 mm cockles *Austrovenus stutchburyi* (see Figure 38), and sites with high mussel (*Xenostrobus pulex*) densities (see Figure 54) also had high barnacle densities. These sites presumably provide enough hard substrate for attachment (most of the barnacles sampled came from cockle shells). Barnacles were mostly 1–6 mm wide (Figure 32).

Table 7: **Characteristics of sampled *Eliminius modestus* populations on the Farewell Spit tidal flats.**

Characteristic	Value
occurrence and density	
number of sample sites recorded at	29
total number of individuals sampled	1 099
average density all sites (no. per m^2)	243
average density where present (no. per m^2)	1 610
median density where present (no. per m^2)	255
maximum density (no. per m^2)	12 186
width	
number measured	1 099
average width (mm)	3.3
standard deviation	1.7
range	1–11

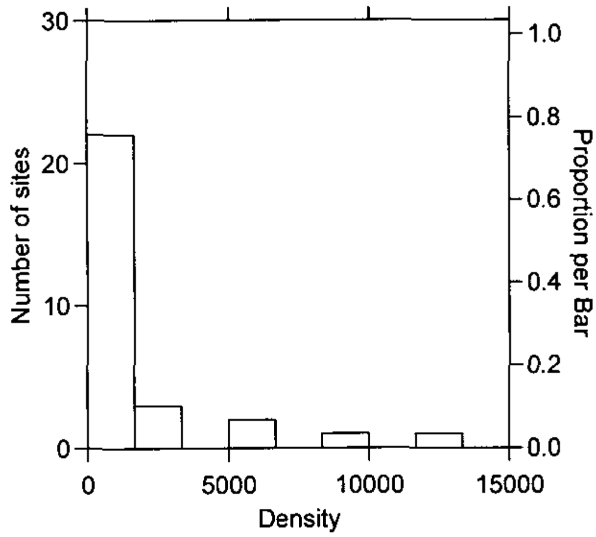

Figure 30: **Frequency distribution of *Eliminius modestus* densities (no. per m²) at the 29 sample sites where they were recorded.**

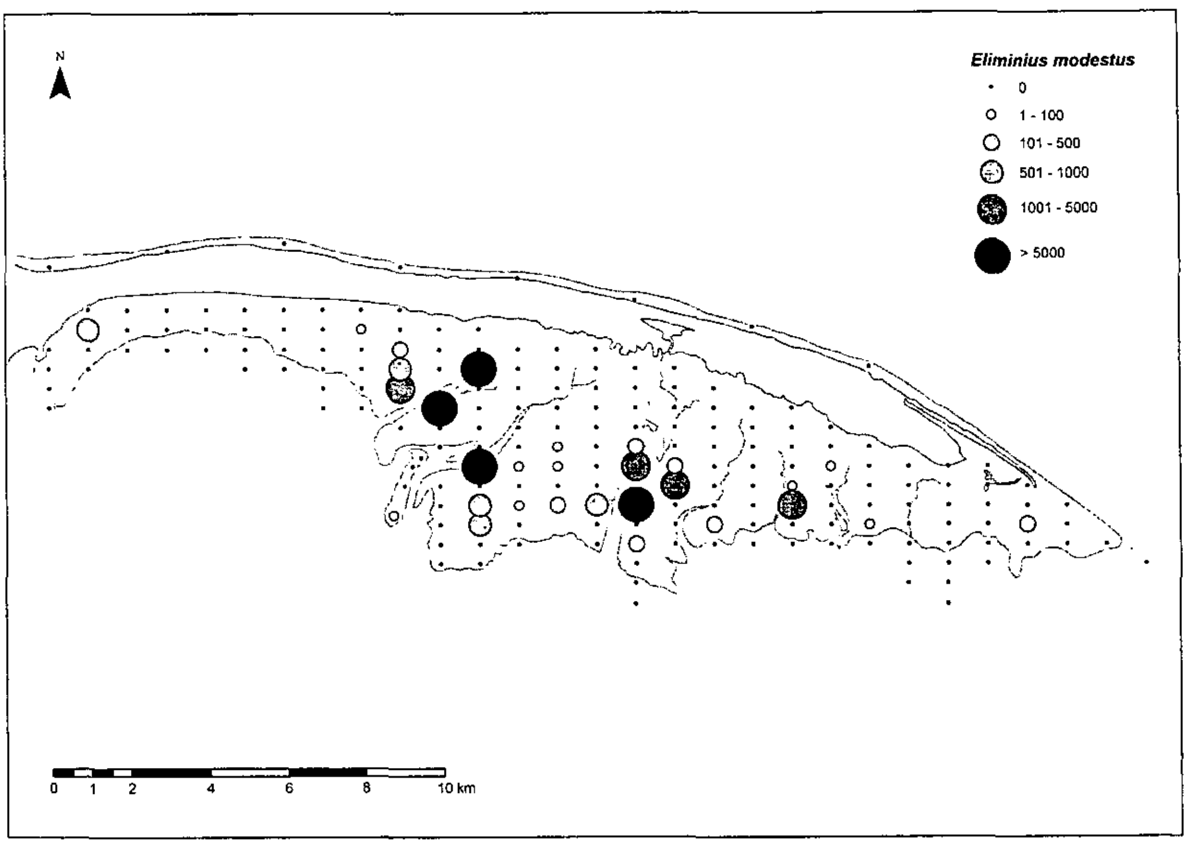

Figure 31: **Distribution of *Eliminius modestus* on the Farewell Spit tidal flats.**

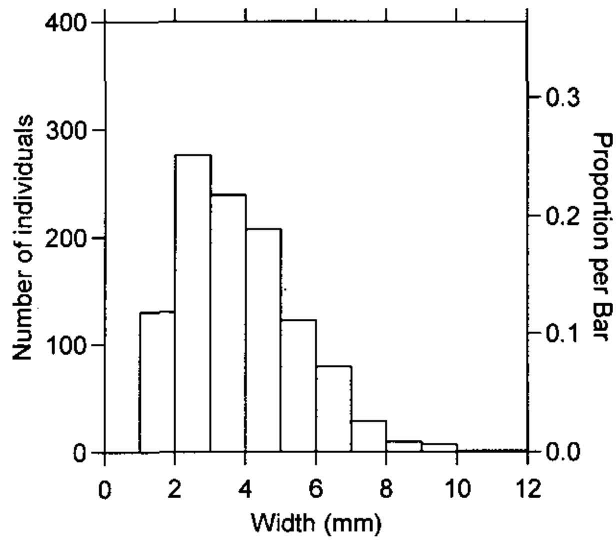

Figure 32: **Carapace width distribution of *Eliminius modestus* on Farewell Spit. N = 1099 specimens.**

4.3 Mollusca: Bivalvia

4.3.1 *Austrovenus stutchburyi*

The cockle, *Austrovenus stutchburyi*, was the most widespread species on the Farewell Spit tidal flats, present at over two-thirds of the sample sites (Figure 33; Table 8).

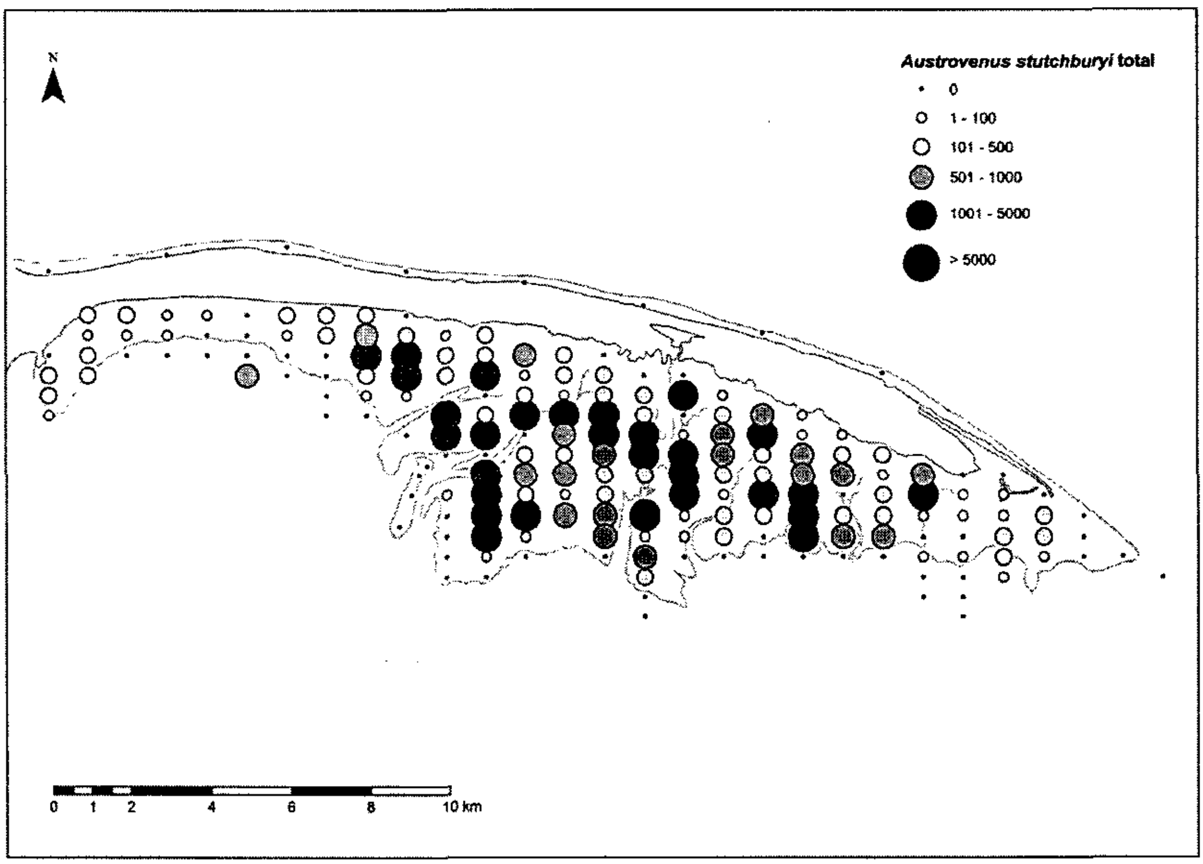

Figure 33: **Distribution of *Austrovenus stutchburyi* on the Farewell Spit tidal flats.**

Table 8: **Characteristics of sampled *Austrovenus stutchburyi* populations on the Farewell Spit tidal flats.**

Characteristic	Value
occurrence and density	
number of sample sites recorded at	131
total number of individuals sampled	1 923
average density all sites (no. per m^2)	431
average density where present (no. per m^2)	631
median density where present (no. per m^2)	255
maximum density (no. per m^2)	4 522
length	
number measured	1 918
average length (mm)	16.8
standard deviation	9.3
range	1–50

It was also the most numerous, with a median density of 255 individuals per square metre in the sites where it was found (Table 8; Figure 34). The size structure was bimodal, with one peak at 4–5 mm, another at 20–24 mm, and a long tail out to 50 mm (Figure 35). These peaks presumably represent separate cohorts of cockle, and there is a clear change in the distribution across the tidal flats with size. The smallest individuals were found throughout the upper and middle tidal flats (Figure 36), but individuals became progressively restricted to the lower parts of the tidal flats as they became larger (Figures 37–40).

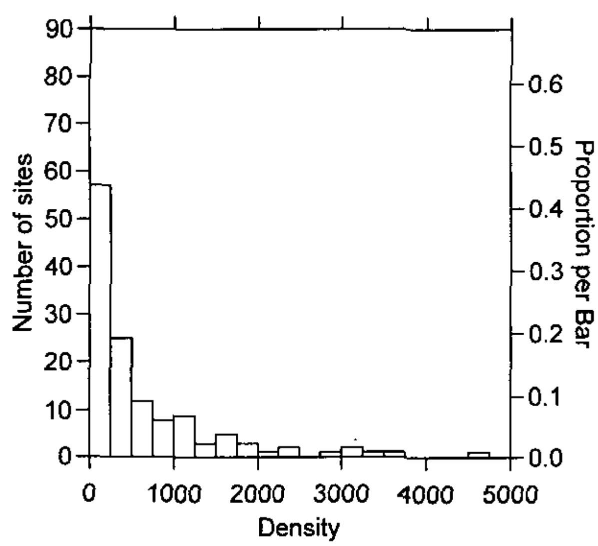

Figure 34: **Frequency distribution of *Austrovenus stutchburyi* densities (no. per m^2) at the 131 sample sites where they were recorded.**

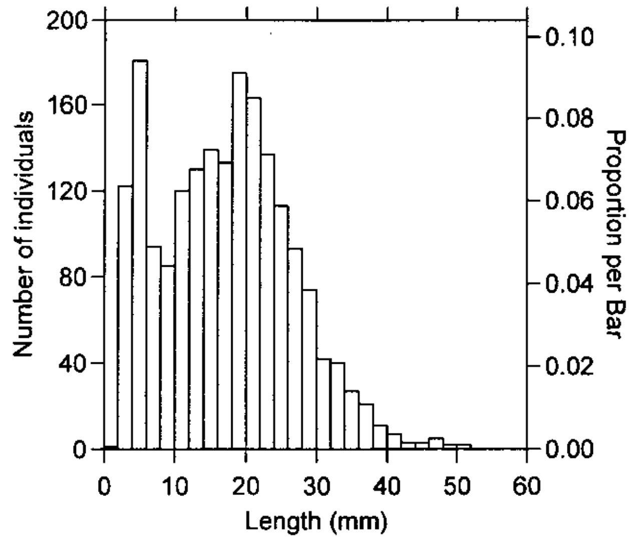

Figure 35: **Length distribution of *Austrovenus stutchburyi* on Farewell Spit. N = 1918 specimens.**

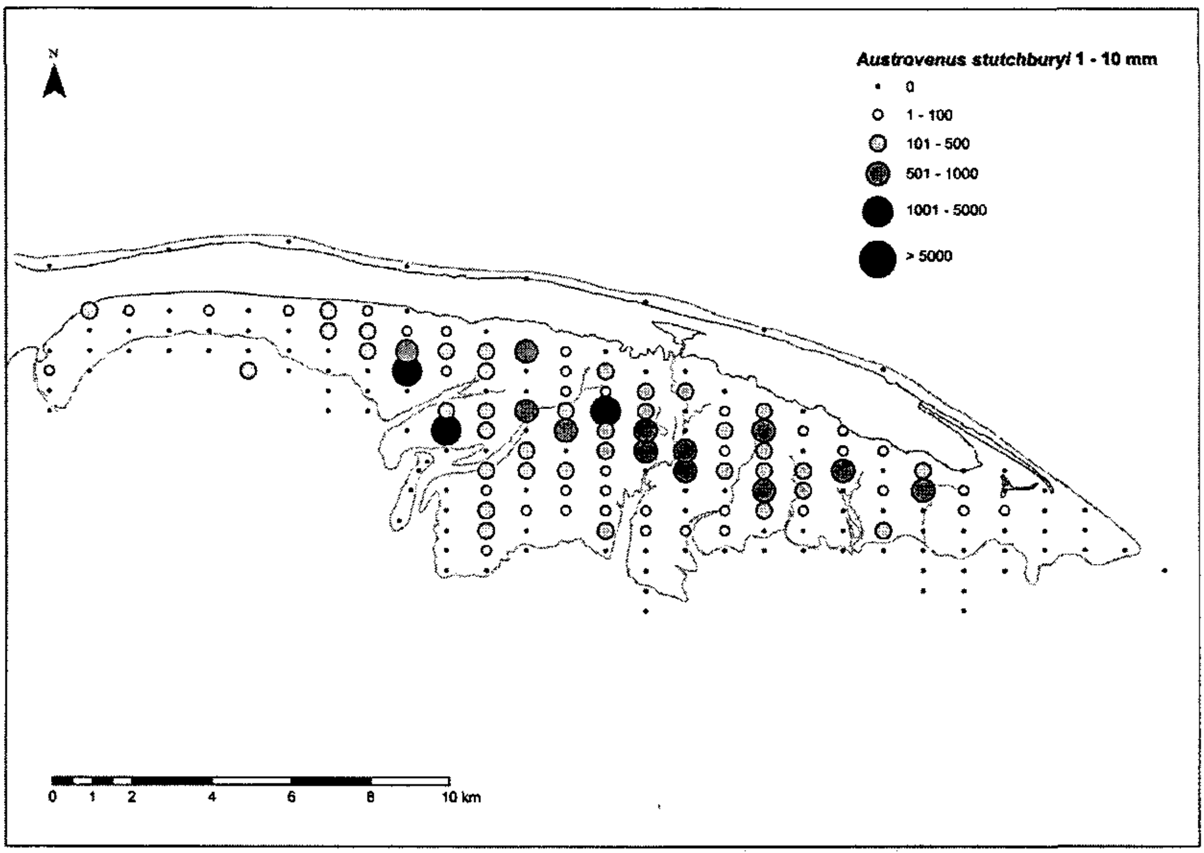

Figure 36: **Distribution of *Austrovenus stutchburyi* 1–10 mm on the Farewell Spit tidal flats.**

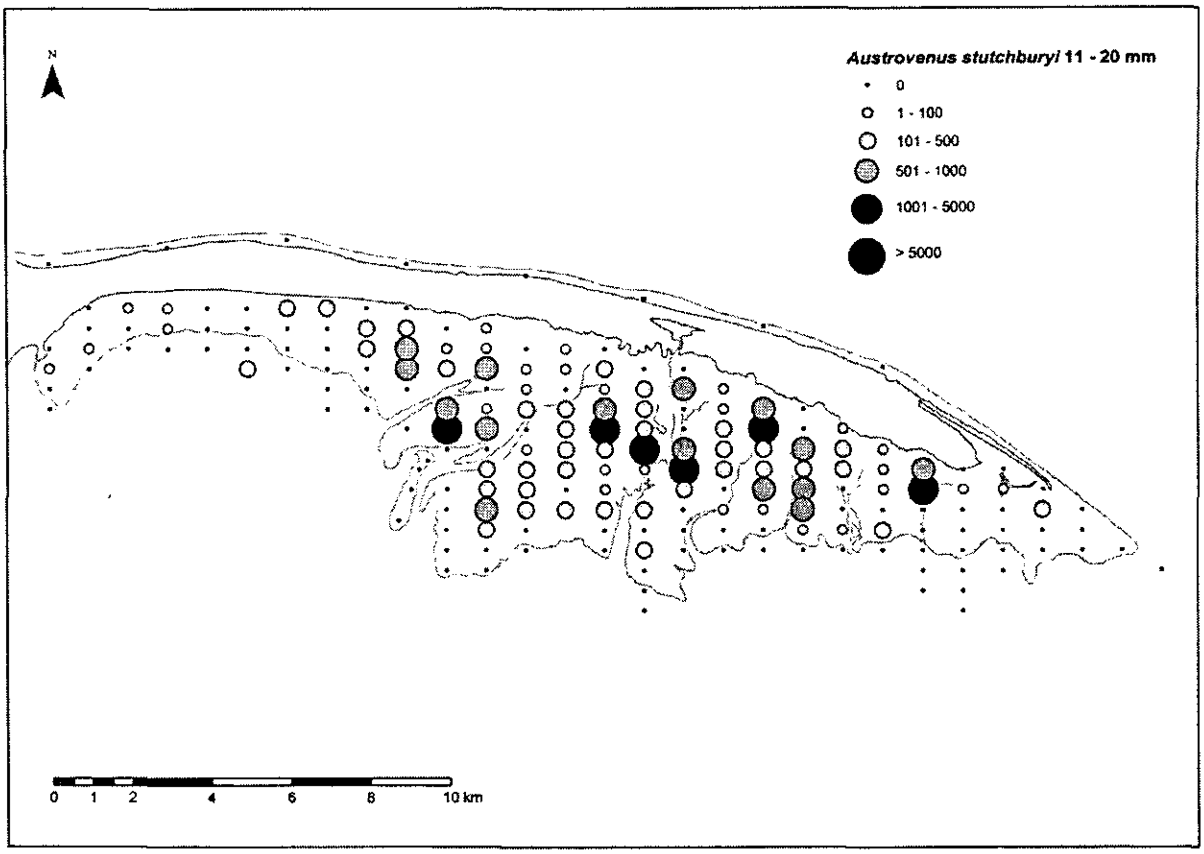

Figure 37: Distribution of *Austrovenus stutchburyi* 11–20 mm on the Farewell Spit tidal flats.

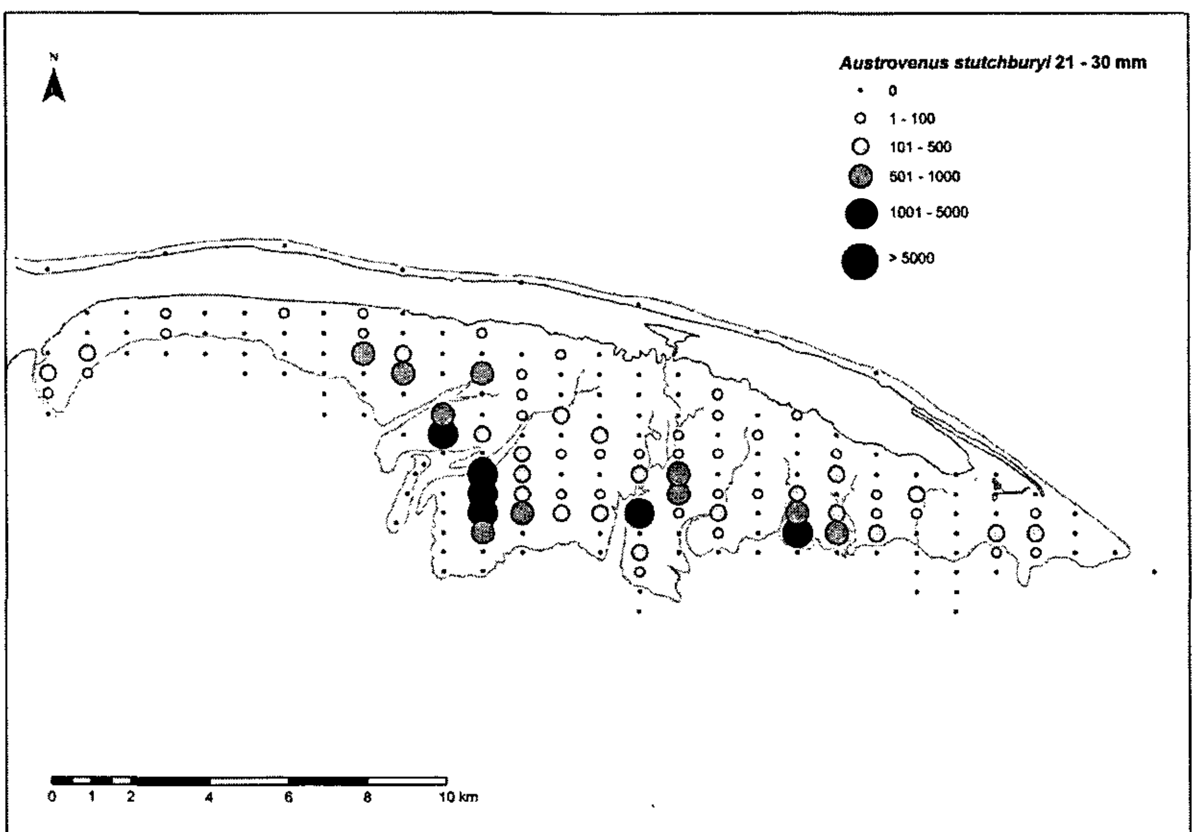

Figure 38: Distribution of *Austrovenus stutchburyi* 21–30 mm on the Farewell Spit tidal flats.

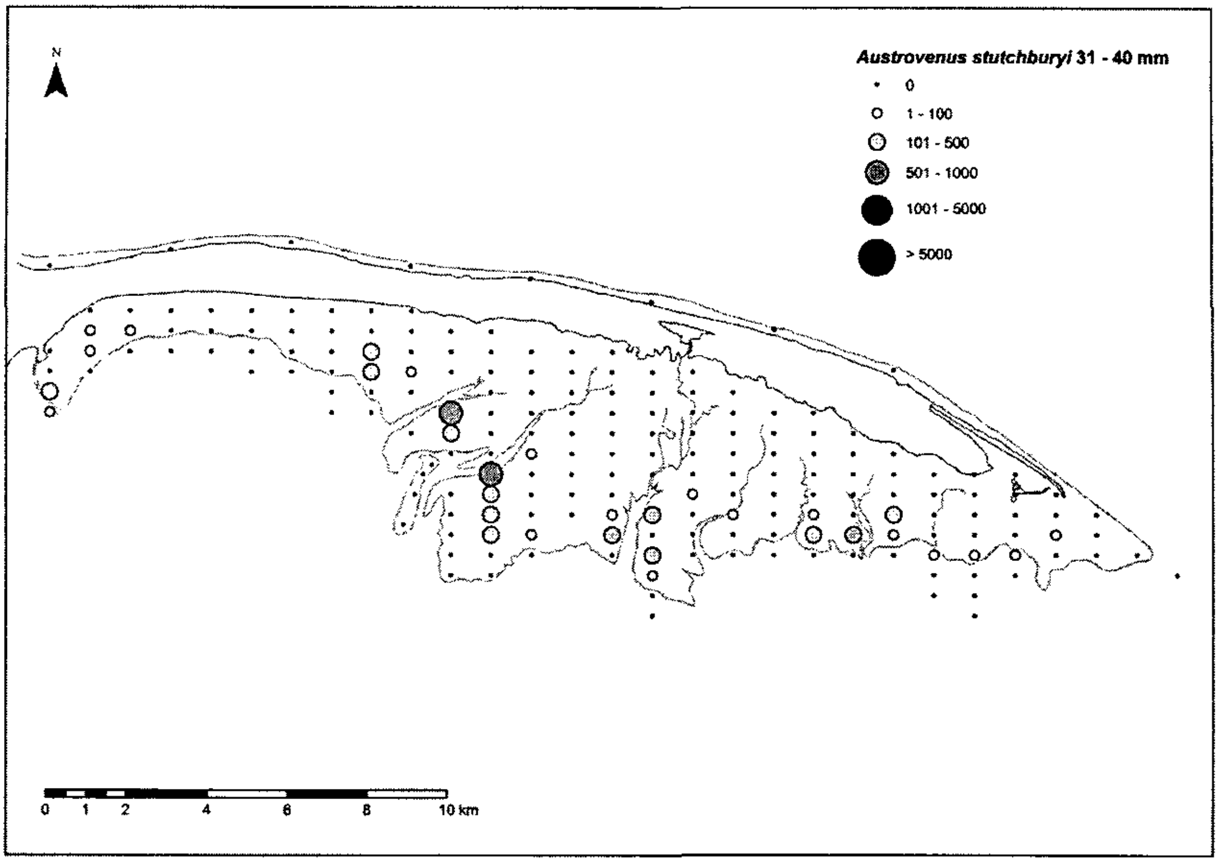

Figure 39: Distribution of *Austrovenus stutchburyi* 31–40 mm on the Farewell Spit tidal flats.

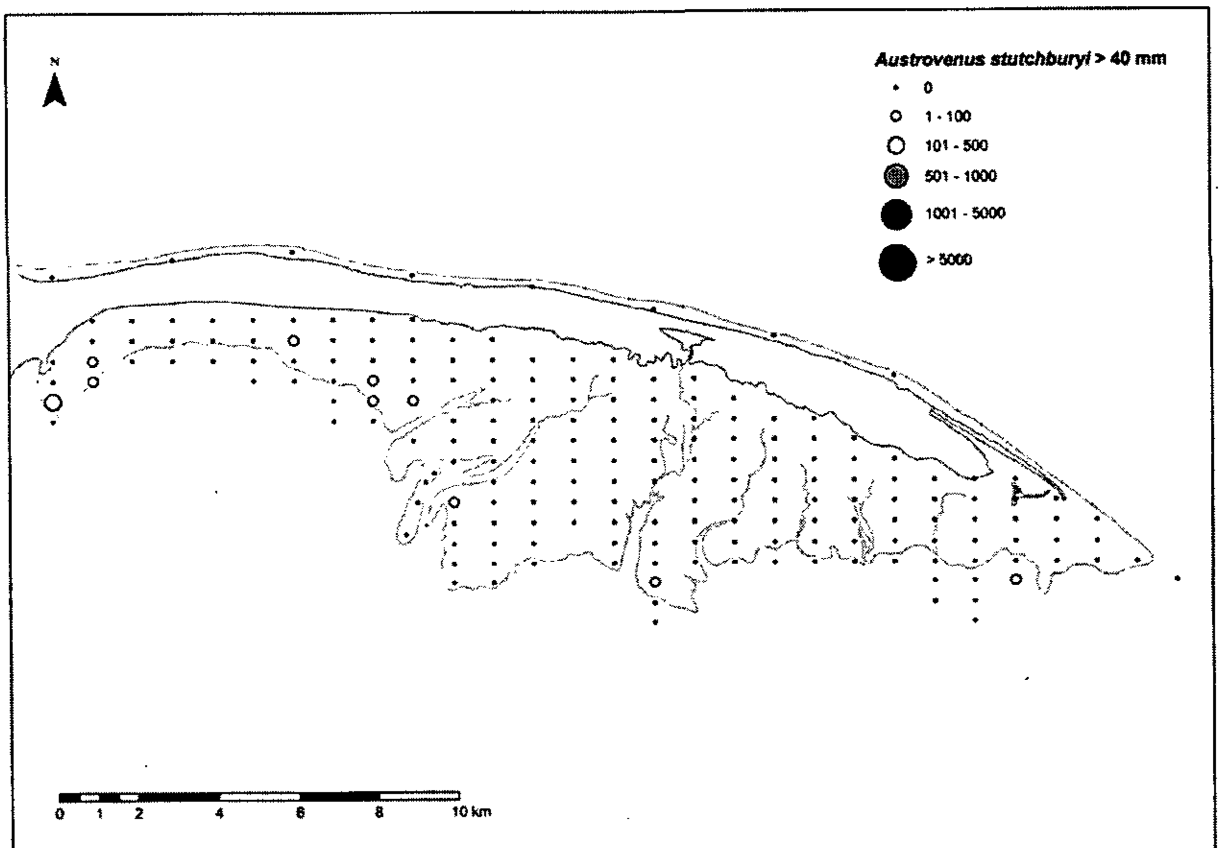

Figure 40: Distribution of *Austrovenus stutchburyi* greater than 40 mm on the Farewell Spit tidal flats.

4.3.2 *Macomona liliana*

The wedge shell, *Macomona liliana*, was less widespread and abundant than *Austrovenus*, occurring in only one-quarter of the sample sites, generally at low densities (Table 9; Figure 41). The size structure was also bimodal, with a peak at 6–8 mm and another at 18–20 mm, before declining steadily to the maximum length of 33 mm (Figure 42). If anything, the distribution pattern on the flats was the opposite to that of *Austrovenus*: small individuals were found throughout the tidal flats (Figure 43), whereas larger individuals were found predominantly at higher tidal levels (Figure 44).

Table 9: Characteristics of sampled *Macomona liliana* populations on the Farewell Spit tidal flats.

Characteristic	Value
occurrence and density	
number of sample sites recorded at	46
total number of individuals sampled	99
average density all sites (no. per m^2)	20
average density where present (no. per m^2)	91
median density where present (no. per m^2)	42
maximum density (no. per m^2)	467
length	
number measured	96
average length (mm)	14.8
standard deviation	8.4
range	3–33

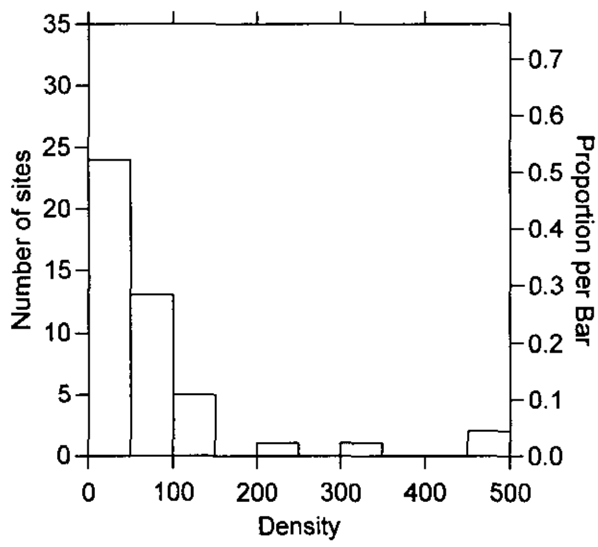

Figure 41: Frequency distribution of *Macomona liliana* densities (no. per m^2) at the 46 sample sites where they were recorded.

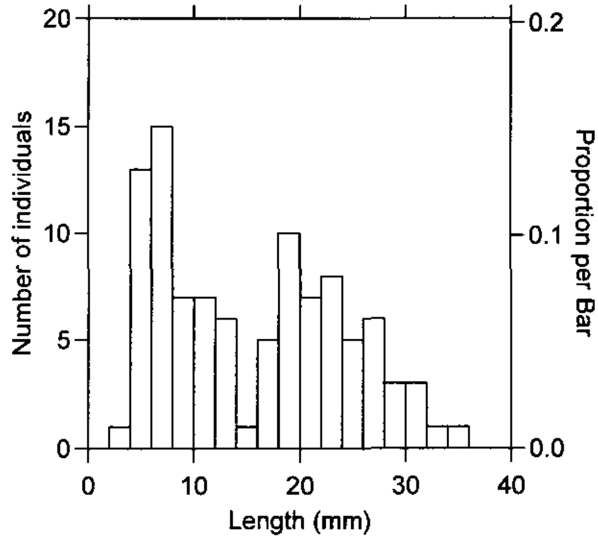

Figure 42: Length distribution of *Macomona liliana* on Farewell Spit. N = 96 specimens.

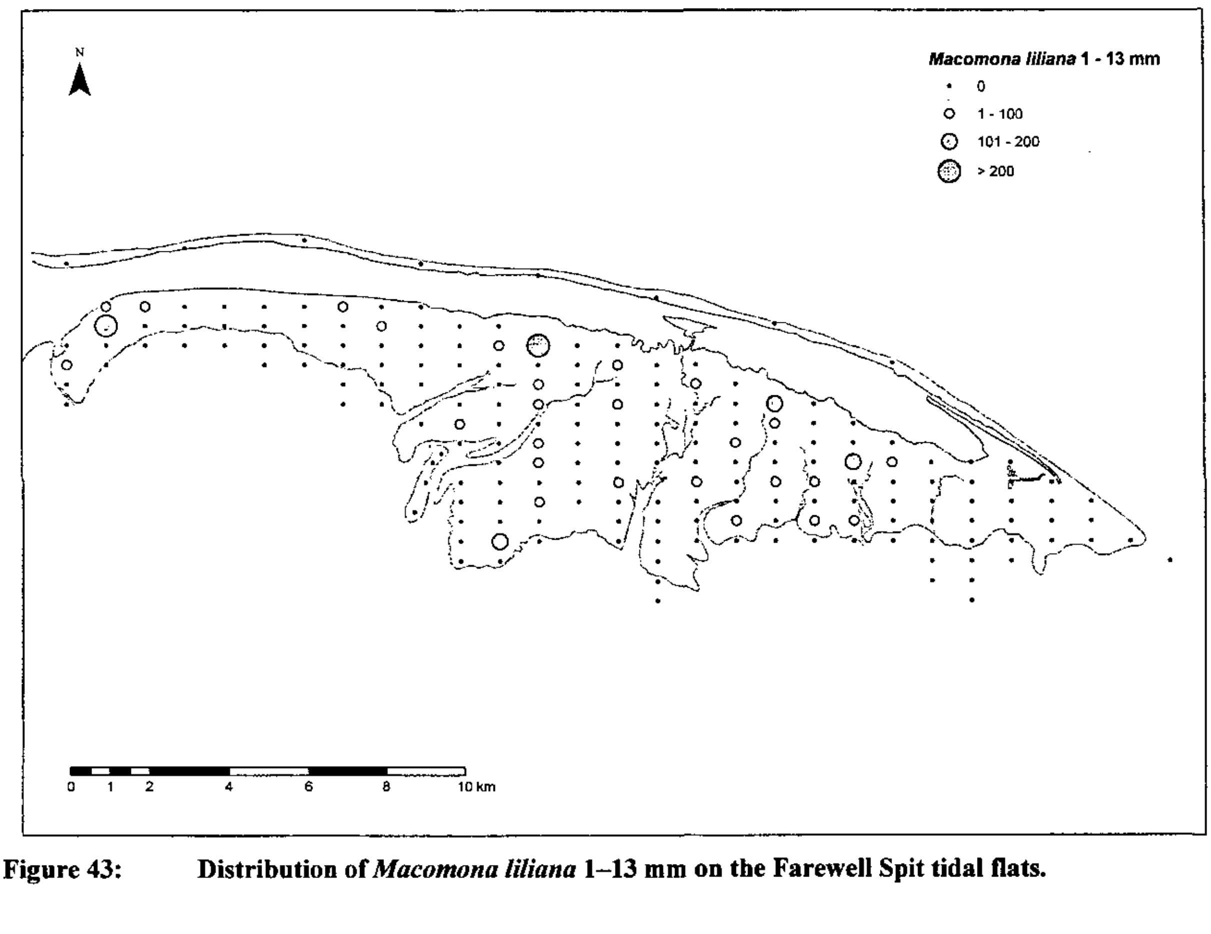

Figure 43: Distribution of *Macomona liliana* 1–13 mm on the Farewell Spit tidal flats.

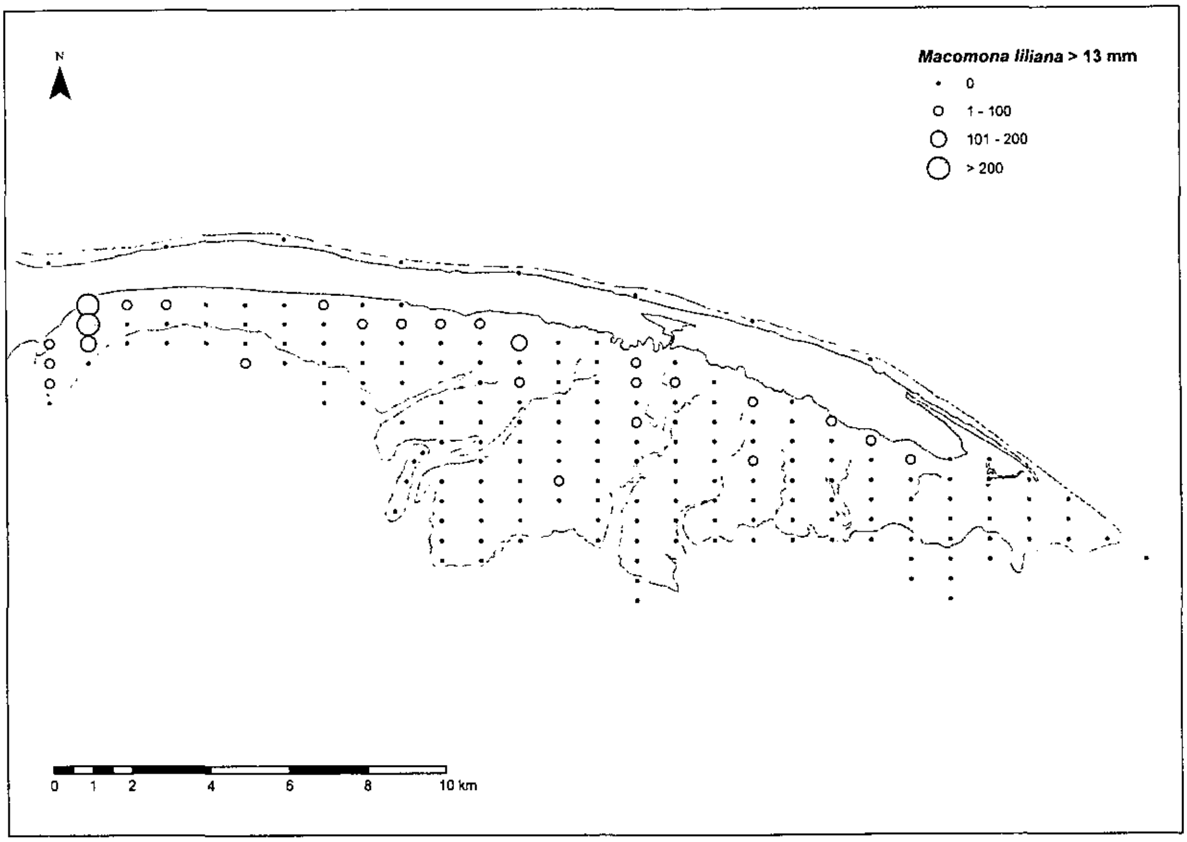

Figure 44: **Distribution of *Macomona liliana* greater than 13 mm on the Farewell Spit tidal flats.**

4.3.3 *Nucula hartvigiana*

The nutshell, *Nucula hartvigiana*, was found at less than one-quarter of the sample sites, but was often abundant where it was present (Table 10; Figure 45), particularly on the eelgrass-rich central flats (Figure 46). The smallest of the common intertidal bivalves present, nutshell sizes were slightly skewed towards individuals smaller than the mode of 6 mm (Figure 47).

Table 10: **Characteristics of sampled *Nucula hartvigiana* populations on the Farewell Spit tidal flats.**

Characteristic	Value
occurrence and density	
number of sample sites recorded at	42
total number of individuals sampled	630
average density all sites (no. per m^2)	112
average density where present (no. per m^2)	544
median density where present (no. per m^2)	106
maximum density (no. per m^2)	2 675
length	
number measured	630
average length (mm)	5.6
standard deviation	1.4
range	1–9

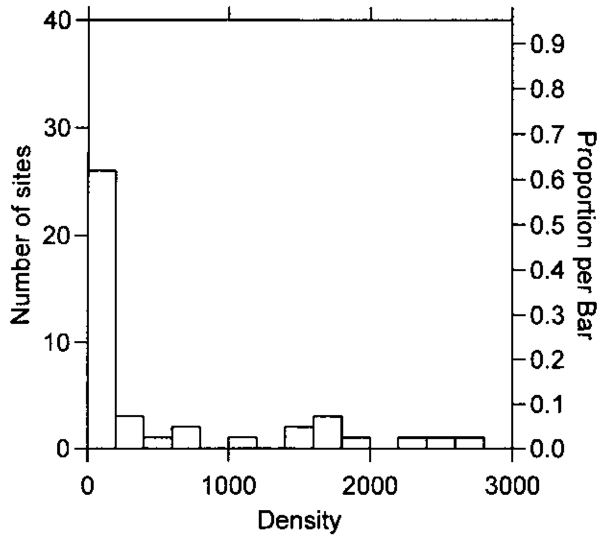

Figure 45: **Frequency distribution of *Nucula hartvigiana* densities (no. per m²) at the 42 sample sites where they were recorded.**

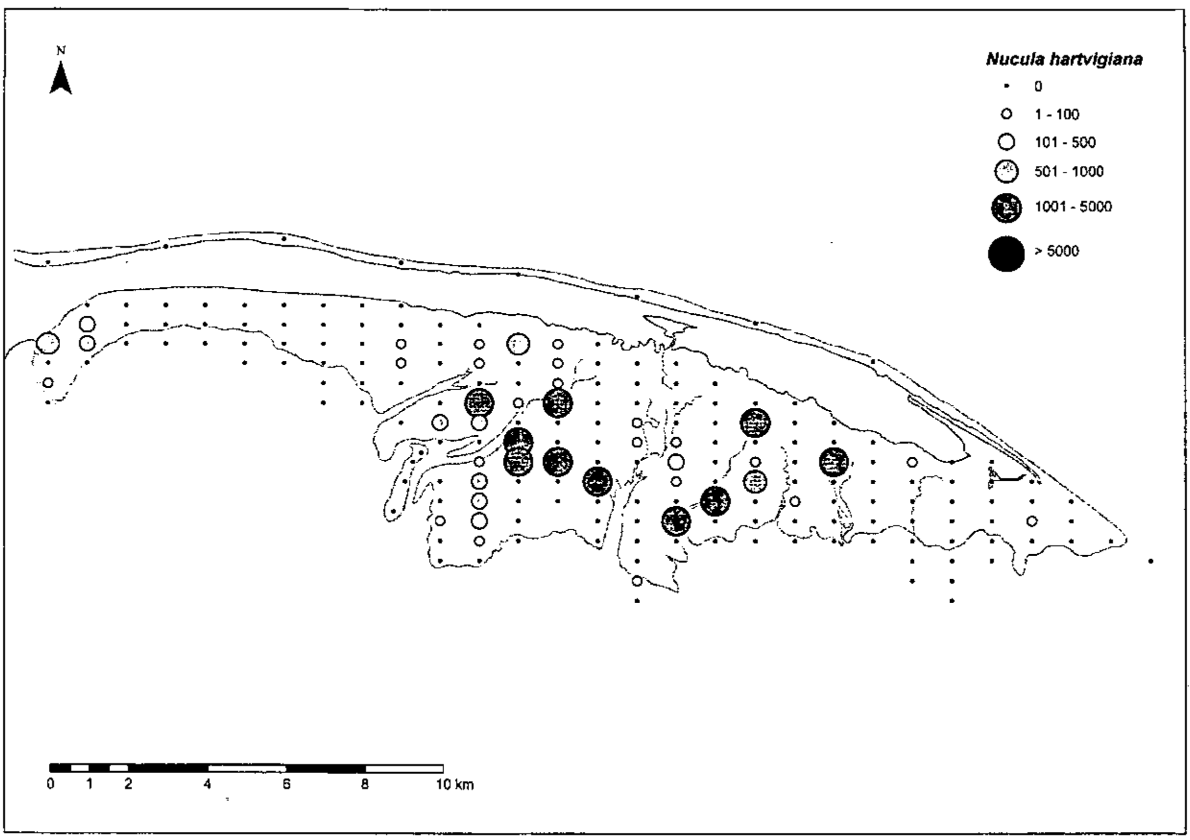

Figure 46: **Distribution of *Nucula hartvigiana* on the Farewell Spit tidal flats.**

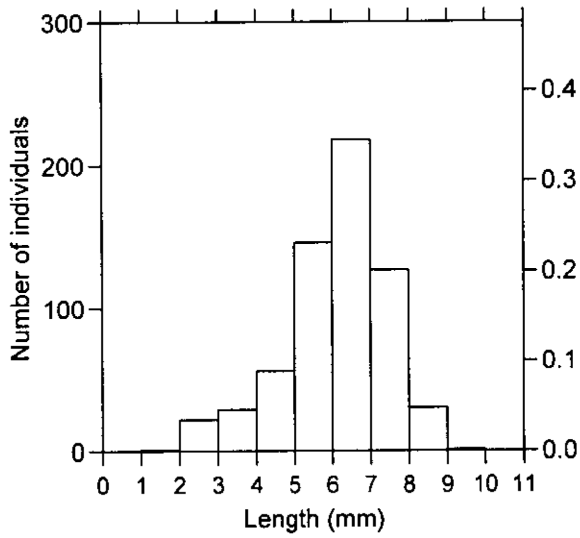

Figure 47: **Length distribution of *Nucula hartvigiana* on Farewell Spit. N = 630 specimens.**

Nucula densities were positively associated with the eelgrass (*Zostera*) surface coverage (Figure 48), with only low *Nucula* densities where *Zostera* was absent or scarce (cover score 1 and 2), and highest densities where *Zostera* cover was near-total (scores 6 and 7) (ANOVA, $F_{5,186} = 43.966$, $P < 0.001$, $R^2 = 0.542$). *Zostera* explained slightly less of the variation in *Nucula* densities if *Zostera* biomass (including subsurface root material) was used instead of surface cover (Figure 49) (linear regression, $F_{1,190} = 81.922$, $P < 0.001$, $R^2 = 0.300$).

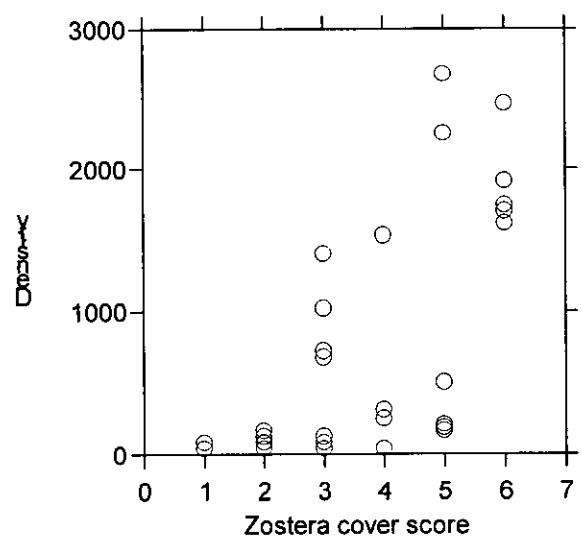

Figure 48: ***Nucula hartvigiana* densities (no. per m^2) in relation to surface coverage of the eelgrass *Zostera*.**

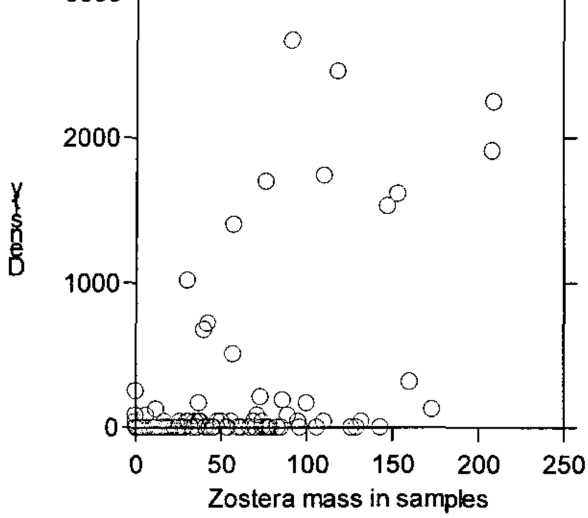

Figure 49: ***Nucula hartvigiana*** **densities (no. per m^2) in relation to the biomass (g fresh mass per set of core samples) of the eelgrass *Zostera.***

4.3.4 *Paphies australis*

Pipi, *Paphies australis*, occurred at almost one-third of the sample sites, and although numbers were sometimes very high (nine sites had densities of 2165–17 111 individuals per square metre), most sites had only low densities (median = 127 individuals per square metre) (Table 11; Figure 50). The vast bulk of the pipi sampled were small, 2–6 mm long, though some older individuals about 40 mm were found (Figure 51). The highest densities of pipi were at the extreme seaward edge of the tidal flats and generally comprised the small size-classes (Figures 52 and 53). This contrasts with the distribution of first-year pipi given by Morton & Miller (1973), in which settlement occurred on the upper beach.

Table 11: Characteristics of sampled *Paphies australis* populations on the Farewell Spit tidal flats.

Characteristic	Value
occurrence and density	
number of sample sites recorded at	57
total number of individuals sampled	1 691
average density all sites (no. per m^2)	330
average density where present (no. per m^2)	1 232
median density where present (no. per m^2)	127
maximum density (no. per m^2)	17 111
length	
number measured	1 690
average length (mm)	5.6
standard deviation	7.2
range	1–44

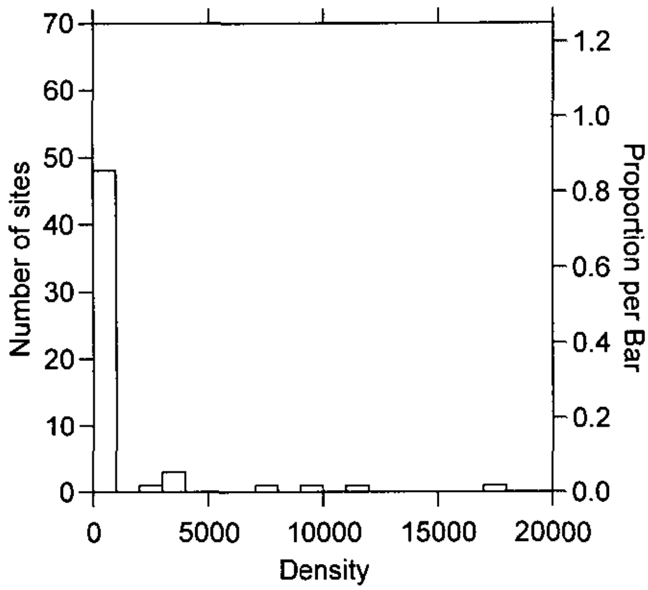

Figure 50: Frequency distribution of *Paphies australis* densities (no. per m^2) at the 57 sample sites where they were recorded.

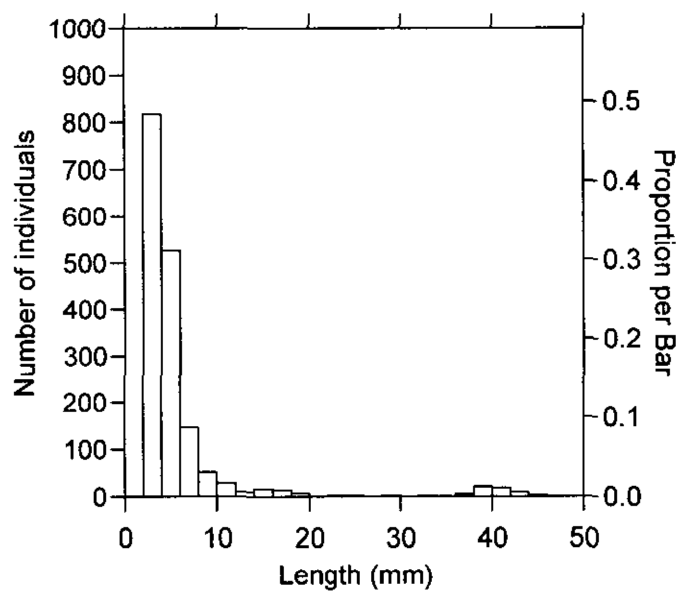

Figure 51: Length distribution of *Paphies australis* on Farewell Spit. N = 1690 specimens.

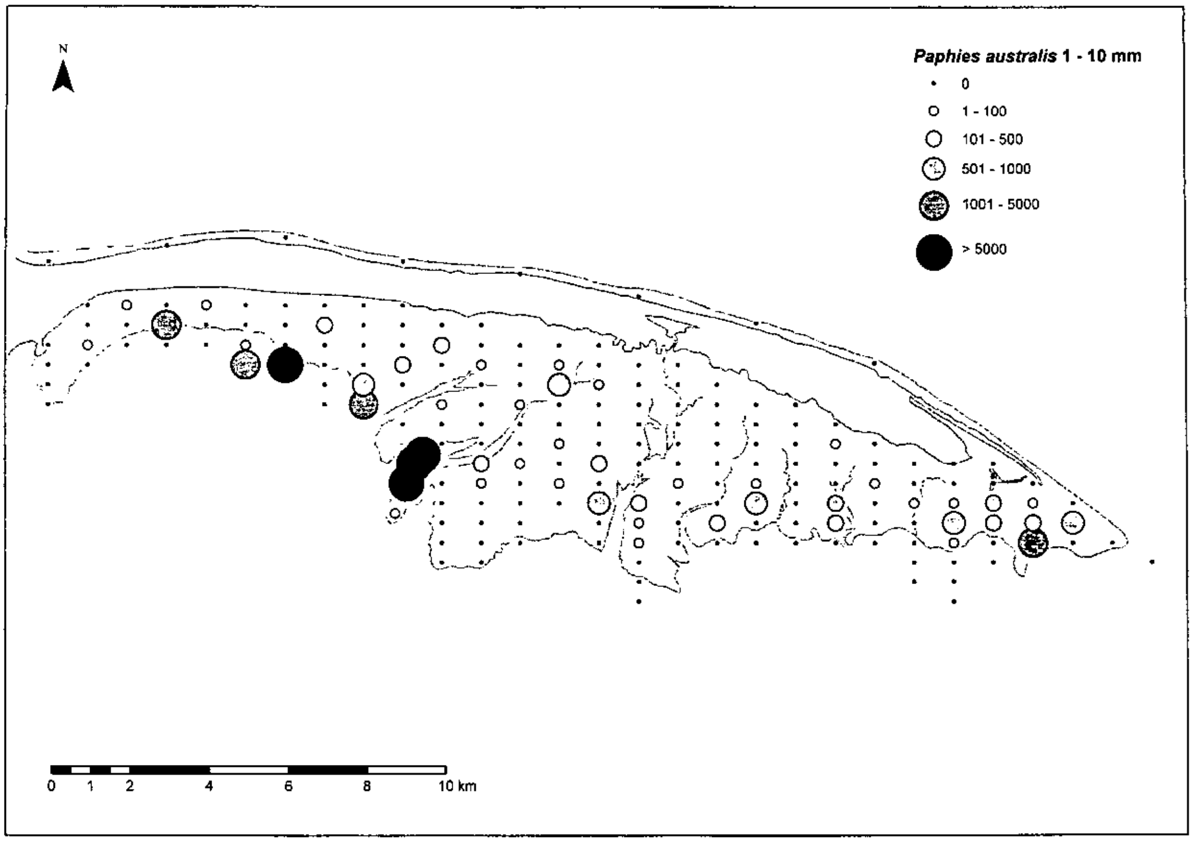

Figure 52: Distribution of *Paphies australis* 1–10 mm on the Farewell Spit tidal flats.

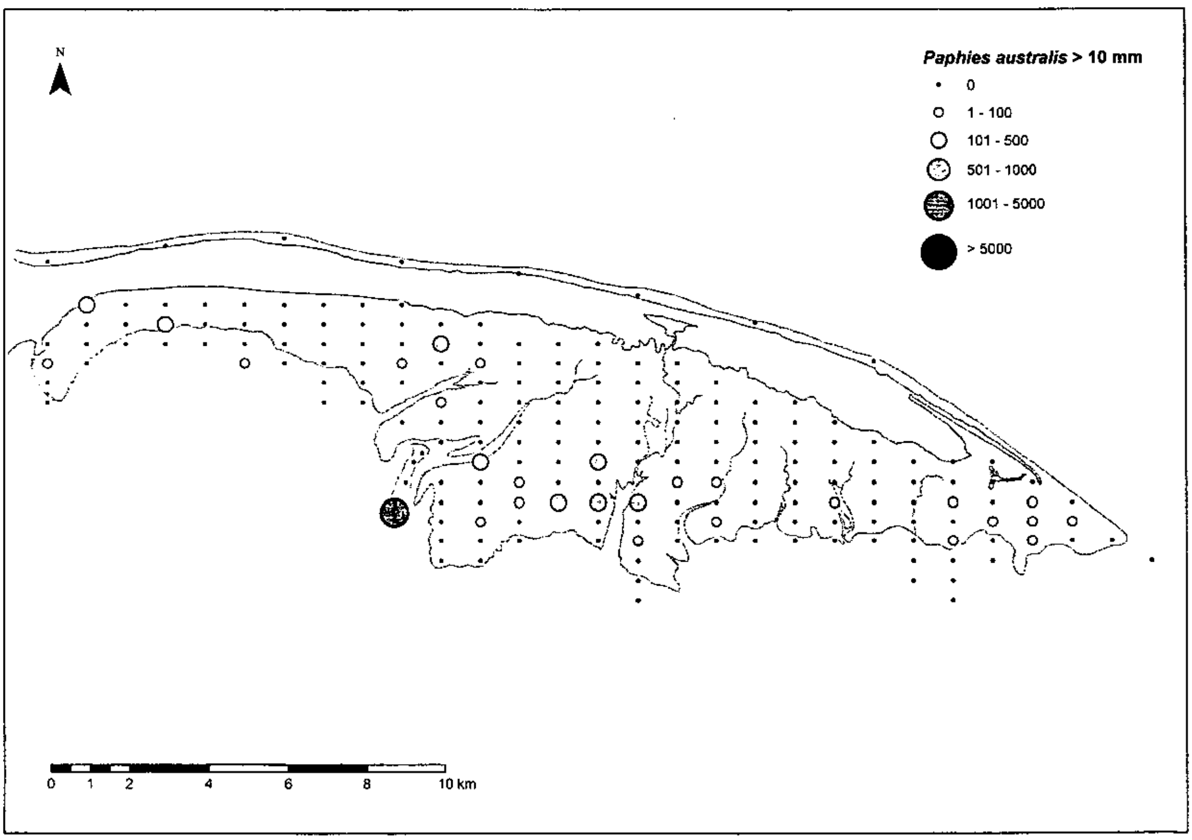

Figure 53: Distribution of *Paphies australis* greater than 10 mm on the Farewell Spit tidal flats.

4.3.5 *Xenostrobus pulex*

The small black mussel, *Xenostrobus pulex*, occurs patchily on the Farewell Spit tidal flats, forming localised, high-density beds, and is also found attached to hard substrates such as large cockle (*Austrovenus stutchburyi*) shells and pieces of whale bone. *Xenostrobus* occurred at only 11 mid- to lower-level sampling sites (Figure 54) but reached high densities at some of those sites (Table 12; Figure 55). The size distribution showed a main peak at 4–5 mm, with smaller peaks at 9 and 12 mm (Figure 56), but whether the latter peaks represent different cohorts or reflect sample size inadequacies is not known. Battley (1996) referred to this taxon as *Modiolus neozelanicus*.

Table 12: Characteristics of sampled *Xenostrobus pulex* populations on the Farewell Spit tidal flats.

Characteristic	Value
occurrence and density	
number of sample sites recorded at	11
total number of individuals sampled	104
average density all sites (no. per m^2)	22
average density where present (no. per m^2)	400
median density where present (no. per m^2)	42
maximum density (no. per m^2)	1 656
length	
number measured	101
average length (mm)	17.8
standard deviation	4.5
range	1–19

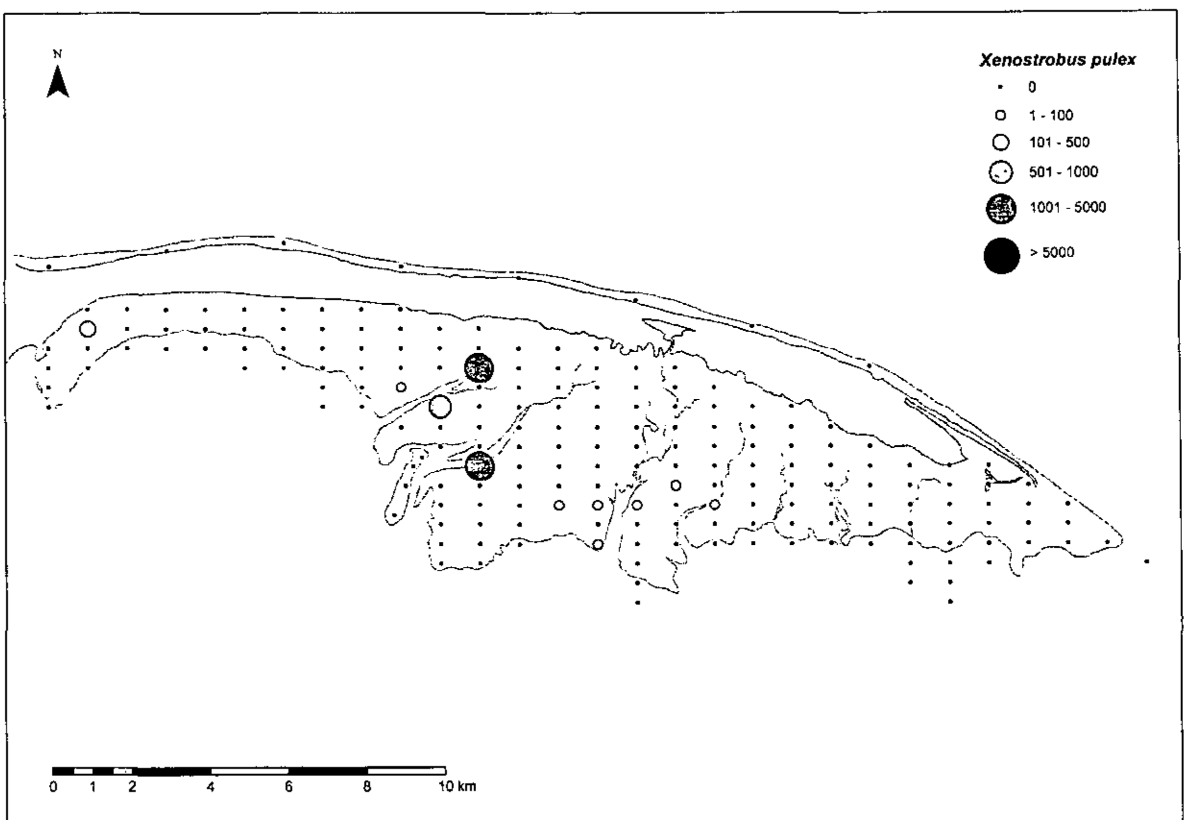

Figure 54: Distribution of *Xenostrobus pulex* on the Farewell Spit tidal flats.

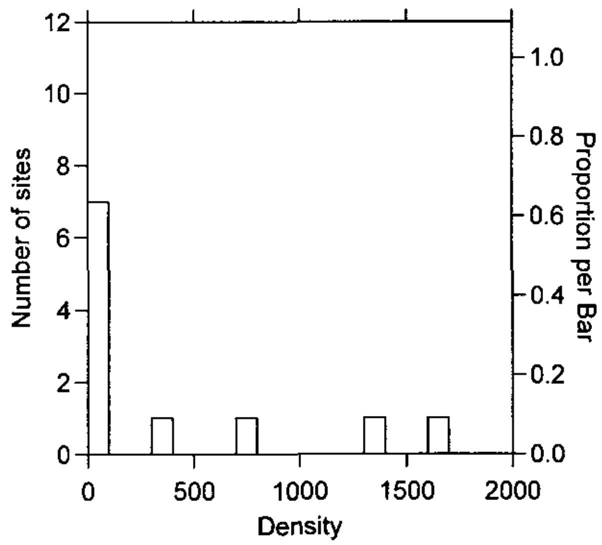

Figure 55: **Frequency distribution of *Xenostrobus pulex* densities (no. per m^2) at the 11 sample sites where they were recorded.**

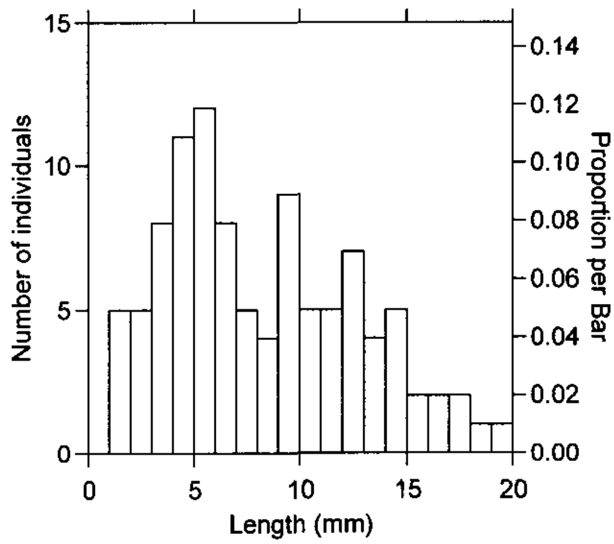

Figure 56: **Length distribution of *Xenostrobus pulex* on Farewell Spit. N = 101 specimens.**

4.4 Mollusca: Gastropoda

4.4.1 *Cominella glandiformis*

The scavenging whelk *Cominella glandiformis* was present at over a quarter of the sample sites, though generally in low densities (at 35 of the 54 sites only one individual was recorded in the samples) (Table 13; Figure 57). From 2 to 24 mm long, there was no obvious pattern to their sizes (Figure 58). Whelks were found across the central flats, and at the base of the spit near Puponga (Figure 59).

Table 13: **Characteristics of sampled *Cominella glandiformis* populations on the Farewell Spit tidal flats.**

Characteristic	Value
occurrence and density	
number of sample sites recorded at	54
total number of individuals sampled	106
average density all sites (no. per m^2)	23
average density where present (no. per m^2)	82
median density where present (no. per m^2)	42
maximum density (no. per m^2)	382
length	
number measured	106
average length (mm)	12.8
standard deviation	6.1
range	2–24

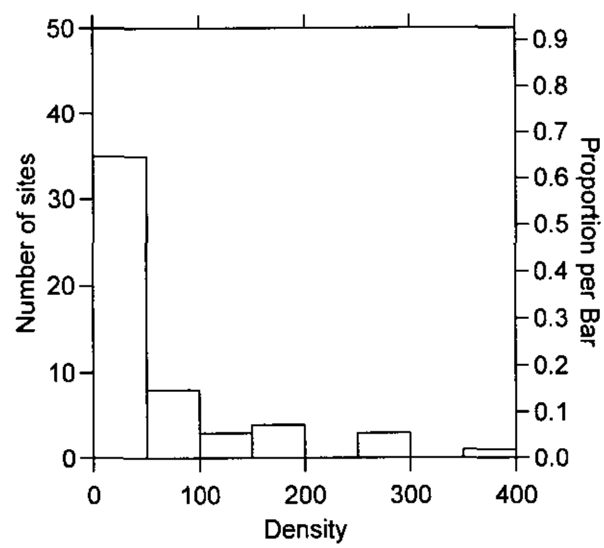

Figure 57: **Frequency distribution of *Cominella glandiformis* densities (no. per m^2) at the 54 sample sites where they were recorded.**

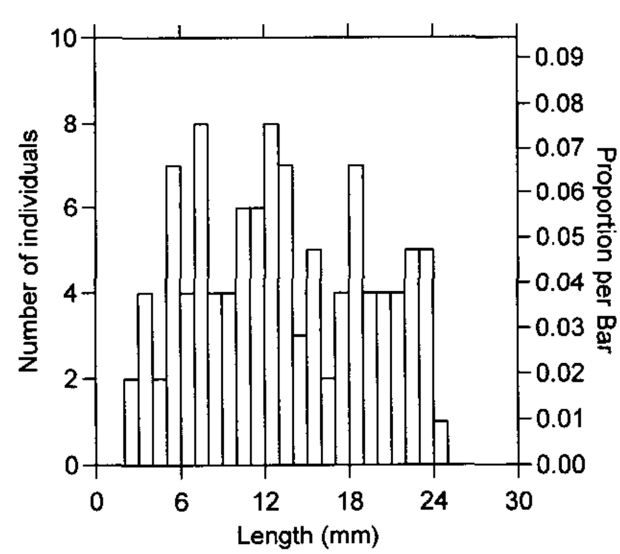

Figure 58: **Length distribution of *Cominella glandiformis* on Farewell Spit. N = 106 specimens.**

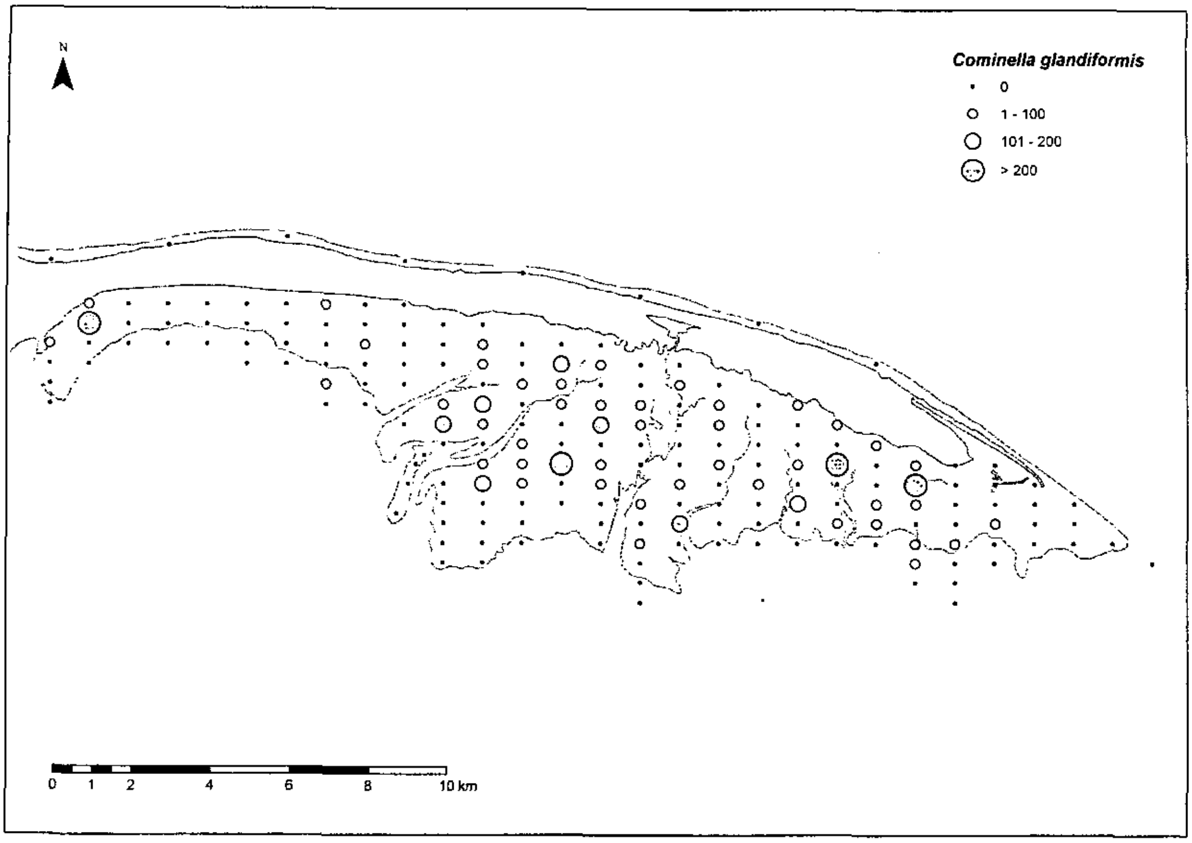

Figure 59: **Distribution of *Cominella glandiformis* on the Farewell Spit tidal flats.**

4.4.2 *Diloma* spp.

The top shells of the genus *Diloma* were difficult to differentiate from *Micrelenchus tenebrosus*, but *Diloma* appeared to occur infrequently and in low densities across the central flats (Table 14; Figures 60 and 61). They were mostly 2 or 3 mm long (Table 14; Figure 62). Both *D. bicaniculata* and *D. zeylandica* were identified.

Table 14: **Characteristics of sampled *Diloma* spp. populations on the Farewell Spit tidal flats.**

Characteristic	Value
occurrence and density	
number of sample sites recorded at	20
total number of individuals sampled	32
average density all sites (no. per m^2)	7
average density where present (no. per m^2)	67
median density where present (no. per m^2)	42
maximum density (no. per m^2)	170
length	
number measured	32
average length (mm)	3.1
standard deviation	1.4
range	2–7

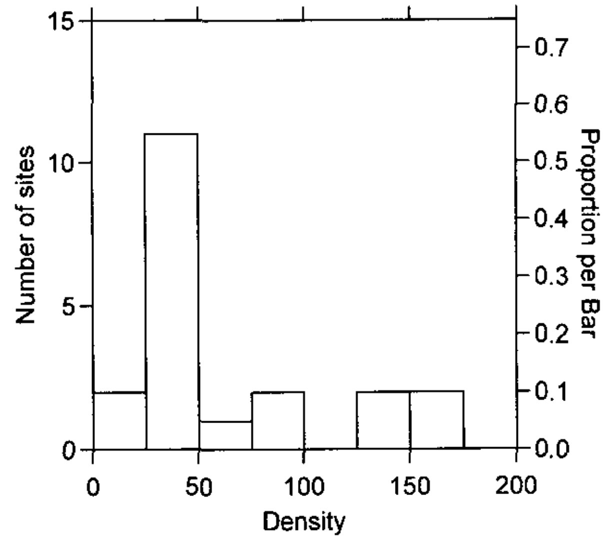

Figure 60: Frequency distribution of *Diloma* spp. densities (no. per m^2) at the 20 sample sites where they were recorded.

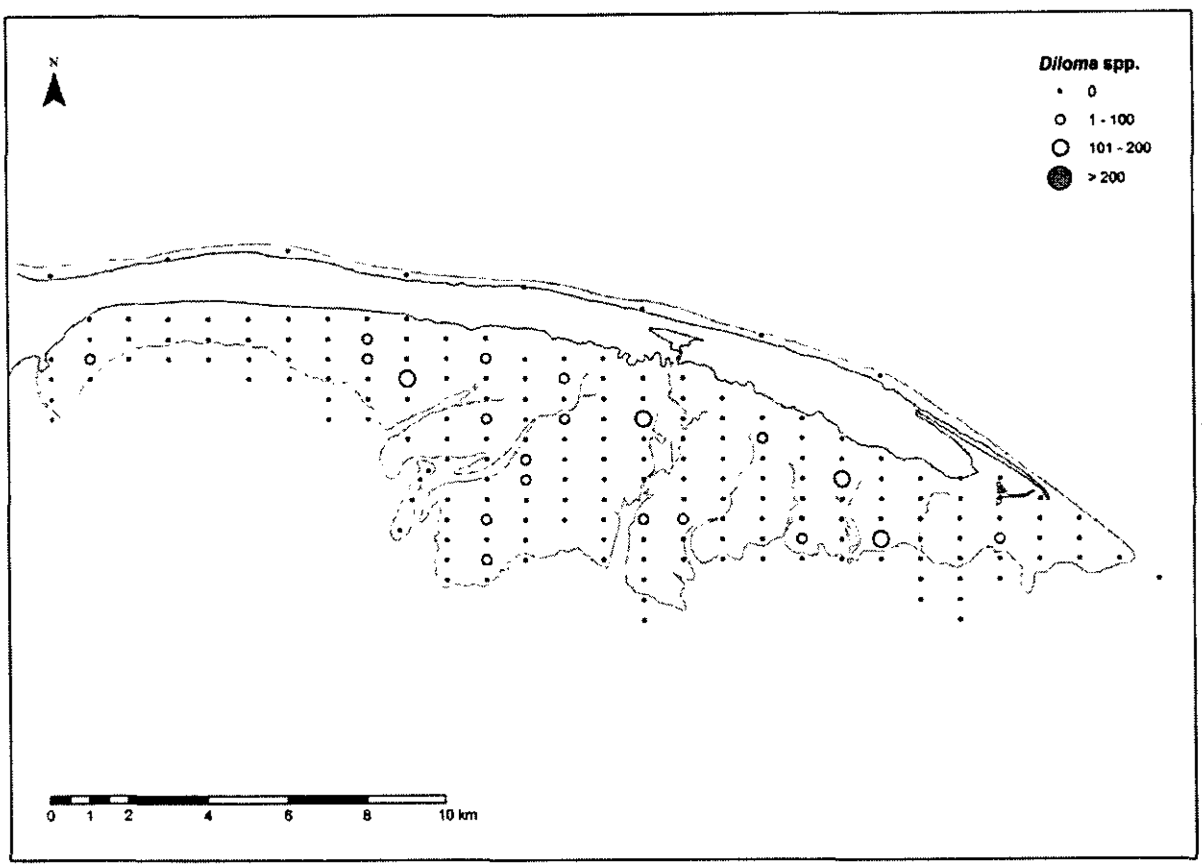

Figure 61: Distribution of *Diloma* spp. on the Farewell Spit tidal flats.

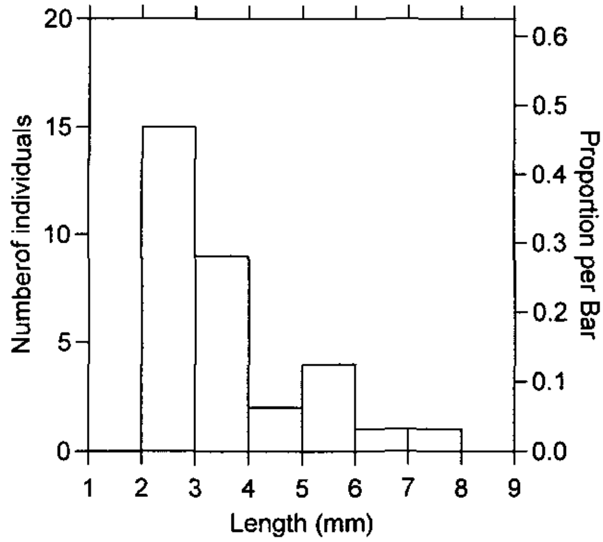

Figure 62: **Length distribution of *Diloma* spp. on Farewell Spit. N = 32 specimens.**

4.4.3 *Eatoniella* sp. cf. *lambata*

Eatoniella (probably *E. lambata*) are extremely small (mostly 2 mm: Table 15; Figure 63) snails that were patchily distributed across the tidal flats (Figure 64). Most of the sites where *Eatoniella* were present had only moderate densities (< 250 individuals per square metre), though a small number had high densities (1000–2000 individuals per square metre; Figure 65). While they are generally found on *Zostera*, there was no clear relationship between *Eatoniella* densities and *Zostera* cover.

Table 15: **Characteristics of sampled *Eatoniella* sp. populations on the Farewell Spit tidal flats.**

Characteristic	Value
occurrence and density	
number of sample sites recorded at	47
total number of individuals sampled	340
average density all sites (no. per m^2)	67
average density where present (no. per m^2)	271
median density where present (no. per m^2)	85
maximum density (no. per m^2)	2038
length	
number measured	340
average length (mm)	2.0
standard deviation	0.2
range	1–3

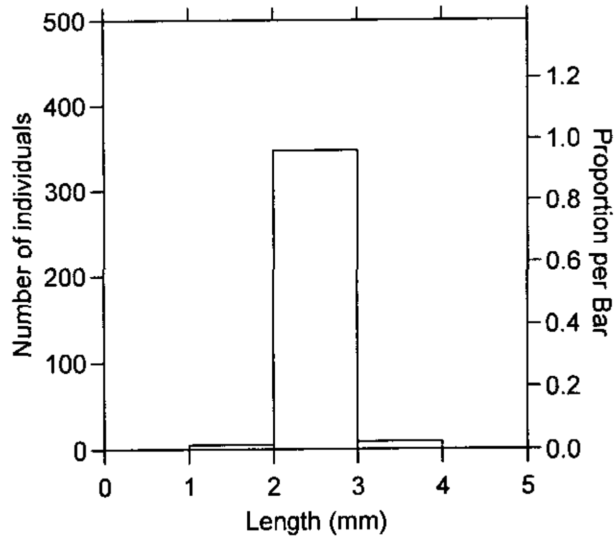

Figure 63: Length distribution of *Eatoniella* sp. on Farewell Spit. N = 340 specimens.

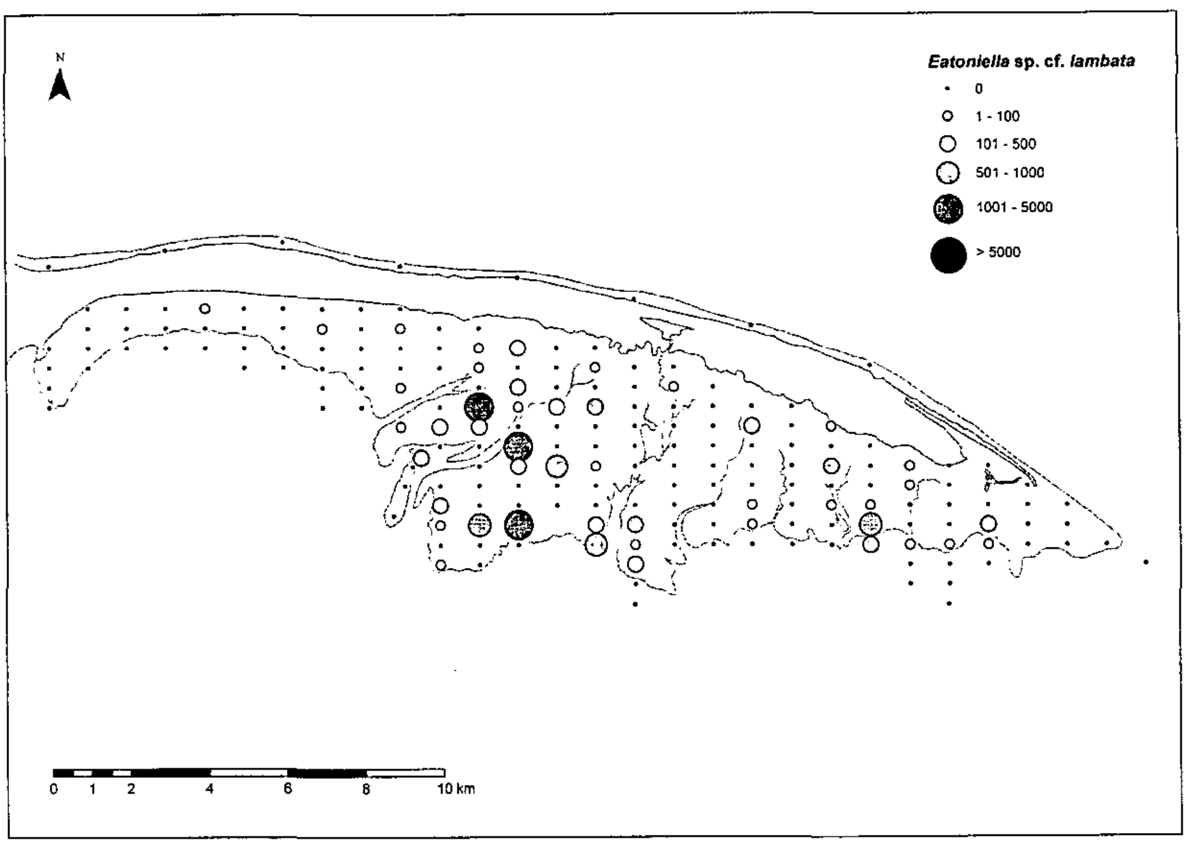

Figure 64: Distribution of *Eatoniella* sp. on the Farewell Spit tidal flats.

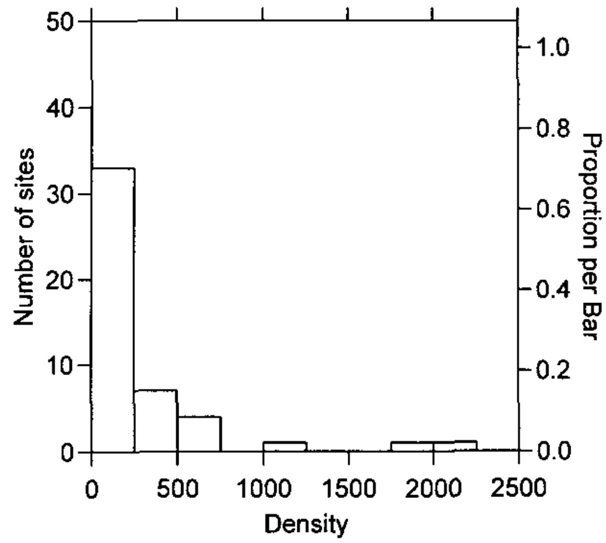

Figure 65: **Frequency distribution of *Eatoniella* sp. densities (no. per m^2) at the 40 sample sites where they were recorded.**

4.4.4 *Micrelenchus tenebrosus*

The top shell *Micrelenchus tenebrosus* was more widespread and more numerous than *Diloma* spp., occurring at low to moderate densities (mostly less than 300 individuals per square metre) (Table 16; Figure 66) on the tidal flats. They were widely distributed across the mid to lower tidal levels, predominantly on the large central flats (Figure 67). Most individuals were 2–7 mm long, but two larger individuals were present (Figure 68).

Table 16: **Characteristics of sampled *Micrelenchus tenebrosus* populations on the Farewell Spit tidal flats.**

Characteristic	Value
occurrence and density	
number of sample sites recorded at	34
total number of individuals sampled	229
average density all sites (no. per m^2)	50
average density where present (no. per m^2)	298
median density where present (no. per m^2)	85
maximum density (no. per m^2)	2 548
length	
number measured	229
average length (mm)	5.0
standard deviation	2.6
range	2–22

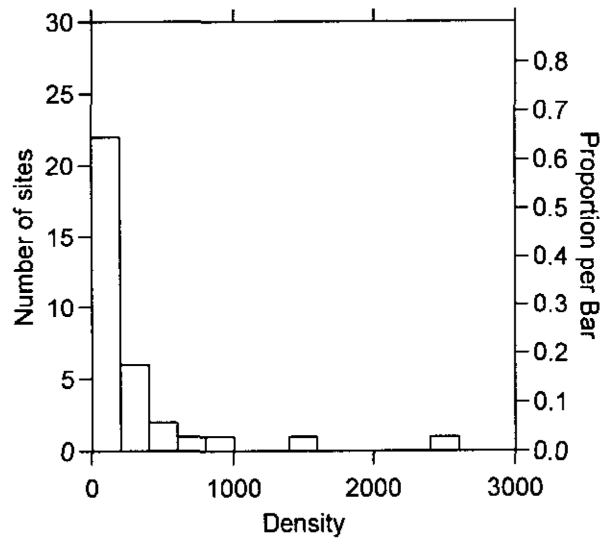

Figure 66: **Frequency distribution of *Micrelenchus tenebrosus* densities (no. per m²) at the 34 sample sites where they were recorded.**

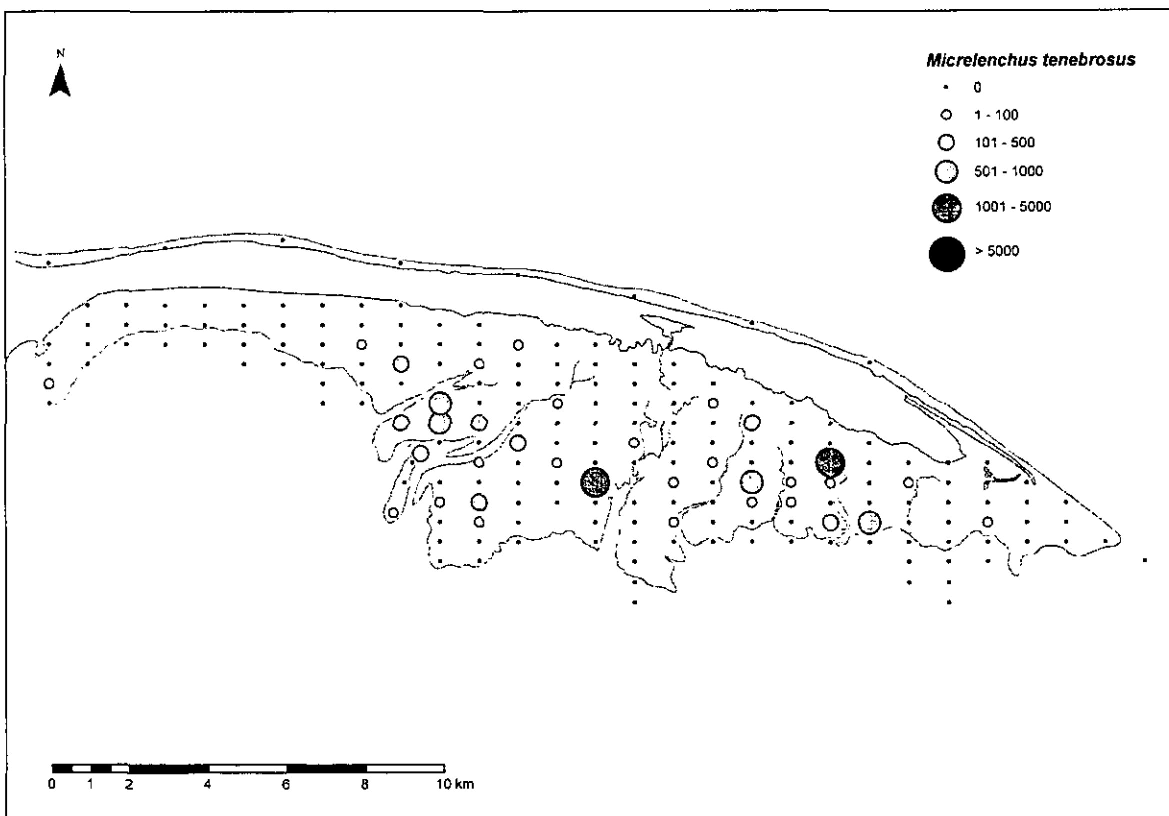

Figure 67: **Distribution of *Micrelenchus tenebrosus* on the Farewell Spit tidal flats.**

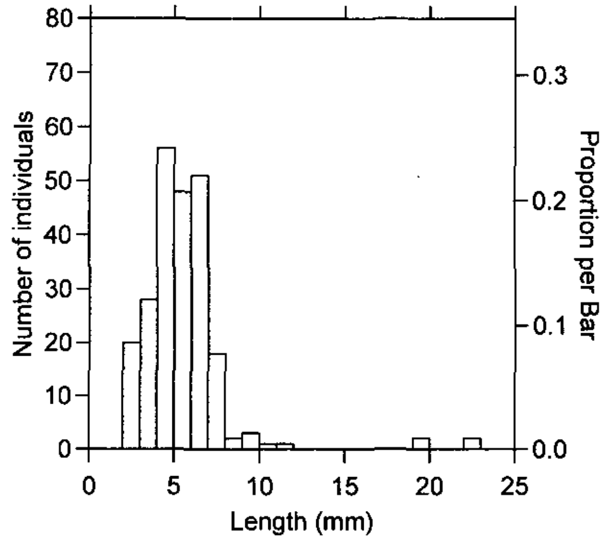

Figure 68: **Length distribution of *Micrelenchus tenebrosus* on Farewell Spit. N = 229 specimens.**

4.4.5 *Notoacmea helmsi*

Notoacmea helmsi is a limpet that was found in few sites on the Farewell Spit tidal flats. Two distinctive subspecies exist: the nominate form (which was found in high numbers attached to pipi *Paphies australis* shells at one site near the extreme low-water mark: Figure 69), and *scapha*, a

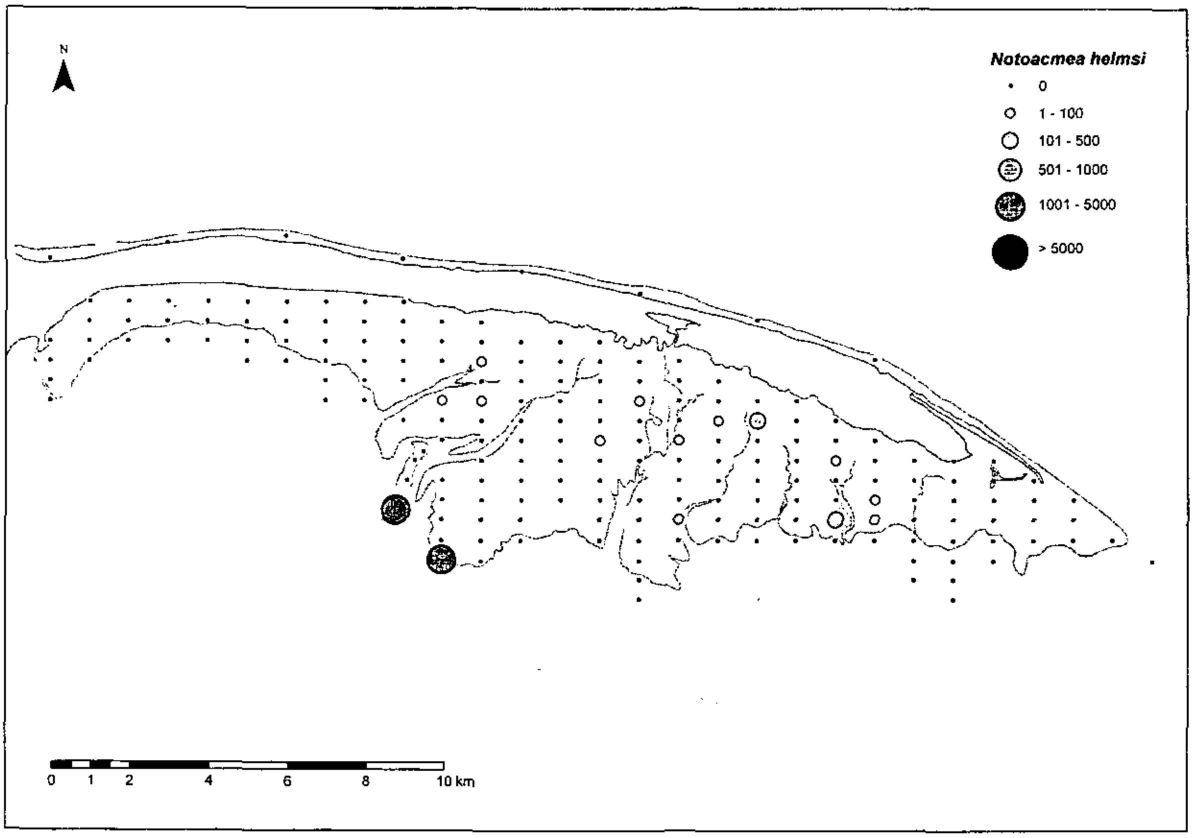

Figure 69: **Distribution of *Notoacmea helmsi* on the Farewell Spit tidal flats. *N. helmsi helmsi* occurred at the two sites with greater than 500 individuals per m^2 on the south-west edge of the central flats; all others records refer to *N. helmsi scapha*.**

specialised *Zostera* form, which is narrower and has parallel sides. This *Zostera* form was found at only a small number of sites with *Zostera* cover scores of 2–7 (Table 17; Figure 69). This is thought to be a genuine reflection of their relatively sparse density based on subjective field observations, but they could have been overlooked during sorting of dense *Zostera* samples. Of the 123 individuals found, only 19 were of the *Zostera* form. The limpets had a unimodal size distribution with most individuals being 3 or 4 mm long (Figure 70).

Table 17: Characteristics of sampled *Notoacmea helmsi* populations on the Farewell Spit tidal flats.

Characteristic	Value		
	helmsi	*scapha*	combined
occurrence and density			
number of sample sites recorded at	2	13	15
total number of individuals sampled	104	19	123
average density all sites (no. per m^2)		4	10
average density where present (no. per m^2)		62	145
median density where present (no. per m^2)		42	42
maximum density (no. per m^2)	1 231–3 185	170	1 231
length			
number measured	104	19	123
average length (mm)	3.8	3.1	3.7
standard deviation	1.0	1.2	1.1
range	1-6	1-5	1–6

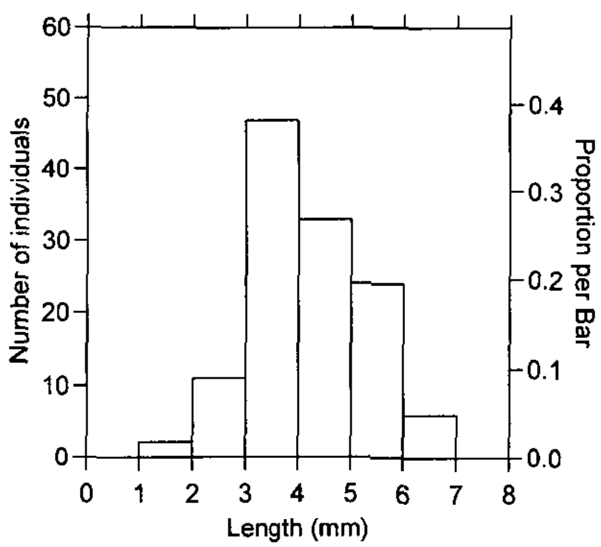

Figure 70: Length distribution of *Notoacmea helmsi* on Farewell Spit. N = 123 specimens.

4.4.6 *Zeacumantus* spp.

The horn shells *Zeacumantus lutulensis* and *Z. subcarinatus* were not systematically separated during the study, though both are present on the Farewell Spit tidal flats. They were widespread, being found at a third of the sampling sites (Table 18) at low to moderate densities (Figure 71).

Table 18: Characteristics of sampled *Zeacumantus* spp. populations on the Farewell Spit tidal flats.

Characteristic	Value
occurrence and density	
number of sample sites recorded at	65
total number of individuals sampled	292
average density all sites (no. per m^2)	58
average density where present (no. per m^2)	188
median density where present (no. per m^2)	127
maximum density (no. per m^2)	722
length	
number measured	291
average length (mm)	15.1
standard deviation	5.0
range	2–26

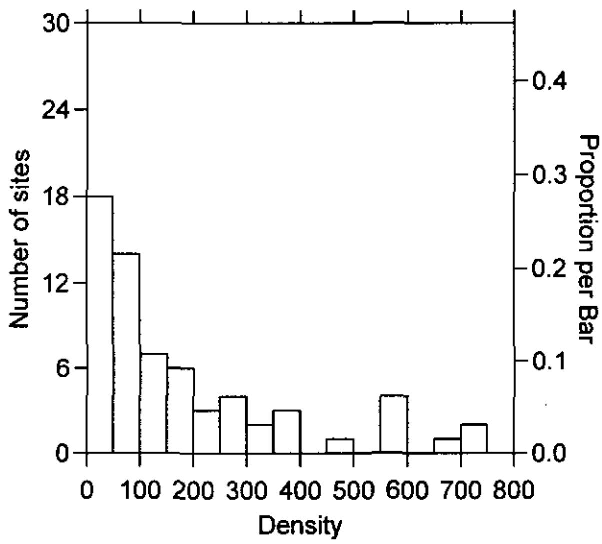

Figure 71: Frequency distribution of *Zeacumantus* spp. densities (no. per m^2) at the 65 sample sites where they were recorded.

They were mostly found on the mid to upper tidal flats, particularly along the central sections of the spit (Figure 72). Three size peaks were found (Figure 73), at 6, 13, and 19–20 mm. The first may represent the smaller species, *Z. subcarinatus*, and the larger two could represent separate cohorts of *Z. lutulensis*.

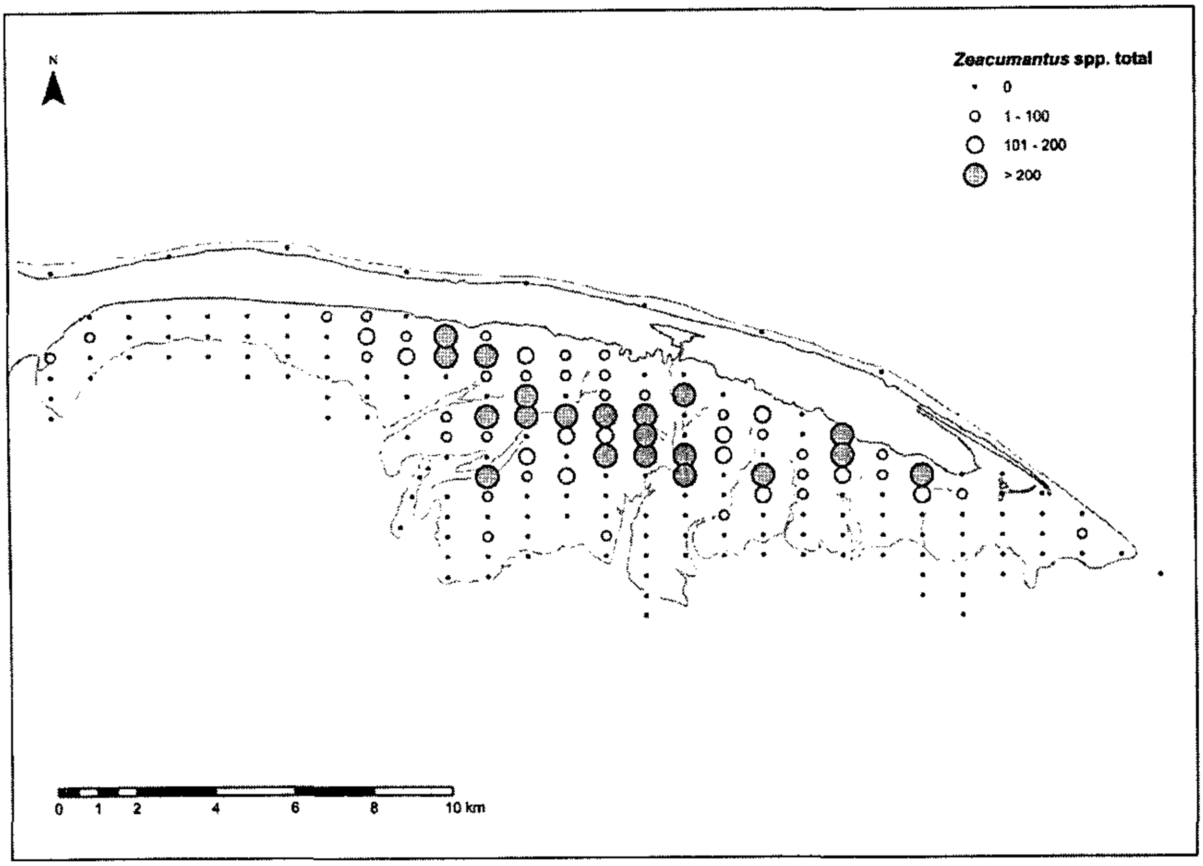

Figure 72: **Distribution of *Zeacumantus* spp. on the Farewell Spit tidal flats.**

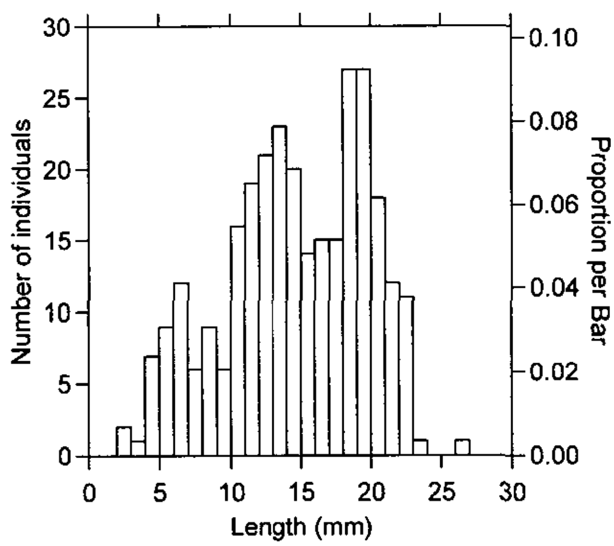

Figure 73: **Length distribution of *Zeacumantus* spp. on Farewell Spit. N = 291 specimens.**

4.5 Annelida: Polychaeta

4.5.1 Capitellidae

Capitellidae were the third-most widespread polychaete taxon on the Farewell Spit tidal flats, being recorded at one-third of the sample sites (Table 19). Most sites had capitellid densities of less than 200 individuals per square metre, but higher densities occurred at two sites (maximum 2590 individuals per square metre) (Figure 74; Table 19). These are not particularly high densities for Capitellidae. Highest densities were found on mid-level sites on the large central tidal flats, and they occurred in sites across the entire tidal range, from adjacent to saltmarsh down to the extreme spring low water mark. (Figure 75). Most complete capitellids were between 6 and 16 mm long (Figure 76), though the size distribution was skewed up to a maximum of 45 mm. As discussed earlier (Section 2.2.1), lengths for polychaete samples are almost certainly underestimates because of breakage of worms during sieving. Although no attempt was made to identify most capitellids to genus or species, *Capitella capitata* and *Heteromastus filiformis* were both recorded in samples, with *H. filiformis* being the most abundant (R. Asher, Cawthron Institute, Nelson, pers. comm. 2004).

Table 19: Characteristics of sampled Capitellidae populations on the Farewell Spit tidal flats.

Characteristic	Value
occurrence and density	
number of sample sites recorded at	65
total number of individuals sampled	357
average density all sites (no. per m^2)	77
average density where present (no. per m^2)	226
median density where present (no. per m^2)	85
maximum density (no. per m^2)	2 590
length	
number measured	159
average length (mm)	18.5
standard deviation	7.1
range	6–45

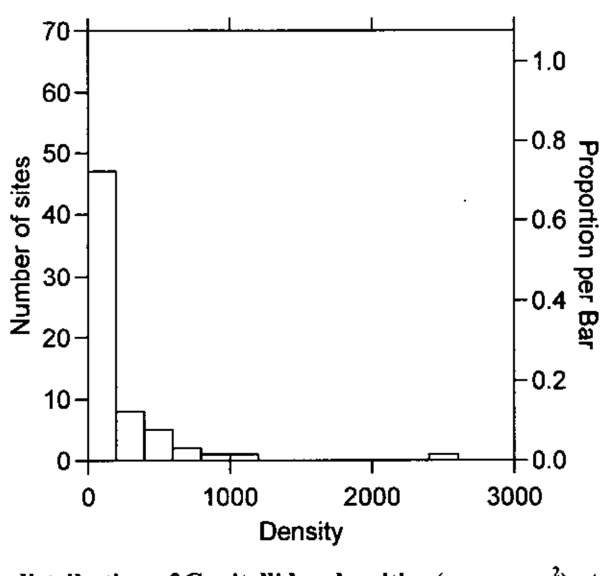

Figure 74: Frequency distribution of Capitellidae densities (no. per m^2) at the 65 sample sites where they were

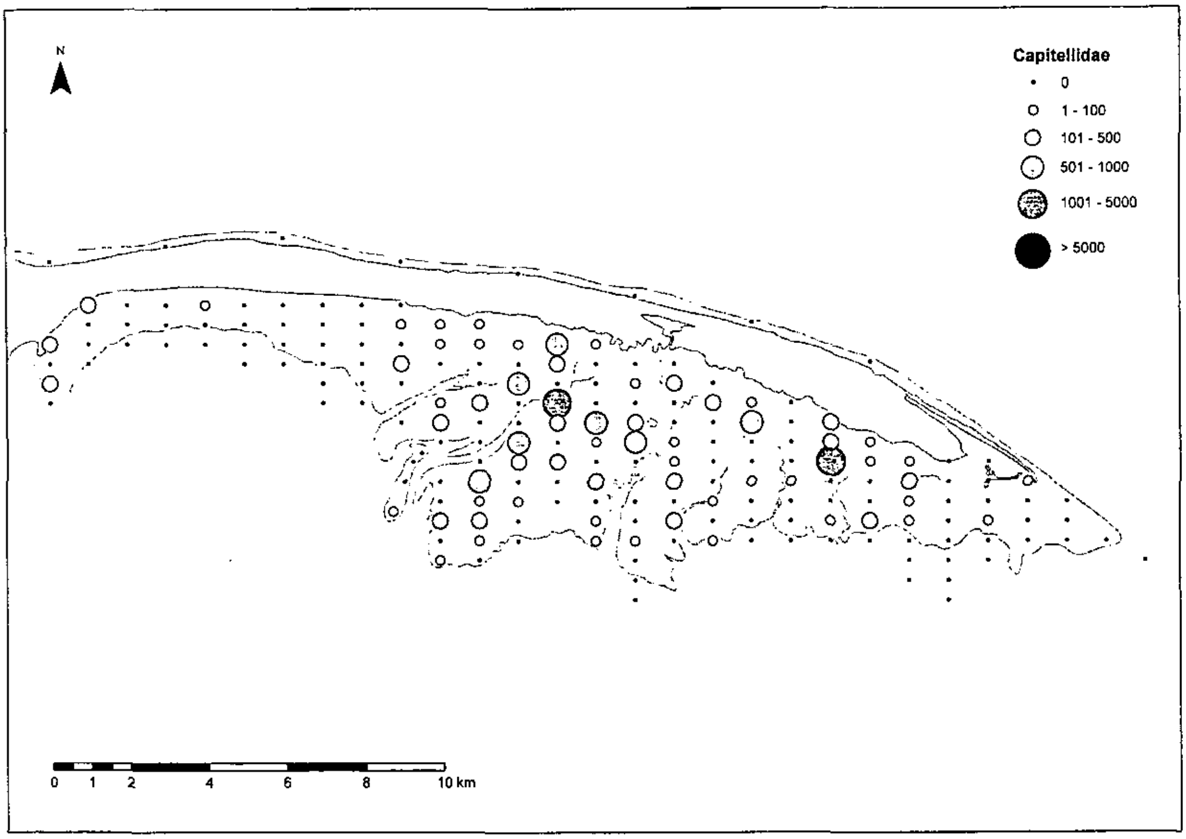

Figure 75: **Distribution of Capitellidae on the Farewell Spit tidal flats.**

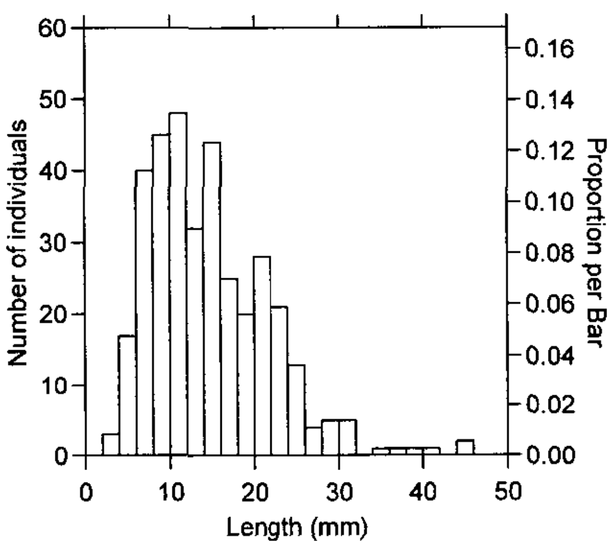

Figure 76: **Length distribution of Capitellidae on Farewell Spit. N = 159 specimens.**

4.5.2 Glyceridae

The distinctive predatory worms of the family Glyceridae were widespread in low numbers on the tidal flats. They were present at just over a quarter of the sample sites (Table 20), in densities of under 100 individuals per square metre (Figure 77). Highest densities were generally towards the seaward edge of the tidal flats (Figure 78). Half of the measurable worms were 15 mm or less in length, but many individuals were up to 50 mm long, and two were over 80 mm (Figure 79). The genus *Hemipodus* was recorded in the samples.

Table 20: Characteristics of sampled Glyceridae populations on the Farewell Spit tidal flats.

Characteristic	Value
occurrence and density	
number of sample sites recorded at	50
total number of individuals sampled	96
average density all sites (no. per m^2)	21
average density where present (no. per m^2)	79
median density where present (no. per m^2)	42
maximum density (no. per m^2)	212
length	
number measured	78
average length (mm)	19.6
standard deviation	15.3
range	2–85

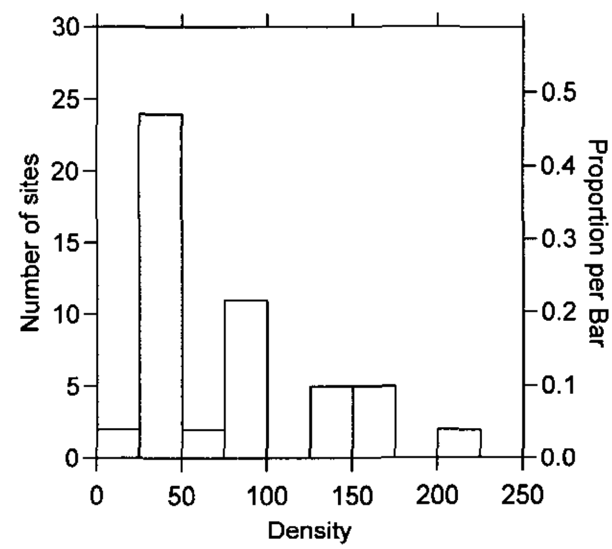

Figure 77: Frequency distribution of Glyceridae densities (no. per m^2) at the 50 sample sites where they were recorded.

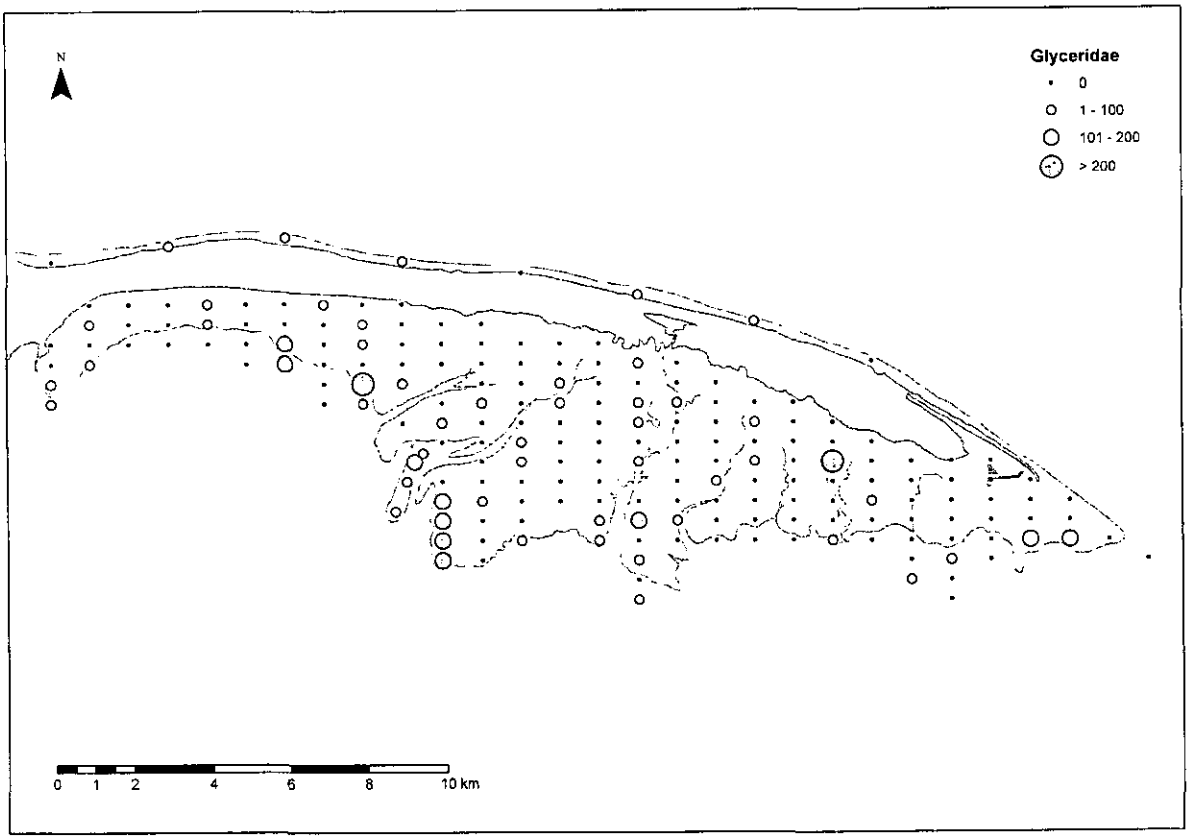

Figure 78: **Distribution of Glyceridae on the Farewell Spit tidal flats.**

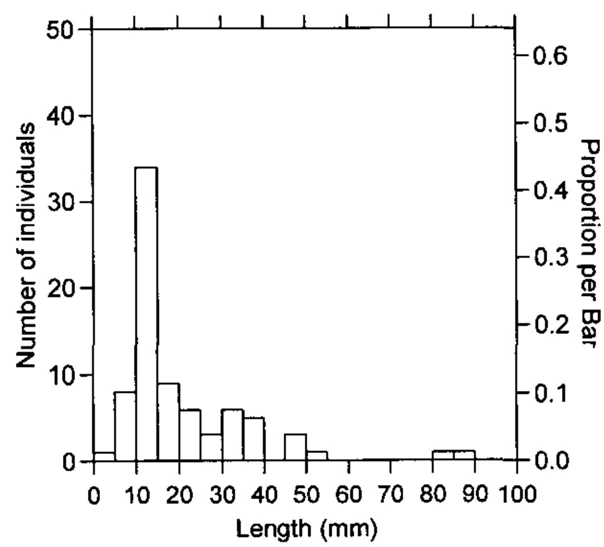

Figure 79: **Length distribution of Glyceridae on Farewell Spit. N = 78 specimens.**

4.5.3 Maldanidae

Two genera of bamboo worm, *Clymene* and *Macroclymenella*, were present in samples, though they were not routinely separated in this study. Maldanids were present at about one fifth of the sample sites, in low to moderate densities (Table 21; Figure 80). They had a disjunct distribution, occurring on upper-level flats on the central flats, and also towards the seaward edge of the flats (Figure 81). This may reflect the distribution of the two taxa, as all *Clymene* records were from the upper tidal flat sites, whereas all *Macroclymenella* records were from close to the low tide edge. In Section 5, the maldanids are split into two taxa, Maldanidae 1 being the lower flat individuals, Maldanidae 2 being the upper flat individuals. Less than half of the worms sampled were intact after processing, most being between 20 and 30 mm in length (Figure 82).

Table 21: Characteristics of sampled Maldanidae populations on the Farewell Spit tidal flats.

Characteristic	Value
occurrence and density	
number of sample sites recorded at	39
total number of individuals sampled	77
average density all sites (no. per m^2)	16
average density where present (no. per m^2)	83
median density where present (no. per m^2)	42
maximum density (no. per m^2)	340
length	
number measured	36
average length (mm)	28.1
standard deviation	13.4
range	8–78

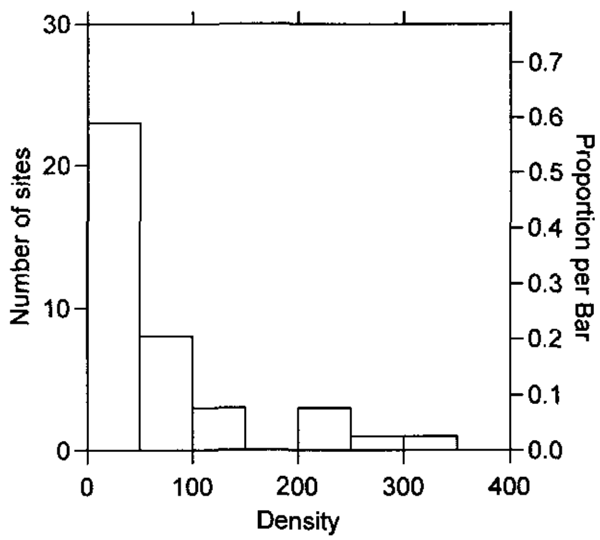

Figure 80: Frequency distribution of Maldanidae densities (no. per m^2) at the 39 sample sites where they were recorded.

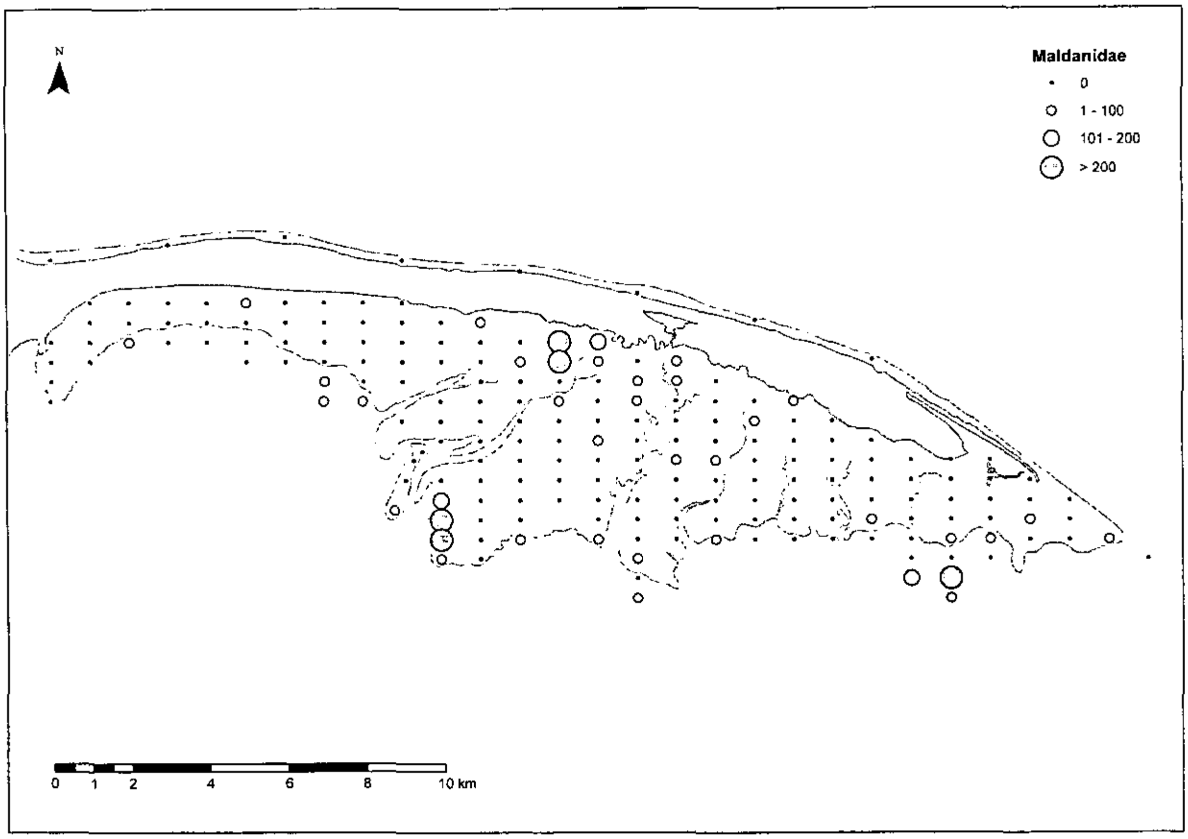

Figure 81: **Distribution of Maldanidae on the Farewell Spit tidal flats.**

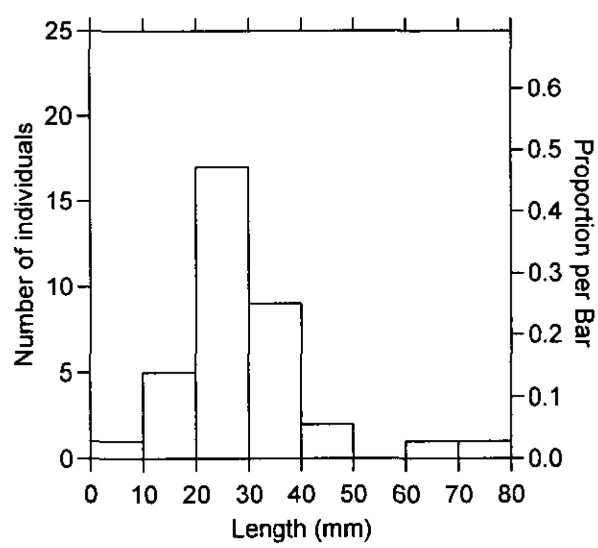

Figure 82: **Length distribution of Maldanidae on Farewell Spit. N = 36 specimens.**

4.5.4 Nephtyidae

Nephtyidae were found at only 15 sites (Table 22). They occurred in lower-level tidal flats along the length of the spit (Figure 83), but never in high densities (Figure 84). Most worms were 10–30 mm long, though larger individuals reached 80 mm (Figure 85). Of those identified to genus, most were *Aglaophamus*; *Nephtys* was also recorded.

Table 22: Characteristics of sampled Nephtyidae populations on the Farewell Spit tidal flats.

Characteristic	Value
occurrence and density	
number of sample sites recorded at	15
total number of individuals sampled	29
average density all sites (no. per m^2)	6
average density where present (no. per m^2)	81
median density where present (no. per m^2)	42
maximum density (no. per m^2)	212
length	
number measured	18
average length (mm)	25.6
standard deviation	15.5
range	10–80

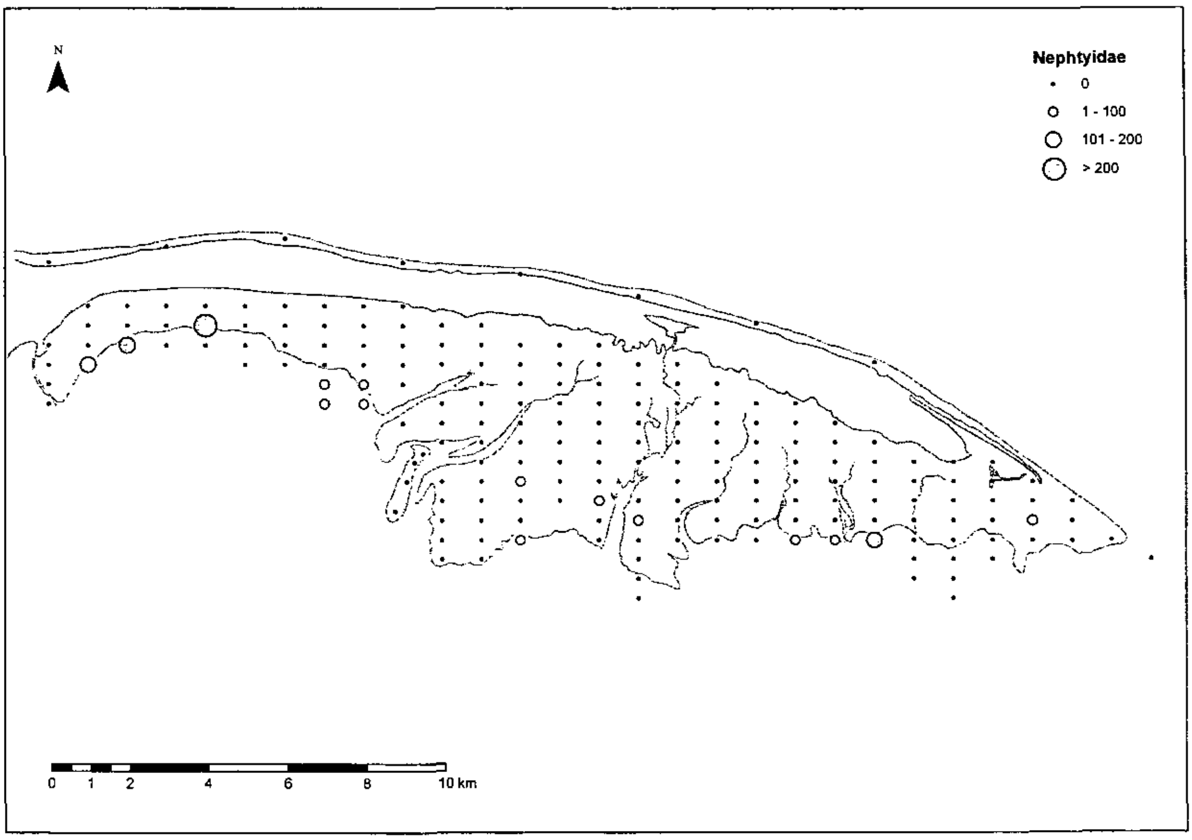

Figure 83: Distribution of Nephtyidae on the Farewell Spit tidal flats.

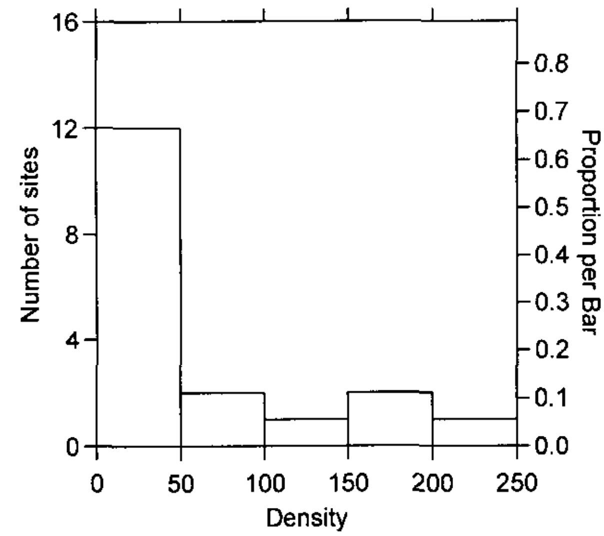

Figure 84: **Frequency distribution of Nephtyidae densities (no. per m^2) at the 15 sample sites where they were recorded.**

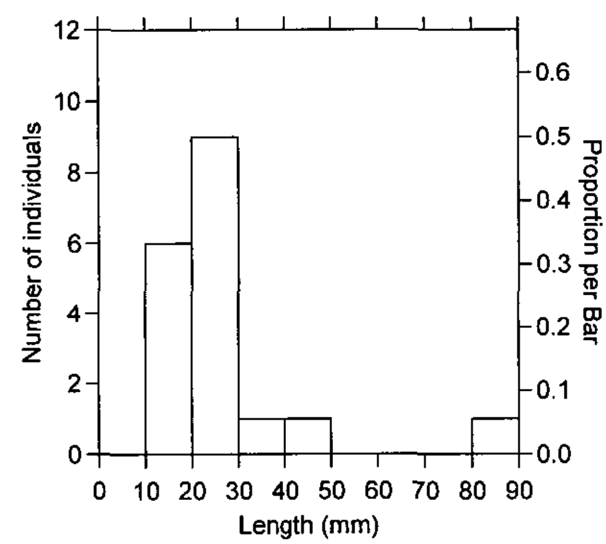

Figure 85: **Length distribution of Nephtyidae on Farewell Spit. N = 18 specimens.**

4.5.5 Nereididae

The most widespread polychaete group on the tidal flats (and the fourth-most widespread taxonomic group overall), Nereididae were encountered at more than half the sampling sites (Table 23). They were typically found in low densities, most sites having fewer than 100 individuals per square metre (Table 23; Figure 86). Their distribution across the tidal flats was fairly even, the only major gaps in their occurrence being at largely lower-level outer sites in the first 10 km along the spit and along the outer third of the spit (Figure 87). Most intact Nereididae were between 5 mm and 12 mm long (Figure 88), though one extremely large individual (230 mm) was recorded on the outer flats (site HH607050: see Appendix 1 for location).

Table 23: **Characteristics of sampled Nereididae populations on the Farewell Spit tidal flats.**

Characteristic	Value
occurrence and density	
number of sample sites recorded at	97
total number of individuals sampled	230
average density all sites (no. per m^2)	50
average density where present (no. per m^2)	99
median density where present (no. per m^2)	85
maximum density (no. per m^2)	425
length	
number measured	154
average length (mm)	17.2
standard deviation	20.8
range	4–230

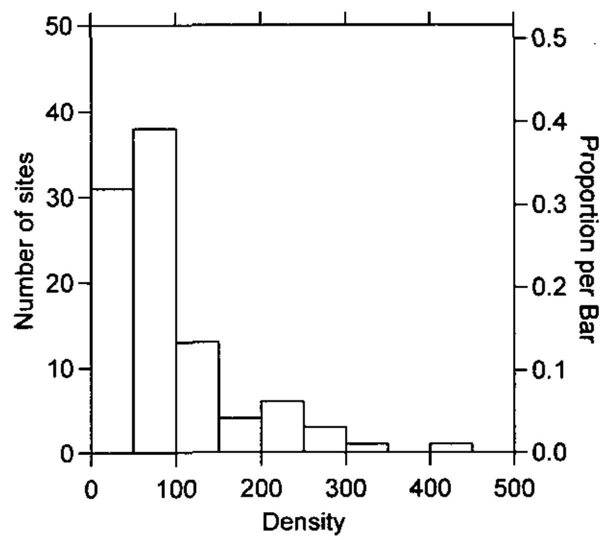

Figure 86: **Frequency distribution of Nereididae densities (no. per m^2) at the 97 sample sites where they were recorded.**

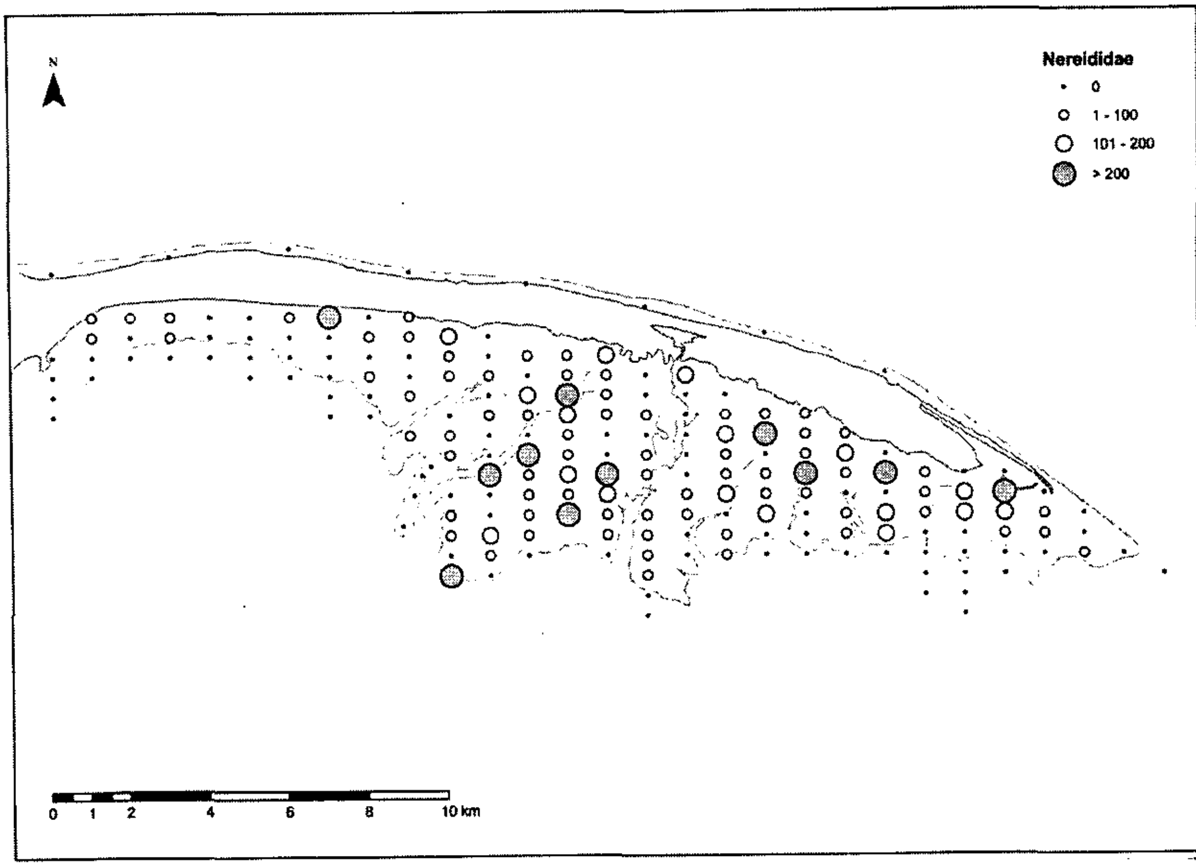

Figure 87: **Distribution of Nereididae on the Farewell Spit tidal flats.**

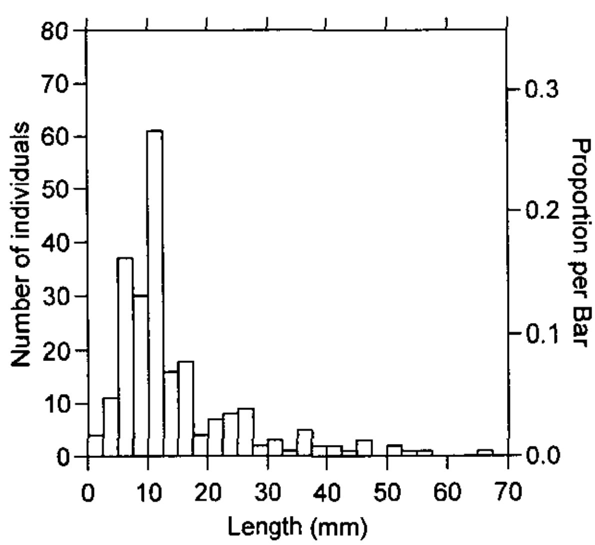

Figure 88: **Length distribution of Nereididae on Farewell Spit. N = 153 specimens. One 230 mm individual is not shown.**

4.5.6 Orbiniidae

Orbiniid worms were found at about one-fifth of the sampling sites (Table 24; Figure 89), at generally low densities (less than 100 individuals per square metre) (Figure 90). One site near the base of the spit (AA6076000) was an exception, with a density of almost 700 individuals per square metre. Being highly prone to breakage during sieving, only 21 of the 77 orbiniids were intact; most of these were 5–20 mm long (Table 24; Figure 91).

Table 24: Characteristics of sampled Orbiniidae populations on the Farewell Spit tidal flats.

Characteristic	Value
occurrence and density	
number of sample sites recorded at	37
total number of individuals sampled	77
average density all sites (no. per m^2)	17
average density where present (no. per m^2)	87
median density where present (no. per m^2)	42
maximum density (no. per m^2)	679
length	
number measured	21
average length (mm)	16.7
standard deviation	8.9
range	6–44

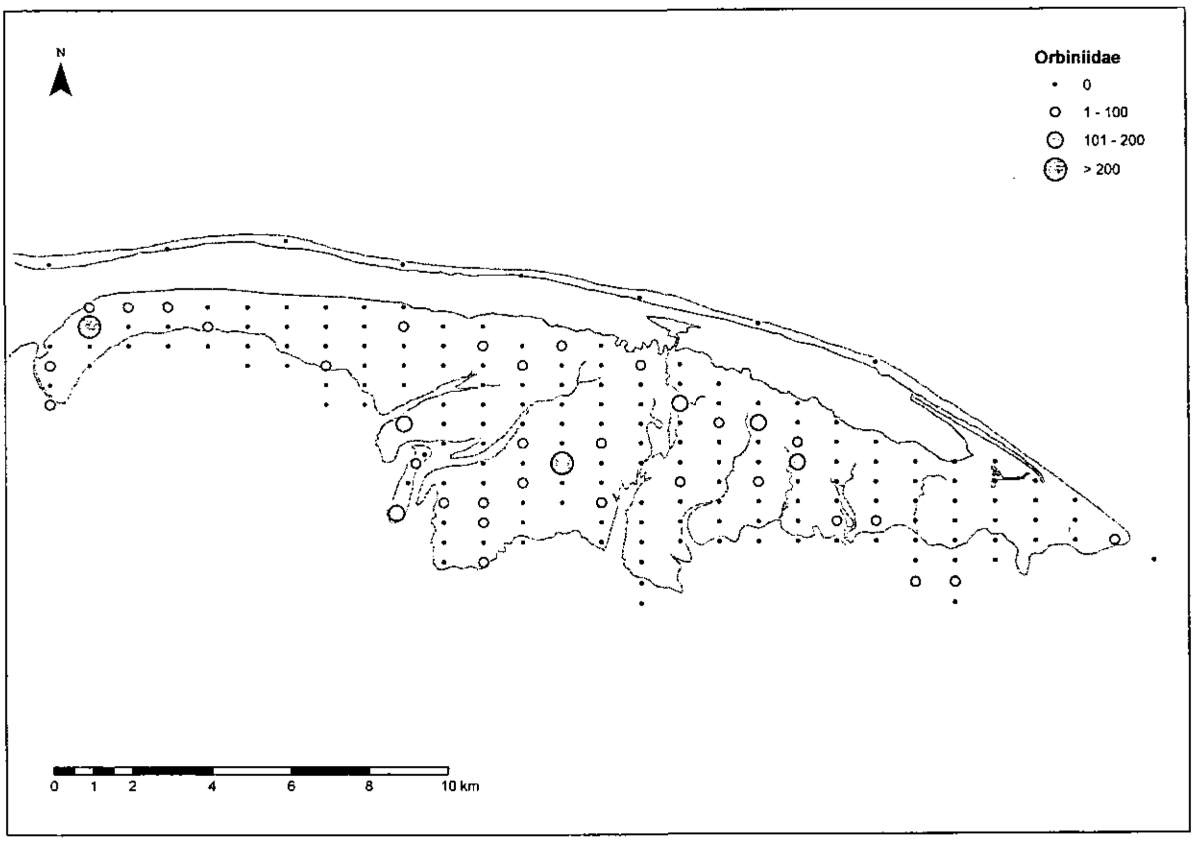

Figure 89: Distribution of Orbiniidae on the Farewell Spit tidal flats.

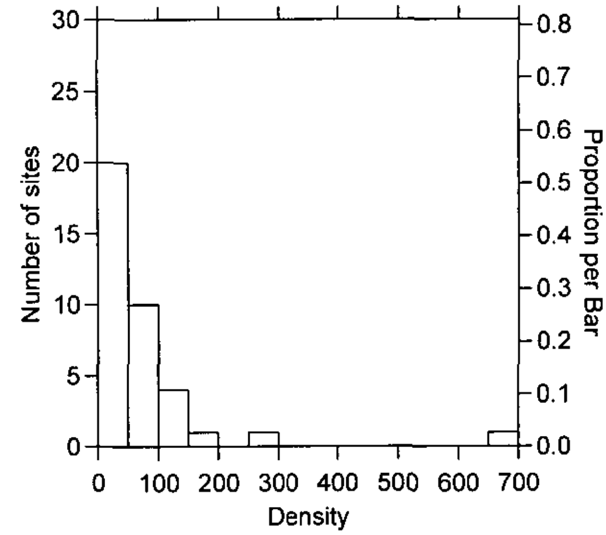

Figure 90: **Frequency distribution of Orbiniidae densities (no. per m^2) at the 37 sample sites where they were recorded.**

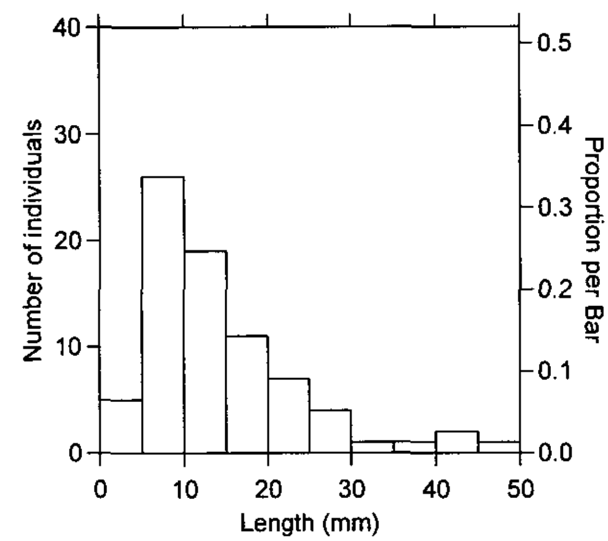

Figure 91: **Length distribution of Orbiniidae on Farewell Spit. N = 21 specimens.**

4.5.7 Oweniidae

The tube-building worms of the family Oweniidae were the most patchily distributed taxon on the Farewell Spit flats. Recorded at only 15 sites, densities ranged from 42 to 5647 individuals per square metre (Table 25; Figure 92). They were found predominantly on mid-level to outer tidal flats across the central parts of the spit (Figure 93). Because their tubes are constructed primarily from small mica flakes they are extremely tough, and consequently almost all Oweniidae found were intact. Lengths were fairly normally distributed around a mode of 20–25 mm (Figure 94).

Table 25: **Characteristics of sampled Oweniidae populations on the Farewell Spit tidal flats.**

Characteristic	Value
occurrence and density	
number of sample sites recorded at	15
total number of individuals sampled	270
average density all sites (no. per m^2)	56
average density where present (no. per m^2)	761
median density where present (no. per m^2)	127
maximum density (no. per m^2)	5 647
length	
number measured	256
average length (mm)	20.7
standard deviation	8.0
range	4–44

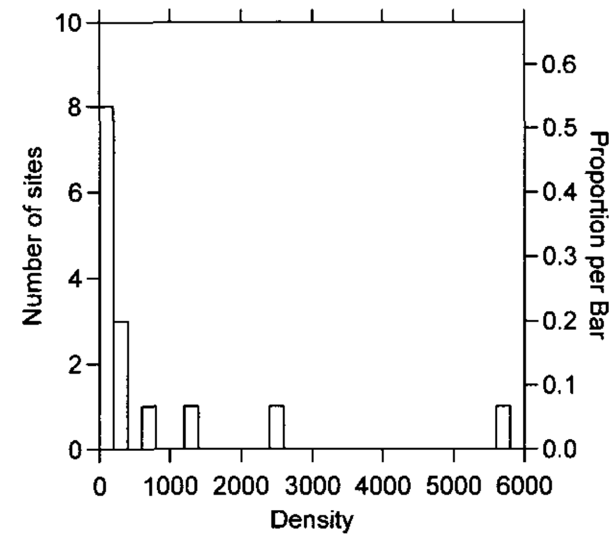

Figure 92: **Frequency distribution of Oweniidae densities (no. per m^2) at the 15 sample sites where they were recorded.**

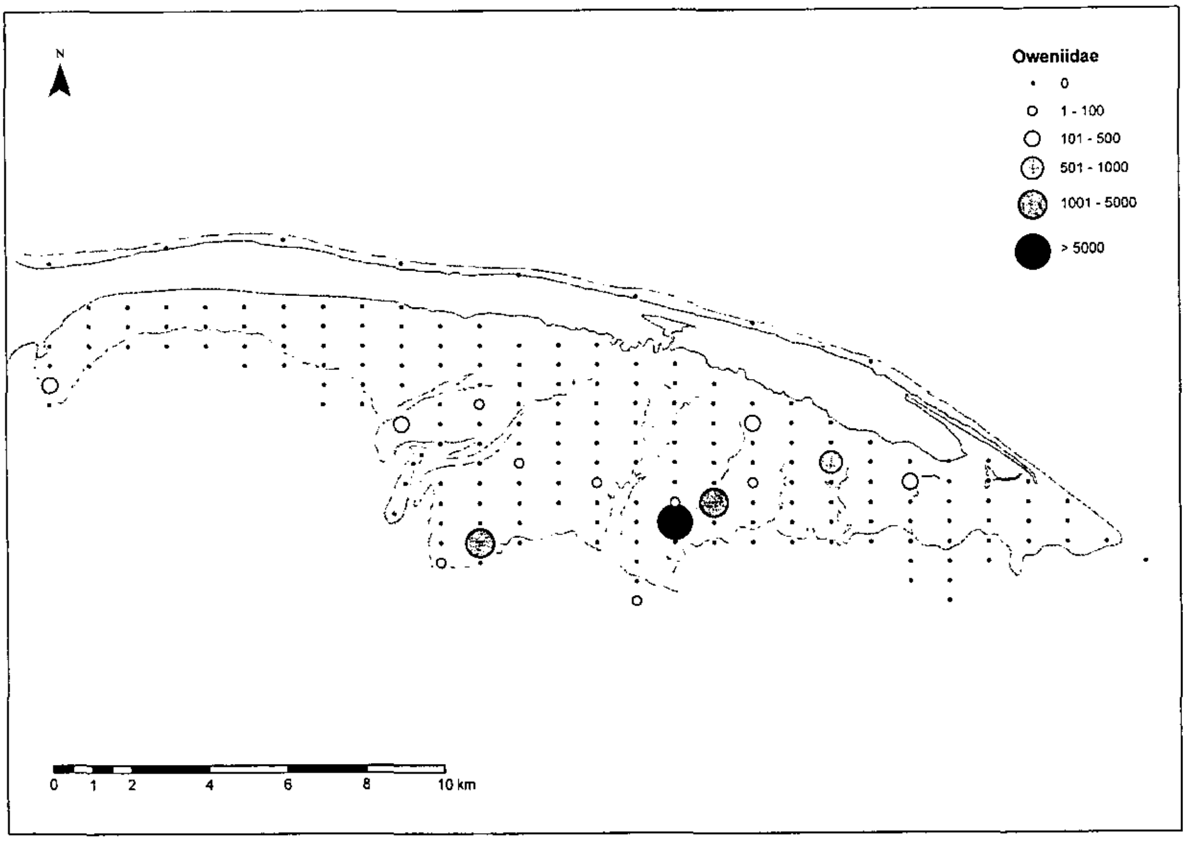

Figure 93: **Distribution of Oweniidae on the Farewell Spit tidal flats.**

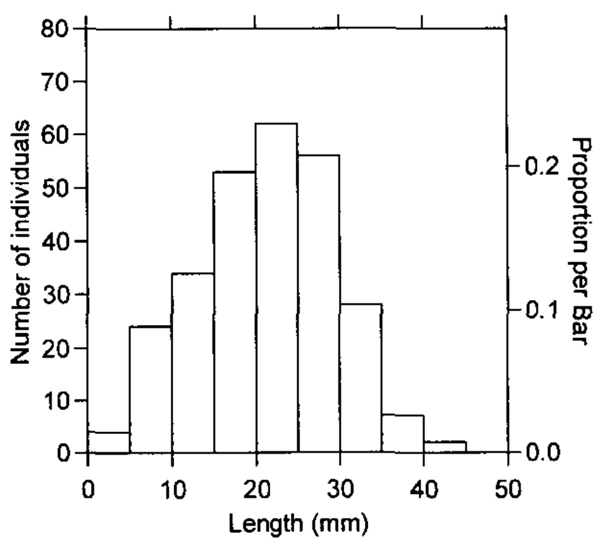

Figure 94: **Length distribution of Oweniidae on Farewell Spit. N = 256 specimens.**

4.5.8 Scalibregmatidae

Scalibregmatidae are short, stout polychaetes that with one exception were found only on the central flats of Farewell Spit (Figure 95). Overall, Scalibregmatidae were found at only 16% of the sampling sites, and even on the central transects where most were found, they occurred at only 24% of the sites. There was a wide range of densities (Table 26; Figure 96): almost half the sites had fewer than 50 individuals per square metre, and the remainder had densities fairly evenly spread up to almost 900 individuals per square metre. Scalibregmatidae typically curled inwards on their ventral side, and had to be 'bent open' to get a length measurement. Bearing in mind that length measurements on this taxon may be less accurate than for other worms, it is clear that Scalibregmatids are short worms, most being 4–16 mm long (Figure 97). Being rather fat worms, however, their biomass is proportionately greater for their length than any of the other worms discussed here. *Travisia olens* was not found during this survey.

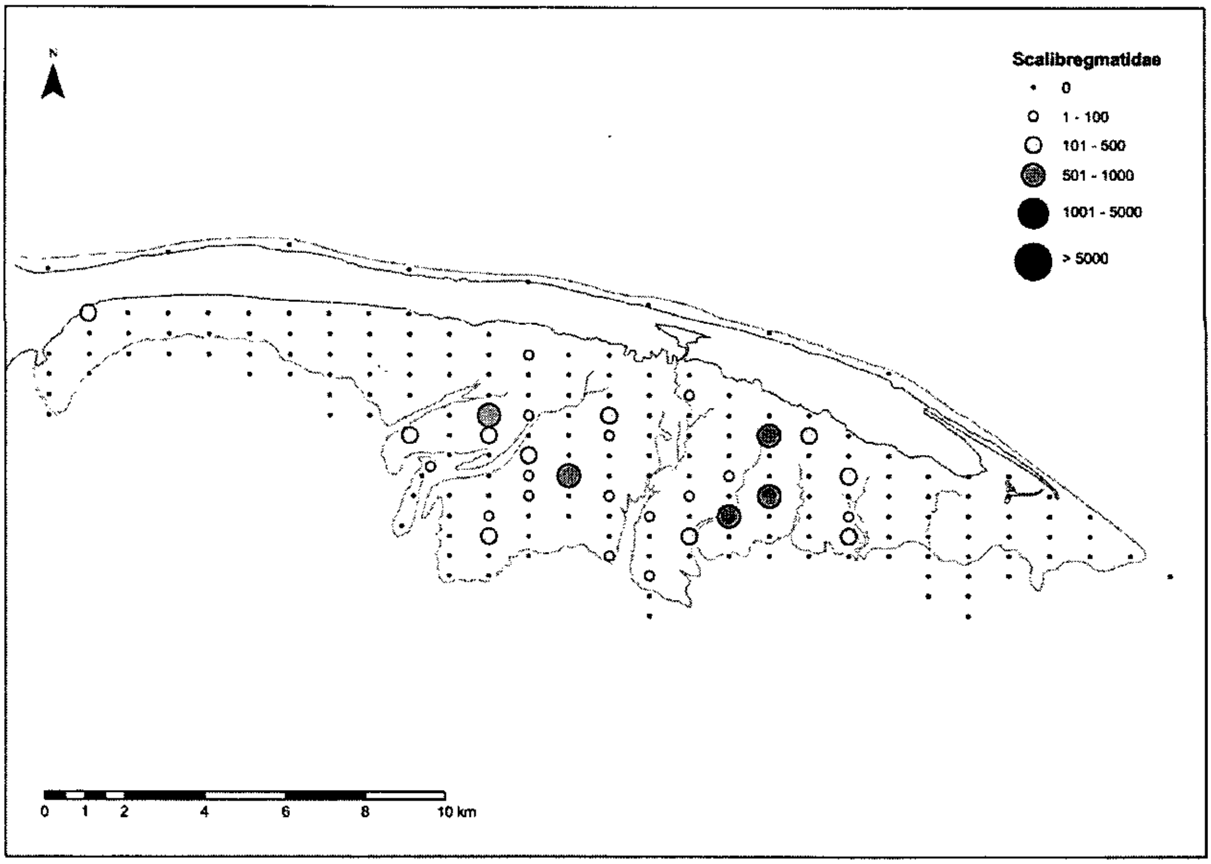

Figure 95: Distribution of Scalibregmatidae on the Farewell Spit tidal flats.

Table 26: Characteristics of sampled Scalibregmatidae populations on the Farewell Spit tidal flats.

Characteristic	Value
occurrence and density	
number of sample sites recorded at	30
total number of individuals sampled	155
average density all sites (no. per m^2)	32
average density where present (no. per m^2)	220
median density where present (no. per m^2)	106
maximum density (no. per m^2)	891
length	
number measured	83
average length (mm)	12.5
standard deviation	5.9
range	4–35

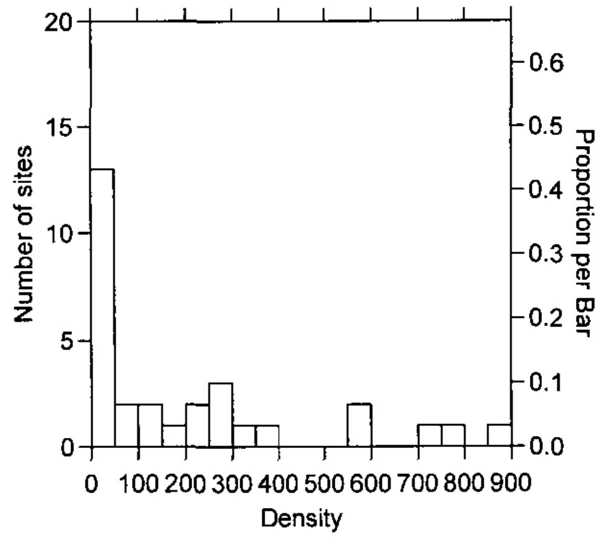

Figure 96: **Frequency distribution of Scalibregmatidae densities (no. per m²) at the 30 sample sites where they were recorded.**

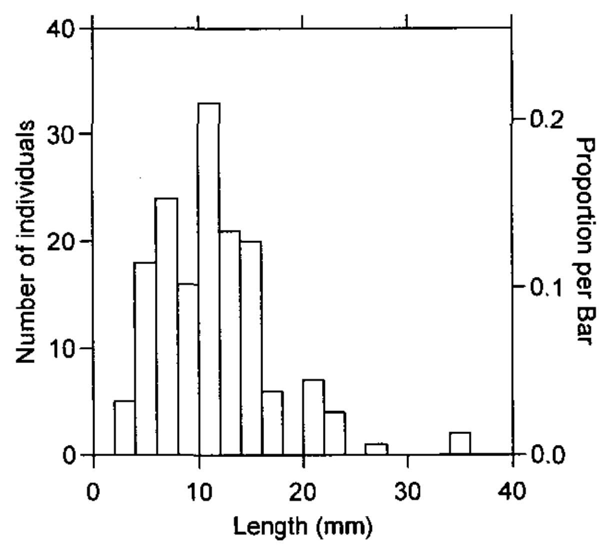

Figure 97: **Length distribution of Scalibregmatidae on Farewell Spit. N = 83 specimens.**

4.5.9 Spionidae

Far and away the most numerous worms on the tidal flats were those of the family Spionidae, over 1700 individuals being recorded during the study (Table 27). Present at just under half the sample sites, they were the most widespread worm after the Nereididae. Their average density where found of 836 individuals per square metre is highly affected by the extreme skew in the density distribution (Figure 98) (maximum of 21 527 individuals per square metre); the median density is much lower at 127 individuals per square metre (Table 27). Spionids were found in most transects along the spit, from sites high on the flats down to sites near the spring low tide mark (Figure 99). The high densities (greater than 1000 individuals per square metre) all occurred on the mid to upper-level tidal flats. The size distribution of the spionids was truncated at the smallest lengths (Figure 100), suggesting that our sampling missed the extremely small individuals. While the bar 'width' in size plots varies in this chapter between different taxa (and are therefore not always strictly comparable), a similar plot for the

Nereididae (see Figure 88) did not show such an extreme truncation. From the modal size of 4–6 mm, the spionid size classes tapered off quite evenly to the maximum plotted of 33 mm.

Table 27: Characteristics of sampled Spionidae populations on the Farewell Spit tidal flats.

Characteristic	Value
occurrence and density	
number of sample sites recorded at	80
total number of individuals sampled	1 737
average density all sites (no. per m^2)	328
average density where present (no. per m^2)	836
median density where present (no. per m^2)	127
maximum density (no. per m^2)	21 527
length	
number measured	435
average length (mm)	14.1
standard deviation	7.7
range	2–115

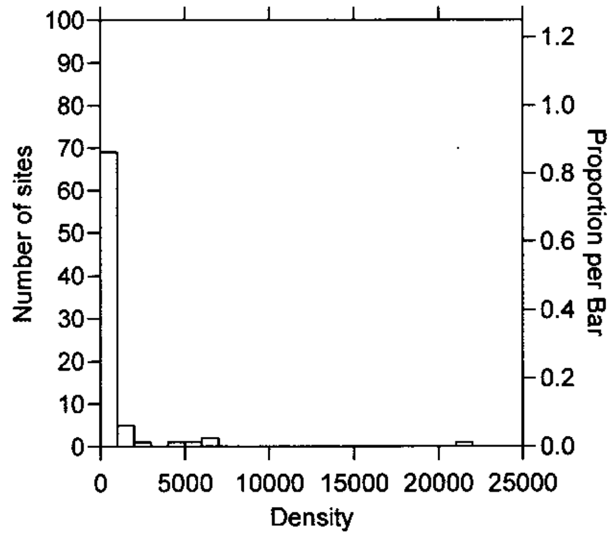

Figure 98: Frequency distribution of Spionidae densities (no. per m^2) at the 80 sample sites where they were recorded.

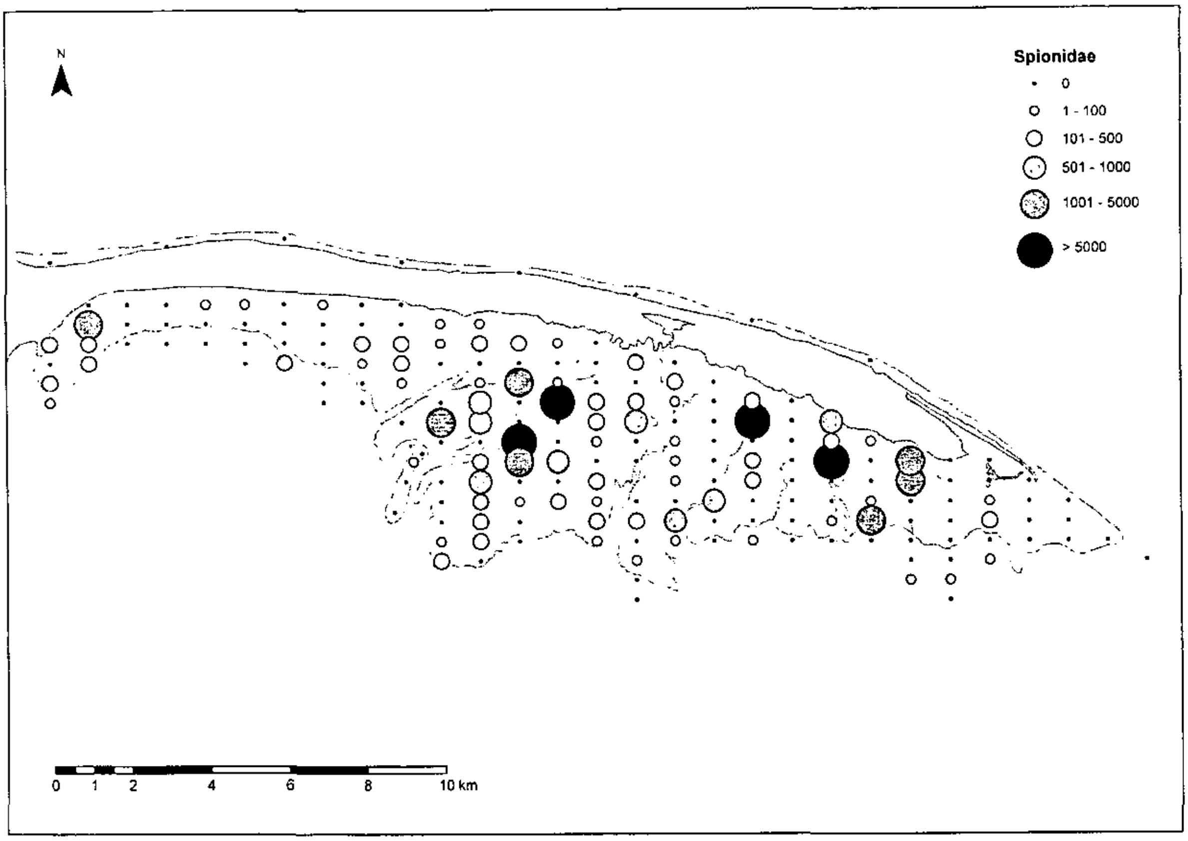

Figure 99: **Distribution of Spionidae on the Farewell Spit tidal flats.**

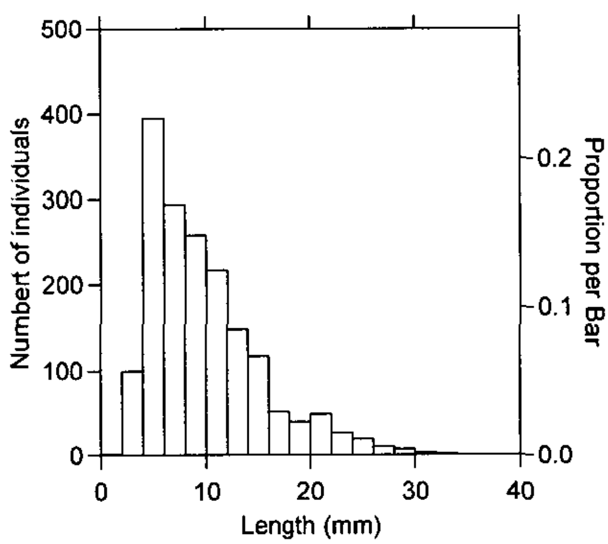

Figure 100: **Length distribution of Spionidae on Farewell Spit. N = 433 specimens. Two specimens of 65 mm and 115 mm are not shown.**

4.5.10 Syllidae

Syllidae were only a small component of the polychaete fauna of the tidal flats, being found at 14 widely spaced sites along the spit (Table 28; Figure 101). Densities at most sites were low (fewer than

100 individuals per square metre; Figure 102). Only 15 individuals were measurable; most of these were between 5 mm and 20 mm long (Table 28; Figure 103).

Table 28: Characteristics of sampled Syllidae populations on the Farewell Spit tidal flats.

Characteristic	Value
occurrence and density	
number of sample sites recorded at	14
total number of individuals sampled	34
average density all sites (no. per m^2)	7
average density where present (no. per m^2)	103
median density where present (no. per m^2)	75
maximum density (no. per m^2)	425
length	
number measured	15
average length (mm)	12.5
standard deviation	6.4
range	5–30

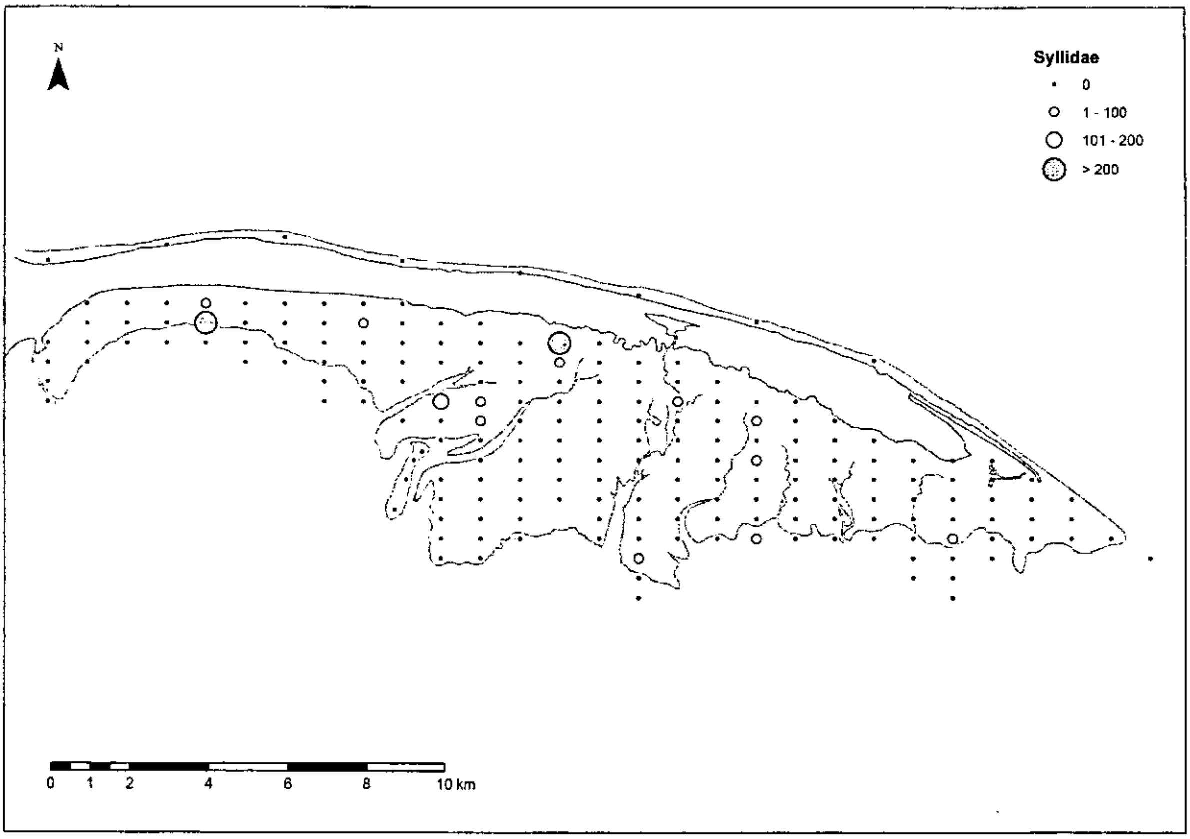

Figure 101: Distribution of Syllidae on the Farewell Spit tidal flats.

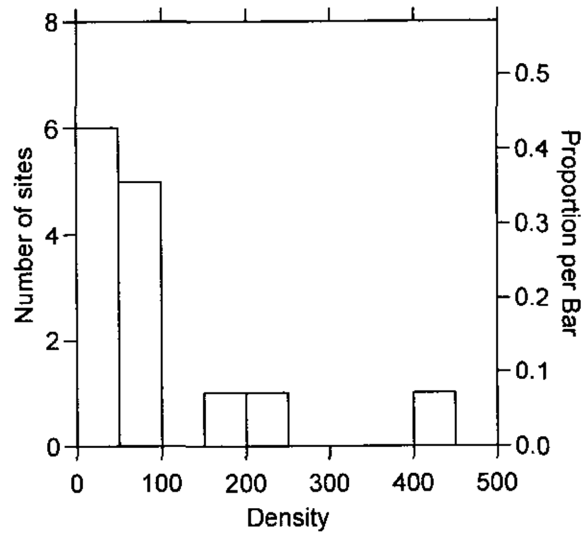

Figure 102: **Frequency distribution of Syllidae densities (no. per m^2) at the 14 sample sites where they were recorded.**

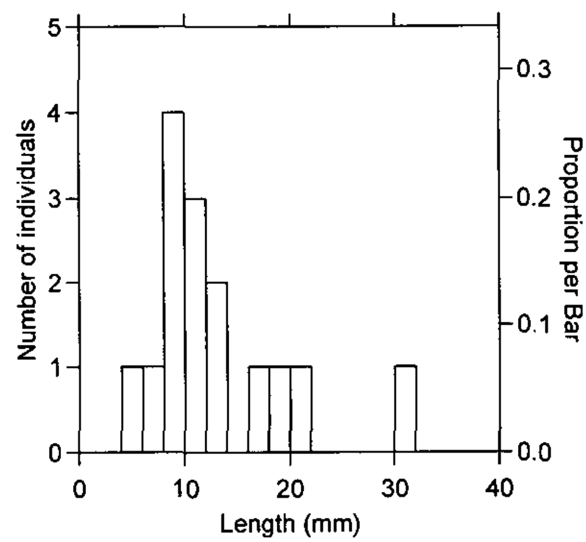

Figure 103: **Length distribution of Syllidae on Farewell Spit. N = 15 specimens.**

4.6 Cnidaria: Anthozoa

4.6.1 *Anthopleura aureoradiata*

The anemone *Anthopleura aureoradiata* is a regular commensal of the cockle, *Austrovenus stutchburyi*, the shells of which provide one of the few hard substrates on the sandy tidal flats. Although not all cockles had anemones attached, only 3 of the 45 sites where *Anthopleura* was recorded (Table 29) lacked cockles. The distribution of *Anthopleura* on the tidal flats therefore resembles that of *Austrovenus*, particularly the larger size classes (see Figures 38 and 39), occurring widely across the central flats and towards the tip of the spit, but particularly on lower tidal level parts (Figure 104). Densities were low at half the sites (median of 85 individuals per square metre) (Table 29), but were considerably higher in the other half (Figure 105). The peak density of almost 1300 per square metre occurred where cockles were present at a similar density (1400 individuals per square metre). Although measurements from a soft-bodied organism such as an attached anemone are undoubtedly less reliable than those from many other taxa, the *Anthopleura* sampled mostly had a pedal disc width of 2–4 mm, though larger individuals of up to 12 mm were found (Table 29; Figure 106).

Table 29: Characteristics of sampled *Anthopleura aureoradiata* populations on the Farewell Spit tidal flats.

Characteristic	Value
occurrence and density	
number of sample sites recorded at	45
total number of individuals sampled	210
average density all sites (no. per m^2)	47
average density where present (no. per m^2)	201
median density where present (no. per m^2)	85
maximum density (no. per m^2)	1 274
width	
number measured	210
Average width (mm)	3.8
standard deviation	1.8
range	1–12

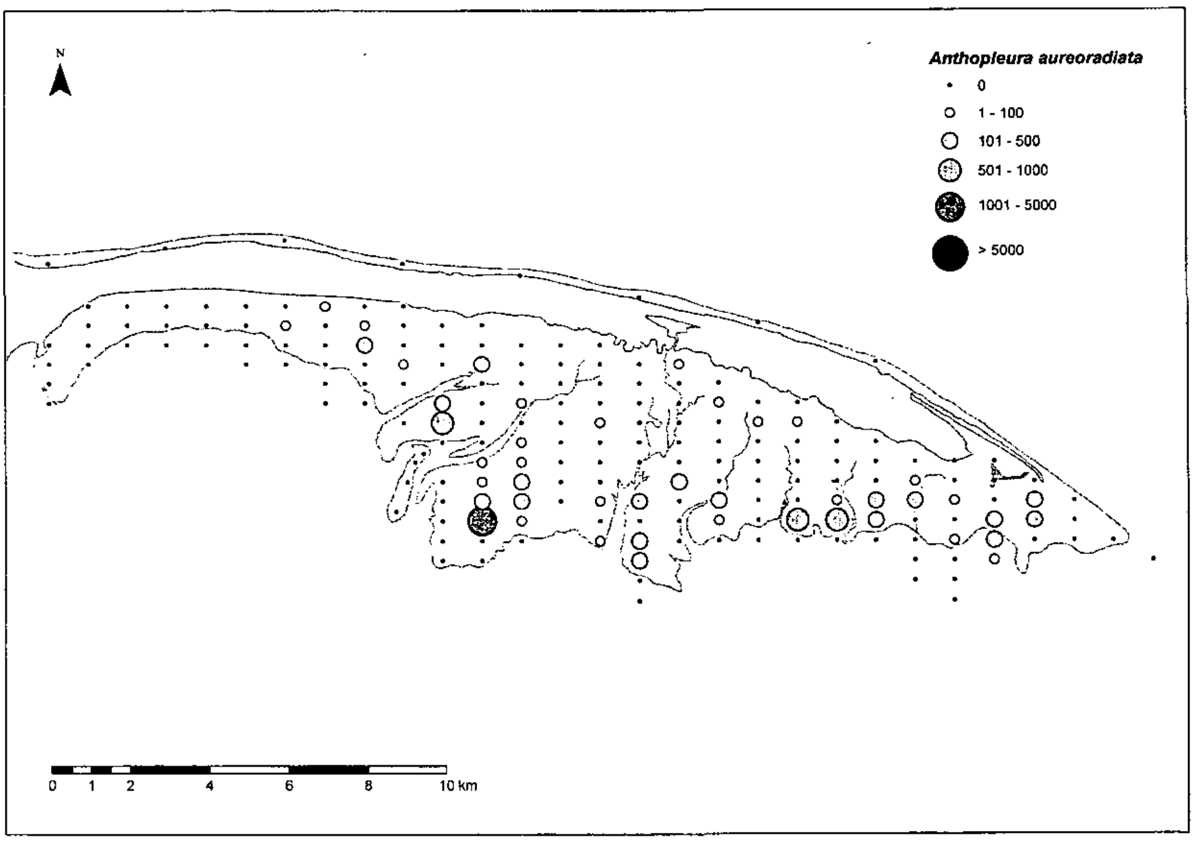

Figure 104: Distribution of *Anthopleura aureoradiata* on the Farewell Spit tidal flats.

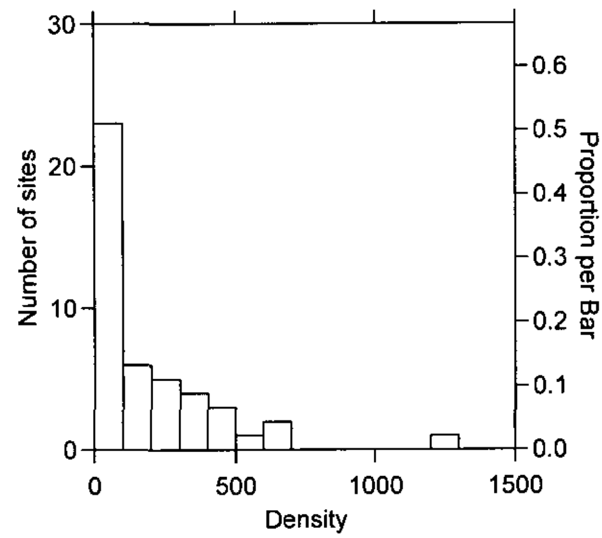

Figure 105: **Frequency distribution of *Anthopleura aureoradiata* densities (no. per m^2) at the 45 sample sites where they were recorded.**

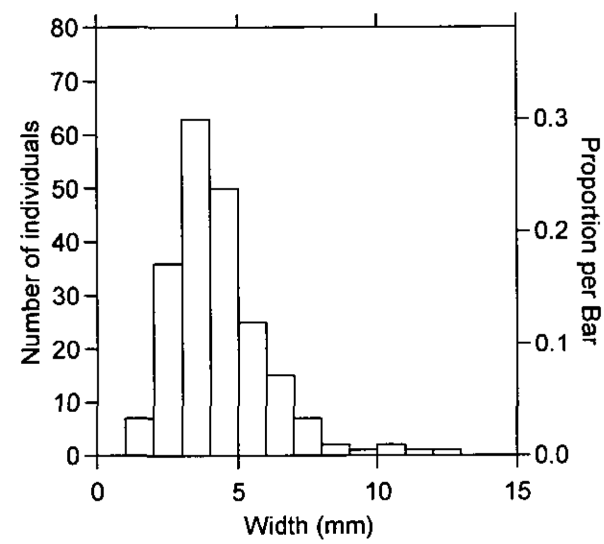

Figure 106: **Width distribution of *Anthopleura aureoradiata* on Farewell Spit. N = 210 specimens.**

4.6.2 Edwardsia tricolor

Edwardsia tricolor is a free-living anemone that was found at only a few sampling sites (Table 30). Although present at a reasonably high density at one site (510 individuals per square metre), most sites where it occurred had a density of only 42 individuals per square metre (meaning only one individual was recorded) (Figure 107). Found mostly on upper and mid-level tidal flats (Figure 108), lengths ranged from 2 mm to 25 mm (Figure 109).

Table 30: **Characteristics of sampled *Edwardsia tricolor* populations on the Farewell Spit tidal flats.**

Characteristic	Value
occurrence and density	
number of sample sites recorded at	17
total number of individuals sampled	43
average density all sites (no. per m^2)	10
average density where present (no. per m^2)	107
median density where present (no. per m^2)	42
maximum density (no. per m^2)	510
length	
number measured	43
average length (mm)	10.7
standard deviation	6.3
range	2–25

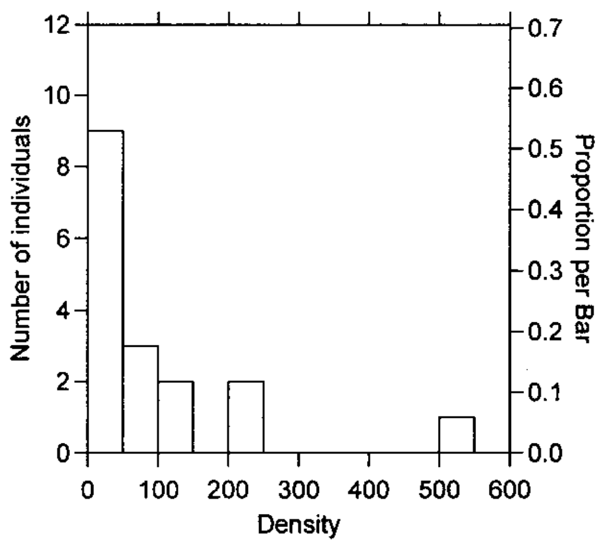

Figure 107: **Frequency distribution of *Edwardsia tricolor* densities (no. per m^2) at the 17 sample sites where they were recorded.**

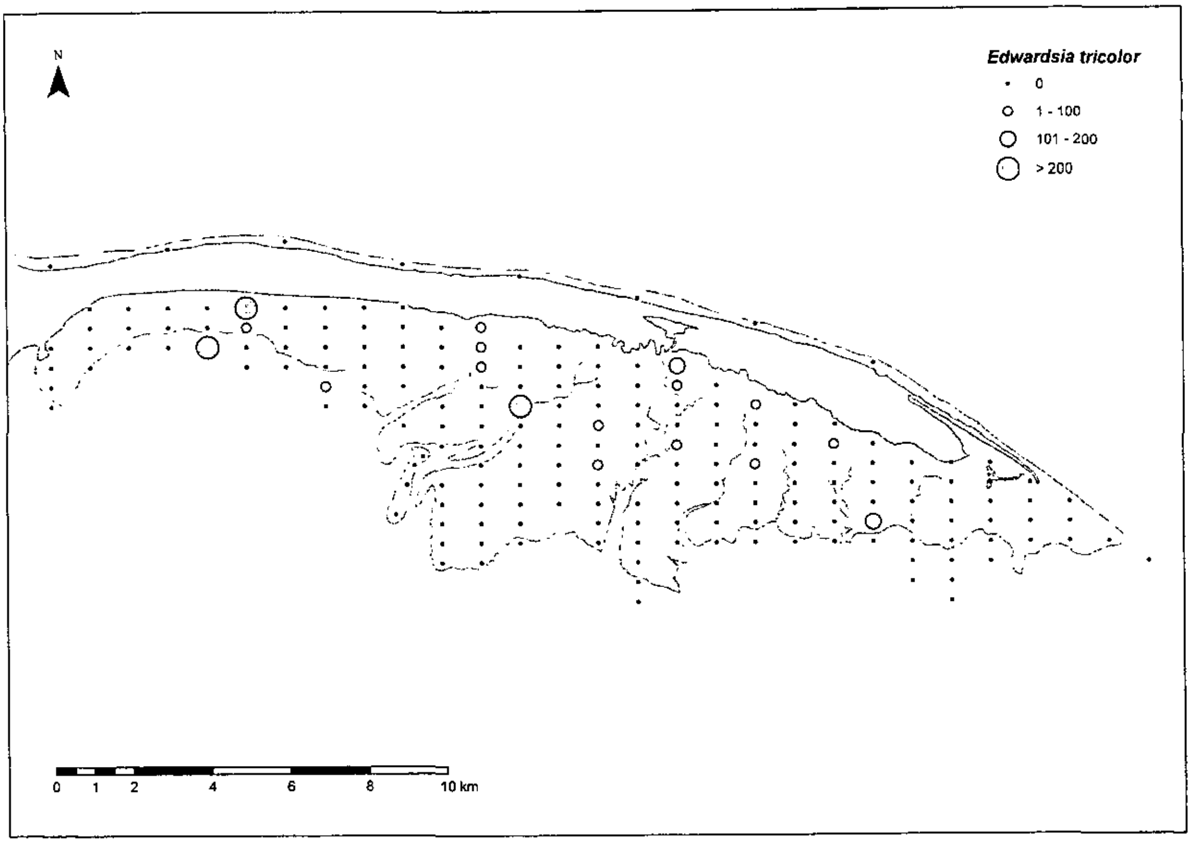

Figure 108: **Distribution of *Edwardsia tricolor* on the Farewell Spit tidal flats.**

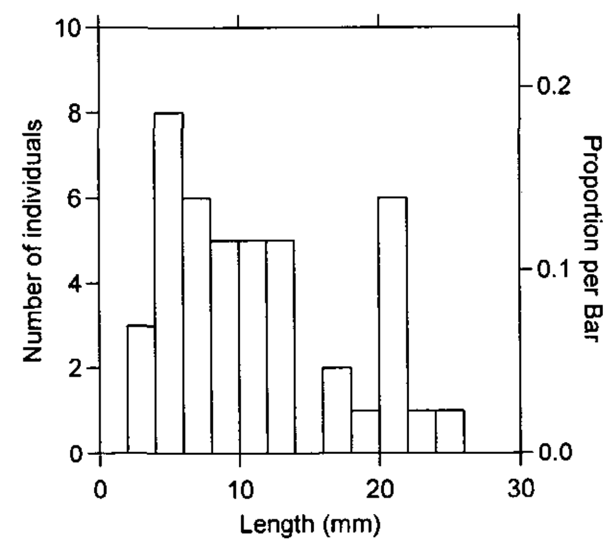

Figure 109: **Length distribution of *Edwardsia tricolor* on Farewell Spit. N = 43 specimens.**

4.7 Nemertea

Nemerteans were widely spread across the Farewell Spit tidal flats (Figure 110), but in low densities (Table 31; Figure 111). Of the 33 sites where they were found, only single individuals were recorded at 28. Nemerteans were especially prone to breaking up during sieving, so only 15 of the 40 individuals could be measured (and some of these were curled and therefore hard to measure accurately). Most of the measured individuals were less than 20 mm in length, though five were 30–60 mm long (Table 31; Figure 112). Two partial individuals were at least 86 and 100 mm long.

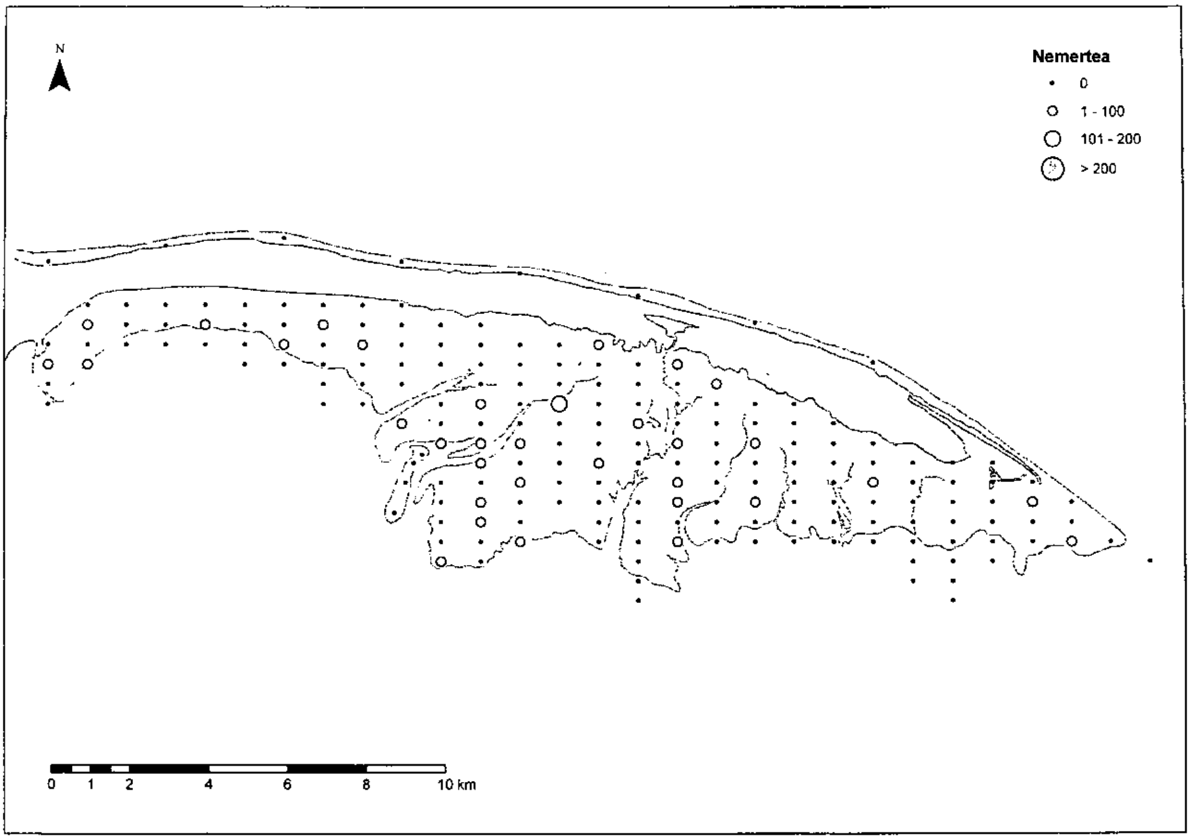

Figure 110: Distribution of Nemertea on the Farewell Spit tidal flats.

Table 31: Characteristics of sampled Nemertea populations on the Farewell Spit tidal flats.

Characteristic	Value
occurrence and density	
number of sample sites recorded at	33
total number of individuals sampled	40
average density all sites (no. per m^2)	9
average density where present (no. per m^2)	52
median density where present (no. per m^2)	42
maximum density (no. per m^2)	170
length	
number measured	15
average length (mm)	19.9
standard deviation	15.0
range	6–60

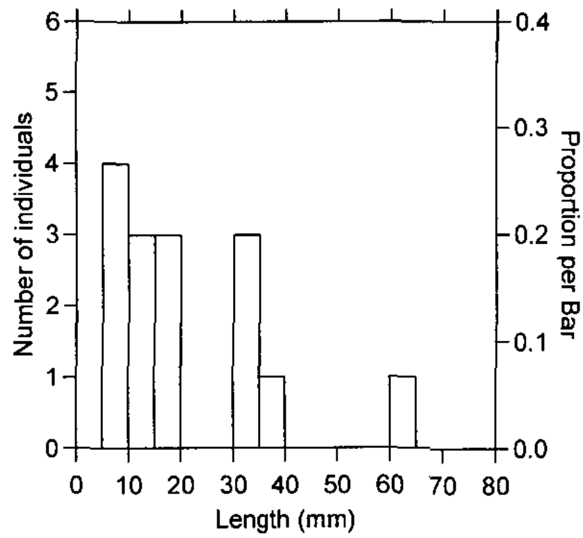

Figure 111: **Frequency distribution of Nemertea densities (no. per m²) at the 33 sample sites where *they were recorded.***

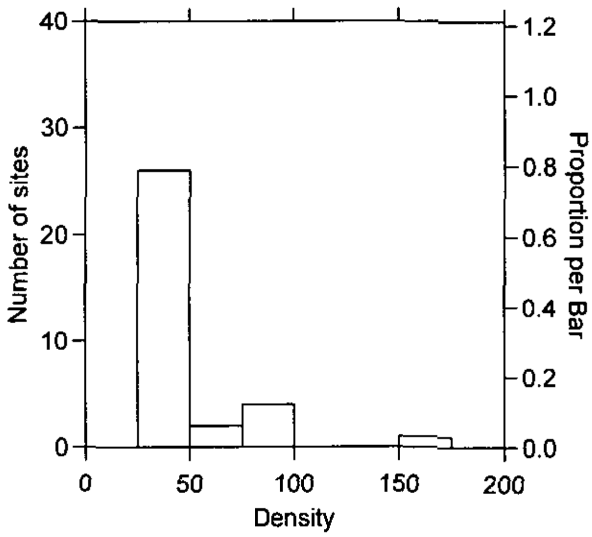

Figure 112: **Length distribution of Nemertea on Farewell Spit. N = 15 specimens.**

4.8 Less common taxa

Brief details are given of those taxa recorded only infrequently during the survey. The locations of sample sites are given in Appendix 1. In the terminology used, the letter(s) give the easting, the number the northing.

Annelida: Polychaeta

Ampharetidae. Recorded at one site (GG6074500, *Zostera* score 2, coarse sand 0.5%); seven individuals. Single individuals also recorded at two sites on the ocean beach.

Amphinomidae. A single specimen collected from the surface near site G6073500.

Arenicolidae. Six individuals recorded at four sites on the central flats (FF6072500, H6073000, I6072000, and I607500). *Zostera* cover ranged from 1 to 4, and coarse sand from 0.4 to 2.2%.

Cirratulidae. Nineteen individuals recorded at four sites: D6075500, G6073000, GG6074000 and K6072500. Three of the sites had moderate to high *Zostera* cover (score 3–6) and 0.5% coarse sand; the fourth site had no *Zostera* and 28.6% coarse sand.

Lumbrineridae. One individual recorded at JJ6070500, a sea-edge site with little *Zostera* (score 2) and coarse sand (0.5%).

Magelonidae. The attractive shovel-headed worms were found at six sites, from the upper beach on the inner part of the spit, to one of the most seaward sites on the central flats (C6076000, CC6076500, DD6074000, DD6074500, DD 6075000, and FF607000). Sites had no *Zostera*, but had various coarse sand components (0.4%, 0.9%, 7.4%, 8.0%, 18.4%, and 22.4%). Seven individuals were found.

Opheliidae. Eight opheliids were found at GG6075500 and H6072000. The sites had little coarse sand (0.4%) but contrasting *Zostera* cover (2 and 6). *Armandia maculata* was present in the samples.

Paraonidae. A single paraonid was found at FF6072500 (*Zostera* score 2, coarse sand 0.4%).

Pectinariidae. Two gold comb worms were found, at G6073000 (*Zostera* score 5, coarse sand 0.5%) and KK6071000 (*Zostera* score 5, coarse sand 2.1%).

Phyllodocidae. Three paddle worms were recorded, at EE6073500 (*Zostera* score 5, coarse sand 38.3%), F6076000 (*Zostera* score 2, coarse sand 6.6%), and J6073500 (*Zostera* score 6, coarse sand 1.2%).

Sabellidae. One from site J6073500 (*Zostera* score 6, coarse sand 1.2%).

Serpulidae. Four *Pomatocerus caeruleus* were found at FF6074000 (*Zostera* score 6, coarse sand 2.4%). An unidentified serpulid was at GG6072500 (*Zostera* score 5; no sand data available).

Terebellidae. Two terebellids were found in coarse sediments, at D607500 (*Zostera* score 1, coarse sand 31.1%) and G6072500 (*Zostera* score 3, coarse sand 19.1%).

Mollusca: Bivalvia

Amphidesma subtriangulatum (Mesodesmatidae). One tuatua was found in the easternmost sample of the spit (O607000) in conditions similar to the ocean beach (exposed, bare sand, high coarse component of 19.9%). Forty were found in sampling along the ocean beach.

Arthritica bifurca (Lasaeidae). Twelve individuals of this tiny (1–2 mm) reddish bivalve were sampled at eight sites on the central flats. All sites had high eelgrass cover (scores of 3, 3, 4, 5, 5, 5, 5, and 6) and low coarse sand (0.4–1.2%).

Divaricella huttoniana (Lucinidae). Two lace cockles were found on the inner Spit, at CC6076000 and DD6074000. Both sites had no *Zostera* and fairly high coarse sand content (8.0% and 35.9%).

Divariscintilla maori (Galeommatidae). Two individuals of this species, which is commensal with mantis shrimps (living in their burrows), were found at JJ607050.

Mactra sp. (Mactridae). A single small (2 mm) *Mactra* sp. was recorded at E6074500 (*Zostera* score 1, coarse sand 24.9%).

Perna canaliculus (Mytillidae). One 20 mm green mussel was sampled at KK6071000. Other individuals were noted incidentally between sample sites on lower-tidal flats.

Solemya parkinsonii (Solemyidae). The distinctive brown razor mussel was found at two sites (D6075000 and G6073000). Four individuals (three whole and one damaged) were found. Well known to occur in *Zostera* beds, only one of the sites where it was found on the spit had eelgrass present (scores of 1 and 5 respectively, with coarse sand of 31.3% and 0.5%)

Tawera spissa (Veneridae). A single individual found near the sea edge on the central flats, at H6070500 (*Zostera* score 3, coarse sand 0.4%).

Venerupis largillierti (Veneridae). Single individuals at FF6075000 (*Zostera* score 3, coarse sand 2.4%) and FF6074000 (*Zostera* score 6, coarse sand 2.4%). This is a typical inhabitant of *Zostera* meadows (Morton & Miller 1973).

Zenatia acinaces. One otter shell found at I6071000 (*Zostera* score 6, coarse sand 2.3%).

Mollusca: Gastropoda

Amalda sp. (Olividae). Ten olive shells were found at eight sites at or near the spring low-tide edge. Eelgrass cover was low (mostly score 1, with single sites with score 2 and 3), and coarse sand was variable (four sites <2.1%; the others were 13.6%, 18.4%, 30.8%, and 37.0%).

Haminoea zelandiae (Haminoeidae). Three bubble shells were found, at G6072500, H6072500, and H6075500. Sites had light eelgrass cover (score 2–3) and varying coarse sand content (0.4%, 0.4%, and 19.1%).

Rissoina (Rissoinidae). One snail at G6073000 (*Zostera* score 1, coarse sand 8.3%).

Trochidae. One 2 mm individual at KK6071000 (*Zostera* score 5, coarse sand 2.1%).

Turbo smaragdus (Turbinidae). Six cat's eyes found at three sites: FF6074000, II6071500, and K6072500. All had high *Zostera* cover (6, 4, and 6) and low coarse sand (2.4%, 2.2%, and 0.4%).

Turbonilla sp. (Pyramidellidae). One found at F6070500 (*Zostera* score 1, coarse sand 8.7%).

Xymene sp. (Muricidae) One boring whelk found at K6072500 (*Zostera* score 6, coarse sand 2.4%).

Mollusca: Polyplacophora

Acanthochiton zelandicus (Acanthochitonidae). A single example at FF6074000 (*Zostera* score 6, coarse sand 2.4%).

Chiton glaucus (Chitonidae). Eleven green chitons were found at seven sites, most of which had high eelgrass cover (scores of 2, 2, 3, 4, 5, 5, and 6). Coarse sand content was variable (0.5%, 2.2%, 2.4%, 4.6%, 5.0%, 54.9%, 71.1%).

Arthropoda: Maxillopoda

Copepoda. Only one copepod was found, at FF6072500 (*Zostera* score 2, coarse sand 0.4%).

Arthropoda: Ostracoda

Ostracoda. Singles found at G6073000, GG6074000, H6073000, and I6071000. All are in the middle of the central flats, and had high *Zostera* (3–6) and low coarse sand (0.5–2.3%).

Arthropoda: Malacostraca

Caprellidae. Eleven skeleton shrimps were recorded at four sites, mostly at the sea edge on the outer part of the spit (I6070500, 1; I6074500, 2; II6070500, 7; N6070500, 1). Sites had low eelgrass cover (1–3) and varying coarse sand content (63%, 1.2%, 1.2%, and 17.1% respectively).

Isopoda: Valvifera. Two individuals from the family Valvifera (genus *Euidotia*) were found in the samples. This isopod is a long, bright green species that lives in dense eelgrass. It was recorded at site G6073000, a site with high eelgrass cover (score 5; coarse sand 0.5%).

Mysidacea. Eight individuals at six sites, three of which were near the tide edge and three in the mid-flat. *Zostera* scores were low at most sites (1, 1, 1, 2, 3, 4), and coarse sand was low at four (0.4–4.7%) and high at two (37.0% and 45.6%).

Squilla armata. Eleven found at 10 sites with generally low eelgrass cover (1, 2, 2, 2, 2, 2, 3, 3, 3, 4) and little coarse sand (nine sites 0.4–2.6%; one site 30.8%). Most sites were moderately high on the tidal flats.

Decapoda

Cyclograpsus lavauxi (Grapsidae). One smooth shore crab found on the upper tidal flats at H6075500 (*Zostera* score 2, coarse sand 0.5%).

Helice crassa (Grapsidae). Single tunnelling mud crabs found at two sites near the saltmarsh.

Hemigrapsus crenulatus (Grapsidae). Single hairy-handed crabs sampled on the mid-lower flats, in samples at EE6073500, F6073500, and II6072500. Two sites had high eelgrass (score 5; coarse sand of 38.3% and 4.6%); the third had sparse cover (score 2, 0.4% coarse sand).

Macrophthalmus hirtipes (Ocypodidae). Eleven stalk-eyed mud crabs were recorded at seven sites on the central flats. All sites had moderate to high eelgrass scores (3, 3, 5, 6, 6, 6, 6) and little coarse sand (0.4–2.3%).

Pontophilus australis (sand shrimp). Four individuals at two sites, A6074500 (*Zostera* score 3, coarse sand 54.9%) and K6072000 (*Zostera* score 6, coarse sand 0.4%).

Arthropoda: Insecta

Empididae (Diptera). One dance fly imago at EE6075000.

Hexatomini (Tipulidae). Four crane fly larvae at EE6076500 and EE6075000.

Neoscatella (Ephydridae). Five shore fly larvae fairly high on the shore, at I6075000.

Philanisus plebeius (Trichoptera, Chathamiidae). Eight larval caddis flies at five mid-level sites on the central flats. Most were in dense *Zostera* beds (scores 3, 4, 6, 6, 6) with low coarse sand (with one exception: 2.3%, 45.6%, 0.4%, 2.4% and 1.2% respectively).

Echinodermata

Fellaster zelandiae (Echinoidea). A single sand dollar found near the spit tip at N6070500.

Holothuroidea. Twenty-eight sea cucumbers were recorded at 22 sites across the spit, from near the salt marsh to the extreme low-water line. Most specimens were not determined to species but *Trochodota dendyi* was identified.

Ophiuroidea. One tiny (2 mm) brittle star, at G6073000 (*Zostera* score 5, coarse sand 0.5%).

Patiriella regularis (Stelleroidea). Thirteen cushion stars present at nine sites on the inner flats (transects A–CC) and the central flats. Those on the inner flats tended to have low *Zostera* cover (scores 1, 1, 1, 3 and 3), but those on the central flats had fairly high cover (4, 5, 5 and 6). Coarse sand content was low at seven sites (0.4–5.0%), high at two (22.4% and 54.9%).

Coscinasterias calamaria (Stelleroidea). Large numbers of the large red eleven-armed seastar were incidentally noted at the sea edge, especially where beds of large pipi occurred (near EE6071000).

4.9 Ocean beach

Ten core samples taken at eight sites along the ocean beach contained 54 individuals of five groups: 2 Ampharetidae (Polychaeta), 5 Glyceridae (Polychaeta), 1 Flabellifera (Isopoda), 6 Amphipoda and 39 tuatua (*Amphidesma subtriangulatum*). Overall densities ranged from 42 to 679 individuals per square metre, most of which was tuatua at 0–510 individuals per square metre.

5. BENTHOS COMMUNITIES IN RELATION TO ENVIRONMENTAL FACTORS

Describing patterns of abundance in a taxon-by-taxon way can reveal obvious differences in the occurrence and distributions of taxa. However, this approach gives little insight into the factors underlying these distribution, and whether there are groups of species (that we might refer to as communities) that respond similarly to environmental conditions. Multivariate approaches are needed to reduce the mass of information in the sampling matrix (192 sites x 83 identified taxa) to just a few dimensions that can be interpreted in an ecological context. In this section we use three main techniques to seek structure in the species and habitat data: Principal Components Analysis (PCA), Indicator Species Analysis, and Cluster Analysis. All analyses were performed in PC-Ord, version 4.0 (McCune & Mefford 1999). .

The analyses used two matrices. The first was the site x taxon matrix, in which the densities were log10(n+1) transformed to reduce the scale of the differences in abundances. The second was a habitat matrix, which contained the *Zostera* surface cover score, *Zostera* mass, and the percent coarse sand in the substrate, for each sample site.

Because many taxa were recorded rarely, the dataset was trimmed of uncommon taxa. Initially, all taxa that occurred in only one site were removed, as was the one site that had no animals present, and any sites that were lacking sediment data. Ocean beach samples were also not included in the analyses. This reduced the dataset to 187 sites and 57 taxa. The dataset was further reduced by removing taxa that totalled five individuals or fewer (leaving 187 sites and 45 taxa), and then those totalling 10 or fewer (187 sites and 39 taxa). Trial analyses were done with all three datasets; results were very similar for the three datasets, but the smallest one had fewer taxa that were seemingly significant mainly because of their rarity. Analyses discussed here were done on the dataset containing all taxa in which more than 10 individuals were recorded. Four taxa were split into subclasses for analysis: *Austrovenus stutchburyi* into five size-classes (1–10 mm, 11–20 mm, 21–30 mm, 31–40 mm, and greater than 40 mm); *Paphies australis* into two size-classes (1–13 mm, greater than 13 mm); *Notoacmea helmsi* into two subspecies (*helmsi* and *scapha*); and Maldanidae into 'lower' and 'upper' flat taxa ('Maldanidae 1' and 'Maldanidae 2' respectively).

5.1 Principal Components Analysis

A PCA was performed on the variance-covariance matrix. The first three axes generated explained 40.9% of the variance in the data (22.9% by axis 1, 10.9% by axis 2, and 8.4% by axis 3). Eigenvalues for the first four axes were larger than the corresponding broken-stick eigenvalues, indicating that they were, in effect, significant axes. Although plots of the sampling sites in relation to Axes 1–3 indicated there were no discrete groups of sites, there was nevertheless a gradient of sites evident from the *Zostera* cover scores. This was most obvious in the plot of Axes 1 and 3 (Figure 113), where *Zostera* cover increases from the right-hand side (no or little eelgrass) to the lower left corner (high eelgrass cover).

This is reinforced by the correlations of the two continuous habitat variables to the axes. *Zostera* mass was strongly negatively correlated with axis 1 (r = -0.650; *Zostera* mass decreases as you move along axis 1; Figure 114), while the proportion of coarse sand grains was positively correlated to it (r = 0.191; sites with a high coarse sand component sit towards the right-hand end; Figure 115). The third axis provided more separation, based on the proportion of coarse sand grains but not on *Zostera* mass (percent coarse sand, r = -0.192; *Zostera* mass, r = -0.099).

Neither variable was strongly correlated with Axis 2 (*Zostera* mass, r = -0.108; percent coarse sand, r = -0.019).

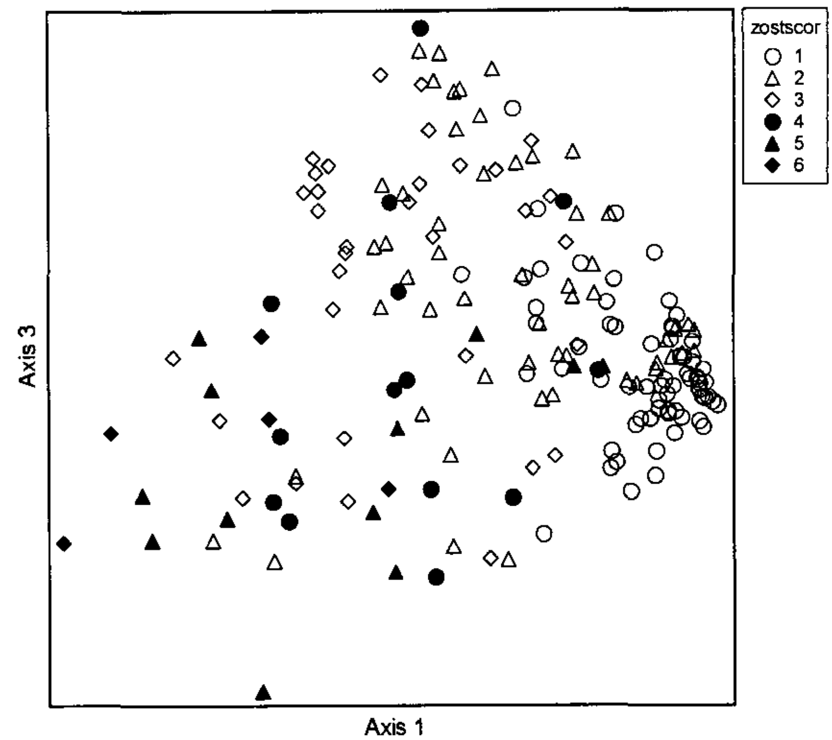

Figure 113: **Plot of Axes 1 and 3 of a Principal Component Analysis, identified by *Zostera* surface cover score ("zostscor"). Points are individual sample sites, based on their taxon abundances.**

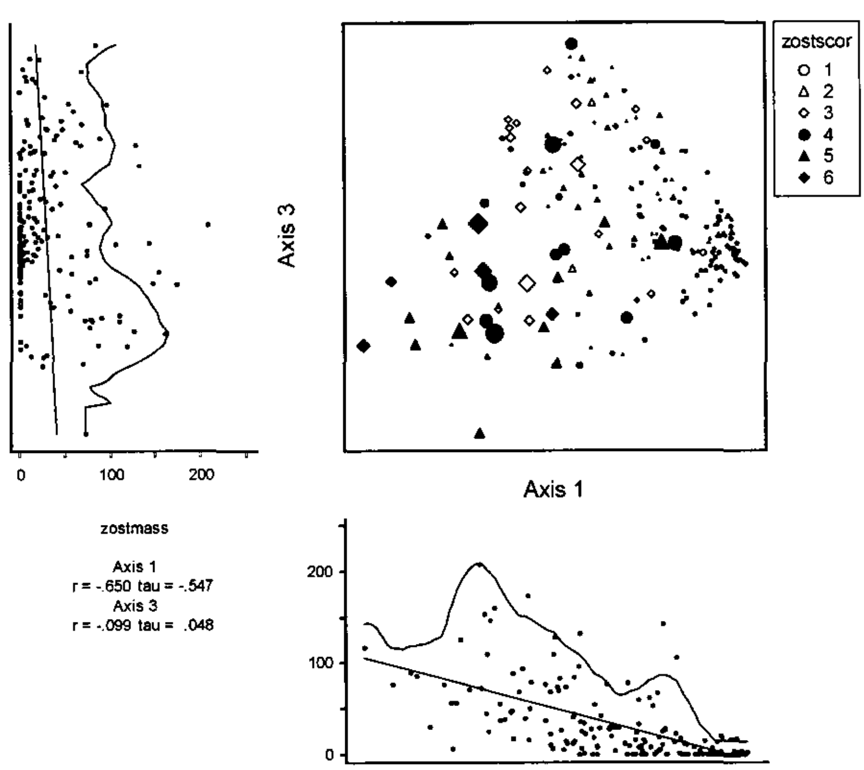

Figure 114: **Correlations of the mass of *Zostera* ("zostmass") to Axes 1 and 3 of a Principal Component Analysis. Points in the main plot are proportional to *Zostera* mass.**

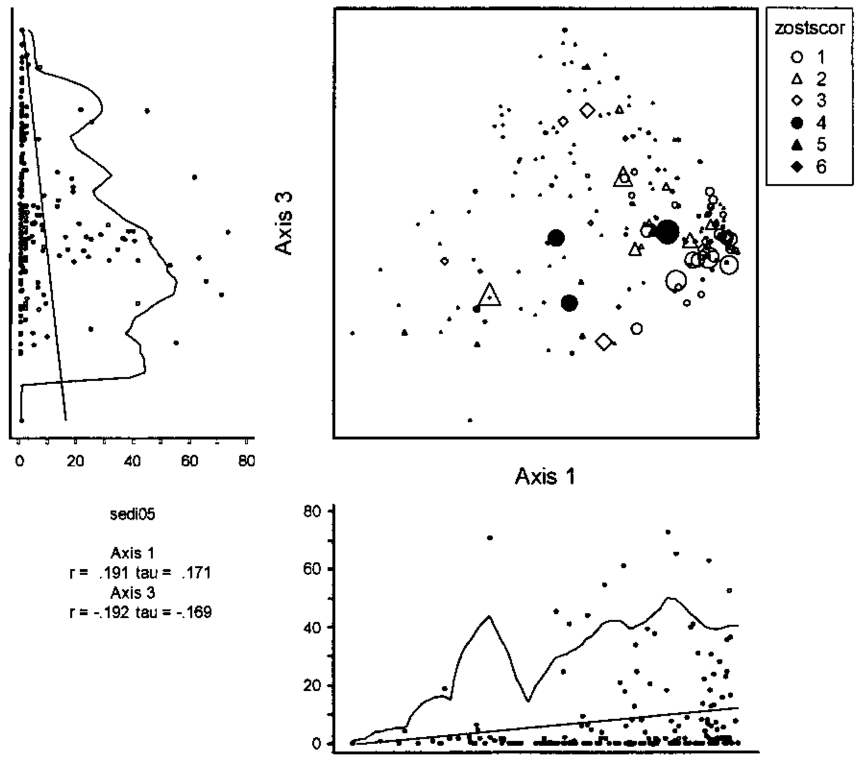

Figure 115: Correlations of the percent of coarse sediment ("sedi05") to Axes 1 and 3 of a Principal Component Analysis. Points in the main plot are proportional to the coarse sand proportion.

The main data can also be correlated to the axes (Table 32), suggesting that the distribution of some of the taxa on the tidal flats reflects differences in *Zostera* cover and sediments. Of the 23 taxa with correlations of 0.33 or above (an arbitrary cut-off point), all correlations with Axis 1 were negative. This suggests that abundances of a substantial proportion of the fauna on the Farewell Spit tidal flats increase with the amount of *Zostera* present. Three taxa had positive, though lower, correlations with Axis 1: *Amalda* at 0.227, Maldanidae 1 at 0.256, and Nephtyidae at 0.244. There was a mix of positive and negative correlations with Axes 2 and 3.

5.2 Indicator Species Analysis

Another approach to quantifying the relationship between benthos and the environment is to use an Indicator Species Analysis (Dufrene & Legendre 1997). In this, the question asked is whether there are any taxa that are particularly good indicators of certain environmental conditions. Environmental variables are summarised as categories, and each taxon's occurrence at sites in those categories is then summarised. First, for each taxon the relative abundance in each category is calculated (i.e. what percentage of the total individuals occur in each category). Secondly, the relative frequency in each group is calculated (what percentage of the sites in each category the taxon occurs in). Finally an indicator value is calculated, which summarises the relative abundance and relative frequency for each taxon across the categories. This is the 'percentage of perfect indication'; a value of 100 would mean that all individuals occurred in that category, and all sites in that category contained that taxon. A Monte-Carlo simulation is also run (1000 times) to calculate the probability that the indicator scores could occur by chance.

Table 32: Correlations between individual taxa and the first three Principal Component axes. Only correlations of 0.33 and above are shown.

Taxon	Axis 1	Axis 2	Axis 3
Amphipoda			0.453
Anthopleura	-0.382	0.436	-0.420
Arthritica	-0.344		
Austrovenus 0–10 mm	-0.779		
Austrovenus 11–20 mm	-0.773		
Austrovenus 21–30 mm	-0.584	0.396	-0.467
Austrovenus 31–40 mm			-0.522
Capitellidae	-0.686		
Cominella	-0.588		
Cumacea	-0.372		0.505
Diloma	-0.422		
Eatoniella	-0.362		
Eliminius	-0.364	0.453	-0.395
Flabellifera	-0.369	0.669	0.337
Glyceridae		-0.335	
Halicarcinus	-0.556		
Macomona	-0.450		
Micrelenchus	-0.553		-0.398
Nereididae	-0.449		0.384
Notoacmea subsp. *scapha*	-0.375		
Nucula	-0.644	-0.351	
Oweniidae		-0.357	
Paphies 1–13 mm		0.528	
Paphies >13 mm		0.610	
Scalibregmatidae	-0.470		
Spionidae	-0.659	-0.473	
Zeacumantus	-0.691		0.331

In the Farewell Spit data, *Zostera* score (1–6) was used as the environmental grouping. Seventeen taxa were statistically significant indicators (Table 33). All of these taxa increased with *Zostera* score (*Anthopleura* and *Austrovenus* 21–30 mm and 31–40 mm peaking at score 5). This may partly be a consequence of the unequal number of sites in each category; with only five sites with score 6, it is easier for a taxon to be recorded at a high proportion of these than it is in a group with large numbers of sites, but most of these taxa clearly increase in occurrence and abundance as the density of *Zostera* increases. It is worth bearing in mind that the *Zostera* scores are only a coarse assessment of the eelgrass cover without any strong biological reasoning to the cut-off points. If we reduced the number of categories (for instance combining categories 5 and 6), the associations with high *Zostera* scores would become stronger. The only taxon to be recorded only at the highest *Zostera* level was the crab *Macrophthalmus*. As only 11 individuals were recorded, it is hard to know whether this apparent restriction to high-density eelgrass is real. Other taxa that seem to be especially strongly associated with high eelgrass levels are the limpet *Notoacmea helmsi scapha* (a known *Zostera* associate), the tube-building polychaetes Oweniidae, *Nucula hartvigiana*, and the stout polychaetes Scalibregmatidae.

No taxa were significantly indicative of bare sand, though two infrequently recorded taxa were recorded primarily in areas with little eelgrass. The olive snails, *Amalda* sp., (10 individuals at eight sites), and the skeleton shrimps Caprellidae (11 individuals at four sites), occurred only at sites with *Zostera* scores of 1–3. Their infrequent occurrence, however, makes them statistically poor indicators of those habitats.

Table 33: Significant indicator taxa, based on an Indicator Species Analysis. Only taxa with P<0.05 are shown. *Zostera* group with the highest score is given in bold. For reference, the number of sites and total number of individuals recorded is given.

		Indicator scores per *Zostera* category						N	N
Taxon	P	1	2	3	4	5	6	sites	indiv
Anthopleura	0.001	0	3	3	9	**36**	2	45	210
Austrovenus 1–10 mm	0.036	0	6	15	16	18	**25**	87	532
Austrovenus 21–30 mm	0.007	1	5	5	17	**30**	9	73	514
Austrovenus 31–40 mm	0.038	1	2	2	12	**24**	0	32	125
Capitellidae	0.003	0	3	13	4	13	**39**	65	357
Cominella	0.015	0	4	5	4	20	**27**	54	106
Diloma	0.018	0	0	1	3	13	**25**	20	32
Glyceridae	0.008	6	2	2	2	6	**32**	50	96
Halicarcinus	0.006	0	2	10	1	12	**33**	42	82
Macrophthalmus	0.001	0	0	0	0	0	**55**	6	11
Micrelenchus	0.002	0	0	3	4	24	**33**	34	229
Notoacmea subsp. *scapha*	0.001	0	0	1	0	1	**58**	13	19
Nucula	0.001	0	0	7	6	6	**51**	42	630
Oweniidae	0.001	0	0	1	0	4	**69**	15	270
Scalibregmatidae	0.001	0	0	4	4	13	**50**	30	155
Spionidae	0.003	1	3	9	9	16	**35**	80	1737
Syllidae	0.031	0	1	0	3	0	**22**	14	34

5.3 Cluster Analysis

Having examined whether the fauna of the different sites reflect environmental gradients (PCA) and whether there are taxa that are strongly indicative of certain environmental conditions (Indicator Species Analysis), we can attempt to define groupings of species based on their similarity of occurrence. Cluster Analysis was performed on the main data matrix, which had been transposed so that taxa, rather than sites, were the items being grouped. Alternative dendrograms were generated using the Sorensen (Bray-Curtis) distance measure, and a variety of linkage methods (Nearest Neighbour, Farthest Neighbour, Group Average, and Centroid). Of these methods, the Farthest Neighbour linkage gave the lowest chaining (sequential addition of small groups, so that few groups are evident; 24.8% c.f. 28.6–84.7%) and is shown here.

The resulting dendrogram (Figure 116) reveals a number of groupings.

(1) A quartet that is well separated from all others: *Amalda*, Nephtyidae, Glyceridae, and the 'seaward' Maldanidae.
(2) A tight grouping of Amphipoda, Flabellifera, Nereididae, and Cumacea.
(3) A slightly less-tightly bunched group of small *Austrovenus stutchburyi* (1–20 mm), *Zeacumantus*, *Cominella glandiformis*, *Halicarcinus*, and *Macomona liliana*, with Capitellidae, Spionidae, and *Nucula hartvigiana* closely linked nearby, while *Eatoniella*, *Micrelenchus tenebrosus* and Scalibregmatidae branched off the same stem.
(4) A group in the lower half of the plot, of *Anthopleura aureoradiata* and *Austrovenus stutchburyi* 21–40 mm, *Paphies australis*, *Eliminius modestus*, and *Xenostrobus pulex*.

5.4 Synthesis

Maps of the distribution and abundance of various macrobenthic invertebrates on the Farewell Spit tidal flats (Section 4) showed that most taxa were more abundant on the large central flats, much of which had moderate to high *Zostera* cover. A simple plot of the number of taxa recorded at different *Zostera* surface cover scores (see Figure 17) showed increasing diversity as eelgrass cover increased. Most taxa had reasonably wide distributions, suggesting that there were no spatially discrete habitat patches with distinct invertebrate communities, at least on the scale of sampling we used.

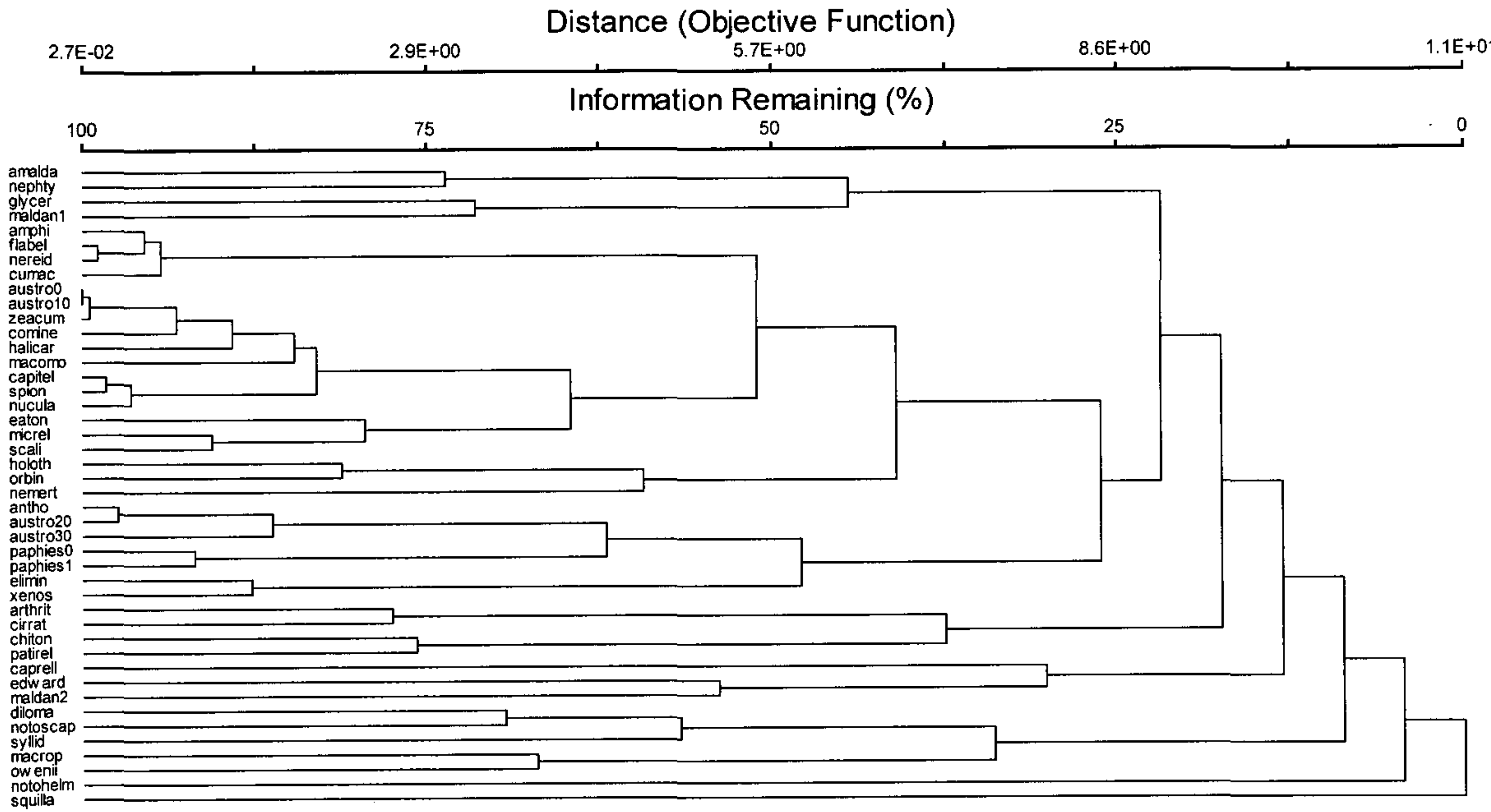

Figure 116: *Cluster dendrogram of groupings of common taxa on the Farewell Spit tidal flats, generated with the Sorensen distance and farthest neighbour linkage method.*

The PCA indicated that there were no major groups of sites. Instead, there was a general gradient from sites with low eelgrass cover to those with high eelgrass cover (see Figure 113).

The PCA and Indicator Species Analysis both indicated that there were moderate associations between the macrobenthos and the presence or density of *Zostera* beds. In the PCA, 21 taxa were moderately to strongly negatively correlated with Axis 1, which reflected a decrease in the surface cover and biomass of *Zostera*. These taxa were more abundant in sites with high *Zostera* cover. Correlations with Axes 2 and 3 were more varied, which may reflect secondary associations with different sediment composition. The Indicator Species Analysis found that 17 taxa were significant indicators of high *Zostera* cover; 14 of these also had moderate correlations with Axis 1 in the PCA (and two more had correlations of –0.258 and –0.313). Most of the taxa that the Indicator Species Analysis recorded as significant occurred in four or more *Zostera* classes. These taxa seem to be *Zostera* 'generalists', occurring wherever *Zostera* is present but being most abundant in dense beds. One taxon that was an almost significant indicator ($P = 0.063$) of moderate *Zostera* cover was the Cumacea, which peaked at categories 3 and 4.

Cluster analysis indicated some major groupings of taxa that are consistent with the results of the PCA.

Group 1 taxa (*Amalda*, Nephtyidae, Glyceridae, and the seaward Maldanidae) were distinctive largely because of their limited distribution on the flats and their occurrence primarily where there was little eelgrass. *Amalda*, Nephtyidae, and Maldanidae 1 were found only near the spring low-tide waterline (e.g., see Figures 81 and 83). Although all were found at sites with eelgrass present (maximum *Zostera* scores of 3, 5, 5 and 6 respectively), all were commonest where eelgrass was absent. *Amalda*, Nephtyidae, and Maldanidae 1 were all positively correlated with Axis 1 of the PCA ($r = 0.227$–0.256), reflecting a general association with low *Zostera* cover.

Group 2 taxa (Amphipoda, Flabellifera, Nereididae, and Cumacea) were all widespread and found in all *Zostera* categories. All were negatively correlated with Axis 1 of the PCA, but they also had equally large or larger positive correlations with Axis 3. These taxa may be responding as much to low coarse sand content as to increasing *Zostera* cover. Cumacean densities were highest at *Zostera* scores 2–4, and the extremely high densities of Amphipoda and Flabellifera occurred at scores of 1–4.

Group 3 taxa (*Austrovenus stutchburyi* 1–10 mm and 11–20 mm, *Zeacumantus*, *Cominella glandiformis*, *Halicarcinus*, *Macomona liliana*, Capitellidae, Spionidae, *Nucula hartvigiana*, *Eatoniella*, *Micrelenchus tenebrosus*, and Scalibregmatidae) all had strong negative correlations with Axis 1 of the PCA, and can be thought of as being true *Zostera*-taxa. They showed mixed correlations with Axes 2 and 3 (some positive, some negative, sometimes within the same taxon), which might indicate different sand tolerances. Nine of the 12 taxa were indicative of high eelgrass in the Indicator Species Analysis; the exceptions were *Eatoniella*, *Zeacumantus*, and *Macomona*.

The strongest link between taxa in Group 4 (*Anthopleura aureoradiata* and *Austrovenus stutchburyi* 21–30 mm and 31–40 mm, *Paphies australis*, *Eliminius modestus*, and *Xenostrobus pulex*) was a high correlation with Axis 2. *Austrovenus*, *Anthopleura*, *Eliminius*, and *Xenostrobus* also had moderate to strong negative correlations with Axis 1. The similarity in response of these taxa is not surprising; *Anthopleura* lives predominantly on large *Austrovenus* shells, and *Xenostrobus* and *Eliminius* both require firm substrates for attachment. *Xenostrobus* is generally found in localised hummocky areas of firm eelgrass. Distribution maps for these taxa show that they all were found low on the tidal flat or near to major tidal channels. For *Austrovenus* 21–40 mm, this distribution was a consequence of a seaward shift with age (see Figures 36–39). In contrast, *Paphies* spat were concentrated in a few extremely high-density sites at the extreme lower edge of the tidal flats (see Figure 52). Seven of the eight sites with densities of more than 1000 small *Paphies* per square metre had no eelgrass present, and all but one site had high coarse sand content (average 37.6%, range 13.3–73.3%; the remaining site had 0.4% coarse sand). Many spat were present in three adjacent sites along a sand island in a channel; next to this was a dense patch of larger pipi, and the presence of large numbers of the eleven-armed seastar (*Coscinasterias calamaria*) and eagle rays (*Myliobatis tenuicaudatus*) suggests that substantial populations of large pipi were also present nearby (and subtidally). Hence, although Axis 2 was not well explained by *Zostera* mass or coarse sediment, features of Group 4 taxa suggest that low tidal elevation and proximity to channels may be reflected in it. The subgroups in this group (*Austrovenus* and *Anthopleura*, *Paphies*, and *Eliminius* and *Xenostrobus*) were not at all closely linked, so this branch may simply represent broad-scale distributions rather than any similarity in finer-scale preference.

The patterns indicated in the previous analyses are also evident visually in ordination plots from a Detrended Correspondence Analysis (DCA) of the taxon data (Figures 117 and 118). The two plots show Axes 1 and 2, and 1 and 3, respectively. Most taxa occur in the same general 'axis space', consistent with the idea that the Farewell Spit fauna consists for the most part of taxa that respond similarly to environmental variables, particularly *Zostera*. Some exceptions are clear, though: *Amalda*, Nephtyidae, and Maldan 1 are well separated, with Caprellidae, *Notoacmea h. helmsi*, *Squilla armata*, *Edwardsia tricolor*, Holothuroidea, *Paphies australis*, and *Austrovenus stutchburyi* over 40 mm also peripheral to the main grouping via either Axis 2 or 3. These seem to be the 'sandy' taxa.

This analysis has used only coarse environmental data. Coarse sand data were the only sediment component available for almost all sites, and there were substantial differences in relief and microhabitat that have gone unrecognised in these analyses. Established large eelgrass beds tended to have a mosaic of large pools present, and were often substantially higher than surrounding sandy areas. These areas can form hummocks where the mussel *Xenostrobus* occurs, with bare sandy areas forming alternating ridges and pools. None of this variability has been explicitly accounted for or adequately sampled in this survey. More intensive finer-scale investigations would greatly clarify the habitat relationships of the macrofauna on the tidal flats.

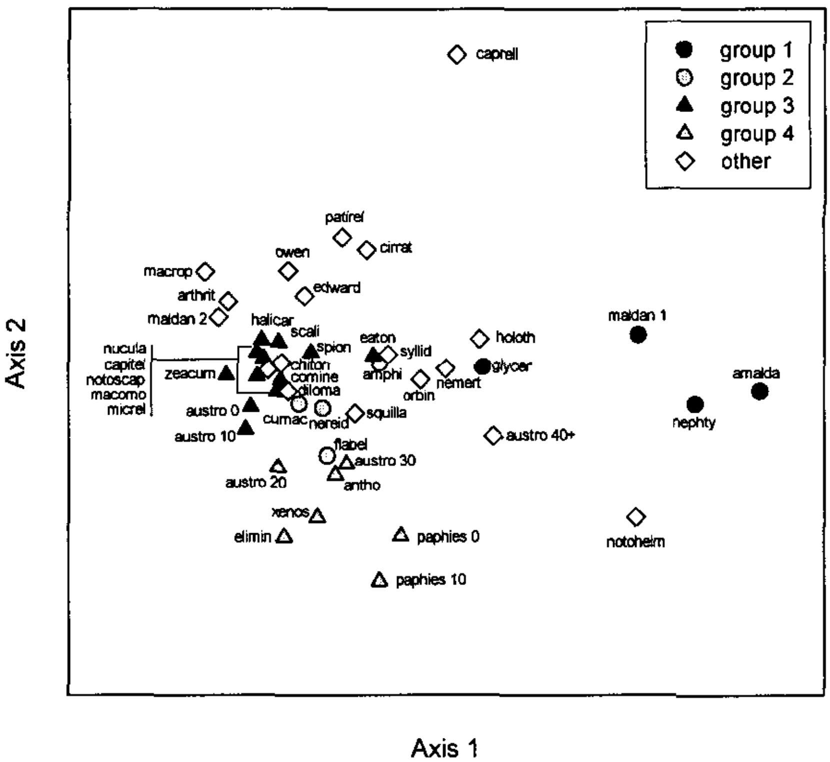

Figure 117: **Ordination plot of Axes 1 and 2 of a Detrended Correspondence Analysis of the species data, with groupings from the Cluster Analysis shown. Abbreviations take the first four to six letters of the family or genus. Notoscap and notohelm refer to *Notoacmea helmsi scapha* and *N. h. helmsi* respectively. Numbers refer to size-classes (*Paphies*, 0 = 1–10 mm, 10 = >10 mm; *Austrovenus*, 0 = 1–10 mm, 10 = 11–20 mm, 20 = 21–30 mm, 30 = 31–40 mm, 40+ = over 40 mm).**

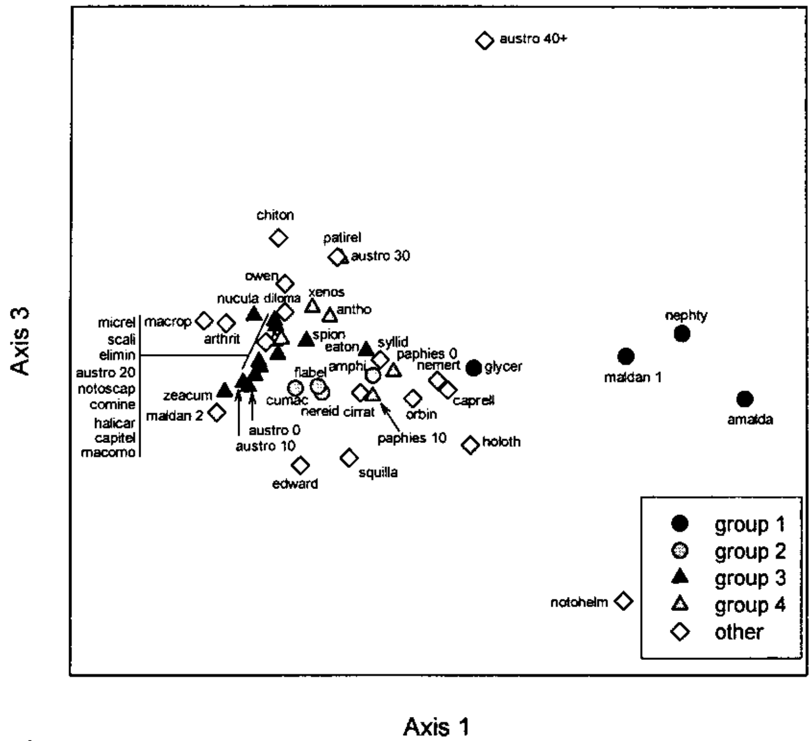

Figure 118: Ordination plot of Axes 1 and 3 of a Detrended Correspondence Analysis of the species data, with groupings from the Cluster Analysis shown.

6. LARGE-SCALE DISTRIBUTION OF FOOD RESOURCES FOR SHOREBIRDS

Not all the macrofauna in an area is relevant as food for every bird species that occurs there. Constraints on the diet of different species mean that only a subset of what is present will provide harvestable food resources. In this section we make a preliminary investigation into the large-scale distribution of food for the dominant shorebirds on Farewell Spit.

There are three main limits to the harvestibility of macrobenthos. *Accessibility* refers to the proportion of the stock that can be reached by a bird (many potential prey are buried too deep to be reached). *Ingestibility* is whether an item can be swallowed or not (many are too large). *Profitability* represents the trade-off between prey density, size and/or condition, and intake rate (which is affected by handling time); some items are simply not energetically rewarding enough or at a sufficient density to be profitable. *Harvestable prey* represent those that are accessible, ingestible, and profitable. None of these limits were directly measured during this survey. Instead, we will describe what is known of the diet of key shorebirds on sandflats in New Zealand (particularly from the studies of Battley (1996) on Farewell Spit) and make a rough breakdown of the grid sampling data into the taxa and size-classes considered to be relevant for pied oystercatchers, bar-tailed godwits and red knots. Descriptions of diet come from studies on the eastern parts of the tidal flats only.

6.1 Diet

6.1.1 Pied oystercatcher (*Haematopus finschii*)

Oystercatchers on Farewell Spit are known to feed on large shellfish (*Amphidesma subtriangulatum* on the ocean beach; *Austrovenus stutchburyi*, *Paphies australis*, *Macomona liliana*, and *Xenostrobus pulex* on the tidal flats) a variety of polychaetes (*Abarenicola affinis*, the scalibregmatid *Travisia olens* and other comparatively long worms, including Maldanidae and probably Orbiniidae), and the anemone *Anthopleura aureoradiata*, which is commonly attached to large bivalve shells. Because oystercatchers open the valves of large shellfish and remove the flesh, there is no ingestibility limit to what can be taken. Bivalves are usually located visually, as are deep-burrowing worms. *Travisia olens*, by comparison, is a shallow-sediment worm that is located by tactile 'sewing'. This worm was not found during the 2003 survey, though it was abundant in 1992–1994 and was present during a pilot study in February 2002.

Macomona liliana is limited as a food source for oystercatchers by the depth it buries itself in the sand. Regular sampling at a site adjacent to the shellbanks at the eastern end of Farewell Spit from December 1993 to December 1994 showed that the proportion of individuals able to be reached by a probing oystercatcher (80 mm deep or less) varied between 76.1% and 0%, with a decline from summer to winter as shellfish buried deeper. Large shellfish bury deeper than smaller shellfish, but as most individuals recorded in this survey were 25 mm long or less, and the predicted depth at which 25 mm *Macomona* occur is within reach of an oystercatcher's bill in summer (Battley 1996), all individuals are included in this analysis.

The only prey for which sizes have been recorded is *Xenostrobus pulex*, from an area of hummocks south of the shellbanks near the tip of the spit (this area did not coincide with the mapping grid in this survey). Oystercatchers fed on mussels 10–26 mm long, preferentially taking 15–23 mm individuals.

Size-selection of pied oystercatchers feeding on cockles (*Austrovenus stutchburyi*) in New Zealand has not been measured, despite estimates of daily prey intake (A.J. Baker quoted by Owen & Sell 1985). Studies elsewhere of the closely related Eurasian oystercatcher (*Haematopus ostralegus*) feeding on the cockle *Cerastoderma edule* have shown that oystercatchers generally select larger individuals, although animals as small as 10 mm will be taken in the absence of larger prey (though prey smaller than 15–20 mm are seldom taken: Goss-Custard et al. (1977), Sutherland (1982), Zwarts et al. (1996)). Above a certain cut-off point, size-selection usually reflects prey availability, with prey up to 40 mm being taken (Goss-Custard et al. 1977).

In this analysis we take the following taxa and sizes to represent the available food for oystercatchers:
Austrovenus stutchburyi, *Macomona liliana* and *Paphies australis* 15 mm and over
Xenostrobus pulex 10 mm and over
All polychaetes 20 mm and longer (Durell et al. 1996)
All *Anthopleura aureoradiata*
All *Holothuroidea*
All *Edwardsia tricolor*

6.1.2 Bar-tailed godwit (*Limosa lapponica*)

Less is known of the diet of bar-tailed godwits at Farewell Spit. Godwits ate predominantly polychaetes on sandy areas, following the tideline out, presumably because worms are shallower in their tubes or more active when covered in water. Birds fed visually on *Abarenicola*, Maldanidae (sometimes stripping the sandy tube), and crabs. *Helice crassa* was sometimes dug out of its burrow near the saltmarsh and dismembered before the parts were eaten. Little is known of godwit diet in eelgrass beds; crabs are certainly taken, and doubtless polychaetes and probably small bivalves such as *Nucula hartvigiana* (which has been found in stomach contents of birds from Northland; P.F. Battley, unpublished data) and *Austrovenus stutchburyi*. There can be sexual differences in habitat choice and diet, as females have much longer bills than males (Higgins & Davies 1996). In the Firth of Thames, in the North Island of New Zealand, some males take small mussels on cobble flats, while females nearby feed on polychaetes in soft mud (P.F. Battley, unpublished data). Zharikov (2002) recorded godwits predominantly feeding on crabs in Moreton Bay, Queensland, Australia, with males feeding exclusively in eelgrass beds, whereas females were divided between eelgrass and sand areas. In all sites in the East Atlantic in which bar-tailed godwit diet has been studied, polychaetes dominated the diet (Scheiffarth 2001). Bivalves (the Baltic tellin *Macoma balthica*) were important at some times in Germany (average length 9.2–13.6 mm in different months), and shrimps and crabs were also taken (Scheiffarth 2001). It is difficult to know what a suitable lower size-limit for polychaetes is. Zwarts & Wanink (1993) showed that long-billed shorebirds (such as godwits) have long handling times on small prey, so are expected to ignore prey below a certain size threshold. We have no information on what this value might be, and have set an arguably low limit of 10 mm. This may be realistic for a stout worm such as a Scalibregmatidae, but an equally long spionid would be energetically much less rewarding. Chironomid larvae have been recorded in godwit faeces in Moreton Bay (Zharikov 2002).

The following taxa and sizes are assumed to represent suitable prey for godwits:
Macomona liliana and *Paphies australis* 15 mm and under
Austrovenus stutchburyi and *Xenostrobus pulex* 10 mm and under
All *Nucula hartvigiana*
All polychaetes 10 mm and over
All crabs

6.1.3 Red knot (*Calidris canutus*)

The diet of red knots on Farewell Spit is reasonably well known, because this species is a mollusc specialist whose diet can be accurately reconstructed from prey remains in faeces (Dekinga & Piersma 1993, Battley 1996). Bivalves form the bulk of the diet on Farewell Spit, primarily pipi (*Paphies australis*) in sandy areas and nutshells (*Nucula hartvigiana*) in eelgrass beds. Cockles (*Austrovenus stutchburyi*) are also taken, especially in areas of eelgrass. Small gastropods (mostly *Eatoniella*, but also *Micrelenchus* and occasionally *Cominella* and *Zeacumantus*) are also taken. Bivalves are located by touch, probably using pressure sensors in the bill tip to detect buried items via pressure gradients in wet sand (Piersma et al. 1998). Gastropods are located by sight. Small Crustacea (Amphipoda and Isopoda) are frequently taken in sandy areas close to shore, where they may provide the bulk of the infaunal biomass (Battley 1996).

Average size of *Paphies australis* taken ranged from 5.5 to 8.2 mm between sites and over three years, with individuals 2–16 mm being recorded. The predicted ingestion limit based on the circumference of the shell and the gape size of knots (30 mm; Zwarts & Blomert 1992) is 22.4 mm. In 1993–1994 it seemed that knots took *Paphies* roughly in proportion to their occurrence up to 12 mm, but did not take prey larger than 14 mm.

Average size of *Austrovenus stutchburyi* taken ranged from 5.1 to 8.0 mm, with a range of 2–15 mm recorded. The predicted ingestion limit is 14.1 mm. Individuals 6–9 mm seemed to be selected for, with those 12 mm or larger taken less frequently than expected based on their availability. Zwarts & Blomert (1992) estimated the maximum size of the cockle *Cerastoderma edule* in Europe able to be ingested by knots to be 12 mm, though dietary reconstructions from faeces collected in the Dutch Wadden Sea indicated that cockles up to 15 mm were taken (Piersma et al. 1993).

No estimates of the sizes of *Nucula hartvigiana* taken by knots have been made, but as they reached only 9 mm in length in this survey, all are probably ingestible by knots. Virtually all *Macomona liliana* are buried too deep in the sand for knots with a bill length of about 31 mm (Higgins & Davies 1996) to reach them (Battley 1996).

The relevant prey items for knots are assumed to be:
Paphies australis 16 mm and under
Austrovenus stutchburyi 14 mm and under
All *Nucula hartvigiana*
All gastropods 5 mm and under
All Amphipoda and Isopoda

6.2 Spatial distribution of potential prey

Densities of potential prey were calculated in three broad categories for each bird species: bivalves, polychaetes, and other (*Anthopleura*, *Holothuroidea*, and *Edwardsia*) for oystercatchers; polychaetes, bivalves, and crabs for godwits; and bivalves, small Crustacea, and gastropods for knots.

We also plotted the relative distribution of the shorebird species at high tide roosts along the spit. Mapping the densities of foraging birds on such an area is almost impossible due to the low densities of birds once they have spread out over the tidal flats, particularly as some birds feed in flocks, and may simply not be located during low tide. However, high tide censuses have been conducted by the Ornithological Society of New Zealand in summer and winter for many years (Schuckard 2002), and the location of birds at high tide should at least partly reflect their choice of feeding location, assuming that birds try to minimise the distance travelled between roosts and feeding grounds. Shorebird counts on the spit are broken up into a series of manageable portions along its length. By plotting the proportion of the birds counted during censuses in relation to the count sections, we can visually compare the general distribution of birds with the maps of potential prey. However, not all of the birds that roost on the spit feed on the spit's tidal flats. Most birds in the first count section (see Figure 120) fly southwest to feed at or past Puponga. Godwits colour-marked further around Golden Bay (Pakawau and Totara Avenue) have been seen in this first section, but not beyond it, so it appears that most of the birds that feed on the spit roost in the three outermost count sections.

Pied oystercatcher

Bivalves were by far the most numerous prey option for oystercatchers. *Austrovenus stutchburyi* dominated this component (86.0% of the suitable individuals), so the spatial distribution of potential

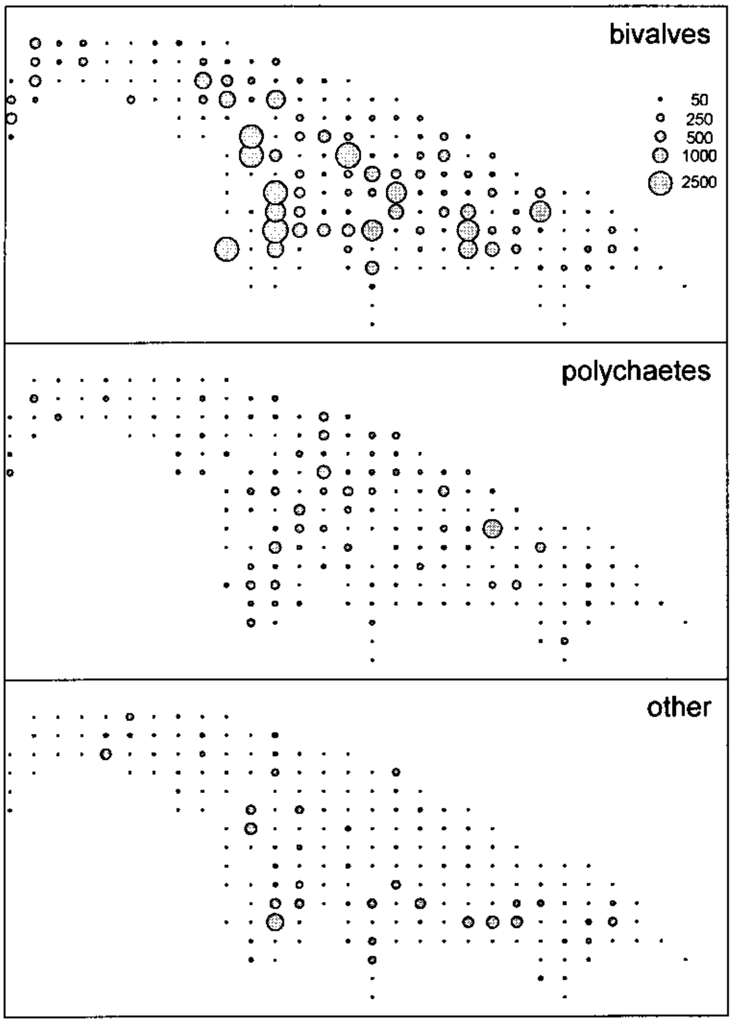

Figure 119: **Spatial distribution of potential prey for pied oystercatchers. Points represent the sampling grid on the tidal flats, and the size of the points is proportional to the density of suitable prey items (numbers per m^2). The smallest points have no potential prey present.**

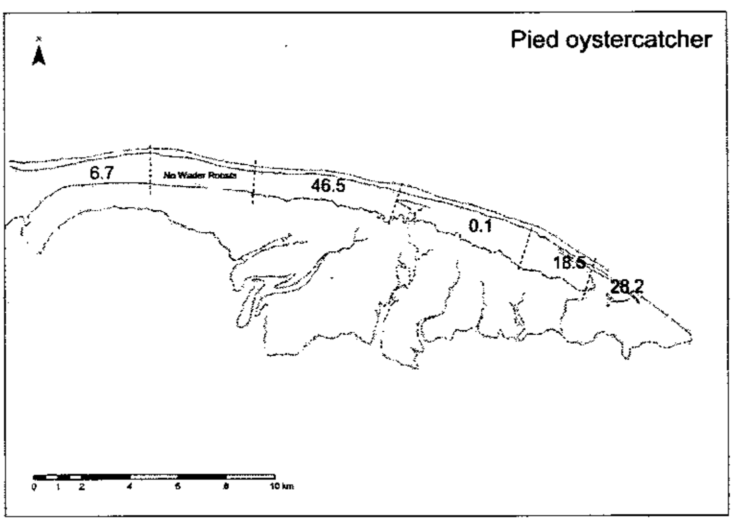

Figure 120: **Relative distribution of pied oystercatcher at high tide on 22 February 2003. Numbers are the percentage of the total census that occurred in given count sections. Total count was 8429.**

bivalve prey (Figure 119) resembles the distribution of cockles (see Figures 37 and 38). The high-density site on the most southwestern corner of the central flats contained numerous large pipi

(*Paphies australis*); this would have been subtidal on most tides so would have been unavailable to feeding oystercatchers. Large polychaetes were found mostly on the central flats but occurred at more than 100 individuals per square metre in less than a quarter of the sites. There was relatively little food on the narrow flats along the western quarter of the spit, on upper-level tidal flats, and around the tip of the spit.

The distribution of birds at high tide (Figure 120) is broadly similar to the distribution of potential food: low numbers on the first two sections adjacent to the rather barren and narrow inner flats, and high numbers on the first half of the central flats, where bivalve and polychaete densities were highest. The low numbers in the central spit may reflect the oystercatchers' tendency to gather in large flocks as much as their choice of feeding location. The presence of substantial numbers on the final section (2375 on the summer census on 22 February 2003) requires explanation, as Figure 119 suggests there is little food present. Historically, large numbers of oystercatchers roost on the beach near the tip of the spit, and these feed on the tidal flats near to the shellbanks, especially southwards towards an area of hummocks that had high cockle populations (Battley 1996). In February 2002, most of the local oystercatchers fed in an extremely high-density bed of large pipi southeast of the shellbanks. In March 2003 no such bed could be located at the same site. Given the scale of sampling used in this study (transects every kilometre, samples every 500 m), substantial but localised cockle and/or pipi populations could have been missed during the sampling. Food resources such as these can be highly dynamic and a much more intensive sampling effort would be required to monitor them appropriately. Oystercatchers were also seen as we approached the outer flats by boat, flying out towards islands south of the flats that were still covered by the tide. There are clearly some resources present but not accounted for in the survey. Another explanation for the mismatch in numbers and apparent prey near the spit tip is that food resources had declined before the benthos survey. In June 2003, oystercatcher numbers at the tip were down by almost 1500 birds, suggesting prey levels may have been lower. A prey item not recorded during the 2003 survey was the distinctively odiferous worm *Travisia olens*. This was an important prey for oystercatchers and godwits near the tip of the spit in 1992–95, but even then showed large density changes within a few months (Battley 1996). In 2002, we recorded 25 individuals from 83 core samples taken on the flats near Mullet Creek on the central flats (see Figure 1) and on the easternmost tidal flats. In 2003, despite taking about 600 core samples, none was recorded. It is unlikely that this absence is merely a consequence of the large sampling grid used, but illustrates the between-year variability that exists in food supply.

Bar-tailed godwit

Because we used a smaller size-limit for suitable polychaetes for godwits than for oystercatchers, more polychaetes are potentially available on the tidal flats for godwits (Figure 121). Moderate polychaete densities occurred over much of the central flats, but densities were low in the inner Spit and around the spit tip. Bivalves, which generally make up less of the diet than polychaetes, were abundant at the four sea-edge sites where small *Paphies australis* were numerous, and fairly even across most of the central and outer flats. Small pipi (*Paphies*) made up 55% of the bivalves, but if the four extremely high-density sites are ignored, then the breakdown of species becomes much more even: *Macomona* 2.8%, *Xenostrobus* 4.2%, *Paphies* 28.7%, *Austrovenus* 29.5%, and *Nucula* 38.9%. Crabs, at least those sampled with our methods, were a comparatively minor food resource numerically; however it must be noted that core sampling is not an efficient way to sample crabs and the data are likely to under-record actual abundance.

The distribution of bar-tailed godwits at high tide (Figure 122) matched the distribution of their main prey, polychaete worms. Again, few were present on the inner parts of the spit, but large numbers occurred in the sections next to central flats where polychaete densities were highest.

Red knot

For bivalve specialist knots, the potential prey map is dominated by the high densities of pipi at sites on the western edge of the central flats (Figure 123). In March 2003, large flocks of knots were flying to the sandy island with the three adjacent sites as soon as the tide exposed it. These were the

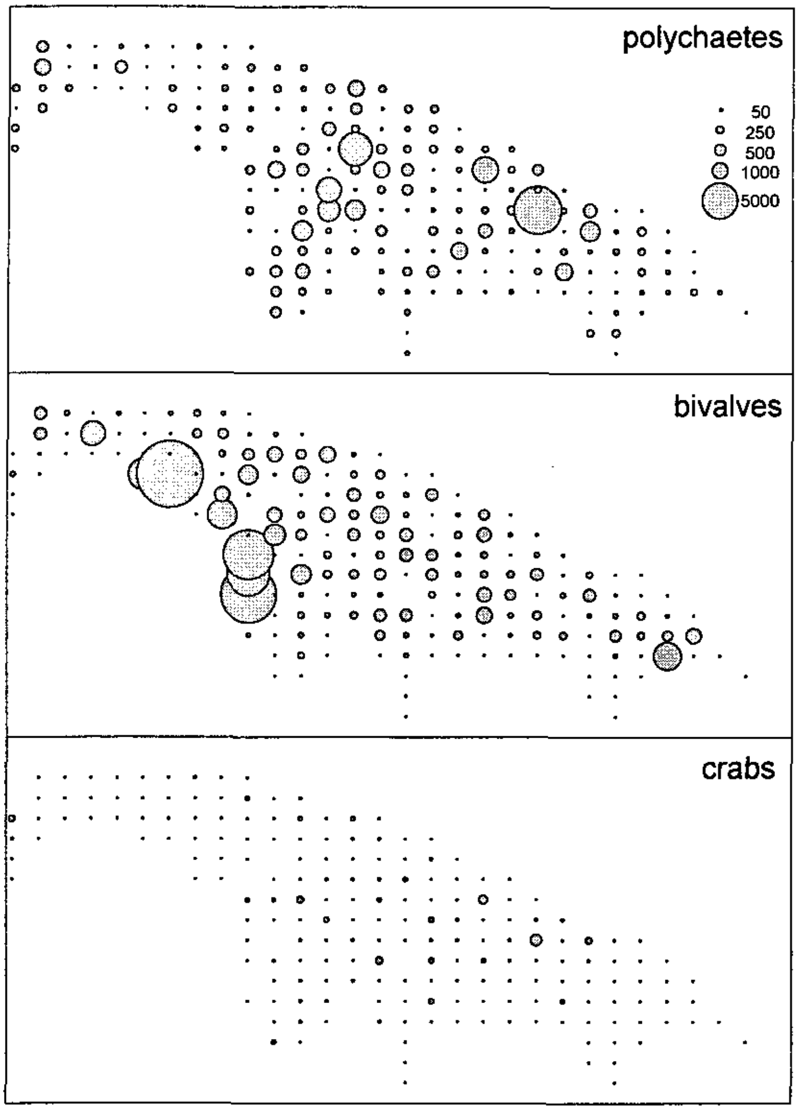

Figure 121: **Spatial distribution of potential prey for bar-tailed godwits. Points represent the sampling grid on the tidal flats, and the size of the points is proportional to the density of suitable prey items (numbers per m^2).**

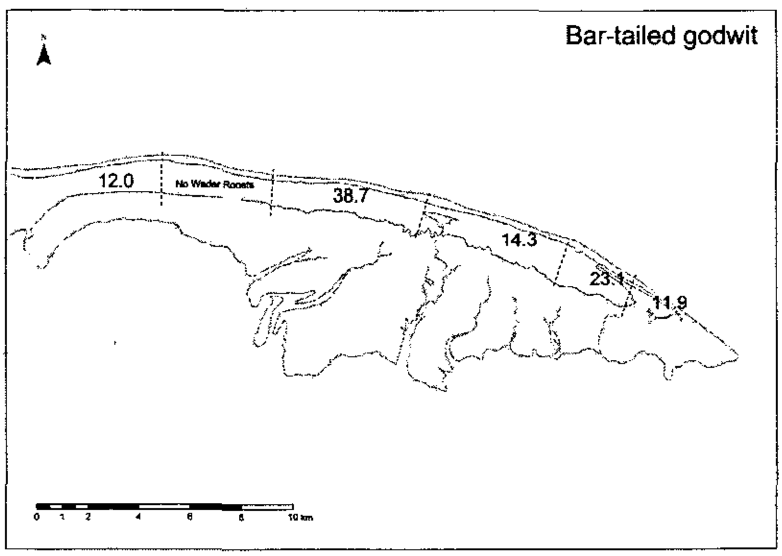

Figure 122: **Relative distribution of bar-tailed godwit at high tide on 22 February 2003. Total count was 12 536.**

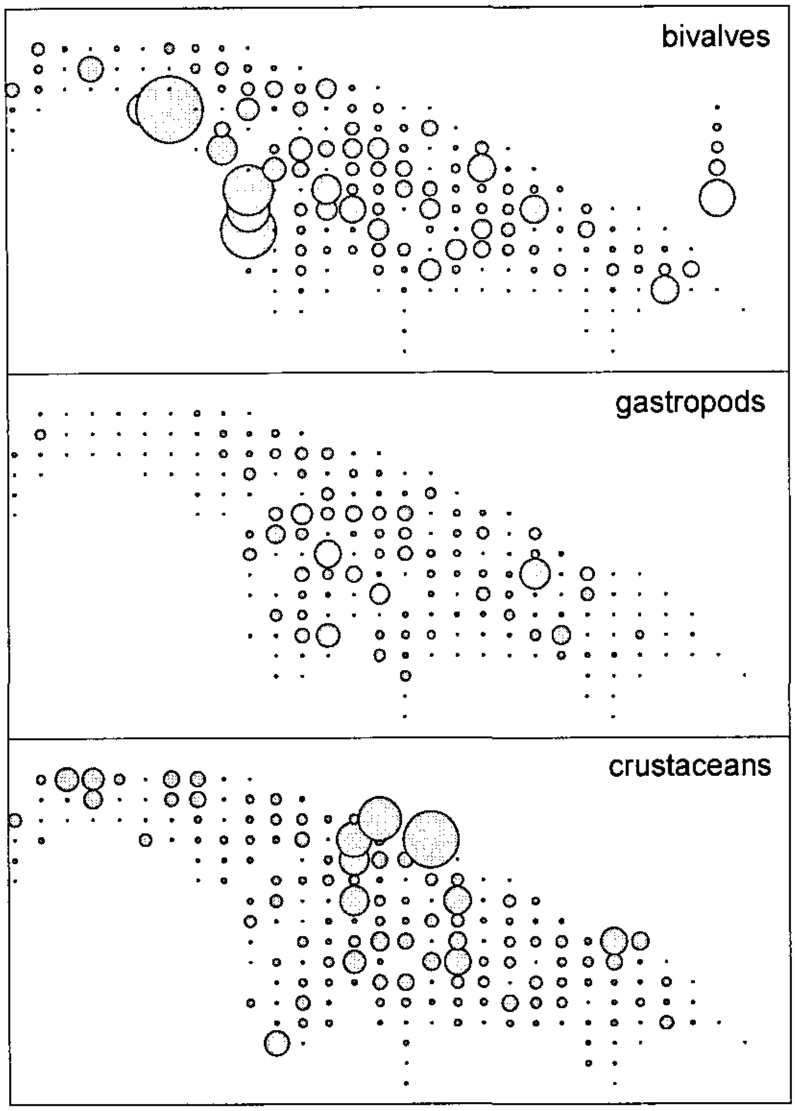

Figure 123: Spatial distribution of potential prey for red knots. Points represent the sampling grid on the tidal flats, and the size of the points is proportional to the density of suitable prey items (numbers per m^2).

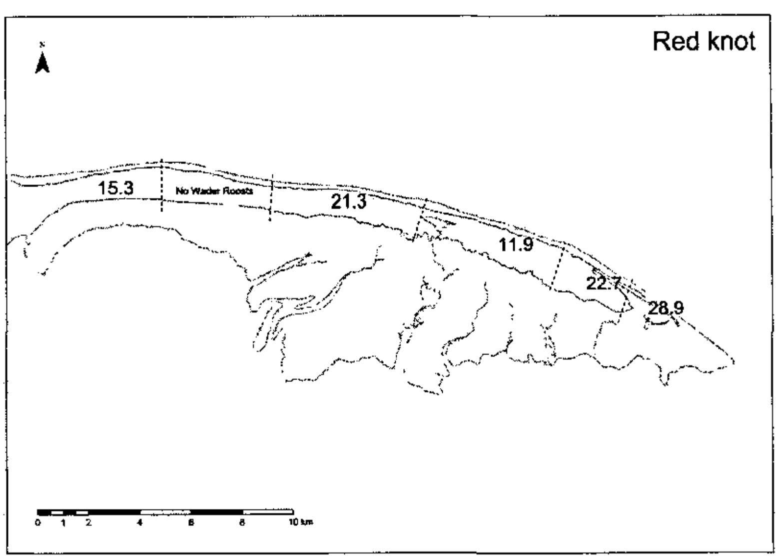

Figure 124: Relative distribution of red knot at high tide on 22 February 2003. Total count was 6229.

only sites with especially high densities of pipi. As with the godwit analysis, *Paphies* made up most (53.0%) of the total shellfish, but one-third of these were present in those four high-density sites. If these were unavailable (as they would be on neap tides), then the relative composition would be *Paphies* 27.0%, *Nucula* 32.3%, and *Austrovenus* 40.7%. Because knots ingest shellfish whole and crush them in their gizzards, the rate at which birds can crush shells is a constraint on their processing capacity (van Gils et al. 2003). Birds should therefore select prey with the most favourable flesh:shell ratio. In terms of the common and accessible bivalves on Farewell Spit, *Paphies* has the best ratio (0.067 g ash-free dry mass (AFDM) flesh: per g dry mass shell, n = 119 measurements), *Austrovenus* the least favourable (ratio of 0.031, n = 75; all data from P.F. Battley, unpublished). The few data for *Nucula* suggest that although it has a heavy shell, it also contains a good return fleshwise (ratio 0.054, n = 8). The least favourable prey, *Austrovenus*, is the commonest on the flats in most places. *Nucula* is the main prey in eelgrass beds, but no studies have estimated the relative intake rate of knots feeding in eelgrass and on sandflats.

Alternative prey types (gastropods and crustaceans) occurred mainly on the central flats (Figure 123). Gastropods were present in moderate densities throughout, while Crustacea were especially numerous high on the tidal flats. This is similar to what Battley (1996) found near the tip of the spit: on the sandy pan just north of the shellbanks, small Crustacea (primarily amphipods, but also isopods and cumaceans) occurred at extremely high densities (17 800 per square metre). They became progressively less numerous out across the sandy flats. Even though the mass of an individual amphipod was extremely low (0.07 mg AFDM), the biomass of small Crustacea at the sites sampled near the shellbanks was generally higher than that of bivalves. Knots sometimes fed for the entire low-tide period on this pan, so they are able to subsist on small crustaceans when the prey are at extremely high densities. The Crustacea we mapped may therefore only be a viable food source at the upper flat sites.

The distribution of knots at high tide did not match the potential prey map well (Figure 124). There were few birds on the inner sections of the spit, but most were found in the easternmost two sections. Three possible explanations for this are: (1) we failed to record a significant food source for knots on the outer spit; (2) the food supply had changed markedly between the census (22 February 2003) and the benthic survey (mid-March 2003); or (3) the distribution of knots reflects more than simply the density of small bivalves. It is certainly possible that there were localised pockets of *Paphies* spat that we did not locate, but we have no information on how much the densities of benthic invertebrates, such as pipi, change over a month. A major difference in the intertidal habitat on the outer spit and the more central portions, however, is the amount of *Zostera* present (see Figure 9). Few small pipi occur in areas with high *Zostera* cover (see Figure 52), and it may be that alternative prey in *Zostera* beds, such as *Nucula hartvigiana*, *Austrovenus stutchburyi*, and gastropods, are less attractive food sources. This is to be expected as the specialised prey-locating method used by knots (see above) might be interfered with by *Zostera* rhizomes.

Other bird species

Although we did not map the distribution of potential food for the other two numerous shorebirds on Farewell Spit (ruddy turnstone, *Arenaria interpres*, and banded dotterel, *Charadrius bicinctus*), maps of their distribution suggest that they also respond to local factors. Turnstone diet has not been studied in detail in New Zealand, but they are known to be extremely adaptable birds. They often occur in rocky habitats, and in New Zealand they also occur in sandy habitats with *Zostera* beds (Higgins & Davies 1996). On Farewell Spit they feed on large sandhoppers (Amphipoda) under beach-washed kelp and wrack, peel back algal mats on sandy pans, toss stones and sticks to examine the ground underneath (hence their English name), extract tiny worms from dead cockle shells, take terminal segments from Maldanidae tubes (P.F. Battley, unpublished data), and eat the crab *Helice crassa* in saltmarsh beds (Robertson & Dennison 1979). Elsewhere they have been recorded feeding on gastropods, bivalves, barnacles, echinoderms, and insects (Higgins & Davies 1996) and a wide variety of carrion, including a human cadaver (Mercer 1966). Their high-tide distribution (Figure 125) coincides with the largest expanse of *Zostera* flats on the spit, though they may also distribute themselves according to how much weed is temporarily available on the ocean beach.

Banded dotterels (Figure 126) are evenly distributed along the outer two-thirds of the spit. They are known to feed on dense *Zostera* beds (Robertson & Dennison 1979, Pierce 1987), and Robertson & Dennison (1979) noted that dotterels flew straight out from roosting areas to the nearby tidal flats, which explained the absence of dotterels on the inner section of the spit. In the recent census, dotterel distribution was not strictly proportional to the area of tidal flat or *Zostera* nearby, and it is possible that the distribution of the sandy pans they both feed and roost in influences their distribution along the spit.

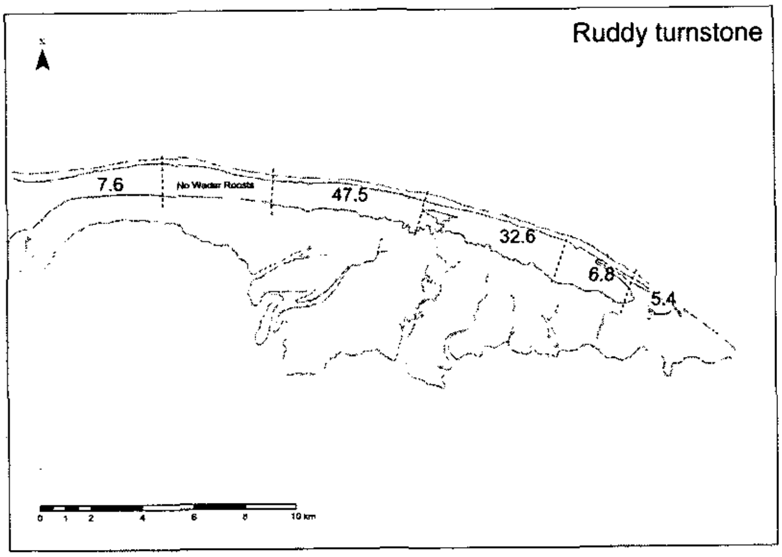

Figure 125: **Relative distribution of ruddy turnstone at high tide on 22 February 2003. Total count was 734.**

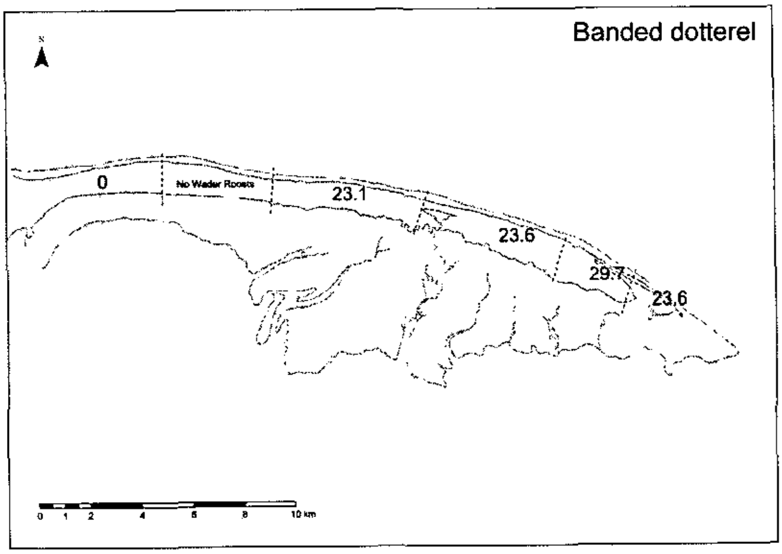

Figure 126: **Relative distribution of banded dotterel at high tide on 22 February 2003. Total count was 593.**

7. GENERAL DISCUSSION

Diversity and distribution of benthic invertebrates

This survey was the most intensive undertaken on Farewell Spit to date, and the taxonomic diversity recorded was unsurprisingly higher than previous limited studies have recorded. We recognised 91 taxa (see Table 2), which were combined into 83 major groups for analysis. This certainly underestimates the species diversity of the spit, as many taxa were not identified to species, particularly the small Crustacea. About nine Amphipoda 'morphotaxa' occurred in the samples, and others have been collected in the past (by P.F. Battley). Although species differences such as these presumably are irrelevant to foraging birds, a detailed taxonomic assessment of reference material from Farewell Spit would be beneficial.

The large-scale distribution of the marine macrobenthos of Farewell Spit largely reflected habitat differences, primarily the presence or density of the eelgrass, *Zostera muelleri*. There were no spatially discrete habitats with distinct faunal communities. Instead, many of the taxa or groups that occurred frequently in the samples increased in abundance as the cover of *Zostera* increased. Typical invertebrates that were characteristic of eelgrass beds included the bivalves *Austrovenus stutchburyi* (small size classes), *Macomona liliana* and *Nucula hartvigiana*, the snails *Cominella glandiformis*, *Micrelenchus tenebrosus*, *Eatoniella* sp., and *Zeacumantus* spp., polychaete worms in the families Capitellidae, Spionidae, and Scalibregmatidae, and the pill-box crabs, *Halicarcinus* spp. Areas without eelgrass have comparatively little infaunal diversity compared with vegetated areas (see Figure 17), but there is a group of taxa that are more commonly found in these sandy sites: *Amalda* sp., the worms Nephtyidae and one Maldanid, Caprellidae, *Notoacmea h. helmsi*, *Squilla armata*, *Edwardsia tricolor*, Holothuroidea, *Paphies australis*, and large *Austrovenus stutchburyi*.

The scale of mapping used was not designed specifically to detect associations between invertebrates and particular habitat types, and the relationships between benthic invertebrates, *Zostera*, and sediments could be better studied at a much finer scale. The purpose of the survey was to describe any large-scale patterns in the distribution of benthos across the whole Farewell Spit tidal flats. The associations between the habitat and the infauna that were apparent are useful in interpreting the main pattern observed, of an increase in diversity and density of many taxa on the large central flats. Farewell Spit is renowned for its eelgrass beds, which are among the largest in New Zealand (G. Inglis, National Insititute for Water and Atmospheric Research, Christchurch, pers. comm. 2004). It is clear that the *Zostera* beds are a major influence on the large-scale distribution of benthic fauna on the spit. Although the scale of sampling used was not suitable for detecting small-scale variability (c.f. McArdle & Blackwell 1989, Thrush et al. 1989), there are obvious large-scale patterns that override the small-scale variability.

There is nevertheless a great deal of local variation present on the tidal flats of Farewell Spit that is not represented in our data. Substantial differences in elevation and surface cover occurred between sample sites, particularly on the central flats, and there may well be benthic 'hotspots' of relevance to birds that we did not record (e.g., small pipi (*Paphies australis*); see Figure 52). The low intensity of sampling also meant that we under-recorded some taxa that may be quite common. The lugworm *Abarenicola affinis*, for instance, is quite numerous high on the tidal flat on the outer Spit, and is fed upon by pied oystercatchers and bar-tailed godwits (Battley 1996), yet was recorded at just four sites in the survey. This is probably partly a result of few of the sample sites being close to the shore edge, but also possibly because *Abarenicola* can burrow deeper than the 250 mm we core sampled, as can the mantis shrimp *Squilla armata*.

For taxa that show little local variation in density, a large-scale survey may give a fair representation of the true distribution, but many taxa show density gradients or patchiness over quite small scales (e.g., 5–30 m: McArdle & Blackwell 1989, Thrush et al. 1989) in apparently homogenous habitat.

This variation may be of interest to those seeking to understand processes behind spatial patterns (Thrush 1991), but it is a problem if it compromises less intensive surveys. In our survey, much of the variation in the distribution of macrobenthos was attributable to major differences in habitat type. We acknowledge that there must also be substantial variation within the samples that simply reflects the local variation that we could not explicitly address. It is perhaps worth bearing in mind differences of scale in mapping exercises and other benthic monitoring schemes: Thrush (1991) cited studies with sites of 0.9 ha as 'large-scale'; our 'large-scale' survey covers an area about 10 000 times larger.

Food supplies for shorebirds

Mapping of potential food resources for shorebirds, based on the survey data, indicated that the distribution of food supplies differed between the bird species (pied oystercatcher, bar-tailed godwit and red knot), though for all species there was little food on the narrow western flats. This fits with the finding that many of the birds that roost on the inner spit do not feed on the Farewell Spit tidal flats, but move to nearby areas in northwest Golden Bay. The distribution of birds at high tide matched the distribution of potential prey inasmuch as most birds occurred in the sections near to and east of the central flats, which held the greatest potential food resources for shorebirds. Differences in the distribution of the various shorebird species suggest that they respond to different factors; differences in diet, and therefore the distribution of suitable prey, could partly explain the differences in distribution.

Little is known of just how suitable the different potential prey types are for these birds. For knots, for instance, the map of small bivalves (see Figure 123) suggests that there are good food supplies from near the tip of the spit to the western side of the central flats, but most of this is *Nucula* and *Austrovenus*, thick-shelled prey that often occur in a subsurface matrix of *Zostera* rhizomes. We located only four sites with especially high densities of small pipi (*Paphies australis*) (see Figure 52), and all of these were at the extreme low-water mark. We saw knots making use of these resources, which would not be available on all tides. During neap tides, the low tide on Farewell Spit can be a metre or more higher than during spring tides; these resources of pipi would be unavailable through much of the fortnightly tidal cycle. Because we do not yet have data on the tidal elevation of the sites, we cannot compare potential prey on spring and neap tides.

Given the extent of *Zostera* on Farewell Spit, and its influence on the infaunal communities, determining how birds respond to *Zostera* cover is important for understanding the consequences of any changes to the intertidal environment. Clearly, high *Zostera* cover is associated with rich infaunal communities. Bar-tailed godwit and red knots are often seen foraging on *Zostera* beds, and it is likely that these beds do provide diverse foraging options. What is not clear is whether these beds are especially good for these species, or whether there is a lack of more easily procured food elsewhere. For knots, bare sand with high pipi densities is probably the optimal habitat. Dense *Zostera*, with its abundant nutshells, might also provide good habitat. But what happens at intermediate levels of *Zostera*?

The attempts to map the potential food resources for shorebirds were extremely coarse. Blanket rules were used to select different polychaetes based on size, despite underlying differences in body form of different taxa, and selectiveness of foraging birds. All the estimates were of numerical abundance, but the harvestable biomass is the relevant value for a foraging bird. Equations have been generated to predict biomass (ash-free dry mass, AFDM) on the basis of body size for some species or groups of taxa on Farewell Spit (Battley 1996), but for some of these (particularly polychaetes) sample sizes were small. Body condition (AFDM per length) also changed considerably within a year for some taxa, but sampling was not carried out over a long enough period to show whether the values at a particular time were representative of the long-term expectation. For instance, both intercepts and exponents of equations relating cockle biomass to shell length changed through the year of sampling. For a 35 mm cockle, the estimated mass increased from 147 mg AFDM in December 1993 to 286 mg AFDM in December 1994. There was a smaller peak in March 1993, but with these data it is not possible to reliably predict the condition of cockles through the year. Likewise, *Macomona* increased in condition through the sampling period and ended up heavier in December 1994 than December 1993. Mussels (*Xenostrobus pulex*) were heavier for their size in June 1994 than February 1994. The most dramatic change was in the polychaete *Travisia olens*. In addition to a more than twofold increase in the relative condition from December 1993 to April 1994, body size increased so that the average worm on the flats near the spit tip increased from 0.92 mg AFDM in December to 19.98 mg AFDM in April. Much more robust data are needed before numerical and size data on the Farewell Spit benthos can be translated into harvestable biomass figures.

Zostera dynamics, and interactions with black swans (*Cygnus atratus*)

Zostera beds are not static, but their rates of change on Farewell Spit have not been measured. Our experience is that light eelgrass cover was more extensive near the tip of the spit in 2002–03 than it was in 1992–1995 (P.F. Battley, pers. obs.). Beyond that, we have no indications as to whether *Zostera* is static, decreasing, or increasing on the spit. Given the apparent importance of eelgrass to the infaunal communities that shorebirds depend on, accurate mapping of *Zostera* is an important step in adequately monitoring the intertidal environment.

The *Zostera* beds of Farewell Spit also provide a food source for the largest congregation of moulting black swans in New Zealand (Williams 1982). From 6000 to 14 000 birds have been counted annually from 1977 to 2002 (N. Deans, Nelson Marlborough Fish and Game, pers. comm. 2004). In coastal areas the main foods of black swan are *Zostera* and sea lettuce (*Ulva* spp.), which they usually feed on in shallow water, preceding the tide as it ebbs and following it as it flows across the flats. It is estimated that each swan may consume 0.25 kg fresh weight of vegetation per day (Sagar et al. 1995), so up to 3.5 t of *Zostera* could be consumed daily on Farewell Spit. Sagar et al. (1995) stated that 'Calculations for Farewell Spit do not suggest an overgrazing problem for the whole area, although there may be local sites where this does occur'. Byrom & Davidson (1992, cited by Sagar et al. 1995), recorded that swans cropped only the leaves of eelgrass and were not observed grubbing for eelgrass rhizomes. Further research may be required to confirm whether this is true. Holes about 10 cm wide can often be found in areas of light to moderate eelgrass cover, including fairly high on the shore. Whether these are made by swans or fish needs to be determined.

There is obviously no direct competition between black swans and the shorebirds of Farewell Spit. They feed on different matter, and swans feed largely in water. The effects of swan grazing on *Zostera* dynamics and nutrient cycling have yet to be studied at Farewell Spit. Swans could plausibly affect the distribution or growth rates of *Zostera* on Farewell Spit. For instance, if intermediate *Zostera* cover inhibits settlement of pipi spat, and swan foraging promotes the spread of *Zostera*, then swan foraging could indirectly influence shorebird populations, such as red knots. The interrelationships between swans, *Zostera*, invertebrates, and shorebirds deserve future study.

Management implications

Farewell Spit and the adjacent tidal flats are listed as a *Wetland of International Importance* under the Ramsar Convention (Site No. 103). The site is of international importance for shorebirds, and has nationally significant *Zostera* beds. A management plan for Farewell Spit Nature Reserve was published in 1990 (Anon 1990) and a new plan is currently under preparation. The 1990 Plan included proposals for species and ecosystem monitoring, and the Nelson/Marlborough Conservancy's Conservation Management Strategy (Department of Conservation 1996) identified monitoring 'intertidal communities of Farewell Spit' as a priority.

Ramsar Convention

Article 3.2 of the Ramsar Convention states that each Contracting Party:

> 'shall arrange to be informed at the earliest possible time if the ecological character of any wetland in its territory and included in the List [of Wetlands of International Importance] has changed, is changing, or is likely to change as a result of technological developments, pollution or other human interference.'

The term 'change in ecological character' was defined in Resolution VII.10, adopted at the 7th Meeting of the Conference of the Contracting Parties to the Convention on Wetlands, in 1999 as:

> '...the impairment or imbalance in any biological, physical, or chemical components of the wetland ecosystem, or in their interactions, which maintain the wetland and its products, functions or attributes.'

The requirement for appropriate monitoring of Ramsar sites, inter alia to allow implementation of the provisions of Article 3.2, is recognised in the 'New Guidelines for management planning for Ramsar sites and other wetlands' appended to Resolution VIII.8, adopted at the 8th Meeting of the Conference of the Contracting Parties to the Convention on Wetlands, in November 2002.

> 'A function of monitoring, in the context of management planning, is to measure the effectiveness of management. It is essential to know, and to be able to demonstrate to others, that the objectives are being achieved. Thus, monitoring must be recognized as an integral component of management and planning. It should be designed to identify and manage change in ecological character of the site.'

It is understood that monitoring will be addressed in the Farewell Spit Management Plan which is currently in preparation (K. Hughes, Department of Conservation, pers. comm. 2004).

Monitoring

Monitoring at Farewell Spit has been largely restricted to waterbird surveys conducted by the Ornithological Society of New Zealand (shorebirds) and Fish and Game New Zealand (black swans). As noted earlier (Section 1) current monitoring of bird populations has revealed population changes, but a lack of information on prey populations and availability have made it impossible to consider potential ecological factors involved in these.

The main purpose of the present survey was to establish a baseline for the development of future monitoring programmes, inter alia to assist in meeting Article 3.2. requirements. The survey was successful in meeting the objectives of providing baseline information on the distribution and abundance of macro-zoobenthic organisms on the intertidal flats off Farewell Spit, with particular reference to prey species for shorebirds. Useful information on the distribution and abundance of *Zostera* and on sediment characteristics was also obtained. By using geographically exact sample sites that are readily relocated by GPS, the same grid can used for future large-scale monitoring. The results of the survey are, however, still a 'snap shot' and do not address seasonal or inter-annual differences. Some changes are evident within and between years, such as with *Travisia olens*. This was the preferred food of oystercatchers near the spit tip in the summer of 1993–94, yet was apparently absent by June 1994. It was present in roughly one-third of samples in the pilot study in 2002, yet was not recorded in 2003.

The present study assessed potential prey populations at the end of summer, at a time when migratory birds were fuelling up before migrating to Arctic breeding grounds. If shorebird predation is a significant pressure (though densities are low compared with many northern hemisphere sites: Zwarts et al. 1990), prey populations could be expected to be depressed at this time due to increased predation rates. This could mean that benthos measurements in a survey such as this one will not represent peak levels, but it could also be argued that this time of year is the most crucial to the Arctic-breeding shorebirds. There is increasing evidence that the level of migratory fuelling achieved is critical to the survival or reproductive success of the individual (Drent et al. 2003, Baker et al. 2004, Morrison et al. 2004) – if birds are to migrate successfully it is necessary that they reach departure weights within the time frame set by their migratory clocks. In view of this, monitoring of prey stocks during or immediately after the period of pre-migratory fattening could be the most sensitive time for assessing potentially adverse changes in ecological character of the site for northern hemisphere shorebirds.

However, it should be recognised that the macrozoobenthos of the Farewell Spit tidal flats are subject to extensive predation by shorebirds throughout the year, as a large population of the endemic pied oystercatcher spends the winter in the area (Schuckard 2002). Shellfish are also subject to extensive predation pressure from eagle rays. Both birds and rays have been shown to influence benthos communities in the Manukau Harbour (Thrush et al. 1994).

Baseline data are of little use if they are not built on. To design management and research that will 'identify and manage change in ecological character of the site', we suggest the following avenues.

- Measure seasonal variation in the densities of key benthic invertebrates at selected sites. This would allow an informed and reasoned decision to be made as to what time of year would be most appropriate for long-term monitoring.
- Periodically repeat surveys of selected parts of the 2003 sampling grid.
- Make accurate measurement of the *Zostera* beds.
- Establish reference markers and initiate detailed monitoring of *Zostera* density at selected sites along the spit.
- Investigate direct and indirect interactions between black swans and *Zostera.*
- Study intake rates and diet choice of shorebirds on substrates with different *Zostera* cover.

8. ACKNOWLEDGMENTS

We are grateful to the many people who have contributed to the success of the project. At the Ministry of Fisheries, Jolene Key was instrumental in getting the project organised and Sian Pratt and Desinee Cunningham provided valuable administrative support.

We are grateful to John Mason and Hans Stoffregen, Golden Bay Area Office, Department of Conservation, for their continuing interest and support. Andrew Baxter at the Conservancy Office, Nelson, also provided valuable input to the initial project design. We are particularly grateful to Geraldine Moore of the Department of Conservation who prepared the benthos maps. The Department has provided extensive logistic support, notably accommodation, vehicles, and use of a boat. Ken Bolt, Maritime Safety Authority, kindly arranged for us to use their accommodation at the lighthouse.

Field work was undertaken by: Rose Blois, Gareth Boyt, Tamsin Bruce, Sue Caldwell, Jo Carson, Kim Collins, Mike Fawcett, Duncan Fergusson, Leighan Field, Neil Freer, Leslie Hadley, Mike Hoverd, Olly Knox, Patrick Liddy, Erina Loe, Julia Melville, Vicky Melville, Kate Morgan, Stuart Nicholson, Karauria Ratapu, Anneka Schuckard, Eva Vervechen, Eigil Wahlberg, and Rob Wilson. Jack Marks kindly assisted with sorting and identification of samples. At the Nelson-Marlborough Institute of Technology, Calvin Tuck and Katrina Marwick allowed us to 'borrow' the Conservation Ranger students to assist in the field work, and Diana Mellor and Duncan Burns allowed us access to microscopes. The Ecology Group, Massey University, also provided microscope access. Thanks also to Ian Henderson of the Ecology Group, Massey University, for statistical assistance.

Peter Field generously allowed us to use his house at Puponga as a field camp. Paddy Gilloolly, Farewell Spit Safaris, provided accommodation at the lighthouse and, together with Ron Marks, met our land and marine transport needs with a sense of humour and tolerance.

GPS units were loaned by Peter Gaze, Graeme Elliot, and Rob Smith (Tasman District Council).

Barry Robertson, Paul Gillespie, and Rod Asher, Cawthron Institute, Nelson, provided advice during project planning, and Rod Asher provided enthusiastic and cheerful taxonomic advice throughout.

In part to support this project, the Department of Conservation and Tasman District Council jointly funded an aerial survey of the Farewell Spit tidal flats, for which we are very grateful.

Mike Beardsell (NIWA) had the unenviable task of editing this report, and we are grateful for his efforts.

9. REFERENCES

Anderson, S.H.; Hammerton, C.A.; Town, F.M. (1978). Intertidal life of Farewell Spit. *Tane 24*: 37–41.

Anon. (1975). Marine Environment of Golden Bay. Unpublished report prepared by the University of Auckland for Shell, B.P. and Todd Oil Services.

Anon. (1990). Farewell Spit Nature Reserve and Puponga Farm Park Management Plan. Management Plan Series 1. Nelson/Marlborough Conservancy Office, Department of Conservation.

Baker, A.J.; González, P.M.; Piersma, T.; Niles, L.J.; Nascimento, I.d.L.S.d.; Atkinson, P.W.; Clark, N.A.; Minton, C.D.T.; Peck, M.; Aarts, G. (2004). Rapid population decline in red knots: fitness consequences of decreased refueling rates and late arrival in Delaware Bay. *Proceedings of the Royal Society of London B 21*: 875–882.

Bartlett, R.M. (1985). Farewell Spit vegetation. Department of Lands and Survey, Nelson, Wellington.

Battley, P.F. (1996). Ecology of migrant shorebirds in New Zealand, focussing on Farewell Spit, North-West Nelson. Unpublished MSc thesis, Massey University, Palmerston North.

Beesley, P.L.; Ross, G.J.B.; Glasby, C.J. (2000). Polychaetes & allies: The southern synthesis. Fauna of Australia. Volume 4A. Polychaeta, Myzostomida, Pogonorphora, Echiura, Sipuncula. CSIRO, Melbourne.

Beesley, P.L.; Ross, G.J.B.; Wells, A. (1998). Mollusca: the southern synthesis. Fauna of Australia. Vol. 5. CSIRO Publishers, Melbourne.

Byrom, A.E.; Davidson, R.J. (1992). Investigation of behavioural patterns of black swan at Farewell Spit and Whanganui Inlet. *Department of Conservation Nelson/Marlborough Conservancy Occasional Publication No. 3*.

Cromarty, P.; Scott, D. (1996). A directory of wetlands in New Zealand. Department of Conservation, Wellington, New Zealand.

Crowe, A. (1999). Which Seashell? Penguin, Auckland.

Day, J.H. (1967). A monograph of the Polychaeta of Southern Africa. *British Museum Natural History Publication 656*. Trustees of the British Museum (Natural History), London.

Dekinga, A.; Piersma, T. (1993). Reconstructing diet composition on the basis of faeces in a mollusc-eating wader, the knot *Calidris canutus*. *Bird Study 40*: 144–156.

Department of Conservation. (1996). Conservation management strategy for Nelson/Marlborough Conservancy 1996-2006. *Nelson/Marlborough Conservancy Management Plan Series No. 10*.

Drent, R.; Both, C.; Green, M.; Madsen, J.; Piersma, T. (2003). Payoffs and penalties of competing migratory schedules. *Oikos 103*: 274–292.

Dufrene, M.; Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs 67*: 345–366.

Durell, S.E.A.l.V.d.; Goss-Custard, J.D.; Perez-Hurtado, A. (1996). The efficiency of juvenile oystercatchers *Haematopus ostralegus* feeding on ragworms *Nereis diversicolor*. *Ardea 84A*: 153–157.

Goss-Custard, J.D.; Jones, R.E.; Newbery, P.E. (1977). The ecology of The Wash. I. Distribution and diet of wading birds (Charadrii). *Journal of Applied Ecology 14*: 681–700.

Gregory, M.R.; Ballance, P.F.; Gibson, G.W.; Ayling, A.M. (1979). On how some Rays (Elasmobranchia) excavate feeding depressions by jetting water. *Journal of Sedimentary Petrology 49*: 1125–1130.

Heiss, W.M.; Smith, A.M.; Probert, P.K. (2000). Influence of the small intertidal seagrass *Zostera novazelandica* on linear water flow and sediment texture. *New Zealand Journal of Marine and Freshwater Research 34*: 689–694.

Higgins, P.J.; Davies, S.J.J.F. (1996). Handbook of Australian, New Zealand and Antarctic birds. Volume 3. Snipe to Pigeons. Oxford University Press, Melbourne.

Howes, J.; Bakewell, D. (1989). Shorebird Studies Manual. *Asian Wetland Bureau Publication No. 55*, Kuala Lumpur.

Hurley, D.E.; Jansen, K.P. (1977). The marine fauna of New Zealand: Family Sphaeromatidae (Crustacea: Isopoda: Flabellifera). *New Zealand Oceanographic Institute Memoir 63*: 1–96.

Inglis, G.J. (2003). The seagrasses of New Zealand. *In*: World Atlas of Seagrasses (eds. Green, E.P.; Short, F.T.), pp. 148-157. University of California Press, Berkley, USA.

Jones, M.B. (1983). Animals of the estuary shore. University of Canterbury, Christchurch, New Zealand.

Les, D.H.; Moody, M.L.; Jacobs, S.W.L.; Bayer, R.J. (2002). Systematics of seagrasses (Zosteraceae) in Australia and New Zealand. *Journal of Systematic Botany 27*: 468–484.

Little, C. (2000). The biology of soft shores and estuaries. Oxford University Press, Oxford.

McArdle, B.H.; Blackwell, R.G. (1989). Measurement of density variability in the bivalve *Chione stutchburyi* using spatial autocorrelation. *Marine Ecology Progress Series 52*: 245–252.

McClay, C.L. (1988). Brachyura and crab-like anomura of New Zealand. *Leigh Laboratory Bulletin 22*.

McCune, B.; Mefford, M.J. (1999). Multivariate analysis of ecological data, Version 4.0. MjM Software, Gleneden Beach, Oregon, USA.

Mercer, A.J. (1966). Turnstones feeding on human corpse. *British Birds 59*: 307.

Morrison, R.I.G.; Ross, R.K.; Niles, L.J. (2004). Declines in wintering populations of Red Knots in southern South America. *Condor 106*: 60–70.

Morton, J.E.; Miller, M.C. (1973). The New Zealand sea shore. 2nd Edition. Collins, Auckland.

Mueller-Dombois, D.R.; Ellenberg, H. (1974). Aims and methods of vegetation ecology. Wiley, New York.

Owen, K.L.; Sell, M.G. (1985). The birds of Waimea Inlet. *Notornis 32*: 271–309.

Parkinson, B. (2000). Common seashells of New Zealand. Reed, Auckland.

Pepping, M.; Piersma, T.; Pearson, G.; Lavaleye, M. (1999). Intertidal sediments and benthic animals of Roebuck Bay, Western Australia. NIOZ-report 1999-3. Netherlands Institute for Sea Research, Texel.

Pierce, R.J. (1987). Observations on distribution and numbers of double-banded plovers in Tasmania. *Stilt 11*: 32–35.

Piersma, T.; Hoekstra, R.; Dekinga, A.; Koolhaas, A.; Wolf, P.; Battley, P.; Wiersma, P. (1993). Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the western Wadden Sea in relation to food, friends and foes. *Netherlands Journal of Sea Research 31*: 331–357.

Piersma, T.; van Aelst, R.; Kurk, K.; Berkhoudt, H.; Maas, L.R.M. (1998). A new pressure sensory mechanism for prey detection in birds: the use of principles of seabed dynamics? *Proceedings of the Royal Society of London, B 265*: 1377–1383.

Powell, A.W.B. (1976). Shells of New Zealand. 5th edn. Whitcoulls, Christchurch.

Powell, A.W.B. (1979). New Zealand Mollusca: marine, land and freshwater shells. Collins, Auckland.

Rafaelli, D.; Hawkins, S. (1996). Intertidal Ecology. Chapman & Hall, London.

Read, G.B. (2004). (Compiler) Guide to New Zealand Shore Polychaetes. Web publication. http://biocollections.org/pub/worms/nz/Polychaeta/ShorePoly/NZShorePolychaeta_begin.htm. Accessed 16-12-2004.

Robertson, B.M.; Gillespie, P.A.; Asher, R.A.; Frisk, S.; Keeley, N.B.; Hopkins, G.A.; Thompson, S.J.; Tuckey, B.J. (2002). Estuarine environmental assessment and monitoring: a national protocol. Prepared for supporting Councils and the Ministry for the Environment, Sustainable Management Fund Contract No. 5096. Ministry for the Environment, Wellington.

Robertson, H.A.; Dennison, M.D. (1979). Feeding and roosting behaviour of some waders at Farewell Spit. *Notornis 26*: 73–88.

Rouse, G.W.; Pleijel, F. (2001). Polychaetes. Oxford University Press, London.

Sagar, P.M.; Schwartz, A.-M.; Howard-Williams, C. (1995). Review of the ecological role of the Black Swan (*Cygnus atratus*). *NIWA Science and Techonology Series No. 25*. NIWA, Christchurch.

Sagar, P.M.; Shankar, U.; Brown, S. (1999). Distribution and numbers of waders in New Zealand, 1983-1994. *Notornis 46*: 1–43.

Scheiffarth, G. (2001). The diet of Bar-tailed Godwits *Limosa lapponica* in the Wadden Sea: combining visual observations and faecal analyses. *Ardea 89*: 481–494.

Schuckard, R. (2002). Wader distribution at Farewell Spit, Golden Bay and Tasman Bay. *Occasional Publication No. 54, Department of Conservation, Nelson.*

Sevon, W.D. (1966). Sediment variation on Farewell Spit, New Zealand. *New Zealand Journal of Geology and Geophysics 9*: 60–75.

Short, F.T.; McKenzie, L.J.; Coles, R.G.; Vidler, K.P. (2001). SeagrassNet manual for scientific monitoring of seagrass habitat. Queensland Department of Primary Industries, Cairns.

Stark. J.D.; Boothroyd. I.K.G.; Harding. J.S.; Maxted. J.R.; Scarsbrook. M.R. (2001) Protocols for sampling macroinvertebrates in wadeable streams. New Zealand Macroinvertebrate Working Group Report No. 1. Prepared for the Ministry for the Environment. Sustainable Management Fund Project No. 5103. Ministry for the Environment, Wellington.

Sutherland, W.J. (1982). Do oystercatchers select the most profitable cockles? *Animal Behaviour 30*: 857–861.

Thrush, S.F. (1991). Spatial patterns in soft-bottom communities. *Trends in Ecology and Evolution 6*: 75–79.

Thrush, S.F.; Hewitt, J.E.; Pridmore, R.D. (1989). Patterns in the spatial arrangement of polychaetes and bivalves in intertidal sandflats. *Marine Biology 102*: 529–535.

Thrush, S.F.; Pridmore, R.D.; Hewitt, J.E.; Cummings, V.J. (1994). The importance of predators on a sandflat: interplay between seasonal changes in prey densities and predator effects. *Marine Ecology Progress Series 107*: 211–222.

van Gils, J.A.; Piersma, T.; Dekinga, A.; Dietz, M.W. (2003). Cost-benefit analysis of mollusc-eating in a shorebird. II. Optimising gizzard size in the face of seasonal demands. *Journal of Experimental Biology 206*: 3369–3380.

Walker, K. (1987). Wildlife in the Nelson region. *Fauna Survey Unit report 42*. Department of Internal Affairs, Wellington.

Williams, M. (1982). The demography of New Zealand's *Cygnus atratus* population. Second International Swan Symposium, Sapporo, Japan, 1980 (eds. Mathews, G.V.T.; Smart, M.), pp. 147–161. International Waterfowl Research Bureau, Slimbridge.

Winterbourn, M.J.; Gregson, K.L.D. (1989). Guide to the aquatic insects of New Zealand. *Bulletin of the Entomological Society of New Zealand 5*: 1–95.

Wright, A.E. (1978). Auckland University field club scientific trip to Farewell Spit, May 1977. *Tane 24*: 1–4.

Zharikov, Y. (2002). Feeding ecology of shorebirds (Charadrii) spending the non-breeding season on an Australian subtropical estuarine flat. Unpublished PhD thesis, University of Queensland, Australia.

Zwarts, L.; Blomert, A.-M. (1992). Why knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. *Marine Ecology Progress Series 83*: 113–128.

Zwarts, L.; Blomert, A.-M.; Ens, B.J.; Hupkes, R.; Van Spanje, T.M. (1990). Why do waders reach high feeding densities on the intertidal flats of the Banc d'Arguin, Mauritania? *Ardea 78*: 39–52.

Zwarts, L.; Cayford, J.T.; Hulscher, J.B.; Kersten, M.; Meire, P.M.; Triplet, P. (1996). Prey size selection and intake rate. *In*: The Oystercatcher: from individuals to populations (ed. Goss-Custard, J.D.), pp. 30-55. Oxford University Press, Oxford.

Zwarts, L.; Wanink, J. (1993). How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Netherlands Journal of Sea Research 31*: 441–476.

APPENDIX 1

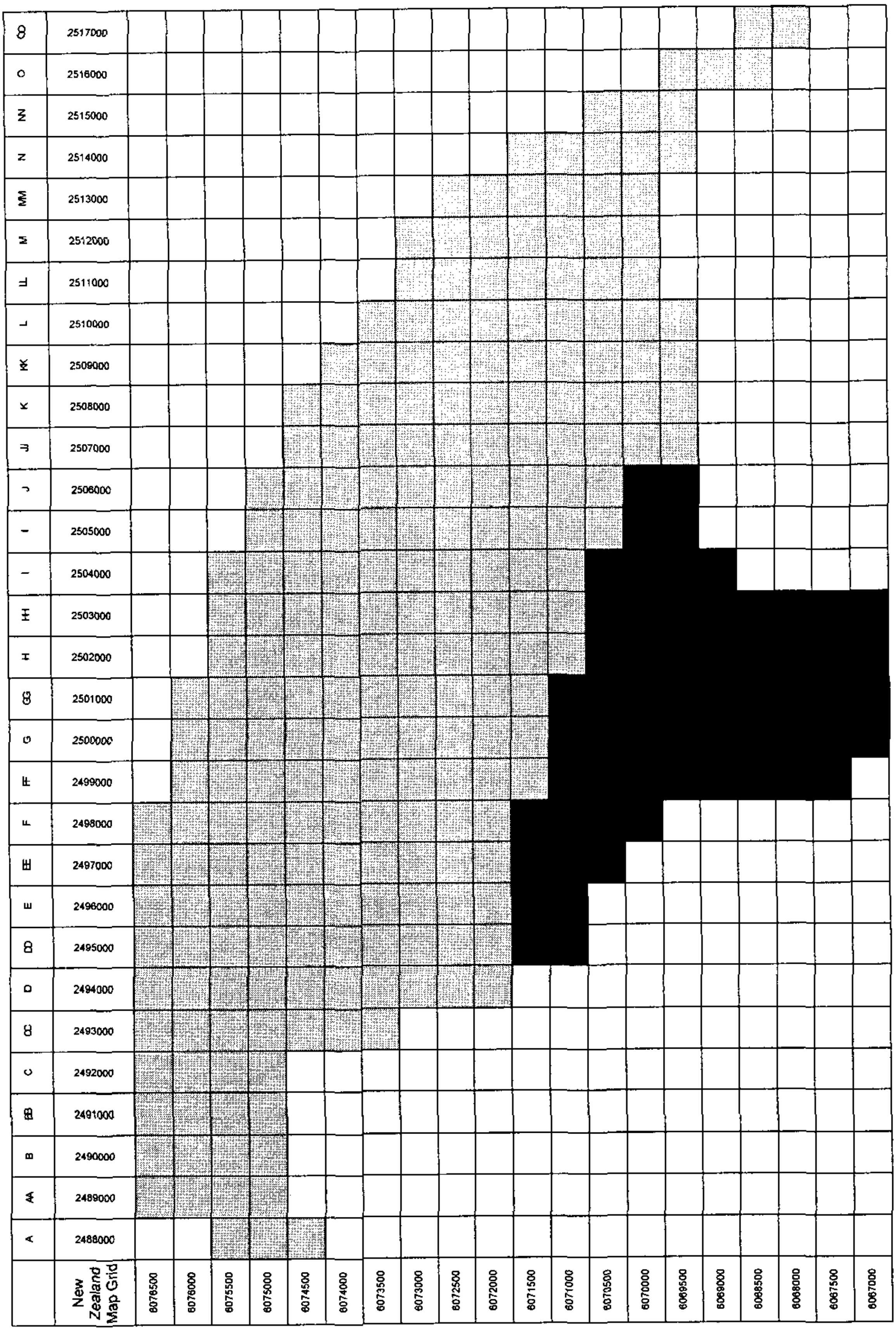

Figure 127: **Layout of proposed sampling scheme, with transect and sample coordinates. Light squares were planned to be reached by foot, dark by boat.**

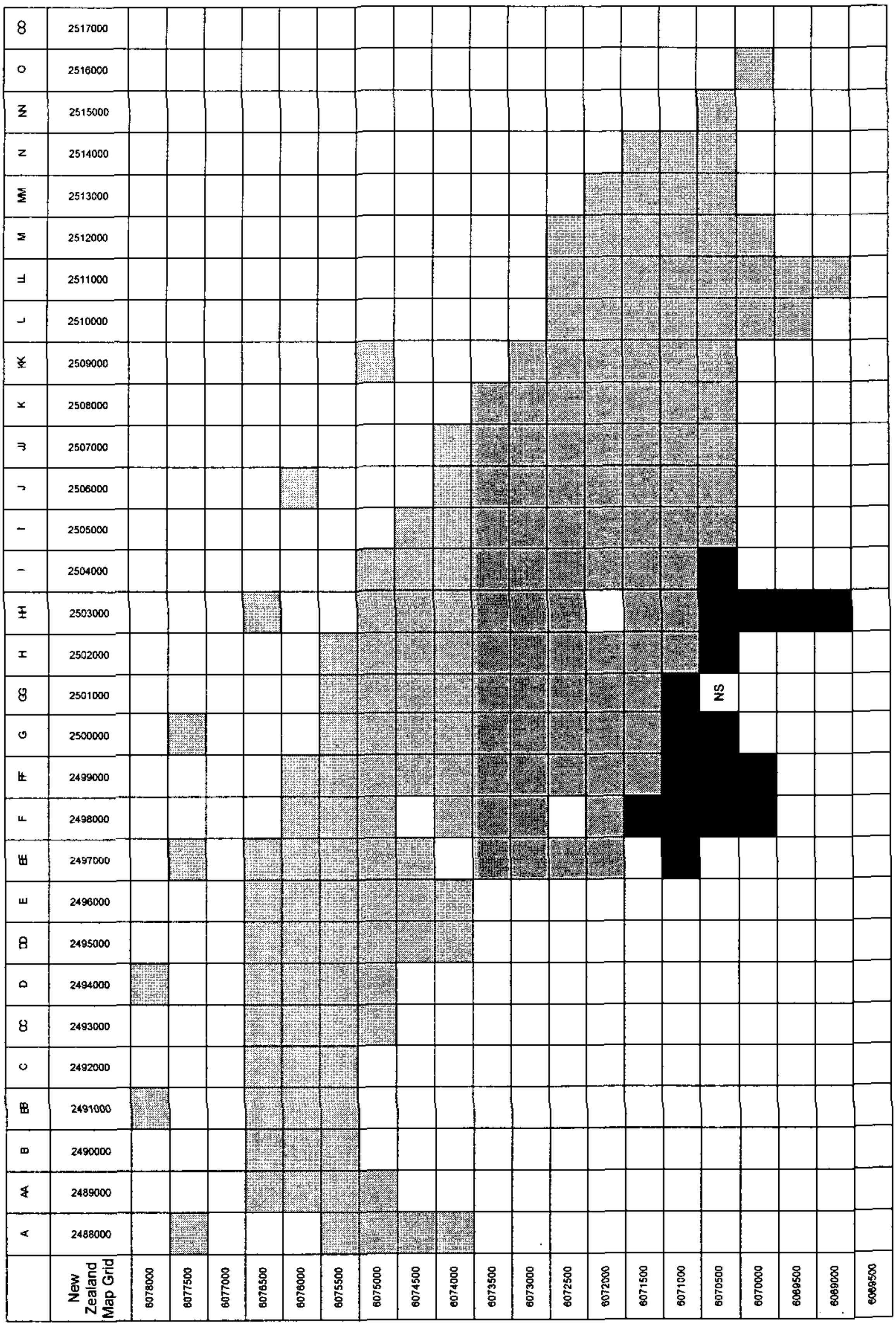

Figure 128: **Layout of achieved sampling. Light squares were reached by foot, dark by boat. NS, not sampled for safety reasons. White squares within the central flats represent channels. Beach samples are the eight squares to the north of the main samples.**

Appendix 2

Hinge-length relationship in *Nucula hartvigiana*

Lengths and two hinge measurements were made of 81 *Nucula hartvigiana* to develop predictive equations for estimating shell length from hinge dimensions. This is a common technique used in studies of the feeding behaviour of shellfish-eating birds.

Shell length was measured under a binocular microscope with an eyepiece micrometer, as were two measurements of the hinge. The first was the hinge height, the distance from the tip of the 'tongue' of shell that protrudes downwards, to the line where the exterior of the shell begins. The second measurement was the hinge+top height, the distance from the tip of the 'tongue' to the top of the shell visible when the shell is horizontal (see Dekinga & Piersma (1993) for illustrations of the equivalent measurements on *Macoma balthica* and *Cerastoderma edule*).

Least-squares regression was used to relate shell length to hinge height and hinge+top height, for both raw and log-transformed data. Results are given in Table A1.1

Table 34: Parameters from regressions of *Nucula hartvigiana* shell length on hinge measurements.

dependent	independent	intercept	exponent	$F_{1,79}$	P	R^2
length	hinge height	1.443	5.119	728.5	<0.001	0.902
length	hinge+top height	1.791	6.046	564.2	<0.001	0.877
log_length	log_hinge height	0.823	0.773	1366.1	<0.001	0.945
log_length	log_hinge+top height	0.899	0.721	1116.0	<0.001	0.934

The best fit was with the log-transformed hinge height, so that

$$\text{log\_hinge length (mm)} = 0.823 + 0.773 * \text{log\_hinge height (mm)}$$

To back-transform the generated log_length value to a raw value, raise $10^{\text{log\_length}}$