Persistence of infaunal polychaete zonation patterns on a sheltered, intertidal sand flat

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Abstract   Macrofaunal   polychaete   densities across a fine-sand intertidal flat in Pauatahanui Inlet, North Island, New Zealand, were examined seasonally from a pair of adjacent transects. Density patterns had shore-normal trends, despite weak tidal-cycle environmental gradients. Abundances frequently corresponded between transects separated by 15 m. *Capitella* sp., *Nicon aestuariensis*, and *Scolecolepides benhami* declined in density downshore,   whereas   *Heteromastus   filiformis* increased. *Microspio maori* and *Axiothella serrata* lacked strong trends. *Boccardia acus'* density was affected by the size and number of the bivalve *Chione stutchburyi*, its substratum. Basic zonation patterns of each species persisted over a 2 year period. Within the density concentrations seasonal cycles were apparent, with some population redistribution attributable to differential mortality (*H. filiformis*), to recruitment (*M. maori*, *A. serrata*), or to migration (*N. aestuariensis*, *S. benhami*).

Keywords   Polychaeta; infauna; benthos; intertidal environment; ecological zonation; population density; seasonal variations; Pauatahanui Inlet

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INTRODUCTION

A sedimentary beach has shore-normal gradients in environmental factors which may influence the abundance of infauna. The result is some form of zonation; a species-specific pattern of density trend with upper shore limits for the marine fauna, and often lower shore limits for specialist intertidal species. Zonation in intertidal infauna has frequently been described (see, e.g., Eltringham 1971; Newell 1979, for reviews). However, knowledge of relationships with environmental factors, the interactions of the biota, and the extent and causes of seasonal variation in zonation is less advanced than for the more readily observed hard shore situation.

On wide intertidal flats of enclosed shores where wave and current action is minimal, beach slopes below high water neap are likely to be gentle and relatively stable, with fine sediments and near-surface water tables. Except where local conditions create a shorewards grain-size gradient (Swinbanks & Murray 1981) or a tide-related salinity regime (Newell 1979), low tide physico-chemical gradients are unlikely to be pronounced. Shore-normal zonation of fauna would not be expected to be strongly developed. Alongshore environmental variation related to local physiography may be present, breaking consistent zonation into mosaic density patterns (e.g., Bassindale & Clark 1960).

This paper reports on the strength of zonation patterns in polychaetes on an apparently uniform, morphologically stable, sand flat within the sheltered waters of Pauatahanui Inlet (Fig. 1). It analyses the consistency of pattern over a short alongshore distance, and the extent of seasonal variation. The local physico-chemical regime is outlined, and its role in influencing zonation briefly discussed.

As yet, little quantitative information is available on the intertidal occurrence of New Zealand infaunal polychaetes. Sedimentary shore fauna descriptions which have some information relevant to polychaete zonation include those of Estcourt (1967 a, b), Morgans (1967 a, b), Wood

(1968), Morton & Miller (1973), Knox & Kilner (1973), Voice et al. (1975), Knox et al. (1977), Knox & Fenwick (1978), and Kilner & Akroyd (1978).

The *Capitella* sp. studied here, a member of the species complex formerly characterised as *C. capitata* (Fabricius), is diagnostically described in Read (1983).

METHODS

Sampling and processing

The sampling strategy aimed to assess population densities and to detect zonation. Two parallel transects were used, normal to the spring tide low water level and separated by 15 m (Fig. 1b). Each was a continuous 2 m wide strip, divided into 20 m zones; a subdivision of the shore sufficient to reveal pattern. Eight zones covered the intertidal flat (160 m), with an additional zone 8 m long at the shore end of the right transect (facing downshore) because of the angle of the shoreline (Zone 1a). Zone pairs 1–8 were at the same tide levels.

For stratified random sampling, random number tables were used to generate unique co-ordinates within each zone for sampling-unit position on a grid of 20 cm squares. Sampling co-ordinates were located accurately on site from permanent marker posts at each end of the transects, using surveyors' tape and a metre rule.

The samples were collected at 3-monthly intervals over a 12 month period, and each comprised 82 sampling-units (proportional allocation of 2 for Zone 1a, 5 each for Zones 1–8). Sampling dates were 14 November 1977, 8 February, 22 May, 21 August, and 16 November 1978. More frequent sampling was not possible because copious fine eel-grass litter made fauna extraction a lengthy process. Sampling-units were undisturbed cylindrical cores of surface area 50.30 cm², taken to 15 cm depth. The deepest burrowing species, *Axiothella serrata* and the bivalve *Tellina liliana*, were adequately sampled by that depth. Cores were sieved through a 500 μm Endecott sieve and the residue fixed in 10%, buffered, seawater formalin containing 20 mg l^{-1} rose bengal stain. A further sample of 24 cores (3 per zone) was taken 19 November 1979 on the left transect only, and processed through both 500 and 250 μm sieves. This sample assessed zonation after a further year, and also indicated juvenile zonation of species with spring settlement.

The fauna and plant litter from each core were separated from shell and sediment by repeated decantation (using 125 μm mesh to prevent attrition losses). Remaining fauna in the shell-sediment residue were extracted during sorting under a stereomicroscope and added to the organic residue. After any large eel-grass rhizomes were removed and examined, and before fauna extraction under the microscope, the organic residue was divided into 2 fractions by further sieving and stirring for 0.5 min in a 1 mm sieve. It was necessary to sub-sample the < 1 mm fraction obtained because of the large amount of fine litter present. A turntable-mounted 1 *l* bowl divided into 10 segments was used (modified from Kott's (1953) whirling sub-sampler). After rotation and settling two 1/10th subsamples chosen by random number were removed with a large-mouthed pipette. Litter settled volume (particles > 0.5 mm) and shell dry weight per core were recorded for most samples. The spionid *Boccardia acus* boring on the cockle *Chione stutchburyi* was assessed by counting the number of U-tubes present.

Statistical treatment

Within- and between-transect differences were examined by Mann-Whitney U and Kruskal-Wallis rank tests (2-tailed probabilities), and correlations examined using Spearman's r_s. Tests were corrected for ties (Gibbons 1971; Lehmann 1975). Tests stated as significant without specified probability levels refer to $\alpha = 0.05$. For other than left with right transect comparisons the 2 transects, or the zone pairs, were treated as a single sample, which for test purposes was regarded as a random sample taken from 1 statistical population of unknown distribution. This procedure was appropriate since the pairs rarely differed significantly (see Table 2; significant tests fewer than the expected number of Type I errors).

Parametric tests on small samples and overall analysis of variance were not used. (Optimum transformations derived by the procedures of Holt et al. (1980) and Downing (1979) were poorer than the (non-normal) original data when tested for normality (χ^2 goodness-of-fit test), were not consistent between samples, and were not improved by excluding sub-sampled data.) However, parametric tests were used to compare overall means of large samples ($n \geqslant 40$). Stratified sample statistics were calculated by standard procedures (Cochran 1977).

Physical environment

Beach profiles were surveyed ($\pm$ 1 mm 100 m⁻¹), and the heights determined relative to orthometric mean sea level. Mean tide levels are inlet mouth records (New Zealand Navy Hydrographic Office Chart 4632, 1975 print). On several days tidal observations were made at the sample site with tide poles to determine local conditions.
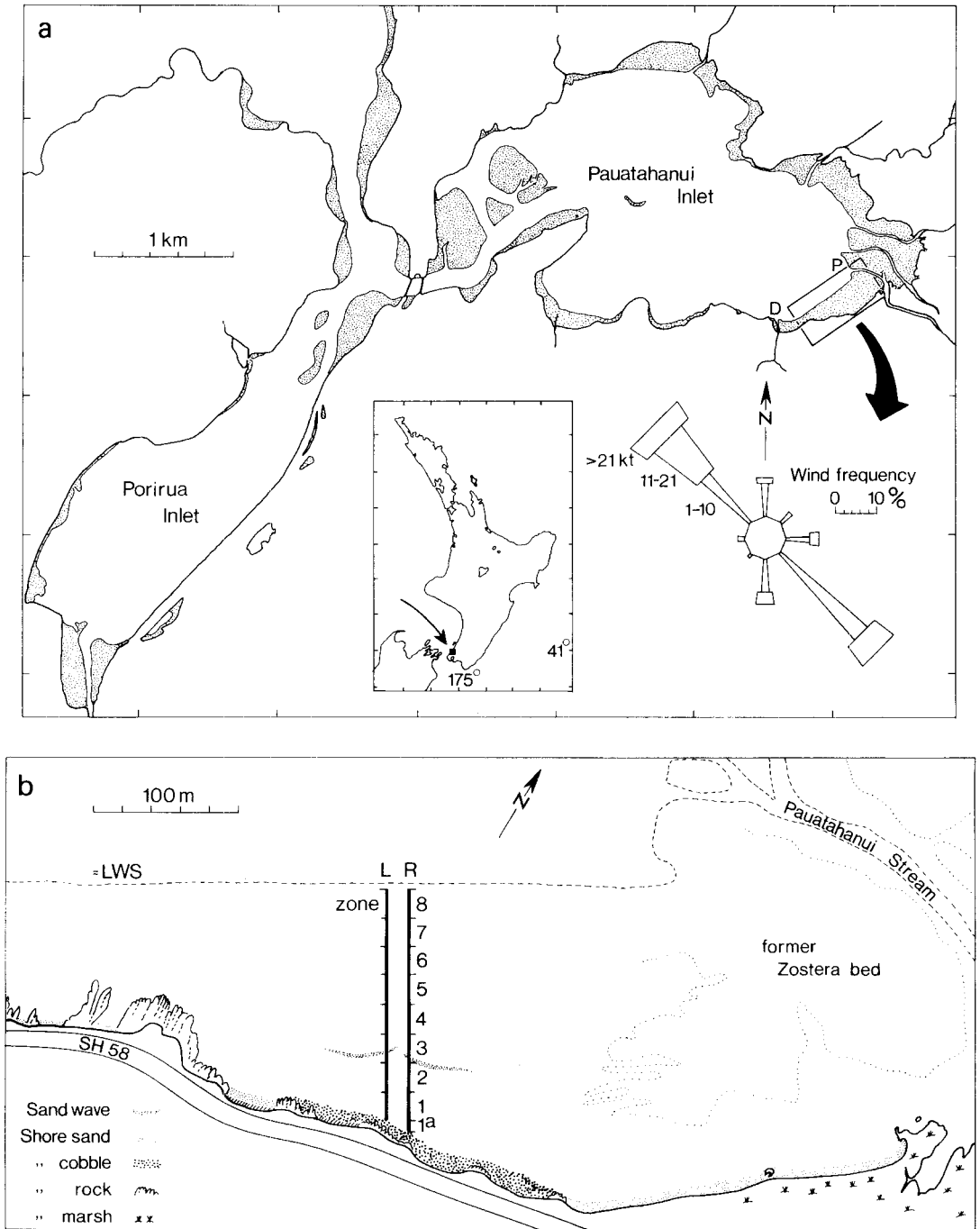
Fig. 1 Site maps. **a.** Porirua Harbour (= Porirua and Pauatahanui Inlets), showing sand flats exposed at approximate mean low water (adapted from Irwin 1978). D = Duck Creek, P = Pauatahanui Stream. Pauatahanui wind rose compiled by New Zealand Meteorological Service from 1976–78 hourly observations. **b.** Transect site morphology, 1979, compiled from plane table mapping and aerial photographs. Left and right transect strips are to scale. Right transect origin metric grid reference 267006E, 600958N; transect-line bearing 327°T.
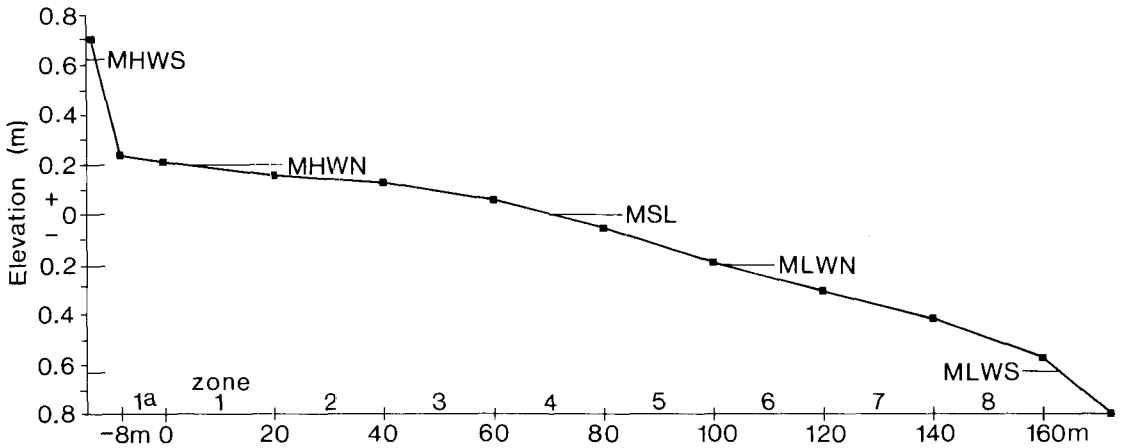
Fig. 2 Profile of transects' site. The levels of zones differed on average by less than 1 cm between the transect pair (March 1979).

Sediment samples of 2 random cores (35 mm diameter to 15 cm depth) were taken in each zone of each transect. Data presented are from a July 1980 sample set. Samples were prepared by settling and siphoning repeatedly with distilled water to remove salts, then dried and weighed. They were then dispersed with sodium hexametaphosphate, wet-sieved through 62 μm sieves, then dried and dry-sieved for 15 min in a mechanical shaker (sieves at 1 φ intervals, 0.5 φ for the 2-4 φ range). Cumulative percentage frequency curves were plotted on probability paper, and Folk & Ward (1957) statistics of mean size (M_z φ), sorting (σ_z φ), skewness (sk $_1$), and kurtosis (K_G) calculated.

ENVIRONMENT

Site location, profile, and sea level

The transects were sited in the southern segment of the wide, eastern inlet, intertidal flats, midway between the tidal channels of Pauatahanui Stream and Duck Creek (Fig. 1a), with origins at the edge of the cobble slope bordering the sand flat (Fig. 1b).

Tidal sea level change within the inlet is semi-diurnal and near symmetrical, with mean spring range 1.25 m and mean neap range 0.4 m (Fig. 2). The sand beach (overall slope 1:210), which begins about high water neap (HWN) level, has a low gradient upper slope (about 1:500, Zones 1-2), which is rapidly covered and uncovered, and a steeper lower slope (about 1:160, Zones 4-8). Observations revealed that meteorologically influenced fluctuation in local sea level and tidal range was substantial and frequent. Precise linking of zonation to

mean levels of the astronomical tide, or use of the critical-tide-level concept advocated by Swinbanks (1982) was therefore inappropriate.

Temperature and salinity

The range of monthly extreme maximum and minimum sediment temperatures (November 1977–February 1979, 12 cm depth) was 6.7–25.8°C, with a winter lowest maximum of 11.8°C and a summer highest minimum of 17.0°C. Upper shore temperatures tended to be about 1°C more extreme than those of the lower shore (Read 1983). The interstitial salinity regime was polyhaline (recorded range 21–32‰ at 5 cm depth, exceptionally 15‰ after prolonged rainfall). Interstitial salinities did not have an intertidal gradient, although lower-shore salinities were less variable (Read 1983).

Sediments

The site of the transects had less silty sediments than adjacent areas (McDougall 1976, 1978), probably as a consequence of having the longest fetch to the prevailing wind (Fig. 1a) of all inlet beaches. The sediments were borderline between fine and very fine sands (125 μm, 3 φ) and moderately well-sorted. Cumulative curves representing the range of variation downshore are given in Fig. 3a. Sediment statistics show that zonal trends were generally closely comparable between left and right transects (Fig. 3b–e). The sediments of Zones 2–8 had silt-clay content (Fig. 3f) of about 2% (3% Zone 6) and showed no trend in M_z values (mean 3.02 φ), but the sorting improved and skewness and kurtosis decreased downshore. In the lowest zone the
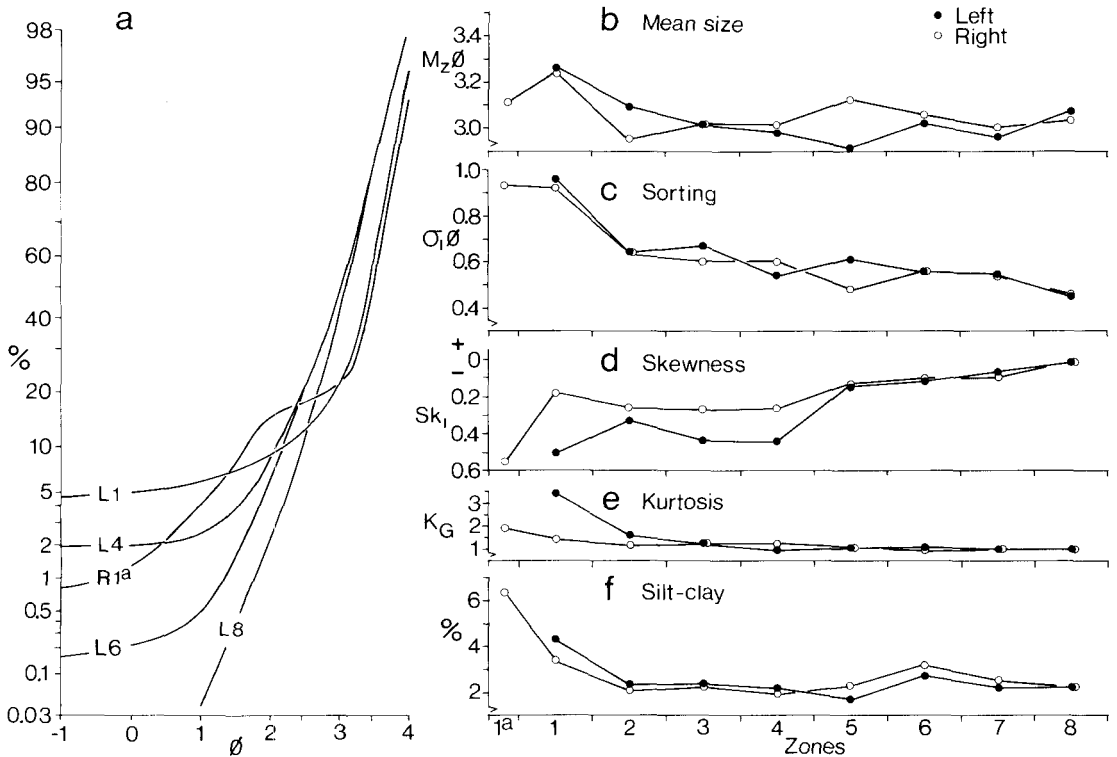
Fig. 3 Sediment grain-size etc. **a.** Representative cumulative percentage probability curves of grain size. L1 = Left transect Zone 1, and so on. **b–f.** Sediment statistics for both transects.

sediments were well-sorted with a near-symmetrical normal distribution.

Sediments within 20–30 m of the cobble shore (M_z 3.1–3.25 ϕ) were finer than those downshore and had silt-clay levels of 3–6%. The mixed distribution of right Zone 1a (Fig. 3a) indicates a submode of coarser sand.

The higher coarse skew occurring in Zones 1–4 was attributable to shell content, which decreased downshore, markedly so from Zone 5 (Fig. 4c). Plant litter content in the sediment, mainly eelgrass, increased downshore to Zone 7 (Fig. 4c), although live *Zostera capricorni* was absent from the area subsequent to a decline of the plant in 1976–77. The redox potential discontinuity level as indicated by an olive-grey to dark-grey colour change (Smith & McColl 1978) was an irregular mottled layer 2–4 cm deep, without consistent zone or seasonal changes. During most of the sampling period the beach surface was featureless, without the sand waves of 1976 (Pickrill 1979), but in early 1979 a solitary shell-covered sand wave grew at Zone 4 and slowly migrated towards the shore (Fig. 1b).

At low tide the water table remained at or very near the sediment surface, which rarely dried. During emersion, water content at 5 cm depth (as weight loss on drying, measured in spring) did not change under overcast conditions, and decreased only by 8% from saturation in clear weather.

RESULTS

Macrofaunal density

Forty-seven species were collected, including 22 species of polychaete (Read 1983). The assemblage was dominated by deposit-feeders, which comprised 95% of the individuals and 32 species, including 8 of the 9 most common species. The 14 species present in more than 10% of cores are ranked in Table 1 according to percentage occurrence and mean overall density over the intertidal strip. Nine species are polychaetes. The small spionid *Microspio maori* was the most frequent and abundant species present, with 20% higher occurrence than next ranked *Capitella* sp. (cf. also Fig. 4). Species with wide intertidal distributions gener-

Table 1 Mean overall density, percentage occurrence, and feeding type of macrofauna with > 10% occurrence in 500 μm sieve sample series, November 1977 to November 1979. Species ranked by mean overall density and percentage occurrence in 434 cores (*Boccardia acus* 270 cores, nemerteans 393). Non-annelids annotated: Mollusca, M; Rhynchocoela, R. Feeding types: D, deposit-feeding; C, carnivorous; S, suspension-feeding.

Species	Density		Occurrence		Feeding type
	Rank	x̄ m²	Rank	%	
Microspio maori Blake	1	4126	1	97.5	D + S
Capitella sp.	2	1939	2	77.6	D
Heteromastus filiformis (Claparède)	3	1777	5	65.1	D
Axiothella serrata Kudenov and Read	4	719	3	76.0	D
Boccardia acus (Rainer)	5	588	6	47.4	D + S
Chione (Austrovenus) stutchburyi (Wood) (M)	6	388	4	66.6	S
Scolecolepides benhami Ehlers	7	386	7	47.3	D + S
Nicon aestuariensis Knox	8	227	8	45.0	D + C
Tellina (Macomona) liliana Iredale (M)	9	107	9	44.5	D
Nemertean sp. 2 (R)	10	86	10	22.9	C
Paradoneis sp.	11	86	12	13.6	D
Boccardia syrtis (Rainer)	12	66	13	12.7	D + S
Oligochaete sp.	13	59	14	11.8	D
Nemertean sp. 1 (R)	14	36	11	14.0	C

ally had occurrence rankings above density rank (e.g., *Axiothella serrata*, the bivalve *Chione stutchburyi*, nemertean sp. 1).

Zonation

The average zonation patterns for each of the 7 most common (major) polychaetes and for all other (minor) polychaete species combined are presented in Fig. 4. The most strongly zoned species were *Heteromastus filiformis* and *Scolecolepides benhami*, concentrated on the lower and upper shore respectively. *Capitella* sp. dropped steadily in density below mid-shore Zone 4, *Nicon aestuariensis* peaked in upper Zone 2 then decreased downshore, and *Boccardia acus* increased downshore to a peak in Zone 6, but had very low Zone 7 density. *Microspio maori* and *Axiothella serrata* were distributed across the flat without pronounced pattern. *M. maori* was numerically dominant in all zones except 6 and 8, where *H. filiformis* was more dense (Fig. 4b). The minor polychaete species mainly occurred on the lower shore, especially in Zone 8 (Fig. 4).

The seasonal changes in overall density of each of the major species are plotted in Fig. 5, and the changes in zone density for each left and right transect separately are shown in Fig. 6–10. High densities mostly occurred in autumn-winter samples (May and August).

Comparison between left and right transects

For each species the similarity of densities between equivalent zones in the 2 transects 15 m apart indicated whether apparent trends or zonation patterns were more widely spread than the 2 m strip of 1 transect; thus detecting the importance of shore-normal trends compared to random density variations. Significant positive correlation existed between seasonal zone means of the left and right transect for all the major species except *Boccardia acus* (Table 2; and correlations of the *B. acus* substratum, *Chione stutchburyi*, were highly significant).

The left and right transect zone distributions were generally not significantly different in each sample (Table 2), nor were the transect pair means. The most strongly zoned species, *Heteromastus filiformis*, showed no significant variation between equivalent left and right transect zones. *Microspio maori* was the only species to have more than 2 zone pairs, of the total of 40, differing significantly. However, there was no overall left- to right-zone inequality (sign test).

Zonation patterns and seasonal changes

Density changes down the shore of the 7 major species were tested for significance (Table 3), as were correlations (at sampling-unit level within zones of high abundance) with distance downshore and litter volume, which respectively represent tide level
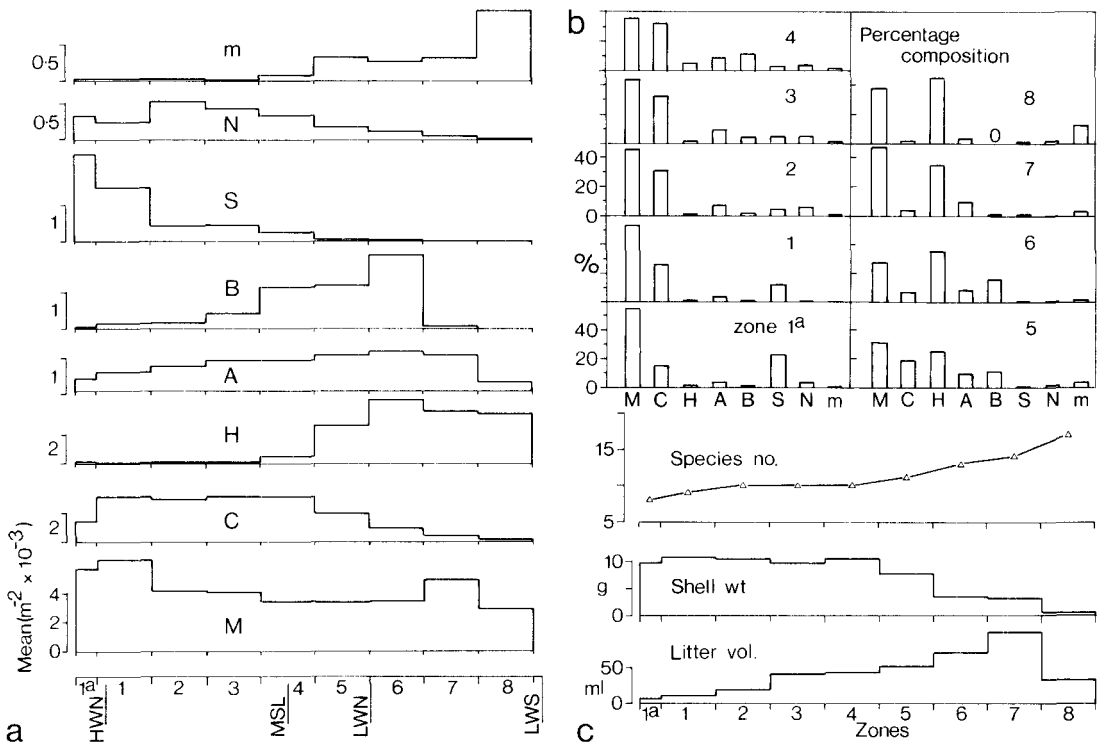
Fig. 4 Overall means per zone (combined data for all transects, November 1977 to 1978 samples). **a.** Density zonation (as thousands per m²). **b.** Percentage composition within zones (percentage of total individuals). **c.** Total number of polychaete species per zone, and zone means of litter volume and shell weight per core (754 ml original volume). M = *Microspio maori*, C = *Capitella sp.*, H = *Heteromastus filiformis*, A = *Axiothella serrata*, B = *Boccardia acus* (May to Nov.), S = *Scolecolepides benhami*, N = *Nicon aestuariensis*, m = minor species summed.

and a potential food resource (Table 4). Significant within-zone density changes between seasonal samples are listed in Table 5.

Microspio maori did not have a strong gradient in density within the intertidal range sampled (Fig. 6a), but between left and right transects there were some concordant densities (e.g., high densities in Zones 3 and 7 in November 1977), and there was zone-pair correlation between transects (Table 2). Significant unevenness in overall zonation occurred only in August and November 1978 (Table 3). Compared to other species *M. maori* had a large number of significant seasonal changes within zones (Table 5), but these changes all followed the overall population trends. The density increases in Zone 1 detected in May and August suggest higher recruitment or superior survival within that zone. *M. maori* was negatively correlated to distance downshore, especially in autumn-winter samples when there were high upper shore densities, and had

almost no correlation to the amount of buried plant litter present (Table 4). The distribution of 250–500 μm sieve fraction 'juveniles' in November 1979 (Fig. 6a) was very similar to the > 500 μm fraction.

Capitella sp. declined in density from mid shore (Fig. 6b). The upper shore was significantly denser in all samples (Table 3) and very few individuals occurred in Zone 8. Density variation within Zones 1–5 was significant in November 1977 and 1978. *Capitella* sp. was negatively correlated with distance downshore, especially in autumn-winter samples, and negatively correlated with plant litter (Table 4). Within individual zones significant seasonal density changes again followed the overall population changes (Table 5). The densities within Zones 7 and 8 dropped significantly between November and February samples and remained at low levels subsequently. As for *Microspio maori*, the 250–500 μm 'juveniles' of November 1979 did not differ in distribution from the 'adults'.

Table 2 Tests of transect pair (left and right) correlation and differences for each major species. Significant tests indicated as * ($P < 0.05$), ** ($P < 0.01$), and *** ($P < 0.001$), with non significant tests blank, and no data as −.

Test	Microspio maori	Capitella sp.	Heteromastus filiformis	Axiothella serrata	Boccardia acus	Scolecolepides benhami	Nicon aestuariensis
[1]Correlation of zone means	***	***	***	***		***	***
[2]Zone pair differences Nov.	zone 8*	zone 4*		zone 2*			
Feb.	zone 1*	zone 1**				zone 1*	
May	zone 4*				−	zone 1*	
Aug.	zones 1**,				−		
Nov.	2*, & 6*				zone 6*		zone 3*

[1]Spearman's r_s (maximum $n = 40$). Correlated over Zones 1–6 only for *Nicon aestuariensis* and *Capitella* sp., Zones 4–8 for *Heteromastus filiformis*, 3–6 for *Boccardia acus*, 2–6 for *Scolecolepides benhami* (zone 1 for this species a special situation discussed later), so that paired zeroes did not exaggerate correlation.

[2]Mann-Whitney U-test ($n = 10$). The test is not sensitive to differences inflated by one extreme value.

Heteromastus filiformis was uncommon above Zone 4 and had significantly uneven zonation on the lower shore (Fig. 7a, Table 3). The dense populations in Zone 8 in November 1977 and subsequently Zone 6 in May, August, and November 1978 are of interest. The density in Zone 8 significantly declined from November to May, and the February-May decline was against the overall population trend (Table 5). Thus in Zone 8 below average survival/recruitment occurred, whereas in Zone 6 the converse occurred, and it replaced Zone 8 as the densest zone. The correlation with downshore distance within Zones 5–8 reversed in sign from positive to negative in conjunction with this change (Table 4). *H. filiformis* was significantly positively correlated with plant litter (Table 4).

Axiothella serrata did not show consistent zonation patterns except in Zone 8 where densities were low (Fig. 7b, Table 3). Zone to zone changes within seasonal samples were otherwise erratic, and left-right zone pairs were not closely matched, although rarely significantly different, and with highly significant overall correlation (Table 2). The seasonal within-zone changes followed the overall density changes (Table 5), with the appearance of a new age group resulting in a large pattern change between November and February (Fig. 7b). *A. serrata* had significant positive correlation with downshore distance over Zones 1–7, and negative correlation when low density Zone 8 was included. Correlation with litter was positive, but became non-significant without Zone 8 densities (Table 4). The November 1979 250–500 µm fraction contained large numbers of early juveniles from a recent spawning. These juveniles were denser on the lower shore.

Zone-specific influences on the density of *Axiothella serrata* and *Microspio maori* have been demonstrated, but correspondence in zone to zone trends between these 2 species abundant across the whole transect was not apparent. Increases and decreases between zones agreed in less than half the possible number of occasions (24 of 60 excluding Zone 8, 33 of 70 all zones). Correlation at the sampling unit level was inconsistent in sign, and significant only in 1 sample (positive in November 1977). Thus there is no indication that the factors operating against survival were the same for both species.

Boccardia acus is a facultative epizoon of the cockle, *Chione stutchburyi*, boring a U-tube into the shell lying buried just below surface, and constructing a short sand-grain tube-extension near the siphons. *B. acus* was significantly zoned, increasing gradually in density downshore to a Zone 6 peak, thus correlating with distance downshore and litter (Fig. 8, Tables 3, 4). The number of *B. acus* per

Table 3 Tests of significant zonation using Mann-Whitney U-test (MWU) and Kruskal-Wallis test (KW) on combined left and right transect data (i.e., $n = 10$ zone^{-1}). Significant tests indicated as * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$), with non significant tests blank, and no test as –.

Species	Zones	Test	Samples				
			Nov. 77	Feb. 78	May 78	Aug. 78	Nov. 78
Microspio maori	1+2:3+4:5+6:7+8	KW					***
	1–4:5–8	MWU				*	
Capitella sp	1:2:3:4:5	KW	***				*
	1–4:5–8	MWU	***	***	***	***	***
Heteromastus filiformis	5:6:7:8	KW	***	***	***	***	***
	1–4:5–8	MWU	***	***	***	***	***
Axiothella serrata	1+2:3+4:5+6:7+8	KW	**	**			**
	1–4:5–8	MWU	***	*			
Scolecolepides benhami	1–4:5–8	MWU	***	***	***	***	***
Nicon aestuariensis	1–4:5–8	MWU	***	***	***	***	***
Boccardia acus	1+2:3+4:5+6:7+8	KW	–	–	***	***	***
	1–4:5–8	MWU	–	–			

Fig. 5 Seasonal variation of major species in overall means per transect pair. a. Thousands per m². b. Hundreds per m². Plot labels as in Fig. 4. See Table 5 for confidence limits.
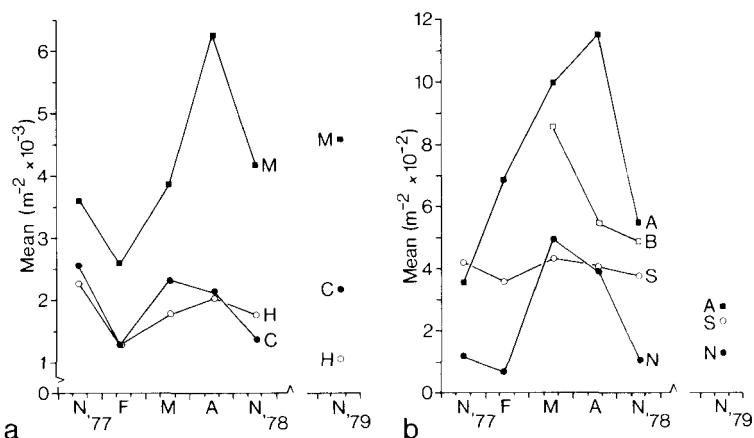
cockle was also highest in Zone 6, whereas *C. stutchburyi* was most dense in Zones 3 and 4. Overall seasonal density changes were not significant (Table 5). *B. acus* density per m² was highly correlated with cockle density ($P < 0.0001$, correlation excluding cockle zero occurrences), but may also have been influenced by the size distribution of cockles and hence the actual area of habitat available for colonisation. The *B. acus* link with cockle size was apparent in a large collection of cockles available from June–July 1976 random samples between Zones 3–6. The size of all cockles over 5 mm length was noted (1 mm classes) together with *B. acus* counts. Cockles of length up to 11 mm had no *B. acus*. All size classes to 28 mm (maximum size 32 mm) had some individuals free of *B. acus*, with overall 42.0% free (32.2% of > 11 mm, total $n = 628$), including 2.2% with old boring scars. *B.*

acus density per cockle was highly correlated with increasing cockle size ($r_s = 0.44$, $P < 0.0001$, $n = 550$).

Scolecolepides benhami occurred in a high density band at the upper edge of the sand flat, with few individuals below Zone 4 (Fig. 9a). The density increased to a peak within 4 m of the cobble zone at the edge of the sand flat, whereas densities of *Microspio maori*, presented for comparison, were highest 12–20 m downshore (Fig. 9b). Comparisons of *S. benhami* density between transects did not often show significant differences (Table 2) because the band of high density was so narrow. Overall population densities did not change significantly during sampling, but *S. benhami* did have a significant density increase between August and November samples in Zone 2, occurring against the trend of a slight overall decrease (Table 5).
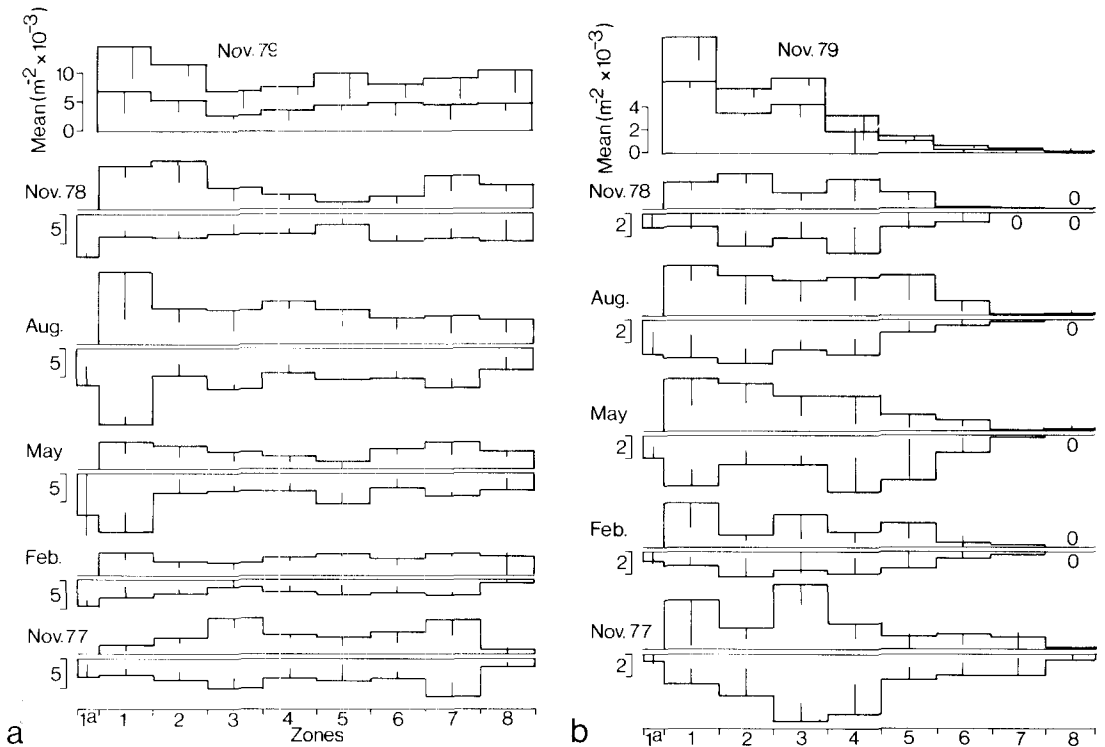
Fig. 6 Seasonal zonation of **a.** *Microspio maori.* **b.** *Capitella sp.*, as zone means (thousands) per m². Left (top) and right (bottom) transects plotted separately for each sample, and variation of zone means indicated as vertical lines 2SE in length (for clarity arising from inner side of the mean only, or from the baseline when greater than the mean). For November 1979 the additional 250 µm sieve density is indicated.

Nicon aestuariensis was significantly more dense on the upper shore with very few individuals in Zone 8 (Fig. 10, Table 3). The substantial May population increase was of juvenile recruits which appeared densely in Zones 2–4, but by August became more evenly distributed with a significant increase in Zone 1 against the trend overall of slight decline (Table 5). The remaining significant within-zone changes followed the overall density changes. Left-right transect correspondence was good, with only the February Zone 3 pairs differing significantly (Table 2). *N. aestuariensis* was negatively correlated with downshore distance and with litter (Table 4).

Zonation of the 4 commonest minor polychaete species is shown in Fig. 10b. *Paradoneis* sp. and *Cirratulus* sp. occurred mainly in Zone 8 but extended upshore to Zones 6 and 7 respectively. *Boccardia syrtis* was present from Zones 2–8 and was significantly more abundant on the lower shore (MWU, $P < 0.01$). *Orbinia papillosa* (Ehlers) occurred mainly on the middle to lower shore.

Polychaetes restricted to Zone 8 were *Prionospio aucklandica* Augener, *Sphaerosyllis* sp., *Goniada* sp., *Glycinde dorsalis* Ehlers, and *Glycera lamelliformis* McIntosh. *Desdemona* sp. and *Microphthalmus paraberrans* Hartmann-Schröder occurred in Zones 6–8, *Aonides trifida* Estcourt occurred only in Zones 5–6, *Scoloplos cylindrifer* Ehlers in Zones 3–4, *Ceratonereis* sp. in 1–1a, generally close to the cobble shore, and *Perinereis vallata* (Grube) in every zone.

DISCUSSION

Zonation pattern

At the Pauatahanui site upshore environmental gradients were not pronounced, because water content of the sediments remained near saturation. Nevertheless, both faunal density variation and the small changes in sediment characteristics had shore-normal orientation. Species abundances varied
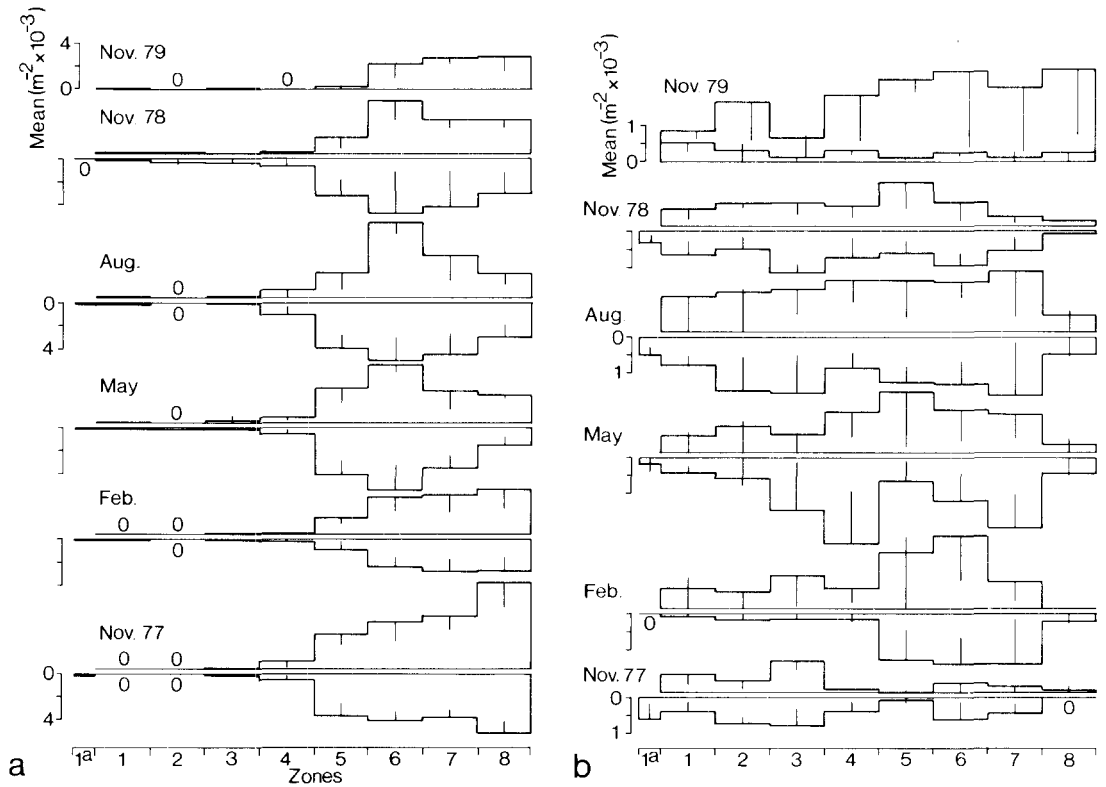
Fig. 7 Seasonal zonation of **a.** *Heteromastus filiformis*, **b.** *Axiothella serrata*. Zone means as thousands per m², and other conventions as in Fig. 6. 250 μm sieve density for *H. filiformis* was zero.

between zones downshore, whereas differences in abundances at 15 m separation of transects were minor and species not obviously zoned correlated between transects. Shore-normal patterns in the latter species would not have been detected with a solo transect.

Microspio maori, Axiothella serrata, and the low density *Perinereis vallata* were the only polychaetes with no strong zonation trend over the tidal range sampled. The upper distribution limits of the first 2 species elsewhere in the inlet lie at an elevation of about 30 cm above the truncated upper shore of the transect site. The density of *M. maori* sometimes showed good correspondence between the transect pair at several beach levels, suggesting shore-normal substratum or hydrodynamic variations did have an effect on mortality or settlement rates.

Axiothella serrata showed the least structured distribution pattern. Although densities were positively correlated with distance downshore to Zone 7, *A. serrata* had low densities in the transiently

emersed Zone 8. Plant litter content of the sediment similarly dropped sharply in Zone 8, but may not have been an important influence, as *A. serrata* correlation to litter was not significant over Zones 1–7. *A. serrata* tolerates continual immersion for many months in laboratory conditions, but in Zone 8 could be more readily accessible to demersal predators.

Zonation of *Heteromastus filiformis*, and of many of the minor polychaete species occurring only on the lower shore, may be a consequence of the longer emersion period and greater variability occurring on the upper shore. They may be predominantly subtidal species whose distributions can extend from the shallows into the lower intertidal. Some previous reports of *H. filiformis* in the intertidal also suggest peak abundance on the lower shore (Estcourt 1967b; Maurer & Aprill 1979). *H. filiformis* has wide salinity tolerances, and a wide range of sediment grades are occupied (Estcourt 1967b; Wolff 1973; Kinner & Maurer 1978), whereas at the Pauatahanui site intertidal changes in salinity

Table 4 Species correlations with downshore distance, and litter content of sediment (Spearman's r_s values, *($P < 0.05$), **($P < 0.01$), ***($P < 0.001$)).

Correlation pair		[3]Zones	Samples ($r_s$values)
[1]Distance	*Microspio maori*	1–8	all (−0.15**), Nov. 1977 & 78 (−0.10), May & Aug. (−0.26**)
	Capitella sp.	1–5	all (−0.19**), Nov. 1977 & 78 (−0.13), May & Aug. (−0.25*)
	Heteromastus filiformis	5–8	all (0.09), Nov. 1977 & 78 (0.25**), May & Aug. (−0.36***)
	Axiothella serrata	1–7	all (0.19**)
	Axiothella serrata	1–8	all (−0.10*)
	Nicon aestuariensis	1–6	Nov. 1977 & 1978 & Feb. (−0.45***), May & Aug. (−0.27**)
	Boccardia acus	1–6	May, Aug., Nov. 1978 (0.47***)
[2]Litter	*Microspio maori*	1a–8	all (−0.03)
	Capitella sp.	1a–5	all (−0.28***)
	Capitella sp.	1a–8	all (−0.24**)
	Heteromastus filiformis	4–8	all (0.30***)
	Axiothella serrata	1a–8	all (0.13*)
	Axiothella serrata	1a–7	all (0.11)
	Nicon aestuariensis	1a–6	May & Aug. (−0.13), Nov. 1977 & 1978 (−0.46***)
	Boccardia acus	1a–6	May, Aug., Nov. 1978 (0.34***)

[1]Distance from start of Zone 1 as 5 m interval classes. Sampling units, all having known co-ordinates, were grouped into these classes.
[2]Litter per sampling unit retained on 500 µm sieve (settled volume). Data of all samples except February and right transect November 1977.
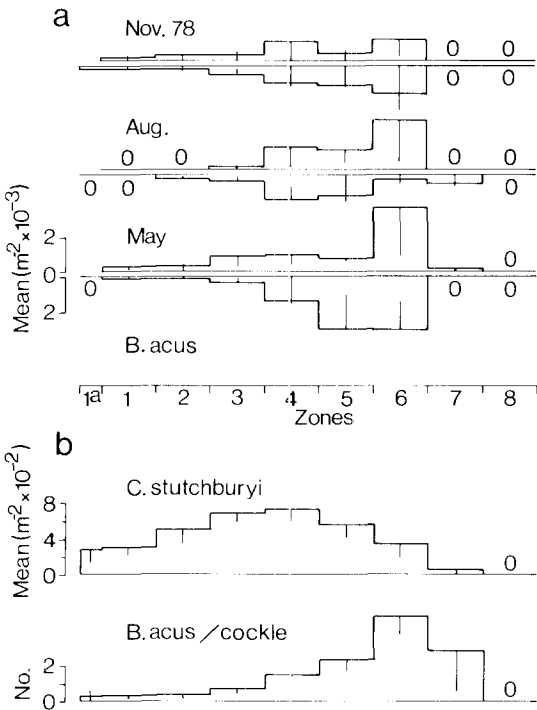[3]Effects from major zonation trends of species were minimised by using restricted ranges.

Fig. 8 *Boccardia acus* variation in zonation and the *B. acus* relationship to *Chione stutchburyi*. Conventions as in Fig. 6. **a.** *B. acus* zone means as thousands per m². **b.** Overall zone means for *C. stutchburyi* (hundreds per m², and *B. acus* (numbers per cockle), using summed data of all transects.

regime and sediment characteristics were relatively minor. *H. filiformis* was positively correlated with litter volume, and small-scale aggregations in patches of buried litter were sometimes observed. Its association with enriched and anaerobic sediment has often been noted (Pearson & Rosenberg 1978; Knox & Fenwick 1981; and references therein).

Scolecolepides benhami, *Nicon aestuariensis*, and *Capitella* sp. were all more abundant on the upper shore. *S. benhami* and *N. aestuariensis* have been recorded in the upper reaches of estuaries and tolerate extremely low salinities (Estcourt 1967a, b; Knox 1976; Knox et al. 1978; Kilner & Akroyd 1978). A possible linkage of zonations with salinity regime was further suggested by the occurrence in Zone 1 only of *Ceratonereis* sp., a known upper estuarine species (Read 1974). There was, however, no pronounced intertidal salinity gradient in the interstitial waters at the site; the data indicate only that the salinity of overlying water drops less frequently on the lower shore, probably because below the neap tide range the surface water of lowest salinity contacts sediment surfaces less frequently (Read 1983).

Scolecolepides benhami does tolerate fully marine salinities. The species occurs occasionally at low densities on sheltered beaches (Morgans 1967b; author's unpub. data). (Morgans' (1967a) report of *S. benhami*, "whose abundant tubes form a sort of 'turf' below MLWS" on an exposed beach (Ingles Bay, Kaikoura) may be a misidentification, as *S.*
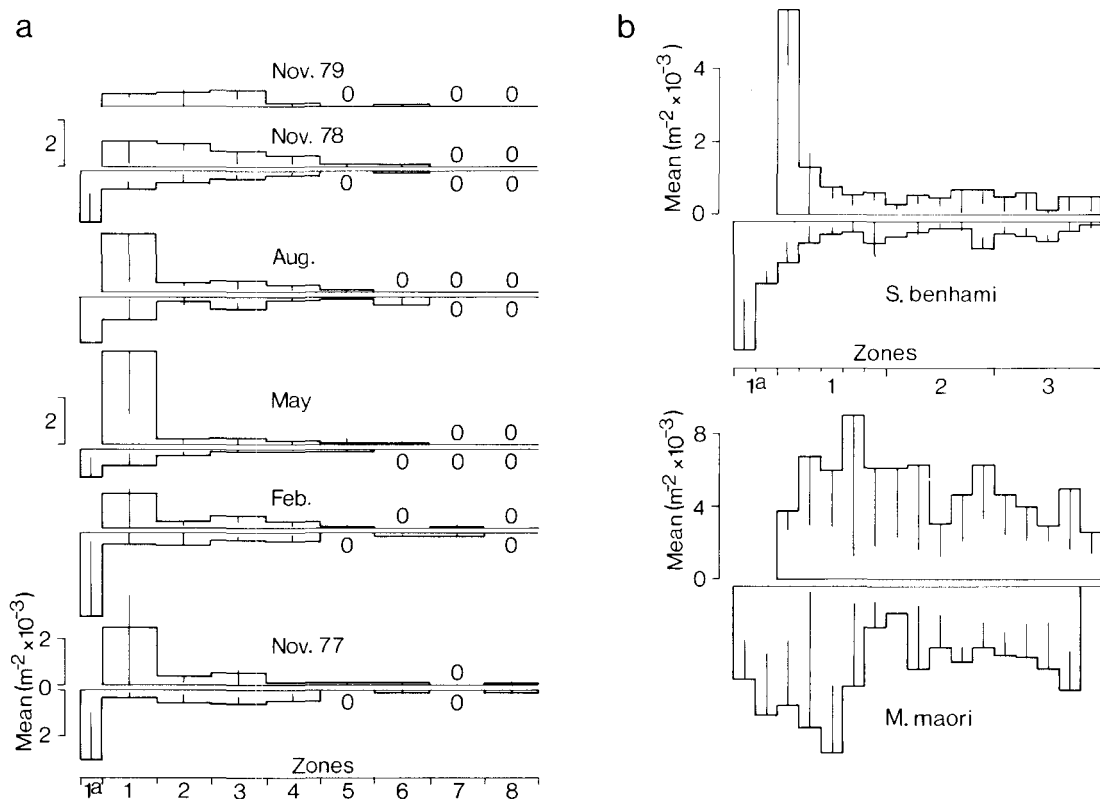
Fig. 9 Zonation of *Scolecolepides benhami*. Conventions as in Fig. 6. **a.** Seasonal zonation as zone means (thousands) per m². **b.** Density trends within zones 1a–3 of *S. benhami* compared to *Microspio maori*. Mean densities are thousands per m² within subzones 4 m long, using sum of all data.

benhami does not form a tube.) Its distribution can also extend to the highest shore levels that are only briefly or even infrequently covered by the tide (Estcourt 1967b; and personal observation). High densities in Zone 1 and 1a of *S. benhami* relate to the proximity of the cobble zone rather than to tide level (Fig. 9b).

Nicon aestuariensis has not been recorded outside estuarine environments. Much higher adult densities (to 6000 m²), have been found elsewhere in oligohaline conditions (Avon-Heathcote Estuary, Estcourt 1967a b; Westshore Lagoon, Knox et al. 1978), and Estcourt (1967b) reported a change to low densities in salinities similar to the Pauatahanui regime. Pauatahanui conditions may not be optimal.

Capitella spp. are more usually found in the shallow subtidal. Dauer and Simon (1975) report a *Capitella* sp. similarly zoned in the upper intertidal in a polyhaline sheltered environment (Tampa Bay, Florida). *Capitella* sp. had a negative correlation with litter volume and an opposite trend in zon-

ation. In contrast, studies showing that *Capitella* species can be cultured on macrophyte detritus (Foret 1975; Tenore 1975) and adjust well to organically enriched situations (Reish 1960; Pearson & Rosenberg 1978) suggest correlation should be positive. *Capitella* sp. occupies the wave-mixed surface sediment at Pauatahanui, whereas the litter distribution reported here is predominantly that of material buried more deeply.

Boccardia acus zonation differed from the density zonation of *Chione stutchburyi*, which is its only suitable substratum at Pauatahanui, although elsewhere the worm also bores on other substrata (Read 1975). *B. acus* density also relates to cockle size. The largest cockles tend to occur low on shore beyond the zone of peak cockle density (Richardson et al. 1979; and personal observation). Although size data were not recorded in relation to transect level, a shift in the cockle size distribution with more larger individuals present is the most likely explanation of Zone 6 *Boccardia acus* density peaks (per m² and per cockle).
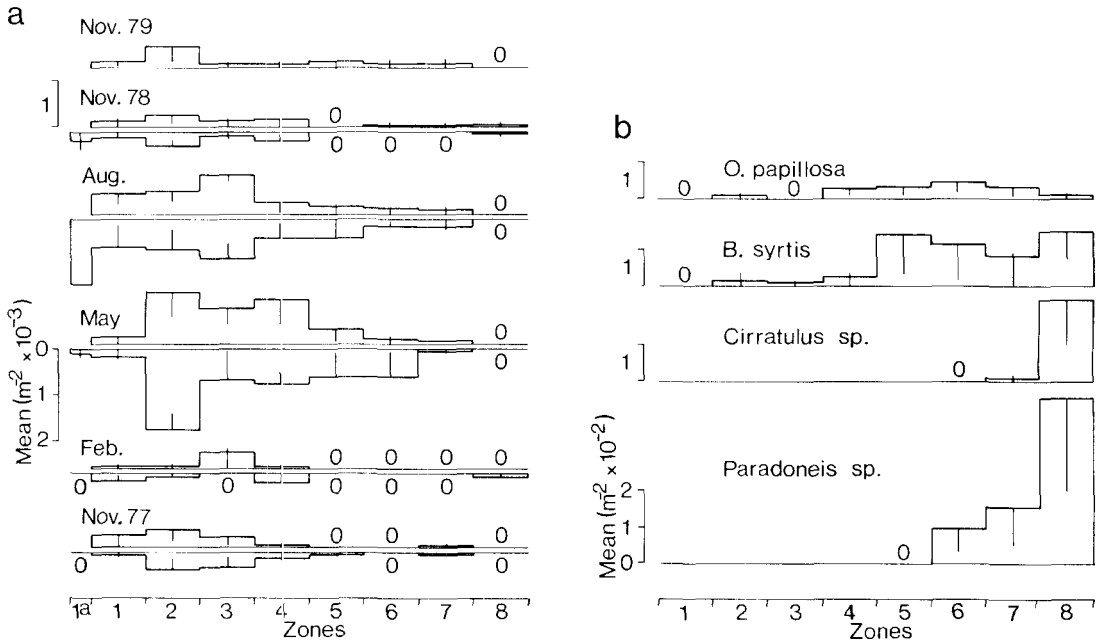
Fig. 10 Seasonal zonation of *Nicon aestuariensis* and zonation of four minor species. Conventions as in Fig. 6. **a.** *N. aestuariensis* zone means as thousands per m². **b.** *Paradoneis* sp., *Cirratulus* sp., *Boccardia syrtis* and *Orbinia papillosa* overall zone means as hundreds per m² from summed data of all transects.

Seasonal zonation changes

Seasonal changes in zonation of intertidal infauna may occur because of erosion, deposition, and profile changes on the shore (Ansell et al. 1972; Moore 1978; Yeo & Risk 1979), or because of the temperature regime (Hager & Croker 1979; Reading 1979), or the salinity regime (Boesch 1977). As well as those forced changes, there will be density changes related to the annual cycle of reproduction and recruitment within a population. After recruitment the zonation of the new age class may differ, temporarily or otherwise, from that of the established individuals. For example, young worms of the surf-shore opheliid, *Thoracophelia mucronata*, were present only low on shore (Dales 1952), and, in contrast, young worms of the sand-flat lugworm, *Arenicola marina*, concentrated high on the shore, then later migrated downshore (Beukema & de Vlas 1979). Additionally, longer-term age differences in zonation might arise when a locally dense population of 1 age group adversely affects subsequent settlement (Woodin 1976).

At Pauatahanui, where seasonal environmental changes were undramatic, the overall density changes related to the cycles of recruitment (Read 1983). The zones of high abundance did not change

during the period examined (exceptions being perhaps *Capitella* sp. with an initial decline in Zone 7, and *Nicon aestuariensis* with a less distinct pattern). Significant seasonal density changes within zones also followed the overall density cycles, except in 3 instances: a more even distribution of upper shore *Nicon aestuariensis* in August; and of *Scolecolepides benhami* in November 1978; and a Zone 8 decline of *Heteromastus filiformis* between February and May. The first 2 changes might indicate movement of individuals as the increases occurred when overall recruitment was not taking place, and the third was mainly attributable to differential high mortality of adults.

There was also evidence of differential recruitment within density concentrations of *Microspio maori* and *Axiothella serrata*. The significant variations between zones may relate to actual differences in juvenile mortality rates between zones, or to active selection by recruits, but chance events during recruitment may also be important.

Table 5 Within-zone density changes (combined left and right transect data) in relation to mean seasonal densities ($\pm$ 95% limits). (* significant overall density change, no data as n.d.). Zones with a significant change occurring against the overall trend are enclosed in parentheses.

Species		Nov. 77	Feb.	May	Aug.	Nov. 78	Nov. 79
Microspio maori	Density m⁻²	3610 ($\pm$410)	2600 ($\pm$350)	3860 ($\pm$550)	6260 ($\pm$770)	4180 ($\pm$480)	4560 ($\pm$750)
	Change ($\pm$)		*−	*+	*+	*−	+
	Zones of significant change		3,7	1,8	1,3,4,6	1,3,4,5	5
Capitella sp.	Density m⁻²	2540 ($\pm$430)	1280 ($\pm$230)	2310 ($\pm$420)	2120 ($\pm$350)	1370 ($\pm$270)	2180 ($\pm$330)
	Change ($\pm$)		*−	*+	−	*−	+
	Zones of significant change		3,4,6,7,8	1,2		1	1,3,6
Heteromastus filiformis	Density m⁻²	2250 ($\pm$240)	1290 ($\pm$210)	1770 ($\pm$220)	2010 ($\pm$270)	1760 ($\pm$230)	1050 ($\pm$250)
	Change ($\pm$)		*−	*+	+	−	−
	Zones of significant change		4,5,8	4,5,6(8−)			6
Axiothella serrata	Density m⁻²	350 ($\pm$60)	690 ($\pm$200)	1000 ($\pm$210)	1150 ($\pm$210)	550 ($\pm$90)	270 ($\pm$90)
	Change ($\pm$)		*+	*+	+	*+	−
	Zones of significant change		5,6,7	4		3,6,7	3,5
Boccardia acus	Density m⁻²	n.d.	n.d.	860 ($\pm$260)	540 ($\pm$210)	480 ($\pm$220)	n.d.
	Change ($\pm$)				−	−	
	Zones of significant change				6		

Species	Scolecolepides benhami			Nicon aestuariensis		
	Density m⁻²	Change (±)	Zones of significant change	Density m⁻²	Change (±)	Zones of significant change
Nov. 77	420 (±310)	-		120 (±40)	±-	2
Feb.	360 (±170)	+		60 (±40)	±-	2,3,4,5,6
May	410 (±220)	-		490 (±90)	±+	2,4(1+)
Aug.	400 (±180)	-	(2+)	390 (±70)	±-	1,3,5
Nov. 78	380 (±90)	-		100 (±30)	±-	
Nov. 79	230 (±100)	-	+	120 (±50)	+	

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