

POPULATION ECOLOGY STUDIES ON

INFAUNAL POLYCHAETES OF PAUATAHANUI INLET

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Submitted for the degree of DOCTOR OF PHILOSOPHY
in ZOOLOGY at the Victoria University of Wellington

June, 1983

'Under the sand at low tide
are whispers, hisses, long slithers,
bubbles, the suck of ingestion, a soft
snap: mysteries and exclusions.'

Fleur Adcock, 'Sea-Lives',
The Inner Harbour. Oxford University Press, 1979.

ABSTRACT

Macrofaunal polychaete densities across a stable, fine-sand, intertidal flat in Pauatahanui Inlet were examined from a set of seasonal samples, 500 μm sieve processed, from a stratified transect pair. Density patterns had shore-normal trends, despite apparently weak tidal-cycle environmental gradients. Zones of high abundance of common species persisted unchanged, but seasonal increase and decline occurred within them, with also some population redistribution attributable to differential mortality/recruitment, or possibly to migration. Correlation analysis did not detect interspecies relationships linked to the abundance and zonation of the common polychaetes, all deposit-feeders.

The population dynamics of six species was investigated from the transect-pair seasonal samples, supplemented by subsequent more finely-sieved samples during dense recruitment periods. The maldanid *Axiiothella serrata* had three identifiable age groups, O, I, and II+, with I plus II+ density to about 550 m^{-2} . The new O group began to appear in October-November, as aggregates below 3 cm sediment depth, believed to represent lecithotropic, direct-developing, siblings from egg masses of the II+ group. Juvenile setiger-total frequencies indicated synchronous adult spawning occurred at varying intervals during an approximate six month

period. Peak density of dispersed, near-surface recruits reached 29 thousand m^{-2} . Setiger-total was the most sensitive indicator of size and age in juveniles of up to about 15 setigers. Zonation patterns were age specific.

The predominantly lower-shore capitellid *Heteromastus filiiformis* had a short summer spawning period with settlement ending before May, when population density was up to 10 thousand m^{-2} . Merger of O group into the adult size range occurred in about one year, and probably first spawning was at the end of the second year, with life span of three years or more.

The nereidid *Nicon aestuariensis* had I+ and older age groups at barely detectable densities. Spawning was probably in late summer although an O group, at about 500 m^{-2} , was not detected until May. The spionid *Scolecopides benhami* had apparently unchanging size structure and density (about 400 m^{-2} transect-wide); new settlement was not detected. High density occurred only in a narrow near-shore strip. *Nicon aestuariensis* also declined down-shore, but more gradually.

The spionid *Microspio* sp. and capitellid *Capitella* sp. were short-lived, near-surface species, with apparently continuous recruitment from planktotrophic and direct-development respectively. A spring recruitment increase created at first a separate modal group of juveniles, and raised *Microspio* sp. density to 45 thousand m^{-2} and *Capitella* sp. to 7 thousand m^{-2} . *Capitella* sp. declined in density downshore, but *Microspio* sp. was only weakly zoned.

The common polychaetes had largely concordant density cycles with settlement (or peak settlement) spring-summer orientated, although 500 μ m mesh processing detected the peak of surviving adults in autumn-winter. Pauatahanui polychaetes as an assemblage, life history traits, links between population structure and zonation, and problems in polychaete population studies are discussed.

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ACKNOWLEDGEMENTS

I am grateful to Dr R.B. Pike for his part in initiating this research; to Dr R.G. Wear and Professor J.A.F. Garrick for their advice and assistance at various stages; and especially to Professor J.B.J. Wells, supervisor during most of this study, for his continued guidance and patience over that time, and his review of the manuscript. Mrs Shirley A. Pledger, Mathematics Department, gave invaluable counsel concerning statistical analyses, and her evaluations of potential methodologies were much appreciated. Mr David Hannon gave willing help in the field with the collection of the main sample series, and Mr George Grainger was an able surveyor's assistant.

Advice on the identity of *Microspio* sp. was given by Dr James A. Blake, Batelle New England Marine Laboratory, Massachusetts, and on *Paradoneis* sp. by Dr John P. Hartley, Oil Pollution Research Unit, Orierton Field Centre, Wales. Dr Geoffrey R.F. Hicks, National Museum, identified the amphipods, and also made useful comments on part of the manuscript. Dr Phillip L. Shaffer, Department of Statistics, North Carolina State University, very generously sent me much information from his unpublished research on *Heteromastus filiformis*. Oxford University Press readily gave permission to use the epigraph quotation.

My most special thanks go to my parents for their support throughout this study, and additionally to my mother for her skilful typing of the manuscript.

Financial assistance was provided by DSIR as part of the Pauatahanui Environmental Programme.

GENERAL INTRODUCTION

In marine sedimentary environments polychaetes are an important and often dominant component of the benthos (Knox 1977). Ecological investigations of benthos have commonly been directed towards describing and comparing communities, usually in relation to sediment characteristics, and latterly often initiated, and subsequently constrained by, requirements for environmental impact assessment. Although regarded as less meaningful than other approaches in terms of ecological theory and practical application (Mills 1975), this research orientation may form a useful foundation for subsequent studies. Much attention is now being directed towards understanding how benthic community structure is developed and maintained. This approach has led to the study of interactions occurring at the species level and between functional groups (trophic, behavioural, spatial etc.), and study of the effects of environmental perturbation and modification. Increased understanding is intended to lead to generalisations, and ultimately to reliable predictive models of benthic communities. However, the population dynamics of individual species and their contribution to community variability has tended to be little emphasised or understood, largely because insufficient detailed information has been available. Such information is as fundamental to predictions as is knowledge of interactions, and also indicates the magnitude of variation typically undetected by 'one-off' baseline surveys.

The comparative lack of population studies is understandable as ideally they require intensive, rigorously-designed sampling programmes and long-term commitment of effort and resources. The number of benthic species to be investigated is very large, but in some hab-

itats, especially in intertidal and estuarine areas, there may be only a small number of numerically important species, and commonly they include polychaete worms. Despite this, surprisingly little is known of population structure and pattern of seasonal change in this group. For widespread, common polychaete species this information can be of value beyond the local area from which it derived.

Population ecology is here defined as the study of the structure, abundance, and distribution of a population, and the influences on it of temporal and spatial variations in the environment. The aim of this thesis is to make a contribution to aspects of population ecology of an integrated assemblage of intertidal polychaetes. Such study has rarely been attempted previously and certainly not in New Zealand. Existing knowledge of intertidal ecology of New Zealand polychaete fauna is sparse (see Section 1), and population analyses are limited to those on *Nicon aestuariensis* Knox, *Pectinaria australis* Ehlers, and *Aglaophamus verrilli* (McIntosh) (Estcourt 1966, 1974, 1975).

This study of polychaete populations was part of a multidisciplinary study of Pauatahanui Inlet and its catchment. In the early 1970's large housing developments began on the southern and north-western hills of the catchment as the first stages of a proposed major urban and industrial complex. However, Pauatahanui Inlet still retained a natural shoreline and a mainly rural catchment, unlike the more human-modified Porirua Inlet that adjoins it (Fig. 1). Public concern for the continuation of scenic and recreational values in Pauatahanui Inlet was aroused when clay and silt, eroded from cut and fill earthworks, built up spectacularly in one bay (see Kennedy 1980, Curry 1981). In response the Pauatahanui Environmental Programme was commenced in 1975 'with the objectives of understanding the present environment or ecosystem, defining its sensitive features, producing data of assistance to planners to enable wise management of this natural

resource as a viable entity, and establishing baselines for monitoring changes resulting from development' (Healy 1980, p.8). The present study is a contribution to the first objective, and hopefully may also have some relevance to the remainder.

Pauatahanui Inlet, the eastern arm of the eustatically-drowned valley system that is Porirua Harbour, is shallow, and almost enclosed, but is largely marine-dominated in water quality. The 4.5 km² area is morphologically stable with 1.1 km² of sandy or silty-sand intertidal flats and banks (Irwin 1976, McDougall 1978). Total average freshwater input during a tidal cycle is less than 5% of the tidal compartment, and only during a few days per year of heavy rainfall are the Inlet waters greatly below marine salinity (Healy 1980, Curry 1981). Two streams at the eastern end, the Pauatahanui and the Horokiwi, contribute 75% of the annual freshwater inflow.

An intertidal area was chosen for the population study because such habitat has naturally-defined limits, and seasonal change within it was thought likely to be of greater range than subtidally. Other considerations were that the shore zone was more likely to be modified by planned developments, and its accessibility readily allowed collection of a large number of sampling units, all from known coordinates. The area selected (Fig. 1) had advantages in that its physiography was comparatively uniform without major changes in sediment type in the near vicinity. Earlier sampling had shown that all common polychaete species of the Inlet intertidal were present.

This thesis comprises five sections. Section 1 describes the physical environment, reports on the relative abundance and trophic grouping of all macrofaunal species, then analyses zonation or shore-normal trends occurring in the more abundant polychaetes, the seasonal changes therein, and also correlations between species. Possible influences on patterns are discussed. Population structure and its

seasonal variation are analysed for *Axiiothella serrata* Kudenov and Read in Section 2, for *Microspio* sp. and *Capitella* sp. in Section 3, and for *Heteromastus filiiformis* (Claparède), *Nicon aestuariensis*, and *Scolecoplepides benhami* Ehlers in Section 4. The population structure of less abundant species could not be studied, but density changes of some of them are briefly analysed in Section 4. Section 5 takes an overview of the information gained, with discussions of the Pauatahanui polychaetes as an assemblage, relevant studies elsewhere, and problems in polychaete population dynamics. Some taxonomic considerations are dealt with as an appendix.

Sections 1 to 4, presenting results, are in the format of self-contained papers, but environment and zonation information in Section 1 is relevant to following sections. The style of bibliographies is the current system of New Zealand DSIR journals.

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SECTION 1

PERSISTENCE OF INFAUNAL POLYCHAETE ZONATION PATTERNS

ON A SHELTERED, INTERTIDAL SAND FLAT

S E C T I O N 1

PERSISTENCE OF INFAUNAL POLYCHAETE ZONATION PATTERNS

ON A SHELTERED, INTERTIDAL SAND FLAT

ABSTRACT

Macrofaunal polychaete densities across a fine-sand, intertidal flat in Pauatahanui Inlet were examined seasonally from a pair of adjacent transects. Density patterns had shore-normal trends, despite apparently 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* sp. and *Axiiothella serrata* lacked strong trends. *Boccardia acus* density was affected by size as well as numbers of the bivalve *Chione stutchburyi*, its substratum. Zones of abundance of species persisted unchanged over a two-year period. Within those zones seasonal cycles of increase and decline occurred, and also some population redistribution attributable to differential mortality/recruitment (*Microspio* sp.,

Heteromastus filiformis, *Axiiothella serrata*), or possibly to migration (*Nicon aestuariensis*, *Scolecocarpus benhami*). Correlation analysis did not detect interspecies relationships linked to the abundance and zonation of the common polychaetes, all deposit-feeders.

INTRODUCTION

On a sedimentary beach there are invariably shore-normal gradients in environmental factors which may influence the abundance of infauna. The expected result of these influences 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 often been described (see e.g., Eltringham 1971, Newell 1979 reviews). However, study of relationships with the environmental factors in the complex three-dimensional habitat, the interactions occurring amongst the biota, and the extent and causes of seasonal variation in zonation, is less advanced than for the more readily observed hard shore situation.

This Section reports on the zonation patterns of the polychaetes of an intertidal sand flat within the sheltered waters of Pauatohanui Inlet (Fig. 1), and analyses the consistency of pattern over a short along-shore distance, the extent of seasonal variation and the occurrence of overt species interaction effects. It is the first part of an investigation of the population structure of an intertidal polychaete assemblage on an apparently uniform, morphologically stable, sand flat. Emphasis is on establishing how well-defined and how variable zonation is, although the role of the physico-chemical regime in influencing zonation is discussed; in particular the importance of effects due to tidal cycle and sediment grade, two primary influences

determining or related to most other factors (Newell 1979, and references therein). Continuous environmental monitoring of selected sites, or comprehensive measurements of the multitude of physico-chemical variables at the sampling unit level were beyond the technical resources available. Analysis concentrates on the numerically dominant polychaetes, but, in order to place this assemblage in ecological perspective, the relative densities of all macrofauna, and the overall trophic structure are analysed in brief.

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 (1967a,b), Morgans (1967a,b), Wood (1968), Morton and Miller (1973), Knox and Kilner (1973), Voice et al. (1975), Knox et al. (1977), Knox and Fenwick (1978), Kilner and Akroyd (1978).

Two important species in the present study unfortunately have as yet no published name. The spionid *Microspio* sp. will be described by Dr J.A. Blake, Batelle New England Marine Laboratory. The status of *Capitella* sp. is uncertain, but it is a member of the species complex formerly characterised as *C. capitata* (Fabricius) (see Appendix).

METHODS

SAMPLING AND PROCESSING

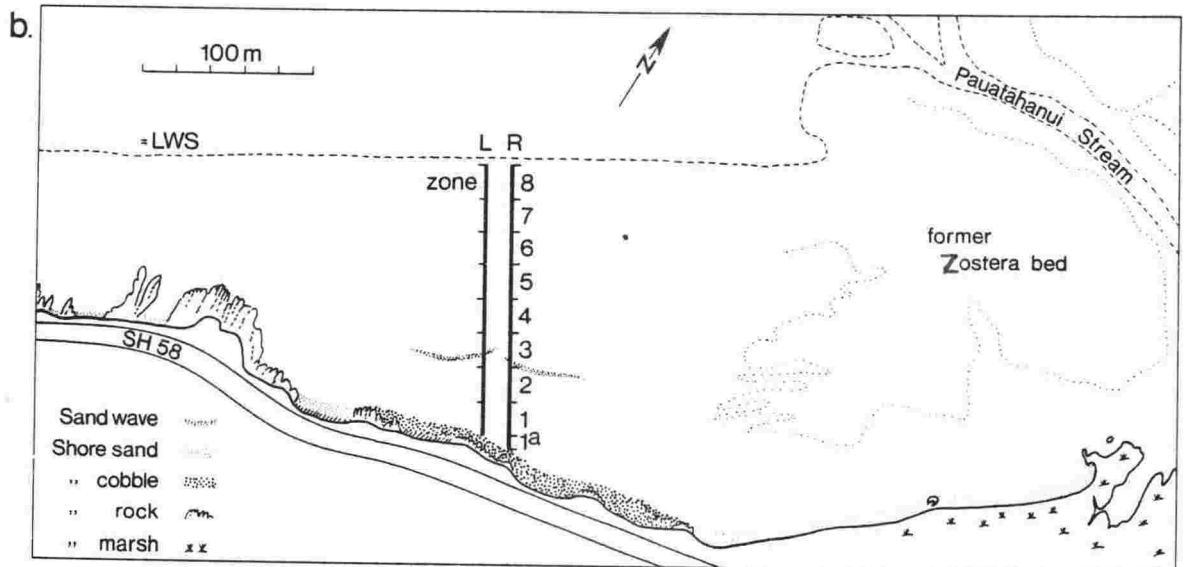
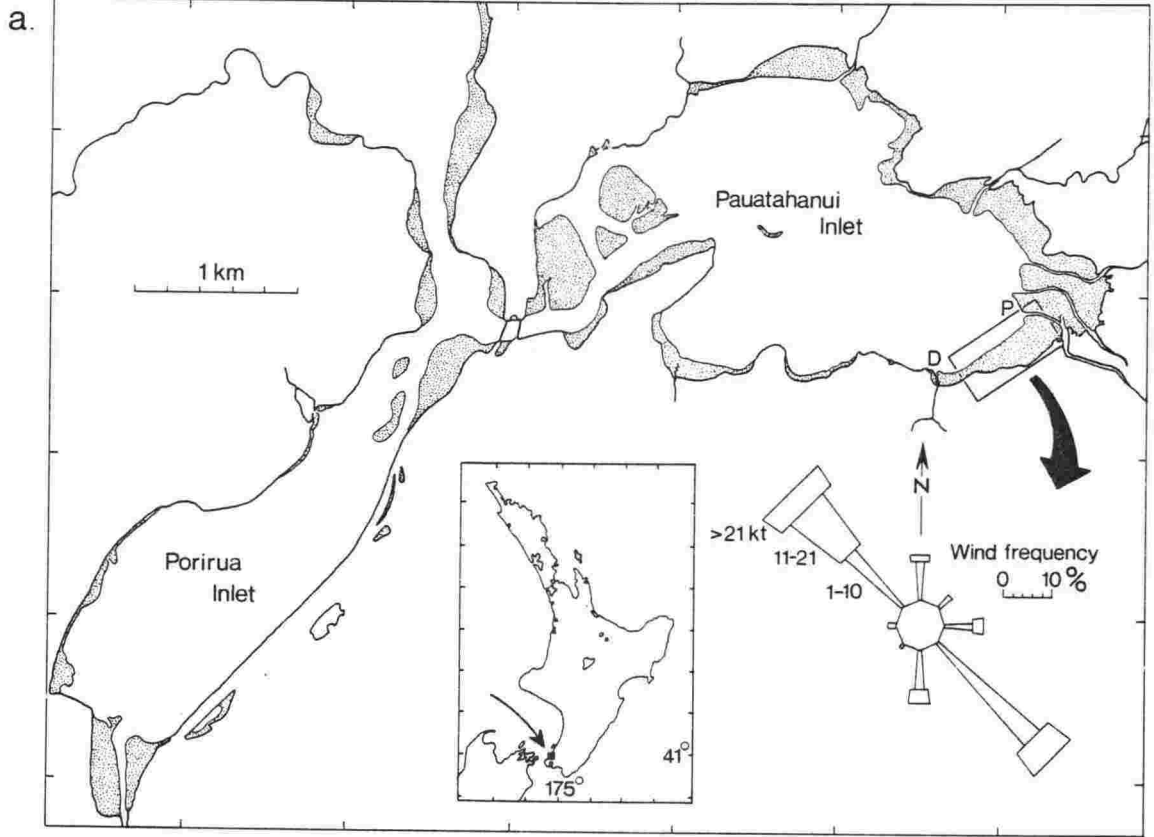
The sampling strategy aimed to assess population densities while also detecting zonation and within-site along-shore variation. Two parallel transects were used, normal to the spring tide low water level and separated by 15 metres. Each was a continuous 2 m wide strip,

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 N.Z. Meteorological Service from 1976-78 hourly observations.

Inset: N.Z. locality map.

b) Detail of transect site morphology, 1979. Left and right transect strips are to scale. The approximate location of *Zostera capricorni* beds in 1977 is outlined. Right transect origin metric grid reference 267006E, 600958N; transect-line bearing 327° T. Map compiled from plane table mapping and aerial photographs.



divided into 20 m zones, a subdivision of the shore sufficient to reveal pattern. For the left transect (facing downshore) eight zones covered the intertidal flat (160 m), and for the right transect an extra zone 8 m long was included at the shore end (zone 1a) because of the angle of the shoreline (Fig. 1b). Zones 1 to 8 were at the same tide levels for both transects.

For stratified random sampling each zone of the transects was considered divided by a 20 cm grid into 1000 squares (400 for 8 m zone 1a). Random number tables were used to generate unique coordinates for the position of each sampling unit. Proportional allocation of units (Cochran 1977) was used when zone 1a was included in the sample (i.e., $n = 5$ for zones 1-8, $n = 2$ for zone 1a). Sampling coordinates were located accurately on site from permanent marker posts at each end of the transects, using surveyors' tape and a metre rule.

Undisturbed cylindrical core samples of surface area 50.30 cm^2 were taken to 15 cm depth. The deepest burrowing species, *AxiotHELLa serrata* and the bivalve *Tellina liliana*, were adequately sampled by that depth. The series of samples was collected at 3-monthly intervals over a 12 month period, and each comprised 82 core samples. Sampling dates were 14 November 1977, 8 February, 22 May, 21 August, 16 November 1978. More frequent sampling was not possible because copious fine eel-grass litter made fauna extraction from each set of 82 cores a lengthy process. Cores were sieved through a $500 \mu\text{m}$ Endecott test sieve and the residue was fixed in 10%, buffered, seawater formalin containing 20 mg/litre 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 $250 \mu\text{m}$ sieves. This sample permitted some assessment of zonation persistence over the two

year period and indicated juvenile zonation of species with spring settlement.

The fauna and plant litter in each core were separated from the shell and sediment by repeated washing and decantation (using a 125 μ m sieve to prevent attrition losses). The shell-sediment residue was sorted under a dissecting microscope to extract remaining fauna, which were added to the organic fraction (mollusc spat in the shell residue passing a 6 mm mesh were not enumerated). After any large eel-grass rhizomes were removed and examined, the organic fraction was further sieved and stirred for a half-minute in a 1 mm sieve to divide it into coarse and fine fractions before fauna extraction under the microscope. Because of the large amount of fine litter present, it was necessary to subsample the <1 mm fraction. A 1/5th random subsample was taken using a turntable-mounted one litre bowl divided into 10 segments (modified from Kott's (1953) whirling subsampler, and in tests giving distributions not significantly different from the Poisson series, $P > 0.05$). After rotation and settling two 1/10th subsamples chosen by random number were removed with a large-mouthed pipette. An application of binomial distribution theory predicts that zone means should remain unaffected by this subsampling method but that zone variances should increase (S. Pledger, pers. comm.). Litter settled volume 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 U-tubes present.

STATISTICAL TREATMENT

Within- and between-transect data-groupings were tested for significant differences by Mann-Whitney U-tests and Kruskal-Wallis tests, and correlations examined using Spearman's r_s . These non-

parametric rank tests were corrected for ties and their significance determined using two-tailed probabilities (Gibbons 1971, Lehmann 1975). All tests stated as significant without specified probability levels refer to $\alpha = 0.05$. For other than left transect to right transect comparisons the two transects, or the zone pairs, were together treated as a single sample, for test purposes regarded as a random sample taken from one statistical population of unknown distribution. This procedure was appropriate since the pairs rarely differed (see Table 4; significant tests fewer than the expected number of type I errors). Parametric tests on small samples and overall analysis of variance were not used, because optimum transformations derived by the procedures of Holt et al. (1980) and Downing (1979) were poorer than the original data when tested for normality (χ^2 goodness-of-fit test). The suggested transformations within species were not consistent between samples, and were not improved by excluding subsampled data.

The central-limit theorem, large sample, normal approximation permitted parametric comparisons of overall means between seasonal samples and between transect pairs. For stratified samples with proportional allocation

$$\text{Overall SE} = \frac{1}{n} \sqrt{\sum (n_z \times s_z^2)} \quad (\text{Cochran, 1977})$$

SE = standard error of mean, n_z = number of sampling units in zone,

s_z^2 = zone variance

Differences between means were tested for significance by t-test after F-test of variances, or approximate t-test (Sokal and Rohlf 1969) for significantly different variances. Degrees of freedom for t values for each species (possible range between $n_z - 1$ and $\sum (n_z - 1)$, depending on zone variances) were approximated by the method of Cochran (1977, p.96).

PHYSICAL ENVIRONMENT

Beach profiles were surveyed (± 1 mm per 100 m), and the heights determined relative to orthometric mean sea level, using a Zeiss Ni2 automatic level. Mean tide levels are inlet mouth records (N.Z. Navy Hydrographic Office Chart 4632, 1975 print). Some tidal observations were made at the sample site with tide poles to determine local conditions.

Salinity data are from measurements taken half-hourly over spring and neap tide cycles, from a 15-day neap to neap period of measurements at low tide, and from approximately monthly low water spring tide observations (1976-78). Salinities (± 0.5 ‰) were measured by hydrometer or refractometer. Interstitial samples were extracted from cores in the field by suction through a sintered glass filter.

Sediment temperature range at 12 cm depth was recorded monthly from buried maximum-minimum thermometers (accuracy on test $\pm 0.5^{\circ}\text{C}$) in zone 5 and zone 1. Wind records are from the Pauatahanui climate station, located at 30 m elevation and a few hundred metres from the sample site.

Sediment samples were two random cores combined (35 mm diameter to 15 cm depth) taken in each zone of each transect. Data presented are from a July 1980 sample set. Samples collected in August 1976 from zone 1 and midshore were also available for comparison. 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 minutes in a mechanical shaker (sieves at 1 ϕ intervals, 0.5 ϕ for the 2-4 ϕ range). Cumu-

lative percentage frequency curves were plotted on probability paper, and Folk and Ward (1957) statistics of mean size ($M_z \phi$), sorting ($\sigma_I \phi$), skewness (Sk_I) 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 the 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 semidiurnal and near symmetrical, with mean spring range 1.25 m and mean neap range 0.4 m (Fig. 2). The profile curve and emersion curves show that the sand beach (overall slope 1:210) begins about 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 showed that meteorologically-influenced fluctuation in local sea level and tidal range was important in frequency and magnitude. Precise linking of zonation to mean levels, 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 to February 1979) was 6.7°C to 25.8°C, with a winter lowest maximum of 11.8°C and a summer highest minimum of 17.0°C (Fig.3). The upper transect zone 1 usually cooled and

heated more than zone 5 year round, as would be expected due to its more frequent exposure to air temperatures, but the difference between the sites was slight. The sediment maximum temperatures were comparable to mean extreme maximum air temperatures during the summer and lower than these in winter, whereas the minima remained about 10°C above air minima (Fig. 3).

Salinities at spring tide low water had a mean of 25 ‰ (n = 31, SD 8.9), ranging between 3.0 and 34.0 ‰. The interstitial salinities measured at zone 5 level at the same time were more constant at mean 28 ‰ (n = 18, SD 2.2) and range 24 - 30.0 ‰ (a mixo-polyhaline regime, Remane and Schlieper 1971). The normally mixo-euhaline (i.e., 30 - 35 ‰) salinities of the main inlet water mass fell substantially below 35 ‰ only after infrequent heavy rainfall periods (Healy 1980). At the transect site after one such an event overlying water salinity was 2 ‰, whereas interstitial salinity was 15 ‰. Observations during both neap and spring tidal cycles showed, however, that the shallow tidal flat waters had an erratic salinity regime also in dry weather. Unpredictable large decreases (>10 ‰), unrelated to tide state, occurred in overlying water, especially near-surface, persisting for periods of less than one hour to several hours. These fluctuations are attributed to the intermittent presence over the site of low salinity water from the adjacent stream discharges.

Interstitial salinities at 5 cm depth took many hours to equilibrate with overlying water and were thus more constant. Interstitial salinities did not have an intertidal gradient, although lower-shore salinities were less variable (see Table 1, Fig. 4).

Fig. 2 Right transect profile and two observed calm-weather emersion curves. Left transect levels differed by less than 1 cm on average (March 1979). Emersion curves 1 and 2 are plots of distance downshore against emersion hours (right hand scale). (Curve 1, range + 0.37 to - 0.44 m, 3 Oct. 1979; curve 2, range + 0.74 to - 0.35 m, 9 June 1979).

Fig. 3 Extreme maximum and minimum sediment temperatures at 12 cm depth, November 1977 to March 1979. The date of reading is indicated by the abscissa symbol. Zone 1 thermometer was lost and replaced in May. Air extremes also shown are Pauatahanui 10 year means 1968-78 (N.Z. Meteorological Service data).

Fig. 4 Low tide salinities over a 15 day neap to neap period. Interstitial salinities at zones 1, 4 and 7 are plotted, together with the overlying water salinity at low water. The position on the transect of low tide mark from zone 1 zero is also indicated (lower). Catchment rainfall (daily figures shown) was negligible during the period except for day one. The neap to spring increase in tidal compartment had no obvious effect on salinities.

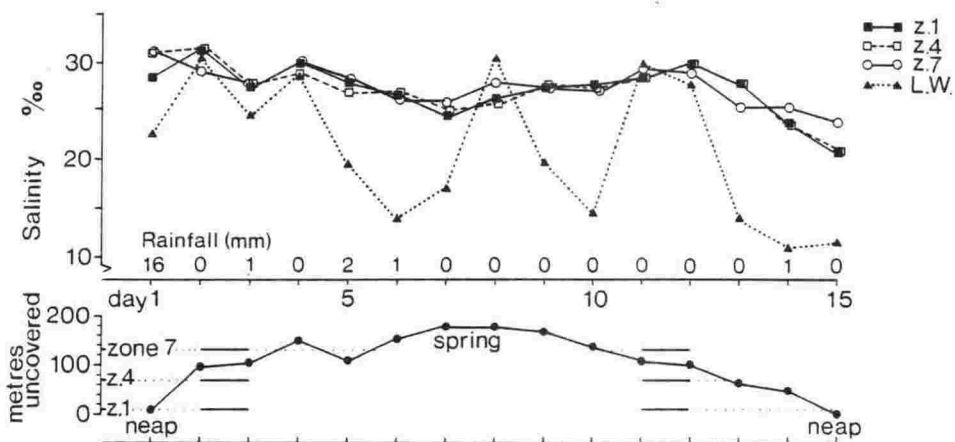
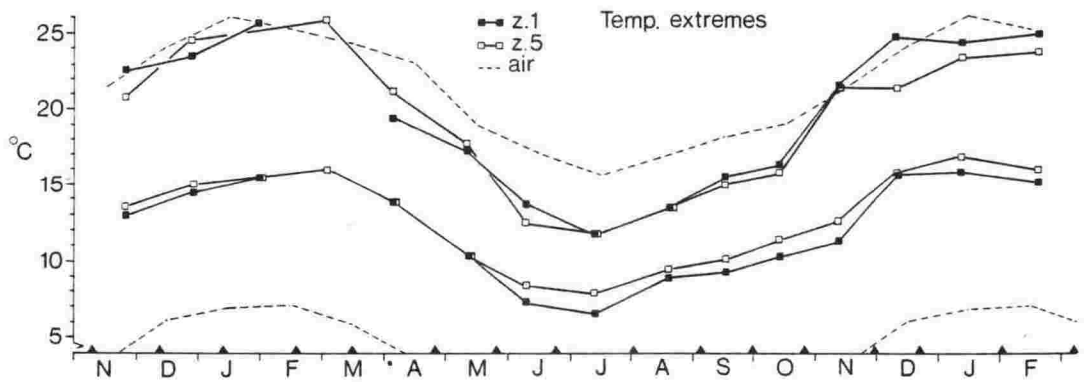
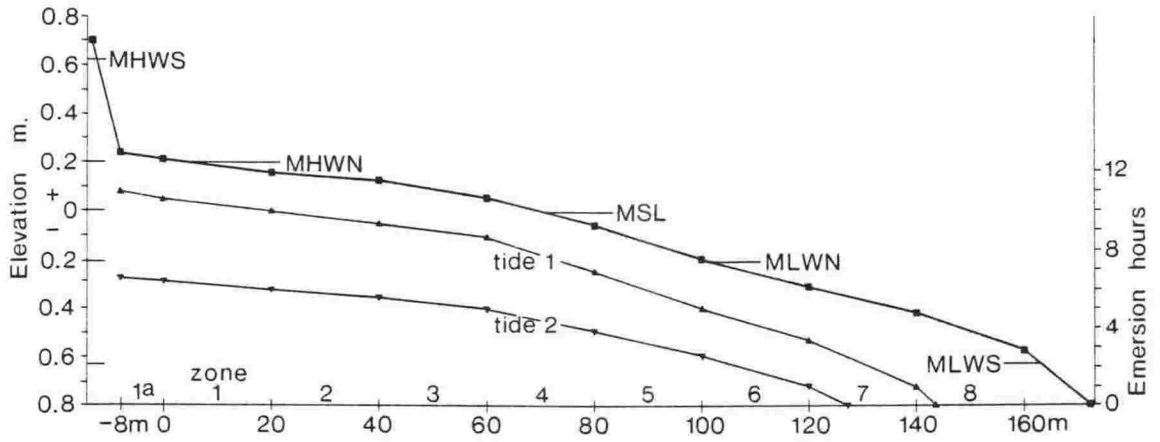


TABLE 1. Interstitial (5 cm depth) and low water salinity measured at low tide over a 15 day neap to neap period (n = 15).

Salinity	Zone 1 interstitial	Zone 4 interstitial	Zone 7 interstitial	Surface water at low water
Mean ‰	27	27	28	21
Range	21-30	21-32	24-31	11-31
SD	2.7	2.8	1.9	7.3

SEDIMENTS

The transects' site had the longest wind fetch to the north-westerly prevailing wind direction of all inlet beaches (2.5 km) and, probably as a consequence of the greater wave exposure, had less silty sediments than adjacent areas (see McDougall 1976, 1978). The sediments were borderline between fine and very fine sands ($125 \mu\text{m}$, 3ϕ) and moderately well-sorted. Cumulative curves representing the range of variation downshore are given in Fig. 5a. Sediment statistics show that zonal trends were generally closely comparable between left and right transects (Fig. 5b-e). The sediments of zones 2-8 had silt-clay content (Fig. 5f) of about 2% (3% zone 6) and showed no trend in M_z values (mean 3.02ϕ), but the sorting improved and skewness and kurtosis decreased downshore. In the lowest zone the sediments were well-sorted with a near symmetrical normal distribution.

Sediments within 20-30 m of the cobble shore (M_z $3.1-3.25 \phi$) were finer than those downshore and had silt-clay levels of 3-6%. The mixed distribution of right zone 1a (Fig. 5a) indicates a submode of coarse sand and was probably related to the proximity of the cobble shore.

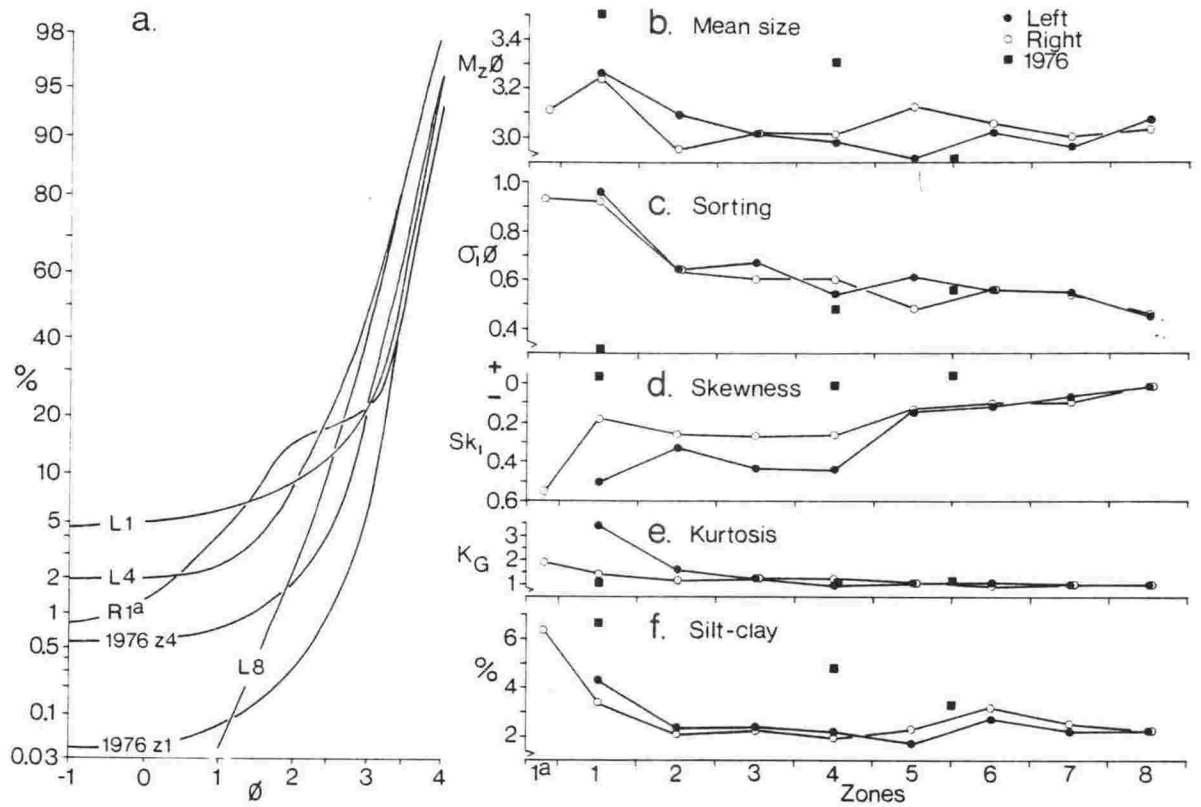


Fig. 5 Sediment grain-size etc.

a) Representative cumulative percentage probability curves of grain size. L1 = left transect zone 1, and so on.

b) - f) Sediment statistics variation with zone.

The higher coarse skew occurring in zones 1-4 was due to shell content, which decreased downshore, markedly so from zone 5 (Fig. 6c). Plant litter content in the sediment (particles >0.5 mm) increased downshore to peak in zone 7 (Fig. 6c). The redox potential discontinuity level as indicated by an olive grey to dark grey colour change (Smith and McColl 1978) was an irregular mottled layer 2-4 cm deep, without consistent zone or seasonal changes.

At low tide the water table remained at or very near the sediment surface, which rarely dried. For example, in spring temperatures water content at 5 cm depth (as weight loss on drying) did not change during emersion under overcast conditions, and dropped up to 8% from saturation in upper and middle zones 1 and 4 in clear weather (zone 7 no change).

LONG-TERM SITE CHANGES

Before sampling began an eel-grass decline occurred during 1976-77 on the Pauatahanui Stream flats. Live *Zostera capricorni*, which was formerly present as intermittent lenses associated with low megaripples from about zone 4 level downshore, was absent during sampling. The upper shore sediments had become less muddy (see Fig. 5b,f), and the beach had flattened from the 1976 megarippled profile reported in Pickrill (1979), possibly as a consequence of the loss of the protective eel-grass. During most of the sampling period the beach was featureless and no obvious surface change occurred. In early 1979 a solitary shell-covered sand wave grew at zone 4 level and slowly migrated towards the shore (Fig. 1b).

RESULTS

MACROFAUNAL DENSITY AND TROPHIC STRUCTURE

As an introductory summary of the faunal assemblage all species are ranked in Table 2 according to mean overall density over the intertidal strip, zones 1a to 8, and to percentage occurrence in cores. Forty-seven species were collected, including 22 polychaetes. The 14 species in more than 10% of cores included 9 polychaetes. Seventeen species had less than 1% occurrence.

The small spionid polychaete *Microspio* sp. was the most frequent and abundant species present, with 20% higher occurrence than the next ranked species *Capitella* sp. (cf. also Table 3, Fig. 6 and see also Fig. 8-12). Species with wide distributions generally had occurrence rankings above density rank (e.g., *Axiothella serrata*, the bivalve *Chione stutchburyi*, nemertean sp. 1), whereas the converse applied for some species with more localised distributions (e.g., *Heteromastus filiformis*, *Cirratulus* sp.). Some small, low density species, occurring only in <1 mm subsamples, gained raised density rankings compared to their occurrence rank (e.g., *Desdemona* sp., *Amphipoda* spp., *Sphaerosyllis* sp.).

The higher of the two densities given for *Axiothella serrata* in Table 2 takes account of the dense aggregations of juveniles occurring in all three November samples in a very small number of cores (maximum 4 out of 82). These aggregations are believed to be undispersed siblings from egg masses in the tube of the female (Section 2), and have been excluded from the subsequent analyses.

In order to outline the trophic structure of the assemblage, the species were also classified by feeding type in Table 2 (after

TABLE 2. Mean overall density, percentage occurrence, and feeding type of all macrofauna in 500 μ m sieve sample series November 1977 to November 1979.

Species	Density		Occurrence		Feeding type
	Rank	$\bar{x} \text{ m}^{-2}$	Rank	%	
<i>Microspio</i> sp.	1	4126	1	97.5	Df+S
<i>Capitella</i> sp.	2	1939	2	77.6	Df
<i>Heteromastus filiformis</i> (Claparède)	3	1777	5	65.1	Db
¹ <i>Axiiothella serrata</i> Kudenov and Read					
November juveniles included	4	1316	3	76.5	Db
November juveniles excluded	4	719	3	76.0	"
<i>Boccardia acus</i> (Rainer)	5	588	6	47.4	Df+S
(M) <i>Chione</i> (<i>Austrovenus</i>) <i>stutchburyi</i> (Wood)	6	388	4	66.6	S
<i>Scolecoplepides benhami</i> Ehlers	7	386	7	47.3	Db+S
<i>Nicon aestuariensis</i> Knox	8	227	8	45.0	Db+C
(M) <i>Tellina</i> (<i>Macomona</i>) <i>liliana</i> Iredale	9	107	9	44.5	Db
(R) <i>Nemertean</i> sp. 2	10	86	10	22.9	C
<i>Paradoneis</i> sp.	11	86	12	13.6	Df
<i>Boccardia syrtis</i> (Rainer)	12	66	13	12.7	Df+S
<i>Oligochaete</i> sp. 1	13	59	14	11.8	Df
(R) <i>Nemertean</i> sp. 1	14	36	11	14.0	C
<i>Cirratulus</i> sp.	15	28	18	4.16	Db
<i>Orbinia papillosa</i> (Ehlers)	16	20	15	8.78	Db
(C) ² <i>Amphipoda</i> sp. 1 and 2	17	15	21	2.77	Df+S?
(C) <i>Macrophthalmus hirtipes</i> (Jacquinot)	18	15	16	7.37	Db
(C) <i>Colurostylis pseudocuma</i> Calman	19	12	19	3.70	Df
(M) <i>Cominella</i> (<i>Josepha</i>) <i>glandiformis</i> (Reeve)	20	10	17	5.07	C
(M) <i>Mactra</i> (<i>Cyclomactra</i>) <i>ovata</i> (Gray)	21=	7.3	20	3.69	S
<i>Desdemona</i> sp.	21=	7.3	28=	0.92	S+Df?
<i>Perinereis vallata</i> (Grube)	23	5.5	22	2.54	C+Db?
<i>Scoloplos</i> (<i>Scoloplos</i>) <i>cylindrifer</i> Ehlers	24	5.1	24	1.62	Db
(C) <i>Halimacarcinus varius</i> Dana	25=	4.1	23	2.07	C
<i>Ceratonereis</i> sp.	25=	4.1	25	1.39	Db
<i>Prionospio</i> (<i>Aquilaspio</i>) <i>aucklandica</i> Augener	27	2.8	26=	1.15	Df+S

TABLE 2. (Contd.)

Species	Density		Occurrence		Feeding type
	Rank	$\bar{x} \text{ m}^{-2}$	Rank	%	
(M) <i>Zeacumantus lutulentus</i> (Kiener)	28	2.7	26=	1.15	Db
<i>Sphaerosyllis</i> sp.	29	2.3	37=	0.23	Df
<i>Aonides trifida</i> Estcourt	30	1.8	28=	0.92	Df
<i>Glycera lamelliformis</i> McIntosh	31=	1.4	30=	0.69	C
<i>Microphthalmus paraberrans</i> Hartmann-Schröder	31=	1.4	30=	0.69	Df
(M) <i>Amphibola crenata</i> (Gmelin)	31=	1.4	30=	0.69	Db
(C) ³ <i>Gastrosaccus</i> sp.	31=	1.4	33=	0.46	Df?+S?
<i>Goniada</i> sp.	35=	0.92	33=	0.46	C
(C) <i>Heterosquilla tricarinata</i> (Claus)	35=	0.92	33=	0.46	C
(Cn) <i>Edwardsia leucomelos</i> Parry	35=	0.92	33=	0.46	C
<i>Glycinde dorsalis</i> Ehlers	38=	0.46	37=	0.23	C
<i>Oligochaete</i> sp. 2	38=	0.46	37=	0.23	Df
(C) <i>Pontophilus australis</i> (Thomson)	38=	0.46	37=	0.23	C+D?
(M) <i>Xymene plebeius</i> (Hutton)	38=	0.46	37=	0.23	C
(M) <i>Diloma</i> (<i>Fractarmilla</i>) <i>subrostrata</i> (Gray)	38=	0.46	37=	0.23	Df+H
(C) ³ <i>Tenagomysis novaezelandiae</i> (Thomson)	38=	0.46	37=	0.23	Df?+S?
(C) ³ <i>T. macropsis</i> Tattersall	38=	0.46	37=	0.23	Df?+S?
(M) <i>Nucula hartvigiana</i> Pfieffer	not quantitative	-	-	-	Db
(M) <i>Notoacmea</i> (<i>Parvacmea</i>) <i>helmsi</i> (Smith)	"	"	-	-	Df+H
47 spp. in total					

TABLE 2. Footnotes

Species ranked by mean overall density and percentage occurrence in 434 cores (*Boccardia acus* 270 cores, nemerteans 393). Non-annelids annotated as follows: Mollusca M, Crustacea C, Rhynchocoela R, Cnidaria Cn. Molluscs <6mm not quantitatively recorded (*Nucula hartvigiana*, *Notoacmea helmsi*, and spat).

Feeding types as follows: bulk deposit-feeding Db, fractional deposit-feeding Df, carnivorous C, suspension-feeding S, herbivorous H, unconfirmed mode ?. See text for further explanation.

¹ *Axiiothella serrata* November juveniles occurred in aggregations but individually would not be retained by a 500 μ m sieve (see text).

² Mostly Lysianassidae sp. but *Paracorophium excavatum* Thomson also.

³ Epibenthic mysids normally absent at low tide.

gut and faeces examination, supplemented by published information and aquaria observations). Secondary feeding modes are given for some species and probable modes indicated by question marks. Deposit-feeders here include all the microphagous species feeding on the organic matter associated with the sediment, including possible specialists on micro-algae. Following Fauchald and Jumars (1979) only macrophagous feeders were designated as carnivores and herbivores. The deposit-feeders were subdivided into 'bulk' deposit-feeders, ingesting large volumes of mineral sediment (*Axiiothella serrata*, *Heteromastus filiformis*, *Tellina liliana*, etc.), and the 'fractional' deposit-feeders, browsing between and on the sand grains, or also ingesting individual grains at times (most of the spionid polychaetes, plus *Paradoneis* sp., *Capitella* sp., amphipods, etc.).

The assemblage was dominated by deposit-feeders as 32 species (68.1%), including 8 of the 9 most common species, were primarily deposit-feeders. Three species were suspension-feeders (6.4%) and 12 (25.5%) were carnivores. Deposit-feeding was presumed a secondary feeding method for three species, and 13 deposit-feeders could potentially feed by other means, mainly suspension-feeding, including bed-load feeding (feeding on bottom-drifting material). Fractional deposit-feeding species (19) outnumbered bulk deposit-feeders (13). Deposit-feeders comprised 95% of the individuals present (inclusive of 64% 'fractional' deposit-feeders), suspension-feeders 4%, and the remaining 1% were carnivores.

ZONATION

The average zonation patterns for each of the seven common (major) polychaetes and for minor species combined are presented in Fig. 6 and Table 3. 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* sp. and *Axiiothella serrata* were distributed across the flat without pronounced pattern. *Microspio* sp. was the numerically dominant species (Fig. 6b, Table 3) in all zones except six and eight, where *Heteromastus filiformis* was more dense. The minor polychaete species mainly occurred on the lower shore, especially in zone 8 (Fig. 6).

The seasonal changes in overall density of each of the major species are shown in Fig. 7, and the changes in zone density for each left and right transect separately are shown in Figures 8-12. 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 two transects 15 m apart showed whether apparent trends or zonation patterns were of wider extent than the 2 m strip of one transect; thus indicating the importance of shore-normal trends compared to random density variations. Significant positive correlation existed between the left and right transect seasonal zone means for all the major species except *Boccardia acus* (Table 4), confirming the general correspondence between transect pairs apparent in Figs. 8-12. Correlation of the *B. acus* substratum, the cockle *Chione stutchburyi*, was significant ($P < 0.001$).

TABLE 3. Polychaete species overall density (mean.m⁻²) and dominance (percentage of total polychaete individuals) per zone (combined left and right transects, November 1977-November 1978).

Species	Zones									
	1a	1	2	3	4	5	6	7	8	
<i>Microspio</i> sp.	density	5 646	6 226	4 167	4 044	3 427	3 396	3 431	4 898	2 895
	% dominance	54.3	52.4	46.7	43.3	35.7	31.7	27.8	47.4	37.9
<i>Capitella</i> sp.	density	1 491	3 157	2 839	3 034	3 097	1 948	919	382	111
	% dominance	14.3	26.6	31.8	32.5	32.3	18.2	7.4	3.7	1.5
<i>Heteromastus filiformis</i>	density	80	76	64	107	501	2 666	4 473	3 602	3 435
	% dominance	0.8	0.6	0.7	1.2	5.2	24.9	36.2	34.9	45.0
<i>Axiiothella serrata</i>	density	358	517	664	823	811	974	1 082	974	207
	% dominance	3.4	4.4	7.4	8.8	8.5	9.1	8.8	9.4	2.7
<i>Boccardia acus</i>	density	66	132	172	411	1 113	1 199	2 014	93	0
	% dominance	0.6	1.1	1.9	4.4	11.6	11.2	16.3	0.9	0
<i>Scolecoplepides benhami</i>	density	2 386	1 499	433	449	250	49	56	8	8
	% dominance	22.9	12.6	4.9	4.8	2.6	0.4	0.4	0.1	0.1
<i>Nicon aestuariensis</i>	density	338	223	545	425	314	158	107	52	20
	% dominance	3.2	1.9	6.1	4.6	3.3	1.5	0.9	0.5	0.3
Minor species	density	40	48	32	44	76	320	282	314	958
	% dominance	0.4	0.4	0.4	0.5	0.8	3.4	2.3	3.1	12.6
All polychaetes	density	10 404	11 878	8 916	9 337	9 590	10 710	12 364	10 323	7 634

¹excludes November juveniles

²May, August, November samples only

Fig. 6 Overall means per zone (combined data for all transects, November 1977 to 1978 samples).

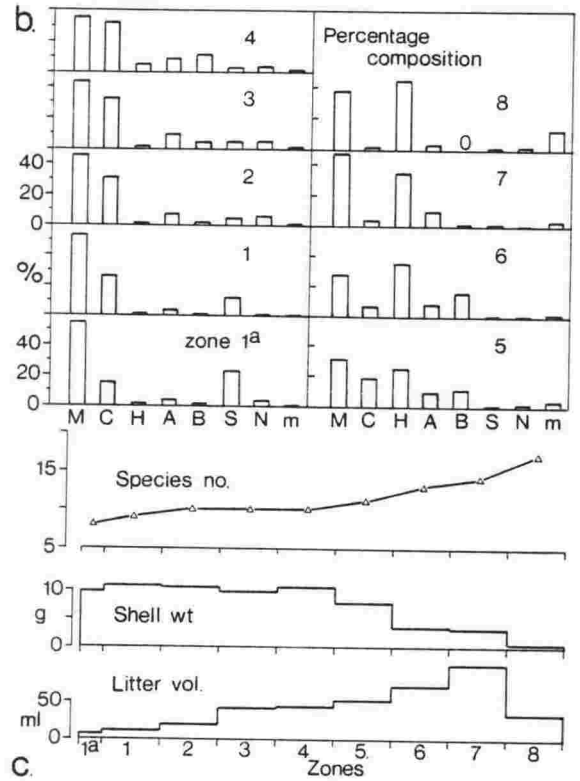
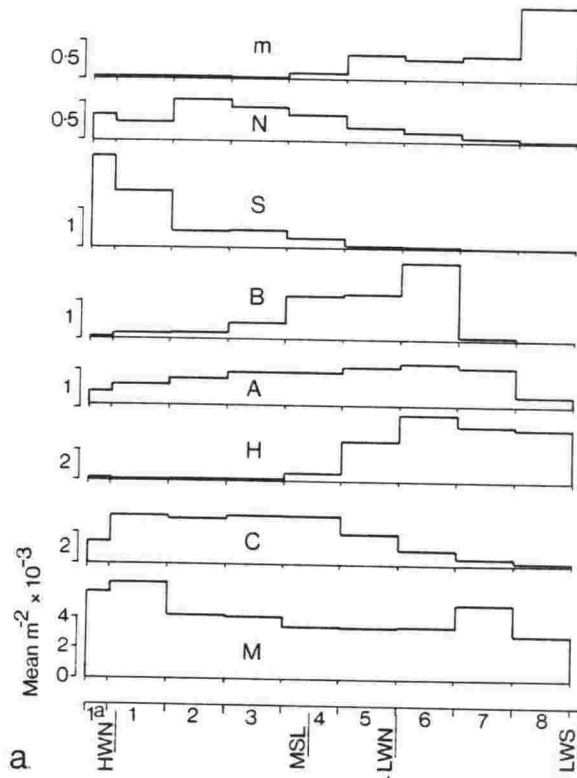
a) Zonation of major species and summed minor species (densities as thousands per m^2).

b) Percentage composition within zones of major species and summed minor species (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).

Plot labels are: M = *Microspio* sp., C = *Capitella* sp., H = *Heteromastus filiformis*, A = *Axiiothella serrata*, B = *Boccardia acus* (May to Nov.), S = *Scolecolepides benhami*, N = *Nicon aestuariensis*, m = minor species.

Fig. 7 Seasonal variation of major species in overall means per transect pair. a) thousands per m^2 , b) hundreds per m^2). Plot labels as in Fig. 6.



c.

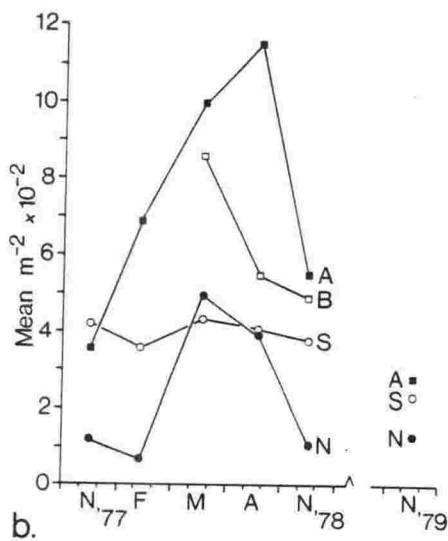
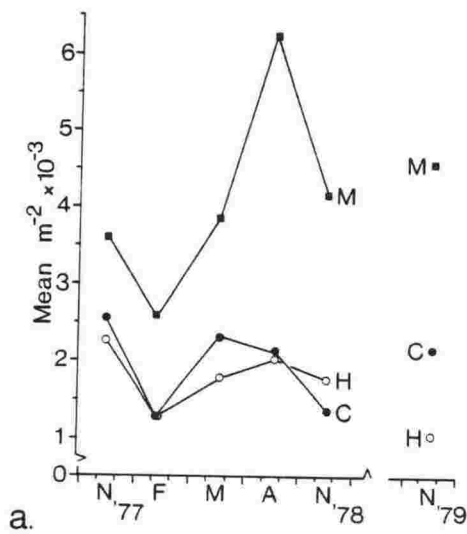


TABLE 4. Tests of transect pair correlation and differences (left and right transects) for each major species. Significant tests indicated as * ($P < 0.05$), ** ($P < 0.01$), and *** ($P < 0.001$), with non significant tests blank, and no data as -.

Test	Microspio sp.	Capitella sp.	Heteromastus filiformis	Ariothella serrata	Boccardia acus	Scolecoplepides benhami	Nicon aestuariensis
¹ Correlation of zone means (maximum n = 40) by Spearman's r _s	***	***	***	***	***	***	***
² Zone pair differences by Mann-Whitney U-test	Nov. zone 8* Feb. zone 1* May zone 1* Aug. zone 4* Nov. zones 1*, 2 & 6**	Nov. zone 4* zone 1**	zone 2*	-	zone 1*	zone 3*	
³ Complete transect pair differences by parametric difference-of-means test, and, in parentheses, Mann-Whitney U-test	Nov. differences by parametric difference-of-means test, and, in parentheses, Mann-Whitney U-test	(*)	*	-	-	*	
⁴ Non-random zone trends (χ ² test)	*		*			*	*

TABLE 4. Footnotes

- ¹ 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 *Scolecoplepides benhami* (zone 1 for this species a special case discussed later), so that paired zeroes did not exaggerate correlation.
- ² Because of the small sample size ($n = 10$) a significant difference occurs only if left and right distributions have little overlap. The test is not sensitive to differences inflated by one extreme value.
- ³ Comparison of left and right transect overall means (Σ zones 1-8) and also zones 1-8 distributions ($n = 80$).
- ⁴ Null hypothesis of 50% synchrony between left and right transects (i.e., both densities increasing, decreasing) tested with χ^2 .

TABLE 5. 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). 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	S a m p l e s				
			Nov. 77	Feb. 78	May 78	Aug. 78	Nov. 78
<i>Microspio</i> sp.	1+2:3+4:5+6:7+8 1-4:5-8	KW MWU				*	***
<i>Capitella</i> sp.	1:2:3:4:5 1-4:5-8	KW MWU	*** ***				* ***
<i>Heteromastus filiformis</i>	5:6:7:8 1-4:5-8	KW MWU	*** ***	*** ***	*** ***	*** ***	*** ***
<i>Axiiothella serrata</i>	1+2:3+4:5+6:7+8 1-4:5-8	KW MWU	** ***	** *			* *
<i>Scolecoplepides benhami</i>	1-4:5-8	MWU	***	***	***	***	***
<i>Nicon aestuariensis</i>	1-4:5-8	MWU	***	***	***	***	***
<i>Boccardia acus</i>	1+2:3+4:5+6:7+8 1-4:5-8	KW MWU	- -	- -	*** -	*** -	*** -

TABLE 6. 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, <i>Microspio</i> sp.		1-8	all	(-0.15) ^{**}	Nov. 1977 & 78	(-0.10), May & Aug. (-0.26) ^{**}
" <i>Capitella</i> sp.		1-5	"	(-0.19) ^{**}	"	" (-0.13), " (-0.25) [*]
" <i>Heteromastus filiformis</i>		5-8	"	(0.09) [*]	"	" (0.25) [*] , " (-0.36) ^{***}
" <i>Axiiothella serrata</i>		1-7	"	(0.19) ^{**}		
" "		1-8	"	(-0.10) [*]		
" <i>Nicon aestuariensis</i>		1-6	Nov. 1977 & 1978 & Feb. (-0.45) ^{***}		May & Aug. (-0.27) ^{**}	
² Litter, <i>Microspio</i> sp.		1a-8	all	(-0.03)		
" <i>Capitella</i> sp.		1a-5	"	(-0.28) ^{***}		
" "		1a-8	"	(-0.24) ^{**}		
" <i>Heteromastus filiformis</i>		4-8	"	(0.30) ^{***}		
" <i>Axiiothella serrata</i>		1a-8	"	(0.13) [*]		
" "		1a-7	"	(0.11)		
" <i>Nicon aestuariensis</i>		1a-6	May & Aug. (-0.13), Nov. 1977 & 1978	(-0.46) ^{***}		

- 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 μ m sieve (settled volume). Data of all samples except February and right transect November 1977.
- ³ Effects due to major zonation trends of species were minimised by using restricted ranges.

TABLE 7. Major species overall seasonal densities per m² compared with within-zone density changes (combined left and right transect data). (* 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
<i>Microspio</i> sp.						
Density m ⁻²	3610	2600	3860	6260	4180	4560
Change (±)	*	*†	*†	*†	*-	+
Zones of significant change	3,7	1,8	1,3,4,6	1,3,4,5		5
<i>Capitella</i> sp.						
Density m ⁻²	2540	1280	2310	2120	1370	2180
Change (±)	*	*†	-	-	*-	+
Zones of significant change	3,4,6,7,8	1,2			1	1,3,6
<i>Heteromastus filiformis</i>						
Density m ⁻²	2250	1290	1770	2010	1760	1050
Change (±)	*	*†	+	+	-	-
Zones of significant change	4,5,8	4,5,6,(8-)				6

TABLE 7. (Contd.)

Species	Nov. 77	Feb.	May	Aug.	Nov. 78	Nov. 79
<i>Axiiothella serrata</i>	Density m^{-2} 350 Change (\pm) ‡ Zones of significant change 5, 6, 7	690 ‡ 4	1000 + ‡	1150 ‡ 3, 6, 7	550 - 3, 5	270 - 3, 5
<i>Boccardia acus</i>	Density m^{-2} n.d. Change (\pm) Zones of significant change	n.d. - 6	860 - 6	540 - -	480 - -	n.d. - -
<i>Scolecoplepides benhami</i>	Density m^{-2} 420 Change (\pm) Zones of significant change	360 - 1	410 + 1	400 - (2+)	380 - -	230 - -
<i>Nicon aestuariensis</i>	Density m^{-2} 120 Change (\pm) Zones of significant change	60 * 2	490 * 2, 3, 4, 5, 6	390 * 2, 4 (1+)	100 * 1, 3, 5	120 + -

The left and right transect pair means, frequency distributions, and zone distributions were also similar, not often differing significantly (Table 4). The most strongly zoned species, *Heteromastus filiformis*, had no significant variation between equivalent left and right transect zones, and *Microspio* sp., a much less zoned species, the most variation. *Microspio* sp. was the only species to have more than two of the total 40 zone pairs differing significantly. However, there was no overall left- to right-zone inequality (sign test). It was also one of three species in which zone to zone trends (increases or decreases, regardless of magnitude or statistical significance) synchronised between left and right transects to a significant level; the others being *Heteromastus filiformis* and *Nicon aestuariensis* (Table 4).

ZONATION PATTERNS AND SEASONAL CHANGES

The significance of zonation within each seasonal sample was tested for the seven major species (Table 5). Within the zones of abundance the densities were further tested for significant correlation (at sampling unit level) with distance downshore and litter volume (Table 6). Correlation with downshore distance would suggest a possible tide-level related density trend, and with litter, a possible trophic relationship. The statistically significant changes within zones between the seasonal samples are listed in Table 7.

Microspio sp. density appeared to be mostly unaffected by intertidal environmental gradients within the intertidal strip sampled (Fig. 8a), but between left and right transects some concordant density changes occurred (e.g., high densities in zones 3 and 7 in November 1977, zone 1 in August, low density in zone 5 in Nov-

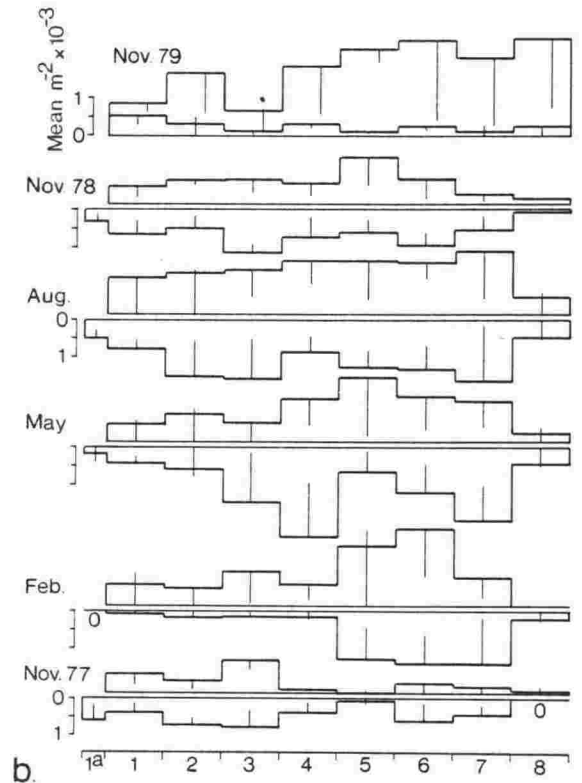
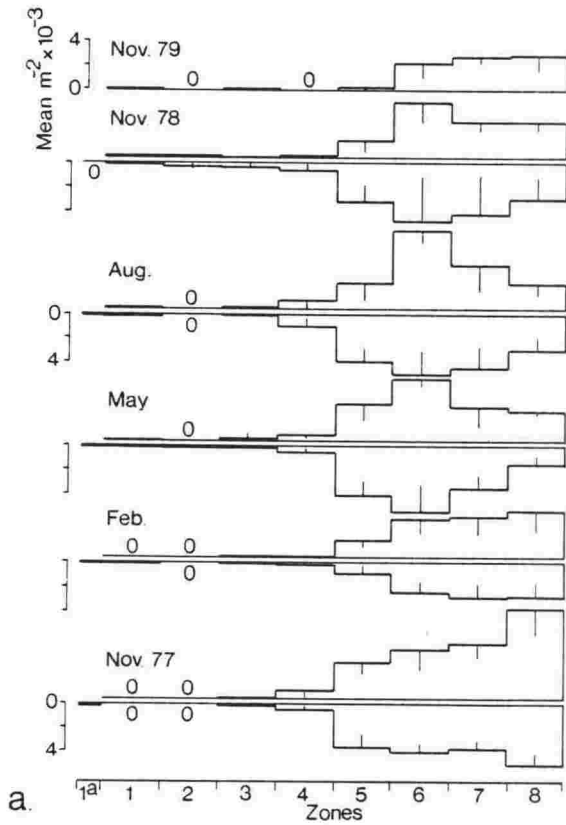
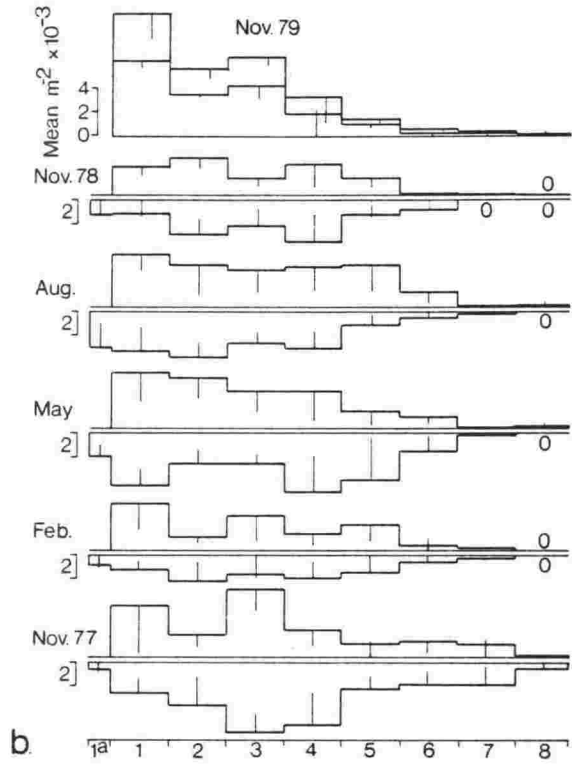
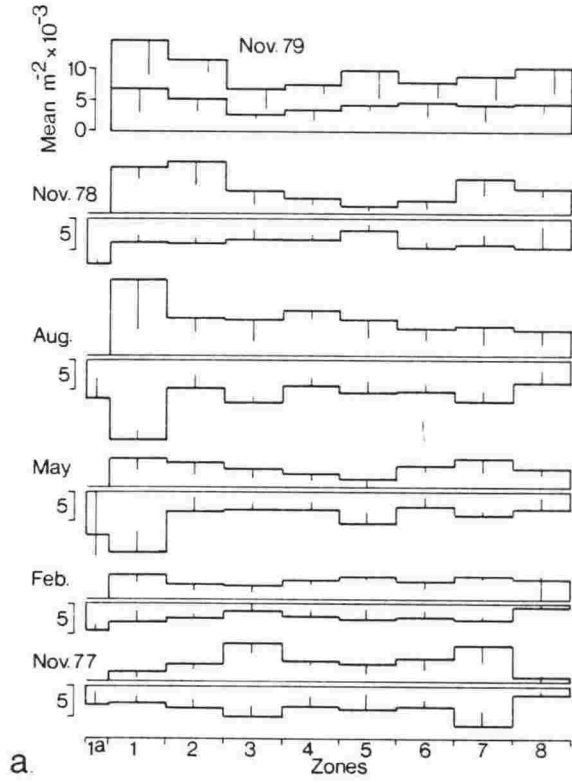
ember 1978), and there was correlation between zone pairs (Table 4). Compared to other species *Microspio* sp. had a large number of significant seasonal changes within zones (Table 7). The changes all followed the overall population trends. The significant density increases in zone 1 in May and August suggest denser recruitment/superior survival at that time. Significant unevenness in overall zonation occurred in August and November 1978. *Microspio* sp. was negatively correlated to distance downshore, especially in autumn-winter samples when there were high upper shore densities (Table 6). *Microspio* sp. had almost no correlation to the amount of buried plant litter present which increased downshore to a zone 7 peak (Fig. 6c, Table 6). The distribution of the 250-500 μ m sieve fraction 'juveniles' in November 1979 (Fig. 8a) was very similar to the >500 μ m fraction.

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

Heteromastus filiformis was uncommon above zone 4 and had significantly uneven zonation on the lower shore (Fig. 9a, Table 5).

Fig. 8 Seasonal zonation of a) *Microspio* sp.,
b) *Capitella* sp., as zone means (thousands) per m².
Left (top) and right (bottom) transects plotted
separately, 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 μ m sieve density is indicated.

Fig. 9 Seasonal zonation of a) *Heteromastus filiformis*,
b) *Axiiothella serrata*. Zone means as thousands per m²,
and other conventions as in Fig. 8. 250 μ m sieve density
for *H. filiformis* was zero.



The dense populations in zone 8 in November 1977 and zone 6 in May, August and November 1978 are of interest. The zone 8 density significantly declined from November to May, and the February to May decline was against the overall population trend (Table 7). Thus in zone 8 below average survival/recruitment occurred, while in zone 6 the converse was the case, and the latter replaced zone 8 as the densest population.

Within zones of abundance *Heteromastus filiformis* was significantly positively correlated with downshore distance in the November samples, but was negatively correlated in the May and August samples (attributable to zones 6 and 8 density changes). It was significantly positively correlated with plant litter (Table 6).

Axiothella serrata did not show consistent zonation patterns except that the zone 8 densities were low (Fig. 9b, Table 5). Zone to zone changes within seasonal samples were otherwise erratic, and left-right zone pairs, although rarely significantly different (Table 4), were not closely similar. As previously mentioned, there was highly significant overall correlation. The seasonal within-zone changes followed the overall density changes (Table 7). The appearance of a new age group was the reason for the large pattern change between November and February (Section 2). *Axiothella 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 (all zones), but became non-significant without zone 8 densities (Table 6). The November 1979 250-500 μ m fraction contained large numbers of early juveniles from a recent spawning of *A. serrata*, and these were denser on the lower shore (Section 2).

Zone-specific influences on the density of *A. serrata* and *Microspio* sp. have been demonstrated (left and right transect corre-

lation), but correspondence in zone to zone trends between these two 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). Thus there is no evidence that the factors operating zone-wide against survival were the same for both species (sampling-unit-level correlation is discussed later).

Boccardia acus is a facultative epizoon of the cockle *Chione stutchburyi*, boring into the shell buried just below surface, and constructing a short sand-grain tube-extension near the siphons. *Boccardia acus* was significantly zoned, increasing gradually in density downshore to a zone 6 peak before decreasing (Fig. 10, Table 5), whereas *Chione stutchburyi* was densest in zones 3 and 4. The number of *Boccardia acus* per cockle was highest in zone 6. No significant overall density changes occurred between the three seasonal samples (Table 7). *B. acus* density per m² was highly correlated with cockle density ($P < 0.0001$, correlation excluding cockle zero occurrences), but was also likely to have been influenced by the size distribution of cockles and hence the actual total area of habitat available for colonisation. The *B. acus* per cockle link with cockle size was apparent in a large collection of cockles available from June-July 1976 random samples between zones 3-6. For all cockles over 5 mm length cockle-size (in 1 mm classes) was noted together with *B. acus* counts. Cockles of length up to 11 mm had no *B. acus*, and all size classes to 28 mm (maximum size 32 mm) had some individuals free of *B. acus*. Altogether 42.0% were free of *B. acus* (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 ($r_s 0.44$, $P < 0.0001$, $n = 550$), as was also apparent from the steady increase in mean density per cockle size group (Table 8).

Fig. 10 *Boccardia acus* variation in zonation and the *B. acus* relationship to *Chione stutchburyi*. Conventions as in Fig. 8.

- a) *B. acus* zone means as thousands per m^2 for May, Aug. and Nov.
- b) Overall zone means for *C. stutchburyi* (hundreds per m^2), and *B. acus* (numbers per cockle), using summed data of all transects.

Fig. 11 Zonation of *Scolecoplepides benhami*. Conventions as in Fig. 8.

- a) Seasonal zonation as zone means (thousands) per m^2 .
- b) Density trends within zones 1a - 3 of *S. benhami* compared to *Microspio* sp. Mean densities are thousands per m^2 within subzones 4 m long, using sum of all data.

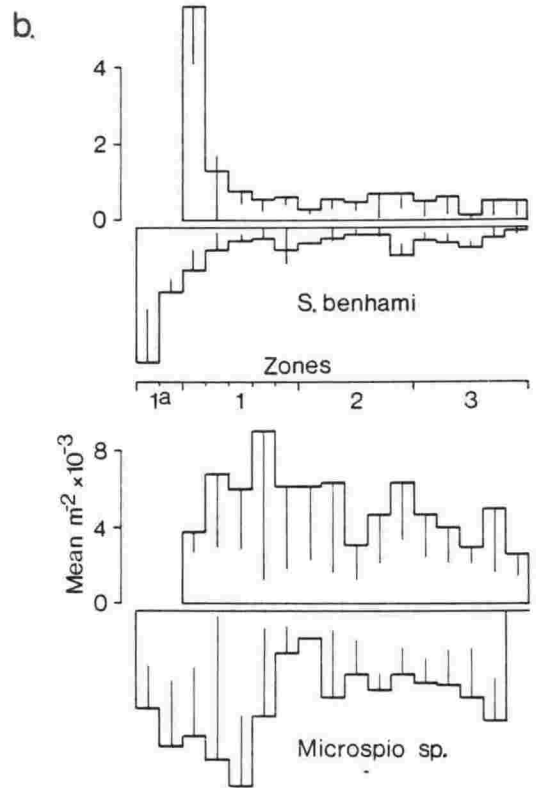
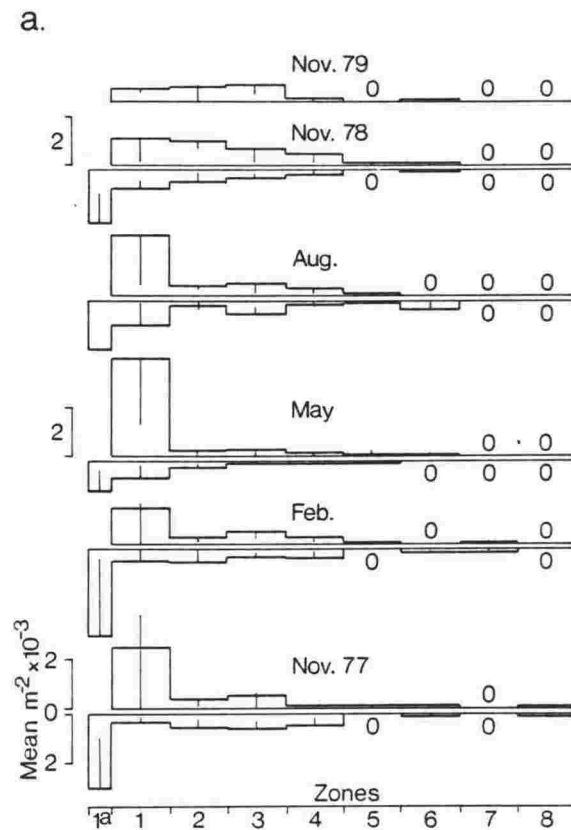
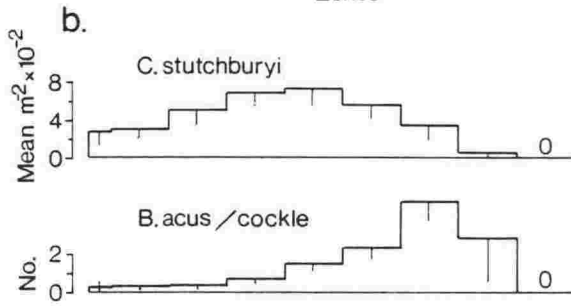
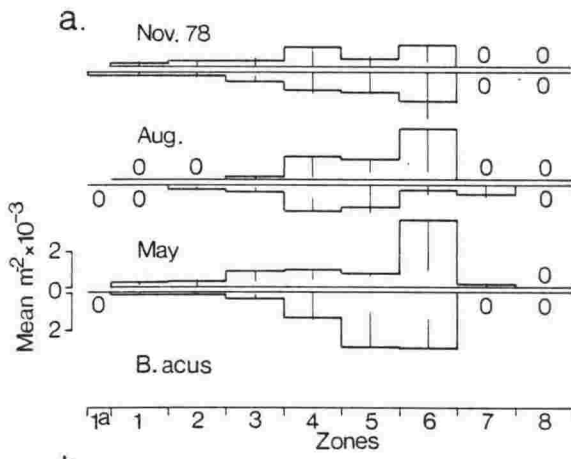


TABLE 8. *Boccardia acus* density within *Chione stutchburyi* size classes (3 mm groups).

Cockle size (mm)	11-13	14-16	17-19	20-22	23-25	26-28	29-31
Mean <i>B. acus</i> per cockle	0.54	1.05	1.48	1.83	2.62	4.11	5.50
Variance	0.968	1.944	2.706	3.400	5.330	10.173	12.70
Cockle no.	68	76	120	136	89	55	6

Scolecopides benhami occurred in a band of high density at the upper edge of the sand flat, with few individuals below zone 4 (Fig. 11a). The density increased to a peak within four metres of the cobble zone at the edge of the sand flat, whereas densities of *Microspio* sp., presented for comparison, were highest 12-20 m downshore (Fig. 11b). Comparisons of *Scolecopides benhami* density between transects did not often show significant differences (Table 4) 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 (Table 7), occurring against the trend of a slight overall decrease.

Nicon aestuariensis was significantly more dense on the upper shore with very few individuals in zone 8 (Fig. 12, Table 5). 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 7). The remaining significant within-zone changes followed the overall density changes. Left to right transect correspondence was good; only the February zone 3

pairs differing significantly (Table 4). Within its zones of abundance (1-6), *N. aestuariensis* was negatively correlated with downshore distance and with litter (Table 6).

Zonation of the four commonest minor species is shown in Fig. 12b. *Paradoneis* sp. and *Cirratulus* sp. occurred predominantly 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* occurred mainly on the middle to lower shore.

Species restricted to zone 8 were *Prionospio aucklandica*, *Sphaerosyllis* sp., *Goniada* sp., *Glycinde dorsalis*, *Glycera lamelliformis*. Amongst the remaining minor species *Desdemona* sp. and *Microphthalmus paraberrans* occurred in zones 6-8, *Aonides trifida* occurred only in zones 5 and 6, *Scoloplos cylindrifer* in zones 3 and 4, *Ceratonereis* sp. in 1 and 1a, generally close to the cobble shore, and *Perinereis vallata* in every zone.

INTER-SPECIES CORRELATION

As interactions amongst species may be one factor affecting abundances and zonation pattern, it was of interest to determine whether, within their coinciding zonation, the major species were associated in any way. Results of Spearman's correlations at the sampling-unit level are summarized in Table 9. Less abundant species were not included because of the high number of zero occurrences, and *Boccardia acus* was represented in the correlation series only indirectly through the occurrences of its substratum, the major non-polychaete, *Chione stutchburyi*. To minimise effects due to coinciding or opposing zonation patterns, only occurrences within the overlapping zones of abundance were correlated (see Table 9). For example, the *Capitella* sp. and *Heteromastus filiformis* correlation was examined over zones 5 and 6.

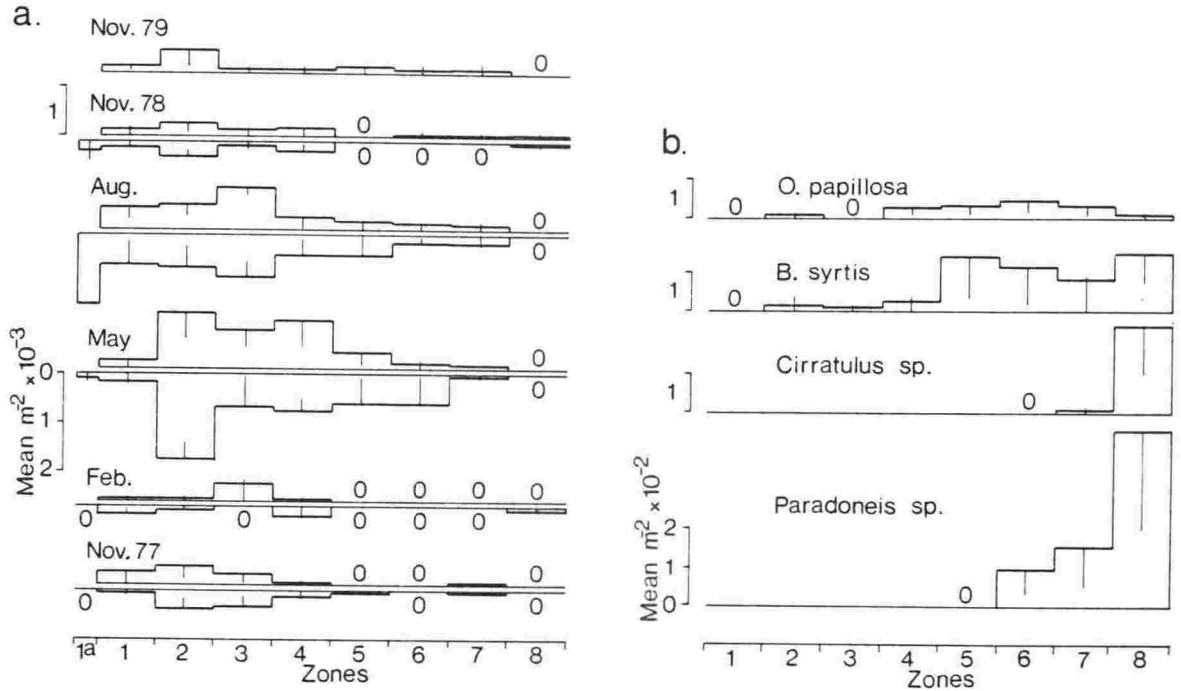


Fig. 12 Seasonal zonation of *Nicon aestuariensis* and zonation of four minor species. Conventions as in Fig. 8.

- a) *N. aestuariensis* zone means as thousands per m^2 .
- b) *Paradoneis* sp., *Cirratulus* sp., *Boccardia syrtis* and *Orbinia papillosa* overall zone means as hundreds per m^2 from summed data of all transects.

This approach assessed the association when both species were present in numbers. Over the whole shore *H. filiformis*, the only abundant species concentrated on the lower shore, will have negative correlation with the species abundant upshore, and similarly those upper shore species will tend towards negative correlation with a species abundant over the whole intertidal. Correlation assessments less influenced by the established zonation were sought.

Correlations potentially indicating interaction amongst species were few. For all samplings combined 15 species pairs gave 4 significant positive correlations and 1 negative, and for each sampling time separately 60 pairs gave 3 negative and 4 positive correlations (Table 9). *Microspio* sp. had significant positive correlation with *Capitella* sp. (combined samples and for November 1978), and with *Axiiothella serrata* (combined samples and November 1977). However, between *Capitella* sp. and *Axiiothella serrata* correlations were not significantly positive except for November 1977, and there was significant negative correlation in November 1978. Correlation of these three species with *Heteromastus filiformis* was not significant except for *Capitella* sp. in one sample (negative in November 1979). *Nicon aestuariensis*, tested when most of the population were O group individuals, had a significant (negative) correlation with *Heteromastus filiformis* only. *Chione stutchburyi* had significant positive correlations with *Capitella* sp. (combined samples, also November 1978) and *Heteromastus filiformis* (combined samples and May 1978), and negligible correlation to other species. *Scolecoplepides benhami*, with its significant numbers occurring only in zone 1, was not tested except with *Microspio* sp., with which a negligible positive correlation occurred (r_s 0.06, zone 1 combined samples).

TABLE 9. Species correlations (Spearman's r_s values). Major polychaete species inter-correlations and correlations with *Chione stutchburyi*. (* $P < 0.05$, ** $P < 0.01$). Effects due to major zonation trends minimised by using restricted ranges. *Nicon aestuariensis* was tested only when numerous (May and Aug. combined).

Correlation pair		Zones	S a m p l e s					
			All	Nov.77	Feb.	May	Aug.	Nov.78 Nov.79
<i>Microspio</i> sp.,	<i>Capitella</i> sp.	1a-6	0.18**	0.23	0.03	0.15	0.10	0.26* -0.10
"	"	5-8	0.08	-0.27	-0.06	0.01	0.22	0.25 0.01
"	<i>Axiiothella serrata</i>	1a-8	0.18**	0.30**	0.21	-0.12	0.18	-0.02 0.12
"	"	<i>Nicon aestuariensis</i>				-0.11		
"	"	<i>Chione stutchburyi</i>	-0.07	0.01	-0.07	-0.18	-0.04	0.03 -0.35
<i>Capitella</i> sp	<i>Heteromastus filiformis</i>	5-6	0.04	0.23	-0.40	0.24	-0.05	-0.1 -0.97*
"	"	<i>Axiiothella serrata</i>	0.04	0.38**	-0.02	0.09	-0.03	-0.33** 0.24
"	"	<i>Nicon aestuariensis</i>				0.02		
"	"	<i>Chione stutchburyi</i>	0.18**	0.18	0.18	0.21	0.10	0.28* -0.03

TABLE 9. (Contd.).

Correlation pair	Zones	S a m p l e s						
		All	Nov.77	Feb.	May	Aug.	Nov.78	Nov.79
<i>H. filiformis</i> , <i>Ariothella serrata</i>	5 - 8	-0.04	-0.19	-0.30	0.29	0.14	0.14	-0.18
" " <i>Nicon aestuariensis</i>	5 - 6				-0.44**			
" " <i>Chione stutchburyi</i>	5 - 6	0.22*	0.20	-0.38	0.52*	0.12	0.16	0.0
<i>A. serrata</i> , <i>Nicon aestuariensis</i>	1a-6				0.04			
" " <i>Chione stutchburyi</i>	1a-6	-0.05	-0.09	-0.16	0.09	-0.09	-0.03	-0.13
<i>C. stutchburyi</i> , <i>Nicon aestuariensis</i>	1a-6				-0.11			

Microspio sp., *Capitella* sp., *Heteromastus filiformis*, and *Axiiothella serrata* had no apparent correlation with the nemerteans which were possible predators of them. The method used to test the association of the two low density nemerteans with the common species was to compare means of the latter, compiled for the alternatives of uncommon species present or absent (Greig-Smith 1964). Differences between means were very small. The nemerteans did not significantly reduce worm density in the cores in which they occurred, and were not located amongst aggregations of potential prey.

DISCUSSION

ZONATION PATTERN

Microspio sp., *Axiiothella 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 two species elsewhere in the inlet lie at an elevation about 30 cm above the truncated upper shore of the transect site. *Microspio* sp. density distribution at some beach levels showed good correspondence at times between transect pairs, possibly indicating sufficient environmental heterogeneity linked to beach level to affect settlement/mortality rates. Alternatively, favourable hydrodynamic factors at a time when numerous larvae were settling from the plankton may have caused heavier settlement at one beach level.

Axiiothella serrata showed the least structured distribution pattern of all the major polychaetes. Correlation with distance downshore indicated higher densities occurred in toto downshore to zone 7. However, it had low densities in the near

constant immersion conditions of zone 8. Continued immersion in itself was not the likely cause as *A. serrata* tolerates this for many months in laboratory conditions, and increasing predation by fish seems unlikely to have caused such a clear drop. Plant litter content of the sediment similarly dropped sharply in zone 8, but may not have been an important influence on *A. serrata* distribution as correlation over zones 1-7 was much weaker than over zones 1-8.

Zonation of *Heteromastus filiformis*, and of many of the minor polychaete species occurring only on the lower shore, may be restricted by the longer emersion times and probable greater variability of the upper shore conditions. They are subtidal species whose distributions can extend into the intertidal from the subtidal shallows. Some previous reports of *H. filiformis* in the intertidal also suggest peak abundance on the lower shore (Estcourt 1967b, Maurer and Aprill 1979). Physico-chemical extremes and disturbance would affect the juveniles near the surface much more than the deep-burrowing adults, which may have low mortality in the intertidal (Shaffer 1979). *H. filiformis* has wide salinity tolerances, and a wide range of sediment grades are occupied (Estcourt 1967b, Wolff 1973, Kinner and Maurer 1978). Therefore, the relatively minor intertidal changes in salinity regime and sediment characteristics are unlikely to have affected its abundance substantially. *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 anoerobic sediment has often been noted (Pearson and Rosenberg 1978, Knox and Fenwick 1981, and references therein).

Scolecoides benhami, *Nicon aestuariensis* and *Capitella* sp. were all more abundant on the upper shore. *Scolecoides benhami* and *Nicon 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 and Akroyd 1978). A possible linkage of zonation with salinity regime on the Pauatahanui site was suggested by the occurrence in zone 1 only of *Ceratonereis* sp., a known upper estuarine species (Smith 1971, Read 1974, as *C. erythraeensis*). There was, however, no pronounced intertidal salinity gradient in the interstitial waters; the data indicate only that overlying water salinity drops less frequently on the lower shore of the site, most probably because below the neap tide range the surface water of lowest salinity contacts sediment surfaces less frequently.

Scolecoides benhami does tolerate fully marine salinities, occurring occasionally at low densities on sheltered beaches (Morgans 1967b, personal records). Morgans' (1967a) report of *S. benhami*, "whose abundant tubes form a sort of 'turf' below MLWS," on an open beach (Ingles Bay) at Kaikoura may be a misidentification, as *S. benhami* does not form a tube. Its distribution can also extend to the highest levels of the shore that are only briefly or even infrequently covered by the tide (Estcourt 1967b, and personal observations). High zone 1 and 1a densities of *S. benhami* relate to the proximity of the cobble zone rather than to tide level (Fig. 11b).

Nicon aestuariensis does not occur outside estuarine environments. Much higher adult densities (to 6000 m^{-2}) have been recorded elsewhere in oligohaline conditions (Avon-Heathcote Estuary at mid tide level, Estcourt 1967ab; Westshore Lagoon, Knox et al. 1978), and Estcourt (1967b) reported a change to low densities in salinities similar to the Pauatahanui regime. If Pauatahanui conditions are not optimal, the slightly more saline regime of the lower shore might be

adversely influencing the success of *N. aestuariensis*. The density trend may also relate to the prolonged immersions and more homogeneous sediments of the lower shore.

Capitella spp. are more usually found in the shallow sub-tidal, and so there is little information available on their intertidal zonation. However, Dauer and Simon (1975) similarly report a *Capitella* sp. zoned in the upper intertidal in a polyhaline sheltered environment (Tampa Bay, Florida). Within New Zealand an Avon-Heathcote occurrence was from a polluted low tide site (Estcourt 1967b), and may not be the same species as at Pauatahanui, although a morphologically similar *Capitella* does occur in the estuary (personal records).

Capitella sp. had a negative correlation with litter volume and an opposite trend in zonation. In contrast, previous studies suggest correlation should be positive. *Capitella* species can be cultured on macrophyte detritus (Foret 1975, Tenore 1975) and adjust well to organically enriched situations (Reish 1960, Pearson and Rosenberg 1978). Possibly in the wave-mixed surface layers occupied by *Capitella* sp. the fine detritus likely to be ingested by these small worms assumes a different distribution than the more deeply buried litter.

Boccardia acus zonation differed from the density zonation of *Chione stutchburyi*, its only suitable substratum at Pauatahanui. Elsewhere the worm occurs intertidally on sandstone reefs and in borings on other molluscs (Read 1975). Therefore, *Boccardia acus* is not necessarily closely adapted to environmental conditions optimal for *Chione stutchburyi*. However, the larger 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 the zone 6 *Boccardia acus* density peaks (per m² and per cockle). Cockles below 11 mm length were apparently too small for *B. acus* to settle on successfully, but 32% of the cockles above that size escaped infestation and densities per cockle were rarely high, suggesting *B. acus* did not have optimal conditions for colonisation.

ZONATION AND ENVIRONMENTAL GRADIENTS

The assumption underlying single transect reports of zonation is that the patterns revealed are representative of a length of beach. Alongshore consistency of zonation pattern on an apparently uniform shore has rarely been studied, but Dauer and Simon (1975) found good correspondence of patterns and densities between three transects spaced 0.8 and 1.6 km apart along a uniform strip of causeway beach (Tampa Bay, Florida). When profile and sediment grade change alongshore large differences in zonation may occur, such as Fincham (1971) reported for amphipods between three transects over a 150 m strip (Port Erin, Isle of Man). In a more extreme case Maurer and Aprill (1979) did not detect faunal zonation and found large differences in macrofaunal density and biomass between two transects 30 m apart in an unstable sand bar and trough environment (Delaware Bay mouth).

On wide intertidal flats of enclosed shores such as Pauatahanui Inlet, where wave action is reduced, beaches are relatively stable with gentle slopes, grain sizes are fine, and water tables remain near surface due to capillary rise, the low tide physico-chemical gradients are not pronounced. The faunal zonation may not be marked under such conditions unless associated sediment grade changes also occur (Newell 1979). However, on sheltered tidal flats the hydrodynamics of water

level rise and fall tends to produce a gradient of decreasing grain size shorewards (Postma 1961, Swinbanks and Murray 1981), and when the enclosed shore is estuarine a tide-related salinity regime may also act to strengthen shore-normal zonation. Concomitant along-shore environmental variation due to local physiography, currents and winds, presence of drainage channels, shell banks, and freshwater inflows may also be influencing distributions. When there are environmental gradients in several directions consistent shore-normal zonation may break up into mosaic density patterns (e.g., Bassindale and Clark 1960).

In the Pauatahanui case the site was apparently uniform for some distance alongshore. Shore-normal environmental gradients were probably not pronounced, although variability increased upshore (in e.g., temperature and salinity). Over much of the intertidal variation in sediments was undramatic, but the small changes in characteristics had shore-normal orientation. The faunal density variation was similarly shore-normal. Species abundances varied 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 environmental effects on the latter species would not have been detected with a solo transect.

Some possible influences on zonation at the Pauatahanui site have been discussed for each species and speculations made as to their importance, but no definite relationships were demonstrated. The data indicate that the contributory causes of zonation limits were relatively constant in their effects. Noticeable density changes of *Heteromastus filiformis* (upshore decline), and *Capitella* sp., *Scolecoides benhami*, and *Nereis aestuariensis* (downshore decline) occurred at about the same level on the shore (around zone 5). The

most likely common influence, directly or indirectly, is the increased rate of change in the durations of emersion/submersion around low water neap level.

Most physico-chemical stresses generating zonation operate at the upper range of a distribution. The species declining down-shore may be specialist intertidal species, but if so, it is only possible to conjecture on what factors contribute to their success in this environment and cause them to be less successful below low water. The accommodation of several of the species to the intertidal is indicated by continued feeding when emersed. *Axiiothella serrata*, *Nicon aestuariensis*, and *Scolecopides benhami* have been observed with bodies partly exposed foraging on surface sediment at low tide. Biotic influences associated with the tidal cycles may occur. Predation pressure by subtidal predators on the near-surface polychaetes would increase with longer periods of submergence. Primary production of surface microflora utilised as food may increase upshore, as has been recorded elsewhere (Cadée and Hegeman 1977).

ZONATION AND SPECIES INTERACTIONS

Interactions among intertidal organisms, commonly further compressing zonation inside the physico-chemical tolerance limit, have long been known from rocky shores (e.g., Lewis 1964). More recently Croker and Hatfield (1980) have found competition-derived zonation contraction occurring seasonally in intertidal amphipods of a sandy shore. It is now well established that negative interactions between polychaetes do occur, especially in dense infaunal assemblages. These interactions range from amensalism (including environment alteration), through competition, to predation (Witte and de Wilde 1979, Weinberg 1979, Whitlach 1980, Wilson 1981,

1983, Levin 1981, Brenchley 1981, 1982). No case having direct zonation effects is known to me, although Dauer and Simon (1976) have suggested a temporary lack of species interactions explained the expanded intertidal distributions of some polychaetes in the first year of recolonisation of a defaunated habitat.

The studies cited above suggest several ways in which the abundant Pauatahanui polychaete species might affect the occurrence of others. They are all deposit feeders, and overlap between the spectra of organic material sought by each may result in competition or amensalism. *Nicon aestuariensis* may also be a predator. Surface-feeding species, *Microspio* sp., *Axiiothella serrata*, *Scolecopides benhami*, *Nicon aestuariensis* and *Boccardia acus* may come in contact, and might possibly consume or disturb settling larvae. *Axiiothella serrata*, a depositor of large quantities of sediment taken mainly from the surface (unpublished data), may disrupt activities of near surface species.

At Pauatahanui negative interactions strong enough to alter zones-of-abundance were, a priori, likely to occur only with *Heteromastus filiformis*, the one major species with a directly opposing zonation pattern to other species; although interactions among other species could have been influencing their abundances. The sampling-unit size involved was too large to detect interactions between neighbouring individuals, but could have been expected to indicate aggregations of one species correlating with depressed or raised abundances of another. The interspecies correlations did not, however, detect effects attributable to interactions at the site. *H. filiformis* did not have an overall negative correlation, except with the juvenile-dominated *Nicon aestuariensis* population. Interaction appears unlikely as *Heteromastus filiformis* feeds well below

surface. Despite the similar zonations of some species and the similar seasonal density patterns of most major species, few significant correlations occurred, and no species pair had consistent positive or negative r_s values for the series of samples. Densities of fauna may have been insufficient to produce interaction effects on a large scale. Survivors of species subject to disturbance or predation as larvae may have been redistributed with time so that the effects of previous negative interactions were not detectable. Combining these two points, Peterson (1979) has suggested competitive exclusion will not occur when negative effects on larvae result in adult densities reduced below carrying capacity. The interacting spionid pair studied by Wilson (1983) may be an example of this.

The weak correlations between Pauatahanui species also indicate the relatively uniform and favourable environment and weak gradients. If the environment had been more heterogeneous, then stronger correlations would probably have been found.

SEASONAL ZONATION VARIATION

Environmentally controlled seasonal changes in zonation of intertidal infauna may occur due to erosion, deposition, and profile changes (Ansell et al. 1972, Moore 1978, Yeo and Risk 1979), due to the temperature regime (Hager and Croker 1979, Reading 1979), and to the salinity regime (Boesch 1977). But, as well as those forced changes, there may be change related to the annual cycle of reproduction and recruitment within a population; also, following seasonal recruitment, a degree of age zonation may be temporarily superimposed on the distribution pattern. Reported polychaete examples include the distribution of the surf-shore opheliid, *Thoracophelia mucronata*, in which young worms were present only low on shore (Dales 1952), and of the sand-flat lugworm *Arenicola marina*, in which young worms always

concentrated high on the shore, and only later migrated downshore (Beukema and de Vlas 1979, Farke et al. 1979). Longer-term age zonation might arise when a locally dense population of one age group adversely affects subsequent settlement (see discussion by Woodin 1976).

At Pauatahanui, where seasonal environmental changes were undramatic, the zones of abundance of the major species did not change during the period of sampling (except perhaps for *Capitella* sp. with an initial decline in zone 7, and for *Nicon aestuariensis* with less distinct pattern). However, there were significant seasonal density changes within those abundance zones. These changes followed the overall density changes of the populations with three exceptions only: a more even distribution of upper shore *Nicon aestuariensis* in August; and of *Scolecoplepides benhami* in November 1978; and a zone 8 decline of *Heteromastus filiformis* between February and May. The first two changes might indicate movement of individuals as the zone increases occurred when overall recruitment was not occurring.

The overall density changes were mainly caused by increased recruitment following the breeding seasons (see later), and not by environmentally-mediated, seasonally-increased mortality. However, significant change or redistribution of density within zones of abundance, attributable to differential mortality or recruitment, did occur in *Microspio* sp., *Heteromastus filiformis* and *Axiiothella serrata*. Thus the density pattern of those species varied within zones of abundance which were persistent. Such variation in mortality and recruitment between zones might result from chance factors, or possibly small changes in the local environment. It might also be a consequence of previously established age zonation and arise from negative adult to juvenile interactions or senescent mortality of an older age group.

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S E C T I O N 2

POPULATION DYNAMICS OF *AXIOTHELLA SERRATA* (POLYCHAETA:MALDANIDAE)

ON A PAUATAHANUI INLET INTERTIDAL SAND FLAT

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ON A PAUATAHANUI INLET INTERTIDAL SAND FLAT

ABSTRACT

The population dynamics of the deposit-feeder *Axiiothella serrata* Kudenov and Read was investigated from seasonal samples, 500 μ m sieve processed, taken from a stratified transect pair, and from subsequent, more frequent, fine-sieved samples during the juvenile recruitment period.

New O group began to appear in October-November, at first below 3 cm depth as aggregations of 4- to 7-setiger juveniles. The aggregations, from 7 to 15 per m^2 and comprising up to 900 juveniles, are believed to represent groups of lecithotrophic siblings developing from sub-surface egg masses without a planktonic larval stage. Juveniles became surface-dwelling and, despite an aggregated origin, were dispersed rapidly over the intertidal.

Juvenile setiger-total frequencies indicated synchronised adult spawning occurred at varying intervals during an approximately six-month spawning period (October to April) in 1978-79. Juvenile

density peaked at about 29 thousand m^{-2} in December 1978 (250 μm sieve estimate), and mortality after recruitment ceased was of the order of 0.02 individual $^{-1}$.day $^{-1}$, or 96% in 6 weeks.

Three age classes, O, I, and II+, were separable by width size-frequencies in November and February quarterly samples, with I and II+ groups merging in May. Densities in November of I plus II+ groups ranged between 270 and 550 m^{-2} between 1977-1979. The density of new recruits varied from year to year, possibly linked to variation in the size of the spawning II+ group.

The number of setigers was the most sensitive indicator of size and age in juveniles of up to about 15 setigers. However, the setiger development rate declined as the total of 22 was approached, hence the relationship of body dimensions to setiger-total had an exponential form. Length combined with width as a volume had a better overall relationship to setiger-total than either individually. Width modes indicated growth from about 110 μm to about 550 μm in the first year and to about 1600 μm in the second year.

Zonation patterns were variable and age-specific, differing even between young and old juveniles. Factors and mechanisms possibly responsible for the dispositions were discussed.

INTRODUCTION

Axiothella serrata Kudenov and Read is found on sheltered intertidal flats of the northern South Island and Porirua Harbour, North Island (Kudenov and Read 1977). A large deposit-feeding species occupying a fragile U- or J-shaped vertical tube, it is an important tide-flat sediment processor, often generating a characteristic cast

and pit topography (Plate 1) by bulk sediment ingestion near-surface and subsequent faecal production.

Axiothella serrata was the most amenable of the Pauatahanui site polychaetes to the analysis of age structure from size-frequencies because it had a large size range during growth from benthic juvenile to adult, and an identifiable O group due to a defined breeding season. The population dynamics of this species was explored using the 1977-78 paired transect samples discussed in Section 1 to establish adult densities and age structure, and additional samples in 1978-79 and spring 1981 to clarify juvenile recruitment pattern.

Most maldanid species are subtidal and their biology is almost unknown. Some of the few intertidal species have been studied, especially the North American *Clymenella torquata* (Leidy). Previous studies on maldanid life history and reproductive biology include Mead (1897), Bookhout and Horn (1949), Newell (1951), Pilgrim (1964), Mohammad (1966), Cazaux (1972), Rowe et al. (1975), but at the time of writing there are no published investigations of the population dynamics of a maldanid polychaete. Whitlatch (1979) reported on work then in progress.

The two common intertidal maldanids of New Zealand sandy shores are *Axiothella serrata* and *Macrocllymenella stewartensis* Augener. While the former appears restricted to central New Zealand, *M. stewartensis* is widely distributed in both Islands (personal records). However, *M. stewartensis* has not been found within Pauatahanui Inlet, although it occurs seaward of Porirua Harbour entrance in the shallow subtidal. Previous references to *Axiothella quadrimaculata* Augener or *A. australis* Augener from New Zealand sandy-shore habitats are misidentifications (e.g., Wood 1968, Morton and Miller 1973, Knox et al. 1977, Knox and Fenwick 1978, Stephenson 1978, Mason and Ritchie 1979, Grange 1982). *Axiothella quadrimaculata*, which does occur in New Zealand, is a very small and distinctive maldanid, which I have found to be an associate of rocky shore algae. *Axiothella australis* is known only from west Australia.

Plate 1. *Ariothella serrata* surface indications.

- a) Pits, feeding scrapes, and casts of *A. serrata* in aquaria.

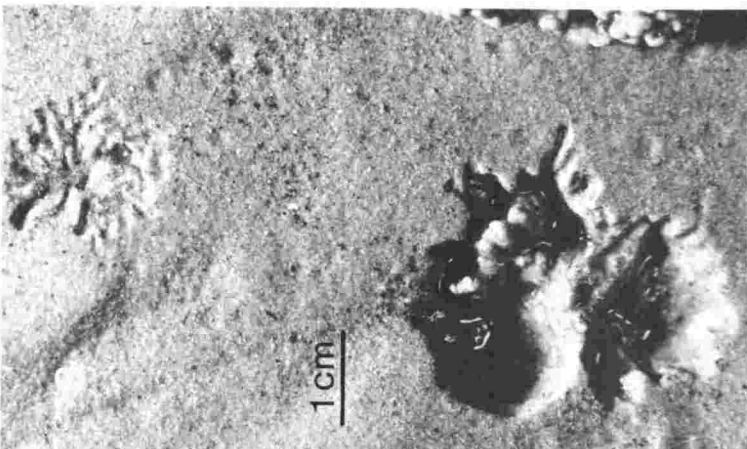
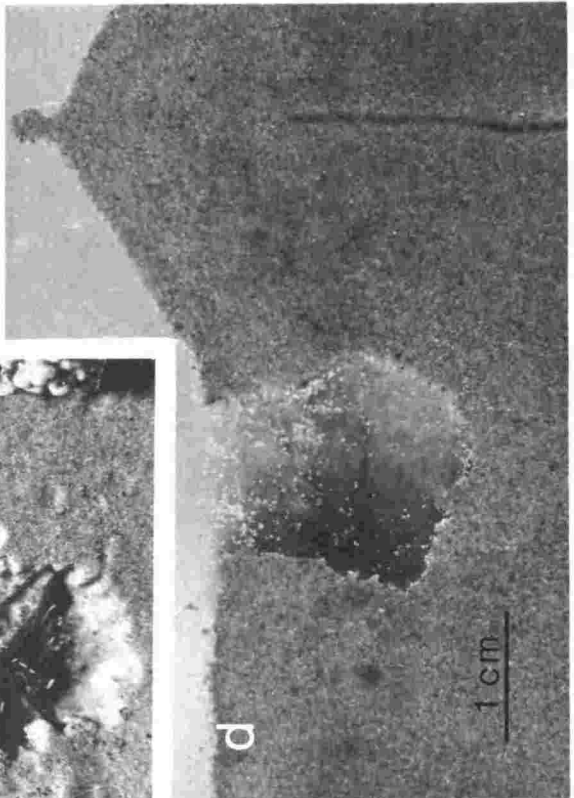
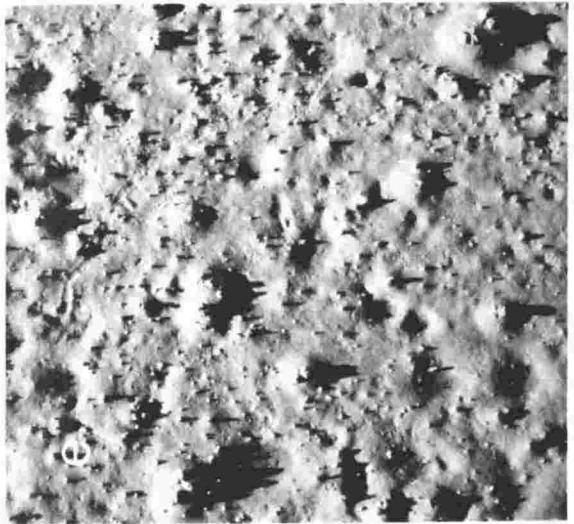
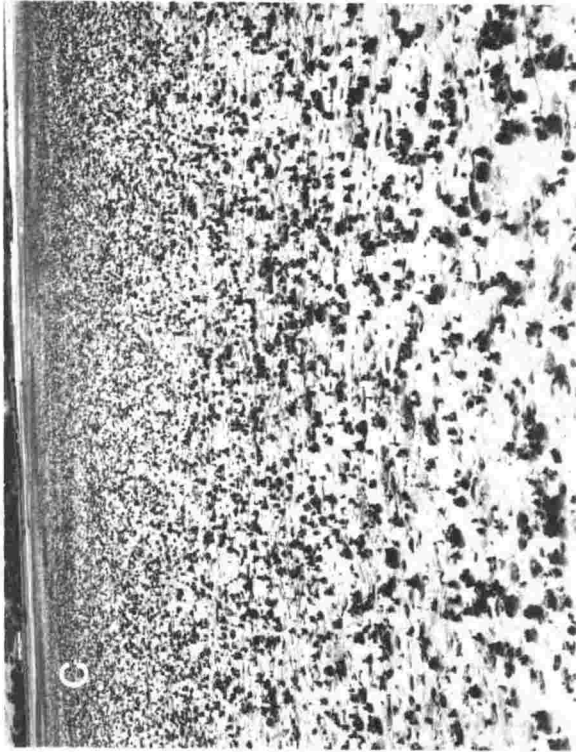
One worm has recently reversed in its tube, and is now casting in the former feeding area.

- b) Dense *A. serrata* terminating where topography rises above low tide water table.

c) and f) Cast and pit topography developed under offshore wind conditions. In f), the close-up view, *Amphibola crenata* faecal trails, and surface traces of smaller polychaete species are visible.

- d) *A. serrata* cast, pit, and tube in aquaria lateral view.

- e) *A. serrata* O group as small casts amongst those of adults. (August, about 9 months post-recruitment).



METHODS

SAMPLING AND STATISTICS

Sampling methods and statistical treatments for the 1977-78 paired transects were stated in detail in Section 1. These samples were taken at 3-monthly intervals from November 1977 to November 1978. The 500 μm mesh used then for processing retained adults and some of the juveniles. A further sample from the left transect, collected in November 1979, was processed through 500, 250, and (in part) 125 μm sieves. However, it was not practical to process these large deep cores (50.3 cm^2 , to 15 cm) in adequate numbers for routine analysis through sieves finer than 500 μm . To study juvenile recruitment, between October 1978 and May 1979 smaller cores, 9.63 cm^2 and 3 cm depth, processed through 250 μm mesh, were used in approximately monthly left transect samples (see Table 11). Also further cores, 1.29 cm^2 area and 3 cm deep, were collected from the left transect in spring 1981 and processed through a 72 μm sieve.

The 3 cm sampling depth used for small cores was sufficient to collect juveniles (see later). The transect width was reduced for small cores (2 m for large cores) to expedite collection of increased numbers of cores. A 1 m strip was sampled for 9.63 cm^2 cores, using a 10 cm grid for random coordinates (2000 units per 20 m zone), and a 0.2 m strip for 1.29 cm^2 cores, using a 2 cm grid (10,000 units per zone). Transects were not paired as in 1977-78 large-core series, because the overall density variation between transects was usually not significant (Section 1).

Differences between means of large samples were tested by t-test (Section 1, statistical treatment). For small samples (less

than 40 cores) an approximation of 95% limits was given by 2SE, and differences between these samples were tested by Mann-Whitney U-test. Juvenile aggregation was assessed with Morisita's index (Morisita 1959; calculated for samples uniformly restricted to 30 cores by random numbers), and tested for significant departure from randomness with χ^2 .

SIZE AND AGE

The indices of size used for *Axiiothella serrata* were length, width, calculated volume, setiger counts and setae counts. The main size measure was setiger-one 'width', taken as the maximum dorso-ventral depth, measured with an eyepiece micrometer to 25 μm classes (adults) or 10 μm classes (juveniles, examined under a compound microscope). Total population size-frequencies were smoothed by grouping in 100 μm classes. For the juveniles, length, total setiger number, and maximum number of neurosetae were also noted, and a volume calculated from length/width data. To calculate volume, the juvenile *A. serrata* body was considered as a uniform cylinder. This is a close approximation, although the posterior third of the body was slightly tapering particularly in youngest juveniles. In setiger counts of juveniles the criterion used to classify part-developed segments was the development of setae. The final segment was included when the neuroseta was near complete in form, although it may not necessarily have penetrated the cuticle. *Axiiothella serrata* develop a fixed total of 22 setigers with any variation as adults (e.g., Kudenov and Read 1977) usually attributable to regeneration in progress.

Size-frequencies were compiled without bias from each random sample by measuring all available individuals, and then expressed proportionately for each class as densities per m^2 , rather than percentages.

Thus between-sample density changes of each size class could be studied. Confidence limits for the density of the groups of size classes considered to represent well-defined age classes were calculated from within-core size data. Note that these limits are valid irrespective of how the age classes have been defined (see later).

AGE CLASSES: When the relative densities and range of size of age classes are sought from size-frequency analysis a basic starting point is inspection of the pattern of pronounced modes. If modes are recognisable in sequential samples and show movement along the abscissa indicating growth, the reasonable interpretation is that such modes signify age classes. However, the size range of successive age classes often overlaps, making density estimation difficult, and when overlap is pronounced the number of age classes may be unclear. To facilitate the analysis each component age class is often assumed to have a gaussian distribution whose parameters can then be approximated by various techniques, ranging from relatively crude graphical procedures (Cassie 1954) to maximum-likelihood interactive computer programs (Macdonald and Pitcher 1979). Complete reliance on this approach is unjustified. Firstly, age classes may have non-gaussian, skewed, size-frequency distributions, requiring at least two curves to fit one age class, or biasing the analysis when undetected; and secondly, spurious groups may be generated, unsupported by other evidence if prior knowledge of the number of component age classes is not available (e.g., Warren 1976). These methods are most suitable for cases in which a preliminary independent estimate of the number and size range of age classes is possible (e.g., McNew and Summerfelt 1978). For acceptable accuracy a reasonable sample size is required, with a minimum of about 50 in each age class (Macdonald and Pitcher 1979). An alternative approximation, acceptable when overlaps are not extreme or highly

skewed, is to assume the overlaps are equal either side of distribution divisions, thus cancelling out.

Analysis of *Axiiothella serrata* age structure was possible because an O group could be identified in all samples. However, application of the quasi-objective fitted-curve method was inappropriate because of obviously skewed size distributions of age classes and the small sample size available for older age classes. The detailed rationale for *A. serrata* age classes is discussed in the results.

SIZE AND SETIGER DEVELOPMENT

Because the number of setigers is a convenient index of juvenile development (see later), it was desirable to study the link between body size and setiger-total. The association was such that exponential or power curve equations were possible simple models. These were tested for their fit to the data by regression analysis of variance (Kleinbaum and Kupper 1978). Exponential curves were superior and will be discussed further. The relationship in linear form is

$$\log_e(\text{size}) = B_0 + B_1(\text{setiger-total})^K$$

where B_0 , B_1 , and K are constants. The natural logarithm transformation required in the equation reduced dimension variances so that they showed no pattern, although still significantly different by Bartlett's test. Models were improved by adjusting exponent K until the minimum residual sum of squares was found. The significance of the relationship was assessed by F test of the ratio of regression mean square/residual mean square (= regression ratio). The fit of each regression line was then quantified by the ratio of lack-of-fit mean square/pure-error mean square (= lack-of-fit ratio). This ratio is sensitive to non-linear trends in the data, although it is also increased by remain-

ing heteroscedasticity and non-normality. The r^2 of the regression shows the strength of association of the variables and is not an indication of the fit of the line.

For morphometric relationships where prediction of both variables may be appropriate (i.e., X from Y, as well as Y from X) the geometric mean regression equation has been given, as advocated by Ricker (1973).

RESULTS

AXIOTHELLA SERRATA TOTAL POPULATION, 1977-79

During the year November 1977 to November 1978, according to estimates using 500 μm mesh, the *AxiotHELLa serrata* population peaked at $1150 \pm 210 \text{ m}^{-2}$ in August, and was lowest in November samples (Fig. 13a). Significant density increases took place between November, February, and May samples, and subsequently a fall occurred between August and November. The November 1978 density of $550 \pm 90 \text{ m}^{-2}$ was significantly higher than the previous November ($350 \pm 60 \text{ m}^{-2}$). The above analysis, however, excludes dense aggregations of very young worms, which occurred in a small number of sampling units in November 1977, 1978 and 1979 samples. Since these young (at 4-7 setigers, and about 110 μm width, 500 μm length) were too small to be retained normally in any number in a 500 μm sieve, their possible origin is discussed below and their density analysed separately.

JUVENILE AGGREGATIONS: Each aggregation of young (henceforth called juveniles as no larval stage is known) is believed to have been composed of siblings coming from a part-developed egg mass within, or attached to, the lower part of the female tube. Losses of juveniles

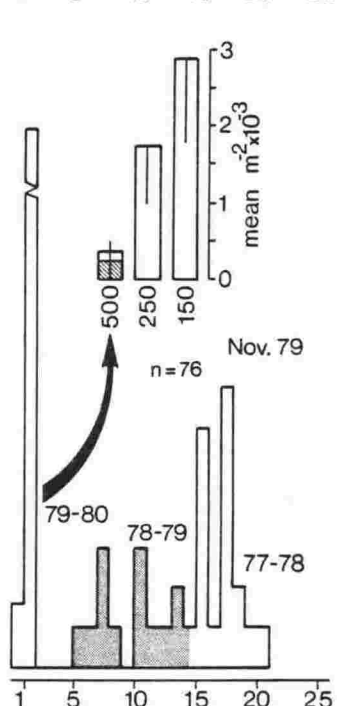
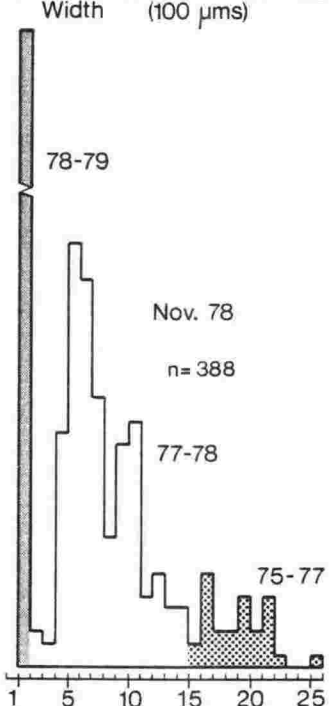
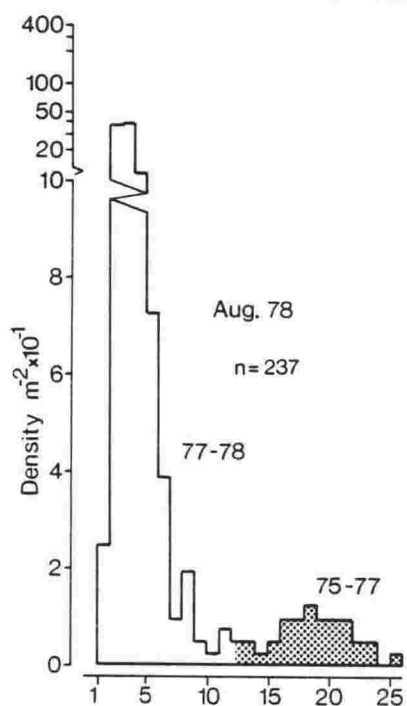
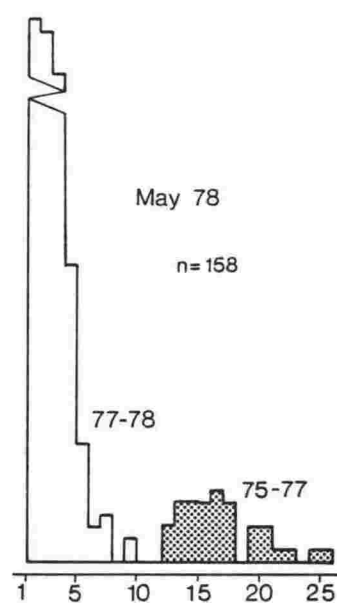
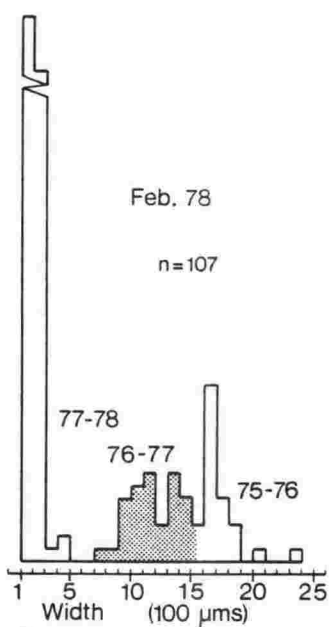
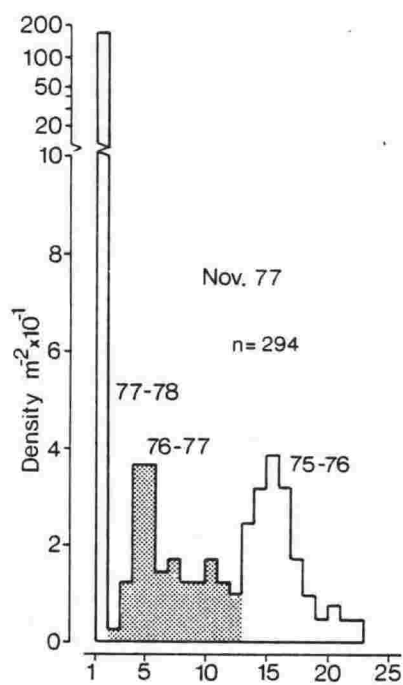
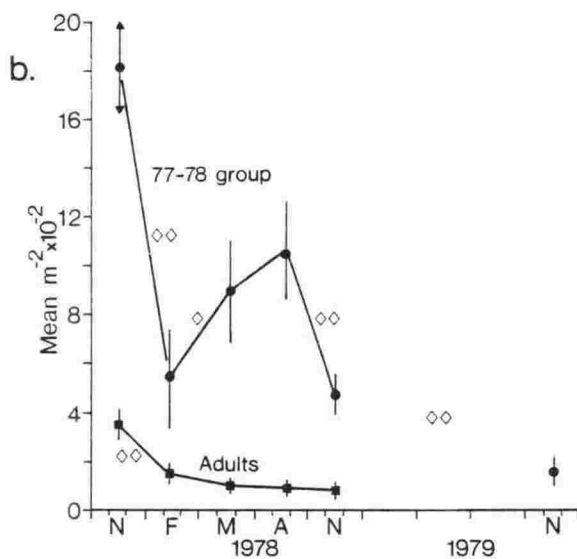
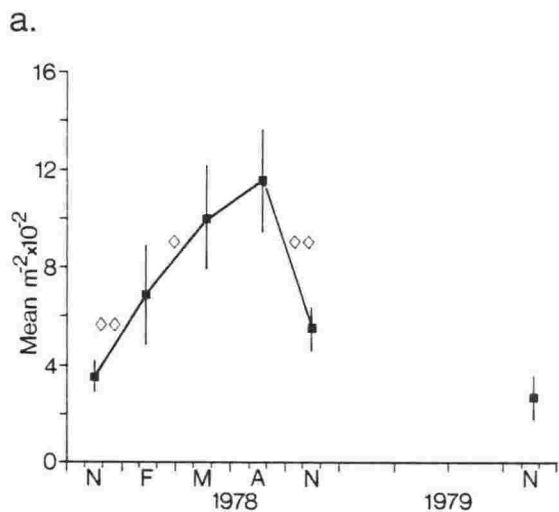
Fig. 13 *Axiiothella serrata* seasonal mean densities as hundreds per m^2 . The limits of the means indicated are 95% confidence intervals (or 2SE for November 1979), which for November 1977 O group were $\pm 2850 m^{-2}$. Diamond(s) indicate $P < 0.05$, ($P < 0.01$) significant differences.

a) Total population. November densities omit new O group appearing then.

b) Adults (1976-77 and prior age classes) and 1977-78 class shown separately. The November 1979 density for the 1977-78 class includes any remnants of prior year classes.

Fig. 14. *Axiiothella serrata* width size-frequencies as tens per m^2 (log scale above $100 m^{-2}$), with suggested age classes labelled and delineated (see text). The oldest age classes include any merged remnants of previous years. Estimates are of the total population from 500 μm sieve samples.

Inset for November 1979 compares the 500 μm sieve O group density (hatched portion represents sibling-mass individuals) with $>250 \mu m$ and $>150 \mu m$ densities (2SE line indicated).



from the samples must have occurred during the 500 μm mesh initial sieving. During later processing of the preserved samples, in which a 125 μm sieve was used, the fragile sand grain tubes of the adult would have been further disrupted, releasing juveniles, which were then retained. In some of the cores young remained attached together in small clumps of secretion and sand. Aggregations did not occur in the numerous shallow cores (0-3 cm depth) taken during the breeding period (see later). In November 1979, when 0-3 cm and 3-15 cm portions of cores were processed separately, the one aggregation occurred in the 3-15 cm portion.

In November 1977 almost all the sibling mass individuals had 6 setigers. In November 1978 five aggregations had approximately equal numbers of 5- and 6-setiger individuals, and one almost all 4-setiger individuals. The juveniles of the November 1979 aggregation were at the 5-setiger stage. Comparison of size and setiger development with near-surface juveniles indicated that the aggregation individuals were much younger, with 5 setigers developed compared to 9-11 (Table 10).

TABLE 10. Size of near-surface, dispersed, *Axiiothella serrata* juveniles compared with deep, aggregated juveniles, November 1979 sample. Setiger-1 width means are from 10 μm size-class data.

Location	¹ Sieve fraction	n	Setiger-total		Setiger- 1 width	
			Mean	SD	Mean	SD
near-surface	>500 μm	14	10.9	1.44	126.9	10.8
" "	500-250 μm	132	9.5	1.54	123.7	12.5
" "	250-150 μm	45	9.2	1.57	114.9	11.2
deep	>500 μm	19	5.0	0.58	102.3	8.7

¹All near-surface (0-3 cm) portions of 24 cores were processed successively through 500, 250, and 150 μm meshes. No juveniles occurred in the 8 deep portions (3-15 cm) passed through 250 μm as well as 500 μm mesh.

Aggregations occurred in 3 of the 82 November 1977 cores (counts of 250, 65, 425 respectively, i.e., a mean density of 1.8 ± 2.8 thousand juveniles m^{-2}), 6 of 82 November 1978 cores (counts of 235, 192, 150, 896, 20, 20, i.e., 3.7 ± 5.9 thousand m^{-2}), and 1 of 24 November 1979 cores (count of 30, i.e., 0.25 ± 0.50 thousand m^{-2}). As an indication of the possible number of juveniles in an aggregation the number of near-mature oocytes carried by gravid females was between three and eight thousand (unpublished data), but it is not known if spawning occurs once and is complete, or is episodic and partial. The number of aggregations per m^2 were respectively 7.3 ± 9.2 , 14.6 ± 11.9 , and 8.3 ± 16.5 . Chances of finding an egg mass during casual digging were therefore low, and no egg masses were ever seen in the field despite extensive collecting of adults during the breeding seasons.

The aggregated juveniles were only part of the total number of juveniles present, but the dispersed older juveniles were at first only sporadically retained by the 500 μm sieve. The duration and pattern of recruitment and densities of near-surface juveniles were assessed for the 1978-79 recruitment period (see later). For the November 1979 sample processed through several sieves the respective estimates of total juvenile density are shown in Fig. 14 inset.

AGE CLASSES: Distinct groups were present in size-frequencies using setiger-one width (Fig. 14). From inspection it was apparent that a new 1977-78 O group began to appear in November 1977 (in fact as aggregated juveniles). Similarly in November 1978 and 1979 subsequent new year groups appeared. According to the 500 μm sieve assessments the O group of November 1977 continued to increase in numbers through February and May samples to August, and was present as

the major group of individuals in the November 1978 size frequency (unshaded in Fig. 14). It was then clear that, at one year old, this 1977-78 age class was the equivalent of the shaded portion of the November 1977 size-frequency. The remaining part of the size-frequency must represent all the older age classes. Thus in November each year three age classes, the O group, I group, and the combined older groups (II+ group) can be identified. Similarly in February 1978 these three groups were apparent, but in May and August the I and II+ were not separable. Together they became the new II+ group in November. Except when recruitment was occurring, age classes declined in density with time, which aided interpretation of size-frequencies.

The division between the 1977-78 age class and older worms was unequivocal in November, February, and May (Fig. 14). From ungrouped data it could reasonably be inferred that the upper size limit of the 1977-78 O group was 1210 μm in August and 1490 μm in November 1978, and for the 1978-79 O group 1460 μm in November 1979. These limits can also be justified from the growth in three months expected for the largest individuals in the O group, estimated from the growth shown by mode individuals (Fig. 14). Note that small shifts in the position of the division between groups would make little difference to the respective densities. By assuming no overlap occurred in August and November it was possible to calculate confidence limits for the O group and adult parts of the population separately, and test for significant density changes in each (Fig. 13b).

Division of the two adult groups was less clear cut. Overlap of I and II+ groups undoubtedly occurred. Approximate density estimates were possible only for November of each year and February 1978, where overlaps were assumed to be equal either side of divisions (Fig. 14, see below and Table 12 for densities).

AGE CLASS DENSITIES: The total adult population (Fig. 13b) was $352 \pm 62 \text{ m}^{-2}$ in November 1977, made up of approximately 170 m^{-2} of the 1976-77 class plus 182 m^{-2} of the older age classes (Fig. 14). The adults declined significantly to $162 \pm 43 \text{ m}^{-2}$ by February 1978 (approximately 68 and 94 m^{-2} of the two groups), and further slowly declined during the year to be $80 \pm 30 \text{ m}^{-2}$ by November 1978. In November 1979 there were approximately 157 m^{-2} of the 1977-78 and older age classes, and approximately 108 m^{-2} of the 1978-79 class. These densities show that 1977-78 recruitment resulted in a large year class as apparently also occurred in 1975-76 (Fig. 14), but 1976-77 and 1978-79 recruitment was comparatively poor, so that after one year the respective age classes were equivalent to, or lower in density than worms one year or more older.

In November 1977 the O group was represented in the $500 \mu\text{m}$ sieve by sibling aggregations at a density of 1810 m^{-2} , with the wide limits of $\pm 2850 \text{ m}^{-2}$ (Fig. 13b). In February 1978, when no aggregations were recorded, the sieve O group population dropped significantly to $540 \pm 200 \text{ m}^{-2}$, but then included older juveniles of 9 to 21 setigers (Fig. 15). The real density of the O group at the time is not known and was probably an order of magnitude higher. In May the sieve O group had increased significantly to $890 \pm 210 \text{ m}^{-2}$, as more juveniles (range 12-22 setigers) became large enough to be held by the sieve. By August the O group population had increased to $1060 \pm 200 \text{ m}^{-2}$, and about one-third had the 22-setiger total of the adults (Fig. 15). The true proportion with 22 setigers may be higher because proportionately fewer large individuals remain unbroken during processing. In August the $500 \mu\text{m}$ sieve probably retained all O group present in the cores because a considerable proportion (48%) were retained even in a 1 mm sieve during processing. Surface casts of the 1977-78 O group

individuals first became large enough to be readily noticeable among those of the adults about August (Plate 1e). By November the O group had declined significantly to $470 \pm 80 \text{ m}^{-2}$. By November 1979 this 1977-78 year class, now two years old, had declined to $<157 \pm 60 \text{ m}^{-2}$ (this estimate includes a small, unknown number of older age class individuals).

AXIOTHELLA SERRATA O GROUP RECRUITMENT 1978-79, 1980-81

1978-79 O GROUP DENSITIES: The annual spawning of *AxiotHELLa serrata* probably began in October or early November from the evidence of aggregated young first appearing in a mid-November 1977 sample. The recruitment of the 1978-79 age class was studied in detail. Frequent samples were taken between October 1978 and May 1979 using 9.63 cm^2 cores to 3 cm depth processed through $250 \mu\text{m}$ mesh. Details of the sampling programme and the juvenile density estimates, etc., are in Table 11. Densities are also plotted in Fig. 16, and size-frequencies in Fig. 17.

The first near-surface juveniles were found on 25 October, whereas none had been detected on 2 and 9 October. Their density was then about 1800 m^{-2} (confidence limits unknown as on this occasion cores were combined then subsampled), and almost all had 6 setigers (range 6-7 setigers, mean 6.1, SD 0.30, $n = 11$). Five days later (30 October) juvenile density was $1490 \pm 530 \text{ m}^{-2}$ and individuals were mainly 7- to 8-setiger stages (range 6-10 setigers, mean 7.6, SD 0.61, $n = 114$). After a further 9 days the 8 November sample indicated a density of about 4.8 thousand m^{-2} and a mean setiger-total of 8.8 (range 6-12 setigers, SD 1.1, $n = 104$). This density estimate may not be representative of the complete transect, as it comes from a non-random sample (consisting of two sets of closely-spaced cores for use in

Fig. 15 *Axiiothella serrata* setiger-total percentage frequencies for the 1977-78 O group in 1978 500 μm sieve samples.

Fig. 16 *Axiiothella serrata* 1978-79 O group mean densities as thousands per m^2 (250 μm sieve). Circled means have 95% confidence limits indicated; other limits are $\pm 2\text{SE}$ from samples <40 cores. Squares indicate two estimates of unknown variance, and abscissa triangles indicate sample dates (see text and Table 11).

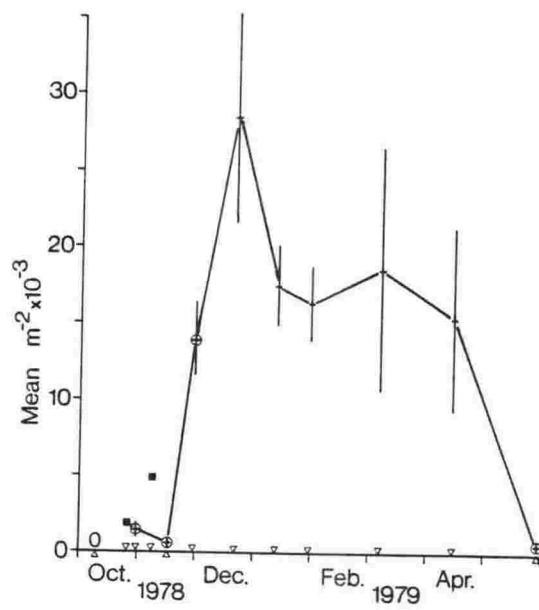
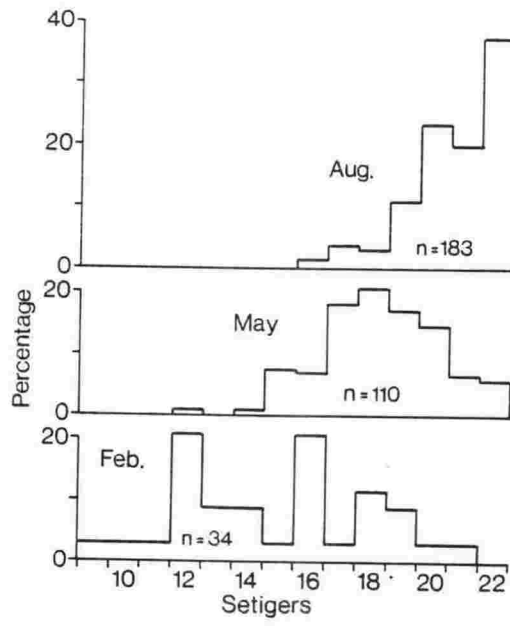


TABLE 11. Sampling programme and near-surface *Axiiothella serrata* juvenile density estimates, October 1978 - May 1979.

Date	No. of cores	Zones	Size-analysis zones	Density m ⁻² (thousands)			SE as % of mean	No./core range	Morisita index
				Mean	± 95% limit	SE			
2 Oct. 1978	10	1-8		0					
9 "	50	1-8		0					
25 "	25	1-8	all	1.83					
30 "	80	1-8	"	1.49	0.53	0.245	16.4	0-15	1.5
8 Nov.	25	4,6	4,6	4.82				0-9	
16 "	40	1-8	all	0.62	0.39	0.18	29.0	0-5	3.2
30 "	64	1-8	1,2,5,7	13.90	2.34	1.14	8.2	0-41	1.7
21 Dec.	7	3,5	3,5	28.50		3.40	11.9	9-34	
12 Jan. 1979	6	3,5	3,5	17.49		1.28	7.3	14-24	
30 "	30	1-8	1,3,5,7	16.28		1.21	7.4	2-29	1.2
6 Mar.	8	3,5	3,5	18.57		3.94	21.2	5-32	
14 April	8	3,5	3,5	15.33		2.96	19.3	4-18	
29 May	52	1-8	all	0.58	0.32	0.15	25.9	0-5	2.6

All transects were stratified random samples except on 8 November.

examining aggregation), and is for that reason shown in Fig. 16 as a separate point. By 16 November juvenile density ($620 \pm 390 \text{ m}^{-2}$) was significantly lower than on 30 October, but mean setiger-total had increased to 9.5 (range 5-13 setigers, SD 1.75, $n = 23$). This sample was collected on the same day as the November 500 μm sieve sample set, with cores taken alongside the larger, deeper cores. However, as previously mentioned, 4- to 6-setiger juveniles occurred in aggregations in the deeper cores at a mean density of 3.7 thousand m^{-2} . These development stage and density differences between two sample depths are more evidence that early development of *Axiiothella serrata* occurs in buried egg masses.

By 30 November, 14 days later, a significant large population increase to 13.9 ± 2.3 thousand m^{-2} had occurred in the near-surface juveniles. They were then mainly 9-setiger juveniles (54% with 9 setigers, range 7-14 setigers, mean 9.2, SD 1.06, $n = 349$). On the next sampling day (21 December) the density of 28.5 ± 6.8 (2SE) thousand m^{-2} was the highest found in the sample series. In subsequent samples from January to April the juvenile density then varied between 19 and 15 thousand m^{-2} (Fig. 16, Table 11), before a large drop to $580 \pm 320 \text{ m}^{-2}$ on 29 May. Setiger size-frequencies had two or more modes during this period (Fig. 17, and see analysis below). By mid-November 1979 the 1978-79 age group further declined to reach a density of approximately 108 m^{-2} .

1978-79 O GROUP SPAWNING GROUPS: Setiger-count size-frequencies as densities per m^2 (Fig. 17a) show large modes of younger individuals at various times. Their occurrence indicates a series of synchronised spawnings by adults. In Fig. 17a the size-frequencies were spaced vertically from each other according to the time in days between samples. Using this scale, lines linking modes of presumed

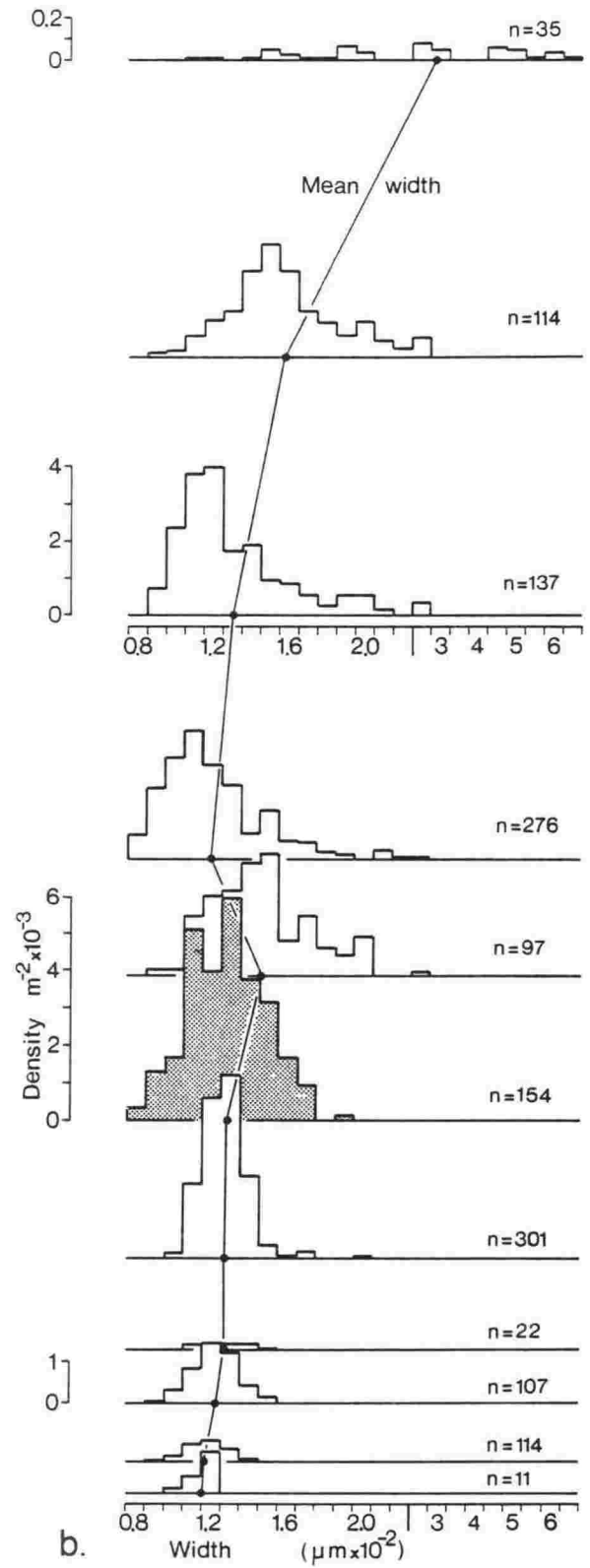
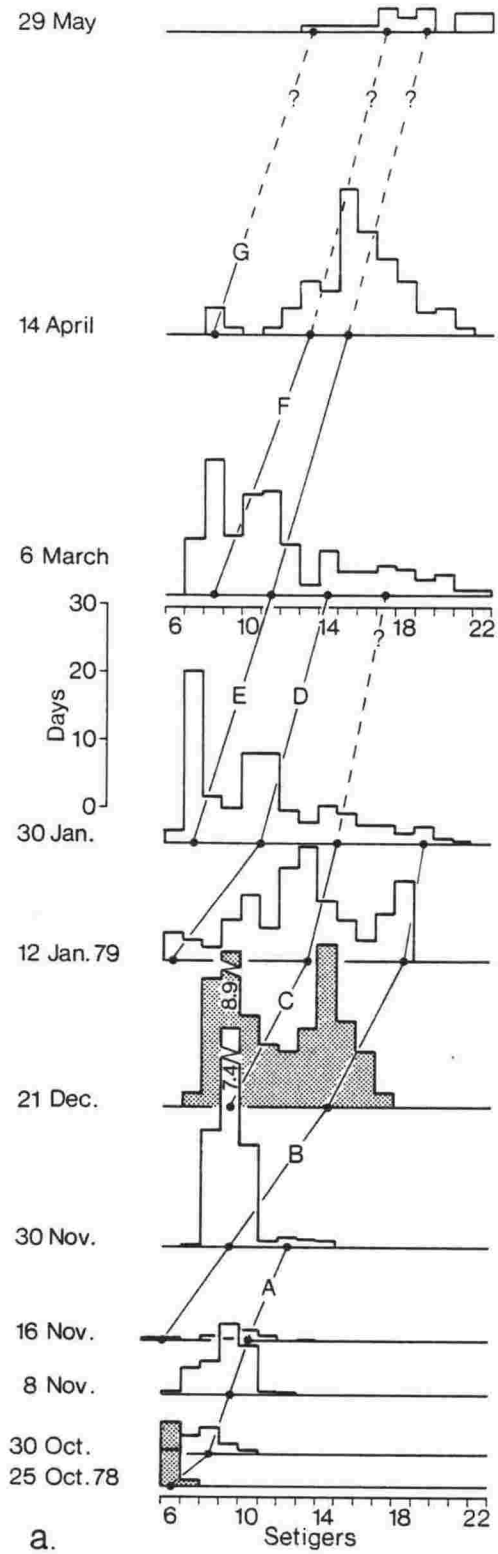
identical spawning groups then indicated their growth. Seven consecutive groups have been identified (labelled alphabetically), each declining in density with time once fully recruited into the population. A small mode of 10-setiger individuals on 12 January may represent another spawning but was not detectable in the next sample. The approximate first appearances of the labelled groups at the 6-setiger stage (where necessary estimated by extrapolation from group B growth) were 25 October, 16 November (+ 22 days), 9 December (+23 days), 12 January (+ 34 days), 26 January (+ 14 days), 26 February (+ 31 days), 5 April (+ 37 days). Thus spawning occurred intermittently over about a 160-day period.

The time elapsing from spawning to when 6-setiger young appear at the surface is unknown. The dates of appearance of 6-setiger groups were distributed over the lunar month, apparently unlinked to the neap-spring tidal cycle. Labelled modes usually occurred in several zones, as shown in the Fig. 18 examples of 30 November and 30 January, although not invariably as mode F occurred only in zone 3 (Fig. 18, 6 March and 14 April). Mode D not detectable in

Fig. 17 *Axiiothella serrata* 1978-79 O group size-frequencies as thousands per m^2 , with distance between samples to time scale. All densities to the same scale (except low density May sample x5). Some overlapping frequencies shaded for clarity. Note that the youngest juveniles were probably underestimated by the 250 μm sieve (see p.92).

a) Setiger-total frequencies linked between samples to show probable identical modal groups (A, B, C, etc.), with possible links indicated by dashed line and query.

b) Width frequencies and mean width. (Note change from 10 μm to 50 μm classes for larger widths).



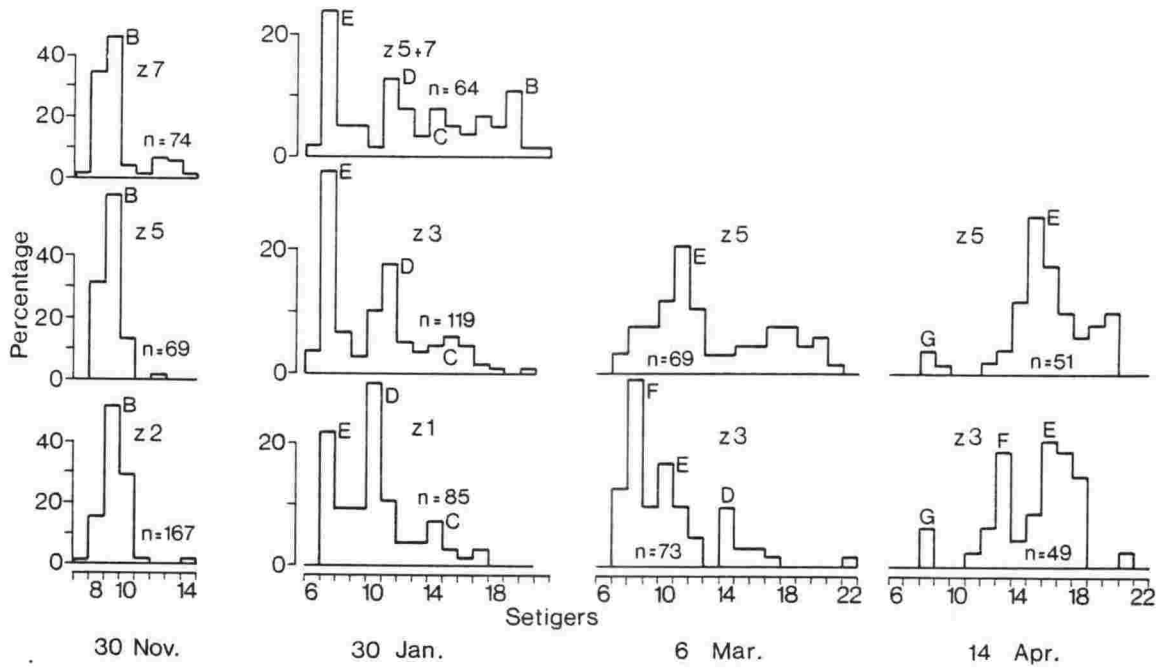


Fig. 18 Zone presence of labelled mode groups (see Fig. 17) within *Axiiothella serrata* 1978-79 O group. Four examples of setiger-total percentage frequencies to show the degree of similarity between zones within each sample. (Number of individuals measured (n) approximates relative densities between zones).

suggest that, in agreement with setiger-total frequency changes, recruitment declined greatly during that period; and in May recruitment had ceased.

1981-82 O GROUP: Some further information on *Axiiothella serrata* juvenile recruitment and depth distribution was obtained from transects in spring 1981. Cores (usually $n = 56/\text{transect}$) were 1.39 cm² to 3 cm depth, split into 0-15 and 15-30 mm portions, and processed through 250 and 72 μm mesh. The recruitment of the 1981-82 O group was first detected on 16 November after transects on 15 September and 13 October revealed no juveniles. *Axiiothella serrata* juvenile density was approximately 26 thousand m⁻². However, as a result of weather conditions little of the beach was emersed and only a few cores ($n = 11$) could be collected. Individuals had up to 10 setigers so, from the growth rates shown within the 1978-79 age class (Fig. 17a), the first spawning probably occurred at around the beginning of the month as in previous years.

A complete transect was taken on 11 December. The surface 15 mm contained 98% of juveniles and their density was then 23.73 ± 6.08 thousand m⁻². As 21% of the total passed through a 250 μm sieve, when the earliest juveniles were present, the previously discussed 1978-79 juvenile densities (250 μm sieve) could be underestimates of the true totals by about that percentage.

JUVENILE MORPHOLOGY AND BEHAVIOUR: Maldanid larval/juvenile morphology has been described by Bookhout and Horn (1948) and Newell (1951), and juveniles of *Axiiothella serrata* did not differ substantially from those accounts. In external morphology *A. serrata* juveniles are miniature adults apart from first lacking a cephalic rim and anal funnel

plus cirri, which begin developing at the 17- to 18-setiger stages. The prolonged ventral anal cirrus of the adult was not present in early juveniles, but the ventral pygidium was characteristically prolonged beyond the anal opening.

Four- and five-setiger sibling group juveniles had yolk- and oil-spheres in the stomach and intestine, whereas the six-setiger and larger near-surface juveniles had ingested food particles, indicating feeding did not begin until the surface sediment was reached. Cilia trochs were not present, but ciliation of the anal and buccal cavities could be seen in live juveniles, and isolated sensory cilia were present anteriorly and posteriorly. The first setae developed were of the adult type, and consisted of one to two notosetae and one rostral hook neuroseta per fascicle. Juveniles were colourless apart from blood vessels, a yellowish gut, and some faint brown pigmentation on the posterior edge of middle segments. A single pair of large red eyespots was present, each located on the ventro-lateral prostomium (occasionally additional smaller spots were present), and in older juveniles diffuse red pigment spots appeared on the cephalic plaque and pygidium.

Early juveniles constantly formed a tube of secretion to which sand grains adhered as they moved. Juveniles in samples were almost invariably enclosed in such a structure, which increased their bulk. Juveniles spent part of the time crawling along the sand surface as well as burrowing when kept in the laboratory in dishes of sand.

JUVENILE DISPERSION: *Axiiothella serrata* juveniles have no ciliary trochs for swimming, but are capable of slow dispersal by crawling on surface. Swimming by vigorous body lashing may be possible, although it was not observed. Further passive, more or less accidental, migration is probable when vigorous wave action stirs up and carries away material from the surface (see discussion).

Because juveniles originate in large aggregations below surface, strong clumping might be expected to persist for some time after juveniles are on surface. However, the data do not confirm this (see Table 11). Aggregation was quantified in complete transects with Morisita's index. Significant aggregation occurred in all, as is normal in benthic samples (see e.g., Downing 1979), but highest Morisita values occurred in low density populations (maximum number per core 5, Table 11, 16 November and 29 May). Similarly the SE as a percentage of the mean was highest in these low density samples. Systematic sampling on 8 November 1978, where cores were spaced along a line at 10 cm intervals, also did not detect any abnormal aggregation of surface juveniles (zone 4, range 0-9 per core, \bar{x} /core 3.5, SD 2.45, 16 cores; zone 6, range 2-17 per core, \bar{x} /core 6.7, SD 4.69, 9 cores).

MORTALITY

Density estimates of successive *Axiiothella serrata* age classes over a two-year period are summarised in Table 12 together with estimates of mortality rate when applicable. Mortality of adults (i.e., the I, II and older year groups) was apparently higher in the first part of the year, especially for the II+ adults. Possibly mortality increased then because of post-spawning deaths during the breeding season. Adult mortality rates ranged from 0.0009 to 0.0070 individual⁻¹.day⁻¹, or a decline of from 0.08 to 1.2 individuals m⁻².day⁻¹. In the O groups comparable mortality occurred in the latter half of their first year (0.0047 and 0.0064 individual⁻¹.day⁻¹). Juvenile mortality could not be estimated while recruitment continued, but by April 1979 recruitment in the 1978-79 O group had almost ceased. The decline then from more than 15 thousand m⁻² to below 600 m⁻² in 45

TABLE 12. Estimates of *Axiiothella serrata* age-class densities per m² and mortality (individual⁻¹.day⁻¹) November 1977 to November 1979.

		A g e c l a s s			
1975-76		1976-77	1977-78	1978-79	1979-80
(& 74-75)					
Starting age (years)	II+	I	O	O	O
November 1977	170	182	*1 810		
February 1978	68 (0.0070)	94 (0.0056)	*540		
May "		96 (0.0040)	*890		
August "		87 (0.0010)	1 060		
November "		80 (0.0009)	470 (0.0064)	4 290	
December "				28 500	
April 1979				15 330	
May "				580 (0.021)	
November "			157 (0.0019)	108 (0.0047)	2 890

*Underestimate

Mortality rates in parentheses refer to the period prior to the sample, and are given when adequate density estimates are available and recruitment was not continuing. For the 1978-79 O group the November 1978 density includes both surface juveniles and juveniles in aggregations; the December sample had peak density, and recruitment had almost ceased by April. The 1979-80 O group density in November is the 150 µm sieve estimate plus deep aggregation juveniles.

days is a 96% loss ($0.021 \text{ individual}^{-1} \cdot \text{day}^{-1}$), and represents an average of $328 \text{ m}^{-2} \cdot \text{day}^{-1}$.

Note the mortality estimates were for the whole transect and thus unaffected by upshore/downshore migration of juveniles (see zonation). Any alongshore emigration occurring was assumed balanced by a similar level of immigration.

ZONATION

The zonation of the total *Axiiothella serrata* population was examined in Section 1 and the conclusion reached that, although there was correlation between corresponding transect zones, the distribution was relatively unstructured, apart from consistent low densities occurring in zone 8. Analysis of *A. serrata* adults and the 1977-78 O group separately (Fig. 19, Table 13) showed that up to August adults were significantly more abundant on the upper shore than the lower shore, except in February when zones became more uniform following more substantial upper shore mortality. The recruiting O group were significantly concentrated towards the mid to lower shore in February, when dense populations were apparent in zones 5-7, and were dense in zones 4-7 in May, but continuation of this pattern was only weakly apparent during the latter part of the year. In zone 8 adult densities were almost negligible and juvenile densities noticeably lower than in zone 7.

Note that the 1977-78 O group had no significant correlation with adult *A. serrata* (Spearman's $r_s + 0.05$, $P 0.4$), or with other abundant polychaete species, with the exception of a November 1978 negative *Capitella* sp. correlation ($r_s - 0.24$, $P 0.02$).

Fig. 19 *Axiiothella serrata* zonation

- a) Seasonal zonation of *A. serrata* adults, November 1977-78 from 500 μm sieve samples. Zone means as hundreds per m^2 , left (top) and right (bottom) transects are plotted separately, and variation of zone means indicated as vertical lines 2SE in length (for clarity arising from the inner side of the mean only, or from the baseline when greater than the mean).
- b) Seasonal zonation of 1977-78 O group from 500 μm sieve samples (isolated aggregates only were recorded in November 1977). Conventions as in a).
- c) O group zone means as thousands per m^2 on left transect from 250 μm sieve samples. 1978-79 group from October to May, plus 1979-80 in November 1979 and 1981-82 in December 1981. Variation of zone means indicated as in a).

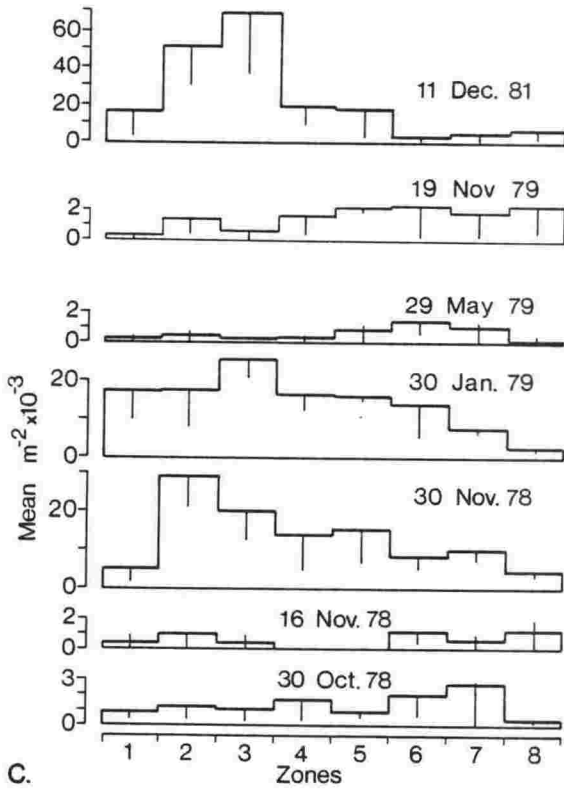
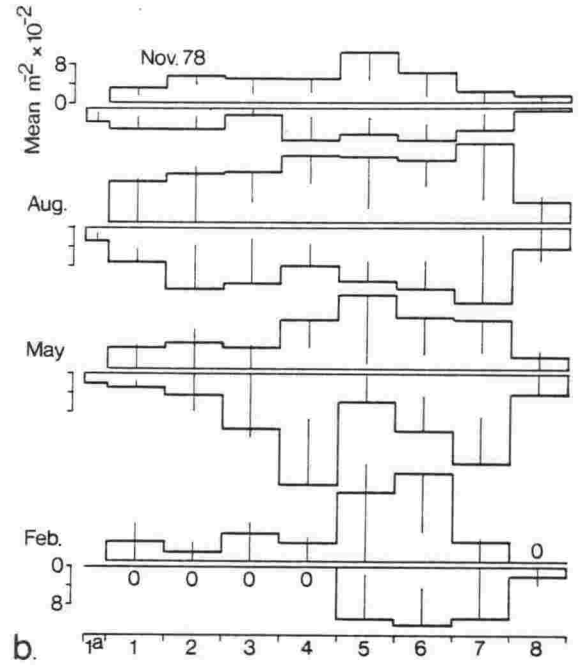
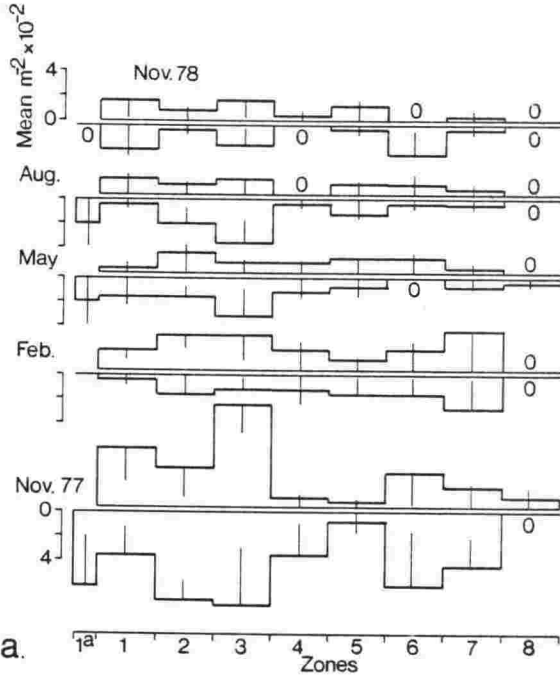


TABLE 13. Tests of *Axiiothella serrata* 1977-78 zonation (500 μ m sieve series) using Mann-Whitney U-test. Significant tests indicated as * ($P < 0.05$), *** ($P < 0.001$), with non-significant tests blank, and no test as - (no data for November 1977 dispersed juveniles).

Age group	Zones	Nov.'77	Feb.'78	May '78	Aug.'78	Nov.'78
adults	1-4:5-8	***		*	*	
O group	1-4:5-8	-	***			

The 1978-79 O group did not at first show a distinct zonation pattern (Fig. 19c), but by 30 November there was an up-shore increase (MWU, $P < 0.05$) with the peak in zone 2. By 30 January densities were more even, but still showing a lower shore decline. By May densities were low and the zonation pattern was (non-significantly) reversed.

The 1979-80 O group had higher downshore density, at least in November 1979 (Fig. 19c, MWU, $P < 0.05$). However, the 1981-82 O group in December 1981 showed a high upshore density (Fig. 19c, MWU, $P < 0.001$), especially in zones 2 and 3.

AGE ZONATION WITHIN THE 1978-79 O GROUP: Mean setiger-totals for zone pairs indicated upper shore juveniles tended to be younger than further downshore (Table 14), and Fig. 18 suggested there was an increase in the percentage of older juveniles downshore.

TABLE 14. Comparison of *Axiiothella serrata* 1978-79 O group mean setiger-totals between two-zone groups, using sum of all samples, 30 October to 29 May.

Zone	n	\bar{x}	¹ Significant differences	s ²	SE
1 + 2	317	9.33	**	3.21	0.101
3 + 4	447	10.54		10.59	0.154
5 + 6	441	11.76		13.17	0.173
7 + 8	136	10.39		12.20	0.300

¹t-test of means (** P < 0.01).

Zone 7+8 mean is significantly higher than zone 1+2 (P < 0.01).

Possibly the high upshore density of early juveniles was sufficient to give these trends. To test this, densities per core were compiled for the upper and lower shores separately (zones 1-4 and 5-8) for the period during which older juveniles (13 setigers and above) were present, the younger juvenile population (6-12 setigers) was still receiving more recruits, and the population was denser on the upper shore (combined data from 21 December 1978 to 14 April 1979 samples). Density of older juveniles was higher on the lower shore (MWU, P < 0.05; zones 1-4 \bar{x} /core 4.5, SD 2.96; zones 5-8 \bar{x} /core 8.2, SD 5.85), whereas younger juveniles were denser on the upper shore (MWU, P < 0.01; zones 1-4 \bar{x} /core 12.7, SD 8.37; zones 5-8 \bar{x} /core 6.5, SD 5.05). Thus during this period early juveniles were concentrated upshore, possibly by the effect of wave action erosion or simply more successful upshore spawning (see discussion). However, the converse pattern for older juveniles suggests that upper shore mortality is higher than on most of the lower shore (zone 8 an exception noted

earlier). This might be due to greater physico-chemical stress up-shore, to continued erosion and eventual stranding on the cobble shore, or perhaps to heavier predation by other infauna.

GROWTH

The rate of growth in size of *Axiiothella serrata* juveniles could not be determined from field samples as recruitment continued over several months. The rate of addition of setigers towards the adult complement of 22 was indicated by the movement of the various modes in the 1978-79 O group setiger-total frequencies (Fig. 17). Because of the time intervals, both between successive appearances of setigers and between samples, only a coarse estimate of the change in rate could be made. During development the rate declined from $2\frac{1}{2}$ days to about $10\frac{1}{2}$ days per setiger. Between the 6- and 15-setiger stages the average rate declined from $2\frac{1}{2}$ to 8 days per setiger. The clearest and most rapid growth was shown by group B of Fig. 17a, which took 14 days from 5- to 9-setiger stage, 21 days from 9 to 14 setigers, and a further 22 days to 18 setigers (total 57 days). From their first occurrence in samples 21- and 22-setiger individuals had developed by at most 97 and 134 days respectively after 6-setiger individuals first appeared.

Some information on the growth of adults can be derived from the movement of the mode in setiger-1 width for the 1977-78 age group (Fig. 14). During the six months from the first spawning the width mode of the group remained about 110 μm while recruitment continued, but individual width increase was in any case slight at first (see size relationships). Subsequently width increased during the next 18 months to about 1600 μm . Largest adults had a width of about 2600 μm .

JUVENILE SIZE RELATIONSHIPS

SIZE AND SETIGER-TOTAL: Juvenile length and width relationships to setiger-total were analysed, based on measurements of 1785 individuals from the 1978-79 O group (to 7 months old), the 1977-78 O group (to August 1978 at 10 months old), and the November sibling mass juveniles. Measurement of soft-bodied, variably contracted *Axiiothella serrata* juveniles extracted from preserved samples includes unavoidable variation. Specimens with the same number of setigers could range from short and thick to long and thin. For example, for 9-setiger juveniles a negative correlation existed between length and width (Spearman's r_s -0.22, $P < 0.01$, n 290), with length tending to increase as width decreased. The range of variation was lessened by the constraints of the tube preventing excessive contraction, and the tendency of worms to be preserved in similar states of contraction. To test if a combination of length and width was a better index of size than either alone, volume was calculated. Width, length, and volume changes during the first ten months' growth are shown in Fig. 20.

Width had lower variation within each setiger-total group than length (mean coefficients of variation, V , of 14 and 23% respectively). Volume data had the highest variation, with an overall mean V of 47%, but mean V to setiger 17 was only 27%. Mean volume values up to 17 setigers increased in a more consistent pattern than length and width means (Fig. 20). Mean width in particular did not increase consistently until about 11 setigers were developed.

The above analysis of size with respect to setiger-total assumes the latter is a reliable correlate of true size. Similarly, setiger-total was earlier used as an index of age (see spawning groups). However, setigers were added at a decreasing rate as the adult total of 22 was approached, while width, length, and volume increased considerably.

Fig. 20 *Axiiothella serrata* juveniles (to 10 months)

size/setiger-total relationships for width, length, and calculated volume, all on arithmetic scales; volume data have different scales for the 4-15 and 15-22 setiger ranges. For each setiger-total the mean size \pm SD and range is indicated. The fitted curves, which were derived by least-squares-regression using all data points, are listed in linear form in Table 15 and discussed in the text. Note that for all three relationships two curves are plotted (5-15, 15-22 setiger ranges).

Fig. 21 *Axiiothella serrata* juveniles (to 10 months)

length/width relationship. For the large number of data points up to 200 μm width, mean length, \pm SD and range, for 10 μm width classes, is shown. For comparison mean widths (for 400 μm length classes) over this range are also shown (large circles). Least-squares-regression lines of length on width and the converse (using all data points over the ≥ 110 μm width range) are shown ($r^2 = 0.8958$), for which the geometric mean (GM) regression was

$$\text{Length} = -165.33 + (1.908 \times \text{width})$$

where length is in $\text{mm} \times 10^2$ units, width in μm .

Inset (displaced ordinate) mean length and width coordinates for each setiger-total are compared with the GM regression line.

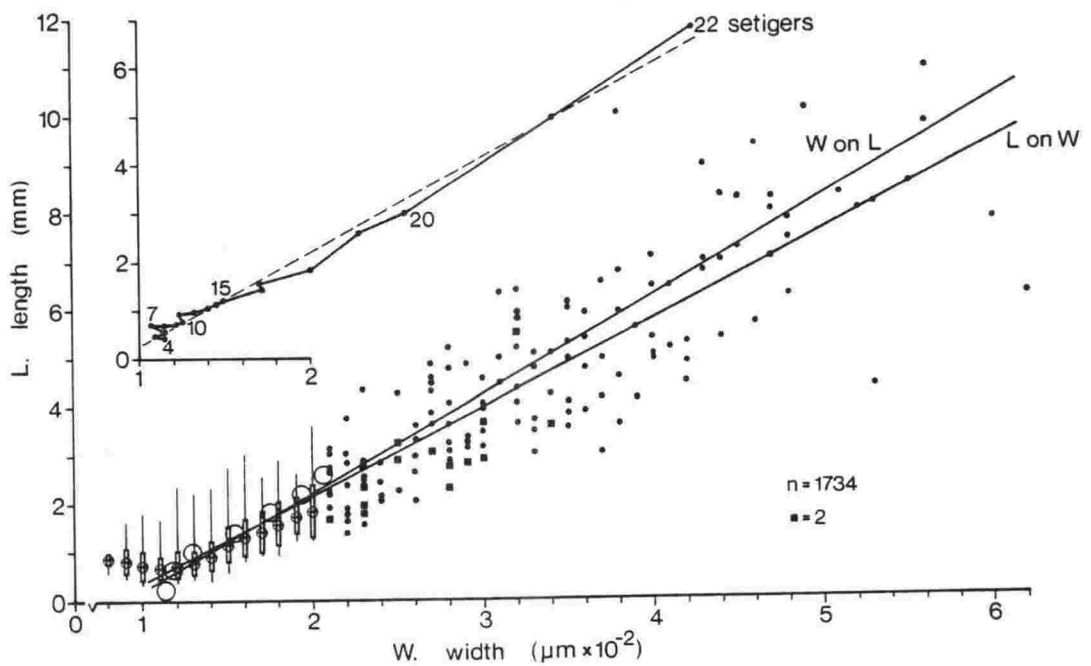
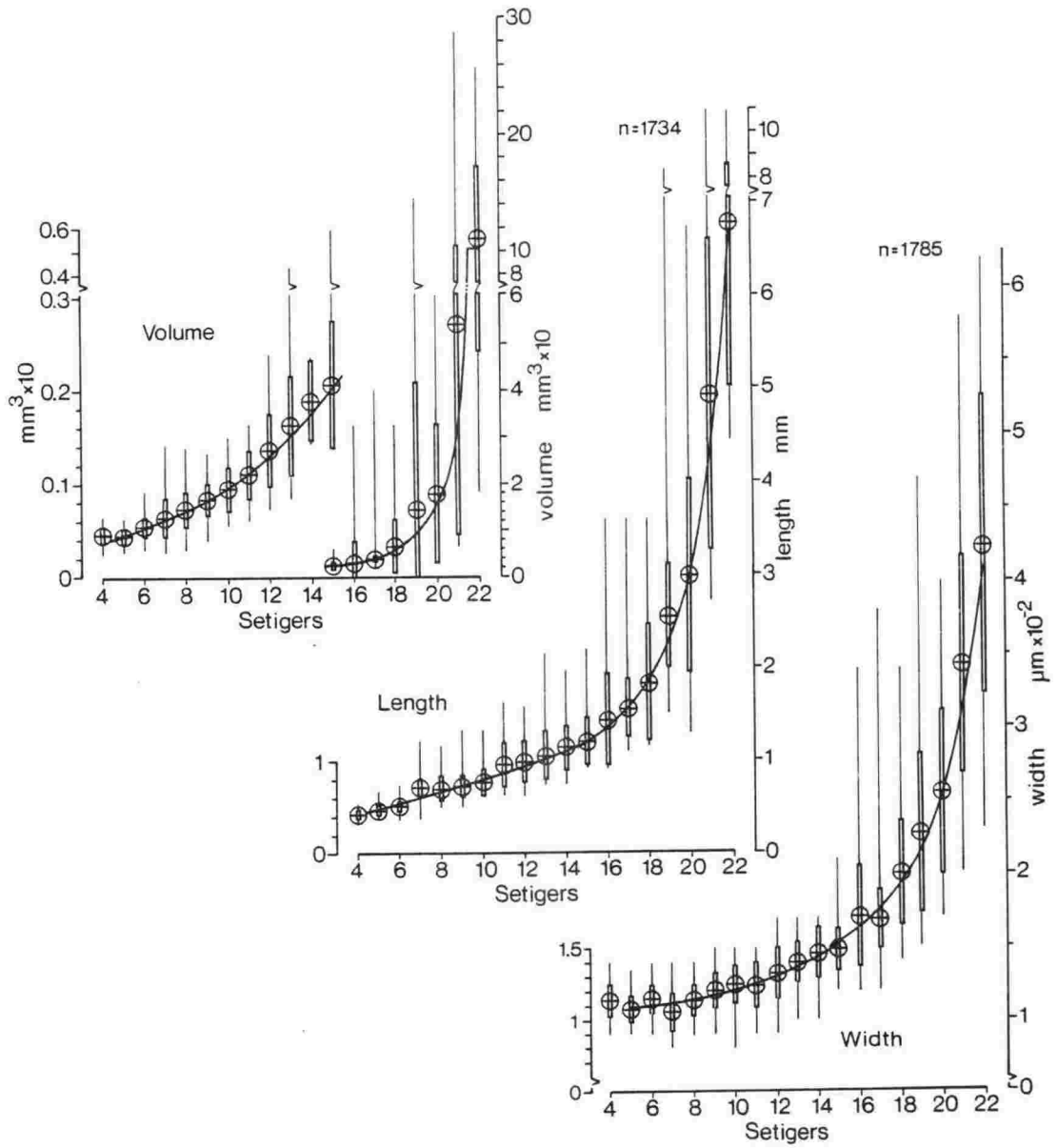


TABLE 15. *Ariotheella serrata*. Exponential regression models of the size to setiger-total ¹relationship where, in linear form, $\log_e(\text{size}) = B_0 + B_1(\text{setiger-total})K$.

Setiger- total range	Size	² Lack-of-fit ratio	Degrees of freedom	r ²	K	B ₁	B ₀	³ 95% Prediction interval	⁴ P.I.(%) at setiger 15
4 - 22	Width	*35.8	17,1766	0.7893	3.8	9.9×10^{-6}	4.721	0.3053	6.09
	Length	*36.6	17,1715	0.8422	1.9	6.4×10^{-3}	3.824	0.4869	9.89
	Volume	*20.1	" "	0.8949	2.9	6.0×10^{-4}	3.947	0.7857	14.31
5 - 15	⁵ Width	*41.9	9,1371	0.3335	2.1	1.24×10^{-3}	4.647	0.2467	4.92
	⁵ Length	*18.2	9,1336	0.5876	0.6	0.3640	2.939	0.3973	8.30
	⁵ Volume	* 4.1	" "	0.7222	0.9	0.2129	2.871	0.4908	9.25
15 - 22	⁵ Width	1.5	6,407	0.7101	5.8	1.8×10^{-8}	4.914	0.3898	7.73
	⁵ Length	* 2.3	6,389	0.7653	5.4	1.1×10^{-7}	4.553	0.5820	12.10
	⁵ Volume	2.1	" "	0.7729	6.0	3.7×10^{-8}	5.025	1.2378	22.70

TABLE 15. Footnotes.

- 1 In all regressions setiger-total had a highly significant relationship to dimension (F test of regression ratio, $P < 0.001$, high F values not tabled).
Regression parameters will give predicted widths in μm ; predicted lengths and volumes were scaled up for working convenience to $\text{mm} \times 10^2$ units, and $\text{mm}^3 \times 10^4$ units respectively.
- 2 Ratio of lack-of-fit mean square/pure-error mean square. *Indicates significantly different mean square values by F test ($P < 0.05$).
- 3 Size \pm 95% Prediction interval (P.I.) gives the expected range of size from the regression line for any setiger-total. The P.I. given is the \log_e value; it changes insignificantly over the setiger range.
- 4 P.I. as a percentage of the predicted size at setiger 15, using \log_e values.
- 5 The fitted curves of Fig. 20.

Thus setiger-total indicated size and age less accurately for older juveniles, and plots of dimensions against setiger development have an overall exponential-like form.

Exponential models were used to compare respective relationships of length, width, and volume to setiger-total (Table 15, Fig. 20). The interesting result from the regression analysis of variance is that lack-of-fit ratios (Table 15) indicated the best fitting relationship (and highest r^2) over the setiger ranges 4-22 and 5-15 was with calculated volume. Thus, under an exponential model, juvenile length and width combined did interact to integrate better with setiger-total than either alone. However, individual lengths and widths were predicted from the equations with greater accuracy than volumes (Table 15) because of the greater variance of volume estimates. The equations demonstrate relationships, and are not advocated for predicting the dimensions of individuals from setiger-totals.

Length and width were highly significantly related (F test of regression ratio). The narrowest individuals (80, 90, 100 μm width classes) had longer mean lengths, and the shortest (0-400 μm length class) had wider mean width than expected for an overall straight-line relationship (Fig. 21). This presumably was due to the presence of more highly expanded or contracted older individuals, as mean widths per setiger-total were all above 100 μm (Fig. 21 inset). The relationship was close to linearity for the data set of ≥ 110 μm width worms, and inspection suggests non-normality in the distribution of lengths of worms below 200 μm width, and increasing scatter in the sizes of larger worms both increased the lack-of-fit ratio to a significant level ($F = 12.3$, tabulated $F_{43, 1480, 0.95} = 1.4$). The coordinates of mean width and length per setiger-total (Fig. 21 inset) lie close to the geometric mean regression line. However, their increases were erratic until 11 seti-

gers were developed, and small until 15 setigers were developed. This confirms setiger-total as the most sensitive indicator of growth and age in juveniles up to about 15 setigers.

SIZE AND NEUROSETAE NUMBER: Juveniles at first have a single neurosetal hook per fascicle, with more developing as size increases, so that older adults have up to about 20. At earliest the second hook appeared in 8-setiger juveniles, the third in 16-setiger juveniles, and by the end of the first year the number on the mid-body setigers, where the maximum occurred, was around 10. Fig. 22 shows how maximum-hook-number per individual relates to body width for the O group. The relationship was highly significant (F test of regression ratio) and close to linearity (lack-of-fit ratio = 4.0, tabulated $F_{187,8,0.95} = 1.98$). As a close relationship to body width has been demonstrated, in itself maximum-hook-number must have potential as an indicator of size and age for older juveniles.

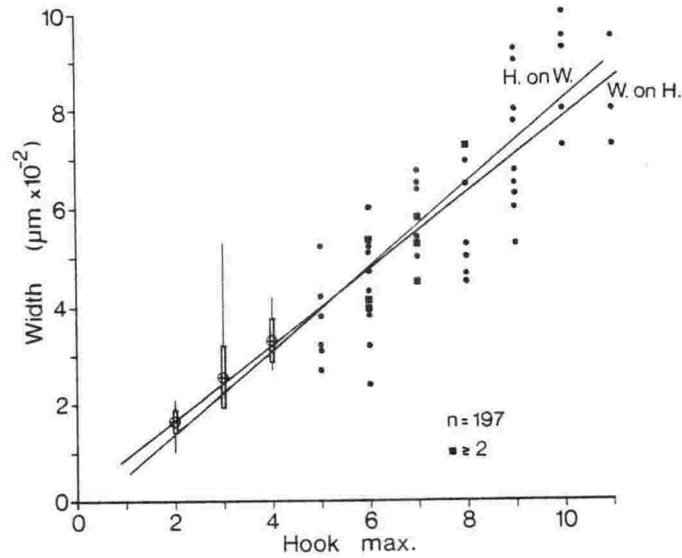


Fig. 22 *Axiiothella serrata* O group width/maximum-neurosetal-hook-number relationship for maximum-hook-number range of 2-11. For clarity the numerous 2-4 hook data points are represented by the mean, \pm SD and range (all data used in regressions).

The least-squares regression lines for width on hook number and the converse are shown ($r^2 = 0.8899$), for which the geometric mean regression equation was

$$\text{setiger-1 width} = -13.10 + (81.66 \times \text{hook number})$$

where width is in μm .

DISCUSSION

The population structure and life history of *Axiiothella serrata* have been outlined. It lives for three years, perhaps longer, and has a prolonged breeding period with intermittent spawning during spring and summer. There is no planktonic stage; juvenile dispersal by means of passive transport mechanisms is localised, but occurs relatively rapidly. Early development occurs within the sediment, probably in a brooded egg mass. As comparable information for other members of Family Maldanidae is sparse, and since the better-known Arenicolidae are related polychaetes with a very similar sediment-processing and burrow-dwelling lifestyle, relevant aspects of arenicolid biology have been included in the following discussion for comparison.

YEAR GROUP RECRUITMENT

Axiiothella serrata spawns first at the end of the second year (unpublished data). Therefore, the large 1975-76 II+ group apparent in November 1977 gave rise to the large 1977-78 O group, and the smaller 1976-77 group gave rise to a similarly small 1978-79 O group. Note that if *A. serrata* is monotelic, there is potential for genetic separation between successive year groups (Olive and Garwood 1981), although if, as is probable, a small proportion of the population survives to breed at the end of their third year, gene flow between year groups would still occur. The apparently alternating year class strength in *A. serrata* may be no more than a coincidental event due to the influence of 'chance' unknown factors on mortality, or a cyclic situation due to the relative reproductive output of the year classes, or even the result

of significant negative age-group interaction. Long-term study would be required to establish whether the pattern was normal.

Evidence of negative adult-juvenile interaction was not obtained, as the 1977-78 O group was positively correlated (non-significantly) to adult numbers per core. Although adult feeding and burrowing activities (Plate 1) could contribute to some juvenile mortality by smothering or ingestion, the question is whether this would affect juvenile numbers seriously, having regard to the comparatively low adult density ($<500 \text{ m}^{-2}$). Previously reported occurrences of adult interference with juvenile settlement, resulting in dominant age classes of long-lived species, are from dense populations (Woodin 1976, Timko 1979). Timko (1979) predicted that intraspecies oophagy was likely to be selected against, but not larviphagy once dispersal had occurred, whereupon it becomes a density-dependent control on recruitment. Interestingly in this regard, in *Arenicola marina* females cease feeding for several weeks after spawning, thus permitting their own eggs and larvae to develop without risk of ingestion (Farke and Berghuis 1979a). However, a negative adult influence on the O group was suggested by Beukema and de Vlas (1979), who found a negative correlation between the annual density of 1½ year old recruits and the previous year's adult density.

SPAWNING AND JUVENILE DEVELOPMENT

The aggregations of *AxiotHELLa serrata* juveniles found between 3 and 15 cm from the surface most probably represent sibling groups developed from egg masses in the female tube. Spawning eggs within the protection of the adult tube is a reproductive strategy used by a variety of polychaetes (Schroeder and Hermans 1975). In the Arenicolidae *Abarenicola pacifica* discharges oocytes to form an 'egg-

tube' within the burrow (Okada 1946, as *Arenicola claparedii*), and spawning within the burrow also occurs in *Arenicola brasiliensis* (Okada 1941, as *A. cristata*), *Arenicolides ecaudata* (Southward and Southward 1958, as *Arenicola ecaudata*), and *A. marina* (Farke and Berghuis 1979a). In *A. brasiliensis* the eggs end up on surface, but in jelly masses attached to the inside of the burrow (Okada 1941).

Spawning strategy is known with certainty for one maldanid species, and with some doubts for another two. *Axiiothella mucosa* spawns its eggs in a surface jelly mass attached to the inside of the tube (Bookhout and Horn 1949). *Clymenella torquata* and *Euclymene oerstedii* (= *Caesicirrus neglectus*) spawn eggs into their tubes, where maturation processes occur before the eggs are fertilisable (Pilgrim 1964). Uncertainty exists as to when, and in what state, the eggs leave the tube. Pilgrim (1964) did not observe spawning in the field, nor did Newell (1951) in an earlier study of *Clymenella torquata*. From the information provided by Pilgrim (1964) the possibility exists that fertilisation and some early development might take place within the female tube.

Approximate early development times of maldanids are known from laboratory studies of three species. In *Axiiothella mucosa* the first four setigers develop three days after fertilisation and almost simultaneously (Bookhout and Horn 1949), in *Clymenella torquata* they develop over the fifth to seventh days (Newell 1951), and in *Clymenura clypeata* over the fourth to seventh days (Cazaux 1972). Six setigers had developed after about 4, 14, and 10 days respectively. The four- to six-setiger *Axiiothella serrata* juveniles found in aggregations might, therefore, be one to two weeks old. After lecithotropic early development, feeding begins when juveniles reach the surface at about the six-setiger stage, the same stage as feeding occurs

in *Clymenella torquata* (Newell 1951). *Axiiothella serrata* juveniles with 22 setigers were recorded in the field some 130 days after aggregations were first found. In comparison, under laboratory conditions the other species developed rapidly. *A. mucosa* developed the full complement of 18 setigers and 20 of the 22 segments in 50 days, and *Clymenella torquata* developed 17 of 18 setigers and the adult total of 21 segments in 41 days (Bookhout and Horn 1949, Newell 1951).

The earliest *Axiiothella serrata* spring spawning recorded was in the latter half of October 1978, and spawning in the first half of November was detected in 1977, '78, '79. '81. The 1978-79 juvenile sampling showed that spawning continued for about five months, apparently as a series of synchronised events. It will be noted that no *A. serrata* juvenile masses occurred in the February 1978 sample, although the subsequent studies showed that spawning continued through February in 1979. Possibly the sample date did not coincide with a spawning event, or more probably aggregation density was below the detection limit, especially if spawning activity progressively decreases. The 1978-79 spawning of *A. serrata* II+ females spread over seven separate occasions would give an average of six aggregations per m^2 each time, assuming each female spawns once, whereas $15 m^{-2}$ were recorded for November 1978.

Nothing is known of how *Axiiothella serrata* spawning is synchronised. One possible mechanism is a periodicity entrained with an environmental variable. However, present data suggest spawning does not occur at uniform time intervals. More conclusive evidence is required, but direct detection of spawning by sampling for *A. serrata* egg masses is impractical. Sampling of surface juveniles provides this information indirectly, although daily sampling would be

required to establish spawning intervals with sufficient accuracy. The search for external factors which may 'trigger' or entrain successive spawnings would be difficult in the absence of a regular periodicity.

Synchronous spawning linked to environmental factors does occur in other maldanids. *Axiothella mucosa* is known to spawn over several months, apparently in the early morning before sunrise, but with unrecorded periodicity (Bookhout and Horn 1949). *Clymenella torquata* and *Euclymene oerstedii* do not have multiple spawnings, but each spawns over a period of a few days coinciding with spring tides (Newell 1951, Pilgrim 1964, Rowe et al. 1975). Among the arenicolids, spawning in *Arenicola marina* is synchronised with tide phases (Duncan 1960, Farke and Berghuis 1979a), and occurs over several months, with geographic variations in the exact periods (Howie 1959, Duncan 1960, Pollack 1979, de Wilde and Berghuis 1979). In *Arenicola brasiliensis* synchronous spawning occurs at about four-day intervals over three months (Okada 1941). Spawning periodicity in the other species studied (*Arenicolides ecaudata*, *A. branchialis*, and *Abarenicola pacifica*) has not been noted, but they have extended breeding periods (Southward and Southward 1958, Okuda 1946).

ZONATION

Axiothella serrata age classes showed more zonation than was apparent for the population as a whole. Juveniles especially tended to be more concentrated within part of the intertidal, although adult zonation also occurred. However, the dispositions still appear to be attributable to 'chance' events and not to the constraints of environmental gradients. Apparently the zones where juveniles concentrated varied year by year.

The effect early *Axiiothella serrata* zonation trends have on subsequent adult zonation is unclear. The evidence from study of adult movement (unpublished data) suggests that migration of adult *A. serrata* does not take place, so distribution patterns result from either differential mortality in both juveniles and adults, or migration of juveniles. Possibly the initial zonation as shown by the dense early juveniles is relatively unimportant, and it is the less apparent zonation of older juveniles which determines later adult zonation. For example, the early zonation pattern of the 1978-79 O group had apparently reversed by May (Fig. 19c) to reveal the trend detected earlier in older juveniles. The 1977-78 O group zonation lasted longer, although barely apparent by November 1978 (Fig. 19b). In February and May this pattern represented that of older juveniles because of the sieve size (500 μ m). Whether the upper shore concentration of adults in November 1977 resulted from early juvenile zonation is unknown, but in May and August 1978 the reappearance of the pattern was due to differential adult mortality.

Adult zonation at the time of spawning might affect early juvenile zonation, although there is little evidence of this. The 1978-79 group were denser on the upper shore, corresponding to adult densities which were (non-significantly) higher on the upper shore. In contrast the 1977-78 group, denser on the lower shore, had an opposing zonation to the adults (but were mainly older juveniles), and the zonation of the 1979-80 group in November 1979 was not reflecting the adult pattern.

The hydrodynamic regime is a probable influence on the dispersal of juveniles. As previously mentioned, juveniles do not remain concentrated around the tube of the parent female, notwithstanding their apparent inability to swim away. Wave disturbance of surface sediment

does occur and may lift juveniles into suspension, and subsequently transport them together with other bed-load material. During strong NNW winds at the Pauatahanui site complete sediment turnover occurred to 10 mm depth and sediment disturbance to 30 mm (technique of Steele et al. 1970). *Axiiothella serrata* juveniles were vulnerable to such erosion because December 1981 sampling showed that 98% of individuals were within 15 mm of the surface. It is likely the tendency was for shorewards transport of displaced juveniles at Pauatahanui as the prevailing winds were onshore. Upshore accumulations (November 1978, January 1979, December 1981) are possibly accounted for by this mechanism. Downshore accumulations (February and May 1978, November 1979) require the influence of unknown local currents or other explanations, such as differential mortality from increased upshore physico-chemical stress, and active attempts to enter the water mass on the ebb tide.

It has been previously observed that erosion and subsequent transport of benthic, infaunal, polychaete juveniles occur (Boaden 1968, Shaffer 1979). Also several cases of apparent active migration via the water mass have been recorded (Simon 1968, Eckelbarger 1974, Farke and Berghuis 1979ab, Dauer et al. 1980), although the circumstances giving rise to these movements are poorly known. The most interesting example for comparison with *Axiiothella serrata* is the recorded dispositions of *Arenicola marina* on the extensive intertidal flats of the Wadden Sea and Brittany. Dense nearshore patches of juveniles occur (Farke et al. 1979, Beukema and de Vlas 1979, Pollack 1979), because larvae and subsequently juveniles tend to be carried upshore (Farke and Berghuis 1979ab). However, later as I group individuals their density decreases nearshore and increases downshore (Beukema and de Vlas 1979, Pollack 1979). Individuals of this age occur in plankton samples, and so the inference is that passive transport downshore occurs (Beukema

and de Vlas 1979). The occurrence of movement both up and down the shore appears to require a behaviour change from entry into the water mass on the flood tide to entry on the ebb. However, the situation requires more investigation; random processes may suffice to give the observed dispositions.

SIZE AND AGE ASSESSMENT

Axiiothella serrata and most other polychaete worms lack structures from which a direct age assessment of an individual can be made, thus restricting population-structure analysis to size-frequency data. Age assessment is hampered by overlapping size ranges of age classes, as occurs in many animals, but with additional variation present because the precise size of a soft-bodied worm is difficult to assess. Setiger-one width measurement allowed separation of the 0 group *A. serrata* individuals from the adults, and also showed the existence of two adult age classes, which were distinct for part of the year. From the decline of the two-year-old group a maximum life span of three, maybe four years appears probable. A comparable age structure has been shown for *Arenicola marina* (Pollack 1979), but a six-year life span has been observed in aquaria (Thamdrup 1935).

The analysis of size in relation to setiger development showed that width measurement was an insensitive index of early juvenile development. Additionally, within a group of juveniles with the same setiger-total the expected inverse relationship of length to width (due to variation in contraction) was demonstrated. Calculated volume gave a better overall fit to setiger-count data than length or width separately.

Besides direct measurement the assessment of size and age may be approached through counts of body parts. The number of setigers was the best indicator of size and age in early juveniles, but less advantageous

for older juveniles because additions came less frequently as the adult total of 22 setigers was approached. For older juveniles the maximum number of neurosetal hooks, possibly a function of body diameter, showed potential as an indicator of normal width of a variably contracted individual. This size measure could be extended to adults, although the number of hooks becomes less readily assessed as size increases and worms become more opaque, necessitating dissection and slide mounting before examination. Setal counts have apparently not been previously used for the purpose of age analysis in polychaetes. In the case of *Axiiothella serrata* the labour involved may not be worthwhile for study of population age structure, but such counts could be a useful aid when the best assessment of the age of an individual was required.

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S E C T I O N 3

POPULATION DYNAMICS OF THE INFAUNAL POLYCHAETES

MICROSPIO SP. (SPIONIDAE) AND *CAPITELLA* SP. (CAPITELLIDAE)

ON A PAUATAHANUI INLET INTERTIDAL SAND FLAT

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ABSTRACT

The population dynamics of *Microspio* sp. and *Capitella* sp. were investigated from seasonal samples, 500 μ m sieve processed, from a stratified transect pair, and from some subsequent, more finely-sieved samples during dense recruitment periods. Both species are small, surface-dwelling, short-lived deposit-feeders, believed to reproduce near year-round but with a spring-summer peak.

Microspio sp. density peaked in August (winter) at about 6 thousand m^{-2} and was lowest in February when estimated by 500 μ m sieve. Size-frequencies were unimodal indicating continuous reproduction, but changes in densities of width classes and shifts in the mode suggested a pre-February settlement peak and an August to February adult decline. Finer sieve samples showed dense larval recruitment occurred during spring, at first creating a separate modal group of

spring recruits (to 37 thousand m^{-2}), and continued through summer before an autumn decline. Width and setiger-total size measures, having a direct functional relationship, gave similar population structure estimates. Size zonation, as well as density zonation, showed no pronounced trend.

Capitella sp. density peaked in May (autumn) at about 2.3 thousand m^{-2} and was lowest in February when estimated by 500 μm sieve. Size-frequencies were again unimodal and, unlike *Microspio* sp., showed only slight seasonal shifts. Variation in settlement was unclear, but the number of egg masses produced was lower in autumn and winter. Finer sieve samples showed juvenile settlement increased to form a modal group in late spring, while at first adult density decreased before renewing by January (ca. 7 thousand m^{-2}). A decline in density and recruitment had occurred by May, and lower densities continued until late spring. Samples processed by 500 μm sieve provided some indication of *Microspio* sp. settlement, but only indicated adult changes in *Capitella* sp. because of smaller worm size.

INTRODUCTION

The small deposit-feeding polychaetes *Microspio* sp. and *Capitella* sp., commonest of intertidal macrofauna at the Pauatahanui transect site, are short-lived species with breeding occurring more or less continuously in the populations. As a result age classes as such do not exist, so that size-frequency data yield less information than can be obtained from long-lived species with discrete breeding seasons. Nevertheless both the *Microspio* sp. and *Capitella* sp.

populations had density and size-frequency changes which can be interpreted meaningfully. These two species are considered together because of population structure and cycle similarities, and because both were assessable by short cores due to their surface-dwelling habits.

The biology of *Microspio* species, and of the related genus *Spio*, is little known. However, descriptions have been given of larval stages and development of *Microspio mecznikowiana* (Claparède and Meczniow 1869, Cazaux 1971), *M. atlantica* (Hannerz 1956), and of *Spio* spp. (Mesnil and Caullery 1917, Okuda 1946, Hannerz 1956, Simon 1967, 1968, Guerin 1972). Sperm may be in spermatophores, but are not necessarily transferred directly from male to female (Claparède and Meczniow 1869, Rice 1978). After an initial development period within an egg string, which is a cylindrical series of capsules attached within the female tube, the larvae become planktonic or, in a second type of development without a planktonic dispersal stage, continue to occupy the egg string while feeding on nurse eggs. Both development types occur in *S. martinensis*, *S. setosa* and *S. decorata* (Mesnil and Caullery 1917, Simon 1967, Guerin 1972). The population dynamics of *Spio* and *Microspio* spp. have not been previously reported.

More is known of the biology of *Capitella* spp. The Pautahanui *Capitella* sp. is a member of the *C. capitata* species complex, at present ill-defined taxonomically and not readily separable morphologically. Grassle and Grassle (1976, 1977, 1978), and Grassle (1979) have used code numbers and letters to refer to ten North American species they have detected. Further discussion of the taxonomy is given in the Appendix. Literature relevant to the population cycles and reproduction of what has previously been called *C. capitata*

is reviewed below and in the discussion. The citations may be considered as referring to several closely related species.

Capitella spp. have been widely reported and have received special attention for their opportunistic capacity to become prominent in organically polluted or disturbed environments (e.g., Reish 1960, Grassle and Grassle 1974, Pearson and Rosenberg 1978, Gray 1979, James and Gibson 1980, and references therein). Reproduction and larval settlement in *Capitella* spp. continue all year in temperate habitats, although seasonal peaks often occur (Rasmussen 1956, Grassle and Grassle 1974, Watling 1975, Dauer and Simon 1975, Foret 1975, Warren 1976a, Dauer 1980, Hannan 1981), and the species Ia and III of Grassle and Grassle (1977, 1978) have a more limited breeding season in winter and early spring. In some populations hermaphroditism occurs (Warren 1976b, Grassle and Grassle 1976, Grassle 1979). After culturing inbred lines, Grassle (1979) suggested the occurrence of hermaphroditism increases under conditions that facilitate inbreeding, such as during a recolonisation.

Early larval development takes place during a period of incubation while the embryos are in an egg mass which lines the tube of the female. From the trochophore stage development may continue as totally benthic or include a planktonic period of variable, but usually short, duration (Eisig 1898, Rasmussen 1956, Reish 1974, Foret 1975, Grassle and Grassle 1976, 1977, 1978). Direct and planktonic development may co-occur in one egg mass (Foret 1975). The larval morphology has been described by a number of authors, among them the first four cited above. Some differences between the sibling species in egg and larval morphology and length of oogenesis have been detected (Grassle and Grassle 1976, Eckelbarger 1980, Eckelbarger and Grassle 1982).

The number of oocytes in each spawning is variable and partly dependent on worm size. Warren (1976a) reported about 10,000 oocytes spawned per female, Reish (1974) 150-200 in laboratory culture, and Grassle and Grassle (1974) at first reported 6-600 oocytes, increasing in number with length of female, later giving an overall range of 30-2000 oocytes, the number varying for each sibling species, depending on food supply (Grassle and Grassle 1977). Their species type IIIa had the lowest number, at 30-50 per batch.

The interval between generations in *Capitella* is 25-60 days, and is dependent on temperature (Reish and Barnard 1960, Reish 1974, California; Grassle and Grassle 1974, Massachusetts; Foret 1975, Mediterranean France). The one-year interval estimated for an estuarine Devon, England, population (Warren 1976a) lacks direct evidence. Worms may spawn two or more times (Reish 1974, after 9-16 day interval; Blackstock and Pearson 1979, after 35-43 day interval).

METHODS

Details of sample collection and statistical treatments have been described in Sections 1 and 2. In brief, a zoned transect pair was sampled quarterly, November 1977 to November 1978, using 15 cm deep, 50.3 cm² cores sieved through 500 μ m mesh, and a further left transect sample in November 1979 was processed through 500 and 250 μ m meshes, the top 3 cm separately. Also additional left transect samples analysed for *Microspio* sp. and *Capitella* sp. were taken on 16 November 1978, 30 January 1979, and 29 May 1979 (24, 24, and 40 cores respectively), using 3 cm deep, 9.63 cm², cores sieved through 250 μ m mesh, and during spring 1981 (15 September, 13 October, and 11 December), using 3 cm deep, 1.29 cm², cores (n = 56/transect) sieved through 72 μ m mesh.

Means of large samples (≥ 40 cores) were compared by parametric test, whereas the Mann-Whitney U-test (MWU), and limits cited as $\pm 2SE$, were appropriate for other sample comparisons.

The analysis of the deep core, 500 μm mesh, samples is presented first, and provides information on changes in the adult population, but little on juvenile recruitment rates in these two species because of their small size. However, combined with analysis of recruitment from later fine-sieve sampling, an integrated interpretation of population structure was possible.

Microspio sp. size was assessed from body width (excluding parapodia) across setiger 6 natural maximum, using 25 μm size classes, which were later grouped into 50 μm classes to smooth size-frequencies. Setiger counts were also used, especially when large numbers of complete juveniles were present. *Microspio* sp. less than about 250 μm width were assessed under the compound microscope, whereas larger worms could be examined under a dissecting microscope. Frequencies were increased proportionately to equal the true number examined under each microscope to avoid bias in setiger counts towards the more frequently complete small worms.

Capitella sp. size was assessed from the body 'width' (here the dorso-ventral depth) at setiger 3-4 natural maximum, measured under a compound microscope using 10 μm size classes, later grouped into 20 μm classes. Thoracic length, used as a size index for *C. capitata* by Warren (1976a), could not be determined accurately for Pauatahanui worms, which were much smaller than those in Warren's study.

Morphometric relationships were examined by regression analysis of variance, and expressed in linear form using the geometric mean regression equation (see Section 2, methods).

RESULTS

MICROSPPIO SP.

POPULATION DYNAMICS FROM 500 μm SIEVE SAMPLES, 1977-79:

Population densities of *Microspio* sp. in November 1977, 1978, and 1979 were not significantly different (3.61 ± 0.41 , 4.18 ± 0.48 , and 4.56 ± 0.75 (2SE) thousand m^{-2} respectively), but during the 1977-78 year densities changed significantly between all quarterly samples (Fig. 23). After 3.61 ± 0.41 thousand m^{-2} in November 1977 the population was at a minimum in February 1978 (2.60 ± 0.35 thousand m^{-2}), then increased (May 3.86 ± 0.55 thousand m^{-2}) to the August maximum of 6.26 ± 0.77 thousand m^{-2} , declining again in November (4.18 ± 0.48 thousand m^{-2}).

The size distribution of *Microspio* sp. was unimodal and also relatively stable (Fig. 24a), suggesting recruitment, hence reproduction, could be nearly continuous and life span short. Some consistent change did, however, occur. For the three November samples the population mode class was 450 μm , but it dropped one class to 400 μm in February, then rose by May to 450 μm , and to 550 μm by August. When the population was divided into three a trend was more clearly seen (Fig. 24a, classes 400 to 500 μm inclusive comprise the shaded middle group). The density of smallest individuals increased from November 1977 to February 1978 (750 to 1240 m^{-2}), declined by half in May (600 m^{-2}) and further declined through August and November 1978 (580 and 380 m^{-2}). Those of middle size declined by half from November to February (2580 to 1320 m^{-2}), then increased through May and August to November (2250, 3250, and 3400 m^{-2}). The largest declined (from 280 m^{-2} in November) to a low of 40 m^{-2} in February, but increased greatly in May and in August (1010

and 2430 m^{-2}), before declining to 410 m^{-2} in November 1978. These changes were consistent with progressive growth of a dominant group formed from a pre-February settlement peak, some individuals of which became large enough to be retained in the sieve in February, before the group as a whole subsequently progressed through the size range and peaked in the $500 \mu\text{m}$ assessment in August. The decline of larger adults from August through November, and inferred on to February, indicates continuous high mortality of about $0.01 \text{ individual}^{-1} \cdot \text{day}^{-1}$, even with recruitment.

POPULATION DYNAMICS FROM $250 \mu\text{m}$ SIEVE SAMPLES, 1978-79:

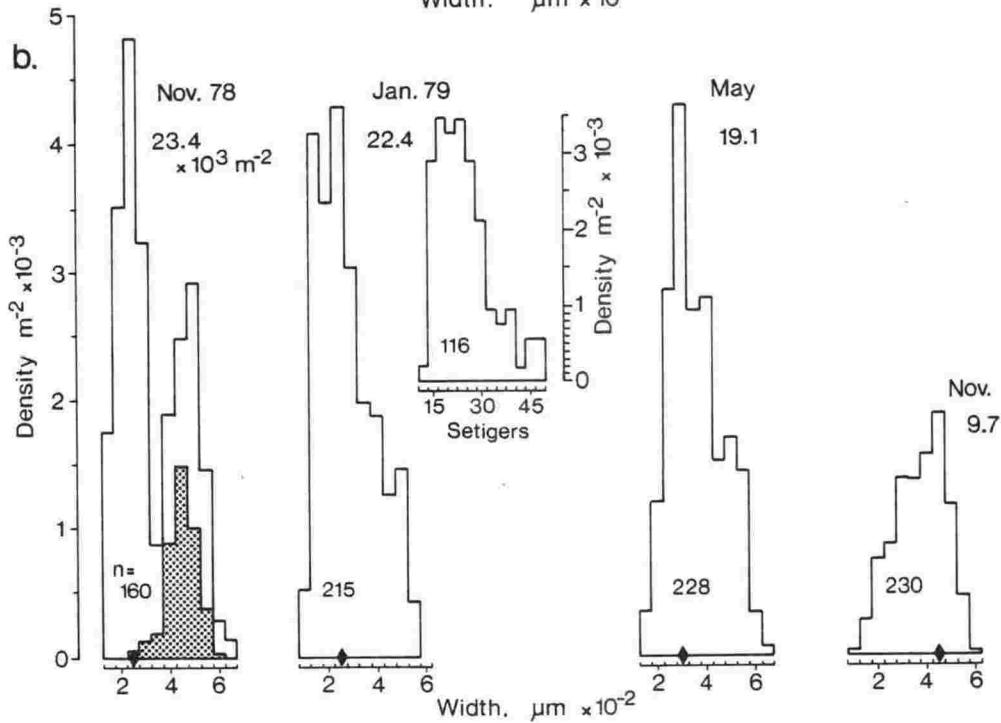
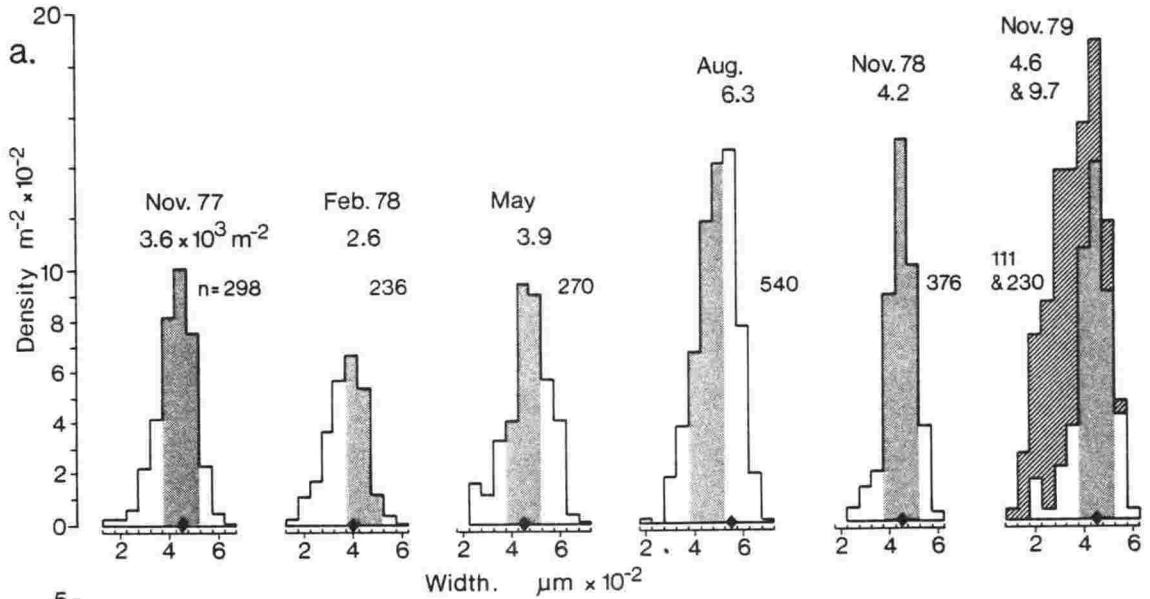
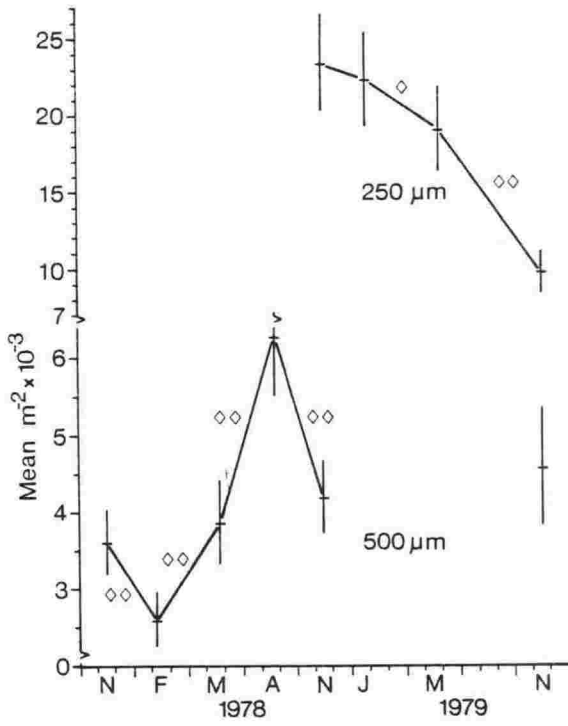
The population structure of *Microspio* sp. revealed by $500 \mu\text{m}$ mesh processing was incomplete as this sieve size allowed a large proportion of small individuals to pass through. The size range of setiger six widths, the widest part of the body, indicates that potentially more than 50% of the retained population could have passed the sieve. In practice in the November 1979 sample 53% of individuals passed the $500 \mu\text{m}$ sieve to be retained on the $250 \mu\text{m}$ sieve. These were mainly juveniles as the percentage of the total $9.73 \text{ thousand m}^{-2}$ population retained by the $500 \mu\text{m}$ sieve for different size classes was 83% for $550 \mu\text{m}$ and above classes, 73% for 500 to $400 \mu\text{m}$ classes inclusive, but 17% for below $400 \mu\text{m}$ classes and 11% for $250 \mu\text{m}$ and below classes (see Fig. 24a). The November 1979 cores, divided as collected into 0-3 cm, 3-15 cm depth portions, also showed that more than 99% of *Microspio* sp. were in the top 3 cm, even though X-rays of sediment blocks revealed *Microspio* sp. potentially could descend 15 cm down existing vertical burrows. Thus cores to 3 cm depth adequately assessed the population.

Fig. 23 *Microspio* sp. seasonal mean densities as thousands per $m^2 \pm 95\%$ limits, or $\pm 2SE$ for 250 μm series and November 1979. Diamond(s) indicate $P < 0.05$ ($P < 0.01$) significant differences. Note scale change.

Fig. 24 *Microspio* sp. width size-frequencies 1977-1979 as densities per m^2 for 50 μm size classes. Mode class (diamond symbol), total population density, and number of individuals measured also indicated.

a) Densities in 500 μm processed samples as hundreds per m^2 , with shaded classes (400-500 μm) clarifying changes in size distribution, and November 1979 250-500 μm sieve estimate added (hatched).

b) Densities in 250 μm processed samples as thousands per m^2 . November 1978 has the 500 μm population estimate superimposed, and inset for January is the setiger-total size-frequency in 3-setiger classes.



In November 1978 *Microspio* sp. density was 23.38 ± 3.14 (2SE) thousand m^{-2} from cores processed using 250 μm sieve mesh, compared with the 4.18 thousand m^{-2} estimate discussed earlier from cores collected alongside and processed using 500 μm sieve mesh (Fig. 23). The difference was mainly due to a distinct modal group of smaller juvenile individuals up to 300 μm class undetected when the larger mesh was used (see Fig. 24b superimposed size-frequencies), with also some less important underestimation of the older group. Subsequently in a late January sample the total population was at about the same density (22.43 ± 3.00 (2SE) thousand m^{-2}), the population $\leq 300 \mu m$ had increased slightly from 13.3 to 15.4 thousand m^{-2} , indicating recruitment continued at the same rate, while the November adult population of $\geq 400 \mu m$ class had decreased from 9.2 to 5.0 thousand m^{-2} . A setiger-count size-frequency (Fig. 24b inset) was similar in shape to the width frequency, suggesting the latter adequately approximated the state of setiger development (and presumably of growth or age) of individuals (see later).

By late May the population density was 15% less than in January at 19.14 ± 2.76 (2SE) thousand m^{-2} , (MWU, a significant decrease, $P < 0.05$). The size classes $< 300 \mu m$ had less than half the density of November and January, but all larger classes had increased. This is consistent with a decline in the rates of reproduction and settlement together with progressive growth of spring-summer settlement peak individuals. By November 1979 a large population decrease had occurred to 9.73 ± 1.33 thousand m^{-2} (MWU, $P < 0.01$), the size-frequency was skewed towards a mode of larger, older worms and, unlike November 1978, dense spring settlement had not yet appeared.

POPULATION DYNAMICS FROM 72 μm SIEVE SAMPLES, SPRING 1981:

To examine the effect on size-frequency of the spring period of recruitment increase, establish the densities at settlement of the earliest post-larvae, and compare the respective depth location of adults and juveniles, a set of three transects was taken in September, October, and December 1981, in which cores were divided into 0-15 mm, 15-30 mm depth portions as they were collected, and sieved through 250 μm , then 72 μm mesh. Table 16 and Fig. 25 summarise the density estimates, and Fig. 26 displays the size-frequency distributions, including depth-zone and sieve-mesh subdivisions. The October transect was to 15 mm depth only. Densities from an approximate division of the population into adult and spring-recruit (juvenile) groups, the two modal groups apparent in the size-frequencies, are included in Table 16. In making the division overlaps were assumed to be equal, cancelling out, an acceptable procedure where densities are high and overlap comparatively small. Setiger-based estimates were probably more accurate due to less overlap, but those width-based gave comparable densities of the two groups (Table 16). Consistent with the division apparent in size-frequencies, the spring-recruit group was widened in December to encompass the increasing size of older recruits.

In September adults comprised about 64% of the 33 thousand m^{-2} , although the existence of a distinct juvenile group showed settlement was occurring. Setiger and width frequencies showed a spring-recruit mode at the 12-setiger, 200 μm classes, and an adult mode at 33-setiger, 400 μm classes (Fig. 26). The sharp division between adults and juveniles suggests settlement rate had recently increased, and/or, coupled with high mortality, had been insufficiently dense to produce many survivors beyond the 19-setiger stage.

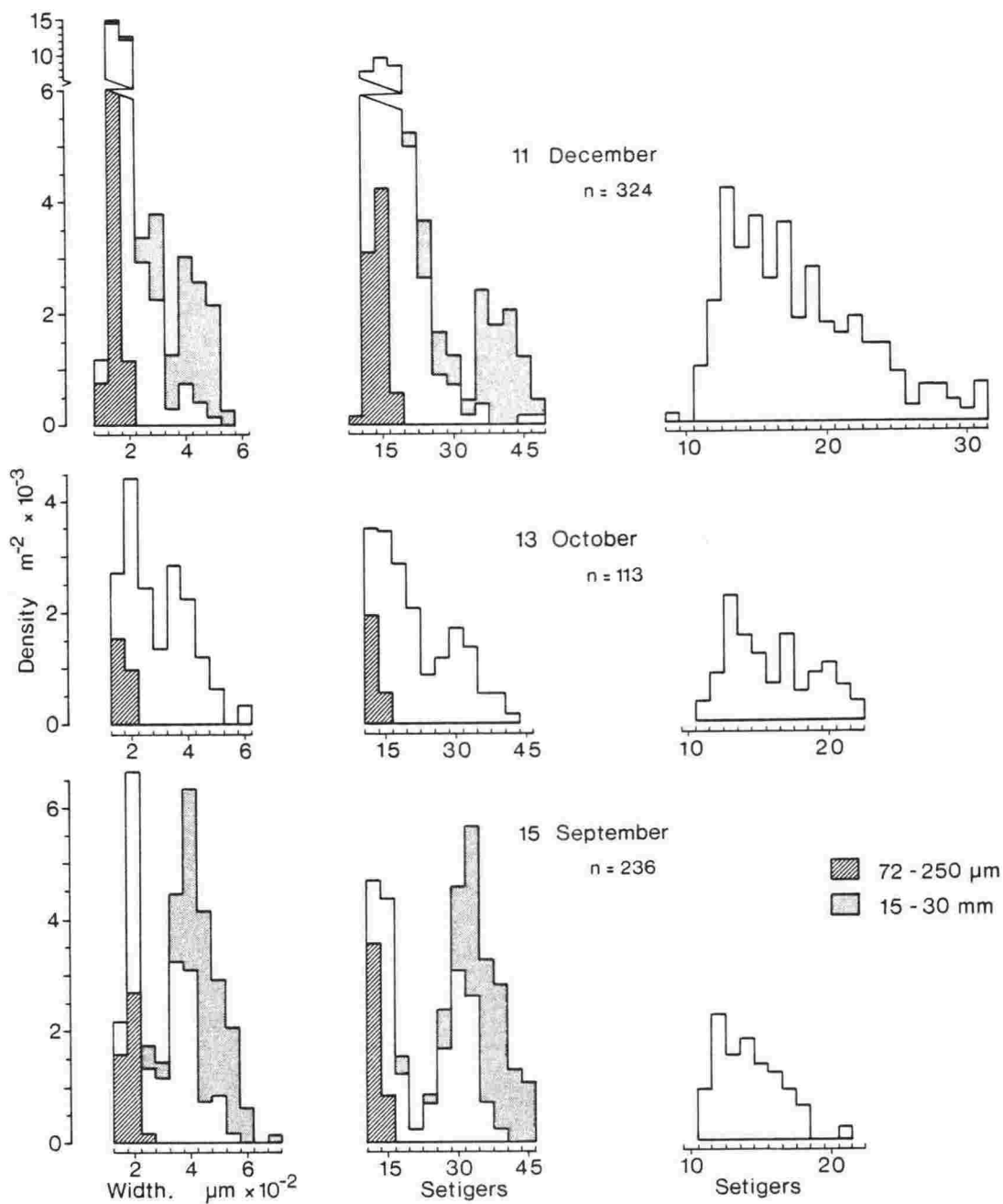
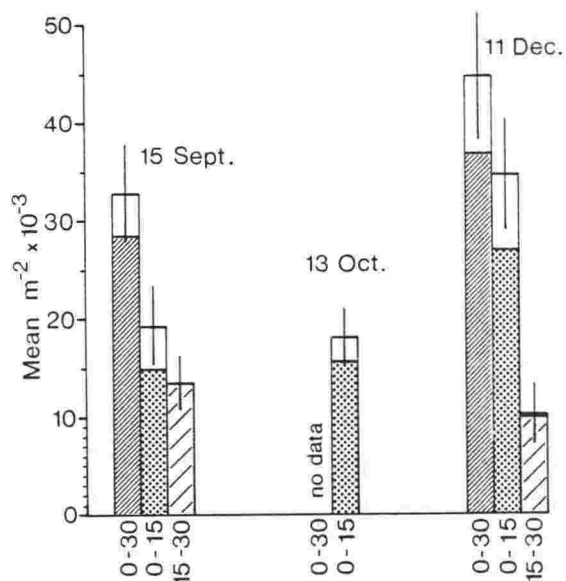
TABLE 16. *Microspio* sp. mean densities as thousands per m² in spring 1981.

Date	Depth (mm)	Mean	± 95% limit	¹ Spring-recruit group		Adult group	
				Width-based estimate	Setiger-based estimate	Width-based estimate	Setiger-based estimate
15 Sept. 1981	0-30	32.75	5.08	12.02	10.76	20.73	21.99
"	0-15	19.29	3.99	11.20	10.26	8.09	9.02
"	15-30	13.46	2.78	0.82	0.50	12.64	12.97
13 Oct. 1981	0-15	18.18	2.88	10.94	11.87	7.24	6.31
11 Dec. 1981	0-30	44.96	6.65	36.95	36.63	8.01	8.33
"	0-15	34.69	5.74	33.39	33.81	1.31	0.89
"	15-30	10.27	3.14	3.56	2.82	6.70	7.44

¹Spring recruits were ≤300 μm width class or ≤22 setigers in September & October, and ≤350 μm class or ≤31 setigers in December.

Fig. 25 *Microspio* sp. mean density estimates, spring 1981, for 0-30, 0-15, and 15-30 mm depths \pm 95% limits (vertical line). Shaded portions are $>250 \mu\text{m}$ sieve fractions.

Fig. 26 *Microspio* sp. spring 1981 size-frequencies, as thousands per m^2 , with 15-30 mm depth and 72-250 μm sieve subdivisions indicated by shadings. For the whole population width frequencies (to left) are in 50 μm classes, with setiger-total frequencies (centre) in 3-setiger classes, and for the spring-recruit population setiger-total frequencies (to right) are in 1-setiger classes.



In October the density to 15 mm depth was slightly (non-significantly) lower at 18 thousand m^{-2} (19 thousand m^{-2} in September). Size-frequencies indicate adult densities may have been dropping, whereas there was little change in recruitment, and an increased number of 17- to 21-setiger older individuals (Fig. 26). On 16 November zones 1 and 2 mean density was 20 thousand m^{-2} to 15 mm depth and 24 thousand m^{-2} to the full 30 mm depth (11 cores). A full transect was not possible due to weather conditions during the spring tide period. Then by early December density had increased greatly to 35 thousand m^{-2} in the surface 15 mm (from October, $P < 0.001$), and 45 thousand m^{-2} to 30 mm. Size-frequencies showed the spring-recruit group had increased from about 11 thousand m^{-2} in September to about 37 thousand m^{-2} , whereas the adult group had declined considerably from about 21 thousand to 8 thousand m^{-2} (or from 64% down to 18% of the total population). The decrease was apparent mainly in the near-surface adults (down to about 1 thousand m^{-2} from 8-9 thousand m^{-2}), whereas the drop in the deeper adult population was less (down to about 7 thousand m^{-2} from about 13 thousand m^{-2} , Fig. 26, Table 16). This apparent differential decline may have been because the surviving September adults were now older and located somewhat deeper. By December about double the number of just-settled post-larvae (to 16 setigers) and three times as many spring-recruits as in September were present. The ungrouped setiger-total frequencies indicate larval settlement occurs mainly at 12 and 13 setigers. The trend suggests that continuation of a high level of reproduction and settlement will fill in the middle of the size-frequency so that it becomes a skewed, near unimodal distribution as in January and May 1979.

As expected, recently-settled individuals were near-surface and older, larger individuals tended to occur deeper in the sediment. No immediate post-larvae (to 16 setigers) occurred below 15 mm and only

low numbers of older spring-recruits (about 6% of the group in September, 9% in December). Adults were denser below 15 mm, especially in December, and especially the larger adults. Overall only 16% of individuals passed the 250 μ m mesh, all young spring-recruits (Fig. 25,26).

The number of egg strings was relatively low in samples despite evidence of high reproductive effort (one in the September sample, two in December, i.e., $140 \pm 340 \text{ m}^{-2}$ and $280 \pm 430 \text{ m}^{-2}$ respectively). However, as egg strings might be located deeper in the burrows than the 3 cm core depth, their near-surface density may not be indicative of the relative spawning activity.

ZONATION: *Microspio* sp. lacked strong density trends in zonation over the intertidal (Section 1), but the density increase in the near-shore zone 1, apparent in May and August, was markedly more pronounced than in other zones. Size-frequencies showed the zone 1 worms were not from new settlement, but rather older individuals similarly present in zone 2 (Fig. 27a). As size-frequencies were similar, better sieve retention of larger individuals was not the explanation of high zone 1 densities. Presumably settlement/survival earlier in the year had been superior in that zone.

However, zonation of *Microspio* sp. juveniles did not show density trends or consistent patterns in subsequent, fine-sieved samples. Size-frequencies also indicated little zonal variation in settlement intensity (e.g., Fig. 27b).

RELATIONSHIP OF SIZE TO SETIGER-TOTAL: The relationship between the two size measures used for *Microspio* sp., body width and the total number of setigers, was investigated using data from the finer-sieve samples to give good coverage of the range of sizes (Fig.28).

Fig. 27 *Microspio* sp. size zonation.

a) Width size-frequencies per zone as percentages for 50 μm classes; May plus August 1978 combined, 500 μm processed samples.

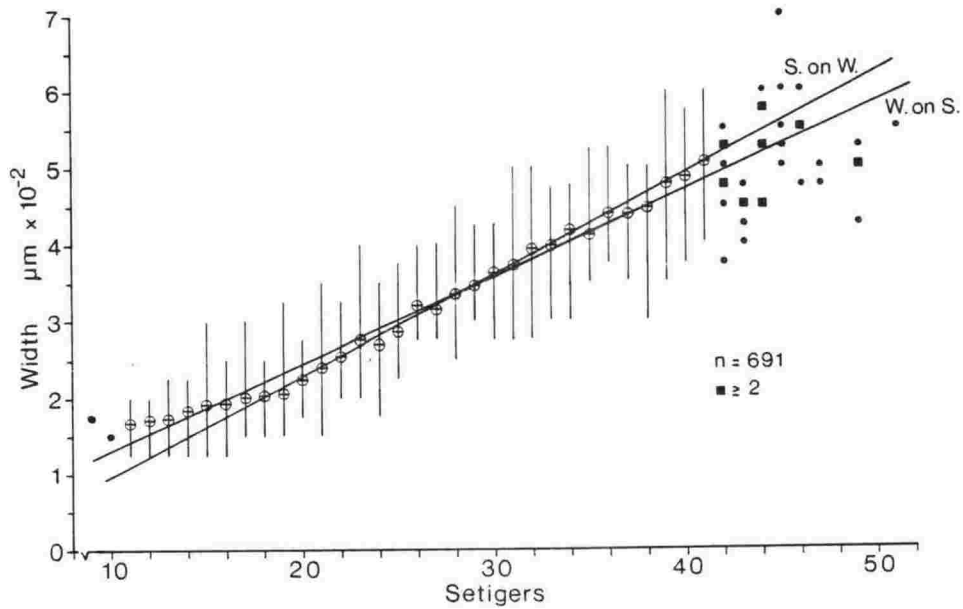
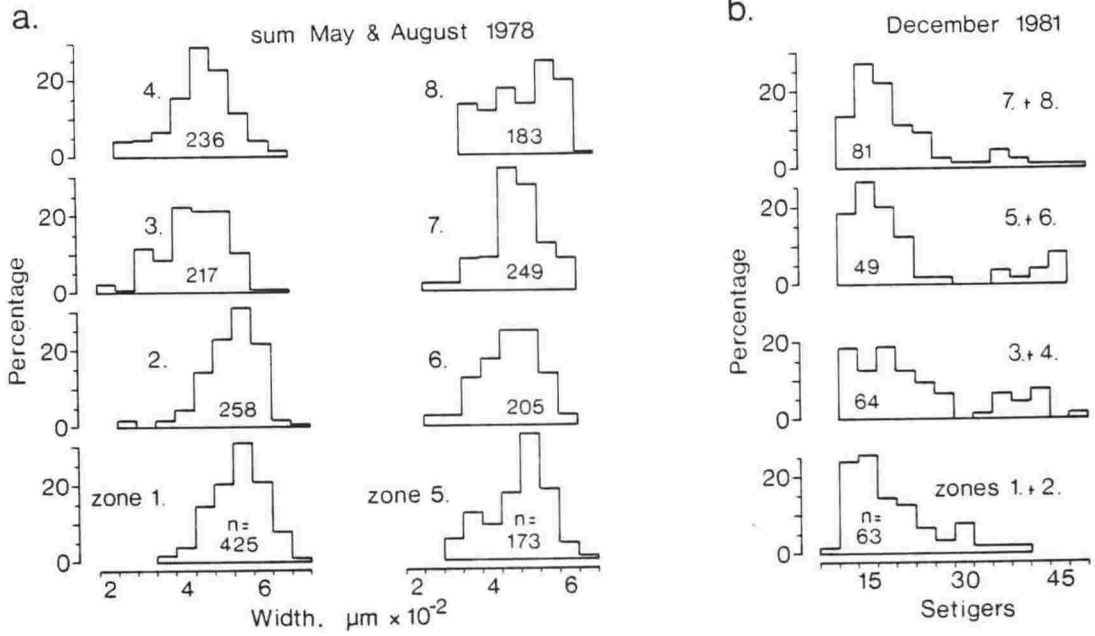
b) Setiger-total size-frequencies per zone as percentages for 3-setiger classes; December 1981, 72 μm processed sample.

Fig. 28 *Microspio* sp. width to setiger-total relationship. For clarity the width data are presented as mean and range (all data used in regressions), except for the few data points at the ends of the setiger range. Width data, recorded in 25 μm classes, were from January and November 1979, September to December 1981 samples ($n = 691$).

Least-squares-regression lines of width on setiger-total and the converse are shown ($r^2 = 0.8665$). The geometric mean regression was

$$\text{Width} = -6.02 + (12.18 \times \text{setiger-total})$$

where width is in μm .



Regression analysis indicated the body width/setiger-total relationship was close to arithmetic linearity (lack-of-fit ratio = 2.62, tabulated $F_{39,650,0.95} = 1.42$). Figure 28 shows that the minimum width of the youngest individuals did not drop below the 125 μm class. There was otherwise a direct relationship between body width and setiger-total. This confirms size-frequency comparisons, wherein the two size measures gave similar results.

LARVAL DEVELOPMENT AND POST-LARVAL MORPHOLOGY: The egg strings in which early *Microspio* sp. development takes place were rarely retained in the deep, coarse-sieved cores (and there are thus no data on their seasonal occurrence), because, unlike many spionids, the species has no sand grain tube in which eggs could be protected and retained during sieving of samples. The egg-number per brood was not high as the largest string obtained had only 142. The stage at which larvae leave the egg string is probably around 3 setigers, as all eggs (about 100 μm diameter) were developing in the strings examined, indicative in spionids of early hatching and a planktonic period of several weeks (e.g., Blake 1969), and also as the oldest larvae seen in strings had 2 setigers. Development in the plankton was not studied.

After settlement at about 12-13 setigers, post-larval *Microspio* sp. at first retain the pigmentation pattern of a planktonic larva. Pigmentation consists of a bar of black pigment, arising from two adjacent chromatophores, present mid-dorsally on setigers 2 to 7, a lateral series of black chromatophores on the posterior surface of the setiger 4 to 6 notopodial lobes, and a chromatophore pair on the dorsal pygidium. Older juveniles and the adults are unpigmented. The group of post-larvae with pigmentation in the December 1981 sample had a mean setiger-total of 14.1, range

9-19 setigers, whereas for those up to 20 setigers without pigmentation (17 of 89, or 19.1%) mean setiger-total was 18.0, range 15-20. Younger post-larvae tended to have more compressed segments, with comparatively squat bodies and less pointed prostomia than the completely metamorphosed individuals.

Post-larval setae are of the adult type. The first neurosetal hook was present from setiger 8 or 9 in the youngest, but anterior hooks were progressively lost in older individuals, beginning from setiger 12 on an 18-setiger worm, from 14 in a 20-setiger worm and from 17 in adults. The characteristic four anal cirri were present in all post-larvae.

CAPITELLA SP.

POPULATION DYNAMICS FROM 500 μ M SIEVE SAMPLES, 1977-79:

Seasonal density changes in the *Capitella* sp. population were all significant except between May and August (Fig. 29). From 2.54 ± 0.43 thousand m^{-2} in November 1977 the density dropped by more than half to 1.28 ± 0.23 thousand m^{-2} in February 1978, then nearly doubled by May (2.31 ± 0.42 thousand m^{-2}), declined slightly by August (2.12 ± 0.35 thousand m^{-2}), and further declined to November 1978 (1.37 ± 0.27 thousand m^{-2}). Annual population as assessed in November fell significantly between 1977 and 1978 and then rose in 1979 to 2.18 ± 0.33 (2SE) thousand m^{-2} (MWU, $P < 0.10$). These densities are means for the complete intertidal strip, but the species is more abundant on the upper two-thirds of the shore (Section 1).

During the period of study size-frequencies remained unimodal and more or less symmetrical (Fig. 30a), and the mode class of the population barely altered. For the three November samples and

also August 1978 it was 220 μm ; in February 1978 it had dropped to 200 μm and remained the same in May. The pre-February population decline was spread over all size classes as was the increase recorded in May. By August, despite a slight overall density drop, there was an increase in the number of larger, older individuals (≥ 260 μm class). Then by November 1978 the population decline was again over most size classes, except density < 200 μm slightly increased. The lack of a pronounced seasonal trend in overall size-frequency suggests either that there was no seasonal trend in recruitment rate, and the density variation related to fluctuation in mortality causes, or that recruits were mostly not retained by the sieve mesh until they had merged into adult size classes.

The changes in density of the egg masses females were incubating indicated reproductive activity was higher in the spring and summer samples than those of autumn and winter, despite lower adult density, [Fig. 29; egg mass density decrease February to May 1978 significant ($P < 0.05$), August to November 1978 increase almost significant ($P < 0.06$), and May to November 1979 increase highly significant (MWU, $P < 0.01$)].

Egg masses of incubating females had a mean of 15.3 embryos, range 1-42 (SD 8.16, $n = 122$), one of the lowest recorded for *Capitella*, although it is probably an underestimate due to some losses by attrition of the mass in processing. The earliest embryos were ovate, 90-160 μm by 140-210 μm . Advanced setigerous larvae often occurred, the largest of which had 14 setigers with a width of 90 μm . A planktonic dispersal period was most probably brief or absent if larvae in all egg masses developed similar numbers of setigers before leaving.

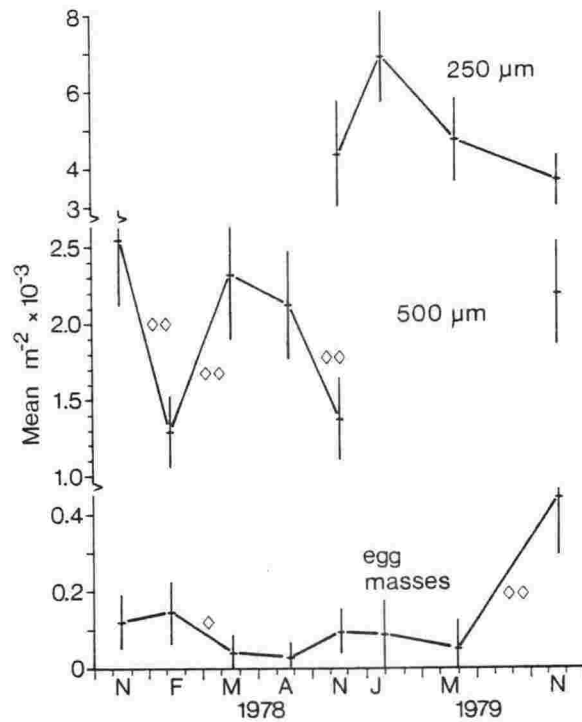


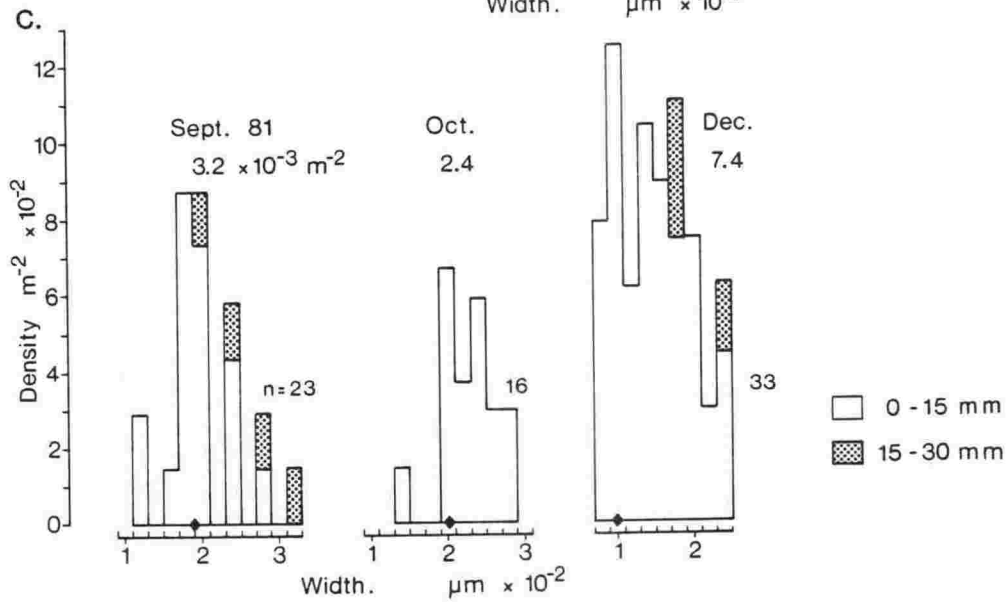
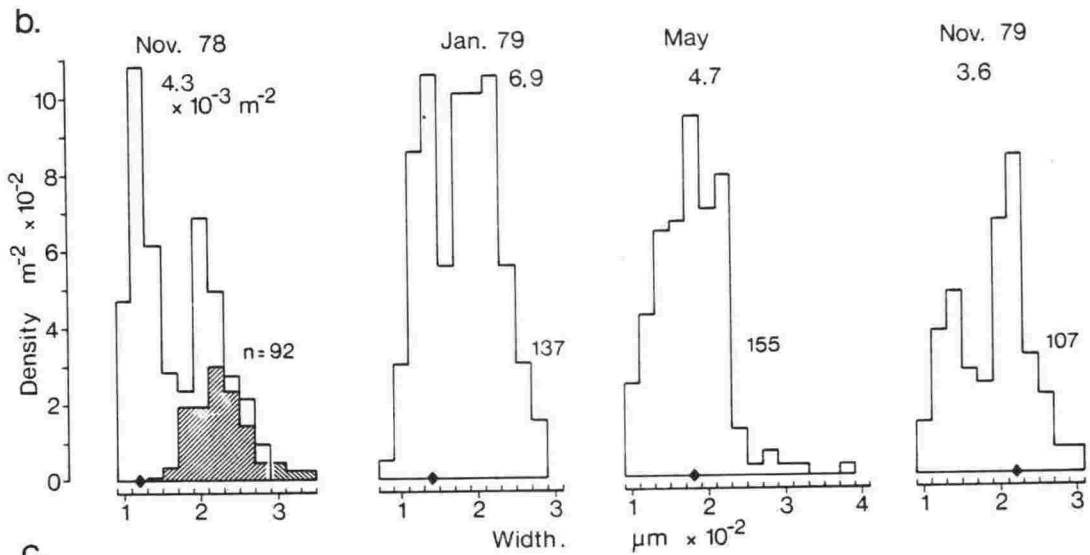
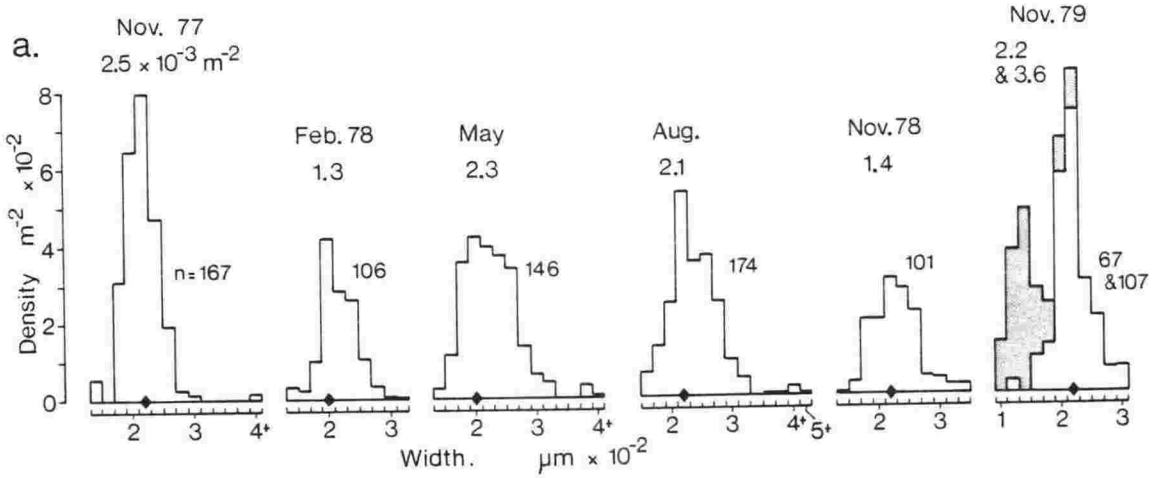
Fig. 29 *Capitella* sp. mean densities 1977-79 as thousands per m² ± 95% limits, or ± 2SE for 250 µm series and November 1979. Diamond(s) indicate P < 0.05 (P < 0.01) significant differences. Egg-mass densities are from 500 µm processed samples in 1978, and 250 µm samples in 1979. Note two scale changes.

Fig. 30 *Capitella* sp. size-frequencies as hundreds per m² for 20 μ m classes (400 μ m and above as 100 μ m classes). Mode class (diamond symbol), total population density, and number of individuals measured also indicated.

a) Densities in 500 μ m processed samples 1977-79, with November 1979 250-500 μ m sieve estimate added (shaded).

b) Densities in 250 μ m processed samples, November 1978-79. November 1978 has the 500 μ m sieve estimate superimposed.

c) Densities in 72 μ m processed samples, spring 1981, with 15-30 mm depth subdivision shaded (October sample to 15 mm only).



POPULATION DYNAMICS FROM 250 μm SIEVE SAMPLES, 1978-79:

Capitella sp. individuals remained small polychaetes at the site, and were retained in the 500 μm sieve partly because their bulk was usually increased due to an attached sand grain and mucous tube. Comparison of 250 μm and 500 μm sieve results for November 1979 showed a distinct group of small individuals was not detected by the 500 μm sieve assessment (Fig. 30a), and when included raised the population density estimate by 67% to 3.63 ± 0.63 (2SE) thousand m^{-2} . The 500 μm sieve had retained 93% of individuals ≥ 200 μm class but only 18% of < 200 μm classes (including 47% of 160 plus 180 μm classes, but 3% of ≤ 140 μm classes). The November 1979 samples also showed that almost all of *Capitella* sp. were in the top 3 cm of sediment (99.6%), and thus the population was sampled effectively by cores only to that depth.

The November 1978 transect using 250 μm sieve processing assessed density at 4.33 ± 1.35 (2SE) thousand m^{-2} (1.37 thousand m^{-2} in 500 μm sieve sample set collected alongside), and similarly showed a distinct 'juvenile' modal group in the size-frequency (Fig. 30b). In this case the coarser mesh retained 69% of the older group ≥ 200 μm class, but only 9% of juveniles in < 200 μm classes (see Fig. 30b superimposed size-frequencies). By late January 1979 the population density had increased to 6.88 ± 1.15 (2SE) thousand m^{-2} (not significantly, MWU, $P = 0.06$). The two size groups were still apparent, but density in intermediate size classes had increased, partly filling the gap between the modes, and adults had become more dense than juveniles.

By late May density had dropped to 4.70 ± 1.06 thousand m^{-2} (MWU, $P = 0.07$), the two size groups had effectively merged, with the

distribution skewed away from the smaller, younger individuals, and more of the largest size classes present. By mid November 1979 two separate modes were again present as noted earlier, surviving adults exceeded juveniles in density, and density had dropped to 3.64 ± 0.63 thousand m^{-2} .

The trends indicate that reproduction and settlement rates were greatest in spring and summer of the November 1978-79 year, and that restocking of the population proceeded at a lower level in autumn and winter, with population structure shifting towards larger, older individuals, and juveniles recruiting at an insufficient rate to maintain a distinct modal group.

POPULATION DYNAMICS FROM 72 μm SIEVE SAMPLES, SPRING 1981:
As for *Microspio* sp., the effect on size-frequency of any spring recruitment increase, the densities of the youngest settling individuals, and the respective depth locations of adults and juveniles, were examined from transects in the spring of 1981 (October transect to 15 mm depth only).

In mid September population density was 2.64 ± 1.15 thousand m^{-2} to 15 mm depth (3.19 ± 1.49 thousand m^{-2} to full 30 mm depth). Then by mid October the 0-15 mm population decreased slightly (non-significantly) to 2.36 ± 0.90 thousand m^{-2} . Therefore recruitment was occurring at a low rate in September and October. The size-frequencies were probably unimodal, with the mode at the 200 μm class, although the Fig. 30c size-frequencies have gaps that are not meaningful because the density of *Capitella* sp. proved too low to obtain adequate numbers from the samples.

By December the population to 15 mm depth increased significantly ($P < 0.01$) to 6.80 ± 1.72 thousand m^{-2} (7.34 ± 1.78 thousand m^{-2}

to full 30 mm). The increase was in the smaller size classes with the population mode at the 100 μm class, and both it and 80 μm classes present for the first time, whereas densities of larger classes $\geq 260 \mu\text{m}$ decreased (Fig. 30c). The 15-30 mm population remained unchanged from its September density of 0.55 thousand m^{-2} . No egg masses occurred in the September sample, and four and three respectively in October and December, or about 560 and 420 m^{-2} . Thus a population build-up had occurred between October and December. The juvenile and adult modal-group pair were not distinct in December as they had been in November of earlier 1978-79 sampling. This stage may be of short duration, thus occurring between samples on this occasion.

The percentage of *Capitella* sp. in the surface 0-15 mm layer was 89%, thus confirming the shallow-burrowing nature of both juveniles and adults. The few that did occur deeper tended to be the larger, older individuals (Fig. 30c). In September and October samples only about 3% of individuals passed through a 250 μm mesh, but in December, when recruitment was heavier, the proportion increased to 26%. Thus, as for *Microspio* sp., 250 μm sieve processing still underestimated the newest recruits.

ZONATION: *Capitella* sp. has an upper shore orientated density zonation, with zones 1-5 regarded as the zones of abundance (Section 1). No indication was apparent in 1977-78 data that markedly heavier settlement continued in any one zone. Similarly changes in size distribution between zones 1-5 were slight (Fig. 31). However, in low tide zones 7 and 8 a small number of distinctly larger individuals was present. This was unexpected as zones of lower density should have fewer survivors reaching the largest sizes. In subsequent transects intertidal zonation persisted as in the pattern described for 1977-78 (Section 1).

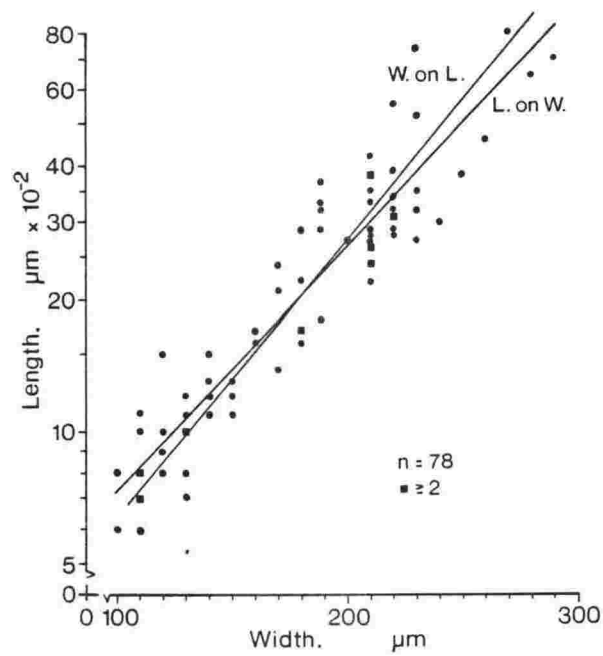
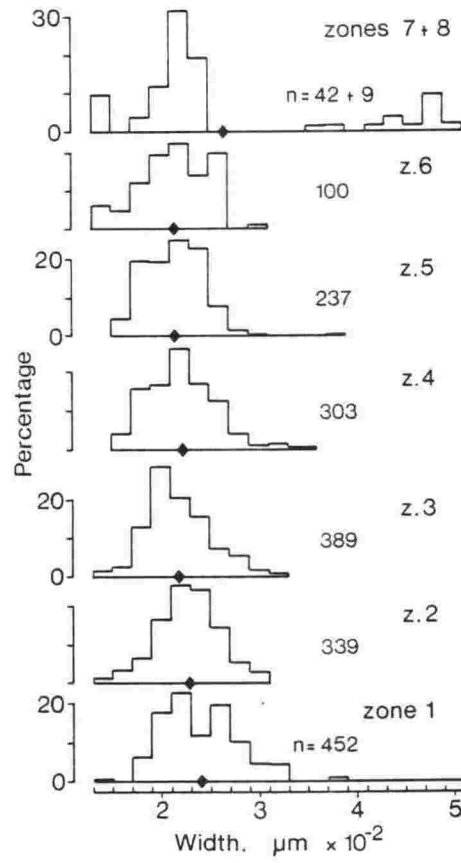
Fig. 31 *Capitella* sp. size-frequencies per zone as percentages for 20 μm classes, using sum of November 1977 to November 1978 500 μm processed samples. Diamonds indicate mean sizes.

Fig. 32 *Capitella* sp. length/width data for the width range of 100 to 290 μm (length to \log_e scale).

Least-squares-regression lines of length on width and the converse are shown ($r^2 = 0.8691$). The geometric mean regression was

$$\log_e (\text{length}) = 0.5286 + (0.01379 \times \text{width})$$

where length is in $\mu\text{m} \times 10^{-2}$ units, and width in μm .



SIZE RELATIONSHIPS: *Capitella* sp. length increased considerably above about 170 μm body width. Regression analysis showed the length/width relationship (Fig. 32) was exponential (lack-of-fit ratio = 1.01, tabulated $F_{18,58,0.95} = 1.75$). From the Fig. 32 equation the predicted length of an adult *Capitella* sp. at 220 μm width, the highest adult mode class, is thus 3.5 mm, showing the small size of most of the population. At 340 μm width, the highest class to which size-frequency distribution was continuous, the predicted length is 18.5 mm. A few larger individuals up to 500 μm class occasionally occurred.

DISCUSSION

MICROSPIO SP.

A consistent pattern of *Microspio* sp. settlement intensity was shown in the three sample series, and some deductions can be made about the population dynamics of the species. Settlement, hence reproduction, probably occurs year round but at a lower level in winter, increasing during spring so that a distinct modal group of juveniles appears, and continuing at the higher level through most of the summer before declining. Adult density falls during spring and early summer, and recovers during autumn as the spring recruits attain the adult size range. The growth and density decline of the spring-summer settlement group indicates a life span of at most a few months beyond the next spring.

There was no evidence from the larval settlement of population-wide synchronised spawning. Also the juveniles were more or less

evenly distributed across the intertidal, unlike those of *Axiiothella serrata*. *Microspio* sp. adults and juveniles have swimming ability and may continuously redistribute themselves.

Age structure of spionid populations has been studied quantitatively rarely, and with little success (e.g., Dorsett 1961, Warwick et al. 1978). Generally they are known from development studies to grow rapidly, and to have generation times shorter than one year. Repeated spawning may occur during the breeding period (Dean 1965, Blake 1969, Guerin 1973, Daro and Polk 1973, Myohara 1979, 1980). *Pseudopolydora paucibranchiata* may spawn at age one month (Myohara 1980), *Polydora ciliata* at 1½ months (Daro and Polk 1973), and *Malacoceros fuliginosus* averaged a three-month generation time and a seven-month life span in culture, with less than five days between broods (Guerin 1973, as *Scolecopsis fuliginosa*). *Paraprionospio* sp. and *Boccardia proboscidea* had one- and two-year longevity respectively (Kudenov 1979, Tamai 1982).

Relevant life cycle information for genus *Microspio* is that *M. mecznikowiana* had produced egg masses after less than six months' recruitment into settlement collectors (Massé and Guerin 1978), and its larvae occurred in the plankton year-round at Arcachon with a peak period from June to September, i.e., summer to early autumn (Cazaux 1971). In the related genus *Spio* poecilogony (polymorphism of larval type) occurs in *S. setosa* between spring and autumn spawnings on the New Hampshire-Massachusetts coast (Simon 1967, 1968). The spring larvae remained within the egg string, feeding on nurse eggs, and metamorphosed at 15-17 setigers without becoming planktonic (Simon 1967), whereas 6-setiger larvae appeared in the plankton in autumn and, after a planktotrophic period, metamorphosed at 18-20 setigers (Simon 1968). Interestingly, in spring *S. setosa* juveniles (to 96 setigers, 30 mm)

were found in large numbers in the plankton at night, showing redistribution of the population occurred after larval settlement (Simon 1967, 1968).

The life cycle characteristics of *Microspio* sp., with its near-continuously reproducing population, brooded early development, seasonal settlement peak, high mortality, and probable short life span and generation time, are thus consistent with those shown in other spionids.

CAPITELLA SP.

The Pauatahanui studies did not establish the presence of a seasonal density and size-structure pattern for *Capitella* sp. as clearly as for *Microspio* sp. This possibly may be because the pattern is less pronounced or more variable, but is also in part because the small size and narrow range of size rendered the species less amenable to study. The 500 μ m 1977-78 sample set always underestimated the total population, and especially underestimated the youngest worms. In contrast to *Microspio* sp., the juveniles were not within the size range sampled by the 500 μ m mesh and, therefore, their recruitment-rate changes were not apparent in that sample set. A second factor, affecting all samples, was that the width frequencies were relatively less sensitive to age-structure changes among adults than in *Microspio* sp.. The adult width range was comparatively compressed, as width increase was slight with growth in length (an exponential relationship), whereas in *Microspio* sp. width increase was directly proportional to growth in length (as represented by setiger-total).

Integration of results indicates that *Capitella* sp. normally has year-round reproduction which occurs at an increased rate

in late spring and summer, at first resulting in a juvenile modal group in size-frequencies. The 1977-78 samples taken with 500 μm mesh show density changes that may reflect those of the adult population but are difficult to interpret in terms of an overall pattern of population structure. In 1978-79 samples, using 250 μm mesh, the recruitment level was high in November, the densest 'young adult' population occurred in January, and the largest individuals occurred in May. Juvenile recruitment apparently had continued at a high level between November 1978 and January 1979 but had declined by May. Later in the year recruitment rate was again high in November. The spring 1981 72 μm mesh samples showed increase in recruitment did not occur until after October, and by December was accompanied by a decrease in the adult density. The data suggest that mortality was high and life span was short, possibly considerably less than one year.

The *Capitella* sp. population is more vulnerable to short-term adverse conditions than that of *Microspio* sp. because a much higher proportion of adults as well as juveniles is in the surface 0-15 mm layer. Fluctuations in mortality rate corresponding to short-term environmental perturbations might partly obscure density effects of longer-term, seasonal, reproductive rate changes, and result in a density pattern that is not constant from year to year. This may explain why February 1978 densities were low compared to November 1977, whereas late January 1979 densities were high compared to November 1978. To examine this, and the related problem of how rapidly age structure can change, a period of sampling more than once a month might be required. A population assessment specifically for *Capitella* sp. could be achieved efficiently using shallow core sampling limited to the upper beach, since the species is near-surface, more abundant up-shore, and did not show age-structure zonation. To improve

age-structure resolution in future studies the use of body width as a size measure might perhaps be augmented by measuring length, or counting capillary-bearing setigers (the number of which may relate to age and size). Counts of the total number of setigers are impractical as the very small posterior fascicles are difficult to detect.

In continuously breeding short-lived species such as *Capitella* sp., and also *Microspio* sp., the size-frequency structure shows the changing rates of breeding and mortality. Unlike annual breeding species such as *Axiiothella serrata*, modal groups do not necessarily represent age classes. Bimodal size structure occurs when settlement rate increases rapidly, and continues until with time sufficient older juveniles survive to fill the gap between adults and juveniles, or until the settlement rate decreases. Modes move to the right with declining settlement rate but their movement lags behind the real growth movement of individuals.

To gain further information from such size-frequencies size-specific rates of mortality, fecundity, and growth need to be obtained. The problem is that laboratory rates are not applicable to the field situation, and the conditions of the latter are difficult to recreate in a manner that still provides the information sought. It is already known for example that *Capitella* spp. populations may increase dramatically when they are initial colonisers, either in sediment rendered artificially azoic, or after environmental disturbance (e.g., Eagle and Rees 1973, Grassle and Grassle 1974, Rhoads et al. 1978, Sanders 1978, Davis and Spies 1980, Sanders et al. 1980). Problems with field experiments begin with the destruction of the initial sediment structure in setting up the experiment. Then the experimental group is exposed to mixing with immigrants of unknown age if the plot has an open surface. Natural predators are excluded if it is covered, and the physical environment may also alter.

Although *Capitella* spp. have been much studied elsewhere in the world, there has been no rigorous investigation which combined size-frequency and density data. Warren (1976a) studied reproduction and size-frequency of a *Capitella* sp. on an unstable, organically enriched spit of the River Yealm estuary, but did not follow density changes because of the fluctuating and patchy occurrence of the population. Size-frequencies based on thoracic length showed recruitment occurred mainly in spring (March to June), although some reproduction year-round was probable. Adults did not show consistent growth trends between samples, and seasonal sexual maturity data were variable and inconclusive. Warren (1976a) suggested age divisions were apparent in the adult population, but these were not convincingly established.

Foret (1975) examined density of males, females, and egg masses monthly in a sewer-outfall-associated population at Marseilles, as background to an experimental study of detergent toxicity. He found autumn (November) and early summer (June) maxima in density of adults, in each case following a high level of reproduction two months before as estimated from egg-mass number. The peak in reproduction during the density maxima had no apparent subsequent effect on density (Foret 1975).

Dense populations of colonising *Capitella* spp. have been mentioned above. *Capitella* species I in particular has a rapid, opportunistic response to disturbed habitats due to its short generation time, year-round reproduction, potential for both hermaphroditism and short-term adaptation, and ability to metamorphose shortly after release from the egg mass (Grassle and Grassle 1977, Grassle 1979). An undisturbed estuarine population in Massachusetts had densities of up to 1500 m^{-2} (Sanders et al. 1965, 210 μm sieve size), whereas populations to more than $200,000 \text{ m}^{-2}$ were recorded colonising similar habitat,

both when oil-polluted and when rendered azoic for experiment (Grassle and Grassle 1974). However, these peaks were short-lived. In comparison maximum densities per zone in the non-perturbed Pauatahanui environment were 5.84, 15.24, and 17.76 thousand m^{-2} for the 500 μm , 250 μm , and 72 μm sieve sample sets respectively.

The near-surface occurrence of the Pauatahanui *Capitella* sp. population corresponds to some *Capitella* recorded elsewhere. Mayou and Howard (1975) reported dense networks of U-burrows just below surface. Whitlatch (1980) found over 70% of individuals within 2 cm of surface, and Myers (1977) found about 70% between 1 and 2 cm depth. This suggests their size was small. In contrast, Warren (1977) found most worms 12-18 cm deep in cores. The Pauatahanui worms were much smaller than Warren's (1976a, 1977) and Foret's (1975) specimens from organically-enriched habitats but similar in size to the Grassles' (1974) populations. Burrow depth is likely to be partly a function of worm size, although as yet this has not been studied.

Cryptic sibling species may or may not coexist at the site. The larger size of a small number of zones 7 and 8 individuals is not thought to be significant in this context as size relates to age and nutrition as well as genotype. It is reasonable to suspect, however, that more than one species occurs in the various habitats and locations within New Zealand. The structure and density variation of *Capitella* sp. at the Pauatahanui site may not apply generally to populations elsewhere. For example, the sediment organic content is relatively low (Smith and McColl 1978) and it is possible this restricts rate of growth. If mean size is larger, as is the case at least at Kahao Bay in the Inlet, then factors such as vulnerability to predation may change. Nevertheless the population is of particular interest because a *Capitella* from a relatively stable, diverse, non-enriched habitat has

not been studied in detail previously. In such habitats the *Capitella* complex was thought 'non-competitive' (Oshida and Reish 1974). The results show that *Capitella* sp. density does not normally fluctuate wildly, although it may have more short-term variation than in other Pauatahanui polychaetes.

SEASONAL CHANGES

Seasonal patterns in both density and size-frequency proposed for *Microspio* sp. and *Capitella* sp. are similar. In late spring both have increased settlement of larvae, and this dense settlement continues through summer while at first an older adult population decreases. In autumn settlement declines and the proportion of adults increases. However, reproduction appears to continue year round, probably with short generation times.

The amount of reproduction and the resulting density cycles are likely to be influenced by external environmental factors, rather than simply related to the number of reproductive individuals. In *Capitella* sp. for example egg mass density was high when population density was low. In *Microspio* sp. peak adult density was probably about August, well before the peak reproductive output. Although for both density cycles could occur if individual maturity was not reached until near 12 months of age (very unlikely considering current knowledge), without feedback from the environment, cycles would not be perpetuated against natural spread in times of maturing.

Rise and fall of settlement intensity may have coincided in timing with temperature, in 1978 for example (Fig. 3), with the more pronounced October-November rise in spring temperatures and the autumn fall which began in March. Temperature is not necessarily a direct

influence (see e.g., Guerin and Reys 1978). Among possible environmental influences on polychaete maturation and spawning, temperature, day length, or both together, have been demonstrated by experiment to be important in several ways (e.g., Clark 1979, Garwood 1980, Olive 1981). A multivoltine, iteroparous, continuously-breeding species has yet to be studied. For *Microspio* sp. and *Capitella* sp. a relatively simple mechanism, such as increasing supply of food micro-organisms as temperatures rise, may be sufficient to produce the observed density cycle.

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S E C T I O N 4

POPULATION DYNAMICS OF SOME INFAUNAL POLYCHAETES

ON A PAUATAHANUI INLET INTERTIDAL SAND FLAT

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ABSTRACT

The population dynamics of capitellid *Heteromastus filiformis* (Claparède), nereidid *Nicon aestuariensis* Knox, and spionid *Scolecopides benhami* Ehlers were investigated from seasonal samples, 500 μm sieve processed, from a stratified transect pair, supplemented with subsequent finer sieve samples.

Heteromastus filiformis had a short summer spawning period, later than previously observed in the Northern Hemisphere. Settlement detected in February had ceased before May, when population density was up to 10 thousand m^{-2} (lower shore, 250 μm sieve processing). Merger of O group with the adults occurred in about one year, and life span was probably more than three years. Density of recruits, and subsequent adult density, varied between years. Larger individuals were deeper in the sediment.

Nicon aestuariensis had I+ and older age groups at barely detectable densities (to 10 m^{-2}). Spawning was probably in late summer, although entry into the population of O group at about 500 m^{-2} was not detected until May. Notable differences from a prior study are discussed.

Scolecoides benhami density did not vary significantly (remaining between $360\text{--}420 \text{ m}^{-2}$ in 1977-78 seasonal samples), and had no appreciable size-frequency changes. No new settlement was detected and juveniles were not present. Possible explanations are discussed. Larger individuals were deeper in the sediment and a few much larger individuals occurred on the lower shore.

Density changes of *Paradoneis* sp., *Cirratulus* sp., and other infaunal polychaetes present at low density, are reviewed.

INTRODUCTION

The capitellid *Heteromastus filiiformis* (Claparède), the nereidid *Nicon aestuariensis* Knox, and the spionid *Scolecoides benhami* Ehlers are the remaining three of the six infaunal polychaete species sufficiently abundant across the Pauatahanui sand flat for population studies. This Section analyses the data on these species from seasonal transects taken in 1977-78, when $500 \mu\text{m}$ sieve mesh was used during processing (Section 1). Subsequent sampling using finer sieves provided verification of the trends found in 1977-78, and did not reveal previously substantially-undetected modal groups of juveniles, in contrast to *Microspio* sp. and *Capitella* sp. (Section 3). The density ranges of the less common species are also summarised in this Section.

Heteromastus filiformis is a deep-burrowing deposit-feeder, of wide habitat range, and near cosmopolitan distribution. This distribution has aroused unconfirmed suspicions that, like *Capitella capitata* (Section 3), *Heteromastus filiformis* might include cryptic species (Kinner and Maurer 1978, Gray 1979). It is rational to expect the species to be polytypic at least. For reasons discussed elsewhere, morphological variation is poorly known (see Appendix). Therefore, comparative morphometric studies as well as biochemical and life-history studies are needed. Meanwhile there has been reasonable agreement that *H. filiformis* as currently understood is a comparatively long-lived species, breeding over a short period when two years old, and producing a larva that is at least intermittently planktonic (see discussion). Shaffer (1978, 1979) has given the most authoritative account of population dynamics, but reproductive biology has not yet been studied quantitatively, nor is larval development fully known.

Nicon aestuariensis, a New Zealand endemic species, is a deposit-feeder and carnivore, restricted to waters of lowered salinity (Section 1). The larvae are lecithotropic, dispersing during a short period in the plankton, and the species is monotelic, metamorphosing to a heteronereid before spawning, although the age at which this occurs is uncertain (Estcourt 1966, and see discussion).

Scolecoides benhami, also endemic, a species attaining large size relative to many other Spionidae, is a deposit-feeder that occurs mainly in estuarine situations, and is abundant at the Paua-tahanui site only on the upper edge of the sand flat (Section 1). Nothing is definitely known of its life-history pattern. Observations of Estcourt (1967) may indicate an extended breeding period.

METHODS

Details of sample collection and statistical treatments have been presented in Sections 1 and 2. In brief a stratified transect pair was sampled quarterly, November 1977 to November 1978, using 15 cm deep, 50.3 cm² cores sieved through 500 μ m mesh, and a further sample from the left transect in November 1979 was processed through 500 and 250 μ m mesh, the top 3 cm separately. Additional 3 cm deep samples processed through 250 μ m mesh were taken in November 1978, January and May 1979, as detailed in Section 3. Means of November 1977-78 samples were compared by parametric test, whereas the Mann-Whitney U-test (MWU), and limits cited as \pm 2SE, were appropriate for other samples, which were less than 40 cores.

Size was assessed by measuring the maximum dorsal-ventral depth at setigers 2-3 in *Heteromastus filiformis*, and at setigers 4-5 in *Nicon aestuariensis*, using 25 μ m size classes for adults and 10 μ m for juveniles. These 'width' classes were smoothed by grouping into 50 μ m units. *Scolecopides benhami* body width including parapodia was measured across setiger 10, and the 25 μ m classes further grouped into 100 μ m units. Positions chosen for measurement were natural maxima in these three species. Separation of the overlapping age classes in *Heteromastus filiformis* by use of fitted gaussian distributions or the equal-overlap approximation was inappropriate (see Section 2, methods).

As a guide to the sexual maturity of the *Heteromastus filiformis* population, monthly samples of about 40 live individuals were examined for gametes visible through the body wall. Gametes were not externally apparent in the other two species.

RESULTS

HETEROMASTUS FILIFORMIS

The highest *Heteromastus filiformis* density occurred in the first sample in November 1977 at 2.25 ± 0.24 thousand m^{-2} , and by February the population had dropped significantly to 1.29 ± 0.21 thousand m^{-2} , but then rose significantly to 1.77 ± 0.22 thousand m^{-2} by May. The further rise by August to 2.01 ± 0.27 thousand m^{-2} , and fall by November 1978 to 1.76 ± 0.23 thousand m^{-2} , were not significant (Fig. 33a). The population in November 1978 was significantly less abundant than in November 1977, and further decreased by November 1979 to 1.05 ± 0.25 (2SE) thousand m^{-2} (MWU, not significant). The above densities are means for the complete intertidal strip, but the species was abundant only on lower shore zones 5-8 (Section 1). The November 1977 zone maximum was 6.34 thousand m^{-2} in zone 8.

Oocytes were visible through the body wall from December to April. The population contained its largest proportion of such obvious adult females in January and February, consistent with late summer spawning. This was confirmed by width frequencies, which showed the recruitment of a distinct O group began by February (Fig. 34a). Earlier there were two modal groups in the November 1977 population: a large adult group, and a less dense group of smaller worms inferred to be juveniles from the 1977 settlement (cf. November 1978). Then by February 1978 there had been a general population decline, with the 1977 class increasing size almost to merge into the adults. The new settlement of 1978, just detectable in February, in May constituted about half the population, and peaked in August, beginning also to overlap the declining adult group. In November the density in the modal group of 1978 juveniles had fallen, while the larger juveniles entering into the

adult size range increased the class densities of small adults. Between November 1977 and November 1978 the mode class of the adult group rose from 400-450 μm up to 550 μm , which suggests that the abundant November 1977 adults may have been predominately still-growing I group individuals, continuing to be numerous as II group by November 1978, compared to the small I group from the 1977 settlement, and so skewing the distribution. If this interpretation is correct, they were then nearly three years old and maximum life span could be longer.

In November 1979 only 1% of the sample population passed through the 500 μm sieve mesh to be retained by 250 μm mesh. Many individuals were theoretically of sufficiently small diameter to pass the coarser mesh given time, and were retained during processing probably because their lengthy bodies and slow movement hindered passage through the mesh. However, underestimation of juveniles is likely to have occurred in February and May samples, and possibly August also.

In November 1978 a sample using 250 μm processed, 3 cm deep cores, collected alongside the 15 cm deep, 500 μm processed cores analysed earlier, gave an estimate of size-frequency structure in reasonable agreement with the coarser meshed sample (Fig. 34b). The population density estimate of 1.08 ± 0.29 (2SE) thousand m^{-2} was 39% lower, due mainly to the non-collection of many larger individuals presumed to be deeper-burrowing. That this was so is shown by the November 1979 sample in which the 28% of the population in the 3-15 cm depth zone were larger, older worms, not juveniles (Fig. 34b).

Fig. 33 *Heteromastus filiformis* density and size zonation.

a) *Heteromastus filiformis* mean densities 1977-79 as thousands per m^2 , \pm 95% limits, or \pm 2SE for 250 μm series and November 1979 (250 μm series to 3 cm depth). Diamonds indicate $P < 0.01$ significant differences.

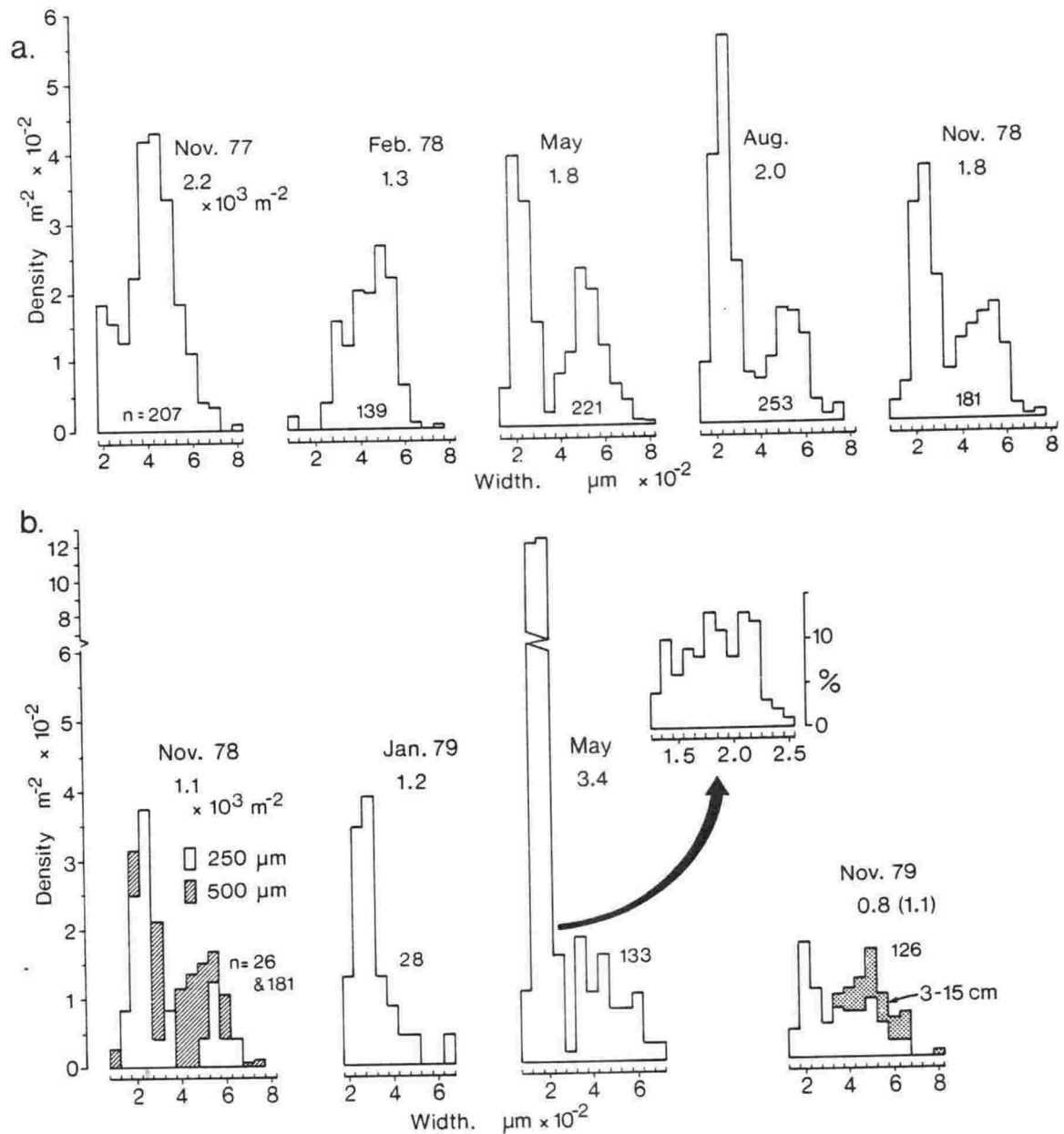
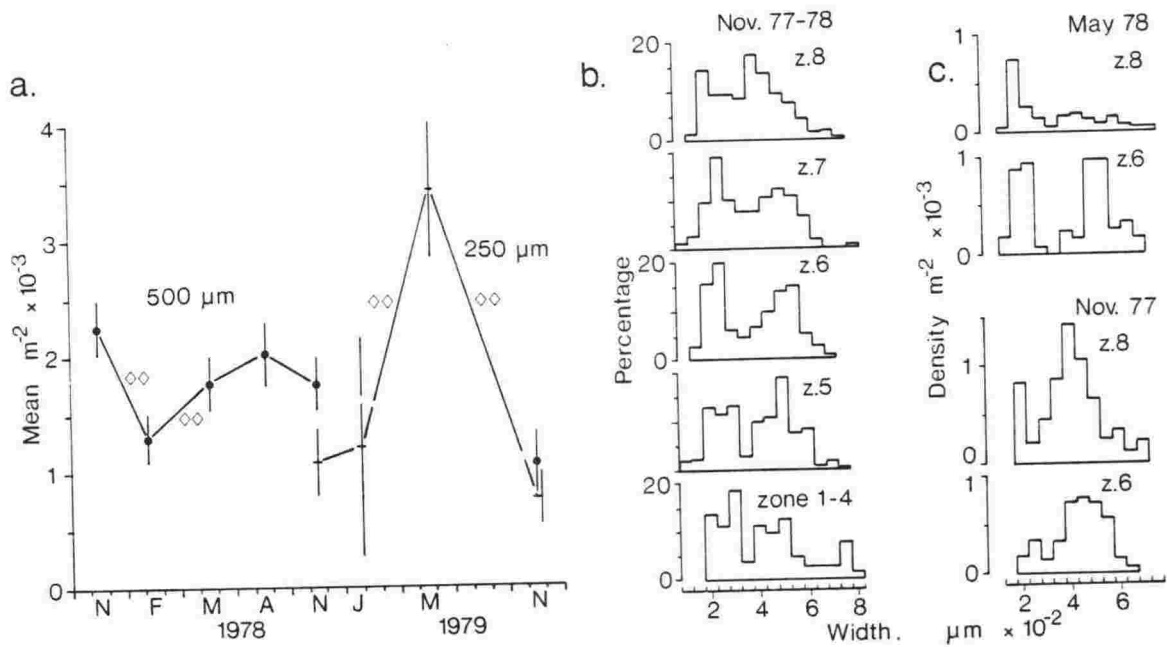
b) *Heteromastus filiformis* size-frequencies per zone as percentages for 50 μm classes using sum of 1977-78 data (totals measured for zones 1-4, 5, 6, 7, 8 were 82, 282, 590, 431, 482 respectively).

c) *Heteromastus filiformis* size-frequencies for zones 6 and 8 as thousands per m^2 for 50 μm classes, comparing November 1977 to May 1978 size-structure changes (see text; totals measured for zone 6 cf. 8 were 103 cf. 189 in November, 125 cf. 62 in May).

Fig. 34 *Heteromastus filiformis* size-frequencies 1977-79 as hundreds per m^2 for 50 μm classes. Total population densities and number of individuals measured also indicated.

a) Densities in 500 μm processed samples, November 1977-November 1978.

b) Densities in 250 μm processed samples. November 1978 (to 3 cm depth) has the 500 μm sieve estimate superimposed (separate sample, to 15 cm depth). May inset shows the juvenile group (≤ 250 μm class) as percentages for 10 μm size classes.



In late January 1979 an estimate of the 3 cm deep population (250 μm processed) was, at 1.21 ± 0.96 (2SE) thousand m^{-2} , almost the same as in November 1978. The size-frequency showed that recruitment had not yet begun, and the mode class had risen from 250 μm to 300 μm . Then by late May settlement was present at about 2.66 thousand m^{-2} , with the mode at the 150-200 μm classes. The population to 3 cm depth had significantly increased (MWU, $P < 0.01$) at 3.43 ± 0.58 (2SE) thousand m^{-2} (Fig. 33a), and maximum density per zone (zone 8) was 9.97 thousand m^{-2} . Mean setiger-total for the May 0 group was 31, range 20-50 setigers (SD 9.3, $n = 22$), and the width distribution lacked an outstanding mode of small individuals, indicating settlement had ceased (Fig. 34b inset). The most-recently-settled individuals encountered were three post-larvae from the February 1978 sample, still with an eyespot and with 16-21 setigers, width 120-140 μm . By November 1979 the 3 cm deep *Heteromastus filiformis* population had dropped significantly (MWU, $P < 0.01$) to 0.75 ± 0.22 (2SE) thousand m^{-2} .

The adult and juvenile pattern of abundance is apparent from the samples. Precise estimates of sequential age-class densities have not been given, as they would have required in some size-frequencies assumptions on slender evidence concerning the flank shapes of overlapping distributions. However, it is clear that by late in 1977 recruit density was low compared to the existing adult group. Recruitment improved in 1978, and again was low in 1979. The adult population declined considerably between November 1977 and 1978, was stable between 1978 and 1979, and, as the 1979 recruit density was low, may have dropped further in 1980. In the 1977-78 year adult mortality rate was highest between Nov-

ember 1977 and February 1978, coinciding with the presumed spawning period. Juvenile mortality between May and November 1979 was about 0.005 individual $^{-1} \cdot \text{day}^{-1}$.

The recruits were not distributed very differently from adults (Fig. 33b), although the pattern of initial settlement is not known. Few adults might be expected to survive in the low density upper shore, but in fact zones 1-4 still had comparable proportions of adults and juveniles (Fig. 33b). *Heteromastus filiformis* had initially high density in low tide zone 8, but abundance later decreased there, and by May 1978 became relatively high in zone 6 (Section 1). Fig. 33c shows that in November 1977 the higher density of zone 8 over zone 6 was noticeable in both adult and juvenile groups. In May the zone 6 increase over zone 8 related as expected to the presence of more young recruits, but also adult mortality/emigration had been less.

NICON AESTUARIENSIS

The comparatively low density *Nicon aestuariensis* population showed a pronounced annual cycle of abundance (Fig. 12, 35). It declined significantly ($P < 0.05$) from $119 \pm 36 \text{ m}^{-2}$ to $63 \pm 37 \text{ m}^{-2}$ between November 1977 and February 1978, then by May had increased nearly eight-fold to $492 \pm 90 \text{ m}^{-2}$, declining non-significantly ($P < 0.1$) by August to $388 \pm 68 \text{ m}^{-2}$, and significantly ($P < 0.01$) to $102 \pm 31 \text{ m}^{-2}$ in November 1978. The November 1979 population was $124 \pm 52 (2\text{SE}) \text{ m}^{-2}$, and there was no significant difference between the three November densities. The above densities are means for the complete intertidal strip, but the species declined in abundance downshore (Section 1).

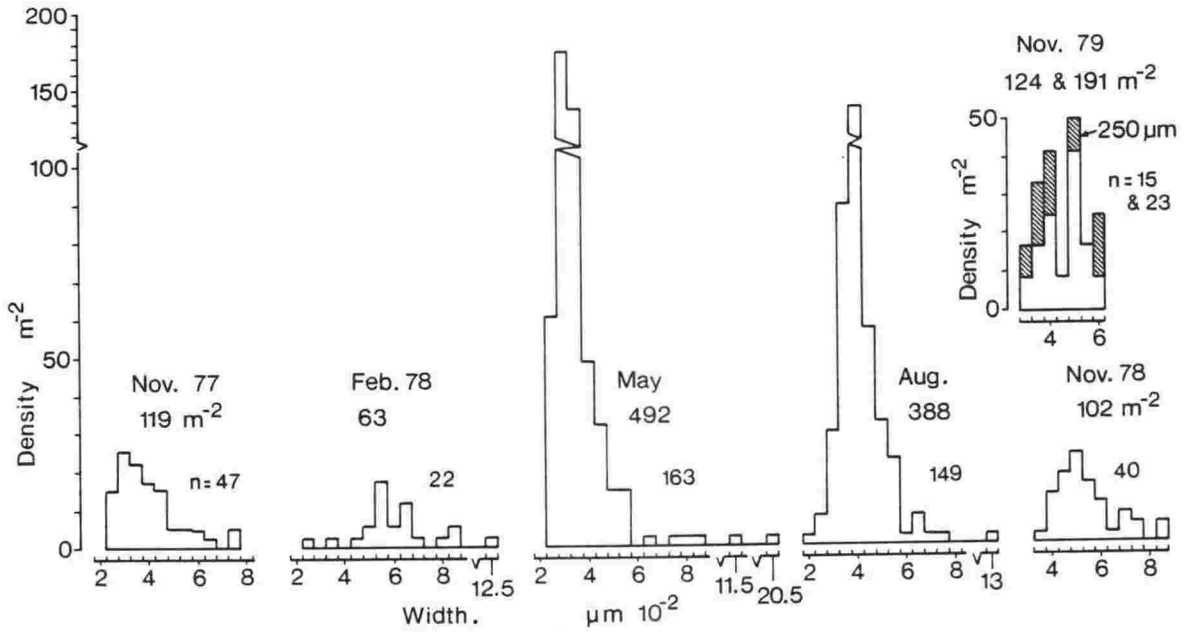
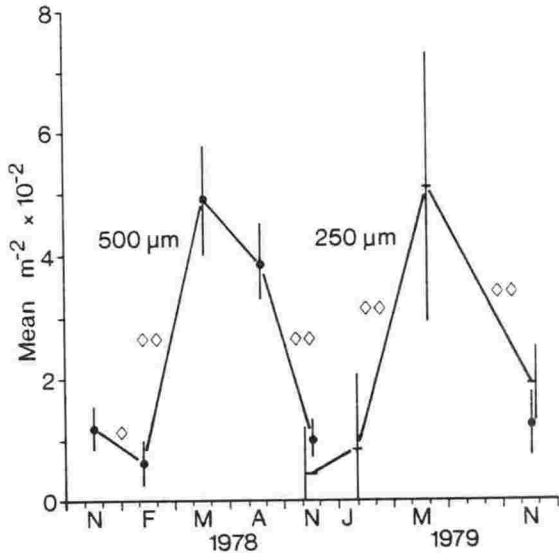
In November 1977 the population mode class was 300 μm with most of the population between 250 and 450 μm classes, and by February 1978 the mode was 550 μm with the bulk of the low density population between 450 and 700 μm (Fig. 36). By May a dense recruitment into the sieve had occurred with mode class at 300 μm . In August, with growth of this juvenile group, the mode was 400 μm , and in November 500 μm .

In 1979 juveniles were not present by late January in 3 cm deep, 250 μm processed cores, but adult population was 86 ± 122 (2SE) m^{-2} . Juveniles had appeared by late May to increase population density significantly (MWU, $P < 0.01$) to 520 ± 220 (2SE) m^{-2} (Fig. 35). In November the density had decreased (MWU, $P < 0.01$) to 174 ± 62 m^{-2} (191 m^{-2} to 15 cm depth). The mode class was 500 μm as in November 1978 (Fig. 36), so the lower November 1977 mode is difficult to explain. Note in November 1979 the top 3 cm contained more than 90% of the population; also double sieving indicated that about 35% of live individuals were not retained by the 500 μm sieve, and the size-frequency of the escapees did not apparently differ from those retained (Fig. 36 inset). This underestimation probably applied to other months, and is likely to have been higher for May recruits.

Adult mortality was 0.0055, and (about) 0.007 individual⁻¹.day⁻¹ for November 1977 to February 1978, and February to May respectively. The May individuals in the 600 to 850 μm classes, with total density about 10 m^{-2} , can reasonably be regarded as I+ young adult survivors, and the few much larger individuals, at up to 5 m^{-2} , as the II+ or older adults. More of the larger individuals (believed to be two or more years old) were collected during regular diggings at the site, but no heteronereids or near-mature worms with oocytes were seen.

Fig. 35 *Nicon aestuariensis* mean densities 1977-79, as hundreds per m², \pm 95% limits, or \pm 2SE for 250 μ m series and November 1979 (250 μ m series to 3 cm depth). Diamond(s) indicate P < 0.05 (P < 0.01) significant differences.

Fig. 36 *Nicon aestuariensis* size-frequencies 1977-79 as densities per m² for 50 μ m classes from 500 μ m sieve processed samples (additional November 1979, 250 - 500 μ m density shaded). Total population densities and number of individuals measured also indicated.



Although O groups were first recorded in May, the settlement had presumably occurred some time before. The mode of the juvenile group in both 1978 and 1979 was 300 μm , although the smallest individuals undoubtedly were not retained in either 500 or 250 μm mesh. In the May 1978 sample complete juveniles up to 350 μm class had a mean of 46 setigers, range 35 to 57 (SD 5.4, $n = 24$), and mean length of 6.0 mm, range 3.8 to 9.8 mm (SD 1.3). In the May 1979 sample the smallest juvenile had 9 setigers but all the rest more than 40 setigers. It can be concluded that, although true mean sizes may have been smaller, spawning must have begun much earlier than May for individuals to 57 setigers and more to occur.

SCOLECOLEPIDES BENHAMI

The population density of *Scolecoclepidus benhami* did not change significantly during the November 1977-November 1978 sampling period (Fig. 37a), varying only between $419 \pm 314 \text{ m}^{-2}$ (November 1977) and $359 \pm 172 \text{ m}^{-2}$ (February 1978). Also the November 1979 density of 232 ± 102 (2SE) m^{-2} was not significantly different (MWU). The size-frequencies were also more or less static, with most individuals of comparatively large size, and without evidence of settlement (Fig. 38). Samples processed with 250 μm mesh in November 1978, January, May and November 1979 had the same size structure as those shown in Fig. 38, and also did not detect settlement. In November 1979 only 10% of the sample population passed through the 500 μm sieve mesh to be retained by 250 μm mesh. The same sample showed that most of the large *S. benhami* were more than 3 cm below surface (Fig. 38, 29% of the total population).

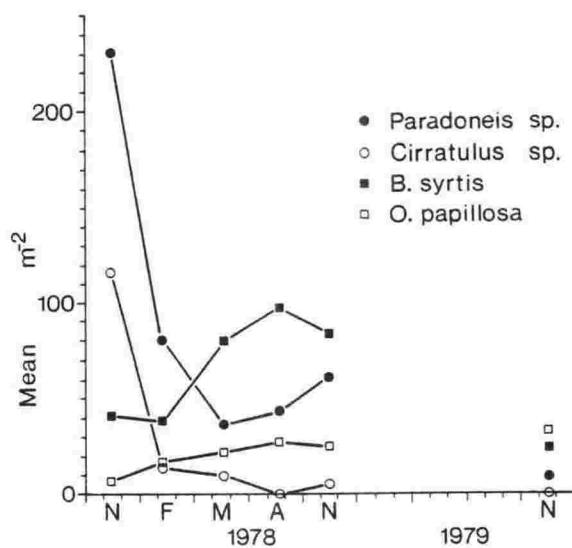
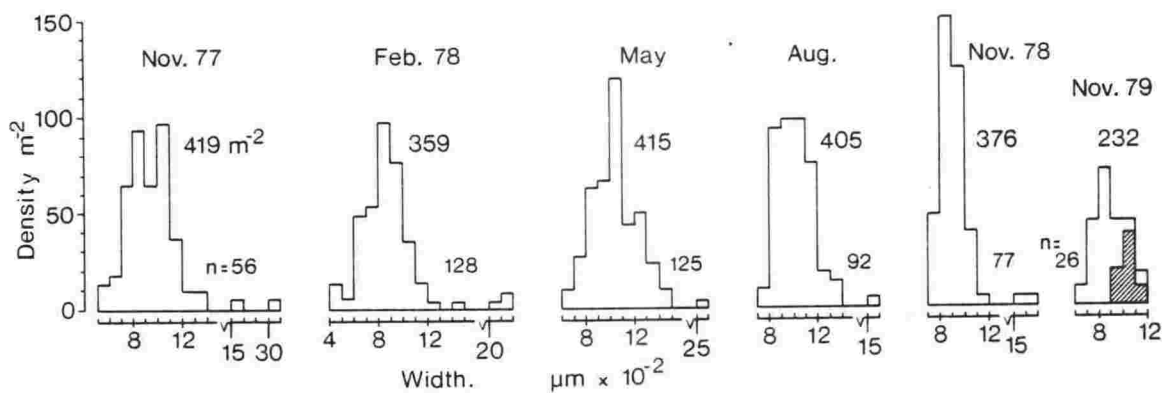
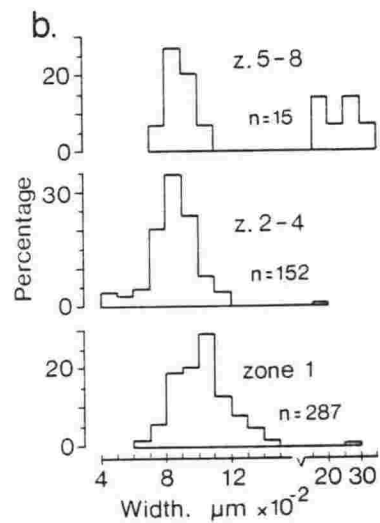
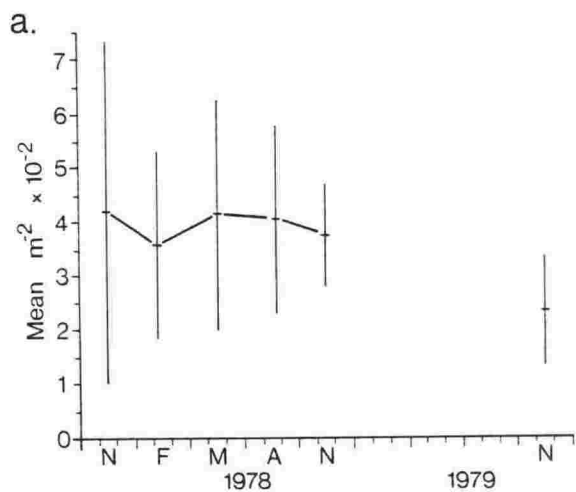
Fig. 37 *Scolecoplepides benhami* density variation and size zonation.

a) *Scolecoplepides benhami* mean densities 1977-79, as hundreds per $m^2 \pm 95\%$ limits ($\pm 2SE$ for November 1979) for 500 μm processed samples. No significant density changes occurred.

b) *Scolecoplepides benhami* size-frequencies per zone as percentages for 100 μm and 500 μm classes, using summed 1977-78 data.

Fig. 38 *Scolecoplepides benhami* size-frequencies as densities per m^2 for 100 and 500 μm classes from 500 μm sieve processed samples. November 1979 hatched area is 3-15 cm depth zone. Total population densities and number of individuals measured also indicated.

Fig. 39 Densities per m^2 of *Paradoneis* sp., *Cirratulus* sp., *Boccardia syrtis*, and *Orbinia papillosa*, 1977-1979, from 500 μm sieve processed samples.



A few much larger individuals occurred, predominantly in downshore zones 5-8 (Fig. 37b). Modal-group individuals from upper shore zone 1 were larger than those in zones 2-8, an effect consistent for all the component samples summed for Fig. 37b.

MINOR SPECIES

Most of the minor species occurred in only part of the intertidal (Section 1), had very low mean densities transect-wide, and were present intermittently in samples (Table 17). Seasonal densities of the four most abundant minor species are shown in Fig. 39. The paraonid *Paradoneis* sp. declined significantly ($P < 0.01$) from 230 m^{-2} to 36 m^{-2} between November 1977 and May 1978, and subsequent increase to 61 m^{-2} in November 1978 was not significant. Also between November 1977 and February 1978 *Cirratulus* sp. declined significantly ($P < 0.01$) from 116 to 15 m^{-2} , and was less abundant in subsequent samples. Both species occurred predominantly in the lower-shore zone 8, and so estimates are based on abundance in relatively few cores. However, their density declines appear to be real events as the high density had occurred in both of the transect pair. It is not known why the species were subsequently less abundant. Seasonal changes in *Boccardia syrtis* and *Orbinia papillosa* were not significant.

TABLE 17. Minor polychaete species density range, November 1977-November 1978, transect means per m², ± 95% limits.

Species	Maximum			Minimum		
	mean	± 95% limits	¹ sample	mean	± 95% limits	¹ sample(s)
<i>Paradoneis</i> sp.	230	182	N7	36	29	M
<i>Boccardia syrtis</i> (Rainer)	97	92	A	39	45	F
<i>Cirratulus</i> sp.	116	48	N7	0		A
<i>Orbinia papillosa</i> (Ehlers)	27	19	A	7.3	8.9	N7
<i>Desdemona</i> sp.	15	34	N7	0		M, A
<i>Perinereis vallata</i> (Grube)	15	15	M	0		F
<i>Scoloplos cylindriifer</i> Ehlers	12	34	A	2.4	6.8	N8
<i>Ceratonereis</i> sp.	12	19	M	0		N7, N8
<i>Prionospio aucklandica</i> Augener	9.7	9.7	N7	0		M, A
<i>Sphaerosyllis</i> sp.	12	34	F	0		N7, N8, M, A
<i>Aonides trifida</i> Estcourt	4.9	7.9	A	0		M, N8
<i>Glycera lamellicornis</i> McIntosh	2.4	6.8	N8	0		N7, F
<i>Microphthalmus paraberrans</i> Hartmann-Schröder	4.8	8.2	N7	0		M, A, N8
<i>Goniada</i> sp.	4.8	7.9	M	0		N7, N8, F, A
<i>Glycinde dorsalis</i> Ehlers	2.4	6.7	N7	0		F, M, A, N8

¹N7 = November 1977, etc.

DISCUSSION

HETEROMASTUS FILIFORMIS

At the Pauatahanui site *Heteromastus filiformis* spawned over a short period, as recruitment had begun by February (late summer) and had ceased probably before May. The resulting O group did not merge into adult-group size classes until one year elapsed, and year groups probably survived for over three years. Sexual maturity was not reached before the second year. *Heteromastus filiformis* had alternate years of higher recruit density. These were the same years as in the maldanid *Axiiothella serrata*, and lead to speculation that the sum of climatic variation may have similarly influenced gamete output or affected the survival of new settlement for both species.

The reproduction and development of *Heteromastus filiformis* is surprisingly little known. Cazaux (1970) and Lacalli (1980) found *H. filiformis* egg masses; Shaffer (1979) was unsuccessful, but thought this may have been because they deteriorated rapidly. Cazaux (1970) and Lacalli (1980) have described some larval stages. The few records of planktonic *H. filiformis* larvae include maximum numbers of larvae in June in the Bassin d'Arcachon (Cazaux 1973), and larvae from April to June in Passamaquoddy Bay (Lacalli 1980). An earlier reference (Smidt 1951) may be a misidentification, and an account of spawning and development (Rasmussen 1956) was later referred to the species *Mediomastus fragilis* Rasmussen (Rasmussen 1973). For New Zealand Estcourt (1967) had noted coelomic oocytes from October to February in the Avon-Heathcote Estuary (December to April in Pauatahanui).

Population structure of *Heteromastus filiformis* has been analysed in the varying detail reviewed below. Shaffer (1979) made an intensive study of intertidal *H. filiformis* in North Inlet Estuary, South Carolina. Density in 500 μm sieve estimates at two separate 10 x 10 m sites ranged from 3-15 thousand m^{-2} with average adult density 5.8 thousand m^{-2} . Densities at the Pauatahanui site were much lower overall, but more comparable within lower-shore zones. North Inlet adults were inferred to spawn in early spring, most probably at the end of their second year. Larvae, suggested as perhaps having a demersal development type, were only once obtained in plankton samples. A larva reared at 20-24°C from laboratory artificial fertilisations metamorphosed in about three weeks. Settlement at 9-setigers or more occurred over about a four-week period in March and April at daily rates of up to 2.3 thousand m^{-2} , giving post-larval densities up to 66.5 thousand m^{-2} . Initial juvenile mortality was about 0.03 individual $^{-1} \cdot \text{day}^{-1}$, whereas adult mortality was mostly low, rising in spring to 0.006 individual $^{-1} \cdot \text{day}^{-1}$ post-spawning. The 0 group, 110 μm minimum width at settlement, was separable from adults only for about four months in size-frequencies compiled from setiger-two widths, compared with about one year at Pauatahanui. Also the adult mode reached 800 μm in winter (cf. 500 μm in Fig. 34), and the largest worms reached 1000 μm width. This more rapid growth and larger size perhaps indicate that the Pauatahanui site sediments provided poorer conditions for growth, i.e., lower temperature and organic content.

Heteromastus filiformis had an annual density of about 225 m^{-2} off the Northumberland coast on an 80 m deep, sandy-silt bottom (Buchanan and Warwick 1974). Over one year 500 μm processed samples were taken at 2-monthly intervals. Interpretation of size-frequencies

compiled from setiger-one widths was of necessity speculative using
fitted gaussian curves, because only in June (early summer) were two

NICON AESTUARIENSIS

A dense recruitment of the *Nicon aestuariensis* O group at the Pauatahanui site at about 500 m⁻² was first noted in May in both 500 and 250 µm processed samples. The size and setiger-development of the individuals suggest that time elapsed since peak spawning could have been several months. During the subsequent year mortality was probably greater than 98%, and the consequent low adult density limited further study of age structure to noting probable presence of II+ individuals.

Estcourt (1966) briefly described *Nicon aestuariensis* larval development from artificially fertilised oocytes reared at room temperature. Free-swimming larvae had developed three setigers after 5 days, became intermittently benthic at 9 days, and at 11 days began feeding and assumed a continuously benthic existence. The furthest-developed larva achieved 6 setigers after 29 days. Estcourt (1966) did not find post-larvae in the field.

It is important to estimate the time elapsed since spawning before juvenile *Nicon aestuariensis* were detected at the Pauatahanui site. *Hediste diversicolor* has similar lecithotrophic larval development to *Nicon aestuariensis* and reaches maturity after two to three years. For this species in a north-east England estuary three months elapsed from spawning to when 18- to 34-setiger juveniles appeared in 500 µm sieve samples, and juveniles were first obtained from the sediment by a decantation method about one month after spawning (Olive and Garwood 1981). However, rapidly-growing nereidid species, maturing in less than one year, may attain 35 setigers after 30-50 days' development (Reish 1957). A conservative estimate of the time span in which peak spawning of *N. aestuariensis* was located is

thus two to four months prior to late May, and therefore no earlier than the latter part of summer (late January-February). In contrast, at night-light samplings in the Heathcote Estuary, heteronereid swarming was at a maximum in early spring (September-October), although it continued at a low level to at least February (Estcourt 1966).

The density and size-frequency data of Estcourt (1966) are not easily compared or reconciled to Pauatahanui data. This is because the Heathcote population was sampled by hand-sorting from large cores taken in the zone of density, and length was used as the size measure. *Nicon aestuariensis* less than 2 cm long were not obtained with the method, but at the Pauatahanui site all were shorter than this, except for the few individuals thought to be two or more years old. The largest adults were about 6 cm long compared to the 25 cm maximum at Heathcote. Age to size relationships probably differed at the two localities, but, if they were similar, then Pauatahanui worms would be two years old before entering Estcourt's assessed population.

The December 1960-November 1961 data of Estcourt (1966) showed mainly two size groups. The group of smaller individuals, with a mode of approximately 7 cm total length, was discernible throughout the year, and static in position; but, expressing Estcourt's raw size data as relative densities, some recruitment to this group could have occurred from December to March. The whole population then declined from 1840 m^{-2} in April to an October low of 760 m^{-2} (subsequent to spawning), and had recovered only slightly by December to 1180 m^{-2} , although previously 1980 m^{-2} in December 1960. From June metamorphosis was common in individuals over 10 cm long. Worms shrunk greatly as they metamorphosed, thus the length-frequencies contracted and distorted. Estcourt (1966) considered growth from 2.5 cm to maturity and spawning occurred in one year.

The important point of contrast established between Heathcote and Pauatahanui populations is the much earlier spawning period in Heathcote Estuary. Also at Pauatahanui growth for three or more years before breeding is more likely than the two-year cycle suggested by Estcourt (1966). Age of maturity at Heathcote requires confirmation. However, like spawning period, this life history trait may differ between the two isolated populations. Recent studies of *Hediste diversicolor* also show differences in traits between populations, although of incompletely resolved extent (Olive and Garwood 1981, Mettam et al. 1982). Knowledge of the population structure of *Nicon aestuariensis* is still incomplete at both New Zealand sites. Study of I group and older classes is not feasible at Pauatahanui, and as the adult population density in the Heathcote is vastly greater, exceeding that at Pauatahanui by a hundredfold, it is an obvious site for future research on the species. However, it would be of interest to determine more exactly the period of settlement and the size at settlement at Pauatahanui. There is a possibility that the *N. aestuariensis* at the site could be juvenile migrants from a denser breeding population nearby.

SCOLECOLEPIDES BENHAMI

The *Scolecoclepidus benhami* population remained relatively static in density and size-frequency, without detectable recruitment. In fact worms less than 450 μm class did not occur. Low density immigration of the sizes recorded must be occurring from elsewhere if the population is not being maintained by an input of planktonic larvae. Migration in the water mass of both ripe adults and juveniles does occur in *S. viridis*, an east coast North America estuarine species (Dauer et al. 1980).

Nothing is known of the reproduction of *Scolecoplepides benhami* or of the type of larval development. Gravid individuals were not seen. The few much larger individuals occurring mainly downshore may be the only worms which have reached the age of maturity, as the bulk of the population were, compared to them, of small size. A prolonged breeding period might be expected in *S. benhami* as in many other spionids (Section 3). However, in a Nova Scotia *S. viridis* population there was a short March spawning following winter gametogenesis (George 1966). Development was holoplanktonic, with larvae, metamorphosing at 9-13 setigers, present until the end of May (George 1966).

In future studies at the site it would be of interest to investigate possible gametogenesis in the dense near shore population. However, more potential lies in finding a dense population elsewhere with a complete size distribution, which would allow age structure and period of recruitment to be studied as well as gametogenesis.

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SECTION 5

POPULATION ECOLOGY STUDIES
ON INFAUNAL POLYCHAETES OF PAUATAHANUI INLET:
AN OVERVIEW

S E C T I O N 5

POPULATION ECOLOGY STUDIES

ON INFAUNAL POLYCHAETES OF PAUATAHANUI INLET:

AN OVERVIEW

INTRODUCTION

Preceding Sections have examined intertidal density patterns and population dynamics of the abundant polychaetes. Some linkages between zonation and population dynamics have already been mentioned. Here a more general view of this aspect will be given as part of discussion of the Pauatahanui polychaetes as an assemblage. Life history traits, the similarity of density cycles, and possible adaptation to inlet life will also be discussed, together with comparable studies elsewhere. Finally, problems in polychaete population studies and their effect on the advancement of knowledge will be reviewed.

PAUATAHANUI POLYCHAETES AS AN ASSEMBLAGE

THE PAUATAHANUI SITE AS A HABITAT: POSSIBLE COMPARISONS

Pauatahanui Inlet is commonly regarded as an estuary, fulfilling the necessary requirements when defined as 'a region containing a volume of water of mixed origin derived partly from a discharging river system and partly from the adjacent sea; the region usually being partially enclosed by a land mass' (Barnes 1974). Its waters are not comparable with extreme estuarine environments of steep, tidally fluctuating, salinity gradients. Pauatahanui Inlet lies instead well towards the marine end of the continuum (see General Introduction and Section 1). It is an enclosed, shallow arm of the sea, large enough to have wave-structured beaches, with waters having much greater physico-chemical fluctuation than those of the adjacent coast. The environment is largely unmodified (see Healy 1980), and the 'moderately polluted' classification in McLay (1976) is unsubstantiated.

The site studied was a relatively uniform, low gradient, intertidal area of very fine sands. Comparable sites occur in various harbours and sheltered coastal areas of New Zealand, but studies of their faunas do not provide sufficient detail or taxonomic rigour to enable extensive comparisons to be made. From the literature and personal observations the components of what may be called a harbour-flat, polychaete assemblage change with locality, or at least vary in relative abundance. While some species such as *Heteromastus filiiformis* and *Scolecopides benhami* occur more or less ubiquitously in the same sediment type, others may not. For instance,

the large, bulk deposit-feeder *Axiothella serrata* is limited to central New Zealand; elsewhere *Macroclymenella stewartensis* or *Abarenicola* spp. may be present. *Microspio* sp. has not yet been found to be as dominant outside the Wellington area. The relative rarity of *Aonides trifida* at Pauatahanui is also of interest considering its high densities in similar habitats elsewhere (personal records, and cf. Estcourt 1967).

Worldwide there are no similar studies of an intertidal polychaete assemblage known to me. However, two studies of sheltered intertidal habitats do contain elements relevant to the present work. Dauer and Simon (1975, 1976a,b, Simon and Dauer 1977, Dauer 1980) report on the recolonisation of a subtropical, fine-sand beach in Tampa Bay, Florida, after a red tide outbreak had caused defaunation. Polychaetes were the most rapid colonisers, comprising 80% of total density in the initial stages, but only 17% two years later (Dauer 1980). Adult immigrants were important (Dauer and Simon 1976a). Unlike Pauatahanui, recurring seasonal density patterns were mostly absent. Instead, the nine most abundant species of the 54 polychaetes recorded were divisible into four groups, depending on their dominance at various times during the period (Dauer and Simon 1976b). Initial wide zonations of some species later contracted (Dauer and Simon 1976b). Zonations of twelve species were reported, and, of the five species with peak abundance on the upper shore (intertidal specialists?), four were said to be estuarine or euryhaline; whereas none of the lower-shore species were (Dauer and Simon 1975, 1976b). The significance of this is unclear as an intertidal salinity gradient was not reported. Dauer (1980) considered 'potential competitive interactions for food ... to be the most important factor explaining the observed ecological patterns', and speculated extensively on

possible occurrences of this among the abundant polychaetes, all deposit-feeders and/or omnivores. However, no detailed comment was made on other possible explanations with greater emphasis on life history traits, environmental preferences, and the influence of non-polychaete taxa.

The other intertidal study of an assemblage is that of Warwick and co-workers on secondary production in the mid-tidal of an estuarine mud flat in Cornwall, England (Warwick and Price 1975, Warwick et al. 1979, Price and Warwick 1980). There were only 11 macrofaunal species but the two polychaetes studied were the most abundant. *Nephtys hombergi*, which had at least three year classes, contributed more than half the total production, and *Ampharete acutifrons*, which was annual, was ranked third behind a bivalve (Warwick and Price 1975). In both species variations in recruitment changed annual production, but less dramatically so in *Nephtys hombergi*, probably due in part to the buffering effect of multiple year classes (Price and Warwick 1980). The production of four meiofaunal-sized polychaetes was also assessed, but detailed population data was not given (Warwick et al. 1979).

There are also several studies giving population data for subtidal assemblages, and a number of single-species studies of polychaete population dynamics. Some of these will be commented on later. None of the single-species studies reports in detail on temporal changes in intertidal zonation.

PAUATAHANUI POLYCHAETE POPULATION CYCLES

Concordance of density cycles among the common species is apparent from Figure 7 and Table 7, with peak density occurring in winter (August). Subsequent examination of population structure

showed that this pattern represented densities of adults, and of the 0 groups when older. A false conclusion would be reached from reliance on densities in the 500 μ m processed samples, without realising these mainly reflected the patterns of the older polychaetes.

Settlement (or settlement peak) and juvenile abundance of five of the common species were spring-summer orientated. The two multivoltine species, *Microspio* sp. and *Capitella* sp., had spring-summer settlement peaks. *Axiiothella serrata* had a spring-summer spawning season, and *Heteromastus filiformis* and *Nicon aestuariensis* did not spawn until the latter part of summer. Seasonal density cycles in other polychaetes were probably absent (e.g., *Scolecopides benhami*, *Orbinia papillosa*), or are largely unknown. *Boccardia acus* and *B. syrtis* may have an autumn-winter peak in year-round breeding (Read 1975, see also Fig.7, 39).

The November 'adult' populations of *Microspio* sp., *Nicon aestuariensis*, and *Scolecopides benhami* were not significantly different over three years, whereas those of *Axiiothella serrata*, *Heteromastus filiformis*, and *Capitella* sp. were. Examination of annual density differences in *Capitella* sp. may not be enlightening since it is a multivoltine species, presumably sensitive to shorter-term changes, but the variation in *Axiiothella serrata* and *Heteromastus filiformis* may have more importance. Years of higher recruit density coincided for the two species. As stated earlier, longer-term study would be required to resolve if the underlying causes were aperiodic environmental ones, or linked to population structure.

Population fluctuations of marine invertebrates have been detected in most long-term studies (Boesch et al. 1976), but as yet the data base is poor. A distinction can be made between the influences that simultaneously affect the whole community, and those

that, by affecting the abundance of individual species, change community structure. Variation due to unstable or patchy substrata (e.g., Rees et al. 1976) is perhaps of less interest than variation in seemingly uniform habitats, where important influences might be biotic interactions, or climatic variation at crucial times, or long-term climatic trends (e.g., Buchanan et al. 1974, 1978). The multitude of possible causes of population fluctuations range from obvious catastrophes (e.g., Dauer and Simon 1976a) to synergistic effects and subtle chain reactions (e.g., Lewis 1977). Boesch et al. (1976) and Pérès (1982) review some of the possibilities.

Fluctuation in *Axiiothella serrata* and *Heteromastus filiformis* may be due to adverse influences on early recruits; a contingency they are unable to compensate for immediately because of their comparatively short spawning periods. As polytelic, or at least perennial species, a comparative failure to recruit normally in one year would result only in a reduction of abundance, and not in eventual local extinction (the 'bet-hedging' reproductive strategy). An example of the comparative effects of recruitment variation in an annual and a perennial polychaete has been mentioned (Price and Warwick 1980). Olive et al. (1981) discuss an interesting situation in co-occurring *Nephtys* spp. with differing years of poor recruitment. Although poor recruit survival did sometimes occur, there was also occasional total reproductive failure, despite presence of mature gametes. Olive et al. (1981) speculated that, as well as possible climatic effects, some form of density-dependent influence on reproduction might be present.

LIFE HISTORY TRAITS

Concepts and hypotheses concerning life history tactics are still in a state of flux. The important assumption that life history traits of each species are being adjusted to optimise indi-

vidual fitness, i.e., the probability of being represented in subsequent generations, may prove less useful than previously thought (Stearns 1976, 1977). The most important traits are believed to be reproductive effort, the age distribution of reproductive effort and mortality, the number and size of young, and the inter-brood interval.

Some of the life history traits of Pauatahanui polychaetes are now known, at least in outline, and they differ between species. An obvious trait is the season of breeding. As already mentioned, breeding was spring-summer orientated in five species and perhaps winter orientated in another two. Seasonal timing of reproduction may indicate the probable latitudinal range of temperate species, with summer-breeding species ranging into lower latitudes, and winter-breeding species into higher latitudes (Hutchins 1947, Moore 1972, Bhaud 1973). For the Pauatahanui spring-summer breeders there is some possibility of a linkage of peak juvenile recruitment with a time of higher food availability in the sediment. Conversely this means energy required to produce gametes must be gained during the winter, and in *Axiiothella serrata*, for example, gametes may constitute about 25% of total weight (unpublished data). Seasonal variation in food available is largely unknown, but slightly higher sediment organic carbon and total nitrogen values were found in summer (Smith and McColl 1978).

The near-surface *Microspio* sp. and *Capitella* sp., breeding apparently continuously, probably with short generation times, heavy input into reproduction, and high mortality, are well placed to take advantage immediately of favourable conditions following any disturbances of the surface. However, conditions on the Pauatahanui flat are seemingly constant and predictable for well-established adults

of deep-burrowing species. *Axiothella serrata* and *Heteromastus filiformis* are successful, with relatively low adult mortality, and a delayed, smaller input into reproduction. *Nicon aestuariensis* and *Scolecopides benhami*, although present in moderate abundance, are perhaps not reproducing successfully at the site. They may be migrants from adjacent populations.

The range of development types of marine invertebrates, from direct to holoplanktotrophic, will variously fulfil the opposing requirements of dispersal to new habitats and maintenance of the breeding populations in their favourable habitats. *Axiothella serrata*, *Capitella* sp., and probably *Heteromastus filiformis* also if it has a demersal larva, readily maintain their Pauatahanui populations because dispersal of offspring is low. In predictable habitats that are of restricted geographic extent selection will favour low dispersal (Jablonski and Lutz 1983). Also loss of dispersal mechanisms permits maintenance of successful genomes in small, cohesive, interbreeding populations (Fauchald 1983).

However, *Microspio* sp. has a lengthy planktotrophic period of development, during which larvae will be carried out of the Inlet and dispersed into unfavourable habitat. One view of the constant reproduction of *Microspio* sp. would suggest it is partly an adaptation to counter this loss of potential recruits (e.g., Woodwick 1977). However, because the favourable habitat is an enclosed inlet, there are possible ways to reduce loss. Behavioural mechanisms aiding estuarine retention of bivalve, barnacle, and crab larvae have been identified (Wood and Hargis 1971, de Wolf 1974, Cronin 1982). This aspect remains to be investigated for *Microspio* sp. The existing balance between the portions of development spent in the egg capsules and in the plankton (0-3 setigers:3-13 setigers) suggests planktonic

mortality of later larvae is not disproportionately higher than that in the sediment. If it were so then the encapsulation period would be expected to be longer (Caswell 1981).

POPULATION DYNAMICS AND ZONATION

Pronounced zonation trends indicate a species which is less successful in part of the intertidal, and thus one that has an effectively reduced overall intertidal density. How has population structure helped explain the zonation patterns? *Heteromastus filiformis* in the low density, upper-shore population were shown to be little different in size structure from those in the lower shore zones of high density. *Capitella* sp. size structure was relatively unchanged outside the zones of high density, except that a number of larger (older?) individuals occurred. The situation in both cases is contrary to the reasonable expectation that in low density areas adults should be proportionately few, because mortality rates are higher in these areas. However, the explanation may be that recruits do suffer the heavy mortality expected at first, but once established have no greater mortality than elsewhere. In both species larger/older individuals were further below surface, and thus more protected from stresses. As 500 μ m processing retained only juveniles that had been settled for some time, the apparent juvenile/adult proportions were more or less the same in all zones. Similar reasoning may explain why the high zone 1 density of *Microspio* sp. was not associated with a difference in size-frequency from zone 2. However, the occurrence of a few much larger individuals downshore from the zones of high density in *Capitella* sp., and also in *Scolecopides benhami*, still appears to be anomalous and inexplicable at present. Smith (1956) similarly reports large down-

shore individuals of *Hediste diversicolor* isolated from the bulk of the population.

Thus knowledge of population structure outside zones of high density raised further questions. However, within the high density zones the information was useful in, for example, understanding the *Heteromastus filiformis* density changes in zone 8, and the *Nicon aestuariensis* zonation expansion during recruitment. Study of *Axiiothella serrata* age structure revealed that the apparent lack of zonation was misleading, and that age groups could at times show zonation trends in opposing directions.

POLYCHAETE POPULATION STUDIES

The study of polychaete populations is in its infancy. Comparatively few studies have been made with primary aims of elucidating structure and dynamics. More often the information has been gained almost as a by-product of studies of reproductive biology, gametogenesis, and larval development, studies of benthic communities, and, most recently, attempts to assess secondary production. Polychaete population studies are still unsophisticated, mostly due to inherent difficulties in censusing, aging, and sexing that will be discussed later. Most attention has centred on size structure rather than on the accurate density assessments that, combined with size structure, greatly improve the deductions that can be made about population dynamics. (Incidentally, 'population dynamics', as used here, is intended to convey density changes in elements of the population, and not merely population density regardless of age/size structure)

Two early studies of polychaete size structure were those of Newell (1948) on *Arenicola marina*, and Dales (1951) on *Hediste diversicolor*. George (1964), studying *Cirriformia tentaculata*, appears to have been the first to incorporate density, rather than simple percentages, into a polychaete size-frequency report. Few studies had been done prior to 1970, but there has since been much greater research effort directed to the polychaete group. As yet no review of polychaete population studies has been published.

AGE AND SEX

ASSESSMENT OF AGE AND SEX: Age assessment is a primary requirement when the structure of populations is being examined. In a number of taxa this is often possible through use of hard-structure annual rings, formed when growth rate changes. Family Nephtyidae, in which the jaws can be so used (Kirkegaard 1970), are so far the only polychaetes this applies to; otherwise size measurement must be used, with its inherent defect of developmental plasticity in the relationship of size with age. Size ranges tend to expand with age so that older age groups overlap. The same problem applies to weight, with the additional difficulty that weight changes with condition.

A major source of variation when measuring polychaete size is the contractile nature of the soft body. Generally length is an unsatisfactory measure, unless standardised conditions can be achieved so that worms are in the same state of contraction (e.g., Hutchings 1973). Length is particularly inappropriate in species that shrink as they become sexually mature (e.g., Estcourt 1966). Also in preserved benthic samples worms are often fragmented or badly twisted. Width measurement near the head has the advantage that it can always

be done, and will give an approximation of size and age, more consistent in species that have a rigid head structure, such as pectinariids (Estcourt 1974), and to some extent also maldanids and other worms that fit tightly into tubes. Volume measurement may be appropriate, although difficult to achieve, and various other body measurements can be used (e.g., Self and Jumars 1978).

Meristic data, applicable when numbers of a body structure increase with age, are an alternative to dimensions. The obvious example, and one used herein, is setiger counts. However, they have been little used except in studies of larval development (e.g., Blake 1969), and only limited information is available on changes in the setiger-total/age relationship (e.g., Hemplemann 1911, Blake 1969, Åkesson 1976, Garwood 1982). Setiger-total size-frequencies for adults have been employed by Dorsett (1961), Gibson (1977), and Garwood (1982). Setiger counts may be relevant to juveniles only, if adults have a fixed setiger-total (e.g., *Axiiothella serrata*), and to polychaetes with relatively few setigers, as the labour involved would be prodigious for some nereids, eunicids, glycerids etc., with several hundred setigers. Possible use of neurosetal counts was discussed for *A. serrata*, and there are likely to be other suitable morphological features in various species.

Polychaetes of most families are not externally sexually dimorphic, and identification of sex is limited to the proportion of the population with developed gonads. Only near-mature worms of species which have free coelomic gametes can be sexed without histological sectioning. This considerably restricts the extent to which population structure can be examined.

CONSEQUENCES OF INADEQUATE AGE AND SEX INFORMATION: If, when examining individuals, many worms cannot be placed unequivocally into an age group, then only statistical-level partitioning of the population is possible. Consequently, other information, such as sex and reproductive state, has lower value, and desirable information, such as confidence limits of age-class density and the spatial distribution of an age class, cannot be obtained. *Axiiothella serrata* was the only Pauatahanui species that could be individually aged, and then only into adults and O group. Other taxa are age-assessed in similar ways; the problems are not unique.

The resolution at the statistical level of an overlapping age-class series was discussed in Section 2, and some of the problems were mentioned. If age classes can be distinguished, their rise and decline in density can be followed, giving the essential information to analyse life history, predict population changes, and calculate energy requirements and production. Knowledge of density variation and recruitment period may well give a more precise estimate of spawning times than determinable from histological sampling.

However, if recruitment is more or less continuous with rapid growth into the adult size range, then size-frequency structure in the sequence of samples will not show the fate of components of the population, but rather represent the shifting balance of recruitment, growth, and mortality rates, none of which can be precisely quantified. Increased recruitment with subsequent high mortality may cause a modal group to be defined for a time (*Microspio* sp. and *Capitella* sp.). The information gained on density changes in *Microspio* sp. and *Capitella* sp. enabled partial analysis of their population dynamics. Techniques based on matrix algebra are being evolved to analyse and predict population changes when age cannot be assessed, or when it is

an inadequate variable (e.g., Caswell 1978, Hiby and Mullen 1980); they still require some independent knowledge of growth and fecundity.

SAMPLING AND DENSITY ESTIMATION

The majority of polychaete population studies have been on infaunal species, presumably because of ease of collection. Potentially sampling of sediments can be very accurate as complete counts of all individuals within the sampling unit are possible, unlike sampling on hard substrates, and in epibiota growths, where quantitative detection of semi-cryptic polychaetes may be very difficult. Also sampling to a chosen design is very much simpler on a flat surface than attempting the same on the complexities of a rocky substrate. A disadvantage of sampling infauna is that changes occur in the habitat (sediment characteristics), that affect faunal abundances, but may not be detectable a priori.

Due to habitat differences, biological interactions, and past events the abundances of infauna vary spatially. It is well known that the dispersion of any benthic population is usually contagious rather than random or regular (e.g., Elliott 1977). This patchiness may occur at several scales (Estcourt 1974, Rees et al. 1976, Findlay 1981). For this reason the use of grab sampling in subtidal, population dynamics studies is best avoided if possible, because sample placement is both poorly controlled and inadequately known. Ideally, for density assessment in both the subtidal and intertidal, each sample should come from within the same defined area, and should be composed of large numbers of small 'randomly-placed' sampling-units to counter aggregation effects (≥ 40 units for parametric statistics without transformations). However, sampling-

unit size should be large enough potentially to contain several individuals of the largest species under study. Excessive numbers of small fauna may be collected, and for Pauatahanui transect samples this was resolved by subsampling the largest cores used.

Obviously intertidal sampling has advantages over subtidal sampling in ease of access and sampling-unit placement. The major complication is that an environmental gradient exists, necessitating a sample from the whole intertidal if an unbiased population assessment is required. This approach was adopted for the Pauatahanui site, and provided the best overall picture of the populations. It allowed detection of anomalies such as the *Scolecoplepides benhami* near-shore density maximum, and the lower-shore large adults of *Capitella* sp. Sampling of two sites at different tidal levels (e.g., Garwood 1982) is less satisfactory, but provides an indication of the variation, and may be a necessary compromise for very wide, non-uniform beaches. However, an intertidal flat four kilometres wide was successfully sampled by Reading (1979) for a study of the bivalve *Macoma balthica*, using small cores in stratified random design.

An important defect in most polychaete population studies is poor assessment of densities. Few researchers appear to have allowed for possible contagion or age-specific differences in the dispositions of their animals. Studies were examined that made use of density estimates for analysis of intertidal, infaunal, polychaete population structure. Only four out of 23 assessed density in a statistically acceptable manner (random sampling in a defined area), and several recently published studies failed to do so. Only one of the four took into account changes in density with zonation (Chambers and Milne 1975).

The explanation for low rigour in density estimation may lie partly in the fact that, while processing and extraction of infaunal

polychaetes from samples is simple, it is also very time consuming. Only relatively crude techniques are available for separating out the fauna, and large amounts of sand and detritus may have to be minutely examined. Much detritus, from which the worms had to be painstakingly picked out, was present at the Pauatahanui site. Because of the time consumed in this, the large-core sample series in 1977-78 was seasonal only, but successfully established the basic outline of population dynamics for most of the common species.

Choice of sieve mesh in benthic sampling is a trade-off, as mesh size decreases, between the increasing sorting time, and the higher efficiency of retention of meiofauna and the smaller 'macrofauna' (see Reish 1959). Examination of Fig. 5a suggests that, for the Pauatahanui site, 250 μm mesh (2 ϕ ; up to 10% of sediment retained) would be borderline in acceptability for processing large cores. Mesh with 500 μm openings (1 ϕ) was used for the 1977-78 sample series, and successfully retained the adults and older juveniles of most species as expected. Subsequent sampling for juveniles used 250 μm and 72 μm meshes. Two species that barely reached macrofaunal size were less successfully sampled by 500 μm mesh.

A high proportion of the polychaete population is near the surface but some adults may be deeper. In a retrospective design for an improved sampling programme, the same quarterly, large-core samples and 500 μm mesh would still be adequate if, in addition, the surface 3 cm was processed through 250 μm mesh, with a small subsample also through 72 μm mesh. To study juvenile recruitment, and also to detect possible short-term changes in *Microspio* sp. and *Capitella* sp., a separate set of more frequent, fine-sieved, near-surface samples would be appropriate.

CONCLUDING REMARKS

This study has examined several polychaete species which show some of the variety of life history patterns known for polychaete worms. Abundant species were multivoltine or perennial, and no annual species were detected. Density cycles were seasonal. Although the situation for *Scolecoplepides benhami* and *Nicon aestuariensis* is unclear, *Axiiothella serrata*, *Heteromastus filiformis*, *Microspio* sp., and *Capitella* sp. appear to have 'robust' life history traits which will enable them to persist if the habitat is mildly perturbed. However, it is a commonplace of benthic ecology that human influences causing permanent changes, e.g., prolonged siltation or eutrophication of the Pauatahanui Inlet, will greatly alter previously-existing abundance rankings and species composition (see e.g., Gray 1981).

As a group of deposit-feeders, the polychaete assemblage is not necessarily a highly interdependent one. The manner in which the fauna partition the available resources is not relevant to population dynamics, except where density-dependent mortality and growth effects occur. Correlations did not detect evidence of potential interactions. However, these may not have overt effects. Also, as suggested by Peterson (1979) and others, biological interactions at the level of colonising larva versus established adult may be the most important.

Some avenues for future research, or points that need further clarification, have been mentioned in previous sections. These include the synchronous spawning of *Axiiothella serrata*, and

aspects of the population dynamics of the two multivoltine species. Long-term monitoring of November populations to study density trends and age-group fluctuations would be of value (see e.g., Price and Warwick 1980). Knowledge of adult-larval interactions, and also of the variation in settlement and mortality of the youngest recruits with respect to adult zonation, may clarify the structure of the assemblage.

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A P P E N D I X

TAXONOMIC NOTES ON

PAUATAHANUI SITE POLYCHAETA

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Table 2 (p.23) includes all the commoner intertidal infaunal polychaetes of the Inlet, and almost all the polychaetes noted at the site. The twenty-two species do not comprise a comprehensive list for the intertidal; the Inlet fauna becomes richer in species at the seaward end. References to the descriptions and New Zealand records of most of the Table 2 species not mentioned below can be obtained from Day and Hutchings (1979), and, for Spionidae, from Blake and Kudenov (1978).

The Pauatahanui site paraonid conforms best to *Paradoneis* according to Dr J.P. Hartley (Oil Pollution Research Unit, Orielton Field Centre, Wales), who will publish a description of the species. *Cirratulus* sp. may be *C. nuchalis* Ehlers. *Ceratonereis* sp., which is similar to a group of Australian species resembling the Madagascarian *C. erythraeensis* Fauvel (see Hutchings and Turvey 1982), may be endemic and undescribed. The three other taxa identified to generic level only, namely, the sabellid *Desdemonia* sp., the syllid *Sphaerosyllis* sp., and the goniadid *Goniada* sp., do not conform to species

previously reported from New Zealand, and presented major identification problems that were not pursued because of the low numerical importance of the species.

FAMILY SPIONIDAE

MICROSPPIO SP.

DIAGNOSTIC DESCRIPTION: Length to 15 mm for 55 setigers; body without pigmentation pattern. Prostomium pointed, with rounded tip. No nuchal antenna; two pairs of black eyes. Caruncle, without defined end, to post setiger 1. Branchiae, absent setiger 1, full-sized from setiger 2, present to near end of body; attached only basally to notosetal lobes. Notosetal postsetal lobes auricular, largest anteriorly, but small on setiger 1 immediately posterior to palps. Neurosetal postsetal lobes smaller, more rectangular, reduced posteriorly. Notoetae capillaries only; neurosetae capillaries to setiger 16, with bifid hooded hooks present from setiger 17, occasionally setiger 16. Hooded hooks up to 9 per fascicle, with companion capillaries reducing in number posteriorly. No sabre setae. Pygidium with 4 anal cirri, the ventral pair largest.

REMARKS: This previously unrecorded small spionid has been found in a number of estuarine areas in New Zealand. Dr J.A. Blake (Batelle, New England Marine Research Laboratory) is publishing a description. *Microspio*, formerly a subgenus of *Spio*, comprises a small group of about 10 species, and is in need of revision to clarify its characteristics and relationships.

SCOLECOLEPIDES BENHAMI EHLERS

- Scolecocarpus benhami* Ehlers, 1907: 14-16, text Fig.4-6, Moeraki, N.Z.—
Estcourt, 1967: 73, Fig.5, Avon-Heathcote Estuary.
Scolecocarpus sp. Estcourt, 1967: 74, Fig.6, Avon-Heathcote Estuary.

REMARKS: Needle-like neurosetal capillaries reported previously anterior to setiger 30 (Ehlers 1907, 'nadelformige'; Estcourt 1967, fig.5, 'acicular') were not often observed. Estcourt suggested these setae were a juvenile character. The *Scolecocarpus* sp. separated by Estcourt 1967, and said always to lack acicular setae, may be an ecophenotype. However, variation within *S. benhami*, both between habitats and over its distribution in New Zealand, merits study. Dr J.A. Blake is currently investigating this species, and also reports (pers. comm.) that the North American *S. viridis* may be two species, both referable to another genus. *S. aciculatus* Blake and Kudenov from Australia would then be the only other member of *Scolecocarpus*.

FAMILY CAPITELLIDAE

HETEROMASTUS FILIFORMIS (CLAPARÈDE)

Capitella filiformis Claparède, 1864: 509-510, Pl.4, fig.10,

Port-Vendres, France.

Heteromastus filiformis. — Eisig, 1887: 839-846, Pl.27,28,32-35,

Gulf of Naples. — Estcourt, 1967: 76-77, Avon-

Heathcote Estuary, N.Z.

DIAGNOSTIC DESCRIPTION (PAUATAHANUI SPECIMENS): Length to 50 mm with >120 setigers; blood-red colour in life. Prostomium thin, pointed. Eyespots present in juveniles, rarely in adults. Twelve thoracic segments, the first asetigerous. Thorax tapering posteriorly, thoracic-abdominal junction often indistinct, but anterior abdominal setigers larger in cross-section, especially dorsally. Setigers in tapering posterior body third campanulate, trapezoid in section, widest ventrally. Parapodial branchiae variably developed dorsal to notosetal fascicle. Pygidium with a long, ventrally displaced, thick-based, cirrus.

Adults with capillaries only in both rami of first 5 setigers, to 8 per fascicle; multifid hooded hooks thereafter, posteriorly decreasing to 1-2 per fascicle in notopodium, about 5 in neuropodium. Hook secondary teeth a descending series of transverse rows of very fine teeth, fewer in shorter abdominal hooks. Capillaries may be absent or mixed with hooks in setigers 4 and 5 of juveniles. Juvenile 12th segment may be transitional in character between thoracic and abdominal.

REMARKS: Claparède's (1864) description was incomplete in several respects. However, the first four anterior segments were stated to have capillary setae and the next six to have long hooks. This combination fits no known genus, although if an asetigerous first segment was also present *Mediomastus* Hartman would be appropriate. Eisig (1887) erected *Heteromastus* as a monotypic genus. He re-described *H. filiiformis* (Claparède) on the basis of his own material, noting the more anterior occurrence of hooded hooks in juveniles (up to setiger 4), but not including this in the generic diagnosis. His rationalisation was that Claparède had described juvenile setal distribution (and also miscounted the number of thoracic setigers?). This is unlikely as Claparède (1864) noted specimens were up to 6 cm length. Only recently-settled juveniles consistently differ in setal pattern from adults (see below). Both Eisig's and Claparède's material is presumed lost, as is type material of the four nominal species listed by Eisig (1887) as *H. filiiformis* subjective synonyms (*fide* Hutchings and Rainer 1982).

Eisig's (1887) designation of *Capitella filiiformis* Claparède as *Heteromastus* type-species was erroneous because Claparède's (1864) description was at variance with *Heteromastus*. Since then conflict between the type-species and Eisig's (exact) diagnosis of *Heteromastus* has assumed greater importance. Small changes in the number of thoracic segments and in the thoracic setal pattern encompass several subsequently-erected capitellid genera. Under Article 70a of Stoll (1964) Eisig's misidentification of the type-species must be resolved by referring the case to the International Commission on Zoological Nomenclature. Under Article 75c(4) of Stoll (1964) a neotype conforming to *H. filiiformis sensu* Eisig cannot be validly designated for

Capitella filiiformis Claparède (cf. Hutchings and Rainer 1982). To maintain the existing widespread usage of *Heteromastus filiiformis sensu* Eisig a suitable course of action would be to request the Commission to suppress the specific name *filiiformis* Claparède, as published in the binomen *H. filiiformis*, and to designate *Notomastus filiiformis* Verrill 1873 as the type-species of *Heteromastus*. Verrill's nominal species is the earliest-published with extant type material which conforms to *Heteromastus filiiformis sensu* Eisig (*vide* Hutchings and Rainer 1982). Meantime *H. filiiformis* (Claparède) remains the appropriate name to use.

Ostensible *H. filiiformis* material from the German North Sea coast, Egypt, Australia, and the U.S.A. north-east coast was examined by Hutchings and Rainer (1982), who found no consistent differences, and apparently did not encounter any variation in setal pattern. Interestingly, branchiae were stated as notopodial in their generic diagnosis, in contrast to diagnoses of neuropodial branchiae in Fauvel (1927), Day (1967), and Hartmann-Schröder (1971), and also to Eisig's (1887) *H. filiiformis* description (Pl.27,28). Hutchings and Rainer (1982) do not comment on this point, although by unstated inference only notopodial branchiae occurred in the material they examined.

Hutchings and Rainer (1982) believed it was highly unlikely that juvenile *Heteromastus filiiformis* had a different setal pattern from adults. However, an ontogenetic setal change does occur, with important consequences for diagnoses, and for identification from existing keys (Shaffer 1979, Fredette 1982). Individuals without capillaries after setiger 3 were considered as newly-settled by Shaffer (1979), who used the increase in number of capillary-bearing setigers as an index of age for early juveniles. At the Pauatahanui

site the youngest *H. filiformis* obtained, a 16-setiger stage, lacked capillaries after setiger 3. The largest worm still to have capillaries on fewer than five setigers had developed 73 setigers.

The extent of natural variation within capitellid species is almost unknown, but, with comparatively few external characters available, emphasis has been placed on the obvious meristic characters when defining genera and species. The number of valid genera is unclear, as Fauchald (1977) and Hutchings and Rainer (1982) have already commented. The generic-level character of thoracic-segment-total does seem constant, irrespective of size and age, in the species where it is readily apparent. In order to clarify existing classification it would be of great interest to determine if this character has biological importance, and if it indeed defines phylogenetic groups.

The taxon known as *Heteromastus filiformis* is widely distributed, and is regarded by Hutchings and Rainer (1982) as cosmopolitan. Also, on the basis of published descriptions, perhaps only two of the five other *Heteromastus* species subsequently described may be soundly differentiated from *H. filiformis*. There is as yet no evidence that soundly-differentiated *H. filiformis* subspecies occur. However, its morphological variation needs to be more thoroughly investigated. The possibility of cryptic *H. filiformis* species has been advanced, most recently by Gray (1982). While this could prove to be the case, it is only speculation at present.

In the past misidentifications between *Mediomastus* spp. and *Heteromastus filiformis* may well have occurred (see Warren 1979). Potential for confusion of juvenile *H. filiformis* with co-occurring *Mediomastus* spp. continues, but workers aware of the possibility have been able to distinguish them (Shaffer 1979, Fredette 1982).

CAPITELLA SP.

DIAGNOSTIC DESCRIPTION: Length to 10 mm and 50 setigers, rarely larger. Adult setiger 3-4 width (largest diameter) about 220 μ m, rarely to 500 μ m. Distal prostomium oval, eyespots rare in adults. Nine thoracic segments, all setigerous. Thorax usually tapering to prominent pre-abdominal intersegmental division. Abdominal setigers longest in mid body, short posteriorly, with setal fascicles on slightly raised ridges. Pygidium an inconspicuous rounded pad.

Capillary setae curved, limbate, up to 5 per fascicle, usually restricted to first 5 setigers only, or less often only on 4 setigers, but may extend to 7th setiger, or only to 3rd setiger. Capillaries may be mixed with hooded hooks on the last one or two capillary-bearing setigers, and may be absent in one fascicle, usually neuropodial. Hooded hooks only on remaining setigers (except 8 and 9), to 4 per fascicle. Hooks typical, with main fang plus rows of minute secondary teeth. Notopodial genital spines of setigers 8 and 9 rarely present, males only; 2 pairs on setiger 8, 1 pair on setiger 9.

REMARKS: *Capitella* sp. collected from two other Inlet sites and from some other New Zealand localities were also examined. Capillary setal distribution in 500 μ m processed, transect site samples was as follows: 1 individual with capillaries to setiger 3, 30 to setiger 4, 46 to setiger 5, 1 to setiger 7 (n = 78, Feb., May, Aug. 1978). Specimens from Mana flats had similar sizes and setal distribution (n = 18, Dec. 1975), but at Kahao Bay there was a higher proportion of worms with capillaries to setiger 3 only, and these were not juveniles (13 to setiger 3, mean width 289 μ m; 30 to setiger 4; 32 to setiger 5; 1 to setiger 7; overall mean width 269 μ m, n = 76, Aug. 1975).

Specimens taken by 500 μm sieve from three estuarine sites elsewhere had similar setal distribution to those of the Pauatahanui transect site [Ohiwa Harbour, 1979, $n = 7$, mean width 240 μm : 1 with capillaries to setiger 3, 3 to setiger 4, 3 to setiger 5. Moncks Bay, Christchurch, Dec. 1976, $n = 8$, mean width 406 μm : 3 with capillaries to setiger 3, 4 to setiger 4, 1 to setiger 5. Waikouaiti River Estuary, Dec. 1976, $n = 18$, mean width 289 μm : 2 with capillaries to setiger 4, 15 to setiger 5, 1 to setiger 6.].

Specimens from organically-enriched sites in Wellington Harbour (five outfall and dock-area sites, 1966-78, sampled by 1 mm sieve) were clearly different and much larger (mean width 1800 μm , to 60 mm length and 80 setigers). Capillary setae were present on the first 7 setigers, less commonly only to setiger 6, or 5, or up to setiger 8, to 20 or more per fascicle ($n = 62$; 2 with capillaries to setiger 4, 3 to setiger 5, 13 to setiger 6, 32 to setiger 7, 12 to setiger 8). Notopodial genital hooks of males were a set of 6 pairs on setiger 8, and 4 pairs on setiger 9. Hooded hooks per fascicle numbered up to 15 in the thorax and 20 in the abdomen. However, these setal differences from Pauatahanui *Capitella* sp. might still relate only to the greater size.

It is not known to what extent setal-pattern differences within *Capitella* spp. resembling *C. capitata* depend on environmental, nutritional, and age differences rather than on genotype. Individuals of the stem subspecies *C. capitata capitata* (Fabricius), *sensu* Warren (1976), as adults usually have only capillaries on the first seven setigers. However, there is believed to be a direct relation between age and increase in number of capillary-bearing setigers, not necessarily ceasing after formation of genital spines at sexual

maturity (Warren 1976). Reish (1977) found variation (capillaries to setigers 4-7) in a population reared from a single *Capitella* sp. (as *C. capitata*). For *Capitella* from the Pauatahanui transect site and from Wellington Harbour there was some direct linear association in least-squares regression of size on the number of capillary-bearing setigers (for each $n > 60$, $r^2 > 0.4$), suggesting age/size differences, but not for the Kahao Bay sample ($n = 76$, $r^2 = 0.005$), in which a similar size distribution occurred for each setal group.

Warren (1976) recognised eight species of *Capitella*. Three of those species were distinguished from *C. capitata* mainly on the distribution of capillaries, and the separated subspecies *C. capitata floridana* Hartman was a very small *Capitella* with capillaries to setiger 4 only, described (as was *C. hermaphrodita* Boletzky and Doyle) from the transient habitat of squid egg masses. Grassle and Grassle (1976) did not report ontogenetic or other setal variation within six cryptic species detected in one area from electrophoretic patterns and some life history study. All except one had capillaries to setiger 7. The one apparent variant J.P. Grassle now accepts is *Capitella jonesi* Hartman (Eckelbarger and Grassle 1982).

Grassle and Grassle have not yet sought status for the cryptic species they have found, but their discovery has now to be considered in any biological research on *Capitella* spp. Currently some researchers ambiguously continue use of the name *C. capitata* (Fabricius), although aware of its uncertain validity (e.g., Tenore 1982). There is both morphological and life-history-trait variation in the confused concept of *C. capitata*. For further refinement of

Capitella taxonomy all means of differentiating the species should be considered together. I suggest on current knowledge species distinct only in setal pattern from *C. capitata sensu* Warren should be regarded as part of a *C. capitata* species complex.

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