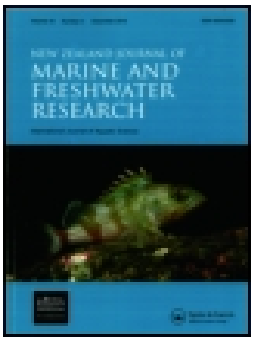

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ECOLOGY OF BENTHIC POLYCHAETES IN THE HEATHCOTE ESTUARY, NEW ZEALAND

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SUMMARY

The distributions of 19 species of polychaetes burrowing in the intertidal sand and mudbanks of the Heathcote Estuary, New Zealand, are related to salinity, sediment grade, and length of time of exposure at low tide. Only *Nicon aestuariensis* Knox and *Scolecolepides benhami* Ehlers appear to be truly estuarine species reaching their greatest population densities in low salinities. Incidental observations of feeding and reproduction are reported.

INTRODUCTION

There have been very few studies of the biology of estuarine animals in New Zealand. The estuarine environment is characterised by steep and variable gradients in environmental factors, and the fauna tends to be specialised to tolerate these conditions (Emery and Stevenson 1957).

In this survey of the polychaetes of the intertidal mudbanks of the Heathcote Estuary the distribution of each species was found to be related to the salinity of the water, the nature of the substratum, and the length of time of exposure to air at low tide. Some observations of feeding habits and reproduction were made. Systematic notes and a key to the species whose ecology is discussed in this paper have appeared elsewhere (Estcourt 1967), and also a description (Estcourt 1966) of the breeding biology of one of them.

Comparatively little work has been done on the biology of the estuary of the Heathcote and Avon Rivers. Thompson (1929) made the first general study and there have since been studies by Bruce (1953), Williams (1960), and Rosenberg (1963) carried out for the Christchurch Drainage Board and principally concerned with the effect of pollution on the biota.

THE HEATHCOTE ESTUARY

The estuary of the Heathcote and Avon Rivers (Fig. 1) near Christchurch lies immediately north of the volcanic mass of Banks Peninsula. Geologically it is a tiny remnant of the arm of the sea which once separated Banks Peninsula from the mountain backbone of

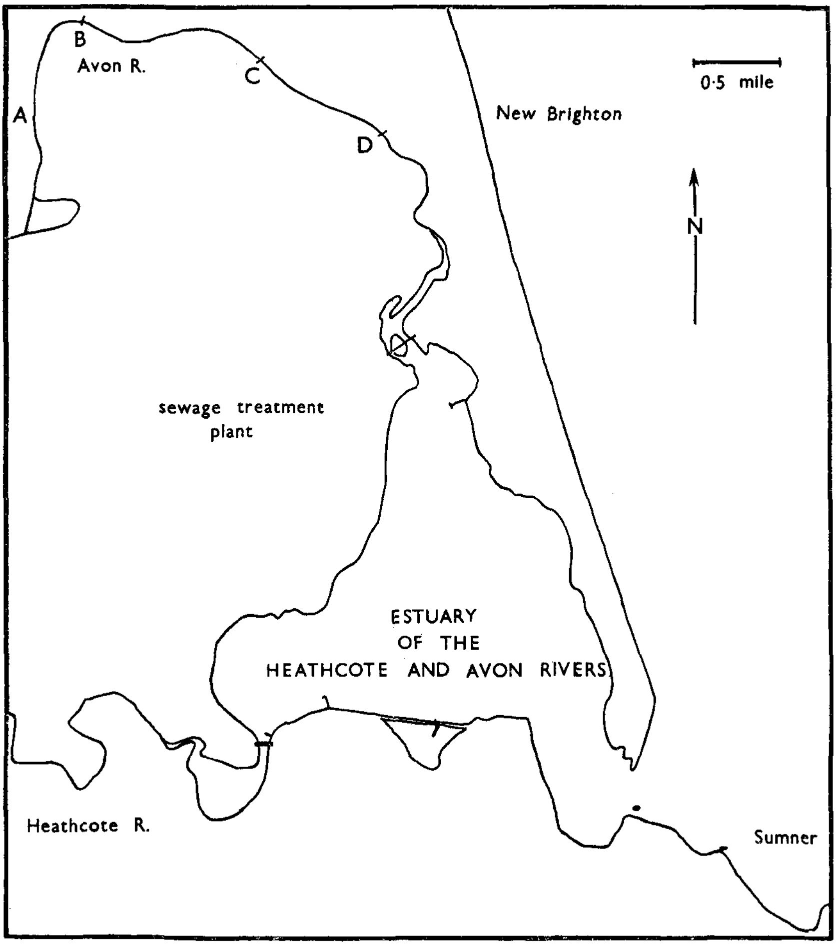

FIG. 1—The estuary of the Heathcote and Avon Rivers. A—Kerrs Reach; B—Avondale Road Bridge; C—Bower Bridge; D—Pages Road Bridge.

the South Island. This bay was filled in when material eroded from the mountains formed the Canterbury Plains and spits built by currents cut off the lagoons of Lake Ellesmere and the Heathcote Estuary. The estuary now has an area of two and a half square miles and is approximately the shape of an equilateral triangle with the outlet to the sea at the south-east corner between the rock of Banks Peninsula and the end of the sandspit which separates it from Pegasus Bay. An isolated rock stack, Shag Rock, stands on the south side of the outlet channel. The Avon River enters the estuary at its northern corner and the Heathcote River at the south-west corner. Both rivers run through very flat country and are tidal for a considerable distance upstream. Their sources and upper reaches are described by Hogan and Wilkinson (1959). Both are largely spring fed, but receive stormwater drains from the city streets which cover a large part of their catchment areas. The effluent from the Christchurch Drainage Board's sewerage treatment plant is discharged into the western side of the estuary near the mouth of the Avon River.

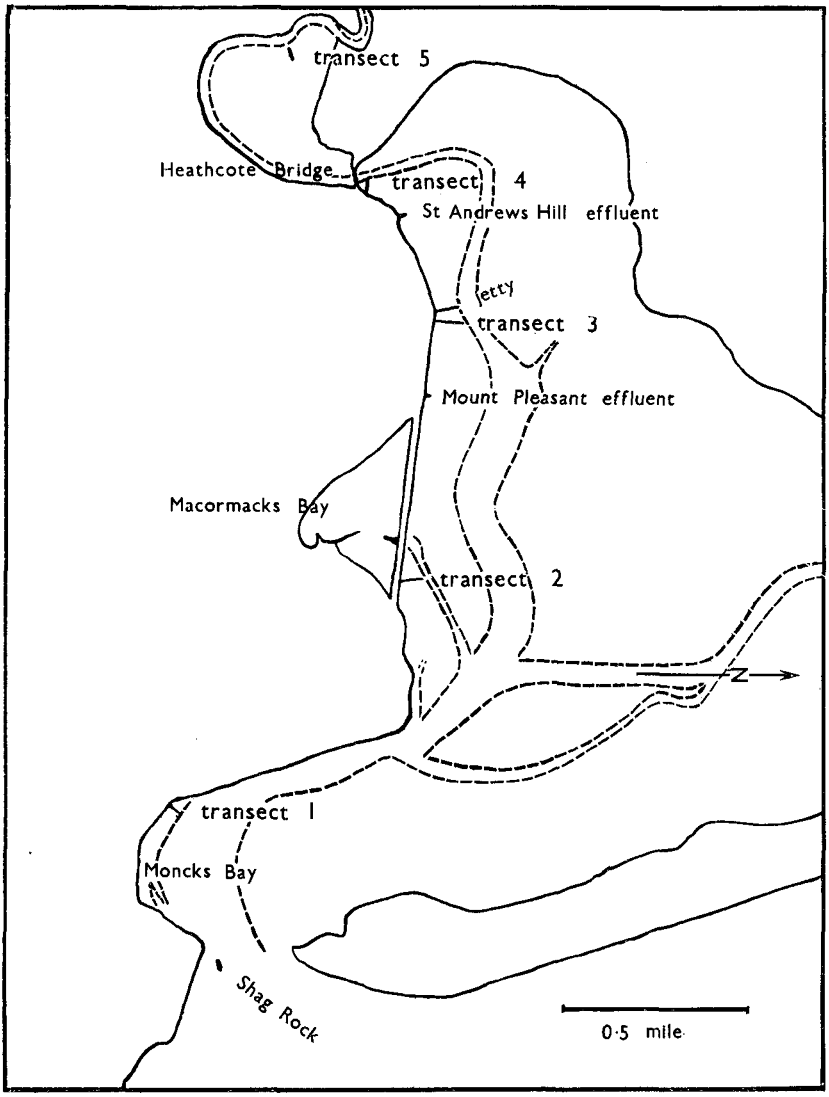

FIG. 2—The southern side of the estuary showing the position of the transects.

The estuary is shallow and mostly intertidal. The banks are sandy near the outlet but gradually change to mud at the river mouths. There is no attached vegetation on the banks except in those areas covered by a dense carpet of *Ulva* in summer. Flats covered by rushes are limited to small areas at the south of the Avon and in the last mile of the Heathcote. The channels (Fig. 2) in the estuary have a very constant pattern (Linzey 1944) but the outlet channel is less stable.

STATION POSITIONS

Sampling of the polychaetes and of their environment was carried out along the south side of the estuary (Fig. 2). The shore line from Shag Rock to the Heathcote Bridge has been reinforced by stone and concrete walls to stop erosion by waves and burrowing crabs. The walls extend below high-water mark of neap tides so that the whole area of the flats is covered by all high tides. Upstream of the Heathcote Bridge the flats are at a higher level and parts of them are dry for two or three days at neap tides.

Five transects from high- to low-water mark were placed at approximately equal intervals along the estuary (Fig. 2) and stations with a known time of exposure to air at low tide were marked on each transect in the following way. The time of high water at a transect was observed and one hour later a peg was driven in at the water's edge. This was station A. A further hour later a second peg was driven in at the new lower position of the water's edge—station B. This process was continued until low tide. Then as the tide rose again the time at which each peg was submerged was noted. From this the time for which each station had been exposed was obtained. The pegs were placed on spring tides and the times later checked on neap tides. The exposure times are set out in Table 1.

TABLE 1—Duration of exposure of the collecting stations (hours and minutes)

Station	*Spring tide*	*Neap tide*
1 B	5 05	5 10
2 B	6 00	5 50
2 C	3 45	3 40
2 E	1 00	nil
3 B	6 35	7 05
3 C	4 45	4 10
3 E	0 45	nil
4 B	6 45	7 30
4 C	5 00	5 00
4 E	1 00	nil
5 A	8 40	not submerged
5 B	7 00	7 45
5 C	5 20	5 10
5 E	1 35	0 30

There is a significant difference between spring and neap tides only at the higher and lower levels on the shore.

Some samples were taken in the unpolluted Avon River, at the localities marked in Fig. 1, for comparison with the polluted Heathcote. At all these places in the Avon polychaetes were found only in the narrow intertidal strip of muddy sand.

AIR TEMPERATURE

Temperatures at the Heathcote Estuary differ significantly from those at the nearest places where records are kept, Christchurch for air temperatures, and Lyttelton for sea temperatures. Thompson (1929) showed that temperatures at the estuary are less extreme than at Christchurch (five miles inland), and records kept during the survey confirm this. During the day in summer the estuary is normally under the influence of a north-easterly sea breeze and very high temperatures occur only when the norwester reaches the coast. No frosts were recorded and no frost was seen anywhere on the flats. Spot readings of air temperature, water temperature, and mud temperature were taken as part of the collecting routine. Maximum-minimum air temperatures for four and one-half months during the winter were obtained from a maximum-minimum thermometer placed in a shaded corner at the east end of the causeway (Fig. 2). It was read at least once a week, and often daily, as collecting trips allowed.

Both Heathcote Estuary and Christchurch air temperatures are plotted in Fig. 3. The Heathcote Estuary maximum temperatures were spot readings, the minimum temperatures were from the maximum-minimum thermometer records, and the data for Christchurch were taken from Garnier (1958).

WATER TEMPERATURE

Figure 4 compares water temperatures from the estuary with sea surface temperatures from Lyttelton (Skerman 1958). The curve for the estuary was obtained by plotting the monthly means of spot readings. The bar graph shows the range between the highest and lowest temperature for each month for the estuary and for Lyttelton. Contact with previously heated or cooled mudbanks causes the wide variation in water temperature. The minimum recorded in the estuary was 70°C in June and the maximum 27°C in February. This was recorded in the shallows as the tide rose over a mudbank which itself had a temperature of 27°C and the temperature dropped as the water became deeper.

SUBSTRATUM TEMPERATURE

Readings were taken 10 cm below the surface by pushing a thermometer into the sand or mud. As the top 10 cm contained most

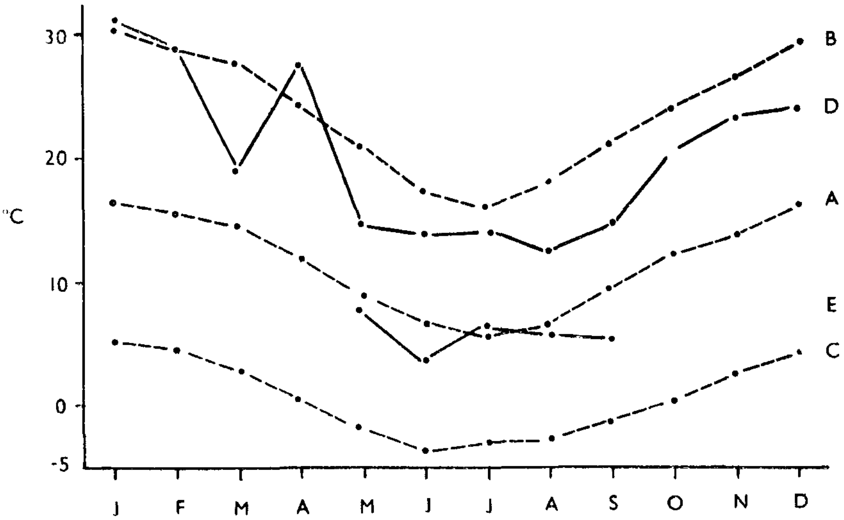

FIG. 3—Air temperatures at the Heathcote Estuary and at Christchurch. A—Christchurch mean monthly temperature; B—Christchurch mean extreme maximum temperature; C—Christchurch mean extreme minimum temperature; D—Estuary observed maximum temperature; E—Estuary extreme minimum temperature.

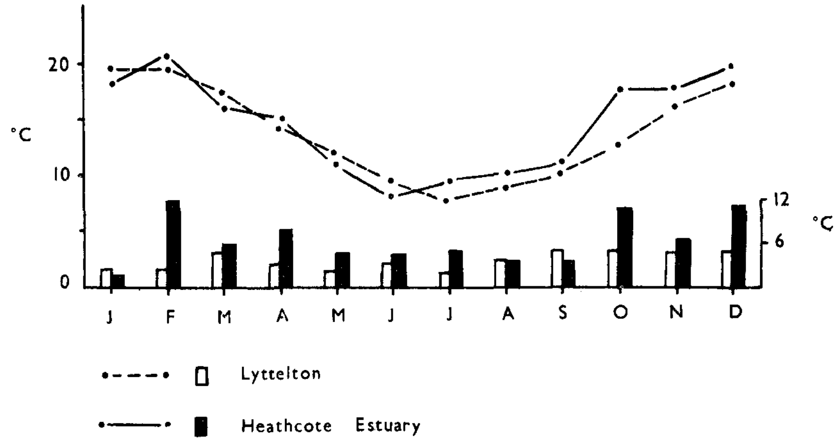

FIG. 4—Sea surface temperatures at the Heathcote Estuary and at Lyttelton. Monthly means above and monthly ranges below.

of the polychaetes a single reading at this depth was considered to be sufficient. When the monthly means of the readings were plotted they gave a curve which was almost exactly the same as the curve for water temperature. This curve (Fig. 4) may be taken as showing substratum temperature also. The minimum temperature recorded was 6°C in July and the maximum 27°C in February.

SALINITY

The hydrology of the Heathcote Estuary is well understood as a result of the studies by Linzey (1944), Bruce (1953), and Hogan and Wilkinson (1959).

Sampling during this survey was designed to establish the minimum salinity at each of the collecting stations. Samples were taken at the water's edge at the various stations as tides and collecting trips allowed. The results are collected in Table 2. Additional samples were taken from the Avon River.

Salinity of samples was determined in the laboratory by titration against silver nitrate, following Barnes (1959). Halides only are measured and the total salt concentration is derived by assuming that the ratio between the major ions is constant and independent of the total salt concentration. This does not hold in estuaries which usually have a higher ratio of carbonate and sulphate to chloride, and of calcium to sodium, than does seawater (Emery *et al.* 1957). For this reason burette readings were taken to the first decimal place only, and the table of corrections given by Barnes was not applied.

TABLE 2—Minimum salinities (expressed in parts per thousand)

Station	*Transect*				
	1 ‰	2 ‰	3 ‰	4 ‰	5 ‰
A		30.3	25.7	25.1	26.9
B	25.0	19.4	17.0	15.7	4.3
C	28.5	18.5	16.9	1.7	3.1
D		8.4	3.7	11.7	0.2
E		32.4	4.3	0.4	0.2

The high salinities at low tide at transect 2 are due to water flowing out of Macormacks Bay. The floor of the culvert through the causeway is at half-tide level so only water of high salinity enters the bay. This water runs out for some hours after the tide has begun to rise in the estuary and maintains high salinities in the channel at the end of transect 2.

Apart from this the salinity rises as the tide rises, so that stations low on the shore have lower minimum salinities and and greater ranges between low and high tide.

The rate of change of salinity is as important as the range (Bassindale 1943), but it seems to be between 12 and 15‰ per hour at all the stations within the estuary so is not likely to affect the species distributions.

Some determinations were made of the salinity of water draining from the sandy sediments. The salinity values were in agreement with the general finding that the interstitial water has a relatively constant salinity intermediate between the maximum and minimum salinities of the overlying water (Smith 1956). A comprehensive programme of determinations of interstitial salinity was not undertaken because there is not enough information on the burrowing habits of the polychaetes to decide which salinity values are relevant. Some species appear to live free in the sand without maintaining an open burrow and are affected only by the interstitial salinity, while others have a distinct burrow or tube through which water could be circulated. These species would be exposed to the full range of surface salinities if they circulated water whenever it was available.

The minimum surface salinity values for each station have been used with the understanding that some species at that station may come in contact only with higher salinity interstitial water.

SEDIMENTS

Sediment samples from most of the stations were analysed for particle size distribution and total organic matter content.

There is no standard method of mechanical analysis of marine sediments. No two workers have used exactly the same technique and their results can be compared only approximately. Most have used a combination of sieving and sedimentation techniques and adopted the Wentworth scale of grain size. Webb (1958) after extensive work on the physical properties of different grades of sand suggested a completely different set of sieves for ecological work. These were not available and the method used by Clark and Haderlie (1960) was followed as nearly as possible for this study.

Samples of the top 10 to 15 cm of the sediment were taken at most of the collecting stations. The samples were oven dried at 105°c and about 60 g weighed out and wet sieved using the following series of wire sieves: 0.42, 0.250, 0.124, and 0.074 mm. The fractions retained by each sieve are described as coarse sand, medium sand, fine sand, and very fine sand in the Wentworth classification. The fraction retained by each sieve was dried and weighed then expressed as a percentage by weight of the whole sample. The perecentage of silt was obtained by subtraction.

The results of the analyses are set out in Table 3. Most of the material retained by the 0.42 mm sieve was shell fragments and detritus, not soil particles.

Table 3—Sediment analyses (figures are percentages by weight)

Station	Particle Size (mm)					Organic Matter
	0.42	0.42–0.25	0.25–0.124	0.124–0.074	0.074	
1 B	2.9	1.5	63.0	1.2	31.4	0.9
2 B	0.4	1.7	46.7	26.5	24.7	2.1
2 C	3.3	16.0	66.7	9.6	4.4	1.6
2 E	0.5	6.7	3.5	12.7	76.6	4.5
3 B	1.4	2.9	26.2	50.3	19.2	
3 C	1.7	4.1	26.3	43.9	24.0	2.1
3 E	9.0	4.0	12.8	40.0	34.2	3.8
4 B	0.7	0.6	3.8	34.9	60.0	2.7
4 C	0.9	0.9	6.7	23.6	67.9	4.0
5 A	0.4	0.4	1.8	11.6	85.8	3.6
5 B	0.4	0.3	1.2	6.4	91.7	4.1
5 D	0.0	1.7	0.4	9.6	88.3	

The total organic matter content of most of the samples was determined by measuring the weight loss after treatment with 6% hydrogen peroxide (Piper 1947). The organic matter content (Table 3) is an indication of the amount of food available to detritus feeding animals.

The distribution of sediments in the Heathcote Estuary follows the pattern usually found in estuaries (Day 1951; Emery *et al.* 1957) with a gradation in particle size along the estuary from fine mud in the upper reaches to sands near the mouth. The vertical changes in particle size reflect the varying strengths of the currents at different stages of the tide. For the same reason the slope of the banks is not uniform; it tends to level out at about mid-tide level in the lower parts of the estuary. Stations 2C and 3C were at this change in slope, but at transect 5 the break in slope was at station A and the flats were covered entirely only by spring tides.

There is an apparent correlation between high silt content and high organic matter content, presumably because silt and organic matter settle out under the same conditions.

The sediments of transects 1, 2, and 3 were sandy, but only down to a depth of 20 to 30 cm. Below this lay clay like that exposed at station 2E. Most of the polychaetes were found in the sand and only a few penetrated into the clay.

POLLUTION

Pollution by domestic and industrial wastes from the city of Christchurch is as important a factor in controlling the distribution of animals in the estuary as are exposure time, salinity, and sediment grade. The effect of pollution as a limiting environmental factor was noted but no work was done on pollution during this survey. Studies of the extent of pollution and its effects in the estuary have been published by Bruce (1953), Hogan and Wilkinson (1959), Williams (1960), and Rosenberg (1963).

Most of the sewage and domestic wastes are treated at the Drainage Board's plant and discharged in the estuary at a point midway between the mouths of the Heathcote and Avon Rivers. This effluent joins the Avon Channel and has no apparent effect on the Heathcote side of the estuary, but pollution from several sources affects the area surveyed. The most important of these is the Heathcote River, which is heavily polluted by wastes from an industrial area. The effects of pollution diminish in the two miles between this area and the Heathcote Bridge.

This recovery is apparently due to dilution of the river water by well oxygenated sea water. Hogan and Wilkinson (1959) found that the water at Long Street, two miles upstream from the Heathcote Bridge, contained barely enough oxygen for fish while the water at the Heathcote Bridge was oxygen deficient only about the time of low water and was completely saturated at high water. At transect 4 (Heathcote Bridge) the polychaetes extended down to low-water mark, at transect 5 about three-quarters of a mile upstream they extended down to mid-tide level, further upstream they were found only at the top of the shore and soon they disappeared entirely. At this point the whole of the area exposed at low tide was black mud covered by a slime (coloured green in summer) of bacteria, blue-green algae, diatoms, and protozoa. Hydrogen sulphide was released when the mud was disturbed. Downstream this slime was restricted to a narrower band near low-water mark and it disappeared at the Heathcote Bridge. The general effect was of two overlapping opposed wedges—a wedge of polychaetes tapering up the shore in the upstream direction and a wedge of pollution tapering down the shore in a downstream direction. This distribution pattern of the polychaetes is ascribed to pollution rather than to salinity because the two species of polychaetes concerned were found in lower salinities in the unpolluted Avon River. Other effluents have only local effects on the polychaetes although the St Andrews Hill effluent may have given an artificial sharpness to the upstream limits of those species which extended past transect 3 but did not reach transect 4.

Once they are sufficiently diluted and oxygenated to be non-toxic the pollutants become available as nutrients supporting a large seasonal growth of *Ulva,* which is available to herbivores and later to detritus feeders. The estuarine area of Saltwater Creek, near the mouth of the Ashley River, and Havelock Harbour at the head of Pelorus Sound, were visited during this survey. They are not polluted and appeared to support smaller populations of animals, especially birds, than does the polluted Heathcote Estuary.

The Christchurch Drainage Board's new sewage treatment plant began operation shortly after this survey was completed. The effluent is now given primary and secondary treatment and held in oxidation ponds before being discharged into the estuary. The initial effects of the decrease in pollution due to this are described in the report by Rosenberg (1963).

COLLECTING METHODS

Collections were made from November 1960 to October 1961, each station being sampled five times at approximately two-monthly intervals. Not all the stations originally established were used. Station 1B was found to be representative of the whole transect, stations 2D and 3D were omitted as they were very similar to the stations above and below, and there were no polychaetes at station 5E because of pollution.

Samples of 0.25 m^2 surface area dug out to a depth of 30 to 40 cm were taken at transects 1, 2, and 3. This sampling unit was used by Spooner and Moore (1940), Stopford (1951), and Raymont (1955) in studies of estuarine macrofaunas. For the present study a sheet steel quadrat, 8 cm deep, with sides of 50 cm, was used. The deep sides stopped the sand collapsing into the hole. Sieving the animals from the sand proved unsatisfactory because the sieve held large quantities of detritus. Instead, each spadeful of sand was carefully broken up by hand and the worms picked out with forceps.

A sampler of steel tubing with a cross-sectional area of 0.01 m^2 was used at transects 4 and 5. At each station two cores about 30 cm long were extracted and the numbers of specimens averaged. With few species, each present in large numbers, this gave an adequate sample. These samples also were hand sorted as the stiff mud was difficult to sieve.

All samples were taken near the peg marking the station, at random, except that care was taken not to sample the same spot on two successive occasions.

The specimens were brought back to the laboratory alive, sorted into species (a stereoscopic microscope was used), anaesthetised in magnesium chloride solution, counted, and preserved in 70% alcohol. Alcohol fixation was not completely reliable and fixation in 10% formalin before storage in alcohol was better. A magnesium chloride solution of 60 g/l of tapwater gave the best results with *Nicon aestuariensis* and was used as standard. This is less concentrated than sea water and other species tended to swell in it. Often this caused the proboscis to evert and allowed easy observation. Magnesium chloride is a nerve poison and cilia on gills and feeding structures could be seen after muscular movement stopped.

Not all species were counted as some of the smaller ones were present in large numbers in the 0.25 m^2 samples. Only the heads of fragmented specimens were counted. All the counts have been converted to population density per m^2. None of the species showed a clear seasonal change in abundance so the average of all the counts from each station has been given in Table 4. Occurrences of the species which were not counted are indicated by a cross in the table.

TABLE 4—Species distributions (explanations in text) × = present

Species	Station														
	1B	2B	2C	2E	3B	3C	3E	4B	4C	4D	4E	5A	5B	5C	5D
Perinereis nuntia var. *vallata*	1	1	2	1	1	1		1	1						
Perinereis nuntia var. *brevicirris*	1		12	1											
Platynereis australis	1		12	2											
Nicon aestuariensis	3	4		1	9	9	6		600	750	530	40	1,157	1,350	396
Aglaophamus macroura	1	25			4	15	2								
Glycera americana	7	6	7	8	1	1	4								
Lumbrinereis sphaerocephala	1														
Orbinia papillosa		64	3		34	12									
Haploscoloplos cylindrifer	227	1	233	170	82	171	106								
Scolecolepides benhami	4			2			8	8,000	2,783	1,517	450	2,150	3,490	2,950	80
Scolecolepides sp.					7	6	8								
Aonides trifidus	×	×	×	×	×	×	×								
Boccardia polybranchia		×		×	×			×	×		×		×		
Prionospio pinnata	×	×	×	×		×	×								
Armandia maculata	1	1	29	17											
Capitella capitata							×	×							
Heteromastus filiformis	×	×	×	×			×								
Abarenicola affinis affinis						5	4								
Pectinaria australis	10	1	1	3			6								

ECOLOGY OF THE POLYCHAETES

The distribution of each species is given in Table 4. The species are tabulated in the same order as in a previous paper (Estcourt, in press) where information on systematics and identification is given.

Day (1951), generalising from reports of European work and observations in South Africa, stated that the maximum changes in estuarine faunas are associated with salinities of 25, 15, 5, and 0.1‰. The distributions of the polychaete species of the Heathcote Estuary fit this pattern.

Minimum salinity 25‰

Lumbrinereis sphaerocephala (Schmarda)

The only specimen taken came from station 1 B. Thomspon (1929) recorded this species as occurring freely over the estuary, especially in stiff mud. There is no apparent reason for its withdrawal from the estuary as the other burrowing species discussed by Thompson have much the same distribution now as they had then.

Minimum salinity about 15‰

Perinereis vallata var. **brevicirris** (Grube)

This species occurred only once at each station. The maximum time of exposure at low tide was 5 h 10 min. The sediments were fine sand at two of the stations and mud at the third. The minimum salinity was 18.5‰.

Platynereis australis (Schmarda)

Specimens were found in both fine sand and mud, uncovered for up to 6 h at low tide. The minimum salinity was 18.5‰. The worms were found in tubes of sand grains close to the surface of the sediment.

Two partially metamorphosed specimens, one male and one female, were collected at station 1 B on 10 August 1961, and swarming heteronereids were collected by students at Kaikoura on the evening of 19 August 1962. The type of larva produced is not known. The reproduction of *Platynereis dumerilii* in the Northern Hemisphere is well understood (Fauvel 1959; Clark 1961) but the reproduction of *P. australis* has not been studied.

Orbinia papillosa (Ehlers)

O. papillosa was found only in fine and very fine sands, with up to 7 h exposure. The minimum salinity recorded at a place where the species occurred was 16.9‰.

It appears to be a detritus feeder. The lobed proboscis is a thin-walled epithelial structure covered with short cilia which beat toward the mouth opening. All specimens had the alimentary canal filled with sand grains. Hartman (1957) quotes a statement that the proboscis is extruded, loaded with nutrient particles, and retracted, carrying food and other particles into the digestive tract. *Orbinia* and *Haploscoloplos* species have pointed anterior ends and burrow by peristaltic movements of the body without using the proboscis.

Specimens with the coelom full of genital products were present in small numbers in all the collections. In the females the region just ventral to the abdominal parapodia becomes distended by two or three eggs which show as a broad white stripe along the side of the animal. The eggs in the rest of the coelom are not visible through the body wall. Males become uniformly pale apart from the gills and parapodial lobes. The anterior region is not affected in either sex. The only species in the genus whose reproduction is known is *O. foetida* (Anderson 1961, as *Aricia foetida*). There the eggs are laid in cylindrical gelatinous cocoons attached to the sand surface and there is no pelagic phase.

Armandia maculata (Webster)

This species was found at stations with up to 6 h exposure, in fine sand and mud. The minimum salinity recorded was 18.5‰. *A. maculata* was found only in the top 2 or 3 cm of sand, where it would seem to be susceptible to drying at low tide. This may be the reason for its infrequent occurrence at the higher levels on the shore. It burrows by "swimming" through the sand with an *Amphioxus*-like movement with only one or one and a half waves of contraction passing along the body at a given moment. It burrows surprisingly quickly for a small animal.

The soft slipper-shaped proboscis of *A. maculata* projects forward past the prostomium. Ventrally it is covered with cilia which beat toward the mouth. The end of a rope of sand grains was seen in the oesaphagus of one specimen as it was anaesthetised. It was rotating slowly in a clockwise direction when looked at from the anterior end in through the open mouth. Larval stages of the related *Ophelia bicornis* have a ciliated oesophagus, but it is not mentioned in the adult (Wilson 1948). *O. bicornis* feeds on detritus and live material such as diatoms among the surface sand grains. *A. maculata* probably has similar feeding habits.

Specimens with eggs in the coelom were taken in July, August, October, and February. Their appearance suggested a breeding season from October to February. *O. bicornis* is the only species in the Opheliidae whose reproduction is known (Wilson 1948). It has a pelagic larva which has been extensively used in work on settling behaviour. *A. maculata* has small eggs about the same size as those of *O. bicornis* and probably also has planktonic larvae.

Minimum salinity about 5‰

Perinereis nuntia var. **vallata** (Grube)

This species occurred only sporadically in the mudbanks, being found more than once only at station 2 C. The maximum time of exposure at low tide was 7 h 40 min, and minimum salinity 1.7‰. It appears to favour a firm substratum as it was found in larger numbers in a gravelly area near the Heathcote Bridge, burrowing in mud between the pebbles.

Aglaophamus macroura Schmarda

A. macroura occurred at stations with up to 7 h 30 min exposure and with a minimum salinity of 3.7‰. This species appears to live free in the sand rather than in a burrow and it is probably influenced more by the salinity of the interstitial water than by the surface salinity.

The stations where *A. macroura* was found had similar sediments (Table 3). In each case most of the sand grains were between 0.25 and 0.074 mm diameter, while the silt content was between 19.2% and 34.2%. These sands were thixotropic (decreased resistance to shear with increased shear stress) flowing easily when disturbed. This property makes the progression of a burrowing animal much easier (Chapman 1949). The related species *Nephtys hombergi* in the mouths of estuaries on the south-western coasts of Britain is limited to similar sediments with up to 34% silt but very little material larger than 0.25 mm (Clark and Haderlie 1960).

A. macroura is apparently limited to sediments of this type for it would otherwise have occurred at stations 2 C and 2 E where the exposure and salinity conditions were similar but the sediments contained a smaller percentage of very fine sand.

There is no information on feeding in *A. macroura* but some species of the very similar genus *Nephtys* are detritus feeders (Sanders 1960) while others are carnivorous (Clark 1962).

Maturing specimens were collected in February and April, and again in July, August, and October. The opaque white tissue under the skin had parted on the dorsal side exposing the blood vessels and the green-coloured gut, and the genital products could be seen in the coelom. This break in the normal uniform white colour made maturing worms conspicuous even in the field. Those species of *Nephtys* whose reproduction is known produce pelagic larvae with trochophore, metatrochophore, and nectochaeta stages (Thorson 1946).

Glycera americana Leidy

The distribution pattern of this species does not reflect differences in exposure and sediment grade, and its penetration into the estuary appears to be limited by low salinity (minimum 3.7‰). *G. americana* was usually found deeper in the sand than the other polychaetes.

Hartman (1950) quotes statements that the species of *Glycera* are carnivorous and others that they are detritus feeders. The small numbers and sporadic occurrence of *G. americana* in the estuary are consistent with a carnivorous habit.

An attempt was made to define the breeding season, but no undoubtedly mature specimen was seen. Epitoky (metamorphosis and swarming) is known in some of the Glyceridae (Hartman 1950) but no sign of it was seen.

Haploscoloplos cylindrifer (Ehlers)

H. cylindrifer was found at stations with up to 7 h 30 min exposure, but in reduced numbers. Different sediment grades did not appear to affect the distribution. The minimum recorded salinity where the species occurred was 1.7‰.

There were large differences in the number of specimens in successive samples which suggested that there might be some aggregation. A chi-square index of dispersal test applied to three sets of three replicate samples confirmed that two of the sets of samples came from populations which were distributed in a significantly non-random manner.

H. cylindrifer appears to have the same feeding habits as *Orbinia papillosa* (above) although the proboscis is not ciliated.

All the collections contained some specimens with conspicuous gonopores and the species may breed all the year round. Pelagic larvae almost certainly belonging to *H. cylindrifer* were present in plankton samples taken at transect 4 on 28 September 1961, 12 December 1961, and 14 December 1961. They were referred to *Haploscoloplos* rather than to *Orbinia* because they occurred in large numbers and because they were very similar to the larvae of *H. fragilis* illustrated by Anderson (1961). The larvae from the Heathcote Estuary had only the prototroch, telotroch, and a narrow longitudinal ventral band of cilia beating toward the mouth; the larvae of *H. fragilis* have an additional ring of cilia on each segment. The Heathcote Estuary larvae were feeding while in the plankton, but *H. fragilis* does not feed until it has settled. Further study of *H. cylindrifer* would be worthwhile as the larvae appear to be pelagic for a longer time than is described for those species whose development is known (Anderson 1961).

Scolecolepides sp.

This form was found in appreciable numbers only in the thixotropic sands at transect 3. A single specimen was obtained from transect 1 and another from transect 4. Specimens were found at stations with exposure times up to 7 h 30 min and salinities down to 4.3‰. Some of the specimens were in tubes of cemented sand grains, others in mucus-lined burrows. The tubes are similar to those of *Boccardia polybranchia* (see below), and it is possible that *Scoleeolepides* sp. had a wider distribution as only small numbers of the tubes were collected and opened.

This form agrees with the one which Thompson (1929) discussed under the name *Spio* sp.

Aonides trifidus Estcourt

A. trifidus was the most abundant polychaete in the seaward part of the Heathcote Estuary. It occurred everywhere from transect 1 to half way between transects 3 and 4, with highest population densities about mid-tide level. No counts of this species were made but comparisons with species of known abundance suggested a maximum population density of 5,000 to 6,000 per m^2. It was found at up to 7 h 30 min exposure and down to 4.3‰ salinity. Changes in sediment grade did not affect the distribution.

Mature specimens were present in collections made in October, November, December, and February. There is no information on the breeding of any species in the genus.

Prionospio pinnata Ehlers

A few counts were made and the maximum population density found was 128 per m^2 at station 1 B. The species occurred at up to 6 h exposure. Its minimum salinity was 4.3‰.

The palps of this species have transverse rings of cilia spaced along the dorsal side in addition to the usual longitudinal ventral ciliated groove. No information on feeding in *P. pinnata* was found but it is presumably unusual in view of the unusual ciliation of the palps.

Specimens with eggs in the coelom were present in all the collections. Some species of *Prionospio* have planktonic larvae (Thorson 1946), but *P. pinnata* has not been studied.

Heteromastus filiformis (Claparede)

Some approximate counts were made and the maximum population density found was 60 per m^2 at station 3 E. The species tolerated up to 6 h exposure and down to 4.3‰ salinity. Apparently some property of the substratum, perhaps drying at low tide, prevented the species occurring at stations 3 B and 3 C where the salinity and duration of exposure lay within the range which it experienced at other stations.

H. fiiliformis has been recorded from estuarine areas in South Africa (Dag, Millard, and Harrison 1952), United States (Stickney 1959), and Britain (Percival 1929; Spooner and Moore 1940) under salinity conditions similar to those in the Heathcote Estuary.

Specimens with eggs in the coelom were taken in October, November, January, and February. Nothing is known of the reproduction of this species.

Abarenicola affinis affinis Wells

This species occurred only at stations 3 C and 3 E where the sediment is thixotropic. Thixotropic sand has been shown to facilitate the burrowing of *Arenicola marina* (Chapman 1949) and the restricted distribution of *Abarenicola affinis affinis* appears to be due to its limitation to sediment with this property.

The surface appearance of the burrows is exactly the same as has been described for *Arenicola marina* and the feeding habits and general behaviour are probably very similar also. The biology of this species in Wellington Harbour has been described by Wear (1962, as *Abarenicola assimilis*). He found it to be a winter breeder and Heathcote Estuary specimens dissected on 30 May 1961 were nearly mature with morulae of sperms with motile tails in the coelomic fluid.

Pectinaria australis Ehlers

P. australis occurred at stations with up to 6 h exposure but in small numbers, except at station 1 B where poor drainage reduced the effective exposure. The minimum salinity where the species occurred was 4.3‰. Differences in sediment grade were not reflected in the distribution.

One specimen from station 3 E had an epizoic colony of a vorticellid protozoan attached to its dorsal shield above the falcae.

The biology of *Pectinaria australis* in Wellington Harbour has been described by Wear (1966). There the main settlement of larvae was in late summer, but there was evidence of an extended breeding period. Adult specimens with eggs in the coelom were collected from the Heathcote Estuary in July, August, October, November, December, and February; but only the February specimen appeared to be ripe. Feeding in *P. australis* has been described by Wear (1966) and a detailed analysis of feeding rates of the North American *P. gouldii* has been made by Gordon (1966).

Minimum salinity 0.4‰

Boccardia polybranchia (Haswell)

The tubes of this species were most common about station 3 B, but the population density was not determined. The worms were found in a tube of cemented sand grains which, near the surface, was strong enough to be easily separable from the sand around it, but below the top three or four centimetres was membranous and difficult to follow. The species occurred at up to 7 h exposure. The minimum salinity of 0.4‰ was recorded at station 4 E. The distribution pattern of *B. polybranchia* does not show any clear relationship to sediment grade although the species did not occur in the comparatively coarse sand at station 2 C, and the specimens from near station 5 B were in a place which was more sandy than the mudbanks nearby.

B. polybranchia occurs in the St. Lucia Estuary in South Africa (Day, Millard, and Brockhuysen 1954), but it apparently does not occur in Northern Hemisphere estuaries where *Polydora ciliata* is the common form. *P. ciliata* has not been recorded from New Zealand.

The palps of *B. polybranchia* are longer in proportion to the size of the body than are those of the other spionids in the Heathcote Estuary which suggests that it feeds on suspended material rather than detritus on the surface of the mud. The mechanism of plankton feeding in *P. ciliata* has been studied (Dorsett 1961) and *B. polybranchia* may feed in a similar way.

Capitella capitata (Fabricius)

C. capitata was common at station 3 E, an incomplete sample giving a population density of 150 per m^2. A single specimen was found at station 4 E. These stations have a maximum exposure of one hour at spring tides and are continuously submerged for several days at neap tides. The lowest salinity recorded was 0.4‰.

The sediment at station 3 E was soft, black, very fine sand, while station 4 E was more muddy. Both were affected by pollution carried by river water, and the sediment sometimes smelt of hydrogen sulphide when disturbed.

C. capitata is found in similar habitats in California, described by Hartman (1947) as "black sandy beaches in quiet water; it sometimes occupies beds of considerable extent especially in estuarine or also brackish water . . . It is euryhaline and can withstand flooding with fresh water." It has also been recorded from South African (Millard and Scott 1954) and British (Percival 1929) estuaries.

C. capitata has been previously recorded from areas affected by organic pollution by Reish (1957). In surveys of the bottom faunas of polluted harbours it was found to be one of the most tolerant species in the macrofauna. However, in the Heathcote Estuary its distribution appears to be controlled by salinity and inability to tolerate long periods of exposure. It does not seem to be capable of exploiting habitats from which other species are excluded by pollution.

According to Reish (1957) it feeds by burrowing into and ingesting the substratum in much the same manner as an earthworm.

Knowledge of the reproduction of this species has been summarised by Thorson (1946). After copulation the female spawns the eggs inside its tube of mucus-cemented sand grains, and remains in the tube until the larvae hatch. The larvae swim for a few days before settling. In the Oresund *C. capitata* seems to spawn all the year round and grows rapidly after settling. It is capable of reproducing all the year round in Southern California, and there reaches sexual maturity in about a month (Reish 1957). In the Heathcote Estuary tubes containing eggs were collected in January, February, and July, suggesting that it breeds all through the year here also. No larvae were seen in plankton samples.

Extending into water which is often fresh

Nicon aestuariensis Knox

The penetration of this species into the Heathcote River was limited by pollution of the river. It extended into lower salinities in the unpolluted Avon River and reached its limit somewhere between the bridge on Pages Road and the Bower Bridge (Fig. 1). The maximum salinity recorded at Pages Road was 14.4‰ at high water of a spring tide, while at high water of neap tides the water was fresh. Worms here are subjected to water containing only a trace of salt for at least half the tides in each fortnight.

The few specimens at station 5 A tolerated exposure for 24 hours at neap tides.

N. aestuariensis was found in largest numbers in the deep stiff mud at transect 5. Small specimens were near the surface but large specimens (15 cm long, 3 mm diameter) were found in burrows as deep as 40 cm. The mud between the burrows was grey in colour and apparently impervious to moisture, while the burrow walls were slimy black mud. The burrows were more or less vertical with their position marked on the surface by a circular depression 2 or 3 mm across. Whether individual worms had separate burrows and whether the burrows were U-shaped or not could not be determined in the field.

Worms anaesthetised in a solution of magnesium chloride isotonic with sea water (80 g/l) distorted, but in a solution of 60 g/l there was no distortion. This suggests that the body fluids have a lower osmotic pressure than sea water, which would reduce the energy expended on osmoregulation in low salinities but might restrict the species to estuarine water.

The abundance of this species in low salinity areas contrasts sharply with its scarcity in the seaward part of the Heathcote Estuary. Its ability to live in low salinities apparently allows it to exploit a habitat which is not available to most polychaete species, but it cannot compete with the other species in the areas which they colonise.

One specimen from station 2 E had fragments of *Ulva* in its gut. All other specimens had the alimentary canal full of sediment and were presumably feeding on detritus. Attempts to maintain worms in aquaria in a thin sheet of mud sandwiched between glass plates were unsuccessful. This failure prevented direct observation of feeding.

The breeding biology of *N. aestuariensis* has been described elsewhere (Estcourt 1966).

Scolecolepides benhami Ehlers

Sc. benhami had the greatest population density of the polychaetes in the Heathcote Estuary and it extended furthest into fresh water. It was found in the banks of the Avon River up to half way along Kerrs Reach, two miles upstream of the Bower Bridge which marks the limit of salt water penetration.

It was found burrowing in the flat behind transect 5, both under rushes and in bare patches. This flat is above high water neap tide level, and in places not shaded by rushes the clay substratum dries out and cracks open at neap tides. The worms were found in material which was warm to the touch and barely moist. In summer a thin surface crust of salt several times formed on these flats and the worms might occasionally be exposed to salinities greater than sea water. They also occurred at stations at low water mark.

The distribution of *Sc. benhami* is like that of *N. aestuariensis,* but it extends further into fresh water and further up the shore, suggesting an even greater ability to exploit a habitat and food supply which is not available to other animals.

Sc. benhami lives in a vertical burrow with a triangular surface opening about 1.5 mm across. The gut was usually full of sand grains and the worm appear to feed on detritus off the mud surface as does *Sc. viridis* (George 1966). The gills are irrigated by a current set up by cilia along the edges of the gills and in a band across the dorsum between the bases of opposite gills. When the gills are in their normal position, arched across the dorsal surface of the body, these cilia draw water in over the head and through the space between the gills and the dorsum.

Some apparently mature specimens were present in all the preserved collections but field observations gave the impression that *Sc. benhami* is a summer breeder. Ripe females are pale green because of pigment in the eggs. A few specimens two or three times larger than average were taken. Many of the average size specimens appeared to be mature, and the part these large specimens play in the life cycle is not known. Incidental observations of the planktonic larvae probably belonging to this species suggest that its reproduction and early development resemble that of *Sc. viridis* (George 1966).

DISCUSSION

The distribution pattern of each species can be explained in terms of its limitation to a particular salinity range, a particular grade of sediment, and a particular amount of exposure (Day 1951). These three factors may not be of equal importance and *Abarenicola affinis affinis* provides an example where the properties of the sediment are the prime factor controlling the distribution. Pollution is also a limiting factor in parts of the Heathcote Estuary.

The largest decrease in the number of species present occurred between transect 3 (15 species) and transect 4 (6 species). The minimum salinity of 5‰ fell in this area and there was the change from sandy to muddy sediments. Pollution from the St Andrews Hill effluent affected the area but appeared to have little influence on the polychaete distributions. The correlated change in salinity and sediment appeared to prevent most species from extending further into the estuary. This agrees with the suggestion by Day (1951) that the euryhaline marine component of estuarine faunas disappears at a salinity of about 5‰.

Only *Nicon aestuariensis* and *Scolecolepides benhami* seem to be truly estuarine species, reaching their greatest population densities in low salinity areas.

Apart from the nereid species, which may eat macroscopic algae, the majority of the species feed on fine detrital particles, either off the surface of the mud or buried in it. An abundance of detritus is characteristic of estuarine environments, and in the Heathcote Estuary a large proportion of it comes from the heavy growth of *Ulva* and other green algae. The volume of algal growth is reported to have decreased since the sewage treatment plant came into full operation (Rosenberg 1963) and there may eventually be some decrease in the populations of detritus feeding animals in the estuary.

Although *Scolecolepides benhami* which penetrates furthest up the rivers was not studied in detail, none of the species appear to have structural reproductive adaptations for estuarine life. However, the developmental stages, which are usually less tolerant than the adults, must be able to adapt to varying salinities.

This study has given information on the habitat requirements of the polychaete species in the Heathcote Estuary but much work remains to be done on feeding, reproduction, and osmoregulation before their ecology can be completely understood.

The Heathcote Estuary supports an abundant and varied polychaete fauna and it is the author's impression that the flora and fauna as a whole are richer than in other estuarine areas he has visited. Estuaries have been little studied in New Zealand, but the surveys planned by the Christchurch Drainage Board to follow changing conditions in this most interesting estuary will make it the best known in the country.

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