DISTRIBUTION OF MACROBENTHIC FAUNA OF SOFT SUBSTRATA IN SWARTKOPS ESTUARY,

WITH OBSERVATIONS ON THE EFFECTS OF FLOODS

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ABSTRACT

The quantitative distribution of the macrofauna inhabiting soft substrata in the Swartkops estuary has been studied in relation to the prevailing abiotic and biotic factors. The most important factors limiting macrobenthic distribution appear to be substrate and competition between communities, while salinity plays only a small rôle. Four major communities have been recognized, each one dominating one reach of the estuary and a minor community dominating the silty heads of creeks. These communities are respectively a *Callianassa* community, an *Upogebia* community, a bivalve community and another *Callianassa* community as one proceeds from the mouth to the upper reaches. The creek community is dominated by four crustaceans and a goby. Biomass values have been recorded and related to the amounts of available food. The effects of floods on the fauna have also been monitored.

INTRODUCTION

Between 1950 and 1954 a qualitative study of the intertidal plants and animals of the Swartkops estuary was made by Macnae (1957). Studies of other South African estuaries were made by Day *et al.* during the 1950's (see Day 1951). The present quantitative study of the macrobenthos inhabiting soft substrata in the estuary was carried out in 1971 and 1972 and formed part of an M.Sc. thesis for the University of Port Elizabeth (McLachlan 1972). The occurrence of a flood during the sampling period provided an opportunity for an evaluation of the effects of floods on the quantitative distribution of the macrobenthic communities of the estuary. As floods are a common occurrence in South African east coast estuaries, occurring every few years (Macnae 1957; Hill 1971), it is important to assess their effects on benthic animals. The flood that occurred during the study period was a particularly severe one, and the observations here may be taken as an indication of the most severe effects of such periodical floods.

A detailed description of the estuary is given by Macnae (1957). The general topography has changed very little since he described the estuary, although the extent of residential areas, communications and the development of salt extraction pans have increased during the intervening period as illustrated in Figure 1. The upper limit of the estuary is a causeway to the north-east of the Perseverance siding and some 16 km from the mouth. The southern boundary of the estuarine basin is formed by a line of low hills and the northern boundary by a low escarpment.

METHODS

In order to evaluate the estuarine environment of the macrobenthic fauna a number of physical and chemical factors were investigated. These were the salinity, temperature, turbidity, pH and

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oxygen content of the estuarine waters and the particle size, shear strength and nitrogen content of the substrate.

The observations of the estuarine waters were made once per month during low and high spring tides. Water sampling was carried out between December 1971 and November 1972 from a boat at ten approximately evenly spaced stations along the estuary (Figure 2, 1–10). Samples of water at the bottom were taken by means of a van Dorn type sampler constructed at the University of Port Elizabeth while surface samples were taken directly from the boat. The pH and oxygen values were obtained *in situ* using a portable pH meter and an oxygen temperature probe. Turbidity was measured *in situ* (except during December 1971 and January and April 1972) using a 20 cm diameter secchi disc. Water temperatures were measured *in situ* using a portable temperature probe accurate to 0,5°C. This was always calibrated with a mercury-in-glass thermometer accurate to 0,1°C. Salinities were determined in the laboratory the same day as the samples were collected, using a freezing point osmometer accurate to 1 mOsm (0,03‰). Values in mOsm were converted to parts per thousand after calibration with chloride titrations. (During February 1972 the water samples were kept frozen for two weeks and then their salinities determined by means of chloride titrations). All water samples were collected and stored in plastic bottles.

Substrate particle size was analyzed by wet sieving following the method outlined by Morgans (1956). At 35 stations along the estuary (Figure 2, 1–37) 1 kg samples of the top 10 cm of substrate were taken at the LWS tide level during January 1972. About 30 g of these samples were wet-sieved with sieves of Wentworth Scale grades between 2 mm and 62 microns (φ −1 to +4). The subsieves were not analyzed further. For determination of the amounts of available food on the surface of the substrate 200 g samples of the top 0,5 cm of the substrate were taken at all of the above-mentioned stations during January 1972. They were analyzed for nitrogen content by means of the microkjeldahl method. The samples were kept frozen in plastic bottles until analyzed. Approximately 30 g of each frozen sample was then thoroughly homogenized and three subsamples, each of 0,5–1,5 g were accurately weighed and analyzed for nitrogen. Differences between triplicates of less than 3% were considered acceptable. Nitrogen values near the lower limit of accuracy for this method were corrected from a curve plotted from analysis of a series of standard solutions of ammonium sulphate. The remainder of each sample, not analyzed for nitrogen, was oven-dried at 105°C for 12 hours and all nitrogen values then corrected to mg per g of dry substrate.

During August 1972 the shear strength of the substrate was measured at 21 of the above-mentioned stations by means of a "Snap On Torqometer" as modified by Hill (personal communication), following the method of Dill & Moore (1965). A vane attached to the torqometer tested the shear strength 2 cm and 10 cm below the substrate surface. The vane was turned very slowly in order to minimize thixotropic effects (Chapman 1949). At each station 10 shear readings were taken at each of these two depths and the mean values calculated. These shear readings give a measure of the compactness of soft substrata.

During December, January and February 1970/71 24 stations along the estuary were sampled for macrobenthos at the LWS tide level (Figure 2, A-W). At each station four areas, each of 0,25 m², were dug to a depth of 30–40 cm. The substrate so obtained was sieved through a 0,25 m² sieve (50 × 50 cm) which had 4 mm mesh. All species collected were identified and

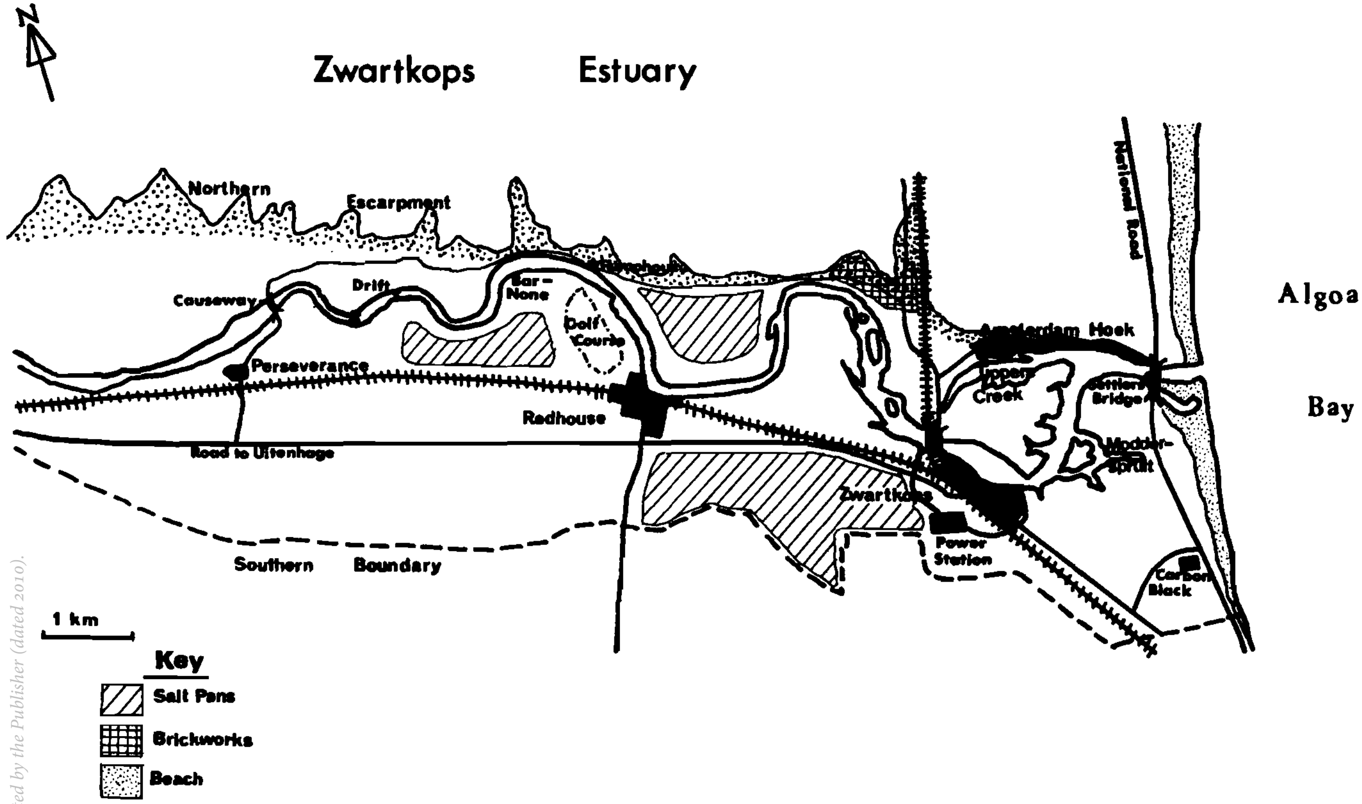

FIGURE 1
Map of the Swartkops estuary showing residential and industrial areas, boundaries and communications.

counted and the total biomass at each station measured. Biomass was taken as wet weights after shells of bivalves and hermit crabs had been removed.

After the floods of April 1971 it was decided to resample the macrobenthos in order to see what changes had occurred. This was done at 35 stations during January 1972, using the same techniques as above, except that the sieve used had a 5 mm mesh, a bait pump was used as well as sieving, and biomass values for all major benthic groups (and not just total biomass values) were measured separately. A similar survey was carried out again in September 1972 in the middle reaches of the estuary where the fauna had changed as a result of the floods. This latter survey was planned to study the recovery of the benthic fauna in these areas after the floods.

RESULTS AND DISCUSSION

The Estuary

The results of the physical and chemical investigations are summarized in Table 1. In this table the estuary has been divided into four reaches, and the mean values for each reach have been tabulated.

TABLE 1

SUMMARY OF IMPORTANT ABIOTIC VARIABLES IN THE DIFFERENT REACHES OF THE SWARTKOPS ESTUARY

Turbidity is given as the mean of all Secchi disc readings.

Factor	*Mouth area*	*Lower reaches*	*Middle reaches*	*Upper reaches*
Normal salinity range (°/$_{oo}$)	33-35	27-37	15-37	1-34
Mean annual salinity (°/$_{oo}$)	34,5	34,3	32,0	26,5
Annual temperature range	15-25 °C	14-28 °C	13-28 °C	13-28 °C
Mean annual turbidity	1,5 m	1,2 m	1,5 m	1,3 m
Mean substrate Md ϕ	2,3	2,6	2,8	1,9
Mean % Subsieves	0,5	17,0	24,0	7,0
Mean shear strength	50 g/cm^2	48 g/cm^2	63 g/cm^2	27 g/cm^2
Mean mgN/g dry sand	0,12	0,40	0,30	0,16

Macnae (1957) divided the estuary into lower, middle and upper reaches, but, as is evident from the above table, the separation of the mouth area is also desirable. This division has been based largely on substrate differences. The extent of these reaches is briefly as follows (Figure 1):

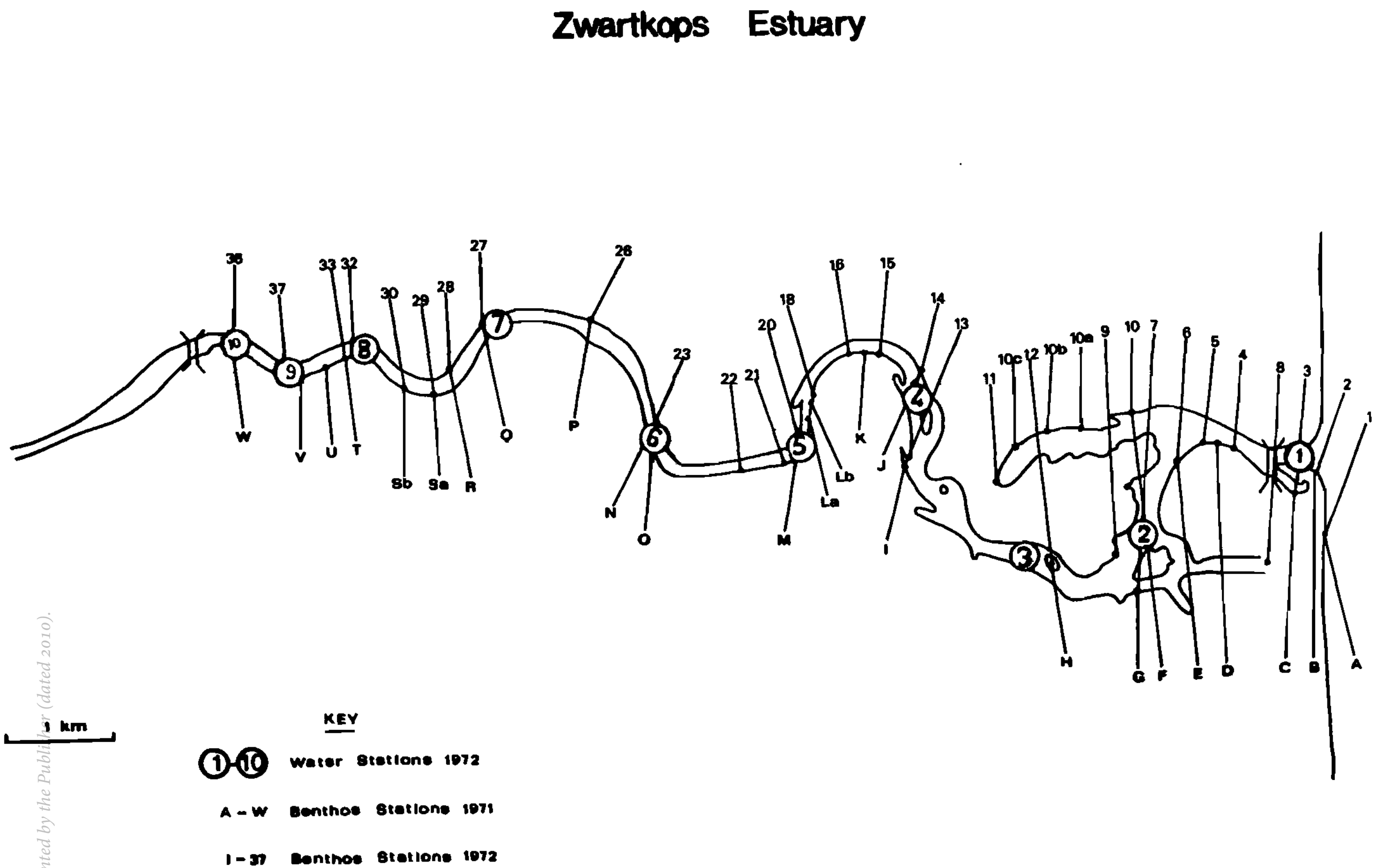

FIGURE 2

Map of the Swartkops estuary showing the water and benthos sampling stations used during this study.

the mouth area extends up the estuary to the start of Tipper's Creek; the lower reaches extend from here to a point halfway between the brickworks and Redhouse; the middle reaches to between the farm Bar-None and the old drift (a ford of stones across the estuary); and the upper reaches from here to the causeway.

It is clear from Table 1 that the salinities recorded in the estuary are too near 35°/₀₀ and generally too uniform for the sub-division of the estuary by means of the salinity boundaries proposed by Day (1951, 1967). The salinity throughout the estuary drops markedly during floods following heavy rains. Five days after the start of the floods of April 1971 surface water samples were taken at the causeway, Redhouse and Swartkops Village. These were found to have salinity values of 0,2°/₀₀, 0,3°/₀₀ and 2,2°/₀₀ respectively. No bottom samples were taken during the floods.

Figure 3 shows graphically the annual range and mean of surface salinities recorded at each of the ten sampling stations. These graphs are based on regular figures and do not include flood conditions. It may be seen that the salinity range increases with distance from the mouth of the estuary. The range at each station depends more on the difference between low and high spring tide samples (taken each month) than on seasonal variation.

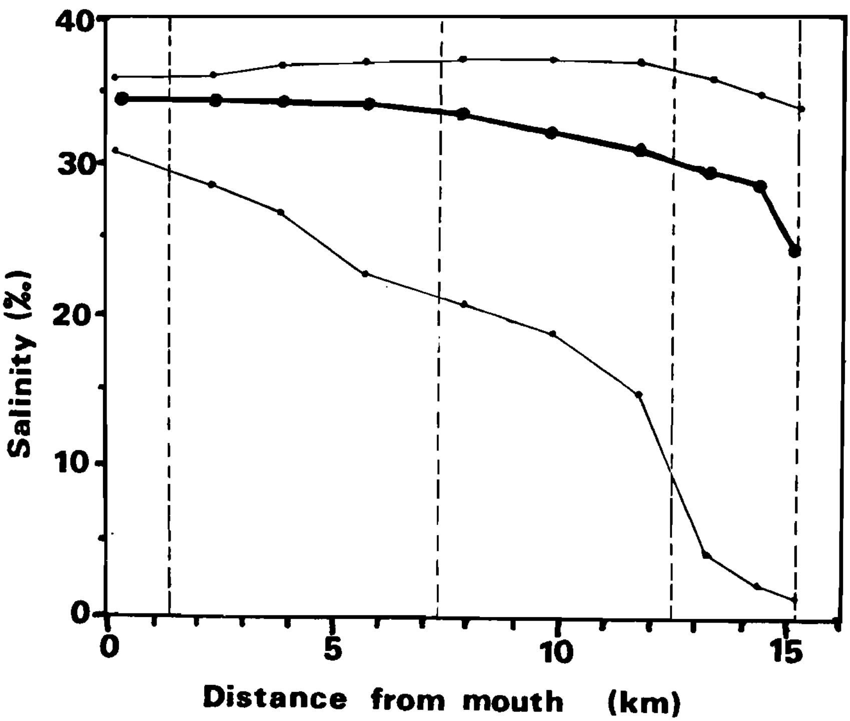

FIGURE 3

The mean annual salinities (heavy line) and salinity ranges (fine line) at 10 stations along the Swartkops estuary from Dec. 1971 to Nov. 1972. Dashed lines indicate boundaries between the different reaches of the estuary described.

pH and oxygen values were found to vary little throughout the estuary during the period of sampling. pH ranged from 7,9–8,3 and dissolved oxygen from 3,3–5,6 ml O_2/litre.

Macnae (1957) noted that, in the catchment areas of the Swartkops River and its tributary the Elands River, a high proportion of the annual rainfall often tends to fall over a period of a few days. This results in minor floods every few years. He also states that the salinity conditions return to normal very rapidly after such floods and that they did so within four days after the floods of 1952. He concluded that such floods have little effect on the estuarine animals. It is evident, however, that the flood recorded during this study was considerably more severe than those referred to by Macnae and some effects on the benthic fauna might be expected.

The salinity at any point in the estuary usually varies by less than 3‰ at different states of the tide and there is very little vertical salinity gradient anywhere in the estuary. The only region where a vertical salinity gradient was established was in the upper/middle reaches between Bar-None and the Drift. This gradient was very variable but was found throughout the year with a mean surface salinity of 29,8‰ and a mean bottom salinity of 41,3‰, the difference being 11,5‰. In all other parts of the estuary the mean differences between surface and bottom salinities during this investigation was less than 1‰.

The results of substrate analyses and measurements of shear strengths are shown in Table 2. The median particle diameter (Mdφ) is given in phi units and not in microns (see McManus 1963). It may be seen from this table that the substrata analyzed are generally well-sorted as the phi quartile deviation values (Qdφ) are fairly low. The positive phi quartile skewnesses (Skφ) obtained in most samples indicate better sorting of larger particles than smaller ones. Most Skφ values are, however, close to zero. The percentage subsieves is a measure of the proportion of fine silt ($<$ 62 microns, $>$ phi 4) in the substrata. The fineness and compactness of the substrata vary considerably along the estuary. The nature of the substrata in the various reaches of the estuary and its relation to the burrowing fauna are discussed in the following section.

The Macrobenthos

In this study the macrobenthos has been divided into communities on the basis of dominant species and an attempt is made to relate the distribution of these communities to the prevailing abiotic and biotic factors. Species lists including the less abundant associated species of benthic animals of the estuary have been published by Macnae (1957).

At practically every station sampled for benthos more than 90% of the biomass of the infauna was made up by one or more of the following species: The mud prawn, *Upogebia africana* Ortmann; the sand prawn, *Callianassa kraussi* Stebbing and a number of species of burrowing bivalves. Each of these three species or groups usually dominates a distinct community.

Figure 4 shows the quantitative distribution of *Callianassa*, *Upogebia* and bivalves along the estuary as found during the survey of 1970/71. Included in Figure 4, for comparison, is a graph of the percentage subsieve material in the substrata along the estuary. Figure 5 is a similar diagram for the survey of January 1972 when the distribution of the communities had changed as a result of the floods of April 1971. A comparison of Figures 4 and 5 indicates the effects of these floods on the benthic fauna. The biomass values recorded during the above-mentioned surveys are shown in Figures 6 and 7. Included in Figure 6 for purposes of comparison is a

TABLE 2

SUBSTRATE PROPERTIES AT 35 STATIONS ALONG SWARTKOPS ESTUARY

Where shear readings went off scale the minimum value has been calculated and this shown by >. The median particle diameter (Mdφ), the skewness of the cumulative curve (Skφ) and the quartile deviation (QDφ) are all expressed in phi units.

Station	*Mdφ*	*Skφ*	*QDφ*	% *Subsieves*	*Shear* 2*cm*	(g/cm^2) 10*cm*	*Remarks*
1	2,19	—0,035	0,26	0,4	—	—	Clean, fine sand
2	1,92	—0,01	0,28	0,2	28	63	Clean, medium sand
3	2,31	—0,01	0,26	0,9	32	73	Clean, fine sand
4	2,42	—0,05	0,16	0,1	17	59	Clean, fine sand
5	2,73	+0,035	0,11	17,8	15	>93	Shelly, muddy, fine sand
6	2,55	+0,32	0,53	15,2	25	46	Shelly, muddy, fine sand
7	2,74	+0,30	0,63	20,0	37	65	Shelly, muddy, fine sand
8	4,61	—	—	67,3	—	—	Very soft, sandy silt
9	2,57	+0,01	0,06	1,3	17	>78	Slightly muddy sand
10	2,57	+0,42	0,57	18,1	—	—	Shelly, muddy, fine sand
10a	2,65	+0,41	0,64	23,3	—	—	Shelly, muddy, fine sand
10b	2,51	+0,30	0,47	22,9	—	—	Shelly, muddy, fine sand
10c	2,87	—	—	47,8	—	—	Shelly, muddy, fine sand
11	4,79	—	—	85,5	—	—	Very soft, sandy silt
12	2,51	+0,29	0,60	19,4	26	51	Muddy, fine sand
13	2,69	+0,34	0,47	18,8	38	>68	Muddy, fine sand
14	2,58	+0,02	0,09	14,9	31	59	Muddy, fine sand
15	2,69	+0,26	0,61	20,0	—	—	Muddy, fine sand
16	2,32	+0,27	0,94	21,9	—	—	Muddy, fine sand
18	2,16	+0,19	0,57	20,0	29	47	Muddy, fine sand
19	2,02	+0,10	0,67	17,9	—	—	Muddy, fine sand
20	1,65	+0,55	0,80	13,4	—	—	Muddy, medium sand
21	2,49	+0,27	0,53	21,7	34	46	Muddy, fine sand
22	2,83	—	—	33,3	40	>92	Silty, fine sand
23	2,58	+0,52	0,85	24,4	46	>93	Silty, fine sand
26	3,14	—	—	40,5	20	>81	Silty fine sand,
27	2,96	+0,01	0,65	16,7	25	>83	Muddy, fine sand
28	1,23	0,00	0,38	0,7	9	22	Clean, medium sand
29	2,55	+0,01	0,58	6,9	29	>79	Slightly muddy, fine sand
30	1,99	0,00	0,32	4,6	15	47	Slightly muddy, medium sand
32	2,41	+0,24	0,78	22,6	8	13	Muddy, fine sand
33	0,87	+0,06	0,36	0,8	—	—	Fairly clean, coarse sand
36	1,95	—0,11	0,45	2,6	—	—	Fairly clean, medium sand
37	1,90	+0,06	0,57	9,6	—	—	Slightly muddy, medium sand

graph of the substrate nitrogen values recorded along the estuary. Figures 8 and 9 illustrate the quantitative distribution of communities and biomass values along the middle reaches of the estuary as found during September 1972. Only the middle reaches were then surveyed as no significant changes had occurred elsewhere. Figure 10 illustrates the quantitative distribution of different bivalve species along the estuary as recorded before the floods. Included in Figure 10 is a graph of the percentage of subsieves in the substrata along the estuary.

The different reaches of the estuary and their macrobenthic communities are discussed commencing with the mouth area and proceeding upstream.

The mouth area is subject to strong tidal currents and has a correspondingly clean, coarse and relatively unstable substratum. Because of its proximity to the sea, the salinity and temperature of the water is relatively stable and tends to correspond to the values obtaining in the adjacent sea. The benthic macrofauna of this part of the estuary is dominated by *Callianassa kraussi* (Figure 4). Because there is relatively little available food here (*c.f.* nitrogen values in Table 1 and Figure 6) the biomass values are low. As the salinity and temperature values recorded here

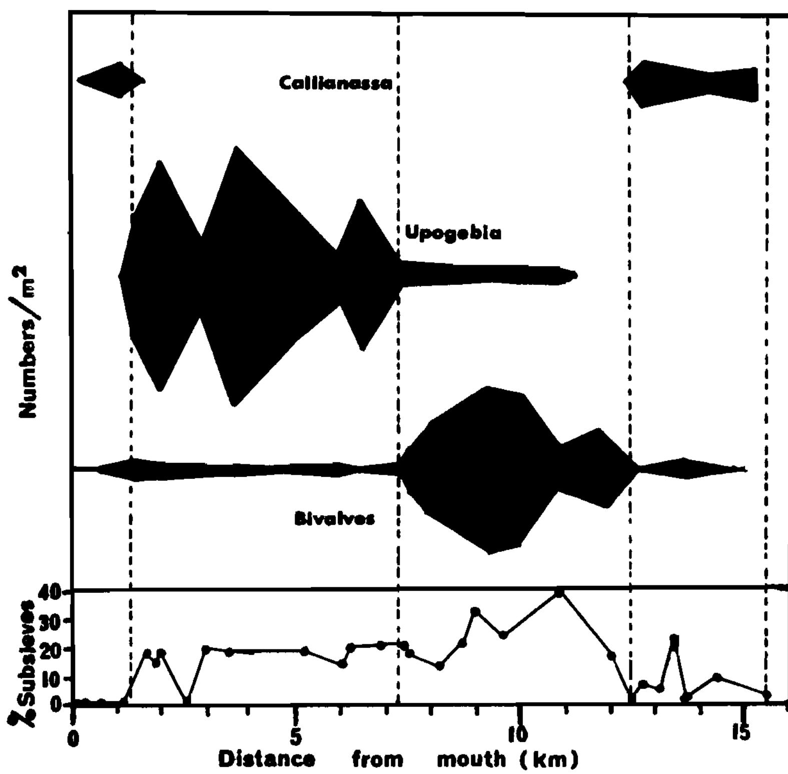

FIGURE 4

The quantitative distribution of macrobenthic communities along the Swartkops estuary during the summer of 1970/71. Included is a graph of the % of subsieves in the substrate at stations along the estuary for comparison. Dashed lines indicate boundaries between different reaches of the estuary.

are very similar to those of the sea, the instability of the sand and its paucity of organic matter are probably the major limiting factors. Animals such as *Upogebia africana*, which construct permanent burrows lined with silt (MacGinitie 1930, 1935; Hill 1967), are unable to colonize this region and the only other common infaunal species is the small bivalve *Psammotellina capensis* Sowerby.

Macnae (1957) recorded both *Donax ringens* (now *D. serra* Röding) and *D. sordidus* Hanley penetrating a mile up the estuary. During this study no specimens of these two species have been found inside the mouth though both are fairly common in the surf on either side of the mouth (Figure 10). The reason for the disappearance of these two psammophilous species from the estuary is uncertain. The construction of the Settlers Bridge near the mouth may have affected the amount of wash and wave action in the mouth area, particularly above the bridge. As *Donax* is generally dependent on wave action to supply its food (Wade 1955, 1967) this is a possible reason for their disappearance. It is also possible that floods (when fresh water penetrates down to the mouth) have prevented them surviving in the mouth region. However, floods appear to have been as common during the period when Macnae studied the estuary as in recent years. Furthermore both species can tolerate dilution to approximately 17‰ for long periods

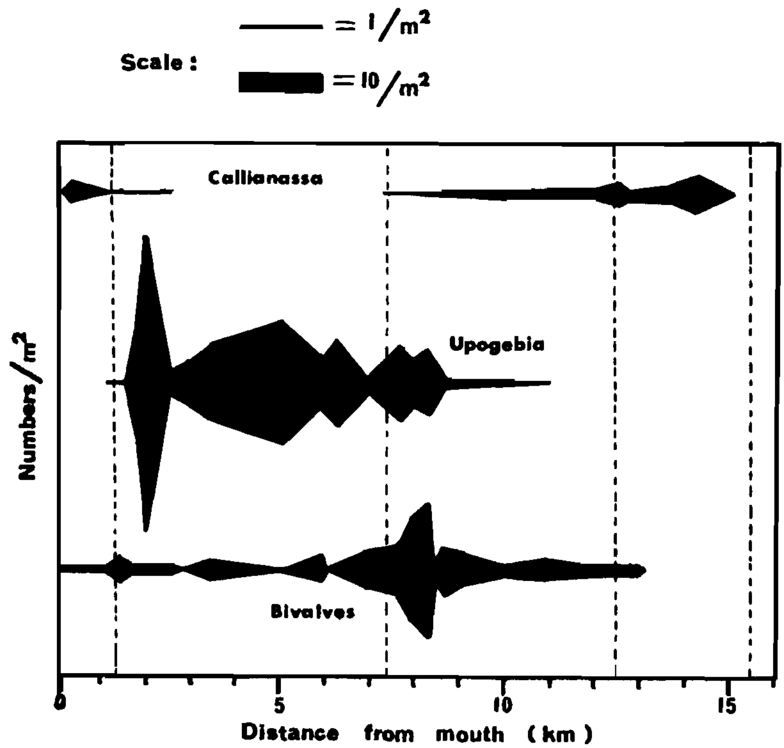

FIGURE 5

The quantitative distribution of macrobenthic communities along the Swartkops estuary during January 1972. Dashed lines indicate boundaries between different reaches of the estuary.

(Hanekom, personal communication). The nature of the substrate does not appear to be limiting as the substrate of the nearby beaches is very similar to that of the mouth area. The most probable reason for the disappearance of *Donax serra* and *D. sordidus* would appear to be the decrease in wave and current action in the mouth area resulting from the construction of the Settlers Bridge.

The *Callianassa kraussi* community stops abruptly where the substrate becomes muddy with a greater proportion of subsieve material (Figure 4). Here there is a narrow zone dominated by the pencil bait, *Solen capensis* Fischer, and thereafter all of the intertidal muds of the lower reaches are dominated by *Upogebia africana*. The zone dominated by *Solen capensis* is only a few hundred metres wide and is characterized by a substrate muddier than that of the mouth

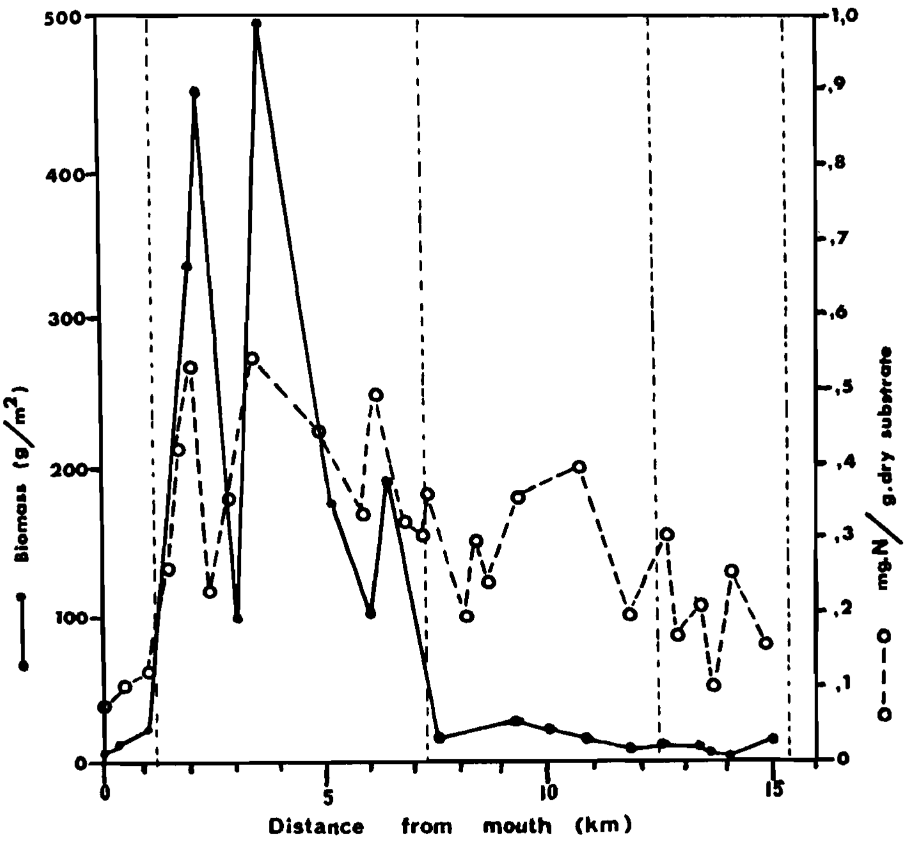

FIGURE 6

Total biomass values recorded at stations along the Swartkops estuary during December 1970 and January and February 1971. Included for comparison is a graph of nitrogen values recorded in the surface of the substrate along the estuary during January 1972. Dashed vertical lines indicate boundaries between the different reaches of the estuary. For key see Figure 7.

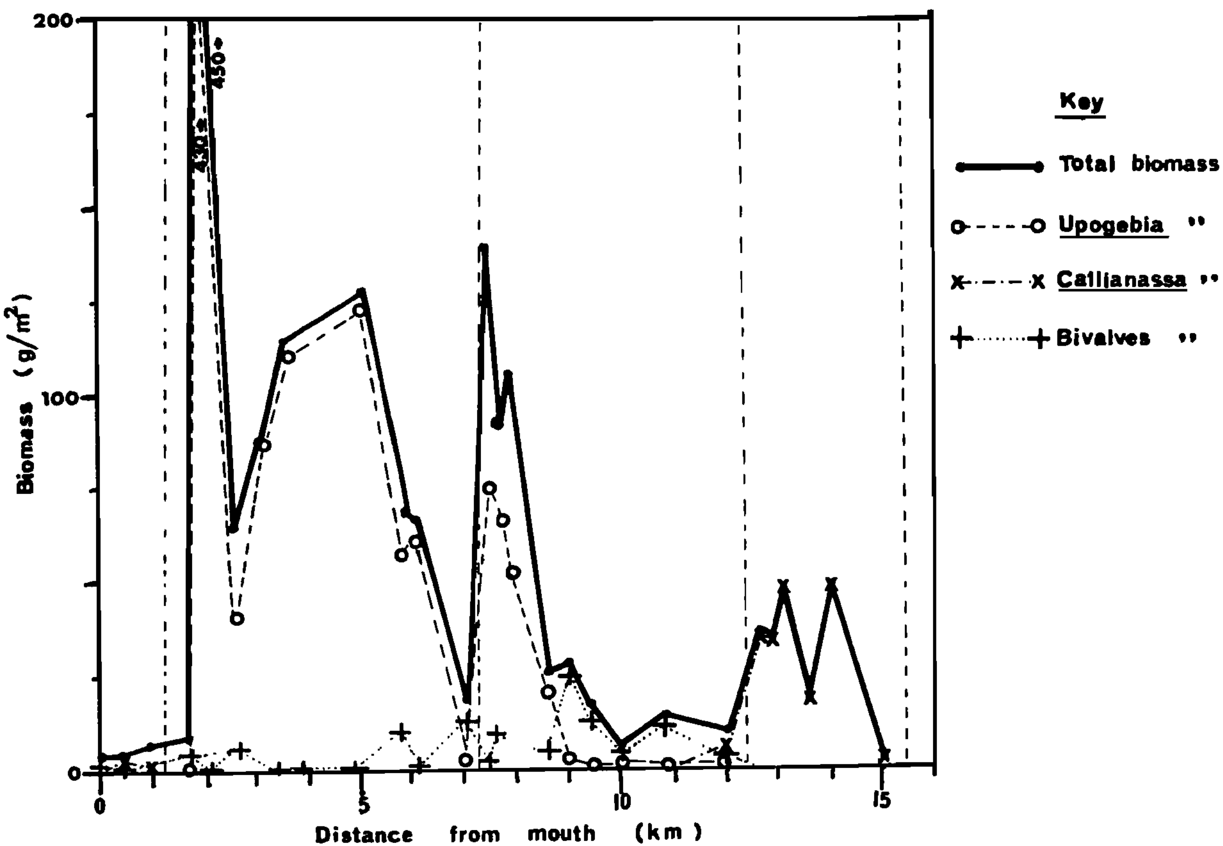

FIGURE 7

Biomass values of major species recorded along the Swartkops estuary during January 1972. Dashed vertical lines indicate boundaries between different reaches of the estuary.

area, but sandier than that of the lower reaches. This zone occurs near Station D (between Stations 4 and 5).

The interaction between the *Callianassa kraussi* and *Upogebia africana* communities is very interesting as, except for areas in the *Solen capensis* community, these two communities do not overlap at all. The salinity at the mouth and throughout the lower reaches is generally very stable and close to that of seawater (Table 1). It is thus well within their tolerance limits. The lower limit for both species is about 3,4°/₀₀ (Hill 1971). Salinity could therefore not limit the distribution of these two communities in these areas. Wooldridge (1968) has found that *Callianassa kraussi* can burrow into practically any estuarine substrate while *Upogebia africana* is restricted to a substrate with not less than 3 % and not more than 65 % subsieves. This explains why *Upogebia africana* does not occur in the sandy mouth area where there is less than 1 % subsieves in the substrate. It does not explain, however, why *Callianassa kraussi* is absent from the muddier middle reaches where the substrate contains 15–20 % subsieves. (*Upogebia africana* has been recorded from one station between the lower reaches and mouth where the substrate contains only 1,3 % subsieves. At this station however the substrate is very compact and contains a relatively large amount of organic matter – 0,24 mgN/g dry sand).

These two anomurans feed in different ways, *Upogebia africana* filtering detritus and small organisms from the water (MacGinitie 1930; Hill 1967) and *Callianassa kraussi* sifting out

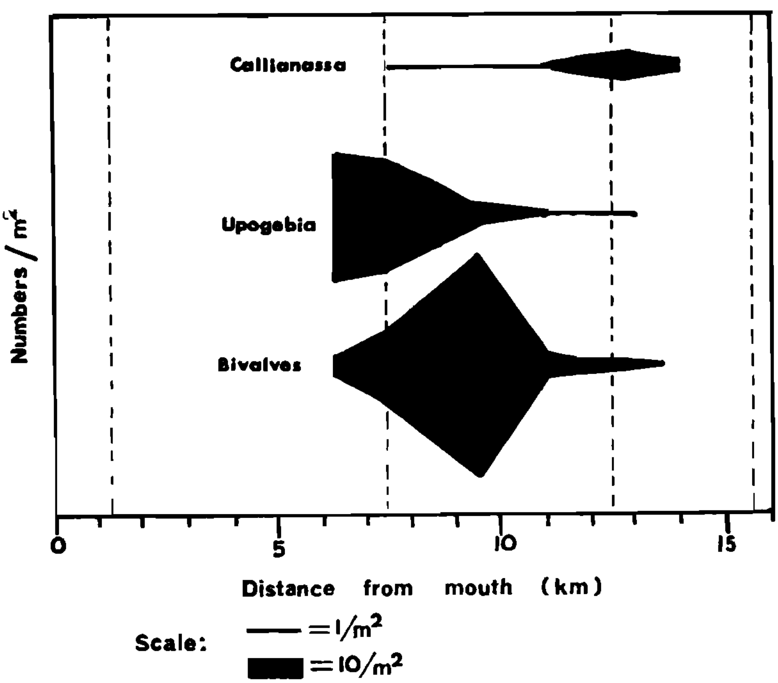

FIGURE 8

The quantitative distribution of major benthic species in the middle reaches of the Swartkops estuary during September 1972. Dashed lines indicate boundaries between different reaches of the estuary.

detritus and micro-organisms buried under the sand (MacGinitie 1934; Macnae 1957). Although these two species can thus not compete directly for food, some form of competition is probably the explanation for the almost complete lack of overlap between them. The excavations of *Callianassa kraussi* tend to keep the substratum soft and unstable and this would make it difficult for *Upogebia africana* to construct burrows. The burrows of the latter on the other hand, might stabilize the mud and thus discourage *Callianassa kraussi*. This interaction between the two species and the substratum might be the basis of competition. Competition may also be important between the *Upogebia africana* and bivalve communities.

The lower reaches, dominated by *Upogebia africana*, consist of extensive mudflats which are partly covered by salt-marsh vegetation. Two large creeks, Tippers' Creek and Modderspruit, branch off the main channel in the lower reaches. The substrate in the lower reaches is generally soft muddy sand containing about 17 % subsieves at the LWS tide level. Relatively large amounts of available food, as indicated by high substrate nitrogen values here (Table 1), make this the richest part of the estuary. Biomass values of up to 500 g/m², made up mainly by *Upogebia africana*, have been recorded. The wind and currents over this fairly shallow muddy bottom (maximum depth of main channel 3 m at low tide) cause the waters of the lower reaches of the estuary to be fairly turbid. In these reaches sea-water enters with every rising tide so the range of salinities and temperatures recorded here are to a large extent moderated by the sea.

The fauna of the creek is most interesting. The results obtained from stations situated in the two creeks have not been mentioned so far as these stations do not lie on the main channel. These results are shown in Table 3. Station 10 lies at the mouth and Station 11 at the head of

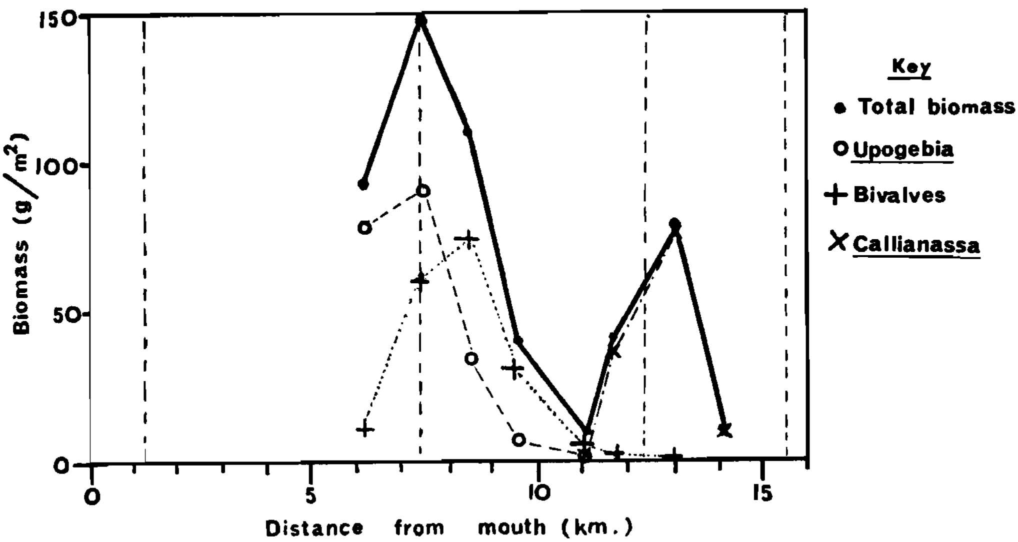

FIGURE 9

Biomass values of major species recorded at stations along the middle reaches of the Swartkops estuary during September 1972. Dashed vertical lines indicate boundaries between different reaches of the estuary.

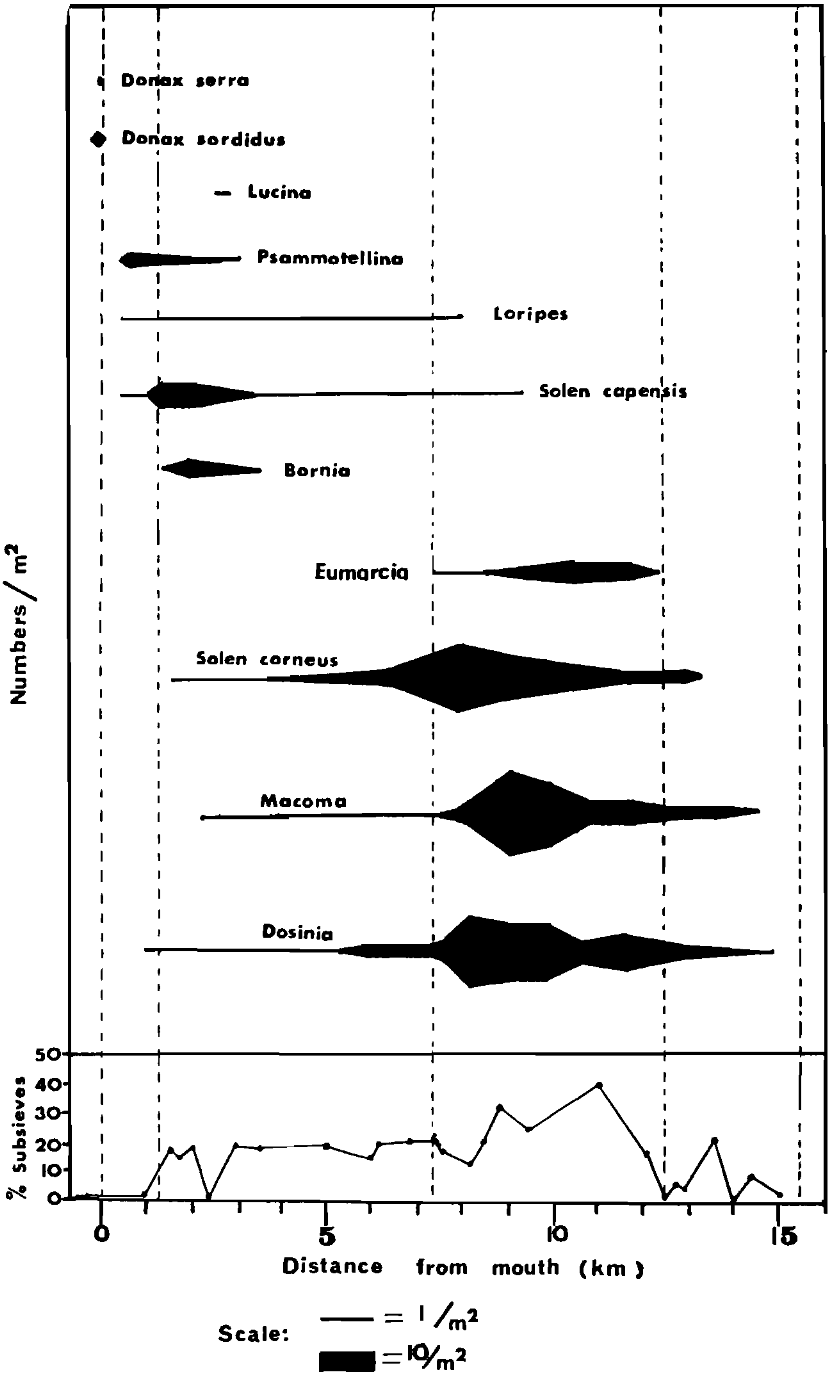

FIGURE 10

Diagram of the quantitative distribution of 11 bivalve species along the Swartkops estuary. Included for comparison is a graph of the % subsieves in the substrate at a series of stations along the estuary. Dashed lines indicate boundaries between different reaches of the estuary.

Tippers' Creek, with Stations, 10a, 10b and 10c in between. Station 8 lies at the head of Modderspruit, but has been placed between Stations 10c and 11 in the table in order of increasing subsieves (silt) content.

Because of the very quiet conditions in such creeks where currents are very slow, considerable quantities of fine matter tend to precipitate out. This tendency is greatest towards the head of the creek where consequently large amounts of detritus and silt are found. The fact that these creeks are surrounded by extensive salt marshes and that they support the growth of much *Zostera capensis* Setchell and *Spartina capensis* Nees adds to the quantities of detritus found in such places.

Table 3

SUMMARY OF AVAILABLE FOOD, SUBSTRATE TYPES AND FAUNA OF MUD OF TIPPERS' CREEK AND MODDERSPRUIT

The six bivalves at Station 10 were all *Solen capensis*; at Station 10a two were *Macoma litoralis* and one *Lucina edentula* (Linn.) and at Station 10b six were *M. litoralis*, two were *S. corneus* and one was *S. capensis*.

Station	*Substrate Mdϕ*	*Subsieves*	*Biomass g/m²*	*NOS/m² U. africana*	*NOS/m² bivalves*	*NOS/m² others*	*Nitrogen mgN/dry sand*
10	2,57	18,1	457	194	6	12	0,54
10a	2,65	23,3	81	42	3	18	0,54
10b	2,51	22,9	56	27	9	51	0,86
10c	2,87	47,8	18	13	0	21	0,90
8	4,61	67,3	310	0	0	264	1,36
11	4,79	85,5	134	1	0	85	1,78

From Table 3 it can be seen that the benthic fauna changes considerably as the substrate becomes finer along such a creek. The numbers of *Upogebia africana* decline rapidly when the substrate contains more than 20% subsieves. Bivalves (*Macoma litoralis* and *Solen corneus* Lamy) which otherwise only occur in the middle reaches of the estuary appear where the substrate contains approximately 23% subsieves, but disappear where the substrate contains 47,8% subsieves. A fauna peculiar to these creeks occurs in large numbers in the siltier areas to reach a peak at Station 8 with 67% subsieves. At Station 11 with 86% subsieves the fauna is not quite as abundant. This "creek fauna" is dominated by the following species: The goby, *Glossogobius giuris* Hamilton, the shrimp, *Palaemon pacificus* Stimpson, the cracker-shrimp, *Alpheus crassimanus* Heller and two small crabs, *Cleistostoma edwardsii* McLeay and *C. algoense* Barnard. Although these five species are not all true members of the benthic infauna, most are found in burrows when the tide is out. *Upogebia africana* is usually absent from the heads of these creeks, where the substratum is too silty. It can not burrow where there is more than approximately 65% subsieves (Wooldridge 1968). The single specimen of *Upogebia* found at Station 11 could quite possibly have moved there from elsewhere. The mud at Station 11 is almost liquid and this small specimen of *Upogebia africana* could not possibly have constructed a permanent burrow there. Despite the absence of *Upogebia africana* from the heads of these creeks, high biomass valuef were recorded (Table 3). These high values almost certainly result from the large quantities os available food in these places.

As can be seen from Figure 4, only occasional specimens of bivalves are found in the lower reaches of the estuary. Besides *Solen capensis*, which has already been discussed, occasional specimens of *Dosinia hepatica*, *Macoma litoralis* and *Solen corneus* occur in the lower reaches, only the latter being fairly common. The tiny bivalve *Bornia africana* Bartsch, which is a commensal in the burrows of the tongue worm, *Ochaetostoma capense* Stephen, is also found in the lower parts of the lower reaches (Figure 10).

Atrina squamifera (Sowerby) (as *A. squamata*) and *Papyridea papyracea* (Bruguiere) (as *Laevicardium natalense*) were recorded by Macnae (1957) in the lower reaches but were not found in the present study, although valves were present. *Lucina edentula* (Linn.) (*Thyasira eutornia*) is very rare in the estuary and only a single living specimen was obtained at Station 10a (Figure 10). The valves of this species are very common in the lower reaches of the estuary and it must have been plentiful in the past. *Loripes clausus* Philippi was recorded in muddy areas in the lower reaches by Macnae (1957), but only three specimens were obtained in the present study these coming from Stations 3, 9 and 21. Valves of this species are common in the lower reaches especially around Stations 5 and 6. *Loripes clausus* would therefore also appear to be less common in the estuary than in the past.

The middle reaches of the estuary, however, are dominated by the bivalves *Dosinia hepatica*, *Macoma litoralis*, *Solen corneus* and *Eumarcia paupercula* (Holten) (Figure 10). Before the floods of 1971 the boundary between the *Upogebia africana* and bivalve communities was fairly distinct and lay approximately 7,3 km from the mouth (Figure 4). After the floods, by January 1972, the boundary had shifted more than a kilometre upstream, to 8,7 km from the mouth (Figure 5). This was a result of the bivalves being decimated in the middle reaches by the floods and of *Upogebia africana* moving up the estuary (*cf.* Figures 4 and 5). By September 1972 (Figure 8) the situation was beginning to return to normal. Due to the recruitment and growth of spat, bivalve numbers were beginning to recover in the middle reaches, and near Redhouse on one occasion 88 one-year-old *Macoma litoralis* were recovered from 1 m^2 of substrate. *Upogebia africana* numbers had also increased a little below Redhouse by September. They will no doubt begin to decline, however, as the bivalves increase and grow. The return to the position recorded before the floods will probably take about two years from the time of the floods, allowing for settlement and growth of spat (McLachlan 1974).

That the bivalve populations of the middle reaches were decimated by the floods is beyond doubt, as dead specimens of *Solen corneus* and *Macoma litoralis* were found at Redhouse shortly after the floods. These two species are the least salinity-tolerant of the bivalve species occurring in the middle reaches of the estuary (McLachlan & Erasmus 1974). The 1971 spat did not seem adversely affected by the floods, however, and large numbers of this year-class of *Solen corneus* were recorded during January 1972, and large numbers of the same year-class of *Macoma* *litoralis* were found during September 1972. The bivalve peak approximately 8 km from the mouth in Figure 5 was due mainly to these high numbers of *Solen corneus*. The bivalves of the middle reaches of the estuary therefore appear to be the only macrobenthic species severely affected by the floods, as no great changes in the number of *Upogebia africana* or *Callianassa kraussi* were recorded.

The factor limiting the downstream distribution of the bivalve community appears to be competition with *Upogebia africana*. Salinity can not limit their downstream distribution as salinity is more favourable in the lower reaches. Neither can substrate be directly limiting as these bivalves have been recorded from both coarser and finer substrata than occur in the lower reaches of the estuary (Figure 10). Both in Tippers' Creek and near Redhouse these bivalves become common when the percentage of subsieve material in the substrate exceeds 20% and *Upogebia* becomes rare or absent.

Bivalves are common in substrata in the middle reaches with up to 40,5% subsieves, but are absent from Station 10c in Tippers' Creek with 47,8% subsieves. It would therefore appear that they can not tolerate more than about 45% subsieves and that they are most abundant between 20% and 40% subsieves in the substrate. *Upogebia africana* is most abundant in the lower reaches in areas where the substrate has between 15% and 20% subsieves.

Considering the evidence from natural distribution it appears that competition from *Upogebia* is probably an important factor limiting the distribution of the bivalves. This competition is probably related to the nature of the substrate. *Upogebia africana* is better adapted to substrata with less than 20% subsieves while the above-mentioned bivalves are most abundant in substrata with 20–40% subsieves.

The distribution of the three common bivalve species in the middle reaches of the estuary is probably related largely to their feeding methods. *Solen corneus*, a suspension feeder which derives its nourishment from the water, predominates in the lower part of the middle reaches below Redhouse (Figure 10). This is probably because it is best able to compete with *Upogebia africana* and because its feeding method relies on a certain amount of water movement which produces relatively coarse substrata (13–22% subsieves). It is the commonest bivalve in areas dominated by *Upogebia africana* (*cf.* Figures 10 and 4). The area near Redhouse has a siltier substrate (25–40% subsieves) than the latter area and here a deposit feeder, *Macoma litoralis*, predominates. The quieter conditions here favour the precipitation of fine silt and detritus over the mudbanks, and the method of feeding of *Macoma litoralis* is adapted to this. It can be seen in Figure 6 that there is a small peak in substrate nitrogen values here, indicating an increased rate of detrital deposition. In the upper middle reaches near Bar-None *Dosinia hepatica* predominates. The substrata become coarser here again (1–17% subsieves) with less available food (Figure 6) and the salinity range somewhat greater than in the middle reaches. As *Dosinia hepatica* is a suspension feeder and also more tolerant of lowered salinities than the previous two species (McLachlan 1972), it is particularly well adapted to this region. All three of these species are, however, common over the whole of the middle reaches. *Eumarcia paupercula* is also quite common (Figure 10). The feeding methods of these animals have been discussed by McLachlan (1972).

The muds of the middle reaches are noticeably harder than those of the lower reaches (Table 2) but it is uncertain whether this is a cause or result of *Upogebia africana* not colonizing these areas. The burrows of *Upogebia africana* tend to render the substrate softer where they are abundant, and bait-digging for prawns softens the substrate further. Biomass values in the middle reaches are lower than would be expected on the basis of the amounts of available food as determined by substrate nitrogen (Figure 6). The shells of bivalves have not been included in the biomass values recorded and the shells on average weigh about four times as much as the soft parts of these animals. The low biomass values recorded in the middle reaches are a result of the low individual body weights and are not due to low animal numbers.

The steep banks of the middle reaches shelter the water from the wind and this, together with the usually slow currents, results in fairly clear water (Table 1). In this part of the estuary the water is not replaced at each high tide. It rather tends to move up and down the estuary with the tides as a plug. The salinity is generally slightly below that of sea-water but it can become diluted after heavy rains or slightly hypersaline during dry periods (Table 1). The narrow intertidal areas (approximately 10 m wide on average) and sparse salt-marsh vegetation limit the extent and richness of the benthic environment which can only be colonized by euryhaline animals. It is worthy of note that Macnae (1957) recorded only occasional bivalves in the middle reaches. The difference between his findings and the numbers recorded here may be due to changes over the past twenty years or to less intensive sampling by Macnae. That some changes have occurred is indicated by the fact that he recorded *Tivela compressa* (Sowerby) from the middle reaches, a species not encountered in this study. That he did not record *Eumarcia paupercula* may have been due to his sampling having been less intensive.

The boundary between the middle and upper reaches of the estuary is not as well-defined as the boundaries between other reaches, and lies between Bar-None and the Drift. In the upper reaches the substrate is coarse and very soft and pebbles and small rocks are common in places. There is, however, a noticeable amount of subsieve material in the substrate here, derived presumably from silt deposited by the river, when it comes down in flood. The substrate nitrogen values recorded here are low, although higher than those recorded in the mouth area. Although much of the upper reaches is protected from the wind by steep banks, the shallow water (less than 1 m at low tide) is easily stirred and it is consequently more turbid than that of the middle reaches. The salinity here is very variable though usually fairly high (mean 26,5‰) so that only very euryhaline animals could survive. The narrow intertidal areas, usually less than 10 m wide, provide a limited benthic environment. The last 200 m of the estuary have a stony bed and no soft substrata are available.

The sands of the upper reaches are, like the sandy mouth area, dominated by *Callianassa kraussi*. There is some overlap between the *Callianassa kraussi* and bivalve communities and specimens of *Dosinia hepatica* have been found throughout the upper reaches. Occasional specimens of *Callianassa kraussi* are not uncommon along most of the middle reaches. This was most noticeable during January 1972 (Figure 5) when specimens of the latter were encountered in many parts of the middle reaches where bivalve numbers had been reduced. *Solen corneus* and *Macoma litoralis* both penetrate a little way into the upper reaches but never occur in high numbers. Diving with SCUBA has revealed that *Callianassa kraussi* dominates the bottom and probably most of the subtidal areas of the middle reaches. Although it is possible that the bivalve and *Callianassa kraussi* communities do compete to some extent, this appears to be limited and other factors seem to restrict the up-stream distribution of the bivalves. Their salinity tolerances seem to be the most important factor as far as this is concerned. *Dosinia hepatica* penetrates the furthest up the estuary, followed by *Macoma litoralis* and *Solen corneus* respectively. *Dosinia hepatica* is correspondingly more salinity-tolerant than *Macoma litoralis* which in turn is more tolerant than *Solen corneus* (McLachlan & Erasmus 1974).

Passing up the estuary biomass values tend to decrease in the middle and upper reaches as the amount of available food decreases (Figure 6). Very large specimens of *Callianassa kraussi* sometimes caused occasional unusually high biomass values to be recorded. (Individuals as long as 15 cm, including the cheliped, have been found). Macnae (1957) recorded only small specimens of *Callianassa kraussi* in the upper reaches. This was most probably because he obtained them by digging, a method really only suitable for obtaining the smaller shallow-lying specimens. The use of a bait-pump allowed the large, deep-lying specimens recorded during this survey to be obtained. The higher biomass values recorded during January 1972 than during 1970/71 are due to the use of a bait-pump in 1972. The wide salinity tolerance of *Callianassa kraussi* is indicated by large specimens being still plentiful in the upper reaches after the floods of 1971. Only in the furthest sandbank up the estuary were their numbers noticeably reduced.

GENERAL CONCLUSIONS

The importance of substrate in determining the distribution of estuarine macrobenthos is obvious from this study. In the Swartkops estuary where the salinity is usually very close to that of the sea, substrate is by far the most important limiting factor influencing the distribution of the macrobenthos.

The biomass values recorded in different regions of the estuary are apparently related to the quantities of available food (measured as substrate nitrogen) occurring in each region for they exhibit the same general pattern of distribution. It is considered that a measurement of nitrogen content provides a more accurate idea of the amount of available food than measurement of organic matter. Much of the organic detritus is indigestible to the estuarine animals while bacteria on the detritus are more easily digestible. When detritus is ingested by estuarine animals practically all of the nitrogen is removed from the faeces while a large portion of the organic matter is undigested (Wernstedt 1942; Newell 1965). The quantity of available food in various parts of the estuary is related to the position and extent of the salt-marshes. The extensive salt-marshes of the lower reaches appear to be the primary source of detritus for the whole estuary. Nitrogen values in the surface of the substrate are highest in the lower reaches, especially the creeks, and decrease rapidly towards the mouth and more slowly upstream. As many of the benthic animals are suspension- rather than deposit-feeders, a measure of nitrogen in the water would probably have been valuable but this was not possible during this study.

A relatively small number of macrobenthic carnivores was found. None were encountered in the middle or upper reaches, only two small specimens of *Natica genuana* Reeve were found in the mouth area and a few *Gorgonorhynchus* sp. and *Glycera convoluta* Keferstein in the lower reaches. The most important predators are therefore probably fishes such as *Lithognathus lithognathus* (Cuvier) and *Pomadasys commersoni* (Lacépède) and wading birds. Natural predation on the benthos must therefore be comparatively light. This might be why such large numbers of, for example, *Upogebia africana*, can be removed by bait gatherers without reducing the populations too greatly.

Bivalves have generally been considered scarce in South African estuaries (Day 1951). The bivalve populations recorded in this study, although not of the magnitude recorded in estuaries in the northern hemisphere are clearly the dominant community in a large part of the Swartkops estuary. Detailed studies of their biology have been carried out (McLachlan 1972). Similar populations may occur in the Knysna estuary, for an examination of Day's (1967) diagram of a transect at Ashford, in the Knysna estuary, reveals that the lower intertidal muds have an infauna dominated by *Dosinia*, *Solen corneus*, *Macoma* and *Eumarcia*. *Upogebia* is also common there. This would seem to be the same community encountered in the middle reaches of the Swartkops estuary. Further investigation might reveal the occurrence of this community in other Cape estuaries.

In general it would appear that the Swartkops estuary has changed very little since the time of the investigations twenty years earlier (Macnae 1957). The construction of the Settlers Bridge appears to have caused some changes in the mouth region and the part of the estuary immediately above Swartkops Village appears to have silted up to some extent and is now a maze of mudbanks and *Spartina*-covered islands. Some differences between the bivalve species found in the mouth region and lower and middle reaches of the estuary in this study in comparison to Macnae's earlier study are recorded. Some of these changes may be related to changes in their habitat.

SUMMARY

1. The quantitative distribution of macrobenthic fauna inhabiting soft substrata in the Swartkops estuary is described in relation to prevailing abiotic and biotic factors.
2. The main limiting factors appear to be the nature of the substrata and competition between dominant organisms in certain communities.
3. Salinity is apparently not an important limiting factor as it is usually close to $35^{0}/_{00}$ over most of the estuary.
4. Five distinct infaunal communities have been recognized, one dominating each of four different reaches of the estuary and one occurring at the heads of tidal creeks.
5. These communities are from the mouth to the upper reaches of the estuary, a *Callianassa kraussi* community, an *Upogebia africana* community, a bivalve community, a second *Callianassa kraussi* community and a creek community dominated by four crustaceans and a goby.
6. Biomass values of benthic fauna of up to 500 gm/m^2 are recorded.
7. The biomass values recorded in different regions are apparently related to the quantities of available food (measured as substrate nitrogen) and both are highest adjacent to the saltmarshes which appear to be the primary source of detritus.
8. Distribution patterns suggest that competition from *Upogebia africana* is probably an important factor limiting the distribution of bivalves.
9. Some changes have occurred in the estuary in recent years. *Donax serra* and *Donax sordidus* have disappeared from the mouth region since the construction of Settlers Bridge.

10. Sampling before and after a severe flood revealed changes in the distribution of the benthic fauna. Reduction in the numbers of bivalves in the middle reaches by the floods allowed the spread of *Upogebia africana* more than a kilometre upstream. Recovery of the original distribution is estimated to take two years.

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