Ecology of southern African estuaries. Part XI. Mngazana: a mangrove estuary in Transkei

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Mngazana is a rich estuary dominated by mangroves and containing a diversity of both invertebrates and fish. Its richness is mainly due to favourable physical conditions. The invertebrate fauna includes temperate, tropical, and subtropical species, predominating in the lower reaches, middle reaches and head respectively. The fish have affinities with the tropics in summer, while in winter many warm-temperate species increase in numbers. In comparison with the fauna of soft substrates, that of rocks has a higher percentage of stenohaline and estuarine forms, and a more restricted distribution. The rocky habitat in estuaries favours greater specialization with respect to salinity tolerance. A high percentage of the biomass of invertebrates in soft substrates consists of detritivores, and the biomass is related to the organic content of the substrate. Mangrove mud has the highest organic content and supports the highest biomass, but few species can tolerate the conditions there. Mangroves are probably the major primary producers in the system.
S. Afr. J. Zool. 14: 149–170 (1979)

Mngazana is 'n ryk riviermond gekenmerk deur wortelbome en 'n verskeidenheid van invertebrate en visse. Dit het gunstige fisiese omstandighede. Invertebrate sluit in gematigde, tropiese en subtropiese spesies wat in die lae, middel en bolope oorheers. Die visse toon verwantskappe met die trope gedurende die somer en baie warm-gematigde spesies vermeerder gedurende die winter. In vergelyking met die fauna van sagte (bodems), het dié van rotse 'n hoë persentasie stenohaliene en riviermond-vorme en 'n meer beperkte verspreiding. Die rotsagtige habitat in riviermonde begunstig groter spesialisasie met betrekking tot soutgehalte verdraagsaamheid. 'n Hoë persentasie van die biomassa van invertebrate in sagte bodems bestaan uit detritus-voeders en is in verhouding tot die organiese inhoud van die bodem. Wortelboom-modder het die hoogste organiese inhoud en onderhou die grootste biomassa, maar min spesies kan die toestande daar oorleef. Wortelbome is waarskynlik die belangrikste primêre produsente in die sisteem.
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Mngazana Estuary is situated just south of Port St Johns in Transkei (31°42′ S 29°25′ E). It is a comparatively short estuary but is particularly rich, with probably the most extensive mangrove forests in the subtropics south of Mocambique. Three mangrove species (*Avicennia marina, Bruguiera gymnorhiza* and *Rhizophora mucronata*) occur in the estuary and Mngazana is the southern limit of the lastnamed species (Macnae 1963). Macnae (1963) has given a general account of the mangroves in southern Africa including those at Mngazana, and Wooldridge (1977) has described the zooplankton of Mngazana.

The Transkeian coastline is a mosaic of forest and grassland with numerous estuaries. Much of the area has been denuded by shifting agriculture, veld burning, over-grazing and erosion. Erosion in particular has been responsible for the degradation of many estuaries, which have become silted up. Advances within the country will inevitably place further pressures on the coastline and particularly on estuaries and there is need for a master plan for the coast line to guide further development of townships, tourism, industry and conservation. Because of this the present survey of Mngazana Estuary provides information on the status of this estuary, and the survey was encouraged by the Transkeian Government and particularly the Department of Nature Conservation. The first survey was undertaken by the University of Cape Town Habitat Group and resulted in a report which was submitted to the Transkei Government (Glyphis 1976) a summary of which is given by Branch (1976).

Methods

Mngazana Estuary was visited for six days in June 1975 by members of the University of Cape Town Habitat Group. Two further trips of seven days each were undertaken by the first author in December 1975 and June 1976 and a final visit of five days by the second author in August 1977. Many staff and students from the University of Cape Town were involved on each trip and the authors acknowledge a great debt to them.

Measurements of physical factors were made at Stations 1 to 9 (Fig. 1). Dissolved oxygen concentrations were measured with oxygen meters and the results corrected for salinity. The transparency of the water was measured with a Secchi disc and salinity with an American Optics salinometer, or by a conductivity meter.

Water samples were analyzed for nitrate, nitrite, silicate and total phosphorus using the standard methods of Strickland & Parsons (1968). The samples were kept cold, and frozen on return to Cape Town two days later. Substrate particle size was determined by dry sieving through a nest of sieves at $\frac{1}{2}$ phi intervals after washing off the silt and clay fraction (less than 62μm). The percentage organic material in the substrate was calculated after combustion of the samples at 540° for 6 hours.

A series of nine transects (T1—T9 in Fig. 1) was undertaken at representative sites along the estuary. Quantitive samples were obtained from 0,25 or 0,125 m^2 quadrats, dug to a depth of 30 cm and sieved through 1 mm sieves. All biomass figures are given in terms of ash-free dry mass, obtained by combustion of whole animals. In the case of molluscs, shells were removed before combustion.

Fish were collected only on the first two trips using two 30 m gill nets of 4 cm stretched mesh, a 20 m seine net of 2 cm stretched mesh, and for juvenile fish a scoop net of 3 m length and 1 mm mesh. The positions at which gill and seine netting were undertaken are shown in Fig. 1.

Description of the Estuary

The catchment of Mngazana is comparatively small (275 km^2) lying largely in the coastal hills. The surrounding steep hills are clothed in dense forest while the less steep areas carry *Acacia* scrub or grasslands or are cultivated with maize. Most of the area was probably originally covered with forest but has been denuded as trees were cut for wood (used primarily as firewood or for building huts) or burnt to allow agriculture. The remaining forests are on shallow rocky soil on steep slopes and their conservation is important. Clearance of forests leads to erosion of the bare soil and the subsoil leaches, rapidly leaving land of poor agricultural potential.

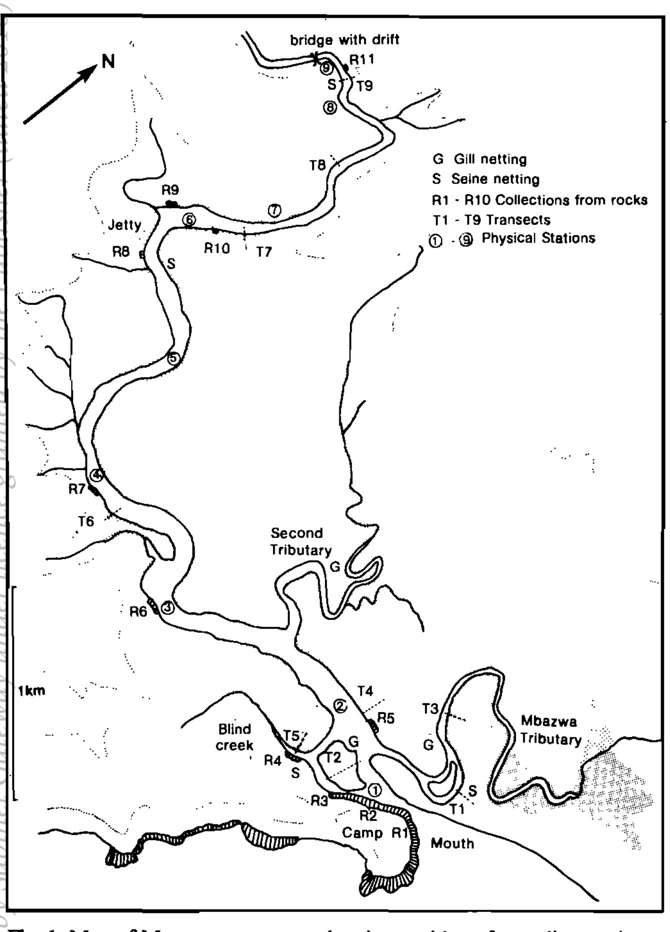

Fig. 1 Map of Mngazana estuary, showing position of sampling stations 1—9 at which physical conditions were recorded, transects T1—T9 where quantitative faunal samples were taken in mud or sand and rocky outcrops R1—R10 where rocky substrates were sampled. The dotted line shows the 15 m contour. Light and dark shading indicates the distribution of sparse and dense mangroves.

Rainfall records are not kept at Mngazana, but Port St Johns (16 km north-east) has an annual average of 1035 mm and the catchment area for Mngazana receives about 850 mm per year (Wooldridge 1977). Rain occurs throughout the year but falls mainly in summer (November—January) with a minimum in July. Wooldridge (1977) records an average of 139 mm in November and 44 mm in July but there are occasional extreme floods: in April 1978 650 mm fell in three days and the river burst its banks spreading from a normal width of about 60 m at the jetty to 800 m.

The Mngazana river is about 150 km long (Macnae 1963) but only the lower 5,3 km are estuarine, the limit of the estuary being effectively marked by a bridge which crosses the estuary (Fig. 1). the weir under this bridge is built up and prevents the tide from pushing further up the river except at extreme high spring tides and the water above is almost fresh.

Broadly speaking the estuary can be divided into four regions using Day's (1951) classification:

The head of the estuary (Station 9)

Salinity very variable, approaching fresh water conditions at times; shallow and fast flowing; bottom of pebbles; fauna of estuarine and brackish water species; mangroves absent.

The upper reaches (Stations 7 & 8)

Salinity still variable; substrate of rocks embedded in mud; fauna transitional, with estuarine and euryhaline marine species; only a narrow band of mangroves.

Middle reaches (Stations 2 – 6)

Salinity more constant; currents lower; substrate muddy; mangroves well developed and *Zostera* beds present; fauna mainly euryhaline marine species.

Lower reaches (Station 1)

Broad lagoon with deep channels; salinity consistently similar to that of sea water; substrate clean sand or rocks; water clear; stenohaline and euryhaline marine fauna.

The west bank of the mouth is bounded by a rocky promontory (Figs. 1, 16) which projects seawards and rises steeply from the estuary. This prevents further movement of the mouth in a westerly direction and protects the mouth from longshore drift minimizing sand deposition in the mouth. Rocky promontories such as these are a common feature of many of the Transkei estuaries with perenially open mouths. The east bank of the mouth consists of sand dunes well vegetated at the crest with *Eugenia capensis* and *Passerina rigida* or by a climax dune-forest in the more established areas. Dominant in these forests is *Mimusops* *obovata.* At the mouth this dune narrows and swings into the estuary where it forms a sandy bar partly stabilized by the pioneering *Scaevola thunbergii* (Fig. 16). This bar narrows the entrance of the Mbazwa tributary into the main river (Fig. 1). The mouth is about 50 m wide and 1 m deep at low tide.

The main estuary receives two tributaries. The first is the Mbazwa which is about 10 km long and drains most of the land between the Mngazana and the eastern mountain ranges; while the second is only 2 km long but drains extensive mangroves. Both tributaries are shallow not exceeding 2 m in depth for most of their length.

The mouth opens into a broad lagoon with central intertidal sand-banks around which channels pass (Fig. 16). The western channel is deep for most of its course (3,5 to 4,0 m). The position of the sand-banks and the depth of the channels are very changeable, due to change in tidal currents and the flow of the river. Despite these extensive changes to the lagoon, flooding has little impact on the main channel at the mouth where the rocky western bank limits its movement.

Above the lagoon the middle reaches of the estuary wind up as far as the jetty, with a fairly constant depth of about 2 — 3 m and a width of 50 — 80 m (at high tide). The outer banks of each curve are deeply eroded forming salting cliffs, while the inner bends slope more gently and are dominated by mangroves (Fig. 1), the roots and pneumatophores of which consolidate the substrate.

Above the jetty there is a short stretch (the upper reaches) where the gradient of the river bed increases sharply and the depth decreases. Both ebbing and flooding tides form a series of rapids over the shallow bolder-lined bed reaching a flow of 1,2 ms^{-1}. This stretch also marks the furthest penetration of mangroves, only stunted stands of *Avicennia* and *Bruguiera* lining the bank. Beyond the rapids is a short stretch of deep water (3 m at high tide) and, at the head of the estuary, a second stretch of progressively shallower water (60 cm at high tide) where the bottom is again lined with pebbles and bolders and overlain with silt. The banks are well-defined, steeply eroded and lined with reeds above the level of high spring tide.

Tidal effects are felt for the full length of the estuary, declining from a spring tide range of 1,7 m just inside the mouth to 0,7 m at the bridge. Certainly the tide would push further up the river if it were not for the weir under the bridge. Tidal exchange is considerable and even at the jetty (Station 6) a range of 1,35 m was recorded. Tidal lag between the mouth and the jetty was about 25 minutes on the rising spring tide.

Physical conditions

Salinity

Figure 2 shows the change of salinity along the estuary. Between the mouth and the jetty salinities remain high but decline rapidly above this point to essentially fresh water conditions at the bridge (Station 9). There is a marked vertical gradient, particularly in the upper reaches where surface salinities are between five—30% lower than the bottom salinities. Wooldridge (1977) recorded similar stratification in the estuary. The surface salinity is markedly lowered by the ebb tide. Vertical stratification has the important conseqence that organisms on, or in the bed

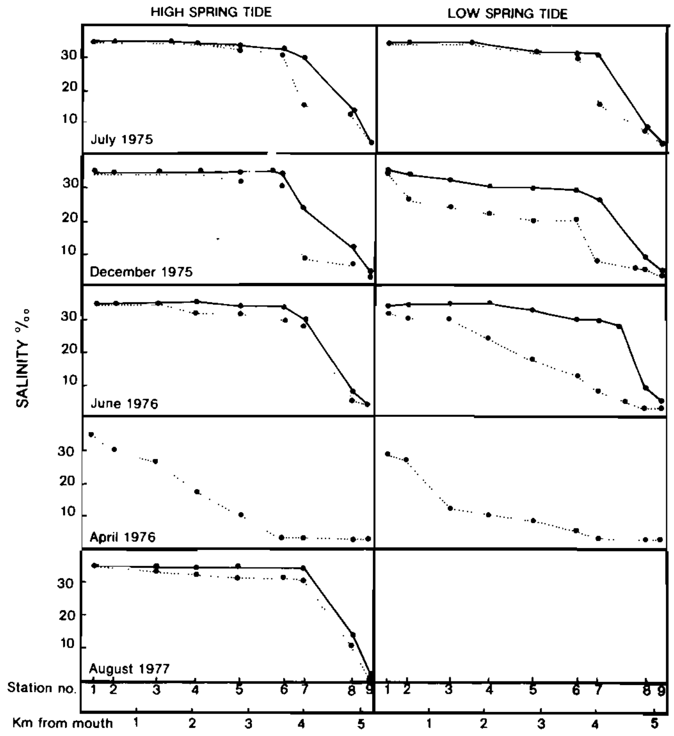

Fig. 2 Salinity gradients from the mouth to the head of Mngazana estuary. Samples from the surface of the water are shown with a dotted line, and those from the bottom with an unbroken line.

scarcely experience tidal salinity changes which are most marked in the surface layers of the water. Although the heaviest rains fall in summer, seasonal variations in salinity are small. Samples kindly collected by Mr A. Rose in April 1976, two weeks after the worst floods ever recorded to that date, show that even after extreme conditions of rainfall the salinities were not excessively reduced, and by June 1976 had returned to normal. It is also likely that stratification would have buffered the effects of flooding. The annual range of salinity is shown in Fig. 13A, and again the great range experienced by surface waters is evident.

Transparency

The water in Mngazana estuary is remarkably clear. Transparency is shown in Fig. 3. Throughout the estuary readings exceed 40 cm, increasing from the head to the mouth.

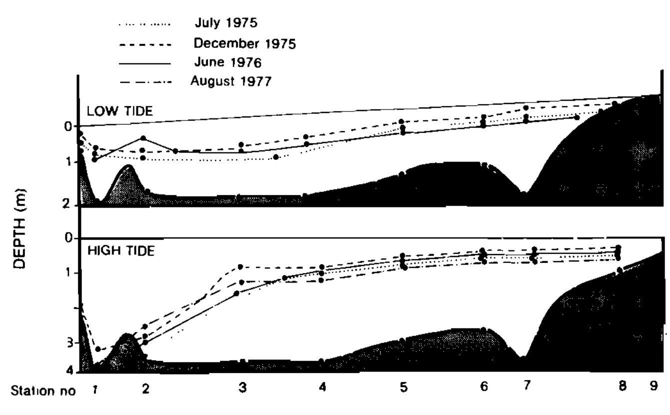

Fig. 3 Measurements of water transparency and depth in Mngazana estuary. The line indicating the surface of the water at low tide slopes to give an indication of the difference in tidal range when compared with the equivalent line for high tide. Transparency is given as the depth at which a secchi disc is visible from the surface.

Seasonal variations are small, but in the lower reaches (Stations 1 & 2) the tidal influence is considerable. With the rising tide, sea water forces its way up the estuary and the bottom becomes clearly visible. This clean water penetrates about 2 km up the estuary giving some indication of the considerable tidal exchange that occurs. Above this point transparency is more constant although it is always greater at high tide. The clear water at Mngazana is in sharp contrast with that of most other Transkeian and Natal estuaries. Mngazana evidently carries a low silt load, partly because its catchment is small and falls in an undeveloped coastal area where comparatively little agriculture is undertaken, but also because the extensive mangroves act as a natural silt trap.

Water temperature and oxygen concentrations

In winter water temperatures decline from 19 to 16 °C from the mouth to the head. Data for June 1975 (Fig. 4) illustrate this trend and also show that there is a slight vertical temperature gradient, the surface waters being about 0,3 to 0,8 °C cooler than the more saline bottom layers. In June 1976 a very similar pattern existed, except that the temperatures were generally 2 °C lower and the temperature gradient was more obvious, surface waters being 0,3 to 2,0 °C cooler.

During summer the main body of the estuary is about 3 °C warmer than in winter but temperatures rise sharply from about 21 °C at the mouth to 26 °C in the upper reaches (Fig. 4) so that the latter part of the estuary experiences a wide annual range of temperature. The vertical temperature gradient is reversed in summer, the cooler saline waters lying beneath the warm layers of fresher water. Bottom waters thus have more stable temperatures because of sea water intrusion. The state of the tide has little effect on water temperature, differences between low and high tide seldom exceeding 2 °C. These small differences may be due to solar heating rather than tidal exchange.

Oxygen tensions are moderately high throughout the system with no obvius gradient along the estuary (Table 1). Values for bottom samples were usually slightly lower than those at the surface. Oxygen levels are highest below the bridge where the water is fresh and turbulent and at Station 7 where the estuary is shallow and forms rapids at low tide. Samples of interstitial water drawn from a depth of 20 cm in the sand-banks and the mangrove mud were respectively 62 and 5% saturated.

Table 1 Dissolved oxygen concentration in Mngazana estuary (ppm).
Figures in brackets indicate percentage saturation

Station	Dec. 1975 High tide		Dec. 1975 Low tide		Aug. 1977 High tide	
	Surface	Bottom	Surface	Bottom	Surface	Bottom
1	8,3(114)	—	7,1(95)	—	6,1(85)	6,2(87)
2	7,5(103)	7,2(92)	6,9(88)	7,1(91)	6,3(88)	—
3	8,1(111)	7,3(98)	6,4(80)	6,3(82)	4,8(73)	5,5(77)
4	7,3(100)	7,3(98)	6,3(81)	6,3(82)	5,9(80)	—
5	7,8(101)	7,2(96)	6,2(77)	5,7(74)	5,4(75)	4,2(58)
6	8,5(113)	6,5(86)	5,9(76)	5,6(72)	5,3(74)	—
7	8,5(113)	6,9(91)	7,2(94)	4,8(64)	4,7(65)	4,4(61)
8	—	—	—	—	—	—
9	—	—	7,7(103)	—	6,9(73)	—

Substrate

The nature of the substrate at various tidal levels on Transects 1—3 and 5—7 is given in Table 2. The mouth of the lagoon, the sandbanks and the sand bar extending into the lagoon (Transects 1 & 2) all have well-sorted fine sand which is clean and has a low organic content. This substrate is quite different from the rest of the estuary. The absence of silt, the low organic content and the well-sorted nature of this fine sand suggests that it is mainly of marine origin, being transported in with the tides or formed from the eastern sand-bar which extends into the lagoon (Fig. 1). The substrate is finer but still well sorted in the middle reaches (Transect 6), while in the mangroves there is a glutinous mud with a very small median particle size, high organic content and a high percentage of silt and clay (Transect 5). To a lesser extent *Zostera* beds also have a high organic content (Transects 3 & 5). At Transects 7 (above the jetty) and 9 (just below the bridge) the river bottom is lined with pebbles, loosely filled in with gravel, and silt so that the median particle size is far higher than elsewhere and the substrate is poorly sorted. At both these sites the river is very shallow and at low tide rapids form so that the substrate is unstable. It is interesting that the narrow band of mangroves in the middle of Transect 7 con-

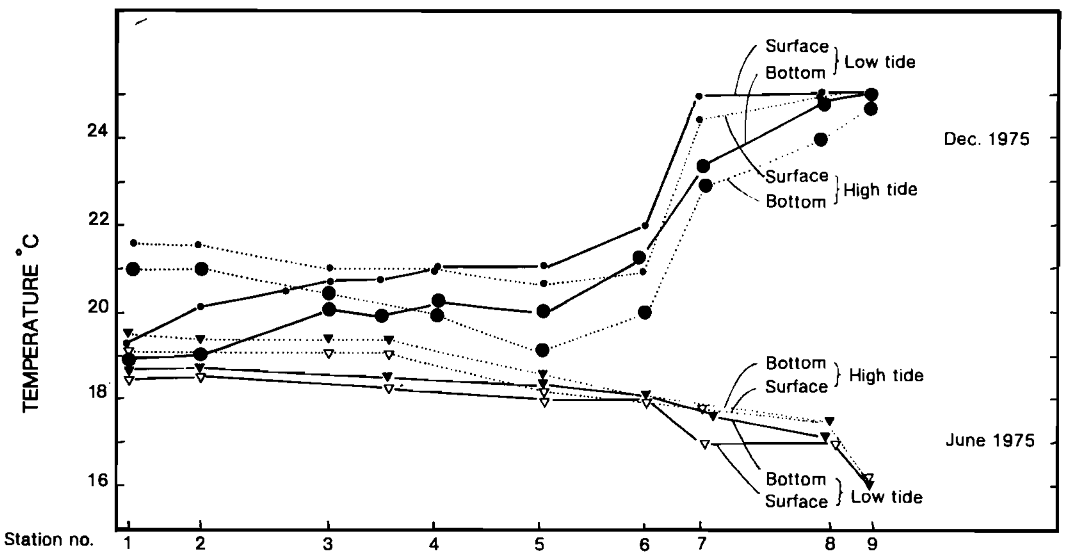

Fig 4. Water temperatures in Mngazana. Data for surface and bottom water samples and for high and low tide. The curves contrast summer (December) and winter (June) conditions.

Table 2 Character of the substrate at various transects. Tidal levels: high water springs (HWS), high water neaps (HWN), midtide (MT), low water springs (LWS) and subtidally 0,7 m below low tide (ST)

Transect number	Tidal level	Median particle size Q	Sorting QdQ	% silt and clay	% organic matter	Comments
1	HWS	2,5	0,15	0,2	1,3	Sand-bank
	MT	2,4	0,12	0,4	1,7	Sand-bank
	LWS	2,3	0,17	—	—	Sand-bank
	ST	1,9	0,13	1,2	0,2	Sand-bank
2	MT	2,4	0,19	1,9	1,4	Sand-bank
	MT	1,8	0,20	2,4	—	Sand-bank
	LWS	2,1	0,14	1,6	0,9	Sand-bank
3	HWS	2,5	0,23	3,2	1,2	Above mangroves
	HWN	3,6	0,46	45,0	7,4	In mangroves
	MT	2,7	0,42	22,0	3,1	In *Zostera* bed
	LWS	2,6	0,42	10,0	3,2	In *Zostera* bed
	ST	2,4	0,23	4,7	1,2	In *Zostera* bed
5	HWS	2,4	0,28	10,3	2,5	Clean sand above mangroves
	MT	3,6	0,46	84,0	11,0	In mangroves
	LWS	2,9	0,48	23,0	4,5	In *Zostera* bed
	ST	2,3	0,42	2,3	4,5	In blind creek: anoxic
6	HWS	1,2	0,89	2,3	0,2	
	MT	2,9	0,35	14,2	4,0	Among *Avicennia* pneumatophores
	LWS	2,9	0,47	10,2	1,4	Anoxic mud
	ST	2,6	0,52	10,2	1,3	Anoxic mud
7	HWS	1,2	1,82	—	—	
	MT	3,2	0,46	23,4	4,2	In mangroves
	LWS	−0,2	1,42	1,2	—	In rapids
	ST	−0,1	1,12	1,2	—	In rapids

tains a very fine well-sorted substrate: testimony to the efficacy of the mangrove rootlet system in retaining and consolidating silt. Particle size is negatively correlated with percentage organic material (Fig. 5), an effect many other authors have previously shown (Newell 1970: 249-251 (summary); Dale 1974). In every case the substrates with a high organic content and a very low particle size are associated with mangroves, or to a lesser extent with *Zostera* beds.

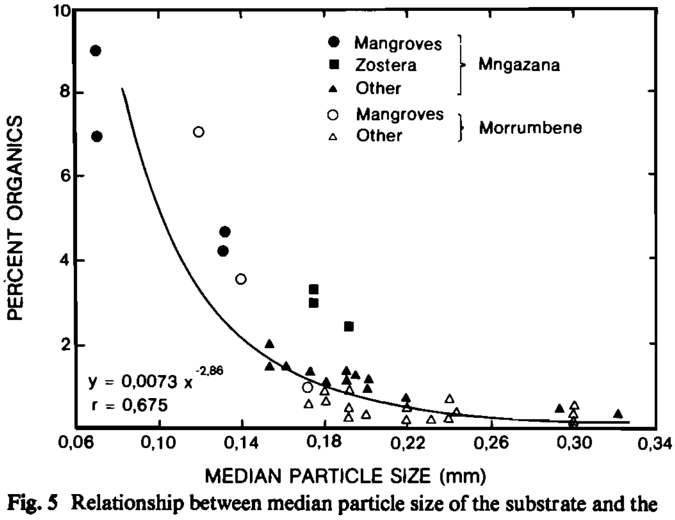

Fig. 5 Relationship between median particle size of the substrate and the percentage of organic material in dry sediments. Data for Morrumbene are drawn from Day (1974) and are indicated by open symbols. Data points for Mngazana are shown as closed symbols.

Water chemistry

Data regarding water chemistry are shown in Table 3 for samples taken at high tide in August 1977.

Total phosphorus values ranged from 0,21—1,21μg-at.l^{-1}. Some high values were recorded in bottom water with the highest on the bottom of a mangrove channel in the second tributary (Station 11). These higher values are probably related to the release of phosphate from organic sediments.

Silicate values ranged from 3,97—55,19μg-at.l^{-1}. Values increased towards the head of the estuary but were low in the incoming fresh water at Station 9. The low concentration in the river water is remarkable in view of the clear trend of concentration up the estuary. Silicate values in bottom water were somewhat lower, perhaps because of the salt-wedge effect in tidal exchange.

Nitrite values ranged from 0,09—0,79μg-at.l^{-1}. Values increased towards the head of the estuary being highest at Station 9.

Nitrate values ranged from 0,38—12,23 μg-at.l^{-1}. High surface values were recorded in the middle reaches (Stations 3 to 7) but the highest value was recorded on the bottom at Station 1. This suggests that the influx of nitrate of marine origin might be significant, particulary in view of the very low value in the river water.

The nutrient data recorded may have been affected by a delay in freezing the samples before analysis, but the ranges of variation recorded are similar to those for other estuaries. Graphical correlations with salinity do not reveal clear evidence of marine or riverine origins. It would appear that the variations in nutrients recorded may have been determined largely by local biological activity.

Vegetation

The Mngazana estuary includes a mangrove swamp covering approximately 340 ha and consisting of three species, *Avicennia marina, Bruguiera gymnorhiza* and *Rhizophora mucronata*. Some specimens of the 'fresh water mangrove' *Hibiscus tiliaceus* are associated with the true mangroves. In addition to the mangrove community a sea-grass community dominated by *Zostera capensis* and a salt-marsh community dominated by species of *Sarcocornia* are important. The low phytoplankton biomass occurring in the estuary indicates that the macrophytes, and in particular the mangroves are the major primary producers in this estuary.

Avicennia marina appears to play a pioneer role both on the seaward fringe and at the landward edge of mangroves. Gently graded shores where accretion is taking place such as on the inside of bends in the estuary are occupied by *Avicennia* saplings. Behind some mangroves in areas which are only covered by spring tides, stunted *Avicennia* trees are also found. They are gnarled and twisted and rarely grow taller than 1,5 m probably because of the high soil salinity in such areas. Where *Avicennia* are well established in favourable areas near the main channels they form groves up to about 10 m high.

Table 3 Mngazana estuary water chemistry

Station	Level	Salinity	Oxygen (ppm)	Total phosphorus (μg-at. l^{-1})	Silicate (μg-at. l^{-1})	Nitrite (μg-at. l^{-1})	Nitrate (μg-at. l^{-1})
1	Surface	35,5	6,1	0,70	5,33	0,28	1,67
	Bottom	35,5	6.2	0,43	5,50	0,27	12,23
2	Surface	35,5	6,3	—	—	—	—
	Bottom	—	—	—	—	—	—
3	Surface	33,8	4,8	0,45	40,57	0,51	8,46
	Bottom	34.6	5.5	1,05	20,45	0,32	4,20
4	Surface	32,6	5,9	—	—	—	—
	Bottom	—	—	—	—	—	—
5	Surface	31,6	5,4	0,50	50,77	0,62	9,75
	Bottom	34,6	4,2	0,68	26,97	0,26	4,85
6	Surface	32,4	5,3	—	—	—	—
	Bottom	—	—	—	—	—	—
7	Surface	31,6	4,7	0,81	55,19	0,68	8,73
	Bottom	34,2	4,4	—	—	—	—
8	Surface	—	—	—	—	—	—
	Bottom	—	—	—	—	—	—
9	Surface	0,16	6,9	0,86	3,97	0,79	0,59
	Bottom	—	—	—	—	—	—
10[a]	Surface	35,3	5,5	0,41	20,28	0,60	0,38
	Bottom	35,5	5,8	0,21	14,33	0,09	—
11[a]	Surface	36,2	4,6	0,54	31,45	0,09	1,02
	Bottom	35,1	4,4	1,21	30,82	0,20	0,97

[a] Stations 10 and 11 were in the second tributary (Fig. 1) 400 m up at the second bend and 1 000 m up at the fourth bend respectively.

Bruguiera gymnorhiza appears to favour firm ground in the protected central areas of the Mngazana mangroves. In a number of places, including along the main channel of the estuary, *Bruguiera* does occur at the water's edge where bank erosion is taking place.

Rhizophora mucronata dominates the fringes of mangrove creeks such as the first and second tributaries of the Mngazana. Here it appears to play a pioneer role, and dense fringing stands exclude other species. A fine clayey substrate is present in such areas, and it would appear that the nature of the substrate is important, as *Rhizophora* also occurs away from channels in areas of waterlogged fine clayey mud.

Although it is possible to distinguish environmental conditions which appear to be favoured by the three species, limiting factors for the species are not obvious. A mixed community of all three species is the most widespread association and all three species do occur in a wide variety of conditions.

A dark felt or 'Bostrychetum' of algae covers the pneumatophores of *Avicennia* and to a lesser extent the knee-roots of *Bruguiera* and the prop-roots of *Rhizophora*. *Bostrychia tenella* and several other species of Rhodophyta make up this characteristic epiphytic community.

Hibiscus tiliaceus appears in a few places where freshwater seepage is evident from behind the mangroves. Some *Hibiscus* flowers are orange rather than the normal yellow form.

The sea-grass *Zostera capensis* occurs in many of the more sheltered shallow channels at levels where it is exposed only at low tide and occurs also at levels somewhat below LWST. *Zostera* is particularly abundant in the lower reaches of the first tributary. Samples indicated the following biomass values per square metre: live 714,0 g; dry 103,8 g; ash-free dry 44,0 g. Small numbers of *Halophila ovalis* occur associated with *Zostera*. *Zostera* supports a dense growth of epiphytic algae and diatoms. The high productivity and shelter provided by *Zostera* attract large numbers and a high diversity of fishes and other marine organisms.

Large areas of saltmarsh occur in the flood-plain area surrounding the estuary, particularly between Stations 1 & 4. Some of these areas are partly intertidal and flooded at least by high spring tides but others are apparently beyond the reach of the tides. These saltmarsh areas are in open stretches between the mangroves and occasonally landward of the mangroves. The vegetation is dominated by species of *Sarcocornia* but *Chenolea diffusa*, *Cotula coronopifolia*, *Triglochin bulbosa*, and *Juncus kraussii* are also common. All of these latter species favour areas near HWST or above. The dominant species in the lower areas of the saltmarshes is *Sarcocornia perennis* which forms prostrate dull-green patches. At a higher level *Sarcocornia decumbens* is the dominant species, forming reddish more erect patches. In the area of Transect T4 there is an intermediate zone of bright green *Sarcocornia perennis*.

Sarcocornia natalensis occurs on the banks at Stations 6, 7 and 8. Several species of reeds, including *Scirpus littoralis, Cyperus textilus* and *Phragmites australis* grow on the banks in the upper reaches, and patches of *Phragmites* appear as far down as Station 4. The distribution of the major aquatic and marginal plant species and the observed salinity range is indicated in Fig. 6.

Station	1	2	3	4	5	6	7	8	9
Salinity :-									
Surface maximum (H.W.winter)	35	35	35	35	34	33	31	13	4
Surface minimum (L.W.summer)	36	26	22	24	20	20	5	6	0
Scaevola thunbergii	◆	—	—	—	—	—	—	—	—
Ipomea pes-caprae	◆	—	—	—	—	—	—	—	—
Caulerpa racemosa	◆	◆	—	—	—	—	—	—	—
Halophila ovalis	◆	◆	—	—	—	—	—	—	—
Zostera capensis	◆	◆	◆	—	—	—	—	—	—
Triglochin bulbosa	—	◆	—	—	—	—	—	—	—
Sarcocornia spp	—	◆	◆	◆	◆	◆	◆	—	—
Chenolea diffusa	—	◆	◆	◆	◆	◆	◆	—	—
Rhizophora mucronata	◆	◆	◆	◆	◆	◆	—	—	—
Bruguiera gymnorhiza	◆	◆	◆	◆	◆	◆	◆	—	—
Avicennia marina	◆	◆	◆	◆	◆	◆	◆	◆	—
Bostrichia spp	◆	◆	◆	◆	◆	◆	◆	◆	—
Juncus kraussii	◆	◆	◆	◆	◆	◆	◆	◆	◆
Cotula coronipifolia	—	—	◆	◆	◆	◆	◆	◆	—
Phragmites australis	—	—	—	◆	◆	◆	◆	◆	◆
Cyperus textilus	—	—	—	—	—	—	◆	◆	◆
Scirpus littoralis	—	—	—	—	—	—	◆	◆	◆

Fig. 6 Distribution of aquatic and marginal vegetation. The presence of a species at or near a station is indicated by a black diamond. An indication of the salinity range is given by the maximum and minimum surface salinities recorded.

Fauna of soft substrates

Transects across sand-banks of the lagoon

Transects T1 and T2 were positioned across the eastern bank of the Mbazwa tributary and across the central sand-banks in the lagoon (Fig. 1). Both sites are lacking in vegetation, have a clean fine sandy substrate (Table 2), and in general share a common fauna. Figure 7 shows the first of these transects with additional data incorporated from the sand-banks. Both areas have a fauna quite distinct from that of the rest of the estuary. Subtidally there is a very poor fauna of only five species, but immediately above LWS the diversity increases. The lower shore and subtidal areas are dominated by the amphipod *Urothoe pulchella*, which is replaced at higher levels by large numbers of *Pontogeloides latipes* and *Eurydice longicornis*. Near the high-tide mark numerous staphylinid beetles (*?Bledius* sp.) burrow into the surface layers of the sand and are associated with carabids (*Axinidium ? africanum*) which prey upon them. *Callianassa kraussi* and *Scolelepis squamata* occur in fair numbers but are restricted to the central sand-banks.

The fauna in these areas is interesting for a number of reasons. There is a high percentage of species which are normally associated with exposed open beaches, including *Hippa adactyla, Donax serra, Ocypode, Pontogeloides* and *Eurydice*; and *Virgularia* which is not usually found in estuaries. The occurrence of these normally marine species relates to the consistently high salinity in the lagoon (Fig. 2)

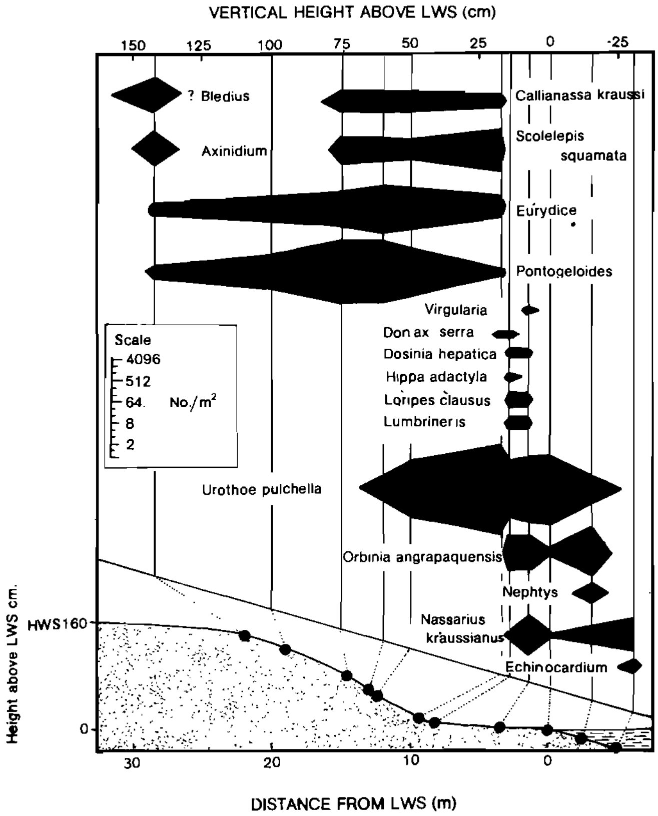

Fig. 7 Transect across the sand banks near the mouth (T1). Data for densities on the central sand banks (T2) have also been included. Asterisks indicate species restricted to T2.

and to the clean sandy substrate which is quite different to that of the rest of the estuary and probably of marine origin. The low organic content of the substrate restricts the fauna, and the biomass of detritus feeders is low. *Eurydice* and *Pontogeloides* are both known to leave the substrate at high tide and feed while swimming in the water above, as evidenced by their occurrence in plankton hauls. Many of the species in the clean sands of the lagoon are filter feeders, scavengers or carnivores.

Parts of the centre banks are overlain with silt and in areas cores of the substrate reveal a stratification with layers of silt being interspersed with clean sand. The silt is evidently of riverine origin and probably deposited after floods, to be covered by clean sand of marine origin. Where the silt is exposed at the surface quite a different fauna is found, including species such as *Macrophthalmus boscii, Paramoera capensis* and *Amaryllis macrophthalma* which replace the clean sand fauna.

Transect across mangroves

Transect T5 was undertaken across a blind creek and through dense mangroves (Fig. 8). The creek experiences comparatively little water movement and although the water is fairly well oxygenated the substrate consists of sandy mud which is black almost to the surface. The lower intertidal region is drained each tidal cycle and the black layer is about 12 cm from the surface of the mud. In this region there is a sparse growth of *Zostera* and *Halophila* which appears to be stunted due to smothering by the fine mangrove mud. Mangroves appear about 25 cm above LWS, *Rhizophora* forming a narrow fringing stand behind which there is a thick growth of mangroves, mainly *Avicennia*, but also containing *Bruguiera and Rhizophora.*

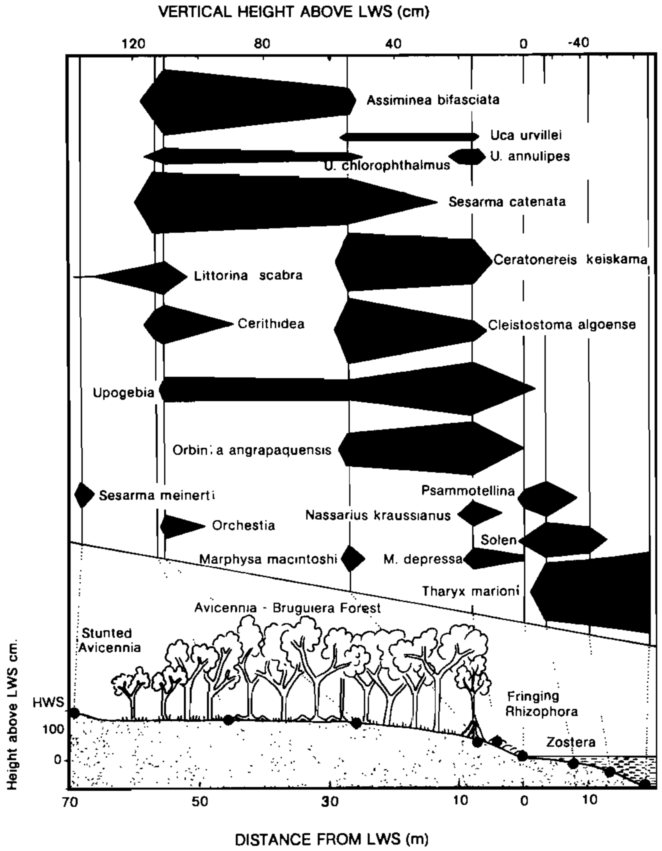

Fig. 8 Transect T5 across blind creek and through mangroves. Scale as in Fig. 7.

Avicennia penetrates furthest on the landward side, stunted individuals occurring almost up to HWS. Throughout the mangrove forest the substrate is typically a fine black anoxic mud, consolidated by the extensive mangrove rootlets and penetrated by the dense upright pneumatophores of *Avicennia*.

The zonation of the fauna is sharply defined. Below LWS the black mud houses few species, dominated by exceptionally dense communities of the polychaete *Tharyx marioni,*a species usually found in deep-water samples from the open sea (J.H. Day *pers. comm.*). In the shallower parts of the creek, *Psammotellina capensis* and *Solen corneus* are also common. At LWS the fauna changes abruptly and a larger number of species occur in the more oxidized sediments of the *Zostera* bed. Two infaunal polychaetes *Ceratonereis keiskamma* and *Orbinia angrapaquensis*, the crab *Cleistostoma algoense* and *Upogebia africana* are the dominant species. There is also a large number of species living on the surface of the mud including *Nassarius kraussiana, Clibanarius longitarsus, Aglaia capensis,* and *Natica* sp. Of the species in the *Zostera* only *Upogebia* extends into the mangroves, declining both in numbers and mean size as it does so.

The mangroves have a distinctly different fauna. Macnae and Kalk (1962), Macnae (1963) and Day (1974) have shown that there are no species which are confined to mangroves, but nevertheless there are species which predominate there and are seldom found abundantly elsewhere. The mangrove substrate places severe limitations on animals for it is very fine and almost totally anoxic and consequently there is practically no infauna. On the other hand the substrate is rich in organic material. There are limited options allowing animals to overcome the restrictions of the substrate in order to capitalize on the rich food source. *Assiminea bifasciata* occurs in vast numbers on the surface of the mud but suffers from intense predation, being eaten by several fish and by *Scylla serrata. Cerithidea decollata* climbs the mangrove trunks, remaining there during high tide but descending to feed on the mud at low tide. Cockcroft (*pers. comm.*) has recently shown *Cerithidea* has marked rhythms of activity, the majority of individuals descending at low neap tide but practically none at low spring tide. *Littorina scabra* climbs and remains on the mangroves feeding on the surface of the trunk. *Sesarma catenata,* the most striking animal in the mangroves, digs firm mud-burrows into the substrate. At low tide, hordes of these crabs scurry between the pneumatophores, feeding on detritus or collecting mangrove leaves which are then dragged down the crab's burrows. At high tide these crabs remain in their burrows although at night many were found climbing in the mangrove trees. Small numbers of *Uca* spp. occur in the mangroves but are much more abundant on the fringe of the mangroves and on the banks of the estuary or at the lower edge of salt marshes. They too form firm burrows in the mud and retreat into these burrows at high tide closing over the mouth of the burrow as they do so. Finally there are species which avoid the substrate by colonizing the algal bostrychetum which clothes the pneumatophores. These include the amphipod *Orchestia rectipalma* and the polychaetes *Perinereis nuntia vallata* and *P. falsovariegata.* Surprisingly, no *Saccostrea* (*Crassostrea*) *cucullata* and few barnacles were found on the mangrove pneumatophores, possibly because of the dense bostrychetum.

Above the mangroves the substrate was compacted and dry and inhabited only by a large crab *Sesarma meinerti* which digs deep tunnels down to the water table, sometimes exceeding 1,5 m in depth. *S. meinerti* scavenges at low tide, descending down the shore into the mangroves and feeding on coarse detritus, bark, lichen and leaves. These crabs are extraordinarily sensitive to the fall of mangrove leaves, emerging from their tunnels in response to a single leaf falling.

Transect across Zostera beds

Transect T3 ran from LWS across dense *Zostera* and up into mangroves. As in the previous transect the fauna changed abruptly at the beginning of the mangroves where the fauna was very similar to that described above for the mangroves of T5, but the *Zostera* beds below the mangroves supported a very diverse fauna summarized in Table 4. The high number of species in the *Zostera* beds can be contrasted with that in the stations below the beds, and with those in the sand-banks (Fig. 7) or mangroves (Fig. 8). Both the number of invertebrate species and their biomass appeared to be related to the biomass of the *Zostera* (Table 4). Many of the species are detritivores, certainly dependant on the high organic content of the *Zostera* beds (Table 2). The most common species were *Cirriformia tentaculata* and *Ceratonereis erythraeensis.* Several penaeid prawns occurred in the *Zostera* beds, and *Palaemon pacificus* was also common.

Transect across salt-marshes

Transect T4 ran across the salt-marshes north of Station 2 (Fig. 9). A steep bank of bare mud rises to 1 metre or more above LWS from where the sparsely vegetated salt-marsh

Table 4 Densities of the more abundant species recorded in *Zostera* beds at T3. Station A was below the *Zostera* beds, B at the lower edge and E near the upper limit

Station	A	B	C	D	E
Height above LWS	1,0 cm	18 cm	32 cm	29 cm	39 cm
Solen corneus	12				
Eumarcia paupercula	7	2			
Cirriformia tentaculata		36	42	245	49
Ceratonereis erythraeensis			250	560	142
Psammotellina capensis			40	8	7
Alpheus crassimanus			20	5	
Macrophtalmus boscii			16	2	
Rhynchoplax bovis			5	20	17
Tharyx marioni				39	16
Orbinia angrapaquensis				16	14
Melita zeylanica				22	16
Grandidierella bonnieroides				32	3
Cleistostoma algoense				44	36
Nassarius kraussianus				26	27
Assiminea bifasciata					27
Dosinia hepatica				7	7
Ceratonereis keiskama					27
Total no. of spp.	2	4	10	16	17
Animal biomass g m^{-2}	2,4	8,9	12,2	9,46	5,22
Zostera biomass g m^{-2}	0	Mean 103,8 (44,0 ash-free)			

extends back to the 'high-water mark' at about 2 m above LWS. The high-water mark is marked by a line of drifted plant litter and a band of *Juncus kraussii*. This would appear to be a flood or wave wash-line as it is above HWS. *Uca lactea annulipes* extends into the fringe of the marsh but *Sesarma meinerti* and *Sesarma catenata* are the dominant animals in the salt-marsh. Two species of *Sarcocornia* and *Chenolea diffusa* are the dominant marsh plants and *Triglochin bulbosa* occurs sparsely near HWN. Live biomass, dry biomass and ash-free dry biomass per square metre were determined from sample quadrats as follows:

	Live biomass	Dry biomass	Ash-free dry biomass
Sarcocornia perennis (grey)	1997,4	106,9	73,8
Sarcocornia perennis (green)	856,0	71,8	48,6
Sarcocornia decumbens	2486,0	171,3	124,9
Triglochin bulbosa	806,6	84,2	61,5
Chenolea diffusa	2912,0	161,4	117,1

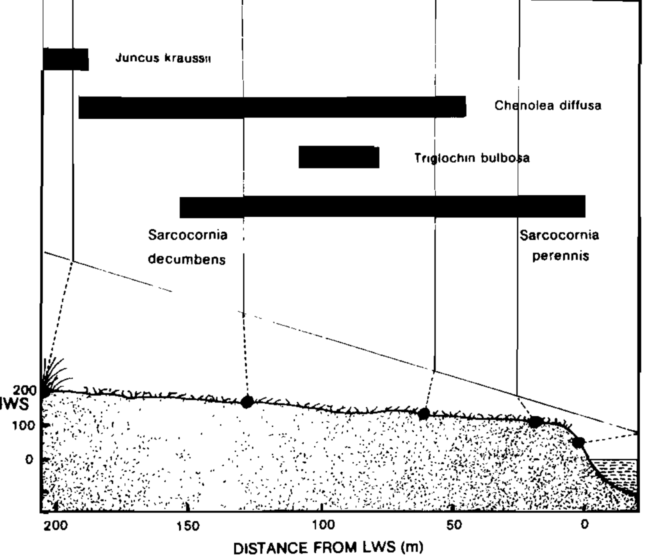

Fig. 9 Transect across the salt-marsh (T4). Scale for fauna as in Fig. 7. Abundance of plants (biomass per unit area) described in text.

Transect T6 across middle reaches

The estuary channel winds through the flood-plain with mangroves predominating on the inner curves and harbouring a fauna similar to that of T5. Transect 6 lay across the outer bank which is steeply eroded and fairly typical of this habitat in the middle reaches (Fig. 10). The substrate consists of fine sandy mud while above HWS the substrate is baked into a dry, very hard soil. The soil above HWS is also very saline and supports only isolated *Avicennia* trees and patches of *Sarcocomia*. Roots from the *Avicennia* extend into the intertidal zone and have a marked influence on the substrate which is more consolidated, finer, and has a higher organic content wherever pneumatophores appear (Table 2). No other plants appear in the intertidal zone.

Subtidally there is a fairly diverse community of polychaetes, bivalves and gastropods but almost all the life is

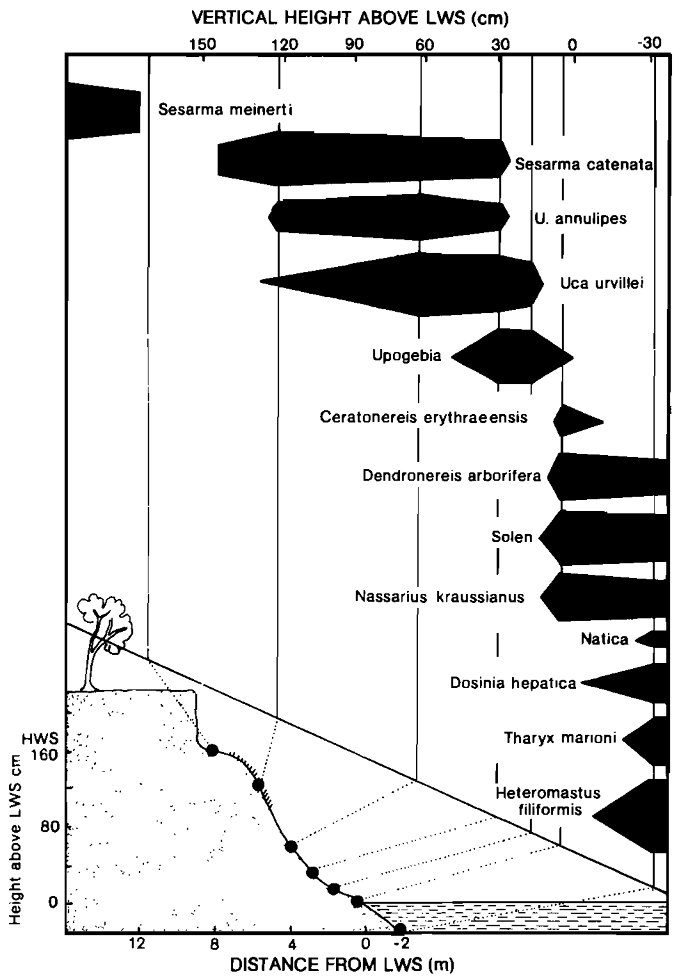

Fig. 10 Transect T6 across the bank of an outside bend of the estuary in the middle reaches. Scale of abundance as in Fig. 7.

confined to the top 10 cm of the substrate, lower layers being black and probably containing little oxygen. At the low-tide mark there is a sharp change in the fauna and the intertidal zone hosts only five species: all in large numbers. The fine mud is saturated with water but black only a few centimetres below the surface. *Upogebia africana* occurs in large numbers in the low intertidal and is the dominant animal on the steep outer banks of the middle reaches. At higher levels *Uca urvillei* and *U. lactea annulipes* are very common throughout the middle reaches although they disappear wherever the bank becomes too steep. The latter crab occupies a wide range of substrates. *U. urvillei* prefers muddier low-lying and wetter areas, but in sandier areas is replaced by *U. chlorophthalmus* which is commonest in or near the lagoon. *Uca vocans* is confined entirely to the cleaner sands of the lagoon. The ubiquitous *Sesarma catenata* is also common on the river banks especially where there are pneumatophores, but is never as abundant as it is in the mangroves. At and above HWS *S. meinerti* again makes its deep tunnels down to the water table and is the only organism which can tolerate the baked substrate. This specialized habit enables *S. meinerti* to penetate far from the water, tunnels being found up to 400 m from the bank of the channel.

Transect T7 above the jetty

Avicennia and *Bruguiera* penetrate further up the estuary than *Rhizophora*, finally disappearaing about 1 km upstream of the jetty. Transect 7 (Fig. 11) crossed the estuary bank and passed through a narrow band of mangroves. The estuary is shallow at this point, and flows swiftly over the channel bed reaching a velocity of 1 m.s^{-1} on the ebb tide. Consequently the bottom is rocky with large pebbles, gravel and sand. Above midtide the substrate changes to a fine compact mud (Table 2) partly because the current decreases as the tide rises, but mainly because the mangrove roots consolidate the substrate. This has resulted in the formation of a muddy knoll on which the mangroves grow while behind the mangroves the substrate is eroded to form a channel which is only submerged at high spring tides or during floods. Above this creek *Chenolea* lines the foot of an earth cliff which is crowned by *Phragmites* (Fig. 11).

The fauna is comparatively sparse and transitional between that of the middle reaches and upper reaches. There are fairly abrupt changes between low tide and the mangrove belt. Below the mangroves the species which predominate in the upper reaches (*Rhynchoplax bovis, Cirolana fluviatilis, Melita zeylanica* and *Orchestia rectipalma*) mingle with those which occur mainly in the middle reaches (*Dendronereis arborifera* and *Upogebia africana*). Although the mangrove belt is narrow it still supports typically mangrove species such as *Cerithidea, Littorina scabra* and *Sesarma catenata*. Above HWS it houses *S. meinerti*, but this crab is more common on the earth cliff. *S. eulimene* characteristically occurs at a higher level and also penetrates further up the estuary than *S. catenata*. None of the *Uca* species occur at or above this transect although colonizing more gently sloping banks about 200 m downstream.

Transect T9 at the head

Two transects were undertaken in the upper reaches at the head of the estuary (T8 & T9) but as they were similar, only

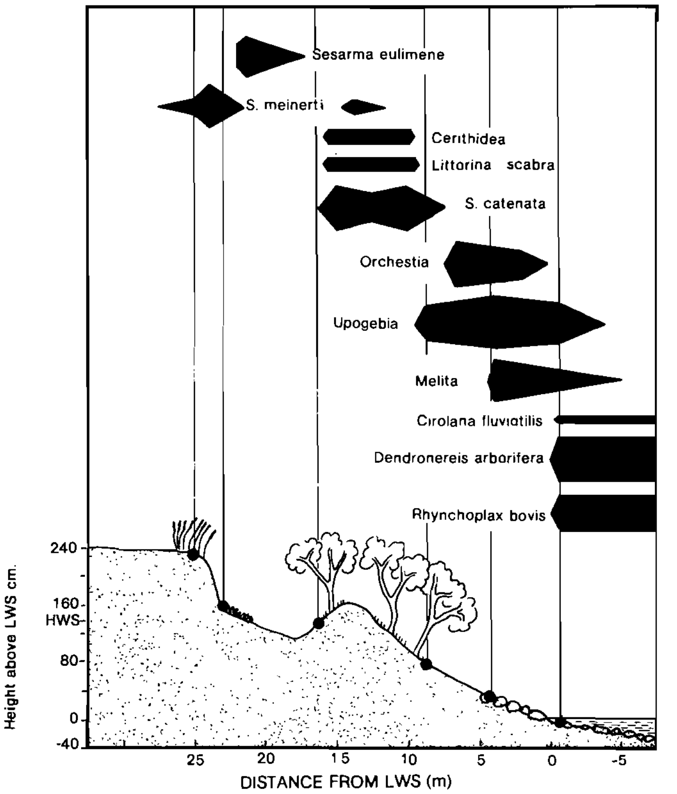

Fig. 11 Transect T7 at the upper reaches of the estuary. Scale of abundance as in Fig. 7.

T9 is described. The upper part of the estuary is narrow below the bridge and the earth banks are steeply cut away dropping between 1 and 2,5 m to the bed (Fig. 12). At low tide the water is ankle deep in most parts but the tidal range is still about 60 cm. Tidal flushing and flooding after heavy rains erode and undercut the bank and the bed is lined with smooth pebbles embedded in a poorly sorted mixture of gravel and mud. Grass fringes the top of the bank but below this the bank lacks vegetation or has scattered tufts of reeds and consists of black earth.

The fauna of the bed is surprisingly rich but quite different from that of the rest of the estuary. Many of the species occurring here are only found in estuaries and in the Mngazana estuary are either confined to the head or predominate there: *Exosphaeroma estuarium, Cirolana fluviatilis, Austrochiltonia subtenuis, Melita zeylanica, Ficopomatus enigmatica, Musculus virgiliae* and *Neritina* sp. which is limited to this region. Two euryhaline marine species become abundant at the head: the amphipod *Corophium triaenonyx* and the crab *Rhychoplax bovis*. Neither species is usually confined to the head of estuaries and their abundance there at Mngazana is evidently related to the nature of the substrate and not the salinity regime. In the Mgazi estuary, adjacent to Mngazana, both species abound in the lower reaches where the banks comprise boulders and pebbles in a sandy mud (a substrate similar to the estuary bed at the head of Mngazana).

At the head of Mngazana the bank consists of a black earthy soil devoid of life betweeen LWS and midtide but above this colonized by numerous crabs. *Sesarma meinerti* is absent and *S. catenata* only present in small numbers, but *S. eulimene* is abundant, forming deep burrows in the glutinous mud, helping to undermind the bank in the process. The amphipod *Orchestia rectipalma* capitalizes on these burrows. The top of the bank is covered with tiny black gastropods (? *Assiminea globulus.*)

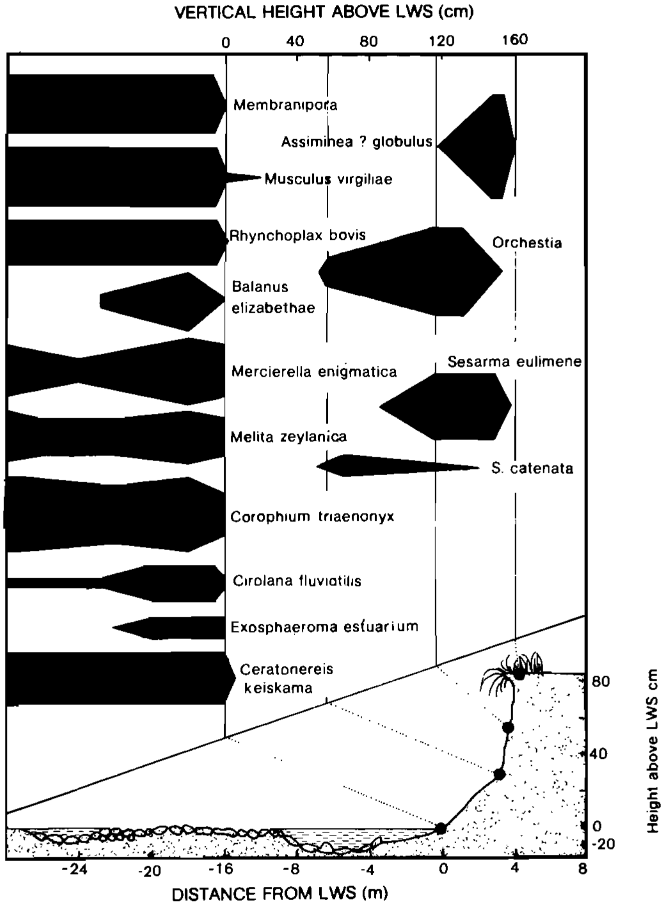

Fig. 12 Transect T9 at the head of the estuary. Scale of abundance as in Fig. 8.

Fauna of rocky shores

The western banks of the mouth and part of the lagoon are rocky and there are isolated outcrops of the rocks down the whole length of the estuary. Collections were made at each of these (Fig 1, R1—R10). The fauna on rocks is of course quite different from that of soft substrates, but as rocks form only a small proportion of the total substrate in the estuary their fauna will be discussed briefly.

At Stations R1 and R2 the substrate consists of large irregular boulders interspersed with flat rock surfaces. The boulders decrease in size towards high tide where a mixture of pebbles and oyster shells forms a coarse rubble. Most of the animals occurring here are typical of an open shore fauna. The high shore supports four species of *Littorina: L. africana* and *L. knysnaensis* in abundance and *L. kraussi* and *L. scabra* in smaller numbers. Under the rocks *Cyclograpsus punctatus* is common. In the upper balanoid zone *Tetraclita serrata* and *Chthamalus dentatus* are abundant together with varius limpets (*Patella concolor, Cellana radiata capensis, Helcion pectunculus* and three *Siphonaria* spp.). The lower balanoid zone contains dense settlements of the oysters *Saccostrea cucullata* and *S. margaritacea*. Under the rocks there is a wide variety of animals, the commonest being the gastropods *Nerita albicilla* and *N. plicata, Turbo coronatus, Oxystele tabularis*, and *Monodonta australis:* the bivalves *Septifer bilocularis* and *Brachidontes variabilis*; the polychaet, *Pomatoleios kraussii*; crabs *Grapsus grapsus tenuicrustatus* and *G. fairmanoiri;* and the isopods *Exosphaeroma kraussii* and *Dynamenella huttoni.* At and below low tide there is an even more diverse fauna.

At Station R3 the rocky shore degenerates into a boulder beach with a much poorer fauna, but the species which do occur here are also found at R1 and R2. The majority of the species at these three stations are typical of the open shore and not usually found in estuaries. They penetrate about 700 m into the lagoon at Mngazana due to a combination of the rocky bank, consistently high saliniteis (Fig. 2), clean water (Fig. 3) and strong tidal currents which prevent the settlement of any silt.

In the middle and upper reaches the rocks are limited to isolated outcrops on the bank, silted to varying degrees. The number of species occupying these rocks is reduced to 15. Some are tolerant species extending from the open shore such as *Cyclograpsus, Saccostrea* spp and three *Siphonaria* spp, but the larger proportion comprises species which are typically found within estuaries: *Eurycarcinus natalensis, Xantho cf. quinquedentatus, Sesarma longipes, Metopograpsus thukuhar, Balanus elizabethae* and *B. amphitrite, Lamya capensis* and *Melampus lividis.*

At station R10 at the head of the estuary, the bed consists of boulders and pewbles supporting a completely different fauna (see Transect T9 for details). This fauna includes *Musculus virgiliae, Corophium triaenonyx, Mercierella enigmatica,* an apparently undescribed species of *Neritina* and *Membranipora* sp. (The latter is morphologically similar to *M. membranacea,* but its restriction to the head of the estuary makes it unlikely that it is this species. Day *et al.* (1954) record *M.? lacroixii* from the head of the estuary of St Lucia, and the Mngazana material is probably the same species). *Balanus elizabethae* also penetrates to the head of the estuary, and dead but attached shells of *Saccostrea cucullata* show that at some stage this oyster occurred at the head of the estuary. The diversity of species at the head is low but the density is very high (Fig. 12).

Thus the rocky shore fauna is divisibile into three: that of the lower reaches is an impoverished open shore fauna; while that of the middle reaches is more typically estuarine but distinct from the fauna found at the head. The number of rocky substrate species declines from the mouth to the head.

Fish fauna

Sixty-two species of fish were collected, including some which extend the known range of their distribution. A species list is given in Appendix 2. Although netting was concentrated in the lagoon and the two tributaries, certain species showed strong preferences for specific habitats. *Psammogobius knysnaensis* occurred only over clean sand, *Glossogobius giuris* preferred a muddy substrate and together with *Coryphopterus multifasciatus* and *Liza macrolepis* occurred as far as the head. *Hepsetia breviceps, Ctenogobius acutipennis, Gilchristella aestuarius* and *Ambassis commersoni* were limited to the upper reaches and the latter two predominated at the head.

Quantitative netting for juvenile fish was undertaken at high tide and revealed a strong preference for *Zostera* beds, where no fewer than 39 species and 4722 individuals were captured from an area of 30 m^2 (Table 5). The abundance of juveniles again emphasizes the importance of estuaries, and particularly *Zostera* beds, as feeding and nursery grounds for juvenile fish, as shown by Wallace & Van der Elst (1975) for Natal estuaries.

Table 5 Numbers of juvenile fish captured over various types of substrate. In each case an area of 30 m² was netted

Substrate	No. of species	No. of individuals
Over *Zostera*	39	4 722
Clean sand in lagoon	2	17
River mud, lower reaches	8	52
Pebble bottom, upper reaches	9	321
Pebble bottom, head	4	426
Mangrove mud	7	87

In winter various species of mullet predominated, particularly *Mugil cephalus. Liza macrolepis, Liza dumerili* and *Myxus capensis.* Other species which were common in winter but disappeared in summer were *Liza richardsoni, Gerres acinaces, Lichia amia* and *Valamugil buchanani.* In summer the mullet were absent or at least scarce following the seasonal pattern described by Wallace (1975a), but other species only appeared in summer: *Parascorpaena aurita, Lutianus fulviflamma, L. vaigiensis, L. argentimaculatus, Pomadasys commersoni, P. hasta* and *Chaetodon linula.* Other species occur throughout the year, the commonest being several species of goby, and *Eleotris fusca, Diplodus sargus, Rhabdosargus holubi and Therapon jarbua.*

Table 6 shows that along the Transkei, Natal and Mocambique coasts the diversity of estuarine fishes increases in a northerly direction and that Mngazana has a high number of fish species in comparison with many other Transkei estuaries (although more extensive sampling is required in some of these estuaries before true estimates of fish diversity can be given).

Discussion

Interaction of physical factors

As Day (1964) has pointed out, many estuaries in Southern Africa suffer from a seasonal rainfall and from erosion of the countryside because of poor agricultural practices. Particularly in Transkei and Natal floods carry down a heavy silt load with consequent siltation and smothering of the estuary, and the water is so turbid that light cannot penetrate. The longer the river, the greater the problem. Short rivers escape this problem for they have small catchments but their discharge is usually too small to keep their mouths continually open. Sand-bars build up across the mouths so that these estuaries are blocked and become tideless lagoons, usually with a poor fauna. Mngazana is one of a few estuaries falling in between these two extremes, short enough to avoid siltation, but with a perenially open mouth. The catchment is about 275 km² (Wooldridge 1977) and being in the coastal belt it has a perennial rainfall. The rock promontory fixing the western bank of the mouth (Fig. 1) minimizes deposition of sand across the mouth, thus helping to keep the mouth open. Erosion in the catchment is minimal as agriculture is limited and many of the valleys are still clothed in coastal forest. As a result the water is remarkably clear (Fig. 3), particularly at high tide. The bulk of the estuary has salinities close to that of sea-water and tidal exchange is experienced the full length of the estuary. The estuary is strongly stratified. Even after floods salinities remain high and as the catchment is small, the effects of floods are not prolonged (Fig. 2). The lower and middle reaches are buffered by the sea and only near the head do salinities and temperatures fluctuate seasonally (Fig. 4). Even here, winter temperatures do not fall very low as there are no coastal frosts, nor does the river drain high mountains. The stability and equable nature of the physical environment is evidenced by the extensive mangrove forests, for mangroves are intolerant of change and excluded from estuaries which close (Hill 1966; Breen & Hill 1969).

Distribution of the fauna

In view of the favourable physical conditions it is not surprising that Mngazana has a rich fauna, with 209 invertebrates and 62 species of fish. These figures can be compared with those for other estuaries on the east coast of southern Africa, drawing on the literature and on the unpublished records of the Zoology Department of the University of Cape Town. To allow for difference in collecting

Table 6 Numbers of invertebrate and fish species found at various estuaries in Transkei, Natal, Zululand and Mocambique. Data from some estuaries have been pooled for various geographical areas. Estuaries are listed in geographical sequence beginning with the most southerly

Locality	Reference	Invertebrates	Fish
Keiskama estuary	Univ. of Cape Town records	51	15
Haven area (Bashee, Mbanyana, Haven)	Univ. of Cape Town records	70	21
Mngazana estuary	Present work	209	62
Port St. John's area (Umgazi, Umzimvubu, Second Beach)	Univ. of Cape Town records	75	28
Port Shepstone area (Umtanvuna, Umzimkulu, Untentweni, Ifafa)	Univ. of Cape Town records	42	31
Umkomaas area (Umkomaas, Isipingo, Umzimbazi, Amalonga, Umgababa, Amanzimtoti)	Univ. of Cape Town records	83	29
Umlalazi estuary	Hill 1966	78	57
Richard's Bay estuary	Millard & Harrison 1959	78	74
St Lucia estuary	Day *et al.* 1954	79	67
	Millard & Broekhuysen 1970	94	88
Kosi Bay estuary	Broekhuyzen & Taylor 1959	108	45
	J. Wallace *pers. comm.*	—	90
Morrumbene estuary	Day 1974	384	114

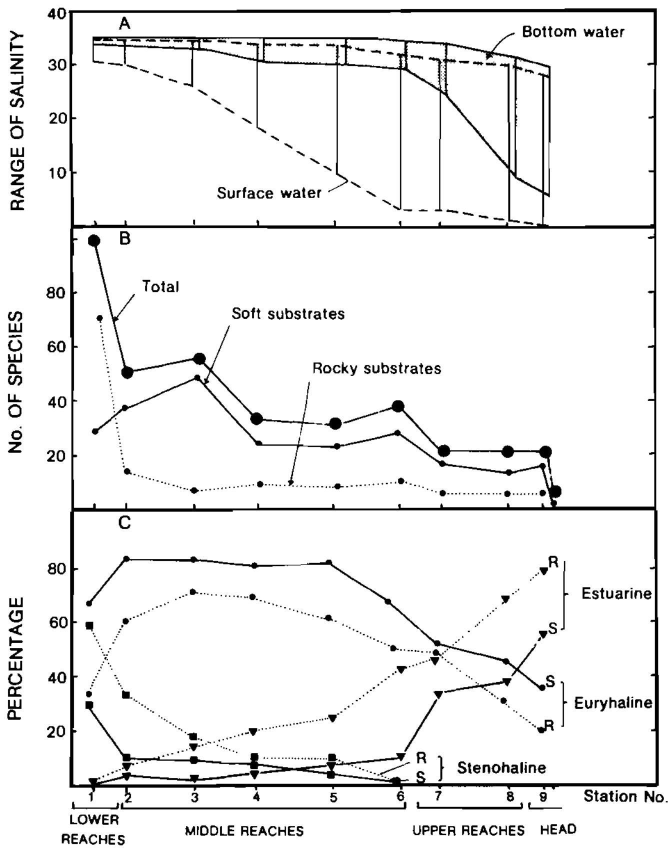

Fig. 13 A. Annual range of salinity experienced in Mngazana estuary. Data drawn from present work and from Wooldridge (1977). B. Change in number of species found down the length of Mngazana and the relative numbers of rocky (R) and soft-substrates species. C. Analysis of faunal components in rocky and soft-substrates in Mngazana. The small fresh-water component contributes 3% at the head and has been omitted. Data expressed as a percentage of the total number of species found in each substrate type at each station.

effort for certain estuaries, data have been pooled for some of the geographic areas (Table 6). In terms of invertebrate diversity, only the rich Morrumbene Estuary has more species than Mngazana. Day (1974) records only 237 invertebrates in a total of 14 Transkeian and Natal estuaries.

Figure 13B shows the change in numbers of species down the length of Mngazana estuary; a steady decline from 100 species just inside the mouth to 21 at the head. This is the normal pattern in most estuaries, and is at least partially due to an increase in osmotic stress. Not only does salinity decline towards the head but both its tidal and annual range increases (Fig. 13A). When the invertebrate fauna is subdivided into rocky substrate and soft substrate species, the two components behave differently. The number of species on rocky substrates declines precipitously from Station 1 to Station 2 (Fig. 13B) and then remains fairly constant throughout the rest of the estuary. Salinity cannot be responsible for this decline for it is high at both Stations 1 and 2 (Figs. 2 & 13A). Siltation does however increase dramatically between these two stations and is probably the main agent limiting rocky-shore species in the estuary, physically smothering them and eliminating the encrusting algae on which many herbivores depend. The importance of silt is strikingly shown near the mouth of Mngazana where two concrete walls have been built out into the channel to form a small jetty. On either side of these walls the rocks are kept clean by the stongly flowing tidal current and support 63 species most of which are typical of the open shore. Between the jetty walls salinity is the same as that in the adjacent channel, but silt deposits on the rocks; and of the 63 species found on adjacent rocks, 56 disappear. In Langebaan Lagoon (which is entirely marine) there is a similar decline in the fauna of rocks as siltation increases in the calmer waters (Day 1959).

In contrast to the fauna of rocks, that of soft sediments increases from Station 1 to Station 3 (Fig. 13B) and the subsequent decline in numbers towards the head of the estuary is not as dramatic. Within the lagoon, animals living in the sand are limited by a low organic content in the clean sands (Table 2), the instability of the sand-banks and the rapid water-flow occurring in the channels and over the shallow sand-banks. At Station 3 the sediment is more stable, has a higher organic content and is partially covered by *Zostera* which supports a rich fauna (Table 4).

Another reason for the more rapid decline of the rocky substrate fauna may be that the animals bear the full brunt of any salinity changes while the infauna of the soft substrate is buffered because the sediments maintain a relatively constant salinity even when salinity changes in the overlying waters (Reid 1930).

Faunal components

Day (1951, 1967) has defined five faunal components in estuaries and these are restated as follows:

- The fresh-water component comprises salt-tolerant species derived from the river and mainly restricted to the head of the estuary.
- The stenohaline marine component consists of forms usually confined to the sea but penetrating into waters of high salinity in the estuary under consideraion.
- The euryhaline marine component extends from the sea, well into the estuary, into waters of variable salinity.
- The estuarine component has evolved from marine forms but is now restricted to estuaries and not found in the sea.
- The migratory component consists of mobile forms which migrate in and out of estuaries, including fish, prawns and cephalopods.

The invertebrate fauna of Mngazana has been analyzed in these terms and Table 7 shows the results, and compares them with three other systems. Most of the species in Mngazana are euryhaline and only a small percentage are truly estuarine, and as Day (1964, 1967) has pointed out, most of the species found in estuaries really comprise marine calm-water species. Table 7 shows that this is true of all three estuaries, but that in Langebaan lagoon (which is a sheltered inlet of the sea and not an estuary) there is a higher proportion of stenohaline species. Knysna and Mngazana are both open, clear-water estuaries with relatively constant salinity and both have a higher proportion of stenohaline species than St Lucia which experiences dramatic changes in salinity in times of drought or flood (Millard & Broekhuysen 1970).

If the faunal components of Mngazana are further subdivided into species on rocks and those associated with sand or mud, a pattern is revealed down the length of the esturay (Fig. 13C). As expected, the stenohaline component

Table 7 Analysis of the invertebrates found at Mngazana (excluding planktonic and migratory forms) and a comparison with three other systems. Results are given as percentage of the number of species analyzed for each system

Component	Mngazana estuary	St Lucia estuary (Millard & Broekhuysen 1970)	Knysna estuary (Day 1967)	Langebaan lagoon (Day 1959)
Fresh water	3	5,7	2,3	0
Stenohaline marine	35	5,7	45,0	67
Euryhaline marine	56	66,7	44,1	21
Estuarine	11	21,9	8,6	12
Number of *spp.* analyzed	165	192	310	117

declines up the estuary, disappearing at Station 6 (end of middle reaches), the euryhaline component increases in the middle reaches and then declines while the estuarine component increases in the upper reaches and at the head. This effect and its relationship to the salinity regime (Fig. 13 A) is well established (Day 1964, 1967) and Wooldridge (1977) has shown a similar pattern for the zooplankton of Mngazana. What is more interesting is the difference between the fauna of the two substrate types. In the lower reaches rocky substrates support a far higher percentage of stenohaline species, and this may be one of the reasons why the faunas of rocks declines so suddenly as one moves up the estuary (Fig. 13B). The smaller proportion of stenohaline soft substrate species declines just as suddenly but is more than offset by the high proportion of euryhaline species occurring in this substrate. Throughout the estuary, but particulary at the head, the fauna of rocks also has a far higher percentage of truly estuarine species (Fig. 13C).

Why should rocky substrates bear higher proportions of stenohaline marine species and estuarine species? Many of the species are sessile or sedentary and in addition they occupy a substrate which is discontinuous both around the coast and even more obviously in estuaries where hard substrates are usually limited to isolated outcrops. Both sessile life and a discontinuous distribution may favour specialization of the species to a narrow range of conditions. One way of testing whether rocky substrate species are more restricted in their distribution is to analyse the percentage of this fauna confined to particular regions of the estuary. Table 8 shows that in comparison with the fauna of sand and mud a much higher percentage of the rocky substrate component is confined to a particular reach of the estuary. This effect is most marked in the lower reaches and at the upper end of the estuary.

Zoogeographic affinities

Four zoogeographic regions are generally recognized around the coast of southern Africa, and are defined as follows for the present analysis: cold temperate (west coast of South Africa); warm temperate (south coast from Cape Point to East London); subtropical (east coast, including Transkei, to southern Mocambique); and tropical (northern Mocambique and northwards including Indo-Pacific.

Table 8 The numbers of species occurring in each of the zones of the estuary, and the percentage of these that are confined to a specific zone. Figures in brackets show the stations considered in each zone. Data are given separately for rocky (R) and soft-substrate (S) species

	Zones of the estuary					
	Lower reaches (1)		Middle reaches (2 — 6)		Upper reaches and Head (7 — 9)	
	R	S	R	S	R	S
No. of species	63	39	11	69	7	17
% limited to this zone	95	34	55	56	100	35

An analysis of the geographic distribution of the invertebrate fauna of Mngazana is given in Table 9. Consideration of the total fauna reveals slightly stronger affinities with the warm temperate province of the south coast rather than the tropics: which is surprising in an estuary dominated by mangroves. This trend is more obvious when considering the rocky substrate fauna alone. Separation of rocky and soft substrate faunas also shows that the former has a higher percentage of species (17% as opposed to 3%) which is restricted to the local sub-tropical province. This supports the suggestion made above that the fauna of rocky substrates may have a more restricted distribution, requiring greater specialization.

If the analysis is applied to the four reaches of the estuary (Table 9) an interesting pattern emerges. The majority of species occurring in the lower reaches extend southwards into the warm temperate province. In the middle reaches most species have tropical affinities. Presumably heating by the sun warms the shallower middle reaches, which in summer have a temperature about 2 °C above that of sea water, making them more hospitable for tropical species. However, in the upper reaches and at the head of the estuary the largest component comprises species of subtropical affinities. As Day (1974) has suggested, the upper portions of the estuary are more likely to be affected by local conditions for they are not buffered by the sea, so it is not surprising that the upper reaches and head have a higher percentage of the local sub-tropical fauna.

If species associated with mangroves are isolated,

Table 9 Analysis of the geographic affinities of the invertebrate fauna of Mngazana (excluding plankton). Data given as percentage for each region of the estuary. Figures for the whole estuary are divided into those for rocky substrates (R), soft-substrates (S) and for the whole fauna (Total)

Centre of geographical distribution	Lower reaches	Middle reaches	Upper reaches	Head	Whole estuary R	S	Total
Warm-temperate	51	25	22	25	46	36	40
Subtropical	26	24	50	51	29	20	24
Tropical	12	42	22	18	21	36	30
Ubiquitous	11	9	6	6	3	8	6
Total	100%	100%	100%	100%	100%	100%	100%
No. of species	94	79	20	16	65	95	160

analysis shows much stronger tropical affinities: 62 % extend northwards into the tropics but fail to penetrate southward into the warm temperate province.

Comparable analysis of the fish (Table 10) reveals that Mngazana has a high percentage of species with tropical affinities. Another interesting feature is that those species with southern affinities appear most often in winter; those whose distribution extends both north and south tend to occur throughout the year at Mngazana; and finally many species of tropical origin appear only in summer. This suggests that there are seasonal movements of fish, tropical species moving south in summer when the waters are warmer, and temperate species extending north in winter. However seasonal disappearance from the estuaries may also be due to a breeding migration, as most species spawn in the sea (Wallace 1975b).

Table 10 Analysis of the geographical distribution of fishes from Mngazana. C = Cold temperate, T = Tropical. Seasonal occurrence in the estuary is given for Winter (Wn), Summer (Sm), or both seasons (Wn + Sm). For definition of components see p.

Centre of distribution	No. of species	Seasonal occurence		
		Wn	Wn + Sm	Sm
Warm-temperate (C-W; C-S; W-S)	12	8	3	1
Ubiquitous (whole coast)	6	0	5	1
Subtropical (W-T)	10	1	7	2
Tropical (S-T; T)	31	5	11	14

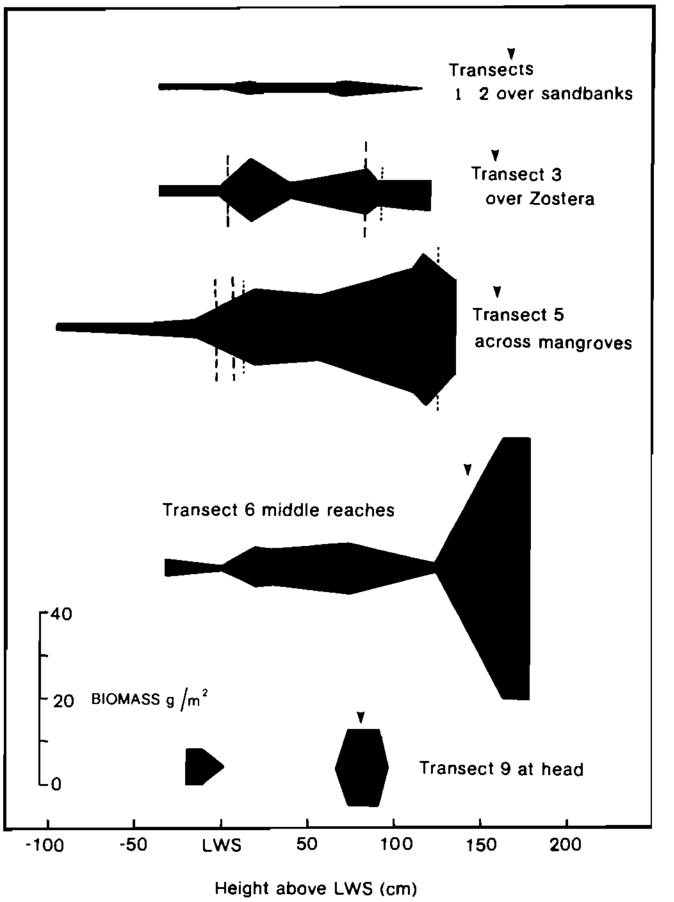

Fig. 14 The distribution of biomass (g AFDW m^{-2}) on 5 transects. Arrows indicate the height of high water springs on each transect, dashed lines show upper and lower limits of *Zostera*, dotted lines the limits of mangroves.

Biomass, sediment and feeding relationships

Figure 14 illustrates the distribution of invertebrate biomass on five of the transects across soft substrates. In the lower reaches the clean sand of Transects 1 and 2 supports a low biomass while the *Zostera* beds contain a much higher biomass. It is in the mangroves (Transect 5) that highest biomass is recorded, although as discussed above, the conditions exclude most species and the high biomass is made up of a few very abundant species. In the middle reaches the open banks have a moderate biomass but high on the banks the value increases enormously due to the large *Sesarma meinerti*. At the head of the estuary biomass is again relatively low, the banks being barren except at the high tide mark and above where *Sesarma eulimene* is mainly responsible for the relatively high biomass.

On all of the transects across soft sediments the biomass is surprisingly low subtidally. In most parts of the middle and upper reaches the mud has a low oxygen content just below the surface and this excludes most burrowing forms except tolerant species such as *Dendronereis arborifera, Tharyx marioni, Ceratonereis keiskamma.* Intertidally the biomass is far higher and tends to increase towards the high tide mark. This is not surprising for many of the species are active when the tide is low, emerging from burrows (*Uca* spp and *Sesarma* spp.) or descending from mangroves (*Cerithidea*) to feed on the surface mud. The only important burrowing form is *Upogebia.* The ash-free dry biomass of a series of samples of *Upogebia* ranged from 159,2 to 254,4 $g.m^{-2}$ (mean 212,0 $m.g^{-2}$) in areas where they were abundant (up to $90.m^{-2}$). Bivalve are largely absent from the intertidal zone.

In Table 11 the biomass of soft substrates has been divided into various feeding types. Filter feeders predominate sub-tidally. This is logical because they can only feed when submerged, and filter feeding has the added advantage that the animal is comparatively independent of the low oxygen concentrations in the mud, deriving both food and oxygen from the water-column. Intertidally the picture changes completely and between 80 and 100% of the biomass is made up of detritivores (a large percentage being *Uca* spp. and *Sesarma* spp.). Figures for the total biomass on each transect reveal the same predominance of detritivores. Only Transects 1 and 2 deviate: their clean sands are too low in organic material to support a high biomass of detritus feeders and many of the species which occur on these transects are filter feeders, scavengers and carnivores. In the high intertidal zone the carnivore *Eurydice longicornis* and *Pontogeloides latipes* are the most important species; but *Eurydice* undertakes rhythmic migrations into the water-column to feed there at high tide and is not dependent on the sediment for food.

As detritus feeders contribute substantially to the invertebrate biomass throughout most of the estuary, some relationship can be anticipated between biomass and the nature of the sediment. Figure 15A shows that as the organic content of the substrate rises, so the biomasss also increases. The highest values for both biomass and organic content are found in the mangrove forests. It is probable

Table 11 Analysis of the feeding types of macrobenthic invertebrates present on six transects. Figures are given as percentages of the biomass in each zone, for the subtidal (ST), intertidal (IT) and the total transect (Total)

Transect	Zone	Percentage of biomass		
		Filter feeders	Detritivores	Carnivores
1 + 2	ST	49	23	27
	IT	64	14	23
	Total	59	16	26
3	ST	68	14	16
	IT	12	83	3
	Total	14	80	6
5	ST	77	7	15
	IT	1	93	5
	Total	4	89	6
6	ST	81	6	13
	IT	<1	99	<1
	Total	4	95	1
9	ST	67	6	27
	IT	0	100	0
	Total	21	70	9

that the mangrove mud supports an even higher biomass than is indicated by sampling, for large numbers of *Sesarma meinerti* descend from their burrows above the high tide mark to feed in the mangroves at night, during the low tide.

The organic content of the substrate is inversely related to particle size (Fig. 5) so it is not surprising that biomass correlates negatively with median particle size.

If the percentage organic content of the sediment is plotted against the number of species captured in a sample of 0,5 m^2 (Fig. 15B) the data are widely scattered, but it is evident that sediments with a low organic content only support a few species. As the organic content increases the community becomes more diverse, and detritivores predominate (Table 11). However relatively few species are found in sediments with a very high organic content (Fig. 15 B). Such sediments are mainly restricted to the mangroves and are extremely fine and smothering, almost completely anoxic, excluding most species from this rich feeding area. A large percentage of the invertebrate biomass has been

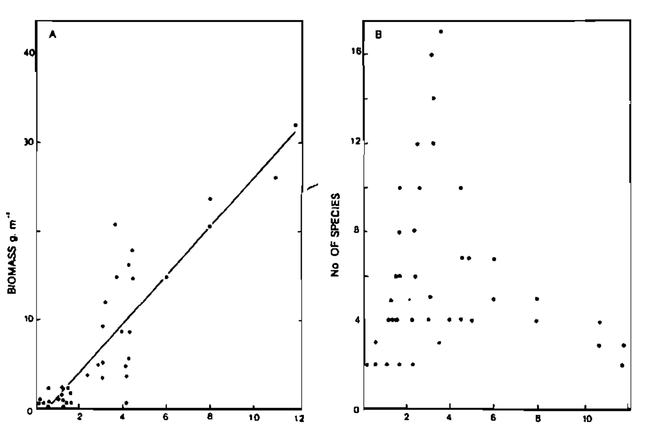

Fig. 15 A. Relationship between biomass and percentage organic content of the substrate. B. Relationship between number of species and percentage organic content of the substrate. Shading indicates the area within which all data points fall.

shown to comprise detritivores and, although more difficult to quantify, the same is probably true of the fish, for although most of the species are carnivores, in winter the mugilids are numerically dominant, constituting 85-90% of the catch.

The question arises as to the origin of this detritus on which so many animals depend. Mangroves are probably the major primary producers in the system. Lugo and Snedaker (1974) quote mean leaf-fall for various mangrove systems as being about 2 $gm^{-2}d^{-1}$ and cite evidence that up to 80% of the total energy budget of mangrove bays may be supplied by export from the mangroves. The clarity of the water suggests that phytoplankton is probably not important in Mngazana, although the zooplankton achieves a high standing crop (Wooldridge 1977). The salt-marshes lie mainly on the flood-plain above normal high tide so that export to the rest of the system is hindered, although periodic flooding may redistribute the detritus. The *Zostera* beds support a wide range of species and seem of particular importance to juvenile fish; but apart from extensive beds on the Mbazwa tributary, the comparatively steep intertidal banks and the resuspension of surface sediments by tidal currents curb its growth in the main estuary.

The decomposition of litter in the mangroves is certainly accelerated by the macroconsumers. The sesarmid crabs in particular scavenge falling leaves and their mechanical breakdown of the leaves will allow faster decomposition by the microflora. Lugo and Snedaker (1974, citing Carter *et al.* 1973) suggest that the macroconsumers reduce the time of decomposition by 60%. Bacterial numbers are inversely related to particle size and positively correlated with the organic content of the sediment (Dale 1974). The very fine mangrove mud with its high organic content is likely to contain high numbers of bacteria.

In Mngazana the major flow of energy is likely to be from the primary production of mangroves, via their decay products to detritivores, and thence to the larger carnivores including fish and birds.

Conservation

The object of this survey was to provide information to the Transkeian Government which is concerned about the rational conservation and utilization of its coastal areas. Recently suggestions have been made that Mngazana might become the site of a harbour in the future. However, it must be recognized that Mngazana is a unique environment on a coast where most estuaries are impoverished by siltation or closure of the mouth. It has some of the best-developed mangroves in southern Africa and mangroves are endangered and becoming increasingly threatened by development. Mngazana has stable physical conditions and supports the richest estuarine fauna and flora known in Transkei. These features make the conservation of Mngazana unquestionably of great importance.

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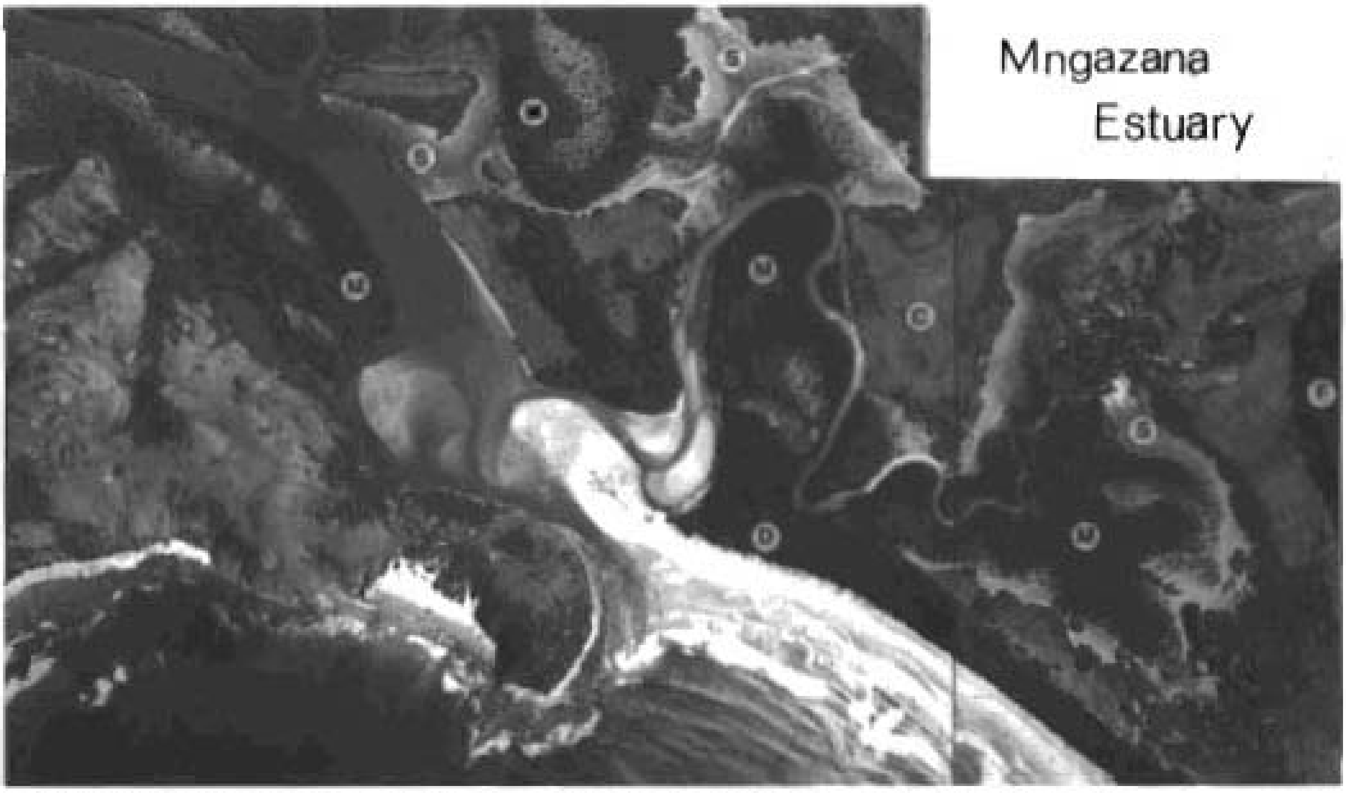

Fig. 16 Aerial photograph, Mngazana, April 1977. C = cultivated, D = dune forest, F = forest, M = mangroves, S = salt-marsh.

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Appendix 1

Faunal list of the invertebrates occurring in Mngazana estuary. Distribution up the estuary is given for Stations 1—9 which refer to the physical stations shown in Fig. 1. Station 1 is at the mouth, and 9 at the head. For convenience, material collected at Transect T3 on the Mbazwa tributary has been included in Station 3. Other material has been allocated to the station nearest to the point of collection.

Relative abundance is indicated by the number of specimens collected at a particular site: R = 1—2; P = 3—20; C = 20—100; A = > 100.

Substrate types: S = clean sand; M = mud; Mn = mangrove mud; MT = mangrove trees; SR = sediment under rocks; R = attached to rocks; P = planktonic; T = terrestrial.

Geographical distribution: C = cold temperate, west coast; W = warm temperate, south coast from Cape Point to East London; S = subtropicaln Transkei to southern Mocambique; T = tropical, northern Mocambique northwards. Asterisks indicate an extension of known records. *Other records:* Records are included from MacNae (1963) as well as unpublished data from T. Wooldridge and H. Champion.

Component: St = Stenohaline; eu = euryhaline;
E = estuarine.

	Distribution down estuary									Sub-	Geo.	Com-
	1	2	3	4	5	6	7	8	9	strate	Dist.	ponent
Coelenterata												
Anemone (unidentified) UMG 27R	P											
Hydractinia kaffraria		P	P	P								
Virgularia schultzii	R									S	C	St
Porifera												
Unidentified UMG 54M	P									R		
Nemertea												
Linaeus sp			P							M		
Unidentified UMG 75C								R		Sr		
Polybrachiorhynchus dayi				P						M	W-T	eu
Sipunculida												
Themiste stephensoni	R									S	C-T	St
Unidentified UMG 28E	R									R		
Polychaeta												
Ceratonereis erythraeensis	R	P	A	P	P					M	U	eu
Ceratonereis keiskamma	R	P	P	P	P	P	C		P	M	W-S	E
Ceratonereis sp.	P									S		
Cirriformia tentaculata		P	A							M	U	eu
Dendronereis arborifera					C			C		M/Sr	S-T	eu
Ficopomatus (= *Mercierella*) *enigmatica*					P	P	C	C	P	R	W-S	E
Glycera tridactyla	P									S	U	eu
Heteromastus filiformis			C	P						M	W-T	eu
Lumbrineris tetraura	P		P							S/M	C-S	eu
Magelona cincta	P									S	T	S
Malacoceros indica			R							M	S-T	St
Marphysa depressa	R									S	C-S	St
Marphysa macintoshi	P	P				P		P		M/Mn	S-T	eu
Mesochaetopterus sp.				P	P					M		
Nephtys capensis	R									S	C-S	eu
Notomastus aberans			R							M	W-T	eu
Orbinia angrapaquensis	C	C	C							S/M	C-W*	eu
Perinereis cultifera	P									S	W-S	St
Perinereis falsovariegata	C	P								Sr	C-T	eu
Perinereis nuntia vallata		P								M	W-T	eu
Polydorella sp.		P								M	S*	
Pomatoleios kraussii	C									R	U	St
Prionospio saldanha	R									S	C-S	eu
Pseudonereis variegata	C									R	C-S	St
Scolelepis squamata	C									S	U	St
Spirorbis sp.	P									R		
Tharyx marioni	R	A	C	P	P					S/M	C-S	St
Thelepus plagiostoma	C									Sr	U	eu
Crustacea												
Amphipoda												
Amaryllis macrophthalma	R									M	C-S	St
Amphithoe africana	R									R	W	St
Austrochiltonia subtenuis									P	M	C-T	E
Caprella equilibra (Wooldridge)	R	R										
Corophium triaenonyx						P	A	A	A	R	W-T	eu

	Distribution down estuary 1	2	3	4	5	6	7	8	9	Sub-strate	Geo. Dist.	Com-ponent
Grandidierella bonnieroides			C							M	S–T	eu
Jassa falcata	P	P (Wooldridge)										
Melita zeylanica			C			C	C	C	C	Sr/M	C–T	E
Orchestia rectipalma	R	P			P	P	P	P	A	M	C–S	eu
Paramoera capensis	P									M	C–S	eu
Podoceras sp.			P							M		
Talorchestia ancheidos		(Wooldridge)				P				P		
Urothoe pulchella	A									S	C–W*	eu
Isopoda												
Cirolana fluviatilis						R	P	P	C	Sr	W–S	E
Cirolana sp.								P				
Corallana africana		Recorded by Wooldridge. All Stations.								P		
Cyathura carinata				P	R	P	R	R		Sr	C–S	eu
Dynamenella huttoni	C						R			R	C–S	St
Eurydice longicornis	A					P				S/P	C–S*	eu
Exosphaeroma estaurium							P		P	Sr		E
Exosphaeroma hylocoetes									P	Sr		E
Exosphaeroma kraussii	P									R	C–W	St
Ligia natalensis	C									R	W–S	
Pontogeloides latipes	A									S/P	U	St
Sphaeroma terebrans						C				R	W–T	eu
Cirripedia												
Balanus algicola	P									R	C–S*	St
Balanus amphitrite		P	P	P		P	P			R	W–T	eu
Balanus elizabethae		P	P		P	C	P		P	R	W–S	E
Balanus venustus	P									R	S	St
Chthamalus dentatus	A									R	U	eu
Octolasmis cor		On gills of *Scylla serrata*									S	E
Tetraclita serrata	A									R	C–S	eu
Cumacea												
Iphinoe truncata		P	P	P	P	P	P	P		S		
Mysidacea												
Mesopodosis africanus							C	A	A	P	S–T	E

	Distribution down estuary 1	2	3	4	5	6	7	8	9	Sub-strate	Geo. Dist.	Com-ponent
Tanaidacea												
Apseudes digitalis					R	R	R			Sr,P	W–S	E
Macrura												
Alpheus crassimanus		P	C							M	W–T	eu
Alpheus edwardsi			P							M	S–T	St
Alpheus hippothoe			R							M		St
Betaeus jucundus		(Wooldridge) P				P				P	C–S	eu
Metapenaeus monoceros		P	C							M	S–T	eu
Palaemon pacificus		P	C							P/S/M	C–T	eu
Panulirus homaris	R									R	S	St
Penaeus canaliculatus			C							M	S	eu
Penaeus indicus		Recorded by H. Champion, *pers. comm.*										
Penaeus japonicus			C		P					M	W–T	eu
Penaeus monodon		Recorded by H. Champion, *pers. comm.*										
Synalpheus anisocheir			P							M	C–S	St
Anomura												
Callianassa kraussi	P									S	C–S	eu
Clibanarius longitarsus		P	P							M	S–T*	eu
Coenobita caripes		Recorded by Macnae (1963)										
Hippa adactyla	R									S	S*	St
Upogebia africana		C	P	A	A	A	C			M	C–T	eu
Brachyura												
Calappa hepatica			R							M	S*	St
Cardisoma carnifex		Recorded by Macnae (1963)								T	S–T	E
Charybdis helleri		R									S–T*	St
Charybidis sp.						R						
Cleistostoma algoense		A	P							M	W–S	eu
Cleistostoma edwardsii	R										C–T	eu
Cyclograpsus punctatus	A	P								R	C–S	eu
Eurycarcinus natalensis	P	P	P		P	P				R/M	S–T*	eu
Grapsus fairmanoiri	P									R	S–T	St
Grapsus grapsus tenuicrustatus	P									R	S–T	St
Hymenosome orbiculare			R							M	C–S*	eu

	Distribution down estuary 1	2	3	4	5	6	7	8	9	Sub-strate	Geo. Dist.	Com-ponent
Macrophthalmus boscii	R	P								M	S-T	eu
Macrophthalmus grandidierri			P							M	S-T*	eu
Matuta lunaris	R									S	S-T*	eu
Metopograpsus thukuhar	C	P		P	P	P				R/Sr	W-T	eu
Ocypode madagascariensis	P									S	S-T*	eu
Pilumnus longicornis						R				Sr	T	
Portunus pelagica	R									S	S-T	eu
Rhynchoplax bovis			C			P	P	P	A	M	S	E
Scylla serrata		P	P	P	P	P	P	P	P	M	W-T	eu
Sesarma catenata		A	A	A	A	A	A	P	P	M	W-T	eu
Sesarma eulimene		P				C	C	P	A	M	S-T	eu
Sesarma guttata						R				S	S-T	eu
Sesarma longipes					R					R	T*	eu
Sesarma meinerti		C	C	C	C	C	C			M	S-T	eu
Thalamita picta						R				R		
Thaumastoplax spiralis	R									S	C-S	eu
Uca chlorophthalmus (= *gaimardi*)		C	P	A	A	P				M	S-T	eu
Uca lactea annulipes		A	P	A	A	A				M	S-T	eu
Uca urvillei		P	P	P		P				M	S-T	eu
Uca vocans (= *marionis*)		P	P							S/M	S-T	eu
Varuna litterata								P	P	Sr	W-T	eu
Xanthid (unidentified) UMG 39B								R				
Xantho cf. *quinquedentatus*	P	P		P	P					R/M		eu
Insecta												
Axinidium ?africanum	C									S		
Chironomid larva				R						M		
Gerrid *?Halobates*						C	P			P		
Staphylinid *?Bledius*	C									S		
Tipulid larva	R									S		
Aranaea												
Thalassius spenceri		R			R					T		
Pyconogonida												
Nymphopsis cuspidata	R									R	C-S*	St

	Distribution down estuary 1	2	3	4	5	6	7	8	9	Sub-strate	Geo. Dist.	Com-ponent
Bryozoa												
Bugula dentata						P					W-S	eu?
Membranipora sp.									A	R	S?	E
Mollusca												
Polyplacophora												
Acanthochiton garnoti	P									R	C-S	eu
Chiton tulipa	R									R	C-S*	St
Dinoplax gigas	R									R	C-S*	St
Dinoplax validifossus	P									R	S	St
Ischnochiton oniscus	P									R	S-T*	St
Bivalvia												
Arca gibba		P								R	S-T	St
Arca obliquata	C									R	W-T	St
Brachidontes variabilis	P									R		St
Cryptodon eutornus (= *Lucina edentula*)	(Recorded by Macnae 1963)									S		
Donax serra	R									S	C-S	St
Dosinia hepatica	R		C	P	P					S/M	C-T	eu
Eumarcia paupercula			P							M	W-T	eu
Lamya capensis				P	P	C				R/M	W-T	E
Loripes clausus	P									S	W-T	eu
Macoma litoralis	(Recorded by Macnae 1963)									S	W-T	eu
Musculus virgiliae								P	A	R	W-S	E
Ostrea algoensis	P									R	W-S	St
Perna perna	C									R	W-T	eu
Psammotellina capensis	C		C							S/M	W-S	eu
Saccostrea cucullata	A	C		P	P	P		Shells		R	W-T	eu
Saccostrea margaritacea	C	P		P						R	W-T	eu
Septifer bilocularis	P	P								R	S-T*	St
Solen capensis-corneus	R	C	C	C	C					M/S	C-S S-T	eu
Tapes corrugatus		P		P	P					R/Sr	C-S*	St
Tellina gilchristi		R								S/M	C-T	St
Gastropoda												
Aglaia capensis		P		P						M	C-S*	eu
Assiminea bifasciata		A	P		A	P				Mn	W-S	eu
Assiminea ?globulus									A	M		eu
Burnupena lagenaria	P									R	W-S	St
Cellana capensis	P									R	S-T	St
Cerithidea decollata		A	A		A	A	A			Mn	W-T	eu

	Distribution down estuary 1	2	3	4	5	6	7	8	9	Substrate	Geo. Dist.	Component
?Cerithium morum	C									R		St
Clavatula kraussi	P									R	C-S	St
Haminea natalensis		P	P							M		eu
Helcion pectunculus	P									R	C-S	eu
Helcion pruinosus	P									R	C-S	St
Littorina africana	C									R	W-T	St
Littorina knysnaensis	A									R	C-S	eu
Littorina kraussi	P									R	S	St
Littorina scabra	C	P	P	C	C	C	P			R/Mt	S-T	eu
Melampus lividus		C		C		C				M/R	S-T	E/eu
Monodonta australis	P									R	S	St
Morula granulata	P									R	S	St
Nassarius kraussianus		P	C	C	C	P				M	C-T	eu
Natica gualteriana	R	R								S/M	S-T	eu
Natica tecta	R				R					S/M	C-S*	eu
Nerita albicilla	A									R	S-T	eu
Nerita plicata	P									R	S	St
Nerita polita	P									R		St
Neritina cf. *ateria*									P	Sr	S*	E
Notarchus leachi			R							M	W*	eu
Onchidella capensis						C					W*	
Oxystele tabularis	A									R	W-T	St
Oxystele variegata	P									R	C-S	eu
Patella concolor	P									R	S	St
Patelloida profunda	P									R	S-T	St
Peristernea forskalii forskalii	P									R	S	St
Peronia peronii									C	R	S-T	eu
Polinices tumidus			P							M	S-T*	eu
Pteropurpura incurvispina	C									R	S*	St
Serpulorbis aureus n. sp.	C									R	endemic new sp.	
Siphonaria aspersa pallida	P									R	C-S	
Siphonaria capensis	P									R	C-S	eu
Siphonaria deflexa	A									R	W-S	eu
Siphonaria oculus	C	C		C	C					R	W-S	eu
Strombus mutabilis	P									R		St
Stylocheilus longicauda			P									
Terebralia palustris	Recorded Macnae (1963)									M	S-T	eu
Thais gemmulata	P									R	S-T*	St
Turbo coronatus	C									R	S-T	St
Echinodermata												
Cucumaria sykion	R									R	W-S	St
Echinocardium cordatum	R									S	W-S*	eu
Holothuria cf. *parva*			R							M	T*	eu
Patiriella exigua	P									R	C-S	eu
Pentacta doliolum	R									R	C-W*	St
Hemichordata												
Balanoglossus sp.	P									M		

Appendix 2

The occurrence of fish in the lower reaches (LR), middle reaches (MR) and at the head (H) of Mngazana estuary.

Relative abundance is given as P (1—20), C (20—100) or A (>100 specimens collected). Wn and Sm indicate occurrence in Winter or Summer.

The geographic range is given by C = cold temperate (west coast); W = warm temperate (south coast); S = subtropical (Transkei to southern Mocambique); T = tropical (Northern Mocambique, northwards).

	Occurrence LR	MR	H	Season	Geog. Dist.
Pisces					
Acanthopagrus berda	—	P	—	Wn	S-T
Ambassis commersoni	—	P	—	Wn + Sm	S-T
Ambassis natalensis	—	A	—	Wn + Sm	T
Argyrosomus hololepidotus	P	P	—	Wn + Sm	C-S
Arothron hispidus	P	P	—	Wn + Sm	C-T
Arothron immaculatus	P	P	—	Wn + Sm	S-T
?Bathygobius saldanha	—	P	—	Sm	
Bothus pantherinus	P	P	—	Wn	S-T
Chaetodon lunula	P	—	—	Sm	S-T
Coryphopterus multifasciatus	—	A	P	Wn + Sm	S-T
Coryphopterus nudiceps	P	C	P	Wn + Sm	C-S
Ctenogobius acutipennis	—	C	—	Sm	S-T
Ctenogobius nebulosus	P	—	—	Sm	T
Diplodus cervinus	—	P	—	Sm	C-T
Diplodus sargus	—	P	—	Wn + Sm	C-T
Dules rupestris	P	—	—	Wn + Sm	T
Dules taeniuris	P	—	—	Sm	S-T

	Occurrence LR	MR	H	Season	Geog. Dist.
Eleotris fusca	C	C	P	Wn + Sm	S-T
Elops machnata	P	P	—	Wn + Sm	W-T
Epinephelus spp.	P	P	—	Wn + Sm	T
Fistularia villosa	—	P	—	Sm	S-T
Gerres acinaces	—	P	—	Wn	W-T
Gerres punctatus	P	P	—	Wn + Sm	S-T
Gilchristella aestuarius	—	C	A	Wn + Sm	C-T
Glossogobius giuris	—	A	P	Wn + Sm	S-T
Glossogobius cf. *giuris*	—	P	—	Sm	
Heposetia breviceps	—	A	P	Sm	C-W
Leiognathus equula	—	P	—	Sm	S-T
Lichia amia	P	P	—	Wn	C-S
Liza dumerili	C	A	—	Wn + Sm	W-S
Liza macrolepis	A	A	A	Wn + Sm	S-T
Liza richardsoni	P	P	—	Wn + Sm	C-S
Liza sp. cf. *macrolepis*	A	A	—	Wn + Sm	
Lutianus argentimaculatus	P	P	—	Sm	S-T
Lutianis fulviflamma	P	P	—	Sm	S-T
Lutianus vaigiensis	P	P	—	Sm	S-T
Monodactylus argentius	C	C	—	Wn + Sm	S-T
Mugil cephalus	P	A	—	Wn + Sm	C-T
Mugil sp.	P	—	—		
Myxus capensis	P	P	—	Wn	S-T
Omobranchus sp.	—	—	P	Wn + Sm	S-T
Parascorpaena aurita	P	—	—	Sm	S-T
Periophthalmus sobrinus	—	P	P	Wn + Sm	S-T
Platax pinnatus	P	P	—	Wn	S-T
Platycephalus indicus	P	—	—	Wn + Sm	W-T
Pomadasys hasta	—	P	—	Sm	W-T
Pomadasys commersoni	P	P	—	Sm	W-T
Pomatomus saltatrix	P	—	—	Sm	S-T
Psammogobius knysnaensis	A	—	—	Wn + Sm	C-S
Pterois volitans	—	P	—	Wn + Sm	W-T
Rhabdosargus holubi	C	P	—	Wn + Sm	W-S
Rhabdosargus sarba	P	P	—	Wn	S-T
Sarpa salpa	P	A	—	Wn + Sm	C-T
Saurida undosquamis	—	P	—	Wn	S-T
Solea bleekeri	—	P	—	Wn	W-T
Sphyraena japonica	P	P	—	Wn + Sm	W-T
Therapon jarbua	P	C	—	Wn + Sm	W-T
Valamugil buchanani	P	P	—	Wn	S-T