A CONTRIBUTION TO THE ECOLOGY OF THE UMLALAZI ESTUARY

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INTRODUCTION

The Umlalazi river in Zululand is undergoing large scale changes due to deposition of mud from cultivated areas and a simultaneous rapid colonisation by mangroves chiefly *Avicennia officinalis*. The result is that open mud banks are being consolidated, shallows are changing into mangrove swamps and eventually into dry land. Much useful information can be obtained from the study of aerial photographs and in the case of the Zululand coastal rivers we are fortunate in having two series of photographic surveys by the Trigonometrical Survey. The photographs of the Umlalazi were made in 1937 and in 1960 and are reproduced in Fig. 1. The spread of mangroves and mud banks is obvious. In view of these changes it was felt that an ecological survey should be undertaken in order to record the present physical conditions and animal life in the estuary. As the mangrove invasion progresses the estuary will become narrower, shallows will disappear and tidal currents will become stronger. This should result in an increase in the fauna associated with mangrove swamps and a decrease in the shallow water fauna.

ACKNOWLEDGEMENTS

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GENERAL DESCRIPTION

The Umlalazi river rises on the Ngoye ridge near the town of Eshowe in Zululand. Near Eshowe the river has been dammed and water is drawn off for the town. From here, at an altitude of 480 metres, it drops down the eastern side of the Ngoye ridge to the coastal plain across which it flows for about 30 kilometres, receiving on the way, a large tributary, the

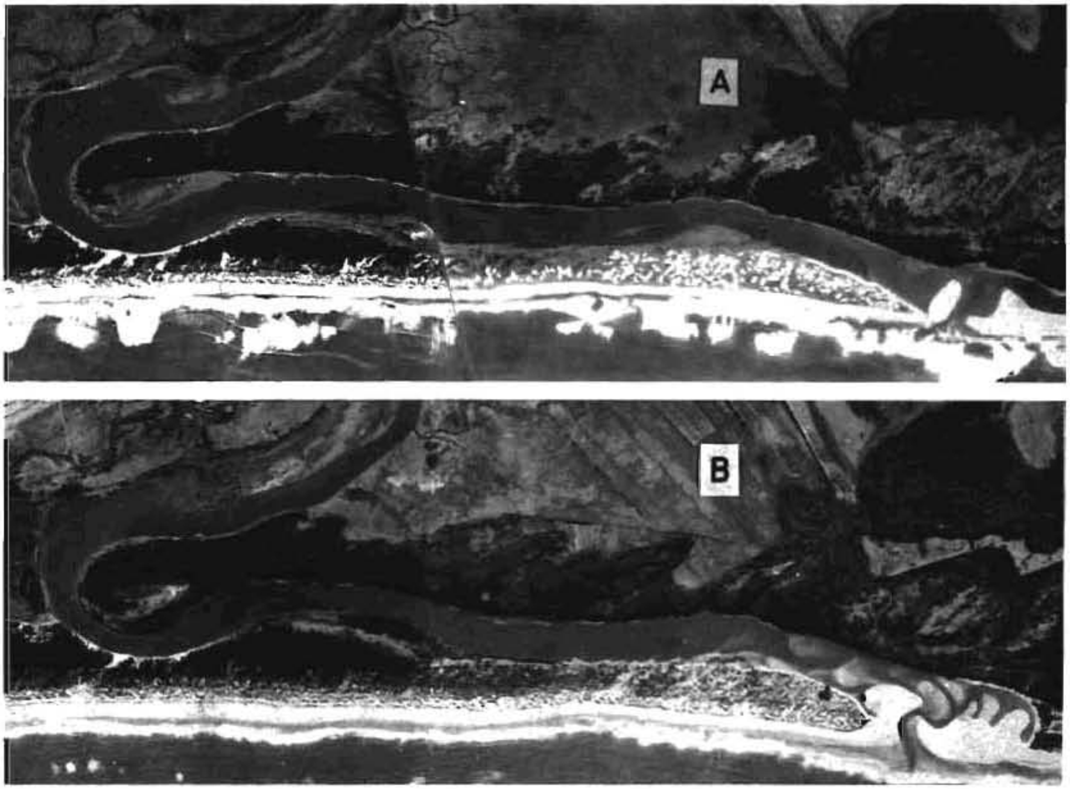

Fig. 1. Aerial photographs of the Umlalazi Estuary. The Head region is not included. (A) 1937, (B) 1960. Aerial Photographs reproduced under Government Printer's Copyright Authority No. 3492 of 10/3/65.

Mkukuze, as well as other minor streams draining the Ngoye. The river when it flows off the ridge is clear and fast running. When it reaches the plain and especially the cultivated areas it becomes muddy and changes into a slow moving river with dense vegetation of bush, trees and creepers on the banks. Eight kilometres from the mouth, at Balcombe's Rocks (Fig. 2) the water becomes brackish; this point was taken as the upper limit of the estuary. For the purposes of this survey the estuary was divided into the following regions:

1. The Head, stretching from Balcombe's Rocks to the Railway bridge;
2. The narrow part of the estuary from the railway bridge to the Lake and the Lake itself;
3. The Channel, from just above the Sandbank to Bishop's Trees;
4. The Mouth Region, from Bishop's Trees to the sea.

1. **The Head:** This part of the estuary is about 2·5 km. in length and 100 metres wide. The bank consists of hard clayey mud and is 2 metres in height. At its foot is a narrow beach which

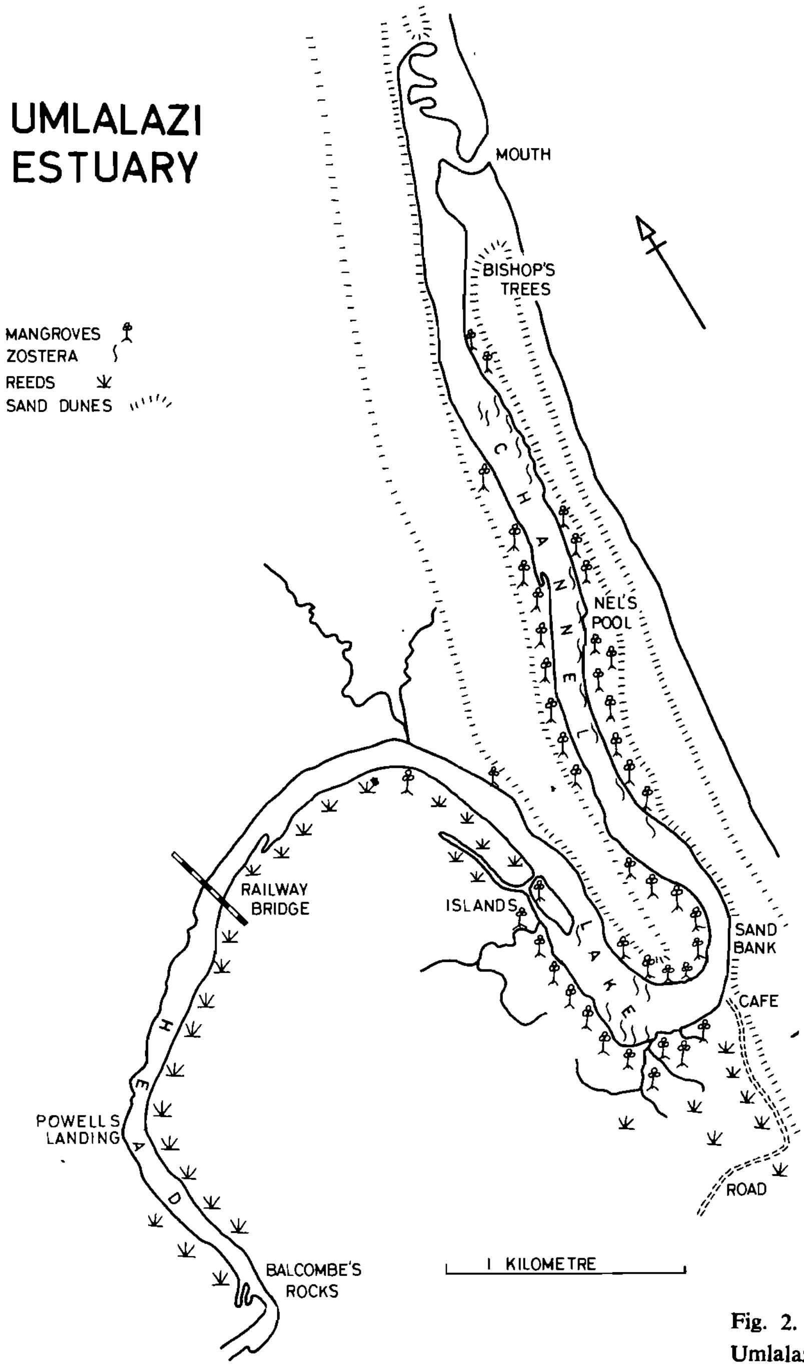

Fig. 2. Map of the Umlalazi Estuary.

slopes steeply into the water and there is virtually no shallow margin. The beach has been colonised by the reed *Phragmites communis.* At higher levels the freshwater mangrove *Barringtonia racemosa* occurs. At two places there are rocky outcrops. At the upper end of the Head at Balcombe's Rocks there are a series of rounded boulders at the foot of the eastern bank. There are a series of low reefs which are two hundred meters above the rail bridge exposed at low tide on the northern side of the estuary.

2. **The Lake:** This region includes the 1·5 km. long channel from the railway bridge to the Lake. This channel, like the Head is bordered by high banks with reeds at the margin, but *Barringtonia* has been replaced by *Avicennia* and *Bruguieria.* The channel curves round to the south and enters the northern end of the Lake at the Islands.

The Lake is the widest part of the estuary, it is between 200 and 300 metres in width and about 700 metres long. The southern end is used as a mooring for boats and this is the only part of the Umlalazi estuary which is easily accessible by road apart from private farm roads to the Head. The Lake is roughly rectangular with its long axis running north–south, i.e. parallel to the sea shore. The eastern bank is backed by a high sand dune which forms a peninsula between the Lake and the upper part of the Channel. The shore along this bank is sandy except at the southern end where thick mud marks the inside of the sweeping curve into the Channel. Mangroves occur along the shore where it is muddy and behind the mangroves *Hibiscus tiliaceus* is common. Elsewhere coastal bush and grass comes right down to the water level. The southern, western and northern banks of the Lake are characterised by a wall of mangroves behind which lie extensive salt marshes, the low lying areas of which are covered at high tide. These marshes have a typical vegetation of *Arthrocnemum*, *Juncus* and *Phragmites.* Mangroves, chiefly *Bruguieria* border the channels which have been dug to drain the marsh.

3. **The Channel:** From the southern end of the Lake the estuary first runs directly towards the sea and then, at the Sandbank, turns and runs northwards for 3 km. to Bishop's Trees, parallel to the sea shore and only a few hundred metres from the sea. The whole channel runs between two sand dunes. The currents in the Channel are strong and the substratum of the shore depends upon whether the current flows in the centre of the estuary or on one side. For example at the Sandbank the current is strong on the outside of the curve, the shore and inshore bottom is clean sand and there is a small beach backed by an eroding sand dune. The water is deep. On the opposite bank the water is shallow and there is deep soft mud supporting a dense growth of mangroves. At Nel's Pool the current is in the centre of the estuary and both banks are mud. Below Nel's Pool the estuary widens to about 200 metres. Strong tidal currents and eddies in this part prevent much deposition of mud and the substratum is mainly sand or muddy sand. *Zostera* grows in the shallows.

4. **The Mouth Region:** The estuary from Bishop's Trees to the mouth is characterised by fast currents and continually changing sand banks. The present position of the mouth is about 0·8 km. south of its position as shown by aerial photographs taken in 1937. The old mouth

site is now covered by a 10 metre high sand dune supporting a small *Casuarina* forest. The channel of the old mouth now forms a blind inlet some 200 metres long and 25 to 30 metres wide to the north of the present mouth. This inlet is slowly silting up.

The western bank of the mouth region is formed by a high sand dune which is rapidly eroding into the estuary. To prevent this erosion from silting up the river, a loose wall of granite boulders was laid down at the foot of the dune in 1962.

PHYSICAL CONDITIONS

Salinity

Salinities were determined by means of Knudsen's tables from specific gravities measured with a Twaddell hydrometer and simultaneous temperature readings. Salinities measured in this way are not as accurate as those obtained by titrations with silver nitrate but I feel that in an estuary a hydrometer gives sufficiently accurate results because the differences in salinity are large and changes are rapid. The hydrometer is also extremely convenient in the field. It is possible to obtain results immediately on station and if the readings indicate anything interesting a large number of them can be taken rapidly.

In order to obtain an overall picture of the variations, and to trace water movements, salinities over the whole length of the estuary were measured at High Water Spring (H.W.S.), Low Water Spring (L.W.S.), High Water Neap (H.W.N.), and Low Water Neap (L.W.N.). Readings were taken on the surface and at intervals of 0·6 metre down to the bottom except in the case of H.W.S. when readings were only taken at the surface and at 1·2 metres. Using the results obtained sections of the estuary were drawn up as shown in Fig. 3. In order to establish whether these readings which in each case were based on one tide could be regarded as typical, spot readings were taken at different dates at various points and depths. The differences were on the whole small, and it is suggested that Fig. 3 represents fairly typical conditions in the latter half of 1963. These conditions can be altered by several factors, for example variations in tidal range as a result of wind or difference in the size of the mouth.

Vertical salinity gradients are fairly common in the Umlalazi estuary. These occur firstly, where incoming sea water meets estuarine water; secondly where estuarine water backs up fresh river water at the Head at high tide; and thirdly after heavy rain. It is thus possible to record vertical salinity gradients at almost any point in the estuary under the right conditions.

Fig. 3 shows that the maximum and minimum salinities occur at high water springs and low water neaps respectively. This corresponds to the maximum and minimum water level. In the Umlalazi estuary low neap tide level is at a lower level than low spring tide. The same effect has been observed in the Severn estuary (Bassindale 1943) and in Kosi Bay (Day 1951). The volume of sea-water which enters the mouth during high spring tides does not have time to escape before the next tide starts rising in the sea. After floods had occurred in July the mouth of the estuary was extremely wide and deep and for about 6 weeks the low spring tide level dropped to well below the low neap tide level exposing large areas of the bottom never normally uncovered. This was only a temporary condition, the sea soon restored the

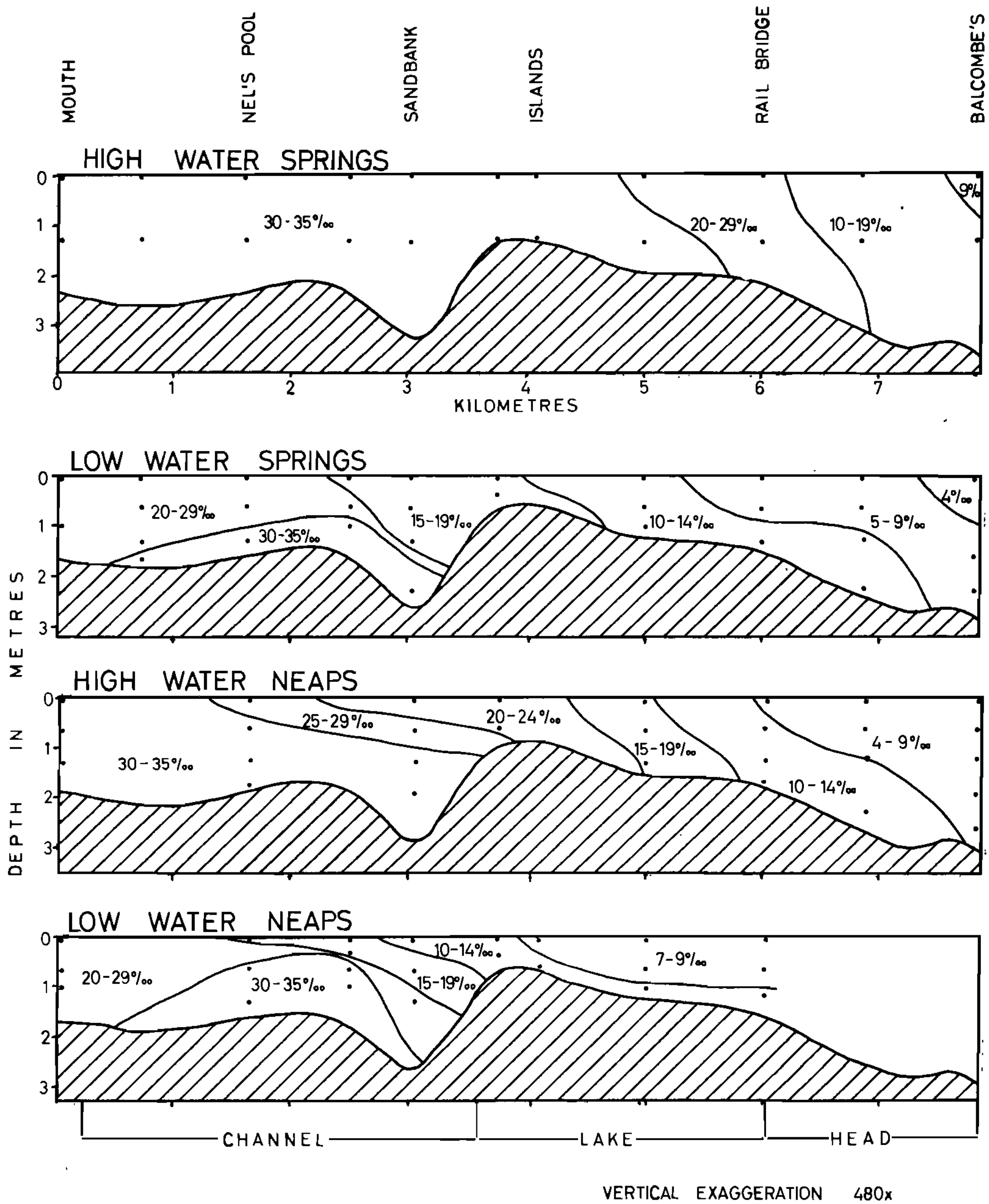

Fig. 3. Longitudinal sections of the Umlalazi Estuary at various tides showing distribution of masses of water of different salinities.

sandbanks and the mouth to its former narrow state and the low spring tide after a few months was higher than the low neap tide level.

As a result of the lower level at neap tides, water of lowest salinity is found at this time. At low tide in the Channel a normal horizontal gradient exists on the surface. But measurements show that the water in the mouth is less saline than the deep water higher up in the estuary, i.e. along the bottom there is a reversed horizontal salinity gradient. This is probably due to water of low salinity from higher up in the estuary flowing out over the denser, more saline bottom water in the region of Nel's Pool. Further down the estuary near the mouth, the currents are strong due to the presence of large sandbanks which narrow the estuary and force the water to flow in winding channels (Fig. 1). These currents cause mixing of the surface and bottom water resulting in water of salinity intermediate between the surface and bottom layers at Nel's Pool. The extensive mixing which occurs in the mouth region on outgoing tides is shown by the churning up of clouds of sand.

Fig. 3 shows that most of the surface water at Nel's Pool at L.W.N. must at H.W.N. have been higher up the estuary—above the Lake. The deep water at Nel's Pool at L.W.N. was only at the top of the Channel, and was not pushed into the Lake by the rising tide. The outgoing surface water, therefore, must flow out more rapidly than the bottom water.

The salinity of the bottom layers of the central part of the Channel never dropped below 30‰ although the surface salinity may be only 17‰. At H.W.N. sea water penetrates into the upper Channel and in the region of the Sandbank a vertical salinity gradient forms. This gradient is not very marked higher up in the Lake where the tidal effect seems merely to be a damming up of estuarine water. In the Head a vertical gradient is again found where the rising tide causes slightly heavier saline estuarine water to push in underneath lighter river water. The same effects are seen at H.W.S. only on a larger scale due to the much larger volume of sea water which enters the estuary. At this time there is no stratification in the Channel or in the Lake as sea water fills them. Above the Lake there is a marked vertical gradient where heavier sea water pushes in beneath backed up estuarine water. Higher up at the Rail bridge this gradient is absent and the water is well mixed and uniform from surface to bottom. In the Head the vertical gradient is formed as at H.W.N. except that the salinities are higher.

Although the catchment area of the Umlalazi is small, only 130 square km., the whole of this area is subject to high rainfall, 125 cm. per annum, most of which falls in summer. The rain tends to come in short heavy downpours and is only rarely spread over a long period. The effect of these short periods of heavy precipitation is a sudden large increase in the volume of fresh water entering the estuary, forming a layer over the saline estuary water. A typical example of this layering is shown in Fig. 4 where a layer of nearly fresh water 1½ metres thick formed after two days of rain totalling 3·8 cm., which is not particularly heavy for the region. This marked stratification is usually of short duration, being broken down by large movements at spring tides which restores normal salinity conditions. Most of the fresher water is apparently lost to the sea by flowing out over the deeper saline layers. During the period in which a surface layer of almost fresh water is present the animals in the intertidal zone are exposed to very low salinity values. Animals which can migrate into deeper water

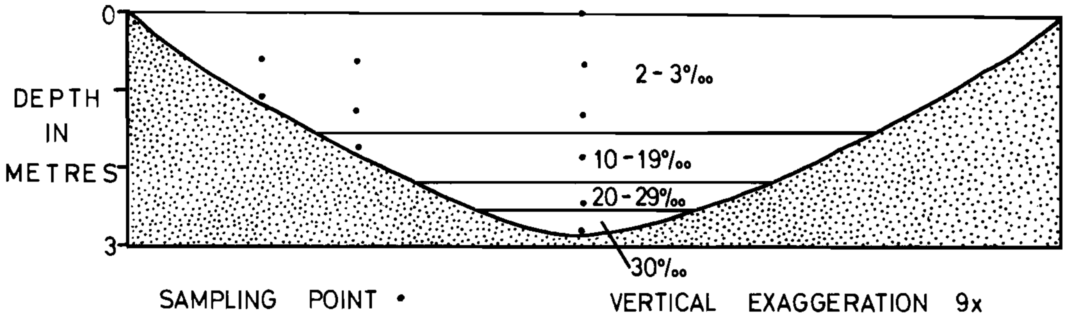

Fig. 4. Cross section of the estuary at the Sandbank on the 24th October, 1963, twentyfour hours after the end of rain lasting 2 days (total precipitation 3.8 cm.) showing the salinity layering which develops.

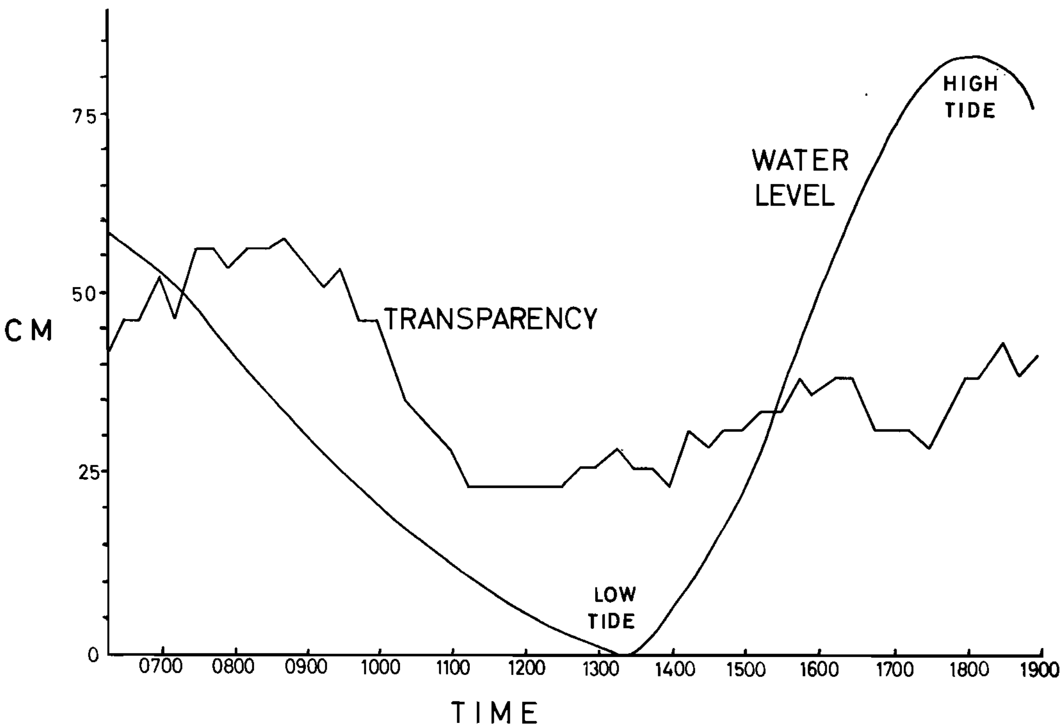

Fig. 5. Transparency and tide measured in the Lake on 9th February, 1963. Explanation in text.

can escape the effects of the stratification because salinities in the deeper water remain high.

Temperature

The temperatures in the Umlalazi estuary undergo a seasonal fluctuation. The temperatures recorded on the surface in daylight in the Lake during 1963 are as follows (Temperatures in °C):

Month	*Mean*	*Maximum*	*Minimum*	*Number of observations*
February	25·7	—	—	1
April	21·0	—	—	1
May	20·0	—	—	1
July	16·7	18·5	15·0	3
August	20·4	23·5	18·0	4
September	22·6	24·0	21·7	4
October	23·1	26·5	19·6	12
November	25·9	27·9	23·3	7

During dry weather the water in the estuary is at a slightly higher temperature on the surface than in the sea due to the warming effects of the sun on the shallow water. The following temperatures were taken at high tide at the Sandbank and in the sea 270 metres away:

Date	*Sandbank*	*Sea*	*Difference*
30th August	23·5°C	20·5°C	3·0°
14th September	22·8°C	21·5°C	1·3°

From the mouth upwards to the head of the estuary there is a gradual increase in the temperature of the surface at high tide as shown by the records in Table 1.

TABLE 1: TEMPERATURE IN °C

	Low Water Neap (8 Nov.)	*High Water Spring (1 Nov.)*	*High Water Neap (8 Nov.)*
Mouth	26·5	23·0	23·1
Nel's Pool	26·8	23·0	25·0
Sandbank	26·5	23·3	25·8
Lake	26·4	23·3	26·0
Islands	26·3	23·4	—
Rail Bridge	26·6	25·8	26·6
Powells	—	27·3	27·0
Balcombe's	—	26·8	26·9

At H.W.S. sea water penetrates as far as the Islands (Fig. 3) and the temperature up to this point is fairly uniform. Upriver from the Islands is dammed-up estuarine water that has been warmed by the sun. At low tide this spreads out down the length of the estuary resulting in uniform temperatures. At H.W.N. cooler sea water penetrates only a short distance and the temperatures in the rest of the estuary remain higher. Thus temperatures at the same place may vary considerably between high and low tide on the same day, for example at the Sandbank:

Date	*High Tide Temperature*	*Low Tide Temperature*	*Difference*
7th September	21·0° (0800)	24·5° (1230)	3·5°
1st November	23·3° (1700)	27·3° (0900)	4·0°

The time of sampling is shown in brackets. The higher temperature at midday on 7th September might have been due to a diurnal variation, but on the 1st November this was not the case, the higher temperature occurring in the morning.

The surface waters are nearly always warmer than the deeper layers, except where there are strong currents or where the water is very shallow. In deeper waters differences in temperatures between the surface and the bottom are nearly always present, for instance in the upper part of the Channel on the 8th November the temperature of the surface water was 26·7°C, 1 metre down the temperature was 23°C, a difference of 3·7°C. These vertical differences are almost invariably associated with salinity differences. Water in the shallow margins is slightly warmer than water in the centre of the estuary. For example at the Sandbank on the 26th October the water in the shallows was 24·8°C, the temperature of the water in the centre of the estuary was 24·2°C. Insolation of pools in mangrove swamps causes temperatures as high as 35°C.

Transparency

The transparency of the water was measured with a 15·5 cm. Secchi disc. Average readings in the estuary in 1963 were as follows (the figures in parenthesis refer to the number of readings):

READINGS IN CENTIMETRES

Mouth	*Lower Channel*	*Upper Channel*	*Lake*	*Above Lake*	*Head*
95 (5)	95 (6)	72 (11)	65 (10)	62 (8)	60 (7)

The low readings higher up in the estuary were probably due to silt in suspension which is precipitated in the central part of the estuary (Lake). The higher readings in the lower regions are due to the presence of clean sea water. It was noticed that as with temperature, the transparency fluctuated with the state of the tide, probably due to the movement up and down the estuary of bodies of water of different transparency. The graph in Fig. 5 was drawn up on the basis of readings taken every 15 minutes over a 12¾ hour period involving an almost complete spring tide cycle in the Lake. On this particular day (9th February) the transparency was slightly lower than average.

There was a sharp fall in readings on the ebbing tide although the outflow of water was slow compared with the inflow of the flood tide. The gradual increase with rising tide apparently confirms suggestions on water movements based on information from salinities. When the tide rises it does so rapidly and because the incoming clearer water is more saline and thus heavier it pushes in underneath the brackish estuarine water and only gradually mixes with the surface layers causing a slow increase in readings instead of the abrupt change that would occur if the estuary water were pushed back in a single mass. At the peak of high tide and on the outgoing tide the current is slower, larger particles which were held in suspension in the strong incoming tidal current settle out and the maximum transparency thus occurs some time after the peak of high tide. However, the whole mass of water is now moving downstream. A few hours after high tide turbid water of low salinity begins to flow downstream over the more saline layer. When this occurs transparency decreases rapidly. Towards the end of low tide the slowing up of the current allows silt to settle slightly and the cycle starts again.

Secchi Disc readings were sharply reduced by rain. The effect of rain is only noticeable about twelve hours after the rain has begun falling. Heavy showers after dry weather can cause readings to drop to as little as 5 cm., although as a rule they only drop to 20 or 30 cm.

Transparency can also be reduced through stirring up of mud by wind induced currents. On the 14th September the low tide reading in the Head was 60 cm.; the following day at the same condition of tide but with a strong wind blowing the reading had dropped to 45 cm.

THE FAUNA

The distribution of the fauna in an estuary is determined to a large extent by the nature of the substratum. In the Umlalazi estuary the substratum could conveniently be divided into three types: sedimenting substrata, eroding substrata and solid substrata.

Sedimenting Substrata

Mud occurs wherever there is little or no current action and in areas which are either permanently submerged or are intertidal. The consistency is dependent upon the current and all gradations from soft soupy mud to fairly firm muddy sand can be found. In the mouth region the blind inlet to the north of the mouth is the only area where mud occurs. There are no strong currents in the inlet and the incoming tide floods slowly over the banks. The mud is sandy and firm and is inhabited by polychaets *Loimia medusa*, *Chaetopterus varieopedatus*, *Nephthys tulearensis* and *Glycera convoluta* and lamellibranchs, *Hemitapes kochii* and *Solen corneus*. The surface fauna consists of large numbers of the gastropod *Nassarius kraussianus*, small specimens of the prawn *Penaeus japonicus* and a few crabs, *Macrophthalmus grandidieri* and *Dotilla fenestrata*.

In the Channel the lower intertidal and sublittoral mud banks have been colonised by *Zostera* which not only consolidates the mud by means of its roots but provides shelter for the epifauna. At higher levels on the shore mangroves and the aerial roots of *Avicennia* form a dense mat. Over the shallow mud banks juvenile fish are abundant. A seine net brings in hundreds of glassies (*Ambassis* spp.) and mullet (*Mugil* spp.), many *Therapon jarbua*, juvenile

Monodactylus falciformis as well as *Lutianus fulviflamma* and *Arothron immaculatus*. At night garfish (*Tylosurus leiurus*), springers (*Elops saurus*) and half beaks (*Hemirhamphus far*) can be seen on the surface together with shoals of mullet.

There are several differences in the components of the fauna of the Channel compared with the mouth region. The common polychaets here are *Glycera convoluta* and *Dendronereis arborifera*. Holes of *Upogebia africana* occur nearly everywhere but the prawn is difficult to dig out and the individuals are small. The large crab *Scylla serrata* digs holes in mud which is consolidated by *Zostera* or mangrove roots. Other crabs found associated with muddy areas in the Channel are *Macrophthalmus grandidieri* and *Thalamita crenata*. The gastropod *Polynices mammilla* is common just under the surface of muddy sand and thousands of the large mangrove snail *Cerithidia decollata* crawl over the soft mud between mangrove roots where *Periophthalmus* is also common.

In the Lake large expanses of mud flats are exposed at low tide. They consist mainly of soft mud but at the Islands and in the south-western corner are made up of sandy mud and have a sparse covering of *Zostera*. The mudflats are rich in mud prawns (*Upogebia africana*), polychaets (*Dendronereis arborifera* and *Glycera convoluta*), and razor shells (*Solen corneus*). Both *Upogebia* and *Solen* although common, are small and are not used for bait by fishermen. The prawn *Metapenaeus monoceros* is common in pools left by the receding tide. The bottom of the lake is soft mud and the only common animal is the gastropod *Nassarius kraussianus*.

In summer in the Channel and the Lake large numbers of swimming prawns, chiefly *Penaeus indicus* but with some *P. monodon* occur in the shallows over the mud banks.

Above the Lake there are no large expanses of mud, the estuary is narrow and the banks are steep.

Eroding Substrata

SAND. The substratum of the mouth region except for the blind inlet is clean sand. The water currents are rapid and the position of sandbanks and channels is continually changing, this results in an unstable environment. The fauna is not rich, consisting of animals which are able to move around and cope with changing conditions. The swimming crab *Matuta lunaris* burrows in the sand, as do the polychaets *Nephthys tulearensis* and *Glycera convoluta*. In semi-permanent sand banks juveniles of the echinoid *Echinodiscus bisperforatus* can be found. The polychaet *Glycera alba* occurs amongst sand at the base of boulders on the west bank. The fauna in the shallows consists of numerous glassies (*Ambassis* spp.), young mullet (*Mugil* spp.), occasional tobies (*Arothron immaculatus*), and the swimming crab *Thalamita crenata*. On the sandy beaches the ghost crabs *Ocypode ceratophthalmus* and *O. kuhlii* predominate whilst the terrestrial hermit crab *Coenobita cavipes* and a more uncommon ghost crab *O. cordimanus* are occasionally seen. Ghost crabs are found wherever there are sandy beaches in the Channel and Lake, but the largest individuals are apparently nearest the mouth. They are also common along the sea shore. Above the mouth the fauna of the sandy regions is sparse and apart from the ghost crabs the only crab is *Dotilla fenestrata*. This crab can be found as far up as the Head. Wherever there is cast up weed on sandy beaches amphipods (*Talorchestia ancheidos*) and small flies occur. The only polychaet recorded from sand high up in the estuary was the ubiquitous *Dendronereis arborifera* which was found just below the rail bridge.

Solid Substrata

Most of the solid surfaces in the estuary are manmade, but hard consolidated mud as well as stranded logs, mangrove roots and two small rocky outcrops provide additional habitats for sessile and burrowing animals.

1. HARD MUD. Near the upper tide levels or above tide level old mud tends to dry out and become hard. The fauna of this hard mud is very different to that of the soft mud because of the obvious difference in the substrata and because the area is either only covered by water for short periods at high tide or is never normally inundated. However, there are occasional beds of hard clayey mud which are completely under water. One of these occurs along the western bank of the lower part of the Channel. This bank is only exposed for brief periods at low tide and is occupied by the burrowing isopod *Sphaeroma annandalei*. Behind the mangroves along the eastern shore there is a 10 metre wide area of consolidated mud, the surface of which is sunbaked hard. On this flat in summer thousands of fiddler crabs (chiefly *Uca urvillei*) and numbers of marsh crabs (*Sesarma eulimene*) are to be found. Similar bare patches of mud inhabited by *Uca* occur amongst the *Arthrocnemum* around the shores of the Lake. These areas are only covered for short periods at high tide. The acres of salt marshes around the Lake are seldom covered by normal tides but over them swarm the marsh crabs *S. eulimene* and *S. meinerti*. The large semi-terrestrial crab *Cardiosoma carnifex* is occasionally found and extends together with *Sesarma* into the edge of the sugar cane plantations which border the marshes.

2. ROCKS. The granite boulders in the mouth region one year after being laid down already supported large numbers of barnacles (*Balanus amphitrite*) and oysters (*Crassostrea cucullata*) as well as the gastropod *Siphonaria oculus*. Several crabs (*Metapograpsus thukuar*, *Grapsus strigosus* and *Cyclograpsus punctatus*) were found living in the crevices between the rocks.

Oysters seem to be limited by lack of a suitable place of attachment, and were not normally found above the mouth. However in 1963 a large metal mooring which was lifted at the southern end of the Lake had several full grown *Crassostrea cucullata* on it indicating at least that other environmental conditions were suitable. The concrete pilings of the rail bridge are covered with a dense population of *Balanus amphitrite*. Just above the rail bridge there are a series of rocky outcrops which are just exposed at low tide. Barnacles are only found on the vertical or overhanging surfaces of these rocks probably due to the film of silt which is present on the horizontal surfaces. 2·5 km. above the rail bridge there is a second series of rocky outcrops but barnacles do not occur there, possibly because of the low salinities—the highest reading recorded was 9‰. These rocks do have numbers of the small lamellibranch *Brachidontes variabilis* in holes and crevices. Macnae (1957) lists *Brachidontes* as one of the animals characteristic of the upper reaches of estuaries in South Africa.

3. WOOD. Embedded in the mud banks of the estuary are several logs which have been washed down from the rivers. These are not as permanent as rocks, but because the currents in the estuary are not powerful, they do not move around except in times of flood, when most are washed out to sea and are replaced by new logs. These logs have a characteristic fauna. On the outside of the wood are barnacles and the serpulid polychaet *Mercierella enigmatica*. There are three common borers, the isopod *Sphaeroma annandalei* which also causes severe damage to wooden boats, and two lamellibranchs—*Martesia striata* and *Teredo ancilla*, the latter first described from the Umlalazi (Barnard 1964). These borers honeycomb the outer wood and cause it to break up creating holes and crevices which are inhabited by the two crabs *Metapograpsus thukuar* and *Rhynchoplax bovis*.

DISCUSSION

Day (1951) has divided an ideal estuary into four regions on the basis of salinity, fauna and flora, currents and substratum. These subdivisions are:

The Head,
The Upper Reaches,
The Middle Reaches, and
The Mouth.

In the Umlalazi the same general pattern can be seen. The Mouth of the Umlalazi stretches from the sea to Bishop's Trees and has been referred to in this paper as the Mouth Region, an area of strong currents, high salinities and colonised by a stenohaline component. The Middle Reaches of Day's subdivision correspond to the Channel of the Umlalazi, stretching from Bishop's Trees to the southern tip of the Lake. This is a region of sandy mud, with high but variable salinity, beds of *Zostera*, mangroves and a fauna of estuarine as well as euryhaline marine forms. Day's Upper Reaches are represented by the Lake as well as the narrower section above the Lake as far as the rail bridge. As described by Day for his ideal estuary, this region has extensive salt marshes, a large amount of silt is deposited here as mud and the fauna is made up of mud loving estuarine forms. Above the rail bridge the conditions alter rapidly, fresh water forms occasionally occur and at low tide the salinity is low: this is the Head of the estuary.

The work of Day and his colleagues has indicated the importance of shelter from wave action in the faunal composition of estuaries in South Africa. However, the evidence presented in this paper relating to salinity variations in the Umlalazi estuary indicates the importance of salinity as a factor in the estuarine environment. Animals living in the mouth region of the Umlalazi may well be there because of the shelter from wave action, but colonisation of the Middle and Upper Reaches could only take place if the colonising species are euryhaline.

Korringa (1956) carried out a series of salinity surveys in Knysna estuary and the results he obtained show an even more marked stratification and possible salinity variation than that found in the Umlalazi estuary.

Although the lowest salinities in the Umlalazi estuary occur at low water neaps, the greatest variation is at spring tides. The actual variation, which is the difference in salinity,

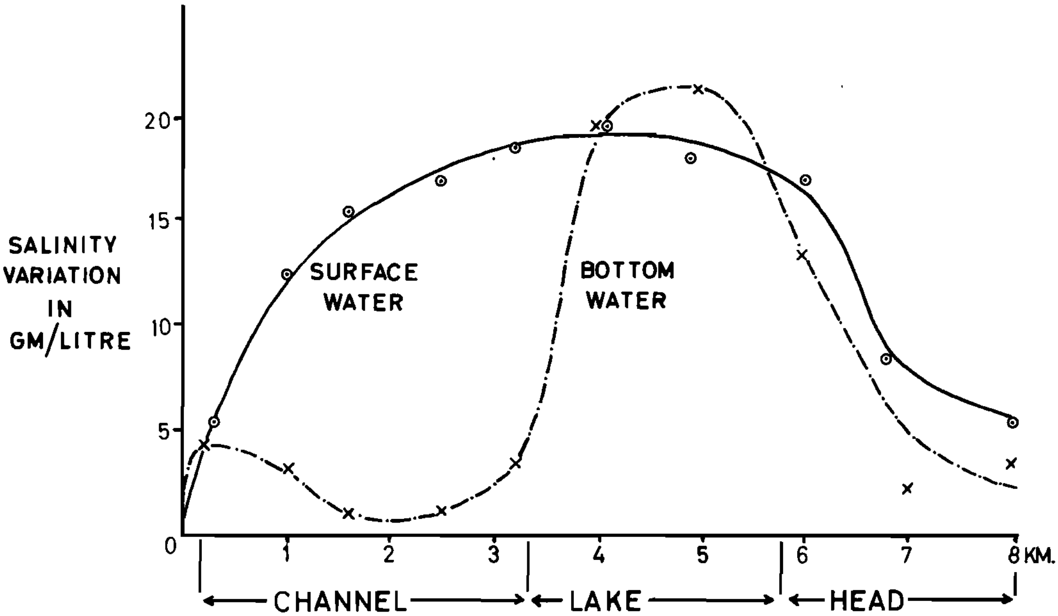

Fig. 6. Variation in salinity between high and low tide along the length of the estuary.

expressed as grams per litre between high and low tide, has been plotted for a spring tide and is shown in Fig. 6. The smallest changes occur at the ends of the estuary, namely near the sea and near the river. The greatest variation is in the Lake. Bassindale (1943) found similar results in the Bristol Channel and Severn estuary. It is interesting to note that in the Umlalazi estuary animals living on the bottom in the Channel are subjected to little salinity variation, whereas those living near the surface are exposed to considerable variation. In the Lake there is little difference between surface and bottom waters.

The most obvious plants in the Umlalazi estuary are the mangroves of which there are two species, *Avicennia officinalis* and *Bruguieria gymnorhiza*. According to local reports which are confirmed by an examination of aerial photographs taken in 1937, there were no mangroves in the estuary before 1940. They apparently made their appearance in the late 1940s or early 1950s although no one seems to know exactly when. The question therefore arises, why were mangroves not present previously?

According to Muir (1937) seeds of *Avicennia* and *Bruguieria* are capable of dispersal by sea and are fairly common in beach drift. Mangrove swamps occur both north and south of the Umlalazi estuary so it seems highly likely that seeds have entered the estuary at times in the past. Macnae (1963) states: "At the estuary of the Umlalazi no mangroves appeared until farming activity had loaded the river with alluvium and this had been deposited in the estuary." This view he based on information given to him by Colonel Vincent, at that time Director of the Natal Parks, Game and Fish Preservation Board, and to a large extent reflects local opinion. However this is not correct since according to a local Game Ranger Mr. M. Austin, and a local farmer Mr. C. Powell, thick mud was present in the Umlalazi as early as 1910–12. Yet the mangroves only appeared about 40 years later. An important point is that Macnae (1963) states that mangroves, especially *Avicennia*, are tolerant of sand since they have become established in sand at Inhaca island as well as at Kosi Bay. The presence or absence of mud was therefore not the deciding factor in the mangrove invasion of the Umlalazi and an alternative explanation is required.

There are a number of estuaries between Durban Bay and the northern border of Zululand. These estuaries fall into three categories:

(1) Those which are open the whole year round, i.e. open estuaries.
(2) Those which are closed for most of the year and only open briefly after heavy rain, i.e. closed estuaries.
(3) Those estuaries which are open for most of the year but for some reason close for a few months every year.

Unfortunately all the estuaries in question could not be visited regularly on a seasonal basis and information as to whether or not an estuary ever closes depends upon local information. The following table lists the estuaries as well as stating whether they fall into the first, second or third category and whether or not mangroves occur:

Estuary	*Type*	*Mangroves*
Kosi Bay	Open	Present
Sordwana Bay	Open	Present
St. Lucia	Open	Present
Richard's Bay	Open	Present
Umlalazi	Open	Present
Siyayi	Closed	Absent
Amatikulu	Occasionally closed	Absent
Inyoni	Closed	Absent
Tugela	Open	Absent
Umvoti (Not visited and information not available)		
Tongaat	Closed	Absent
Sinkwazi	Closed	Absent
Umhlali	Closed	Absent
Durban Bay	Open	Present

From this list it can be seen that those estuaries which are open the whole year round have mangroves, the others do not. The only exception is the Tugela but in this case frequent flooding occurs and mangroves are probably not able to become established. The interesting estuary in the above list is the Amatikulu. This is about 15 miles south of the Umlalazi and although open most of the year does close for a few months. There are no mangroves present and attempts to establish them there by the local Game Ranger have failed. In the list the Umlalazi is regarded as being an open estuary but local enquiries revealed that it formerly closed every year for a few months. Mr. C. Powell was responsible for organising parties to open the mouth to prevent flooding of low lying sugar plantations and he supplied me with information as to the dates when the mouth closed. Since 1945 the estuary closed on the following dates:

October 1945
January 1946
August 1947
February 1949
April 1952.

Since April 1952 the mouth has not closed again. The dates here show remarkable correspondence to the time of the beginning of the colonisation by mangroves, namely the late forties or early fifties. Rainfall records show no apparent link between the closing of the mouth and the amount of rainfall. The closing in August 1947 was preceded by normal rainfall for June and July (8·8 cm. and 8·3 cm. respectively). Closing did sometimes occur after dry conditions, for example in August 1948 when there had only been 1·5 cm. in June and 0·5 cm. in July. Since 1952 there have been occasional long dry periods and yet the mouth has not closed again.

It is therefore suggested that it is as a result of the mouth of the Umlalazi remaining open that mangroves have been able to colonise the estuary and that the silting up which occurred prior to the colonisation was not the prime cause.

The reason why mangroves do not survive in estuaries that close for a few months only is not clear. It is possible that in a closed estuary the salinity may drop below the tolerance of the trees although Macnae (1963) suggests that they are very tolerant to reduced salinity and may even grow to greater heights in low salinities.

If the mouth of the estuary closes in the dry season it is possible that salinities may rise above that of normal sea water, this effect was recorded in the Klein River Estuary in the Cape by Scott (1952). A more plausible explanation is that when the mouth closes the water level rises and drowns the mangroves. Macnae (1963) states on this point, "All species seem to die off if they are continuously under water so that the aerenchyma of the pneumatophores has no access to air". In this connection it may be pointed out that the reason why local farmers were interested in the closing of the mouth was the flooding of their fields as the water level rose.

It is difficult to assess the effect the mangroves are having on the estuary. In a flood in July 1963, extensive silting of the estuary occurred. This silting took place in the Lake and in the Channel and the source of silt is different in the two cases. Silt brought down by the river into the estuary was deposited in the Lake as a fine mud when the force of the current was reduced due to the broadening of the basin—the water flooded over into the salt marshes and formed a huge lake. On the other hand, in the Channel the silt originated from the banks of the Channel itself when these were eroded by the fast flowing water. The presence or absence of mangroves in the Lake made no difference to the amount of silt being brought down by the river and deposited there. However in the Channel mangroves had both a beneficial and a deleterious effect. In places where mangroves were well established very little scouring of the banks took place, i.e. they helped to protect the banks from erosion. By colonising the shallow areas, however, they effectually narrow the width of the estuary resulting in increased current speed and thus increased scouring and erosion of areas not covered by mangroves, e.g. the Sandbank. They also prevent the floodwaters from removing the mud banks which they have colonised and thus contribute doubly to the blocking effect in the Channel.

The dominant mangrove in the Umlalazi is *Avicennia officinalis*. Its thick masses of roots help to consolidate the substratum and in comparison with the situation recorded in 1937 by aerial photographs, this has resulted in an extension of the shoreline into the estuary (Fig. 1). Places where this has occurred are opposite the Sandbank and Nel's Pool. At the southern end of the Lake there used to be a large pool separated from the Lake by a narrow bank. By 1963, Dunn's Pool as it is known locally had completely disappeared beneath an impenetrable forest of mangroves. Opposite the Sandbank and Nel's Pool former tidal mud banks have been colonised by mangroves, more sand and mud has settled around the matted roots and new land has formed. This seems to be the chief result of the invasion, namely a takeover of the shallows. This has occurred mainly at the expense of *Zostera*.

The *Zostera* beds in the Umlalazi in 1963 were insignificant in comparison with those of Richard's Bay where, according to Millard and Harrison (1954), the beds are the richest and most valuable part of the estuary. This difference is reflected in the fauna. For example although the prawn *Penaeus indicus* is the dominant swimming prawn, *P. monodon* also occurs in both estuaries. However in Richard's Bay, *P. monodon* is common and made up 55 per cent of the catch in thick *Zostera*. In the Umlalazi *P. monodon* is uncommon, a few juveniles are usually found but otherwise it only occurs in shoals which enter the estuary for short periods.

Increased turbidity cuts down light penetration, increase in depth of water does the same. Reference to Fig. 5 shows that in the Lake minimum transparency coincides with low tide and maximum transparency approximately with high tide, thus when light reduction through turbidity is at a maximum the water level is low and vice versa. This must limit the depth to which *Zostera* can grow in the Umlalazi. Day (1951) suggests that in the Berg River the muddiness of the water limits *Zostera* to the intertidal region. Macnae (1957) disagrees because *Zostera* plants can develop a long leaf which rises and floats near the surface making the plant to some extent independent of the transparency of the water around it, and he regards the turbidity explanation as an over-simplification. He prefers the suggestion of Tutin (1938) that *Zostera* cannot grow when the bottom is continually being modified by wave action or tidal currents. However Day (1954) points out that in Richard's Bay the *Zostera* is far more luxuriant in winter when the water is clear than in summer when it is more turbid. Obviously light must have some effect on *Zostera*.

Examination of seine netting catches gives the impression that the Umlalazi is not as rich as Richard's Bay. The differences between Richard's Bay and the Umlalazi are due to a variety of reasons. The differences in *Zostera* and its effects on penaeid populations have already been pointed out. In the Umhlatuzi Lake at Richard's Bay large numbers of rhizostomid jellyfish are seen in the shallows. In the Umlalazi on the other hand Rhizostomids are uncommon and the occasional specimens which are found have probably washed into the estuary. The rhizostomids apparently find conditions in Umhlatuzi Lake ideal.

As mentioned above, the tidal differences in most of Richard's Bay are small, whilst in the Umlalazi even above the rail bridge a tidal range of ·6m occurs. This means that the Umlalazi has a much larger intertidal zone than Richard's Bay and it is in the intertidal fauna that many differences are observed. Four species of *Uca* were recorded from Umlalazi and one of these (*U. urvillei*) is present in thousands. The U.C.T. ecological survey failed to find any *Uca* on four visits to Richard's Bay. Macnae (1963) records *Uca annulipes* and *Uca chlorphthalmus* as being common in Richard's Bay although he states in his text that "species of *Uca* were not seen and only a few pellets of pseudofaeces probably of *U. annulipes* or of *U. chlorophthalmus* were noticed". I think that it is fairly safe to assume that *Uca* does not occur at Richard's Bay or is only present in very small numbers. *Uca* is a typical intertidal animal feeding on the interstitial matter in mud and sand and the discrepancy in its distribution between Richard's Bay and the Umlalazi could be explained on the basis of the extent of the intertidal zone in the two estuaries. Similarly the intertidal crab *Dotilla fenestrata* penetrates into the Head of the Umlalazi but it is absent from the Umhlatuzi Lake although it does occur in the channel of Richard's Bay where there is some tidal variation.

Four estuaries have been investigated on the Zululand coast, namely Kosi Bay (Broekhuysen 1959), Richard's Bay (Millard 1954), St. Lucia Bay (Day 1954) and the Umlalazi. The number of species of animals excluding birds found in these estuaries is:

Kosi Bay	173
Richard's Bay	183
St. Lucia	156
Umlalazi	156

A comparison of the number of species which the Umlalazi has in common with the other three estuaries is:

Umlalazi and Kosi Bay	55
Umlalazi and Richard's Bay	68
Umlalazi and St. Lucia	71

Thus nearly half the species which were found in the Umlalazi also occur in St. Lucia and of these 52 occurred in that part of St. Lucia between the Shallows at the southern end of the lakes and the mouth. This is a narrow channel about 100 metres wide and 22 km. long and is remarkably similar to the Umlalazi in topography, fauna and flora. According to Day (1954) the southern end of the lakes, which is the area immediately above the channel, is the richest part of the St. Lucia System.

In 1965 a start was made with dredging the Umlalazi estuary. The estuary is to be deepened and the excavated mud is to be dumped into the marshes and mangrove swamps. Similar work is in progress at Richard's Bay and at St. Lucia where the mud dumped in the swamps has killed the mangroves.

SUMMARY

In the last fifteen years the Umlalazi estuary in Zululand has been colonised by mangroves, chiefly *Avicennia officinalis* (Linn.), which were previously absent. This will probably result in large changes in the physical conditions. The possible causes of the colonisation are discussed and it is suggested that the failure of the estuary mouth to close in recent years may

be the cause. The salinity, temperature and transparency variations in the estuary have been investigated. The 156 species of animals found in the estuary are listed together with their distribution.

FAUNA LIST

The approximate abundance of the species is shown by the following symbols:

P – present,
F – fairly common,
C – common,
A – abundant.

The estuary is divided into five regions as discussed in the text, these are:

(1) Mouth; from the sea to Bishop's Trees.
(2) Lower Channel; from Bishop's Trees to Nel's Pool.
(3) Upper Channel; from Nel's Pool to a point opposite the cafe.
(4) The Lake; including the salt marshes surrounding the Lake and the estuary as far as the railway bridge.
(5) The Head; from the railway bridge to Balcombe's Rocks.

	Mouth	Low. Chan.	Up. Chan.	Lake	Head
COELENTERATA					
Amphisbetia bidens (Bale)	P				
Clytia hemisphaerica (Linn.)	P				
Rhizostomid jellyfish		P	P		
POLYCHAETA					
Chaetopterus varieopedatus (Renier)	F				
Dendronereis arborifera Peters		P	F	F	
Desdemona sp.					C
Glycera alba (Muller)	P				
Glycera convoluta Kef.	P	F	F	P	
Loimia medusa Savigny	C				
Mercierella enigmatica Fauvel	F	F	F	F	F
Namanereis indica (Southern)				P	
Nephthys tulearensis Fauvel	P				
CRUSTACEA: CIRRIPEDIA					
Balanus amphitrite v. denticulata Bloch	C	C	F	C	P
Octolasmis sp. Parasitic in Scylla serrata					
COPEPODA					
Acartia negligens Dana			P		
Acartia sp.				A	
Acrocalanus (? inermis)			P		
Centropages sp.	P	P	F	C	
Clytemnestra (? scutellata)					F

	Mouth	Low. Chan.	Up. Chan.	Lake	Head
Corycaeus speciosus Dana				P	
Ditrichocorycaeus africanus M. Dahl		P		P	
Ergasilus sp.			P	P	P
Eucalanus sp.				P	
Euchaeta (? marina)				P	
Euterpina acutifrons (Dana)		P	P	P	
Halicyclops (? pilifer)				P	
Oncaea sp.				P	
Paracalanus crassirostris f. typica Fruchtl.	F	P	F		
Paracalanus parvus (Claus)	P				
Pseudodiaptomus charteri Grindley				C	
Pseudodiaptomus hessei (Mrázek)				A	P
Temora turbinata (Dana)		P			
ISOPODA					
Cyathura carinata (Kröyer)				P	
Irona melanosticta Sch. & Mein.		Parasitic on Tylosurus leiurus			
Sphaeroma annandalei Stebb.		C	C	C	
AMPHIPODA					
Grandidierella bonnieri Stebb.				C	
Melita zeylanica Stebb.			F	F	
Talorchestia ancheidos Barnard		F	C	C	
DECAPODA: MACRURA					
Leucifer sp.			P	P	
Macrobrachium equidens (Heller)			P	F	F
Metapenaeus monoceros (Fabr)				C	
Palaemon pacificus Stimpson		C	C	F	
Penaeus indicus M. Edw.	C	A	A	A	F
Penaeus japonicus Bate	C	F	F	F	
Penaeus monodon Fabr.	P	C	C	F	
DECAPODA: ANOMURA					
Callianassa kraussi Stebb.		Recorded by Macnae 1963			
Clibanarius longitarsus (de Haan)	F	C	C	F	
Coenobita cavipes Stimpson	P		P		
Upogebia africana (Ortmann)	F	C	F	F	
DECAPODA: BRACHYURA					
Cardisoma carnifex (Herbst)				P	
Cyclograpsus punctatus M. Edw.	P	P			
Dotilla fenestrata Hilg.	F	F	F	F	P
Grapsus strigosus (Herbst)	P				
Illyograpsus rhizophorae Barnard				P	
Lupa pelagica (Linn.)		P	P		
Macrophthalmus grandidieri M. Edw.	P	P			
Matuta lunaris (Forsk.)	F	P			
Metapograpsus thukuar (Forsk.)	F	F	F	F	P
Ocypode ceratophthalmus (Pallas)	F	F	F	F	
Ocypode cordimanus Desm.	P				

	Mouth	Low. Chan.	Up. Chan.	Lake	Head
Ocypode kuhlii de Haan	F	P	P	P	
Pseudograpsus erythraeus Kossmann			P		
Rhynchoplax bovis Barnard	P			P	P
Scylla serrata (Forsk.)		F	F	F	F
Sesarma catenata Ortmann		Recorded by Macnae 1963			
Sesarma eulimene de Man		F	A	A	F
Sesarma guttata M. Edw.			P		
Sesarma meinerti de Man		P	F	C	F
Sesarma plicata (Latr.)		F	F		
Thalamita crenata (Latr.)	F	P			
Tylodiplax blephariskios (Stebb.)				P	
Uca annulipes (M. Edw.)			F		
Uca chlorophthalmus (M. Edw.)	•	P	P		
Uca marionis (Desm.)				F	
Uca urvillei (M. Edw.)		C	A	C	
Varuna litterata (Fabr.)	F			P	P
MOLLUSCA: GASTROPODA					
Cassidula labrella (Deshayes)		Recorded by Macnae 1963			
Cerithidia decollata (Linn.)		A	A	C	
Leucotina natalensis Smith		P			
Littorina scabra Linn.	P	F	F	F	
Nassarius kraussianus (Dunker)	C	C	C	C	
Neritina natalensis					P
Polynices mamilla Lam.	P	F			
Pyrazus palustris Linn.		Recorded by Macnae 1963			
Siphonaria oculus Krauss	P				
MOLLUSCA: LAMELLIBRANCHIATA					
Brachidontes variabilis (Krauss)				P	C
Crassostrea cucullata (Born.)	F		P		
Dosinia hepatica Phil.				P	
Hemitapes kochii (Phil.)	P	P		P	
Macoma litoralis (Krauss)			P		
Martesia striata Linn.		P		P	
Solen (? corneus Lam.)	P		F	F	
Teredo ancilla Barnard		P		P	
CHAETOGNATHA					
Sagitta sp.			P	P	
ECHINODERMATA					
Echinodiscus bisperforatus (Leske)	P				
PISCES					
Dasyatis uarnak (Forskal)*		P		P	
Acanthopagrus berda (Forskal)			F	P	
Acanthurus sp. juvenile		P			
Agriosphyraena barracuda (Walbaum)		P			
Ambassis commersoni Cuv. & Val.			C		
Ambassis gymnocephalus (Lacepede)	A		C	C	P

	Mouth	Low. Chan.	Up. Chan.	Lake	Head
Ambassis safgha (Forskal)*	A	A		C	
Ambassis urotaenia Bleeker	A	P	P	C	
Amblyrhynchotes honckeni (Bloch)			P	P	
Arothron immaculatus (Bloch)	P	F	P	C	
Caranx sexfasciatus Quoy & Gaimard			P	F	
Chaetodont juvenile			P		
Chelonondon laticeps Smith				P	
Chorinemus (? sanctipetri C. & V.)			P		
Coryphopterus natalensis (Gunther)		P			
Ctenogobius acutipennis Cuvier			F	F	
Eleotris fusca (Bloch)			P		
Elops saurus Linn.*		P			
Epinephelus gauza (Linn.)		P			
Epinephelus tauvina (Forskal)		P	P		
Epinephelus spiniger (Gunther)				P	
Gobius sp. (Uml No. 55)				P	
Gobius sp. (Uml No. 80)				P	
Gobius giuris Hamilton				P	
Hemirhamphus far Forskal*				P	
Johnius hololepidotus (Lacepede)	P	P	P	P	P
Kantapus oglinus Smith		F			
Leiognathus equula (Forskal)	P		P	P	
Lutianus fulviflamma (Forskal)		F	P	P	
Monodactylus falciformis Lacepede		F	P	P	
Mugil ramada Cuv.				F	
Mugil (Liza) seheli Forskal	C			C	
Mugil strongylocephalus Richardson	C	C	C	C	
Muraenesox cinereus (Forskal)*				P	
Oxyurichthyes tentacularis (Cuvier)				P	
Pelates quadrilineatus (Bloch)		P			
Periophthalmus cantonensis Osbeck*		F	F	C	
Pisodonophis boro (Hamilton-Buchanan)				P	
Platycephalus indicus (Linnaeus)	F	P	P	P	
Polydactylus plebius Broussonet			P		
Pomacentrid juvenile		P			
Pomadasys hasta Bloch		P	P	F	
Pomadasys operculare (Playfair)*		P	P		
Pomatomus saltator (Linnaeus)		P	P	P	
Promicrops lanceolatus (Bloch)*			P	P	
Pseudorhombus arsius (Hamilton)*			P	P	
Pterois volitans (Linnaeus)	F	P			
Rhabdosargus tricuspidens Smith	C				
Siganus oramin (Schneider)				P	
Sillago sihama (Forskal)	F		P		
Solea bleekeri Boulenger				F	

(*Not identified by Prof. J. L. B. Smith)

	Mouth	Low. Chan.	Up. Chan.	Lake	Head
Strializa canaliculatus (Smith)		C	C	P	P
Syngnathus spicifer Ruppell			F	F	
Therapon jarbua (Forskal)	F	C	F	F	P
Thrissocles malabaricus (Bloch)			P		
Thyrsoidea macrura (Bleeker)..			F		
Trachystoma euronotus (Smith)	F	F	F		
Tylosurus leiurus (Bleeker)	P		P	P	

REFERENCES

BARNARD, K. H. 1950. Descriptive Catalogue of South African Decapod Crustacea. *Ann. S. Afr. Mus.*, 38: 1–837.

BARNARD, K. H. 1964. Contributions to the Knowledge of South African Marine Mollusca. V. Lambellibranchiata. *Ann. S. Afr. Mus.*, 47: 361–593.

BASSINDALE, R. 1943. Studies on the Biology of the Bristol Channel XI. The Physical environment and the intertidal Fauna of the Southern Shores of the Bristol Channel and Severn Estuary. *J. Ecol.* 31: 1–29.

BROEKHUYSEN, G. J. and H. TAYLOR. 1959. The Ecology of South African Estuaries. Part VIII. Kosi Bay Estuary System. *Ann. S. Afr. Mus.* 44: 279–296.

DAY, J. H. 1951. The Ecology of South African Estuaries. Part I. Review of Estuarine Conditions in General. *Trans. Roy. Soc. S. Afr.* 33: 53–91.

DAY, J. H., N. A. H. MILLARD and G. J. BROEKHUYSEN. 1954. The Ecology of South African Estuaries. Part IV. The St. Lucia System. *Trans. Roy. Soc. S. Afr.* 34: 129–156.

DAY, J. H. and J. F. C. MORGANS. 1956. The Ecology of South African Estuaries. Part VIII. The Biology of Durban Bay. *Ann. Nat. Mus.* 13: 259–312.

KORRINGA, P. 1956. Oyster Culture in South Africa. *Union of S. Afr. Div. of Fish Rep.* 20: 287–370.

MACNAE, W. 1957. The Ecology of the Plants and Animals in the Intertidal Regions of the Zwartkops Estuary near Port Elizabeth, South Africa. Parts I & II. *J. Ecol.* 45: 113–387.

MACNAE, W. 1963. Mangrove Swamps in South Africa. *J. Ecol.* 51: 1–25.

MILLARD, N. A. H. and A. D. HARRISON. 1954. The Ecology of South African Estuaries. Part V. Richard's Bay. *Trans. Roy. Soc. S. Afr.* 34: 157–179.

MUIR, J. 1937. The Seed-drift of South Africa. Dept. of Agriculture and Forestry. *Botanical Survey Memoir No.* 16. *Govt. Printer Pretoria.*

SCOTT. K. M. F., A. D. HARRISON and W. MACNAE. 1952. The Ecology of South African Estuaries. Part II. The Klein River Estuary, Hermanus Cape. *Trans. Roy. Soc. S. Afr.* 33: 283–331.

TUTIN. 1938. Autecology of *Zostera marina* in relationship to its wasting disease. *New Phytol.* 37: 50–71.