

# Distribution of fishes in the Mhlanga estuary in relation to food resources

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Food resources play an important role in determining the distribution of fish species in the Mhlanga estuary. Standing crops of detritus and associated micro-organisms, zoobenthos, zooplankton, epiphytic flora and fauna were measured in the upper, middle and lower reaches of the estuary, and the distribution of 20 fish species related to these resources. The distribution of the majority of species correlated with the abundance of preferred food items, except for the Mugilidae where substrate particle sizes influenced the composition of fish in an area.

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Voedselbronne speel 'n belangrike rol om die verspreiding van visspesies in die Mhlanga estuarium vas te stel. Die voorkoms van detritus en geassosieerde mikro-organismes, soöbenthos, soöplankton, epifitiese flora en fauna is in die boonste, middelste en onderste gedeeltes van die estuarium bepaal, asook die verspreiding van 20 visspesies verwant aan hierdie bronne. Die verspreiding van die meerderheid van die spesies was gekorreleer met die volopheid van voedselitems waaraan voorkeur gegee is, behalwe vir die Mugilidae waar substraatpartikelgroottes die samestelling van 'n visgemeenskap in 'n gebied beïnvloed het.

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Little is known about the distribution of fishes within southern African estuaries. During 1978 an investigation was conducted to determine whether the composition of the fish fauna in the Mhlanga estuary was related to the availability of different food resources. The results of the study (Whitfield 1980) indicated that there was a relationship between the diet of the different fish species and food availability. No attempt was made however to relate the distribution of the fish species to their food resources. The aim of this paper is to present data which show that the distribution of most fish species at Mhlanga is directly related to the distribution of particular food categories.

## Materials and Methods

### Study area

The Mhlanga estuary (29°42'S; 31°06'E) is fed by a river 28 km in length with a catchment area of approximately 124 km<sup>2</sup> (Chew & Bowen 1971). The mean annual rainfall within the catchment is about 100 cm, 70% of which falls during summer (October – March) (Brand, Kemp, Pretorius & Schoonbee 1967). The estuary remains closed to the sea for most of the year because the inflow of freshwater from the river is insufficient to counteract the effect of longshore drift maintaining the sand bar across the mouth. Heavy rains during summer result in a flooding of the estuarine lagoon and breaching of the sand bar. The strong outflow of turbid water decreases after a few days thus allowing tidal penetration of seawater into the estuary. In the absence of further rain in the catchment area, the estuary normally closes within 10 days.

### Sampling and biomass estimations

#### Fish

Fish were sampled in January, February, March, May, July, September and November 1978. The estuary was open during March and November and closed during the other sampling periods. The following gear was used; a large seine net (70 m × 2 m × 12 mm bar mesh), small seine net (10 m × 1,5 m × 4 mm bar mesh), fry seine net (3 m × 1 m × 1,5 mm bar mesh), cast net (4 m diameter, 12 mm bar mesh) and gill nets (55, 90 & 125 mm stretch mesh). The topography of the upper reaches precluded the use of a large seine net in this region, with the result that biomass or numerical comparisons of fishes in the different regions on a catch per unit effort basis, were not possible.

The diet of fish species at Mhlanga was determined using

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a modified points system (Whitfield 1980). Substrate particle sizes from the stomach contents of Mugilidae were measured with an eyepiece micrometer in a binocular microscope.

#### Zoobenthos

Zoobenthos were collected using a Zabolocki-type Eckman grab (area covered = 236 cm<sup>2</sup>). Ten grab samples were taken every two months from the lower, middle and upper reaches of the estuary. Each sample was initially sieved with a 1 mm mesh and all organisms retained by the sieve preserved in 10% neutralized formaldehyde. Material which passed through the 1 mm mesh was then washed vigorously in 4% formaldehyde which caused the burrowing forms to emerge and become suspended. The supernatant was passed through a 0,5 mm mesh sieve and the organisms combined with those retained by the 1 mm mesh. The grab sampler did not penetrate below 15 cm depth and deep burrowing zoobenthos such as the sand prawn *Callinassa kraussi* was not captured. The distribution of *C. kraussi* was determined using a prawn pump (72 cm length, 6 cm diameter).

Each zoobenthic sample was washed in the laboratory, causing the animal material to become suspended, and enabling it to be poured through a 0,2 mm mesh sieve. The animals were then identified and counted using a binocular microscope and expressed as Joules m<sup>-2</sup>.

#### Zooplankton

Zooplankton in the water column were collected every two months using a Clarke-Bumpus plankton sampler fitted with a flow meter and a 70µm mesh net. The sampler was held just below the water surface and towed for three minutes at approximately 5 km h<sup>-1</sup>. Day and night samples were collected from the lower, middle and upper reaches of the estuary. All samples were preserved immediately in 4% formaldehyde (Analar grade).

Zooplankton samples were analysed using standard subsampling procedures. Subsamples constituting 10–15% by volume of the parent sample were used. The number of organisms in each taxon present was obtained and expressed as Joules m<sup>-3</sup>.

#### Epiphytic flora and fauna

A minimum number of 30 10cm lengths of submerged *Phragmites* stems were collected using secateurs and preserved in formaldehyde. The reed depths between the water surface and substratum, and densities per m<sup>2</sup> were measured for the lower, middle and upper reaches of the estuary.

In the laboratory epiphytic algae were scraped from the stems using a scalpel, dried, weighed and milled. A subsample of the powder was used for energy determinations. Epifauna were identified, counted and expressed as Joules m<sup>-2</sup>.

#### Benthic floc

Benthic floc is the term used here to describe the mixture of detritus and microorganisms which is found on benthic substrates in the Mhlanga estuary. The sampling apparatus consisted of a metal guide and an open ended perspex container which slid along the guide, removing the upper 2 cm of substrate. The container was closed manually when it reached the end of the guide and the entire sample pre-

served in formaldehyde. Samples were collected from the lower, middle and upper reaches of the estuary.

Each sample was shaken vigorously for exactly 30 sec. and the freed floc poured through a 1,5 mm mesh sieve to remove any large macrophytic debris, crustaceans and molluscs. The floc was then concentrated on Whatman number 40 filter paper by vacuum filtration in a Büchner funnel, scraped from the filter and dried to constant weight. The dried sample was then ground to a powder and a subsample removed for energy determinations.

#### Energy determinations

A Phillipson microbomb was used to obtain energy values for benthic floc, zooplankton, zoobenthos, epiphytic flora and fauna. To produce complete combustion of floc and epiphytic flora samples it was necessary to add 1µl of mineral oil to each pellet. The energy content of the oil was then subtracted from the total Joules measured, to determine the energy content of the sample. All animals were washed, dried to constant weight at 50 °C in a vacuum oven and weighed on a Cahn gram electrobalance. All samples had to be preserved in formaldehyde and therefore energy determinations were restricted to fixed material. However values obtained from the above material should not differ significantly from those of fresh material since formaldehyde is very soluble in water and is a non-coagulant fixative which preserves most lipids (Baker 1966).

#### Physical environment

Salinities were measured using a Goldberg optical salinometer and temperatures with a standard thermometer. Water transparency was recorded with a light meter linked to a submersible photo-electric cell, mounted in the centre of a Secchi disc.

The benthic floc sampling apparatus was used to remove the upper 5 cm of substrate from sampling stations in the lower, middle and upper reaches of the estuary. The particle size distribution was obtained by washing the substrate through a series of standard sieves with mesh sizes of 4, 2, 1, 0,5, 0,25, 0,125 and 0,063 mm. The contents of each sieve were measured by volume and expressed as proportions of the whole sample.

## Results

#### Fish distribution

The catch composition of fishes in the lower, middle and upper reaches of the estuary is shown in Table 1. Each species has been assigned a trophic category based on a detailed assessment of the diet of fishes from Mhlanga (Whitfield 1980). Only species comprising more than 10 individuals were considered for analysis. A biomass assessment revealed that *Ambassis commersoni* and *Sarotherodon mossambicus* showed a preference for the upper reaches; *Glossogobius giuris* and *Myxus capensis* for the upper and middle reaches; *Gerres rappi*, *Liza alata*, *Pomadasys commersonni* and *Valamugil cunnesius* for the middle and lower reaches; *Crenimugil crenilabis*, *Leiognathus equulus*, *Liza dumerili*, *Liza macrolepis*, *Mugil cephalus*, *Rhabdosargus holubi*, *Rhabdosargus sarba* and *Solea bleekeri* for the lower reaches. No biomass pattern was evident for *Gilchristella aestuarius*, *Monodactylus falciformis* and *Terapon jarbua*, but a numerical analysis

**Table 1** Percentage catch composition (biomass and numbers) of fishes in the lower, middle and upper reaches of the Mhlanga estuary. Scientific and common names after Smith & Jackson (1975), dominant food after Whitfield (1980)

Fish species	Common name	Percentage biomass			Percentage numbers			Dominant food
		Lower	Middle	Upper	Lower	Middle	Upper	
<i>Ambassis commersoni</i>	Banded glassy	0,62	1,70	5,29	1,28	7,58	10,09	Zooplankton
<i>Caranx sexfasciatus</i>	Bigeye kingfish	0,17	—	0,07	0,29	—	0,21	Fish
<i>Crenimugil crenilabis</i>	Fringelip mullet	0,92	—	—	0,92	—	—	Benthic floc
<i>Gerres rappi</i>	Evenfin pursemouth	0,28	0,16	—	0,87	0,53	—	Zoobenthos
<i>Gilchristella aestuarius</i>	Estuarine roundherring	0,37	0,03	0,97	15,15	2,42	1,91	Zooplankton
<i>Glossogobius giuris</i>	Tank goby	0,28	0,61	0,68	1,65	9,02	11,36	Zoobenthos
<i>Leiognathus equulus</i>	Slimy	0,10	—	—	0,60	—	—	Zoobenthos
<i>Liza alata</i>	Diamond mullet	9,53	29,43	—	0,40	4,09	—	Benthic floc
<i>Liza dumerili</i>	Groovy mullet	6,99	0,47	0,05	1,63	0,30	0,21	Benthic floc
<i>Liza macrolepis</i>	Largescale mullet	1,90	0,24	—	1,68	0,15	—	Benthic floc
<i>Monodactylus falciformis</i>	Cape moony	0,20	0,31	0,22	0,23	0,53	0,42	Zooplankton
<i>Mugil cephalus</i>	Flathead mullet	18,61	2,72	0,97	4,97	2,12	0,42	Benthic floc
<i>Myxus capensis</i>	Freshwater mullet	8,90	18,70	15,94	4,23	6,44	1,55	Benthic floc
<i>Pomadasys commersonni</i>	Spotted grunter	0,67	0,43	—	0,40	0,23	—	Zoobenthos
<i>Rhabdosargus holubi</i>	Cape stumpnose	6,17	0,37	0,06	7,90	1,06	0,07	Epifauna and flora
<i>Rhabdosargus sarba</i>	Natal stumpnose	0,62	—	—	0,60	—	—	Zoobenthos
<i>Sarotherodon mossambicus</i>	Mozambique tilapia	22,81	17,68	68,15	26,54	32,12	67,40	Benthic floc
<i>Solea bleekeri</i>	Blackhand sole	0,06	—	—	0,43	—	—	Zoobenthos
<i>Terapon jarbua</i>	Thornfish	0,40	0,05	0,66	10,94	8,86	1,84	Zoobenthos
<i>Valamugil cunnesius</i>	Longarm mullet	20,40	27,10	6,94	19,29	24,47	4,45	Benthic floc

indicated that these species were proportionally more abundant in the lower reaches. *Caranx sexfasciatus* was recorded from the lower and upper reaches but was more common in the former area. A total of 5 531 (130 688 g) fishes were captured in the lower reaches, 1 320 (63 320 g) in the middle reaches and 1 417 (24 647 g) in the upper reaches.

The sand particle size preference of mullet species from Mhlanga is shown in Table 2. These particles are ingested together with food items such as diatoms, algae and particulate organic matter. Although there was overlap in the sizes of inorganic particles consumed, there was also a grading with certain species selecting fine particles and other species coarser particles. *C. crenilabis* and *L. macrolepis* consumed similar sized particles.

### Zoobenthos

Energy values of zoobenthos are shown in Table 3 and Fig. 4. Standing crops in the upper reaches were low due to the anaerobic silt substrate and presence of hydrogen sulphide.

The distribution of the sand prawn *Callinassa kraussi* at Mhlanga is shown in Fig. 1. Although most of the population was restricted to the lower reaches, small colonies were present in the middle reaches of the estuary.

### Zooplankton

The energy values of zooplankton in the lower, middle and upper reaches of the Mhlanga estuary are shown in Table 4 and Fig. 4. The energy contribution of fish larvae has been excluded from Fig. 4 since they were not an important food item of fish species at Mhlanga. The calanoid copepod *Pseudodiaptomus hessei* was abundant throughout the estuary and comprised a significant proportion of the diet of many fish species (Whitfield 1980).

### Reed epiflora and fauna

Energy values of epiflora were similar in the lower, middle and upper reaches of the estuary (Fig. 4). Most of the epiflora consisted of filamentous green algae although diatoms, blue-green algae and unicellular green algae were also present.

The distribution of epifauna at Mhlanga is shown in Table 5. The tube-dwelling polychaete *Ficopomatus* (= *Mercierella*) *enigmatica* dominated but *Corophium triaenonyx*, *Musculus virgiliae*, *Chironomus* larvae and *Ceratonereis erythraeensis* were common. The upper reaches had the highest standing crop of epifauna (Fig. 4) because of the abundance of *F. enigmatica* in this area.

### Benthic floc

The highest energy values were recorded in the upper reaches (Fig. 4) due to the input of detritus from the fringing reed swamp and deposition of organic material from the Mhlanga River. The influence of both the river and *Phragmites* swamp decreased towards the mouth.

**Table 2** Sand particle size preference of seven species of grey mullet from the Mhlanga estuary (n = number of stomach contents examined)

Species	Particle size range ( $\mu\text{m}$ )	Particle size mean ( $\mu\text{m}$ )	S.E.	N
<i>Valamugil cunnesius</i>	100–400	212	5,79	110
<i>Mugil cephalus</i>	100–400	257	8,89	63
<i>Crenimugil crenilabis</i>	125–350	276	16,06	14
<i>Liza macrolepis</i>	150–400	278	12,13	39
<i>Myxus capensis</i>	250–400	308	5,81	42
<i>Liza alata</i>	200–450	347	13,34	36
<i>Liza dumerili</i>	100–800	437	19,77	50

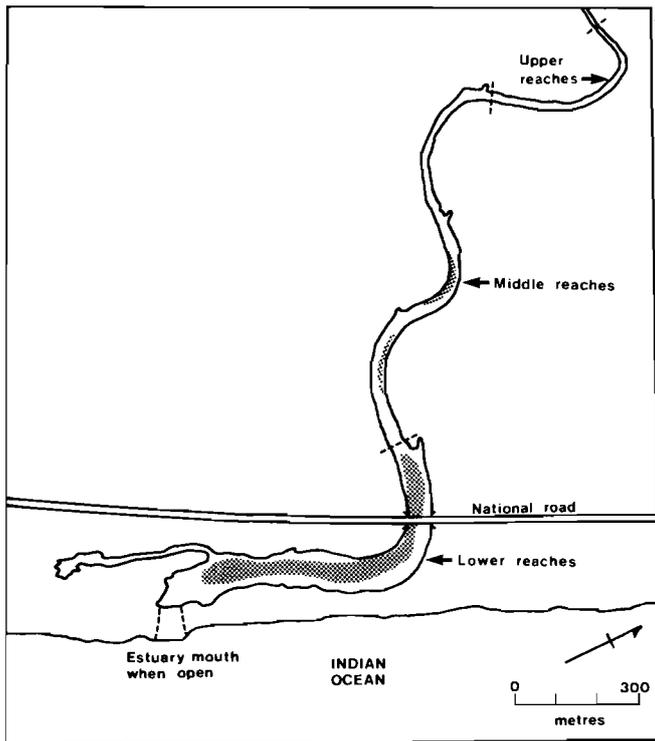


Fig. 1 Distribution of the sand prawn *Callinassa kraussi* (stippled area) in the Mhlanga estuary.

#### Physical environment

The deepest portion of the estuary was in the middle reaches where a depth of 3,2 m was recorded. The water level dropped approximately 1 m when the estuary opened but rose rapidly following closure. Mhlanga was closed during the winter months (April – September) but opened following heavy rains in summer (October – March). Salinities during 1978 fluctuated between 0 and 34‰ but were normally less than 10‰ (Table 6). Following closure of the estuary there was a mixing of saline and fresh water such that the salinity difference between the upper and lower reaches was less than 5‰. Surface and bottom salinity differences during the closed phase did not exceed 4‰. Water temperature differences between the upper and lower reaches of the estuary seldom exceeded 3°C. Water turbidity was linked to river flow and phase of the estuary

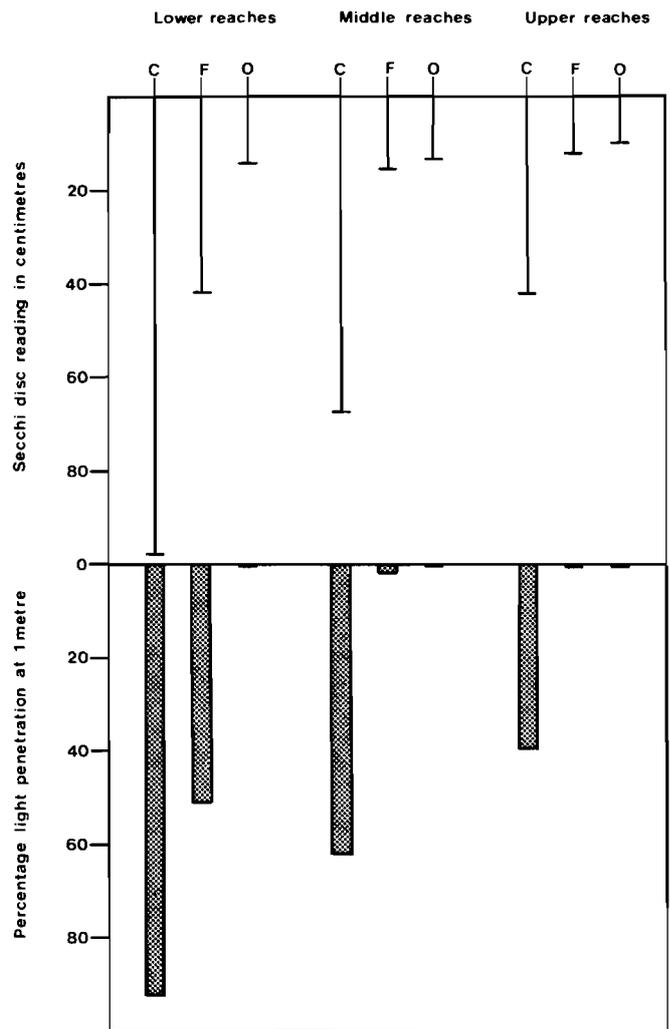


Fig. 2 Water turbidity in the Mhlanga estuary during the closed phase (C), closed phase with river flooding (F) and open phase (O).

mouth (Fig. 2). During the closed phase, sediment loads carried by the river were low and water transparency in the estuary relatively high. Following rains in the catchment area, suspended sediment in the river increased and this material was carried into the estuary. Much of the sediment was deposited in the upper and middle reaches without influencing the lower reaches significantly. When the estuary opened, however, the turbid water flowed into the

Table 3 Energy values (Joules per square metre) of zoobenthos in the lower, middle and upper reaches of the Mhlanga estuary.

Zoobenthos	Lower J m <sup>-2</sup>	Middle J m <sup>-2</sup>	Upper J m <sup>-2</sup>
Amphipoda: <i>Austrochiltonia capensis</i>	1,2	—	—
<i>Corophium triaenonyx</i>	5 316,9	3 358,6	24,2
Bivalvia: <i>Musculus virgiliae</i>	111,9	71,3	—
Copepoda:	66,7	14,9	3,1
Cumacea:	85,8	3,2	—
Insecta: <i>Chironomus</i> larvae	341,2	130,4	100,0
Isopoda: <i>Cirolana fluviatilis</i>	407,8	70,4	—
<i>Leptanthura laevigata</i>	19,7	—	—
Macrura: <i>Macrobrachium equidens</i>	—	—	684,7
Oligochaeta:	162,1	73,9	73,3
Ostracoda:	5,8	3,8	10,8
Polychaeta: <i>Ceratonereis erythraeensis</i>	9 080,3	1 925,4	201,1
<i>Dendronereis arborifera</i>	6 855,7	2 471,5	—

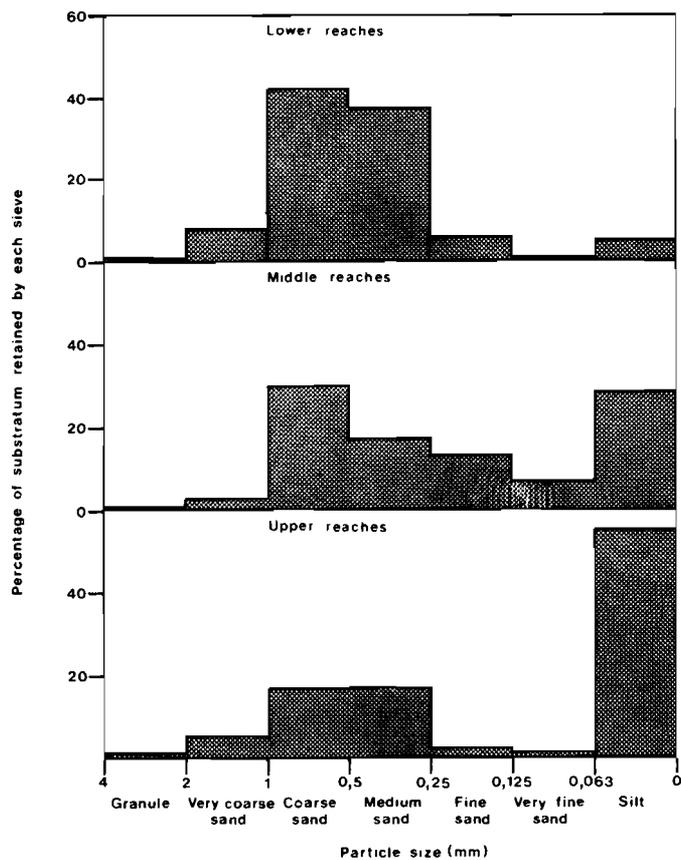


Fig. 3 Substrate particle size composition in the lower, middle and upper reaches of the Mhlanga estuary.

lower reaches, decreasing water transparency in this area (Fig. 2).

Substrate particle size composition in the different regions of the Mhlanga estuary is shown in Fig. 3. Analyses showed that the lower reaches may be classified as medium/course ( $Md\Phi = 1,0$ ), the middle reaches medium/fine ( $Md\Phi = 1,9$ ) and the upper reaches very fine sand/silt ( $Md\Phi = 4,1$ ). Variation in grain size was greatest in the upper reaches ( $Qd\Phi = 1,77$ ) and lowest in the lower reaches ( $Qd\Phi = 0,73$ ).

Table 4 Energy values (Joules per cubic metre) of zooplankton in the lower, middle and upper reaches of the Mhlanga estuary

Zooplankton	Lower $J m^{-3}$	Middle $J m^{-3}$	Upper $J m^{-3}$
Amphipoda:	45,7	32,3	36,9
Bivalve spat:	1,2	0,1	0,2
Cladocera:	25,3	7,3	15,8
Copepoda:			
Calanoida	256,8	398,2	355,9
Cyclopoida	0,6	2,0	1,0
Harpacticoida	0,7	0,4	1,4
Copepodids	5,8	9,3	18,5
Cumacea:	5,0	0,1	0,1
Fish larvae:	1 979,1	160,8	102,8
Gastropod larvae:	1,1	0,2	0,1
Insect larvae:	28,3	19,4	27,9
Macruran larvae:	20,7	22,2	9,9
Nauplius larvae:	178,0	95,9	51,5
Oligochaeta:	—	0,6	0,6
Ostracoda:	0,1	0,9	0,4
Polychaeta:	26,6	13,0	1,7

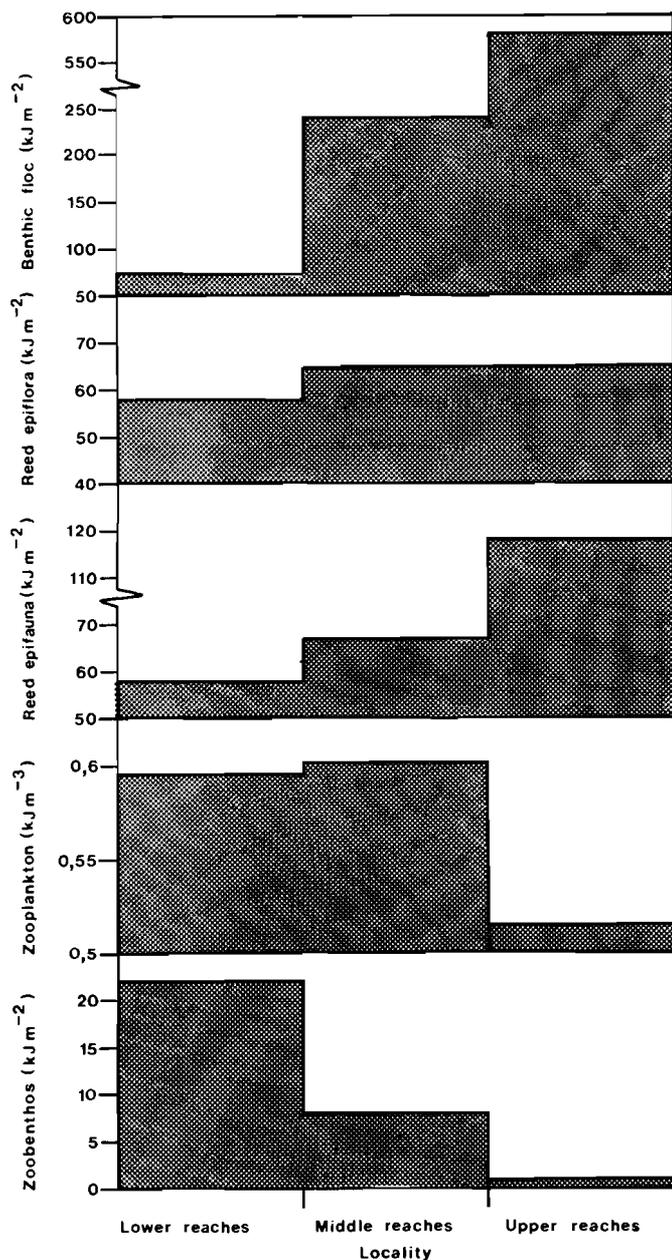


Fig. 4 Energy values of food resources in the lower, middle and upper reaches of the Mhlanga estuary.

Discussion

Gunter (1956) determined that salinity was an important factor governing the distribution of fish species in the Mermentau system (North America), with certain species vacating an area at low salinities but returning when salinities increased. Although this may apply to the fishes inhabiting an open estuary, those marine species resident in temporarily closed estuaries cannot retreat to the sea when salinities decrease. The distribution pattern of fishes in the Mhlanga estuary did not appear to be determined by salinity or temperature since there was no marked gradient of either parameter during the closed phase (Table 6). When the estuary was open a salinity gradient often became established between the lower, middle and upper reaches. This gradient was, however, of short duration and disappeared at low tide.

Blaber (1976) has shown that mullet species at Lake St Lucia consume similar food items and avoid competition by selecting sand particles of different sizes. The diet of mullet species in other Natal estuaries is also similar. but varies

**Table 5** Energy values (Joules per square metre) of reed epifauna in the lower, middle and upper reaches of the Mhlanga estuary

Epifauna	Lower J m <sup>-2</sup>	Middle J m <sup>-2</sup>	Upper J m <sup>-2</sup>	
Amphipoda: <i>Austrochiltonia capensis</i>	347,1	1 604,9	925,3	
	<i>Corophium triaenonyx</i>	1 903,4	49 494,9	27 726,0
	<i>Grandidierella bonnieri</i>	—	104,7	98,7
Bivalvia: <i>Musculus virgiliae</i>	1 481,5	1 835,5	2 052,6	
Brachyura: <i>Sesarma eulimene</i>	—	1 601,1	409,9	
Cladocera:	—	34,0	—	
Copepoda:	93,6	167,1	60,4	
Insecta: <i>Chironomus</i> larvae	5 409,3	2 242,8	2 203,0	
Isopoda: <i>Dies monodi</i>	291,3	492,1	83,3	
Oligochaeta:	—	81,7	126,3	
Polychaeta: <i>Ceratonereis erythraeensis</i>	9 492,8	3 740,4	3 123,3	
	<i>Ficopomatus enigmatica</i>	39 357,2	5 816,2	81 727,9

from one estuary to another, and is determined largely by the occurrence of particular food items on substrates of the preferred particle size of each species (Blaber 1977). Table 2 indicates that most mullet species at Mhlanga select different sized particles and the distribution of certain species can be related to substrate composition. *V. cunnesius* a fine particle feeder (Table 2) was most abundant in the middle reaches where there was the highest proportion of fine sand (Fig. 3). *M. cephalus*, *C. crenilabis* and *L. macrolepis* were medium particle feeders and *L. dumerili* a medium/coarse particle feeder (Table 2). These species were most common in the lower reaches where medium and coarse sand was present in greatest quantities. Whitfield and Blaber (1978a) determined that mullet species at Lake St Lucia also selected those areas where preferred sand particle sizes were most common. Payne (1976) ascertained that the abundance of four mullet species was lowest in the upper tidal region, when compared to the mid and lower reaches. Silt deposition was high in the upper tidal region and may have accounted for the low mullet numbers in this area. Mullet comprised less than 25% of the fish biomass catch composition in the upper reaches of Mhlanga (Table 1) and this may be attributed to the high

silt content of the substrate (Fig. 3). *M. capensis* was however common in the upper reaches, which may be due to the catadromous life history of this species. Bok (1979) found that *M. capensis* occurred mainly in the freshwater zones of eastern Cape rivers with small numbers in brackish water at the head of estuaries. The numbers of *M. capensis* relative to *M. cephalus* increased as the distance upstream from the estuary increased (Bok 1979). There was also an inverse relationship in the distribution patterns (biomass) of these species at Mhlanga (Table 1).

*S. mossambicus* at Mhlanga are benthic floc feeders with 67% of their diet comprising particulate organic matter (Whitfield 1980). This species was most abundant in the upper reaches (Table 1) where benthic floc was most concentrated (Fig. 4). *S. mossambicus* did not ingest large amounts of sand and it would appear that substrate particle size had little influence on the distribution of this species. Mhlanga is the only southern African estuary where *S. mossambicus* has been recorded in the lower reaches during the open phase (Whitfield & Blaber 1979). When a closed estuary opens this species usually retreats to the upper reaches.

*A. commersoni* was also most abundant in the upper

**Table 6** Salinity and temperature data from the lower, middle and upper reaches of the Mhlanga estuary

Estuary mouth	Date		Lower		Middle		Upper	
			‰	°C	‰	°C	‰	°C
Closed	1/5/78	Surface	3	28	2	29	2	29
		Bottom	3	28	2	26	2	25
Closing	9/2/78	Surface	10	30	8	29	2	29
		Bottom	14	28	14	27	12	27
Open	22/3/78	Surface	0	23	0	23	0	24
		Bottom	0	23	0	23	0	23
Open	30/3/78	Surface	30	26	5	27	0	27
		Bottom	34	25	14	25	0	27
Closed	30/5/78	Surface	3	18	3	20	2	21
		Bottom	5	17	4	20	3	20
Closed	7/7/78	Surface	4	17	2	16	1	16
		Bottom	5	17	4	17	4	17
Closed	12/9/78	Surface	2	22	0	22	0	22
		Bottom	2	21	2	21	2	22
Open	24/11/78	Surface	0	29	0	23	0	23
		Bottom	0	27	0	23	0	22

reaches and this may be related to the large numbers of copepods, insect larvae and insects in this region. *A. commersoni* did not appear to be adversely affected by higher water turbidity in the upper reaches (Fig. 2), since it was present in this region when the river was flooding.

*R. holubi* occurred in all three regions but was concentrated in the lower reaches despite the fact that reed epifauna values were highest in the upper reaches (Fig. 4). However *R. holubi* seldom consumed the tubicolous *F. enigmatica* which comprised almost 70% of the epifauna in the upper reaches. Furthermore the high density of this polychaete may have reduced the availability of prey such as *C. triaenonyx* which utilized the intertwining tubes as a refuge. Reed epiflora values were similar throughout the estuary and 25% of the diet of *R. holubi* was derived from this resource (Whitfield 1980). *R. holubi* also fed on zoobenthos which was most abundant in the lower reaches.

The distribution of *P. commersoni* was related to the presence or absence of sand prawn beds (Table 1, Fig. 1). *C. kraussi*, which comprised 65% of the diet of *P. commersoni* (Whitfield 1980) was absent from the upper reaches as was *P. commersoni*. *G. rappi*, an infauna feeder, was also absent from the upper reaches where zoobenthos energy values were low (Table 3, Fig. 4). According to Carriker (1967) high concentrations of detritus and organic material associated with muddy sediment may reduce the oxygen content within the substrate and limit the penetration of infauna not tolerating anaerobic conditions. The large amount of silt and detritus in the upper reaches was therefore not conducive to the establishment of a large zoobenthic community. The presence of *G. giuris* in the upper reaches was therefore surprising but may be explained by the fact that this species captured epifauna rather than infauna. Most zoobenthic foraging fishes were concentrated in the lower reaches of the estuary where this food resource attained values above  $20 \text{ kJ m}^{-2}$  (Fig. 4). Cumacea, which comprised 55% of the diet of *L. equulus*, were concentrated in the lower reaches (Table 3). The slight preference of the piscivorous *C. sexfasciatus* for the lower reaches may be attributed to the abundance of fish larvae and fry in this region (Table 4).

Fish species which showed no biomass zonation pattern were mainly zooplankton foragers, *G. aestuarius* and *M. falciformis*, whose prey ranged from  $0,5 - 0,6 \text{ kJ m}^{-3}$  for the entire estuary (Fig. 4). *T. jarbua* also showed no distinct biomass distribution pattern but was most abundant in the lower reaches where zoobenthos was most readily available. *T. jarbua* captured in the upper reaches were feeding mainly on fish scales removed from living fishes (Whitfield 1979). The high proportion of slow moving *S. mossambicus* in this region may have attracted *T. jarbua* to the area. Whitfield and Blaber (1978b) have shown that fish species such as *S. mossambicus* are more prone to scale removal than faster swimming grey mullet.

Although the distribution of animals in estuaries cannot be attributed to any single factor of the environment (Day

1951), the evidence from this study indicates that the distribution of fishes in Mhlanga estuary was governed largely by food availability.

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