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A SURVEY OF SELECTED EASTERN CAPE ESTUARIES WITH PARTICULAR REFERENCE TO THE ICHTHYOFAUNA

by

Paul D. Vorwerk, Alan K. Whitfield, Paul D. Cowley and Angus W. Paterson

ABSTRACT

The physical environment and ichthyofauna of 10 estuaries, the East Kleinemonde, Klein Palmiet, Great Fish, Mtati, Mpekweni, Mgwalana, Bira, Gqutywa, Ngculura and Keiskamma, was sampled over a four year period. The ichthyofauna of each estuary was sampled once during winter and once during summer in that period, with the physical environment being sampled on two occasions per season. This investigation provides baseline ichthyofaunal and physical information for these estuaries, the majority of which have never been studied before. The fish data presented for these systems includes species composition, relative abundance, richness and diversity, longitudinal distributions and length frequency data. Descriptions of the physical environment within each estuary are also presented.

The permanently open estuaries had a greater proportion of marine and freshwater species relative to the temporarily open/closed systems which were dominated by marine species dependent on estuaries and estuarine resident species. The permanently open estuaries had a higher Margalef's species richness index relative to the temporarily open/closed systems but the Shannon-Wiener species diversity index did not follow any discernible trend. There were minor longitudinal distribution trends when analysing the community as a whole, with patterns for individual species being more pronounced. The length frequency histograms for estuarine resident species differed between estuary types, while those for the marine migrant species were similar in the different estuary types.

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Paul D. Vorwerk[1], Alan K. Whitfield[2†], Paul D. Cowley[2] and Angus W. Paterson[3]

INTRODUCTION

Ichthyological research in the Eastern Cape Province has mostly been conducted in larger permanently open estuaries, including systems such as the Swartkops (Melville-Smith & Baird, 1980; Beckley, 1983; De Wet & Marais, 1990; Marais, 1990; Baird et al., 1996), Sundays (Beckley, 1984; Whitfield & Paterson, 1995; Baird et al., 1996; Whitfield & Harrison, 1996), Kariega (Ter Morshuizen & Whitfield, 1994; Paterson & Whitfield, 1996; Paterson, 1998) and Great Fish estuaries (Ter Morshuizen et al., 1996a; Ter Morshuizen et al., 1996b; Whitfield et al., 1994). Some insight has been provided into the fish assemblages of smaller systems, including the Kabeljous, Seekoei, Van Stadens (Dundas, 1994) and East Kleinemonde estuaries (Cowley, 1998), but in general temporarily closed estuaries have been poorly researched. This lack of baseline information from smaller systems emphasizes the need to document and interpret their fish community structures. There is a particular requirement for additional information such as species composition, richness/diversity indices and the length frequencies and longitudinal distributions of species found in these and other types of estuaries along the Eastern Cape coast. There is a similar need for published data on the physical variability within these systems, e.g. the Great Fish (Ter Morshuizen et al., 1996a; Ter Morshuizen et al., 1996b; Whitfield et al., 1994), Keiskamma (Read, 1983) and East Kleinemonde (Cowley, 1998; Cowley & Whitfield, 2001; Cowley et al., 2001). This study compares the species composition, relative abundance, richness and diversity, longitudinal distributions and length frequency data for the fish communities in 10 Eastern Cape estuaries. A study of the physical variability in these systems was also carried out, but a detailed analysis of the physical data in combination with fish community data has been analysed in another manuscript (Vorwerk et al., submitted).

MATERIALS AND METHODS

PHYSICO-CHEMICAL SAMPLING

Five sites up the length of each estuary were selected, with one site occurring in each of the following reaches; mouth, lower, middle, upper and head reaches. Water temperature was measured at the time of fish sampling using an alcohol thermometer. Water samples were simultaneously collected at the same sites for laboratory analyses of salinity (using a Reichert optical salinometer) and turbidity (using a Hach 2100A turbidimeter). Additionally, a winter and summer set of physico-chemical samples were collected in all the study estuaries during July 1999 and February 2000 respectively. This involved sampling temperature, salinity and turbidity in the water column at 1 m intervals (with a minimum of a surface and bottom sample) at the five sites along each estuary. Sampling was conducted during early mornings (approximately 06h00 in summer and 07h00 in winter) and mid-afternoons (approximately 14h00-15h00) to obtain measurements during the coolest and warmest periods of the day. Information on the area cover of submerged macrophytes in each system were obtained from Colloty (2000). These data are not considered to offer an insight into the long-term variability in these systems, but indicate the physico-chemical variability as recorded during the study period.

During the February 2000 physico-chemical expedition, a sediment sample was collected from each region (mouth, lower, middle, upper and head) of each estuary. These samples were then subjected to organic content and particle size distribution determinations as described in Black (1965). The samples were classed as gravel (>2 mm), coarse sand (2-0.5 mm), fine sand (0.5-0.063 mm), silt (<0.063 mm) or a combination of these categories (Walsh et al., 1999).

The width and depth of the estuary was determined at five sites within each system. In the smaller systems a rope marked at 2.5 m intervals was strung across the channel. A measuring pole was then used at every marker to determine the depth at that point. In the larger systems a Lowrance depth sounder was used to take a reading every 3 sec while crossing the estuary at a steady speed. The full width of the estuary at the point of the cross-section was measured using a graduated rope.

ICHTHYOFAUNAL SAMPLING

The fishes in the different estuaries were sampled bi-annually, during June or July (winter) and January or February (summer), on one or 2-3 consecutive days depending on the size of the estuary (the dates for sampling in each estuary are reflected in Table 1). A range of gear types, including a small and large seine net and a fleet of gill nets were used. Different gear types targeted specific groups and/or size ranges of fishes (Table 2). Fish were identified using Smith & Heemstra (1995) and van der Elst & Wallace (1976). The fish were then assigned to an estuarine association category according to Whitfield (1998).

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Table 1. Dates on which ichthyofaunal sampling was conducted in each of the study estuaries, except the East Kleinemonde which was sampled every year during both seasons.

Estuary	Winter Dates	Summer Dates
Klein Palmiet	15 June 1999	1 February 2000
Great Fish	16/17 June 1999	31 January/ 1 February 2000
Mpekweni	10/12 June 1996	28/29 January 1997
Mtati	1/2 June 1998	26/27 January 1999
Mgwalana	10/12 June 1997	17/18 February 1998
Bira	14/15 June 1999	26/27 January 2000
Gqutywa	11/30 June 1997	17/18 February 1998
Ngculura	3 June 1998	25/26 January 1999
Keiskamma	26/27 June 1996	4/6 February 1997

Table 2. The target groups and size classes (mm standard length) of the different gear types.

Gear Type	Stretch Mesh Size	Target Group	Target Size Classes
Small mesh seine (30 m x 2 m)	1 cm	Estuarine-spawning species	All size classes excluding very small individuals (<10 mm SL)
Large mesh seine (50 m x 2 m)	3 cm	Marine-spawning and freshwater species	All size classes excluding small individuals (< 40 mm SL)
Gill nets (10 m x 2 m)	4.5, 7.5 and 10.0 cm	Marine-spawning and freshwater species	Larger individuals (> 100 mm SL)

Table 3. The number of times each net type was deployed per season in each estuary.

Estuary	Large Seine Net	Small Seine Net	Gill Net			
	Winter	Summer	Winter	Summer	Winter	Summer
East Kleinemonde	8,6,4,7	7,6,4,9	6,4,3,6	7,4,5,6	6	6
Klein Palmiet	0	0	1	1	0	0
Great Fish	8	8	12	8	6	6
Mpekweni	9	8	9	5	12	6
Mtati	10	8	9	9	6	6
Mgwalana	13	7	10	5	6	6
Bira	12	10	9	6	6	6
Gqutywa	4	4	4	3	6	6
Ngculura	6	8	6	8	6	6
Keiskamma	6	9	11	8	18	18

The number of large mesh seine net hauls varied in each system (Table 3) depending on the size of the estuary and a major decline in the rate of collection of new species from that system. In each estuary all possible littoral habitats were sampled, with the exception of areas with submerged obstructions. The net was laid in a semi-circle from the bank by motorised boat and then hauled in by three or four people. All fish captured were identified and measured to the nearest millimetre standard length (SL) before being returned to the water alive.

The small mesh seine net sampling protocol was identical to that used with the large seine except that due to the large numbers of individuals, the fish captured in this net were preserved in formalin and returned to the laboratory where identification and measurements (mm standard length) were conducted.

Monofilament gill nets were used to sample larger individuals of both marine spawning and freshwater species, as members of both groups are known to actively avoid seine nets (Cowley, 1998). The nets were 10 m in length and 2 m in depth consisting of three equal length sections of 45 mm, 75 mm and 100 mm stretch meshes. Generally two nets were used in each reach (upper, middle and lower) of an estuary (see Table 3), although this was changed depending on the size of the system. No gill nets were set in the very small estuaries as these were adequately swept with the seine net gear. The gill nets were deployed in the evening (at approximately 18h00) and lifted the following morning (at approximately 06h00). All fish captured were identified and measured to the nearest millimetre standard length.

SPECIES COMPOSITION, DIVERSITY AND ESTUARINE ASSOCIATION

The richness and diversity of the fish communities in each estuary were expressed using Margalef's richness index and the Shannon-Wiener diversity index respectively. Margalef's index (Equation 1) calculates the number of species relative to the number of individuals in the sample, which reduces sample size bias.

$$d = (S-1)/ \log N \qquad \text{(Equation 1)}$$

Where d is Margalef's index, S is the number of species and N is the number of individuals (Clarke & Warwick, 1994).

The Shannon-Wiener diversity index (Equation 2) incorporates equitability in its calculation (Zar, 1996). This gives a better assessment of composition diversity, as it indicates whether a community is dominated by a few species.

$$H' = - S_i\, p_i\, (\log p_i) \qquad \text{(Equation 2)}$$

Where H' is the resultant diversity, i is the sample number and p_i is the proportion of the total count represented by the ith species (Clarke & Warwick, 1994).

Correlations between these indices and catchment size, mean annual run-off (MAR), estuarine area and linear length were tested using Spearman's Rank Correlation Coefficient (p-values were determined from Zar (1996)).

The species composition of each estuary was presented as a numerical contribution by each species. This was determined by calculating the percentage each species represented of the total catch. Species were categorised according to Whitfield (1998) and the contribution of each category calculated for each estuary, based on the number of species and relative abundance.

LONGITUDINAL DISTRIBUTION ANALYSIS

Longitudinal distributions were investigated using non-parametric multivariate analysis (Clarke & Ainsworth, 1993; Clarke & Warwick, 1994) from the PRIMER Package (Version 4.0, Plymouth Marine Laboratory). The estuaries were first analysed on an individual basis by calculating a catch per unit effort (CPUE) for each species either per seine net haul or gill net in each system. A combined analysis of all the estuaries was also conducted by calculating a catch per unit effort (CPUE) for each species by dividing the total number of individuals of each species caught by the total number of seine or gill net hauls in each reach. Both CPUE data sets were averaged either per season or by combining the seasons. These data were standardised and root-root transformed before producing a Bray-Curtis similarity matrix. The clusters were produced using a group average hierarchical sorting strategy. The relationships between the estuarine reaches, based on their fish communities, were examined using dendrograms and non-metric multidimensional scaling (MDS). Analysis of similarity (ANOSIM) was carried out to determine if the fish communities from each reach were distinct. Where significant differences were found the SIMPER routine (from the PRIMER Package) determined the relative contribution of individual fish species to differences between reaches. A non-parametric Kruskal-Wallis one-way ANOVA (Analysis of Variance) was used to test for differences in densities from both the small and large seines between the different reaches of the estuaries.

LENGTH FREQUENCY ANALYSIS

Length data were analysed for eight of the most abundant species only. These included four estuarine resident species (*Atherina breviceps*, *Gilchristella aestuaria*, *Glossogobius callidus* and *Psammogobius knysnaensis*) and four marine migrant species (*Rhabdosargus holubi*, *Liza dumerilii*, *Liza richardsonii* and *Pomadasys commersonnii*). Data for each species were combined within the two estuary groups: large closed and permanently open. No analysis was conducted on the small closed estuaries due to the limited data sets from these systems. The data were analysed using a Kolmogorov-Smirnov test to detect differences in lengths of fishes in the large closed and permanently open estuaries. Information on age at length was obtained from the following studies: *A. breviceps* (Ratte, 1989), *G. aestuaria* (Talbot, 1982), *G. callidus* (Boullé, 1989), *P. knysnaensis* (Bennett, 1989), *L. dumerilii* (van der Horst & Erasmus, 1981), *L. richardsonii* (de Villiers, 1987), *R. holubi* (Blaber, 1974) and *P. commersonnii* (Wallace, 1975).

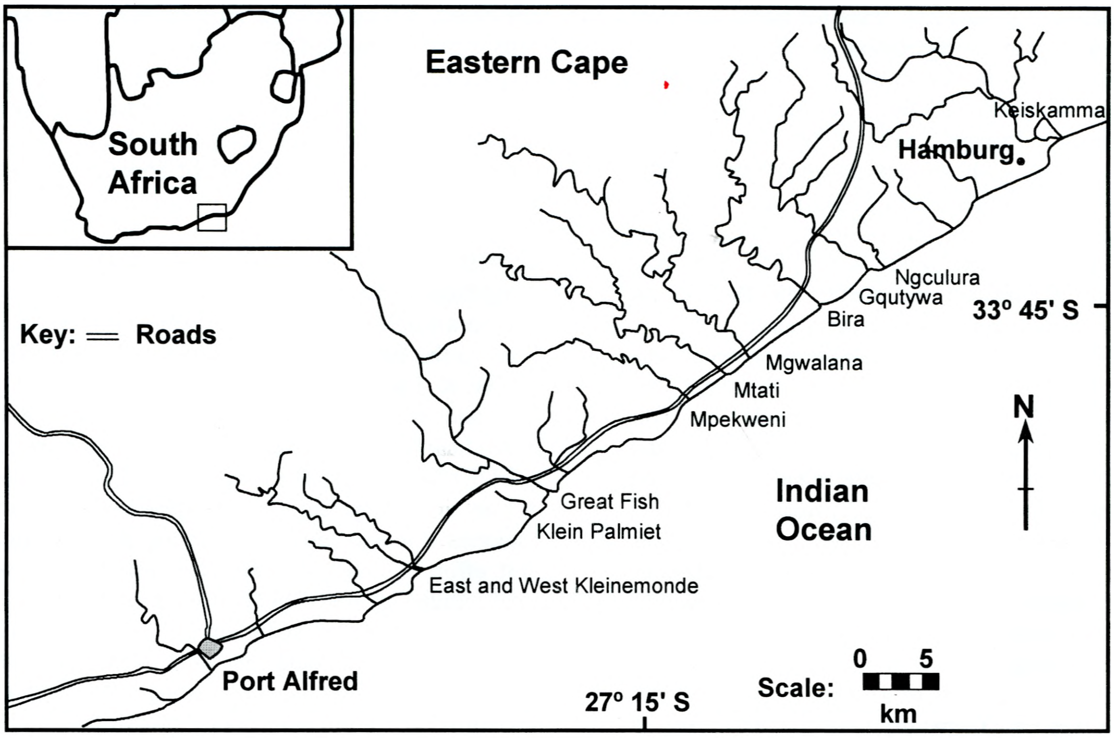

Figure 1: The study area showing the location of each estuary along the Eastern Cape coast.

STUDY AREA

This study incorporated 10 estuaries along a 70 km long stretch of the Eastern Cape coast between the towns of Seafield (33° 32′ 42″ S, 27° 03′ 05″ E) in the south-east and Hamburg (33° 16′ 45″ S, 27° 29′ 50″ E) in the north-west. This area was selected due to the diversity of estuary types and sizes occurring in close proximity. The estuaries investigated include the East Kleinemonde, Klein Palmiet, Great Fish, Mpekweni, Mtati, Mgwalana, Bira, Gqutywa, Ngculura and the Keiskamma (Figure 1).

The estuaries were classed into permanently open, small closed and large closed systems. These distinctions were made based firstly on whether the estuary was either a permanently open or a temporarily open/closed system (predominantly closed during this study). The closed esuaries were further subdivided based on their size, with systems under 5 ha in surface area being referred to as small closed and those with a larger surface area being termed large closed.

EAST KLEINEMONDE ESTUARY

The East Kleinemonde (Figure 2) is a large temporarily open/closed estuary. The township of Seafield surrounds most of the lower reaches of this system, as well as the neighbouring West Kleinemonde Estuary. The coastal road (R72) between Port Elizabeth and East London crosses the estuary approximately 500 m from the mouth.

The estuary is 2.5 km long with a surface area of 17.5 ha. The catchment area is 46 km^2 and provides a mean annual run-off (MAR) of 2 x 10^6 m^3/yr (NRIO, 1987; Badenhorst, 1988). The width of the estuary is approximately 100 m in the lower and middle reaches and narrows down to 25 m in the upper reaches. The main channel has a maximum depth of 2.5 m, with most of the estuary having a littoral zone of less than one metre deep. The cross-sectional area of the system steadily decreases from the mouth (154 m^2) to the head (24.5 m^2), with an average of 82.1 m^2.

The mouth dynamics of this system are well documented (Cowley, 1998). These data demonstrate that open mouth conditions were only evident 2.5% of the time, while overwash conditions appeared to be important in promoting marine influences on the system, occurring 16.4% of the time. During the period 1993-1998 open mouth conditions occurred during every month except March and July, demonstrating the variable nature of the mouth phase (Cowley, 1998).

The winter and summer temperatures recorded during the study period averaged 16.9°C and 26.4°C respectively. The winter temperatures ranged between 14.5°C and 19°C while the summer temperatures varied from 25.4°C to 27°C (Figure 3). These temperatures are below the maximum (27°C) and minimum (14.9°C) values recorded by Cowley & Whitfield (2001).

The seasonal salinities remained relatively constant during the study period with the average winter and summer salinities being 12.7‰ and 14.8‰ respectively. The only large variation was a mouth region sample during summer that had a relatively high salinity of 34‰. The summer salinities ranged from 13‰ to the high of 34‰, while winter salinities ranged between 12‰ and 14‰ (Figure 3). These salinities were generally higher than the 0-27‰ recorded by Cowley & Whitfield (2001).

There were extremely low seasonal turbidity

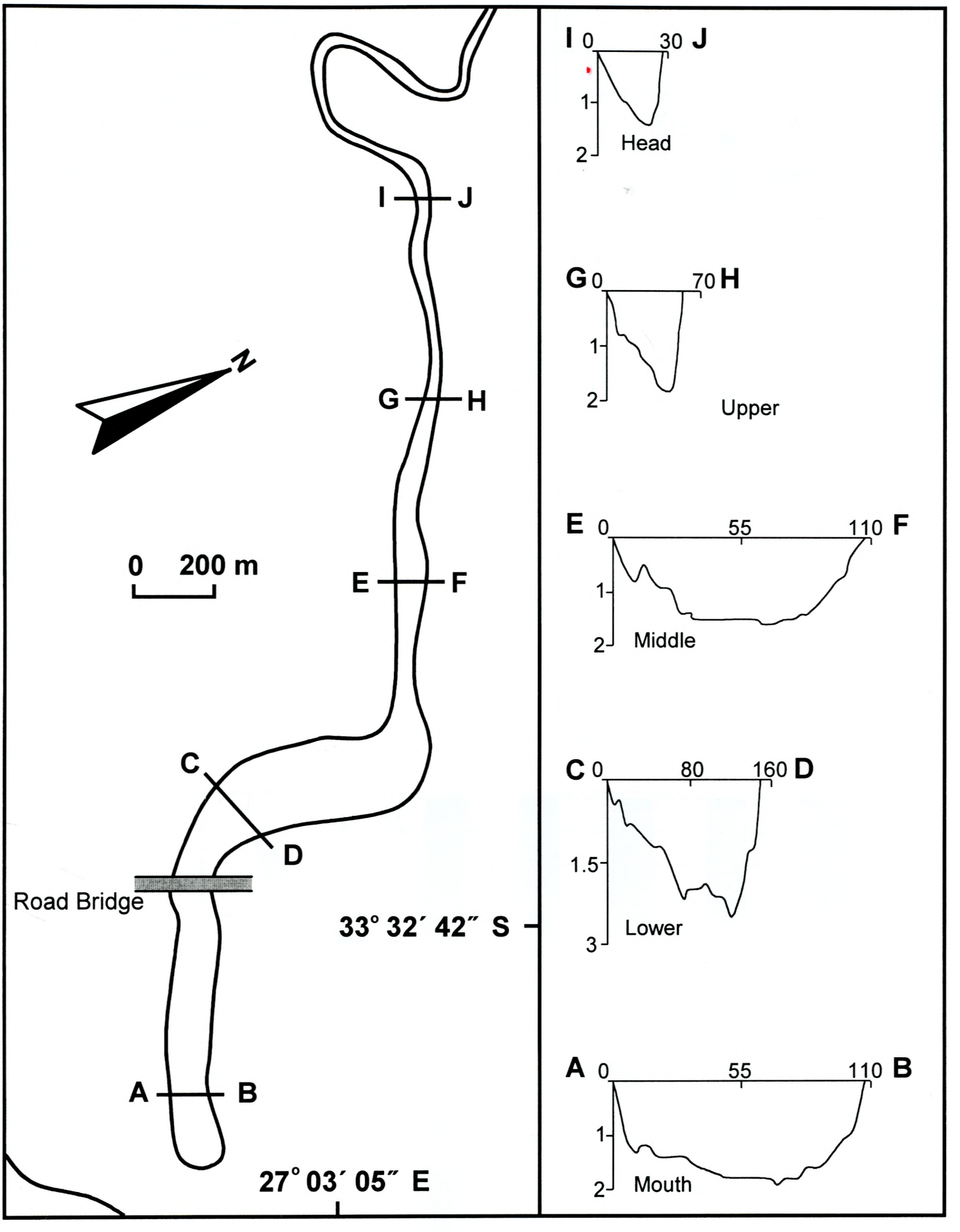

Figure 2: The East Kleinemonde Estuary, showing the size and shape of the system. The cross-sections indicate depths in the various sections of the estuary (drawn from data collected on the 3rd June 1999).

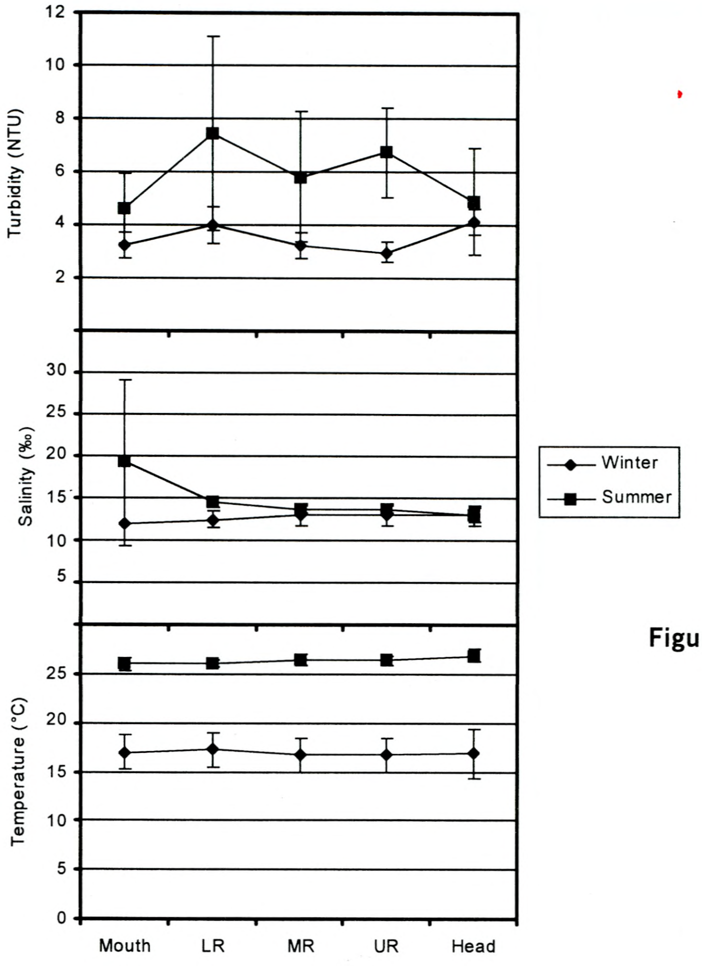

Figure 3: Mean (±S.D.) summer/winter temperature, salinity and turbidity measurements for different localities in the East Kleinemonde Estuary. The mean was determined from morning and midday samples collected in surface and bottom waters on the 3rd June 1999 and 6th February 2000.

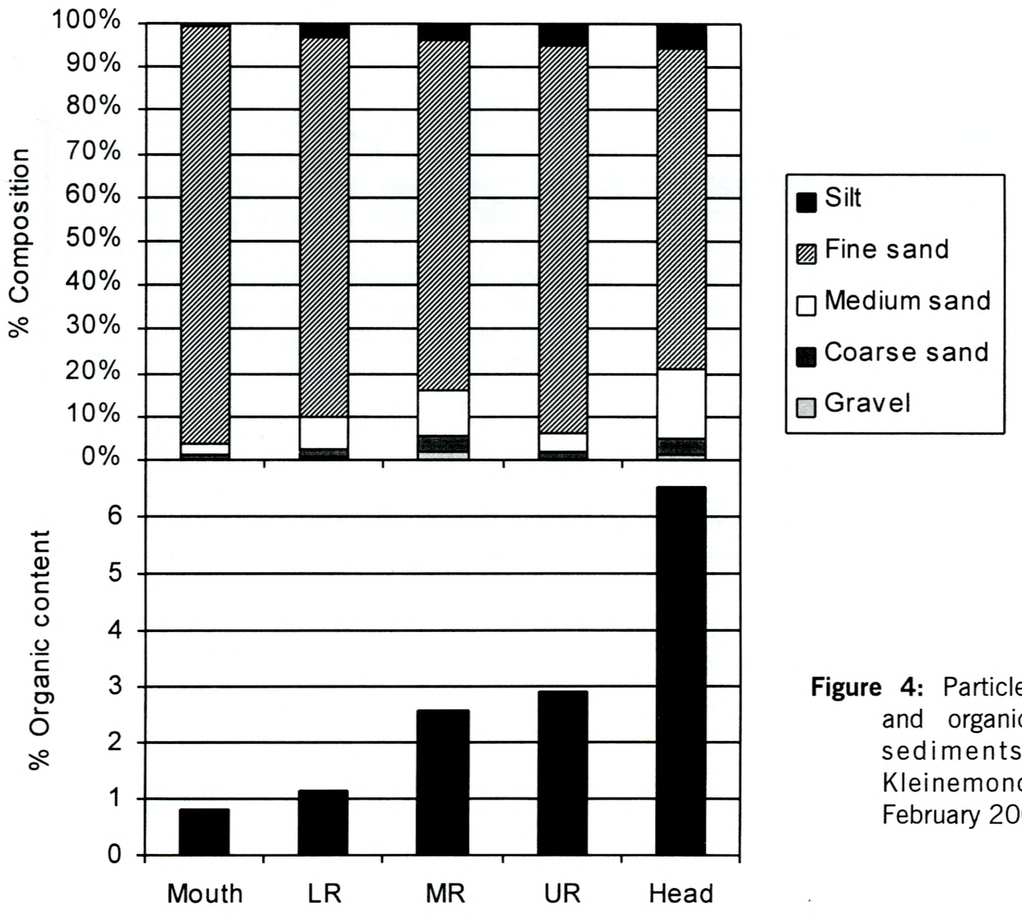

Figure 4: Particle size composition and organic content of the sediments in the East Kleinemonde Estuary (6th February 2000).

variations, with winter turbidities of 3 to 4.5 NTU, and summer values ranging from 3.4 to 11 NTU (Figure 3). The winter and summer averages were 3.5 and 5.9 NTU respectively, with bottom turbidities being generally higher than surface turbidities during both seasons.

Throughout the East Kleinemonde sediment samples comprised mostly fine sands, with a general trend of decreasing larger particles (gravel, coarse and medium sands) as well as silts, from head to mouth (Figure 4). The sediment organic content showed a decreasing trend from head to mouth, although all sites had a relatively low organic content of between 0.8% and 6.5% (Figure 4).

A brief botanical survey was conducted by Adams (1997) and revealed submerged macrophytes, in a continuous band along both banks of the estuary above the road bridge. A salt marsh was recorded on the west bank just above the road bridge and small stands of reeds were noted along the length of the estuary, particularly in the lower and middle reaches.

KLEIN PALMIET ESTUARY

The Klein Palmiet (Figure 5) is a small temporarily open/closed estuary that enters the sea approximately 1 km west of the Great Fish Estuary on the coordinates 33° 30′ 00″ S and 27° 07′ 47″ E. A game farm surrounds the entire estuary, with a farm road accessing the beach on the east bank at the mouth. The recent construction of a dam in the catchment has severely altered the freshwater supply to this estuary.

Prior to construction of the dam the estuarine surface area was 1.44 ha when full, but declined to approximately 0.4 ha during droughts. The catchment is 12.6 km^2 in size and provides a MAR of 0.67 x 10^6 m^3/yr (Smakthin, V., pers. comm.). The water level at the time of sampling was very low, with an average depth of 0.4 m and a maximum of 1.2 m in the centre of the pool near the mouth.

During the study, a single winter and summer physico-chemical sample was collected on the 15th June 1999 and the 1st February 2000. These samples showed very little variation in the salinity and turbidity measurements. The recorded winter salinity was 23‰ while during summer it was slightly higher at 28‰. Similarly the winter turbidity was 5 NTU increasing during summer to 8.1 NTU. Water temperatures showed a greater variation, rising from a winter value of 16°C to a summer recording of 25.2°C.

The sediment of the Klein Palmiet Estuary was dominated by fine sands, which constituted 99.8% of the sample, with all the other sediment sizes contributing less than 0.1% each. The organic content of the sediment was the lowest of all the systems in the study, comprising 0.5% of the sample.

Submerged macrophytes were recorded in the deeper pools near the mouth, although not in very high densities. Stands of reeds were observed along the banks of the estuary although due to the low water levels these plants were approximately 3 m away from the water's edge.

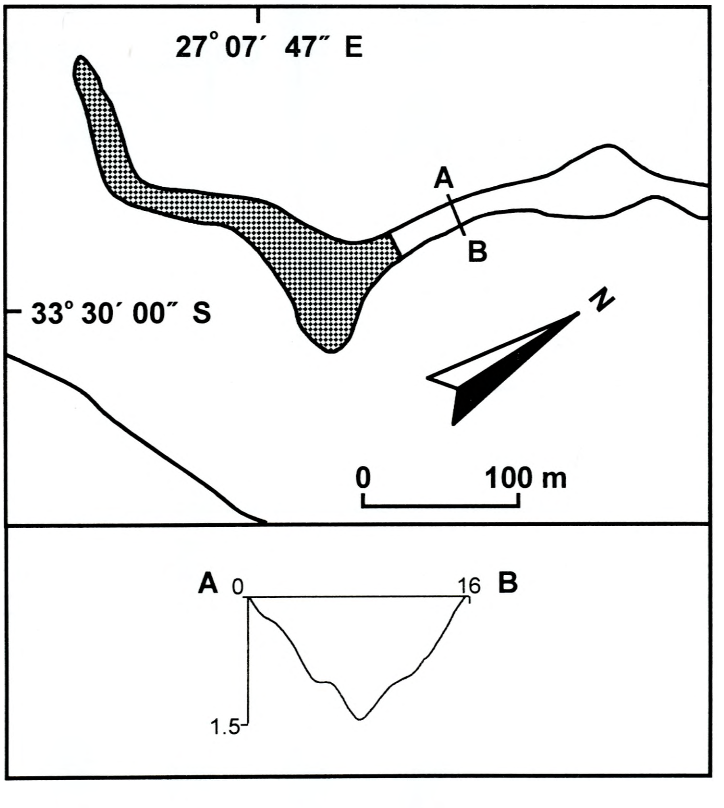

Figure 5: The Klein Palmiet Estuary, showing the size and shape of the system. The cross-section at A-B depicts the depth profile at this point (drawn from data collected on the 15th June 1999). The shaded area indicates the surface area of the estuary that has dried as a result of the dam in the catchment.

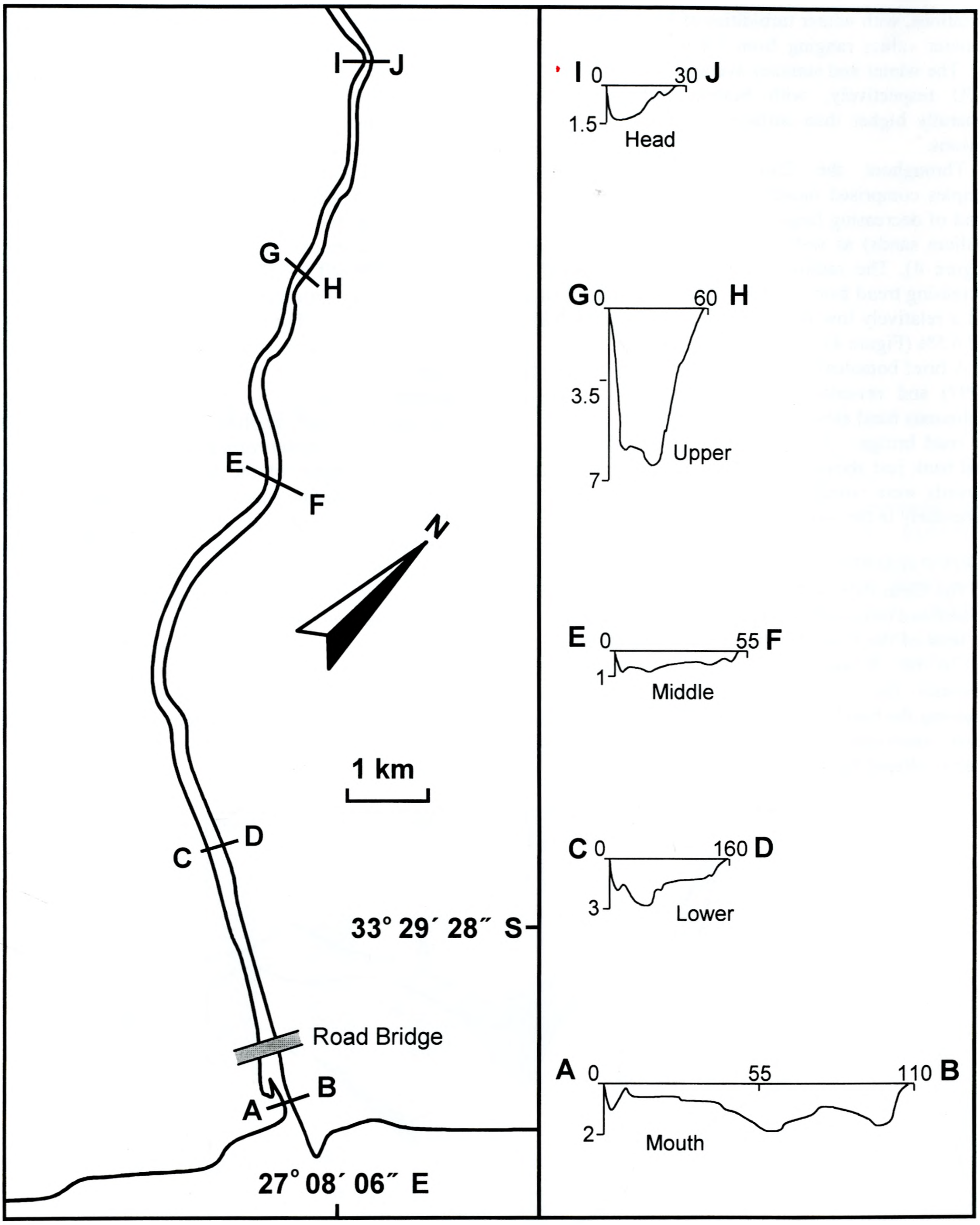

Figure 6: The Great Fish Estuary, showing the size and shape of the system. The cross-sections indicate depths in the various sections of the estuary (drawn from data collected on the 2nd June 1999).

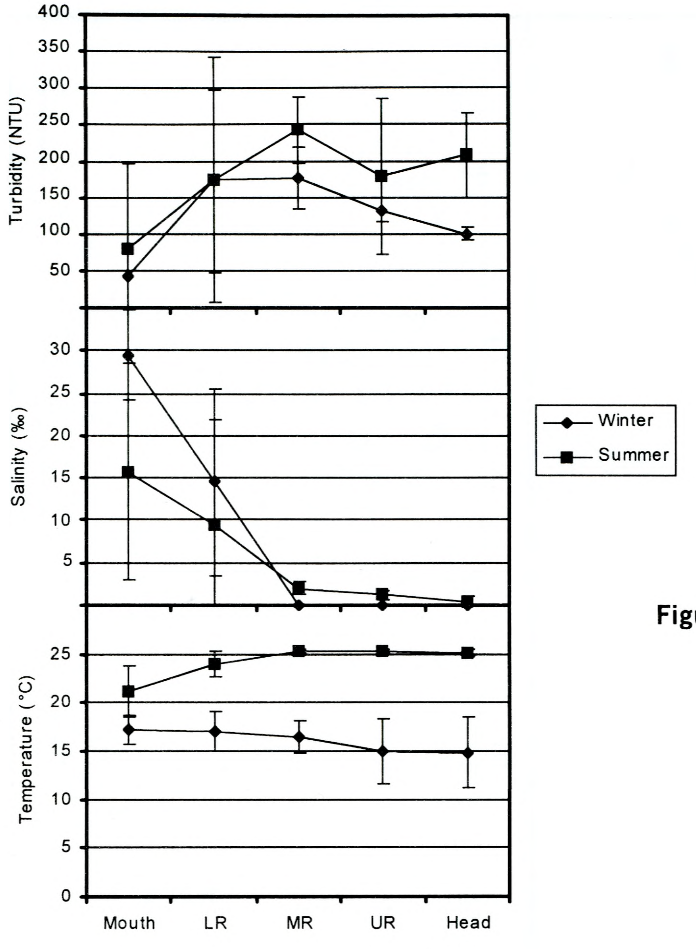

Figure 7: Mean (±S.D.) summer/winter temperature, salinity and turbidity measurements for different localities in the Great Fish Estuary. The mean was determined from morning and midday samples collected in surface and bottom waters on the 2nd June 1999 and the 31st January 2000.

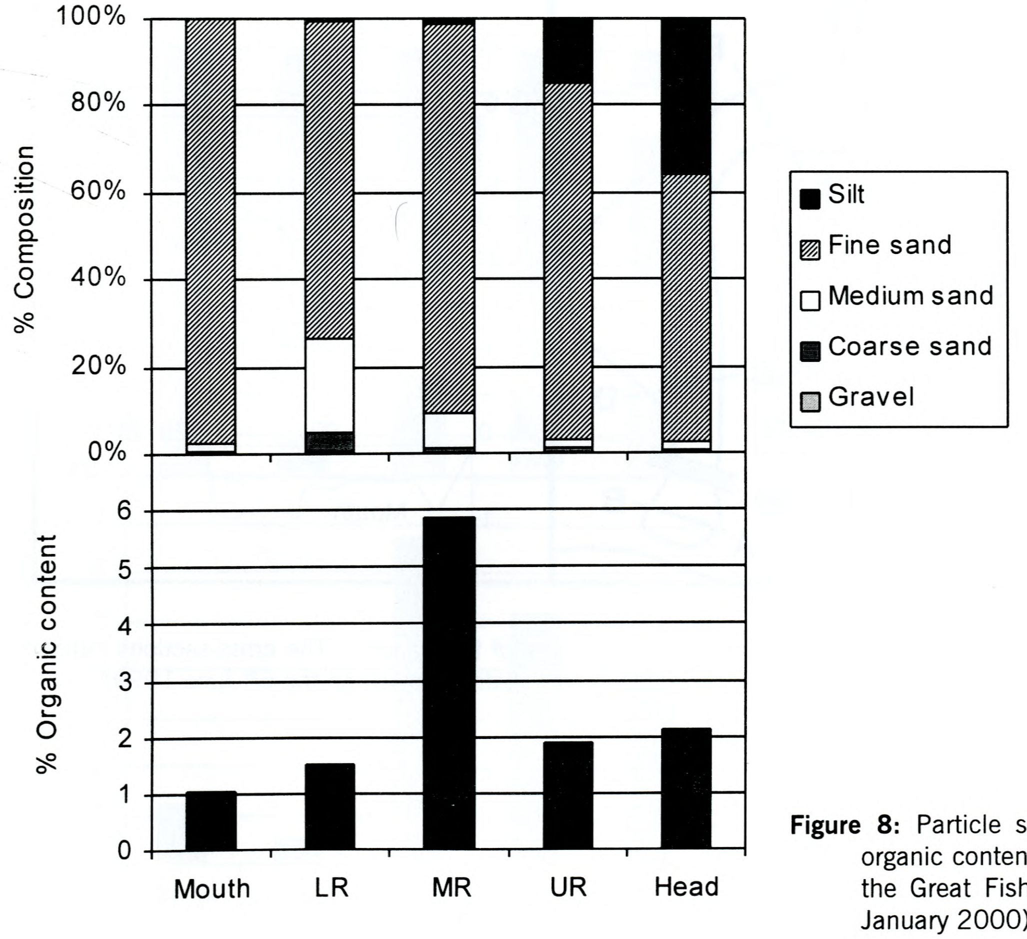

Figure 8: Particle size composition and organic content of the sediments in the Great Fish River Estuary (31st January 2000).

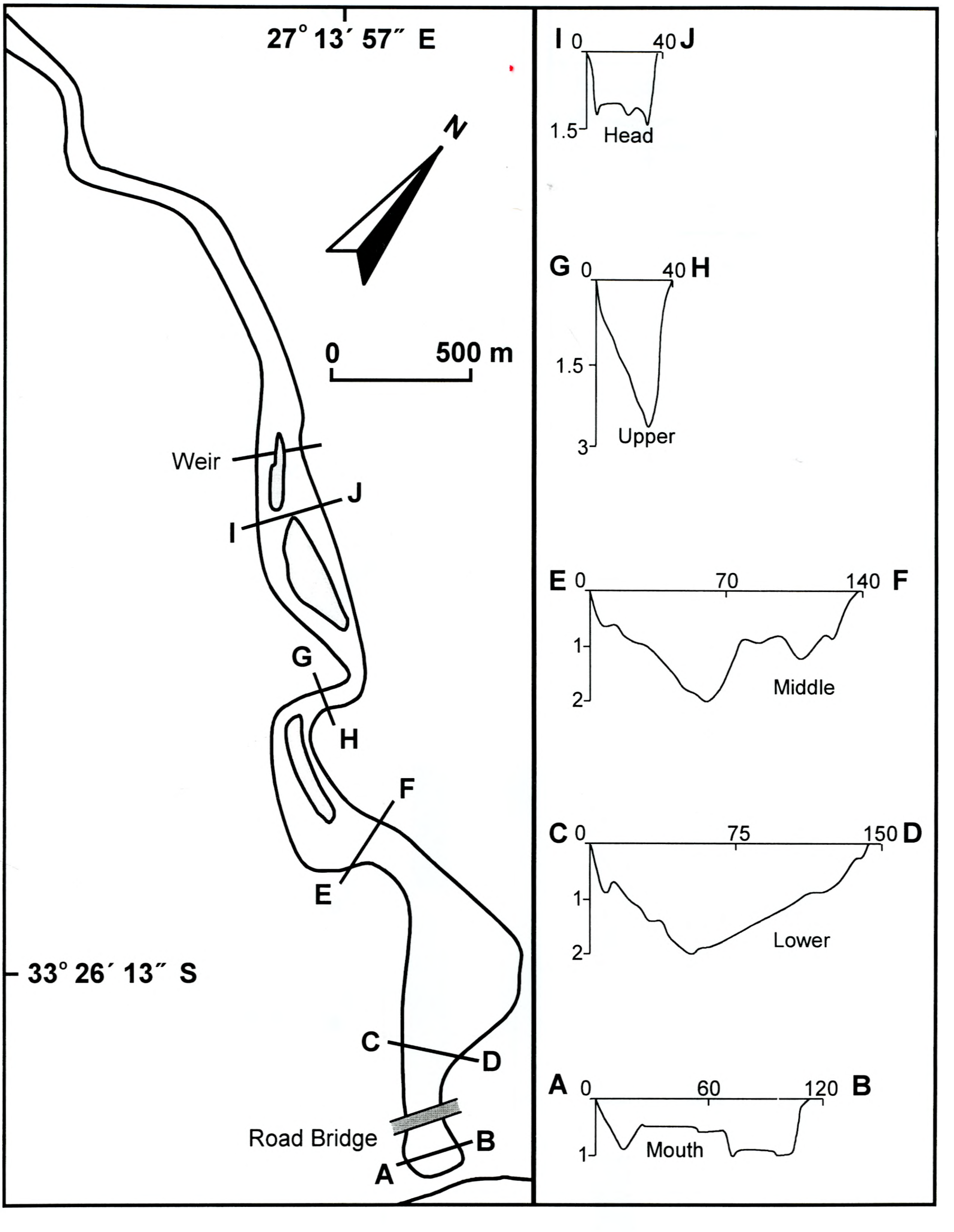

Figure 9: The Mpekweni Estuary, showing the size and shape of the system. The cross-sections indicate depths in the various sections of the estuary (drawn from data collected on the 6th June 1999).

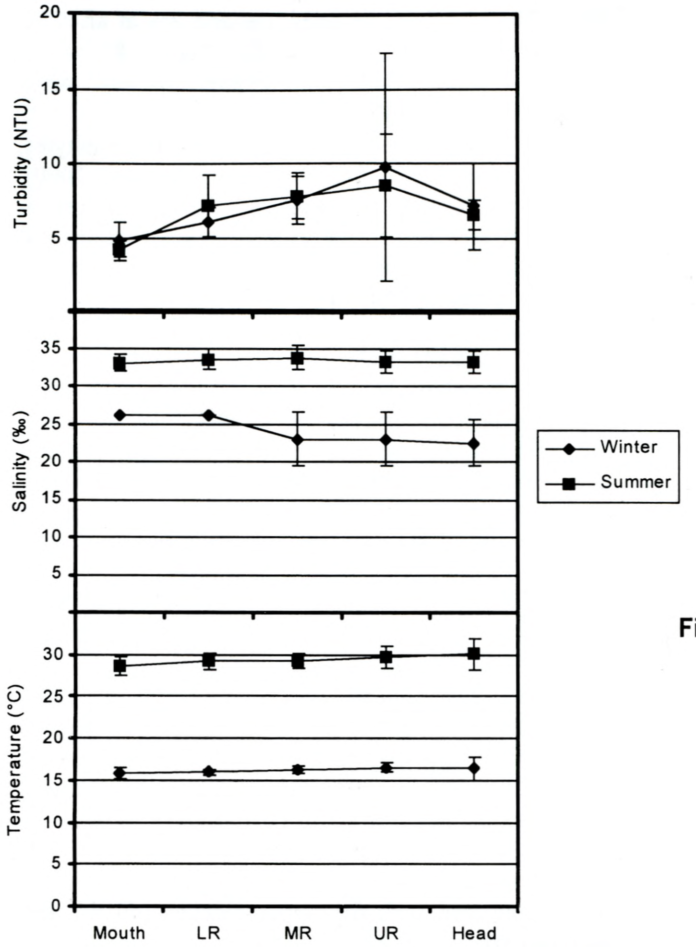

Figure 10: Mean (±S.D.) summer/winter temperature, salinity and turbidity measurements for different localities in the Mpekweni Estuary. The mean was determined from morning and midday samples collected in surface and bottom waters on the 6th June 1999 and the 8th February 2000.

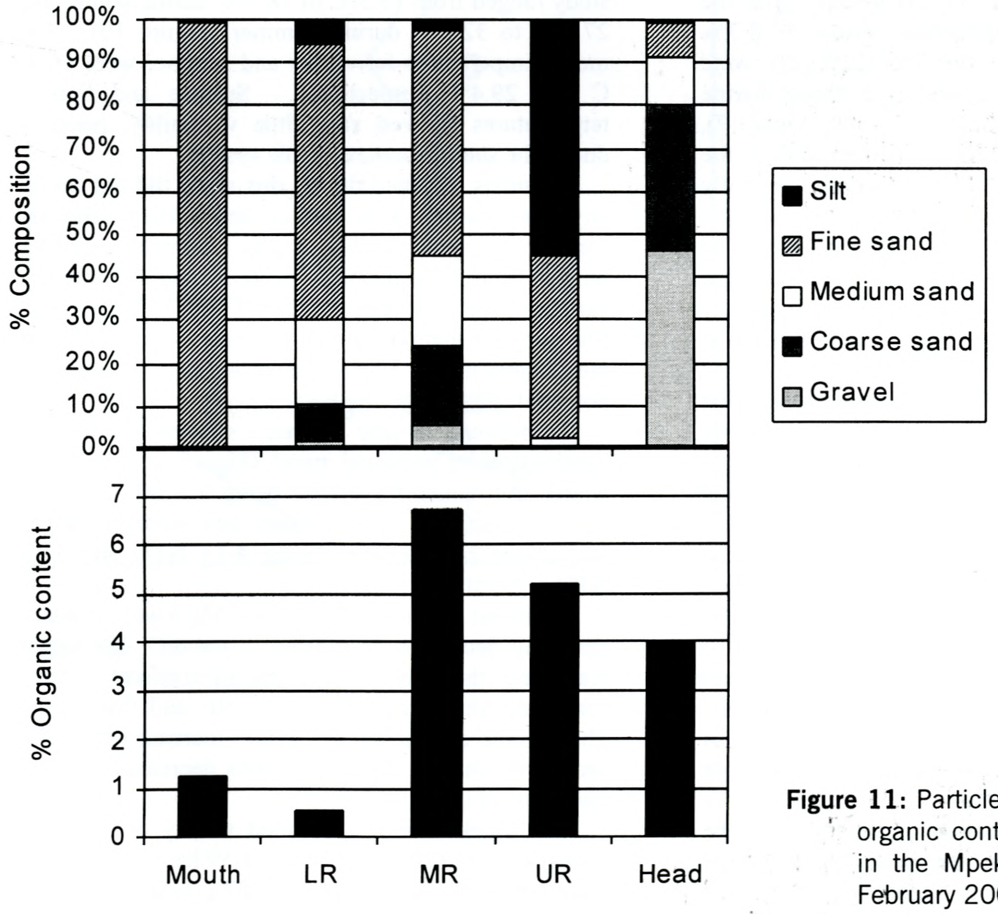

Figure 11: Particle size composition and organic content of the sediments in the Mpekweni Estuary (8th of February 2000).

GREAT FISH ESTUARY

The Great Fish Estuary (Figure 6) enters the sea at 33° 29′ 28″ S and 27° 08′ 06″ E. It has a road bridge crossing the estuary approximately 400 m from the mouth. Due to freshwater input from the Orange River inter-basin transfer scheme the estuary has a perennial river inflow.

This large permanently open estuary has a catchment area of 30366 km^2 and a MAR of 525 x 10^6 m^3 yr^{-1} (NRIO, 1987). The longitudinal length of the system is approximately 15 km, encompassing a total water area of 192.7 ha. The estuary depth and width data were recorded on a neap low tide. There was a large shallow bay near the mouth with two channels flowing through it that were 1.8 m deep. The main estuary channel had a maximum depth of 6.4 m, with shallow intertidal mudbanks on either side, resulting in an average depth of 1.37 m. Even at low tide the estuary was relatively broad, with the narrowest area located in the head-waters (50 m) and the widest area (180 m) being recorded near the mouth (Figure 6). The average cross-sectional area was 106.9 m^2.

The seasonal variability in water temperatures during this study was most noticeable in the upper reaches, with the sea having a moderating influence on the mouth region (Figure 7). The average winter temperature was 16.1°C (range = 12-19°C), while the summer average was 24.2°C (range = 18.6-25.6°C). The temperatures presented by Ter Morshuizen et al. (1996a, 1996b) were within this range, except for an elevated summer maximum (28.5°C).

Salinities recorded during this study reflected the elevated fresh water inputs on this system, with the upper estuary having oligohaline salinities, 0-3‰ (Figure 7). Salinities in the mouth region were generally higher (5-34‰), indicating a strong marine influence at times due to the open mouth (Figure 7). Salinity intruded further along the bottom than in the surface layers, with the surface waters generally having slightly lower salinities (1-2‰ lower in the upper reaches and 5-10‰ in the lower reaches). The average monthly salinity recorded in the middle and upper reaches between November 1992 and January 1995 varied between 0‰ and 15‰ (Ter Morshuizen et al., 1996a; 1996b).

Turbidity also reflected the dual nature of the Great Fish Estuary, with the upper reaches having higher turbidities from the elevated fresh water input and the lower reaches having clearer water as a result of the marine influence (Figure 7). There were no large differences between surface and bottom turbidities, except in the mouth region where surface and bottom readings sometimes differed by up to 100 NTU. The turbidity in this estuary is generally higher than in the surrounding systems, with a winter and summer average of 124.9 NTU and 176.7 NTU respectively. Ter Morshuizen et al. (1996a; 1996b) recorded a mean of approximately 200 NTU in the middle and upper reaches of the estuary.

The particle size distribution of sediments in the Great Fish increased from the head to the lower reaches and decreased again to almost completely fine sand at the mouth (Figure 8). The organic content in the sediment ranged between 1% and 2% at all sites, excluding the middle reach site (Figure 8), which contained over twice the organic content when compared with the other sites.

This estuary has no submerged macrophytes, probably due to the high turbidity (Colloty, 2000). There is a relatively large (199 ha) salt marsh area on the southwest bank in the mouth region. Reeds and sedges do occur intermittently along the banks, covering a total of 16.6 ha (Colloty, 2000).

MPEKWENI ESTUARY

The Mpekweni (Figure 9) is a temporarily open/closed estuary that reaches the sea at 33° 26′ 13″ S and 27° 13′ 57″ E. The coastal road between East London and Port Elizabeth (R72) crosses the estuary 300 m upstream from the mouth. Access to the mouth is limited to a private road through the Mpekweni Sun resort on the northeast bank of the estuary.

This system has a catchment of 65 km^2 and a MAR of 4.0 x 10^6 m^3/yr (NRIO, 1987). The longitudinal length of the estuary is 6 km, encompassing a total water area of 57.6 ha and an average depth of 1.08 m (maximum = 2.6 m). The mouth area is extremely shallow with only one section reaching 1 m in depth. The cross-sectional area decreases from the lower reaches to the head of the system (Figure 9), with an average of 92.3 m^2. The mouth (110 m), lower (140 m) and middle (140 m) reaches are relatively wide when compared with the upper reaches (40 m) and head (40 m).

Water temperatures in the Mpekweni during this study ranged from 15.3°C to 18.3°C during winter and 27.6°C to 32.2°C during summer (Figure 10). The mean temperatures for winter and summer were 16.3° C and 29.4°C respectively. Surface and bottom temperatures showed very little variability, possibly due to the shallow nature of this system.

Salinities recorded during this study did not reveal any stratification, with surface and bottom salinities varying by approximately 0.2‰. Winter salinities ranged from 20‰ to 26‰, while during summer the variation was between 32‰ and 35‰ (Figure 10). The summer increase in salinity may be indicative of the shallow nature of the system and high evaporative potential.

Turbidities in the system showed no depth, longitudinal or seasonal trend (Figure 10), with the winter and summer averages being 7.1 NTU and 6.8 NTU respectively. The winter and summer ranges overlapped considerably, being 4-11 NTU and 3-13 NTU respectively.

Sediment particle sizes in the Mpekweni Estuary generally decreased from head to mouth. The upper reach was the only site that didn't conform to this, consisting almost exclusively of silts and fine sands. The organic content of the system increased from the head to the middle reaches and then decreased towards the mouth (Figure 11).

The Mpekweni has a limited variety of estuarine plants. Colloty (2000) identified 1.59 ha of submerged macrophytes in the estuary and 27.2 ha of supratidal salt marsh on the northeast bank above the road bridge.

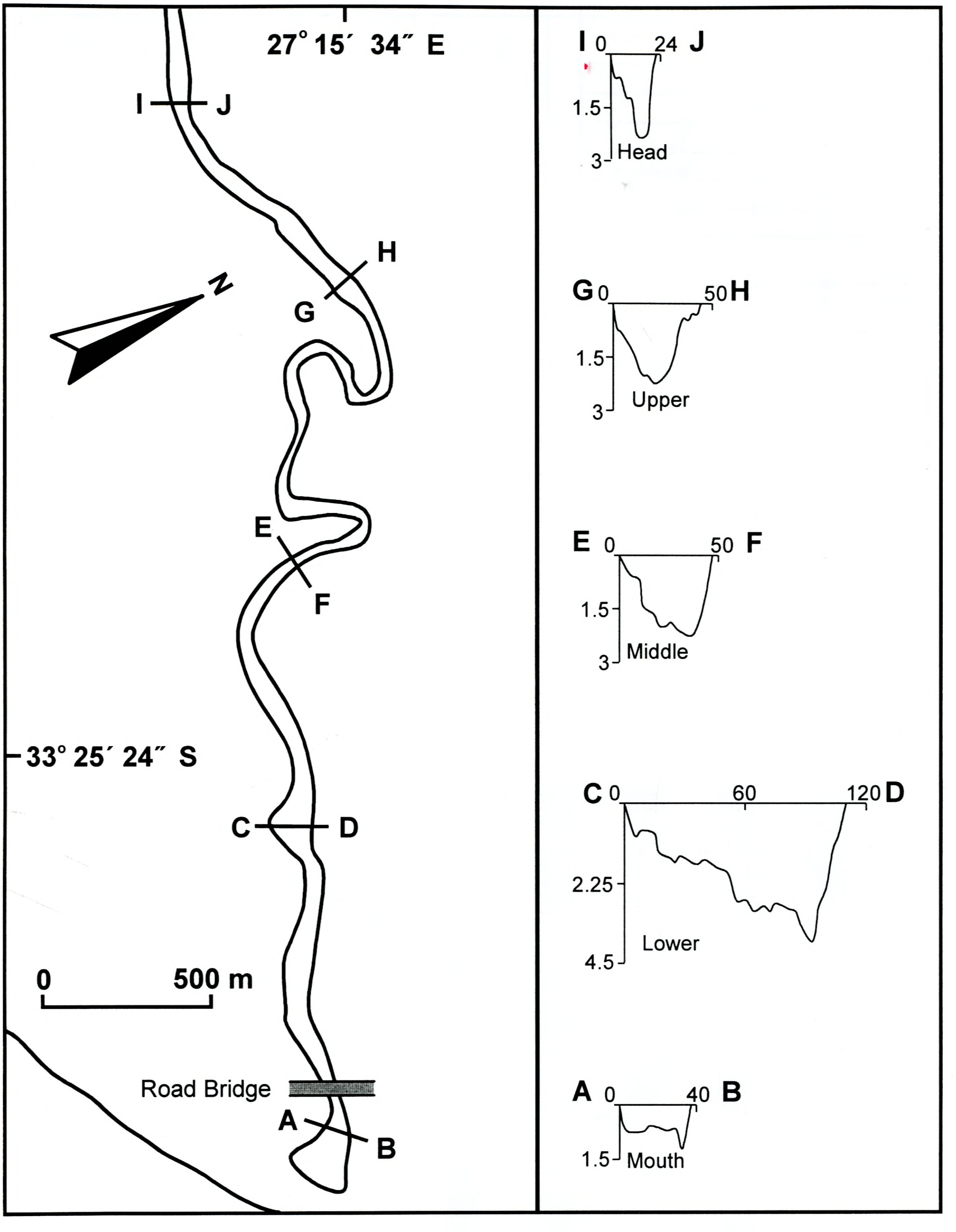

Figure 12: The Mtati Estuary, showing the size and shape of the system. The cross-sections indicate depths in the various sections of the estuary (drawn from data collected on the 31st May 1999).

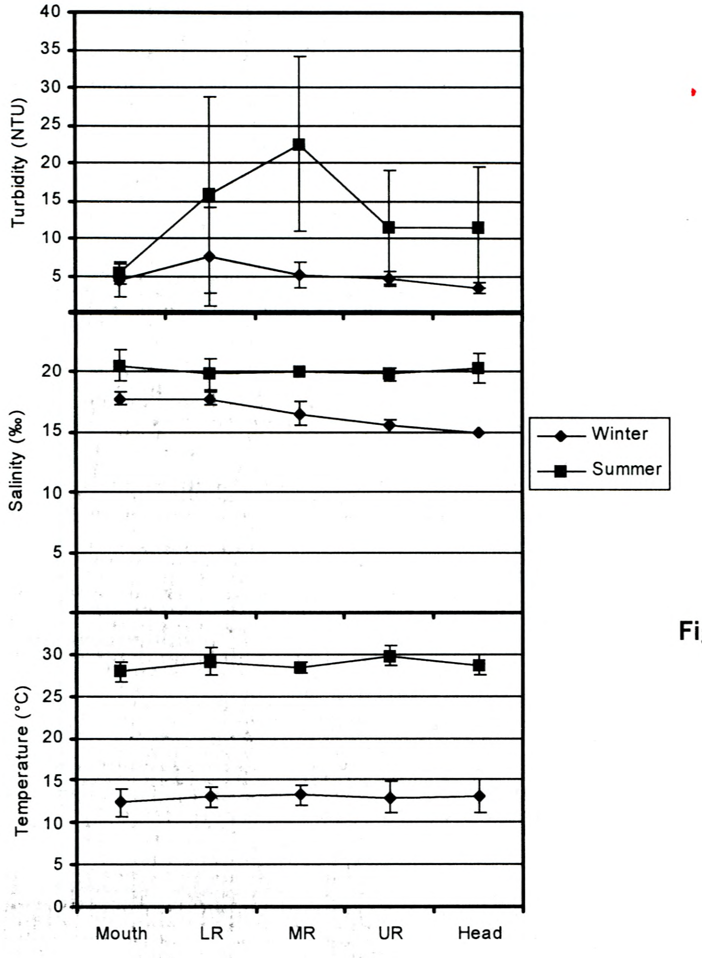

Figure 13: Mean (±S.D.) summer/winter temperature, salinity and turbidity measurements for different localities in the Mtati Estuary. The mean was determined from morning and midday samples collected in surface and bottom waters on the 31st May 1999 and the 9th February 2000.

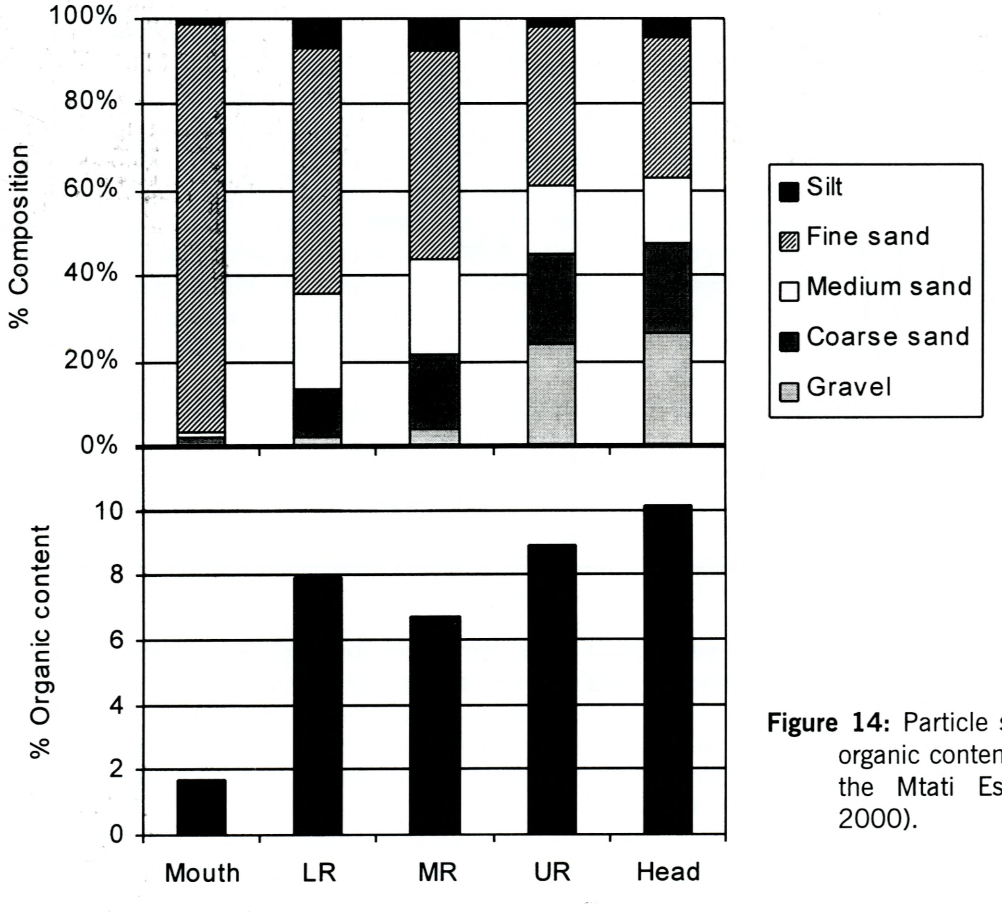

Figure 14: Particle size composition and organic content of the sediments in the Mtati Estuary (9th February 2000).

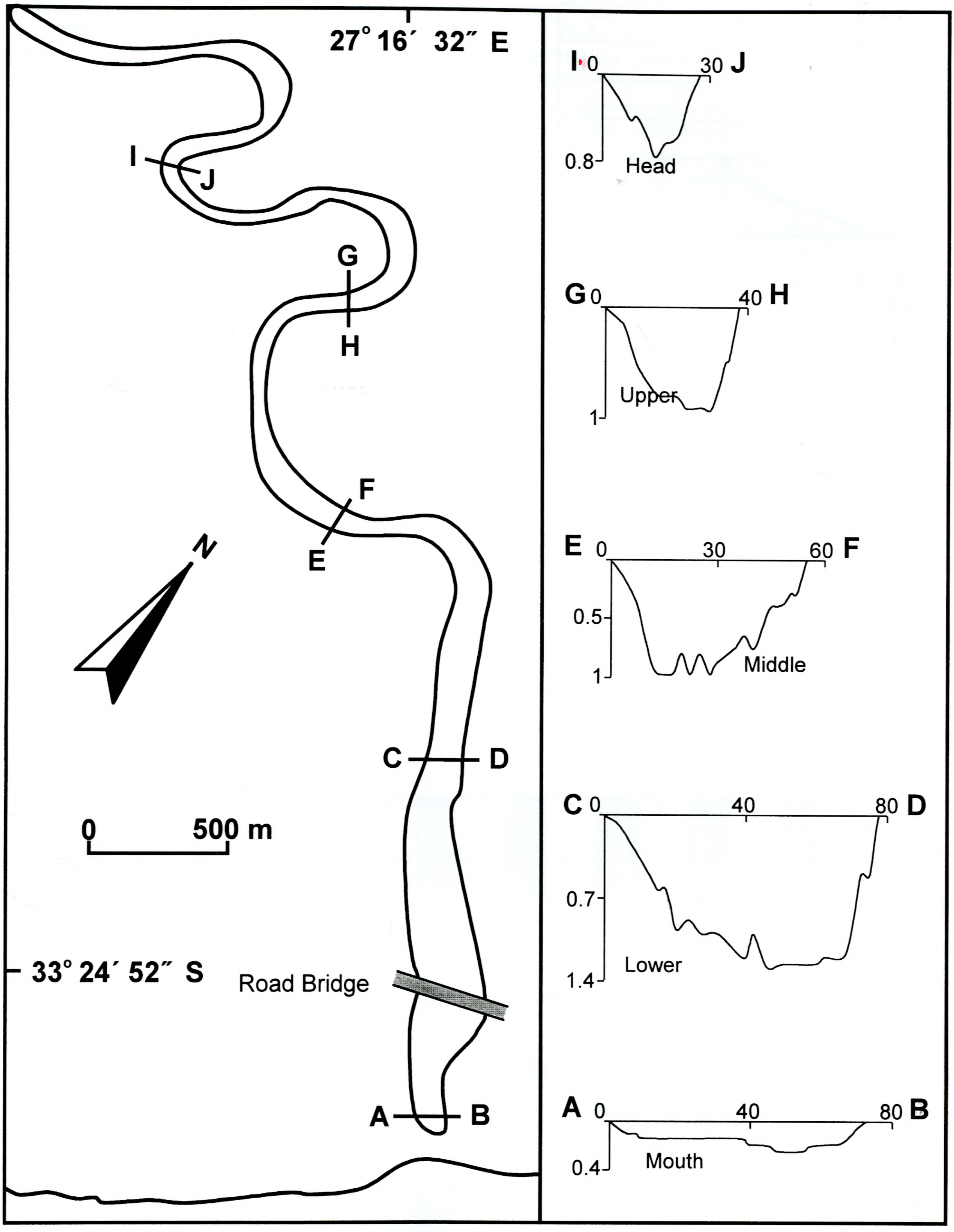

Figure 15: The Mgwalana Estuary, showing the size and shape of the system. The cross-sections indicate depths in the various sections of the estuary (drawn from data collected on the 6th June 1999).

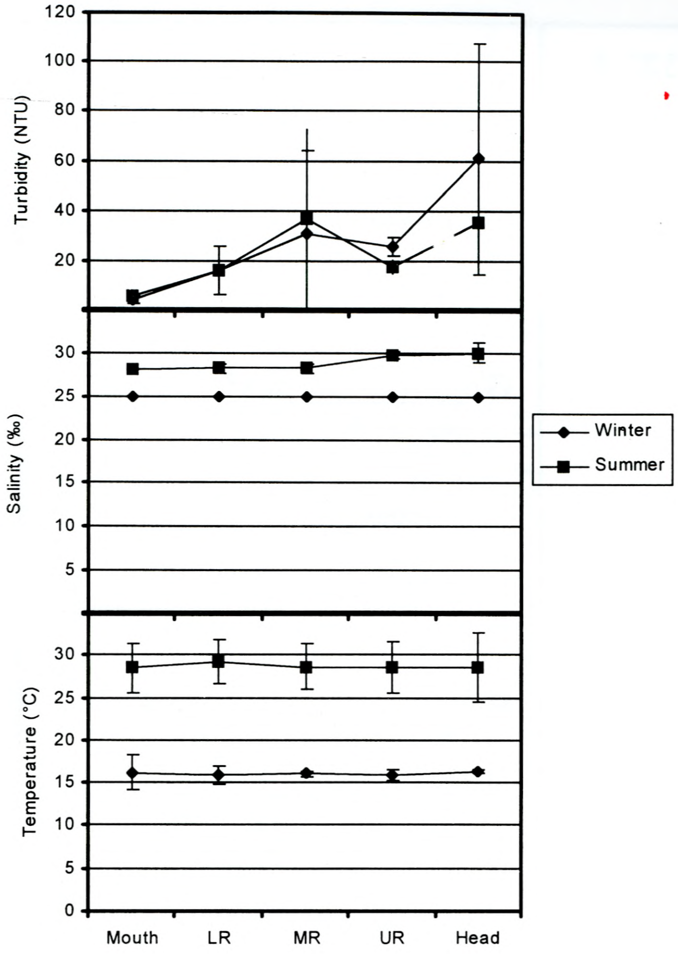

Figure 16: Mean (±S.D.) summer/winter temperature, salinity and turbidity measurements for different localities in the Mgwalana Estuary. The mean was determined from morning and midday samples collected in surface and bottom waters on the 6th June 1999 and the 9th February 2000.

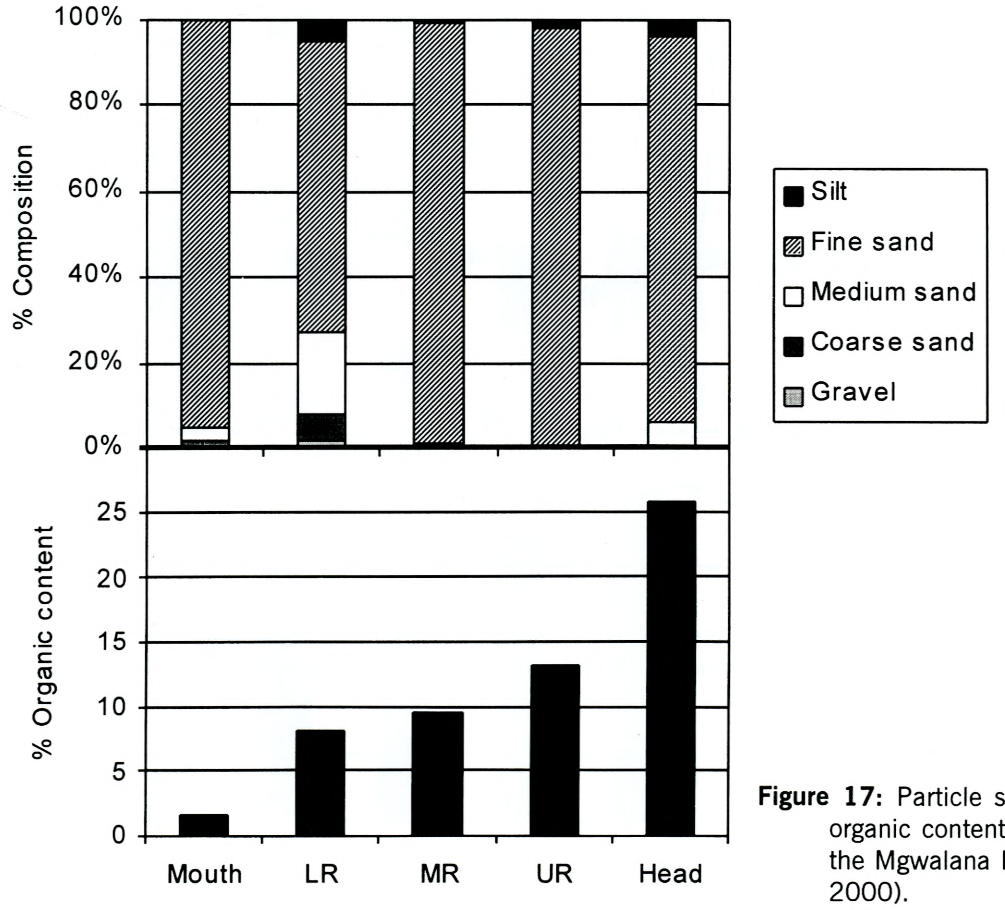

Figure 17: Particle size composition and organic content of the sediments in the Mgwalana Estuary (9th February 2000).

MTATI ESTUARY

The Mtati (Figure 12) is a temporarily open/closed estuary that reaches the sea at 33° 25′ 24″ S and 27° 15′ 34″ E. Anthropogenic impacts are restricted to the road bridge, which crosses the estuary approximately 300 m from the mouth and a small residential development on the northeast bank.

The catchment size of the Mtati is 130 km^2 with a MAR of 8.0 x 10^6 m^3/yr (NRIO, 1987). The estuary has a surface area of 37.9 ha and a length of approximately 4 km. The Mtati is generally a narrow system, with an average width of 57.5 m, except for a bay area above the road bridge where it widens to approximately 110 m. The average recorded depth of the system was 1.6 m, although the main channel was generally deeper than 2 m, reaching a maximum of 3.9 m in the lower reaches. The average cross-sectional area was 57 m^2 although this was mostly due to a relatively high value of 121 m^2 in the lower reaches.

Based on measurements taken on the 31st May 1999 and the 9th February 2000, temperatures in the Mtati Estuary showed a large seasonal variation, with a winter average of 13°C and a summer average of 28.8°C. There was a small range during both seasons, 11-15°C during winter and 27-31°C during summer (Figure 13). There was no evidence of temperature stratification, possibly due to the shallowness of the estuary and the effects of wind mixing.

The salinity throughout the system was fairly uniform with only a small reduction towards the head during winter (Figure 13). The mean summer salinity (20.1‰) was higher than the mean winter salinity (16.5‰) possibly due to the shallow warm waters promoting evaporation during the summer. The overall turbidity in the Mtati was low with an average of 9.2 NTU. Winter turbidities were slightly lower with a mean of 5.1 NTU while the summer mean was 13.3 NTU (Figure 13).

Sediment particle sizes in the Mtati Estuary decreased from head to mouth, with the mouth sample comprising mostly fine sands (Figure 14). The percentage organic content of the sediments also decreased from the head to the mouth (Figure 14). The only site not following this trend was the lower reach site, which had a higher organic content than the middle reaches.

The botanical importance of submerged macrophytes to this system is relatively low, with only 3.2 ha being identified (Colloty, 2000). The main contributors to productivity were the supratidal salt marsh area (54.3 ha) and reed stands along the banks (26.2 ha).

MGWALANA ESTUARY

The Mgwalana (Figure 15) is a temporarily open/ closed estuary reaching the sea at 33° 24′ 52″ S and 27° 16′ 32″ E. Access to the mouth area is limited to a private road through a small holiday resort on the northeast bank. The main anthropogenic influence on this system is the coastal road, which crosses the main channel approximately 400 m upstream of the mouth. Some small walls have been built on the northeastern side of the mouth region in an attempt to stop erosion of the beach access road.

This system has a relatively large catchment area of 200 km^2 and a MAR of 12 x 10^6 m^3/yr (NRIO, 1987). The length of the estuary is 6.5 km and encompasses a total water surface area of 62.9 ha. The mouth area of the Mgwalana is very shallow (less than 0.25 m in depth), with the rest of the system being slightly deeper (average depth = 0.6 m), and having a maximum depth of 1.3 m. The estuary is also narrower relative to the other study systems, having a maximum width of 180 m and an average of 54.4 m. The system has a small average cross-sectional area of 29.7 m^2 with only the lower reaches being higher at 60 m^2.

The Mgwalana revealed little temperature variation along the length of the estuary. Winter temperatures ranged from 14.3°C to 18°C (average = 16.1°C), while the summer range was between 25°C and 32°C (average = 28.7°C) (Figure 16). Similarly, the biannual samples yielded very little variability in salinity, particularly during winter when all salinities were 25‰, while during summer they ranged from 28‰ to 31‰. During summer there was a slightly reversed salinity gradient, with the mouth having a mean of 28‰ and the head having a higher mean of 31‰ (Figure 16).

A turbidity gradient was evident in this estuary, with values at the head (>30 and 60 NTU) being at least triple those at the mouth (<10 NTU) during both winter and summer (Figure 16). This may be due to wind driven mixing of the water column stirring up some of the finer sediments in the upper reaches.

The sediment composition of the Mgwalana Estuary was similar from head to mouth, consisting primarily of fine sands (Figure 17). The only site that did not follow this trend was the lower reaches where there was a higher percentage of medium (18.9%) and coarse (6.9%) sands. The percentage organic content in the estuary decreased from the head (25.6%) to the mouth (1.5%) (Figure 17). The overall organic content of this system and the Keiskamma was relatively high when compared with the other study estuaries.

Colloty (2000) recorded very low densities of submerged macrophytes in the Mgwalana, with a total area cover of only 1.1 ha. There is a small supratidal salt marsh area (7.6 ha) on the northeast bank above the coastal road bridge, but the majority of the primary productivity arises from patches of reeds and sedges along the banks of the estuary (total area cover = 48.8 ha).

BIRA ESTUARY

The Bira (Figure 18) was the largest of the temporarily open/closed estuaries in this study, with a tidal influence extending 9 km up the estuary and encompassing an estuarine surface area of 122.3 ha. The system has a 255 km^2 catchment area and a MAR of 13 x 10^6 m^3/yr (NRIO, 1987). The estuary enters the sea at 33° 22′ 58″ S and 27° 19′ 47″ E. The main coastal road (R72) bridge crosses the system approximately 600 m from the mouth, with access to the mouth area via a road on the northeastern bank.

The Bira is a relatively shallow system for its size,

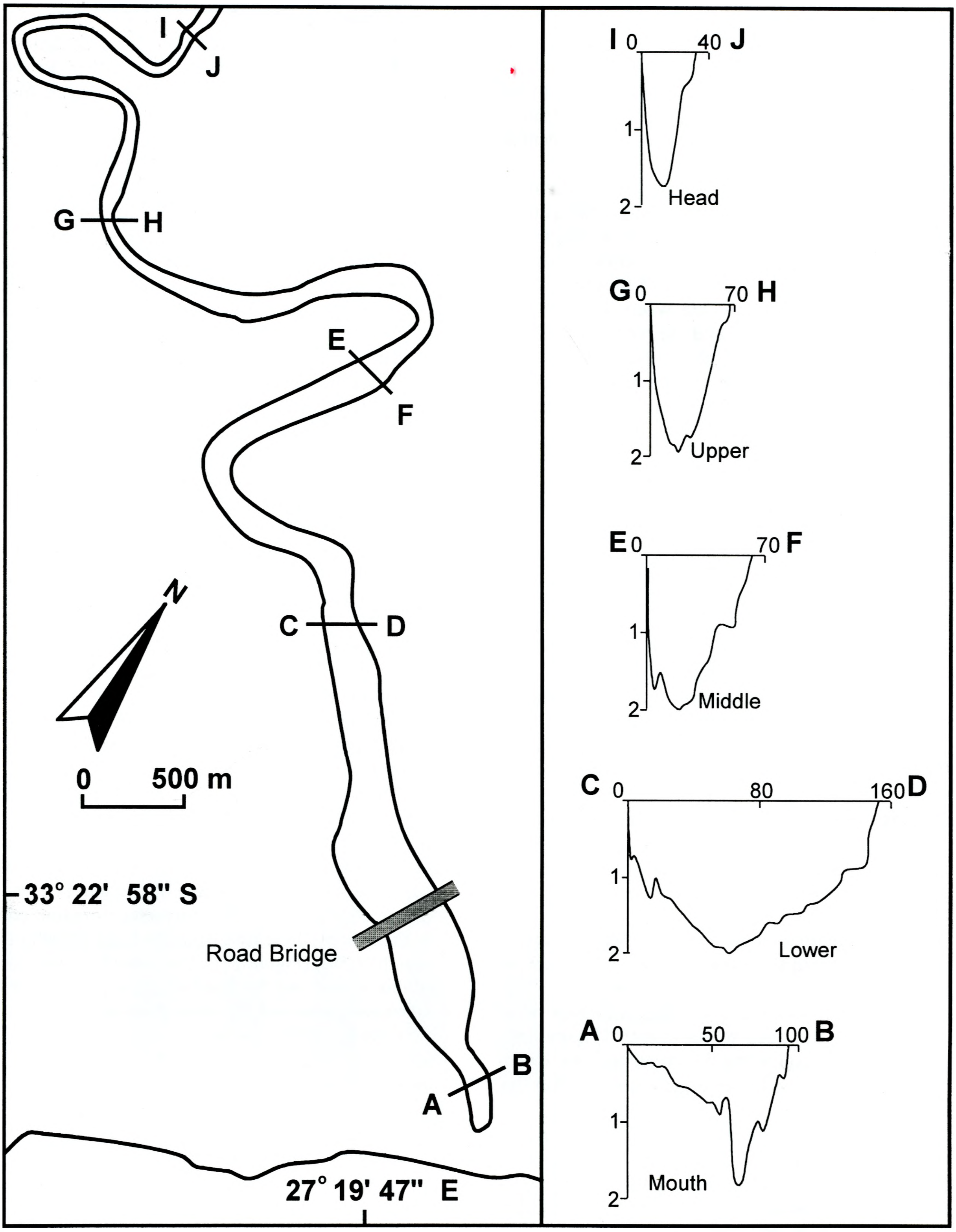

Figure 18: The Bira Estuary, showing the size and shape of the system. The cross-sections indicate depths in the various sections of the estuary (drawn from data collected on the 1st June 1999).

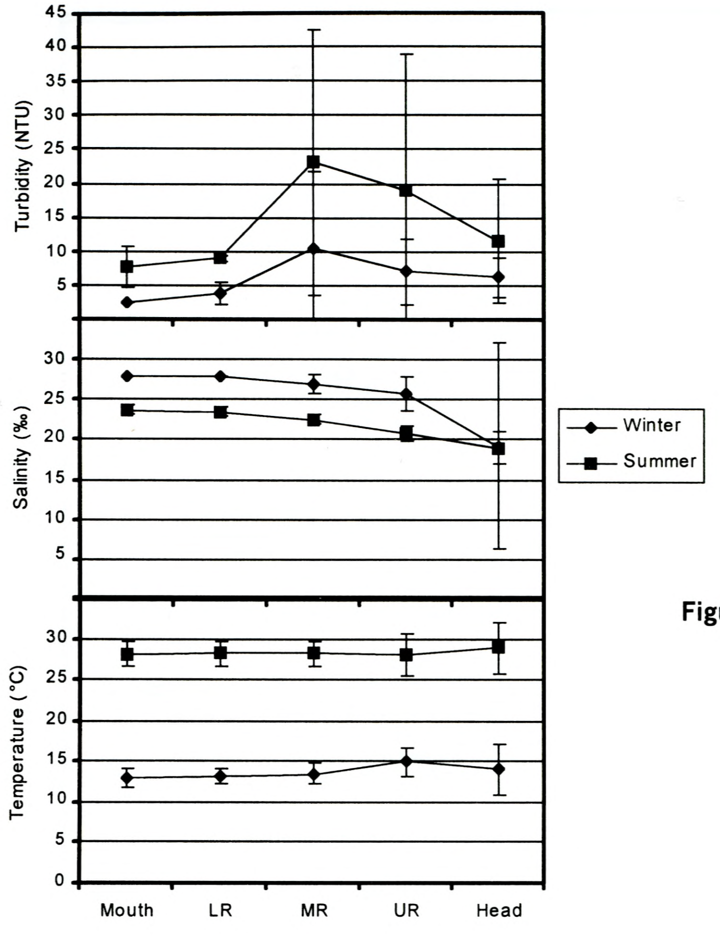

Figure 19: Mean (±S.D.) summer/winter temperature, salinity and turbidity measurements for different localities in the Bira Estuary. The mean was determined from morning and midday samples collected in surface and bottom waters on the 1st June 1999 and the 9th February 2000.

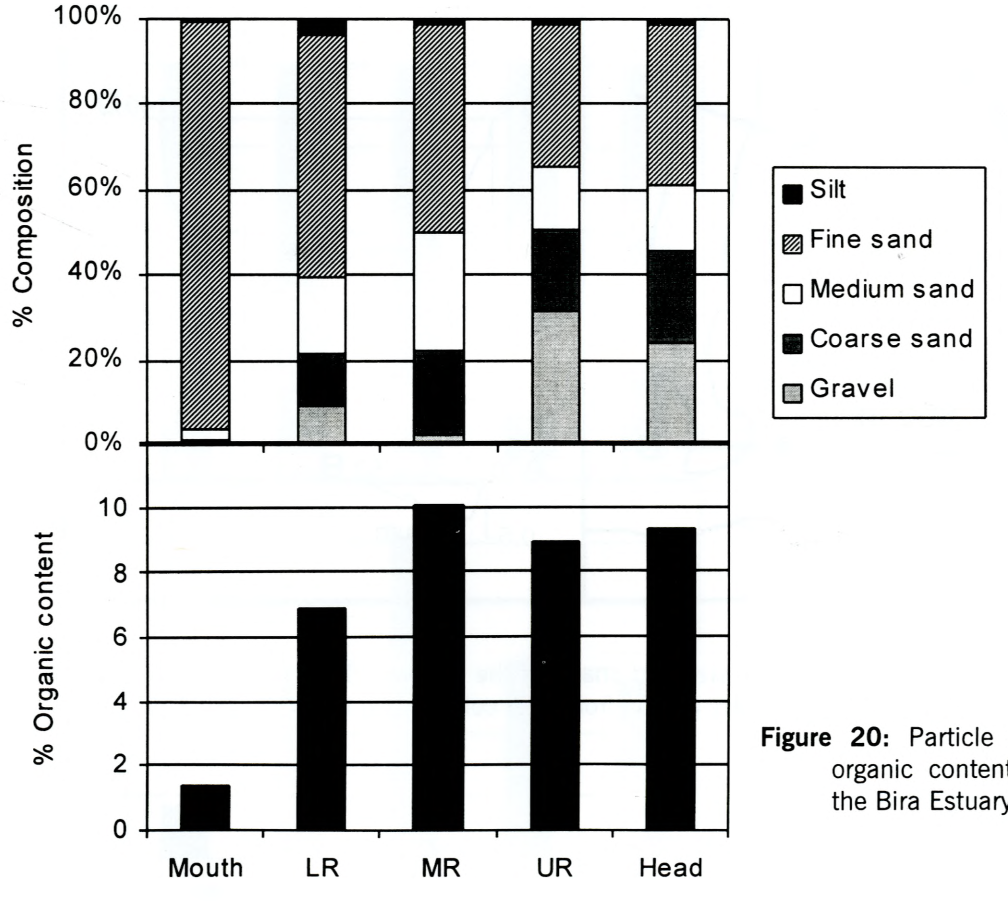

Figure 20: Particle size composition and organic content of the sediments in the Bira Estuary (9th February 2000).

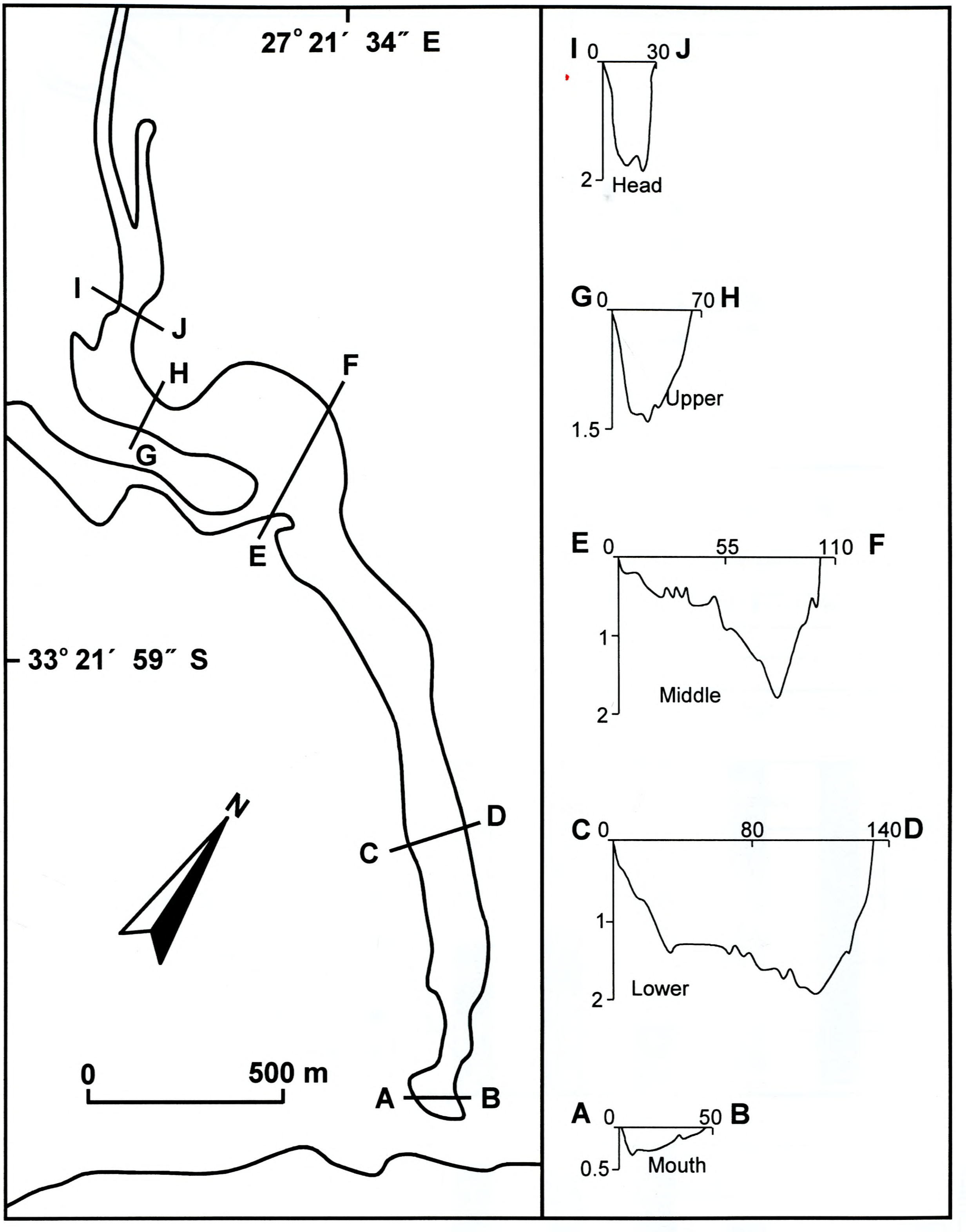

Figure 21: The Gqutywa Estuary, showing the size and shape of the system. The cross-sections indicate depths in the various sections of the estuary (drawn from data collected on the 5th June 1999).

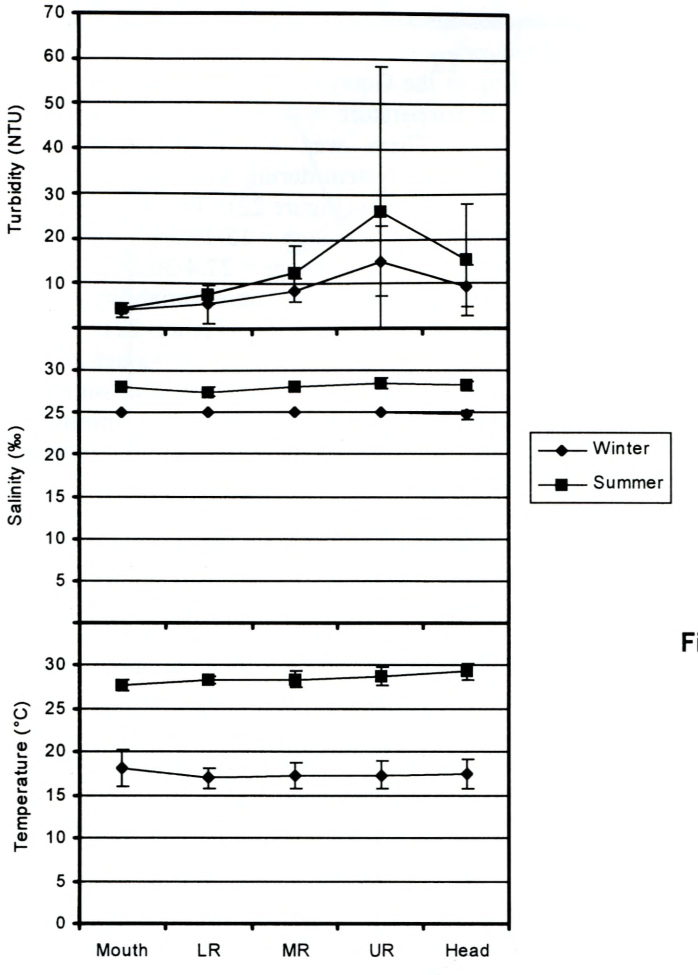

Figure 22: Mean (±S.D.) summer/winter temperature, salinity and turbidity measurements for different localities in the Gqutywa Estuary. The mean was determined from morning and midday samples collected in surface and bottom waters on the 5th June 1999 and the 8th February 2000.

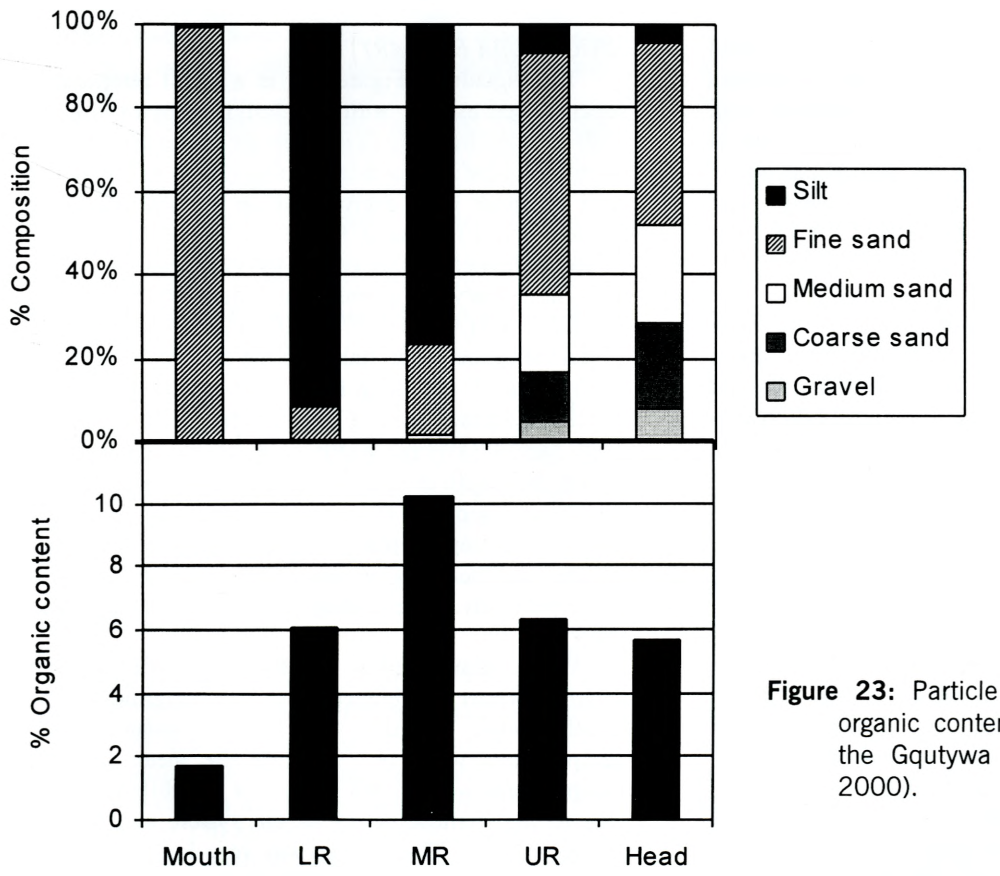

Figure 23: Particle size composition and organic content of the sediments in the Gqutywa Estuary (8th February 2000).

with an average depth of 1.2 m, and a maximum of only 2 m. The mouth area has a fairly shallow bay with a short, deep channel (1.8 m) along the east bank, adjacent to the retaining wall. This bay widens above the road bridge, before the system narrows again towards the head (40 m). The average cross-sectional area is also relatively low at 80.6 m^2, with only the lower reaches exceeding this average at 188 m^2.

The Bira demonstrated very little longitudinal variability in winter and summer temperatures (Figure 19). There was also very little temperature variability with depth, but a large seasonal difference was evident with a winter mean of 13.8°C and a summer mean of 28.3°C.

Salinity variation within the system was very low, with a winter mean of 25.6‰ and a summer mean of 21.9‰. A small longitudinal change in salinity was recorded between the mouth and head of the estuary (Figure 19). There was greater variability in turbidity, with a peak in the middle reaches (Figure 19) that may be due to outflow from a small tributary entering the estuary in this region. The summer turbidity was higher than winter throughout the system, although during both seasons the longitudinal trends were similar.

The sediments of the Bira Estuary indicate a reduction in large particles and an increase in fine sands from the head to the mouth (Figure 20). The percentage organic content of the sediments was relatively low (<10%) throughout the estuary, with the middle, upper and head reaches having a higher organic content than the lower reaches and mouth region (Figure 20).

According to Colloty (2000) the Bira has limited macrophyte primary producers, with a very small area (2.6 ha) of supratidal salt marsh on the northeast bank above the road bridge and a total of only 5.3 ha of submerged macrophytes. There are several patches of reeds and sedges (total area = 15.2 ha), although most of these plants occur on the banks in the lower reaches.

GQUTYWA ESTUARY

The Gqutywa (Figure 21) was one of the most pristine systems in this study, with no direct anthropogenic impacts. The coastal road does not cross this system and the only access to the mouth area is via the beach. This temporarily open/closed system enters the sea at 33° 21′ 59″ S and 27° 21′ 34″ E. The MAR of 6.0 x 10^6 m^3/yr arises from a catchment area of 85 km^2 (NRIO, 1987). The linear length of the estuary is 3 km encompassing a total estuarine surface area of 39.9 ha.

The Gqutywa has a shallow embayment (average depth = 0.9 m) in the mouth region extending up into the middle reaches with one deep channel (1.9 m) along the east bank. The head and upper regions are slightly deeper on average (average depth = 1.0 m), although the channel is slightly shallower at 1.4 m. The system is fairly narrow in the head and upper reaches (27.5 m and 45 m respectively) but widens in the middle and lower reaches (98 m and 137.5 m) before narrowing near the mouth. The average cross-sectional area is relatively low (62.2 m^2), although the lower reaches has a substantially higher cross-sectional area of 165 m^2.

Sampling in the Gqutywa demonstrated very little variability in temperature with depth and distance up the estuary. There was a slight decrease in temperature up the system during winter and a slight increase during summer (Figure 22). The mean winter temperature was 17.5°C (range = 15-19.3°C) while the summer mean was 28.6°C (range = 27.4-30.2°C).

Salinity also revealed very little variability, with only a small seasonal variation (Figure 22). The winter salinities were 25‰ with only two values lower than this in the head region, while the summer salinities ranged between 27‰ and 29‰ (mean = 28.1‰). The summer and winter turbidities showed similar trends, peaking in the upper reaches and decreasing towards the head region (Figure 22). Summer turbidities were generally higher than winter, with means of 13.3 NTU and 8.6 NTU respectively.

Sediment particle sizes in the Gqutywa decreased from the head to the lower reaches, with the mouth having slightly larger particles than the lower and middle reaches (Figure 23). The organic content of the Gqutywa increased from the head of the system towards the middle reaches and then decreased towards the mouth (Figure 23).

Submerged macrophyte densities in the Gqutywa during this study were very low, with a total area cover of 2.5 ha. In addition there was only a small salt marsh area on the northeast bank in the middle reaches covering an area of 1.2 ha. There were reed and sedge patches on both banks (total area = 3.8 ha).

NGCULURA ESTUARY

The Ngculura (Figure 24) is a small temporarily open/closed estuary with two holiday homes situated 500 m away from the system on the northeast bank. It is not used for any form of boating due to its small size and no roads have encroached on the channel. The system enters the sea at 33° 21′ 21″ S and 27° 22′ 23″ E approximately 700 m east of the Gqutywa.

The estuary has a small catchment of 15 km^2 that provides a MAR of 1.17 x 10^6 m^3/yr (NRIO, 1987). Tidal influence, when linked to the sea, is only evident approximately 600 m up the system resulting in a total estuarine surface area of only 1.6 ha. The estuary is very narrow (average width = 14 m), the widest point being the mouth area at 20 m, and the narrowest being the head region at 10 m. The estuary is generally shallow (average depth = 0.8 m) with only the upper reaches and head region being deeper at 1.5m and 1.8 m respectively. The average cross-sectional area was 10.9 m^2.

Water temperatures in the Ngculura showed summer/winter differences but no longitudinal or depth trends (Figure 25). The mean winter temperatures were 16.7°C while the mean summer temperatures were 27.9°C. The low variability may be due to the shallow nature of the system and limited water volume. The salinity was very low throughout the estuary during both seasons, with winter having an average 2‰ and summer 3.2‰ (Figure 25). There was almost no longitudinal or depth variability within

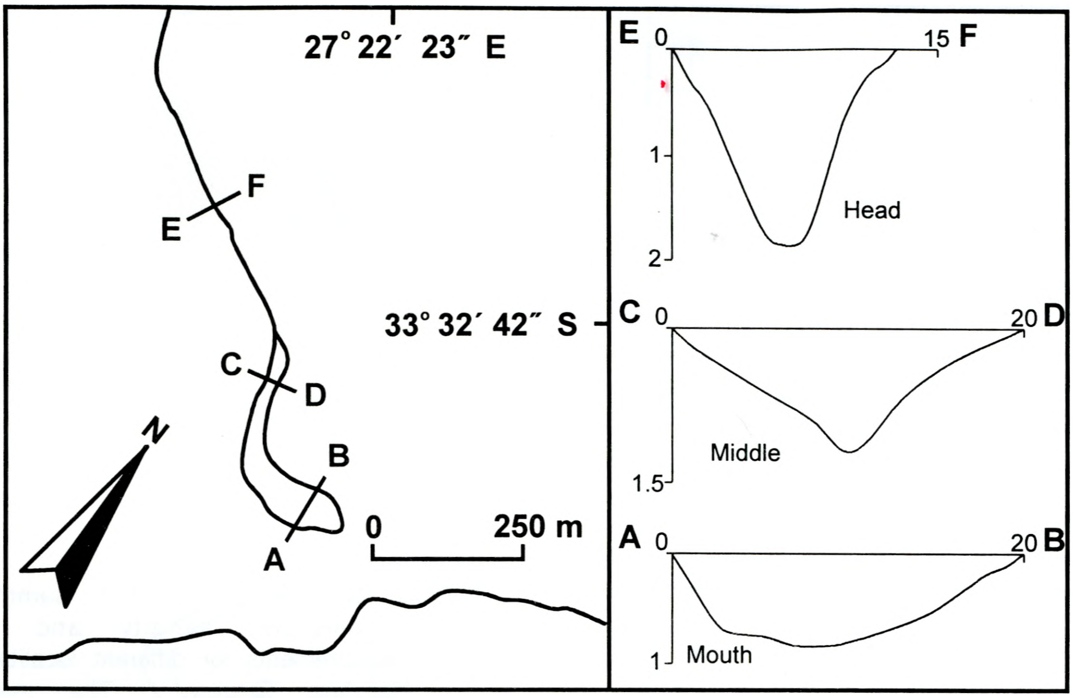

Figure 24: The Ngculura Estuary, showing the size and shape of the system. The cross-sections indicate depths in the various sections of the estuary (drawn from data collected on the 5th June 1999).

the system.

The estuary also had very low turbidities during both seasons, with the winter turbidity being lower than summer (means of 3.9 NTU and 12.8 NTU respectively) (Figure 25). A slight increase in turbidity gradient from mouth to head was evident during both seasons, although barely detectable during winter.

Fine sands dominated the sediments in all reaches (Figure 26). This arises through most of the estuary being situated in a wind blown dune area of the beach, with only the head and upper reaches extending beyond that into a vegetated dune ridge. The percentage organic content was also extremely low in this system, peaking with a value of 6.9% in the upper reaches (Figure 26) where dune vegetation was present.

Colloty (2000) recorded very low macrophyte densities, with no submerged macrophyte beds or salt marsh areas. The only plants present in the system are reeds and sedges, with a relatively large patch near the mouth and a few very small areas further upstream (total area cover = 0.7 ha).

KEISKAMMA ESTUARY

The Keiskamma (Figure 27) is a large, permanently open estuary, with the mouth situated at 33° 16′ 45″ S and 27° 29′ 50″ E. This system represented the eastern boundary of the study area with the small town of Hamburg situated on the southwestern bank.

The Keiskamma has a large catchment (2745 km^2) with a MAR of 170.48 x 10^6 m^3/yr (NRIO, 1987). The estuary is approximately 12 km long, encompassing a total estuarine area of 197 ha. The estuary has an embayment near the mouth with depths ranging from 0.5 m to 2 m. The main estuary channel has a minimum 1.6 m depth, attaining a maximum of 2.7 m in the upper reaches. The average depth is 1.35 m with the middle and lower reaches having relatively shallow banks on either side of the main channel, while the upper reaches and head of the system have steep slopes from the bank into the main channel. The average cross-sectional area is 116 m^2 and the average width is 86.5 m with a minimum of 30 m in the upper reaches and a maximum of 172.5 m near the mouth.

There was little longitudinal variability in winter water temperatures (Figure 28), with a mean of 17.6°C and a recorded range of 15.5°C to 19°C. Summer temperatures increased with distance up the estuary from a mean of 21.3°C at the mouth to 27°C at the head of the system (Figure 28). Summer temperatures ranged from 16°C to 28°C. Read (1983) recorded an identical maximum but lower minimum (12°C) temperature.

Longitudinal salinity trends during both winter and summer decreased from the mouth (31‰ and 31.8‰ respectively) to the head (6.3‰ and 0‰ respectively) thus indicating a perennial fresh water input together with open mouth conditions (Figure 28). The average salinities during winter and summer were 19.5‰ and 11.8‰ respectively.

No longitudinal turbidity trends were evident during winter, although during summer the turbidity increased with distance up the estuary, peaking in the upper reaches (Figure 28). The summer turbidities were generally higher than the winter turbidities with a mean of 74.8 NTU during summer and 15.5 NTU during winter.

Sediment composition in the Keiskamma Estuary did not reveal any distinct trends (Figure 29). The middle reach samples were dominated by silt, and the mouth region by fine-grained sands. Similarly the

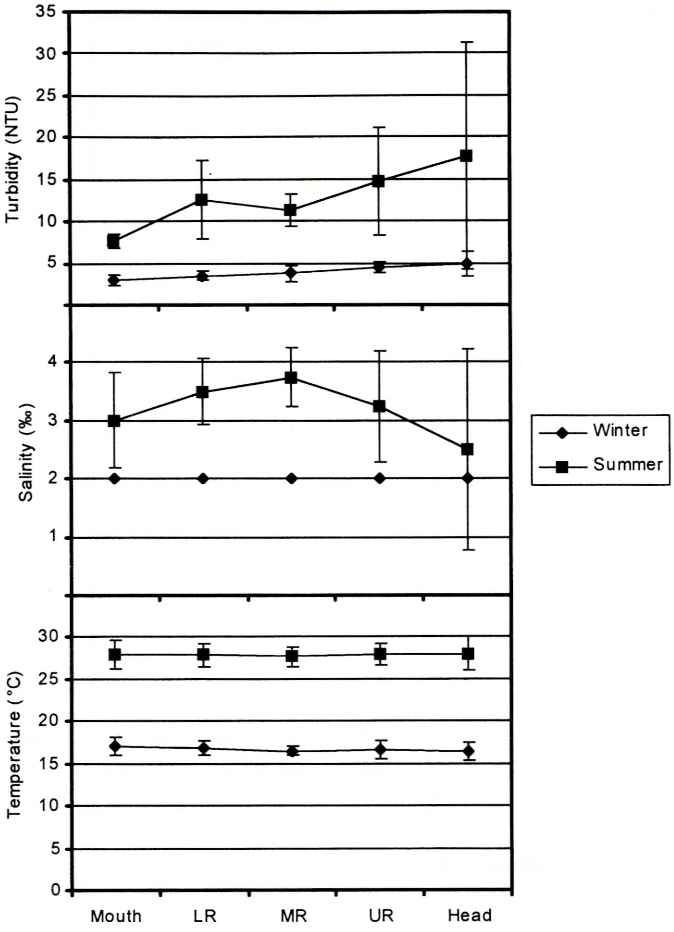

Figure 25: Mean (±S.D.) summer/winter temperature, salinity and turbidity measurements for different localities in the Ngculura Estuary. The mean was determined from morning and midday samples collected in surface and bottom waters on the 5th June 1999 and the 8th February 2000.

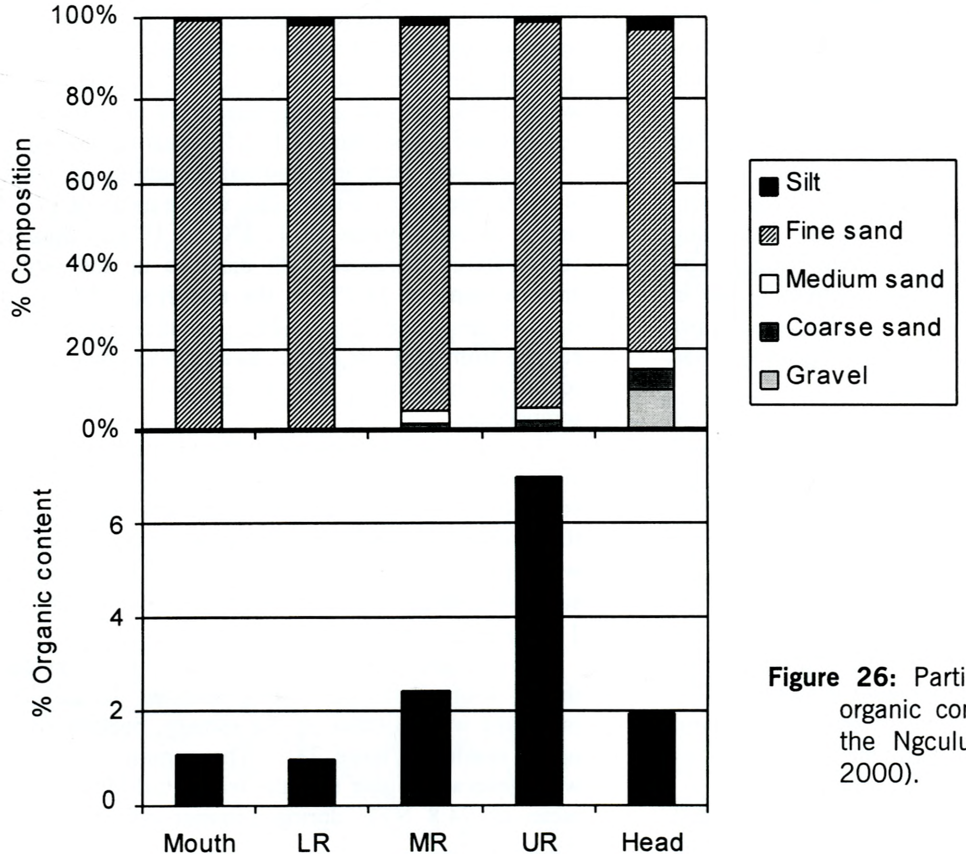

Figure 26: Particle size composition and organic content of the sediments in the Ngculura Estuary (8th February 2000).

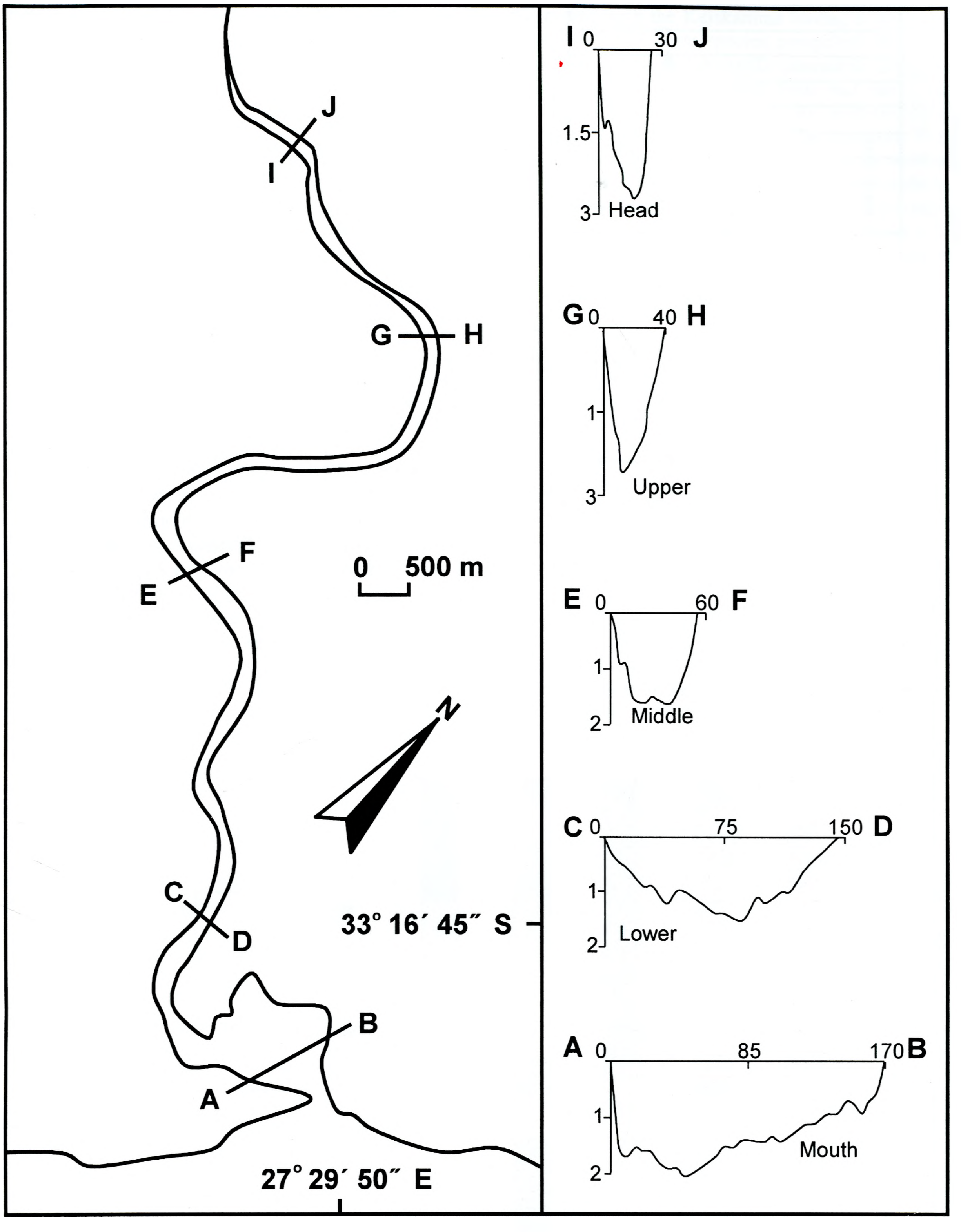

Figure 27: The Keiskamma Estuary, showing the size and shape of the system. The cross-sections indicate depths in the various sections of the estuary (drawn from data collected on the 4th June 1999).

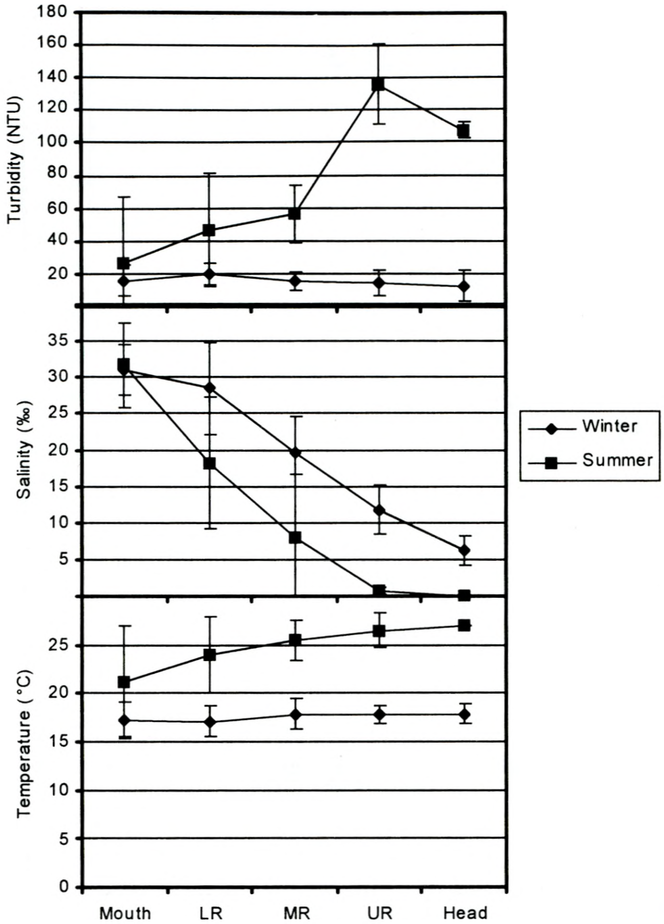

Figure 28: Mean (±S.D.) summer/winter temperature, salinity and turbidity measurements for different localities in the Keiskamma Estuary. The mean was determined from morning and midday samples collected in surface and bottom waters on the 4th June 1999 and the 11th February 2000.

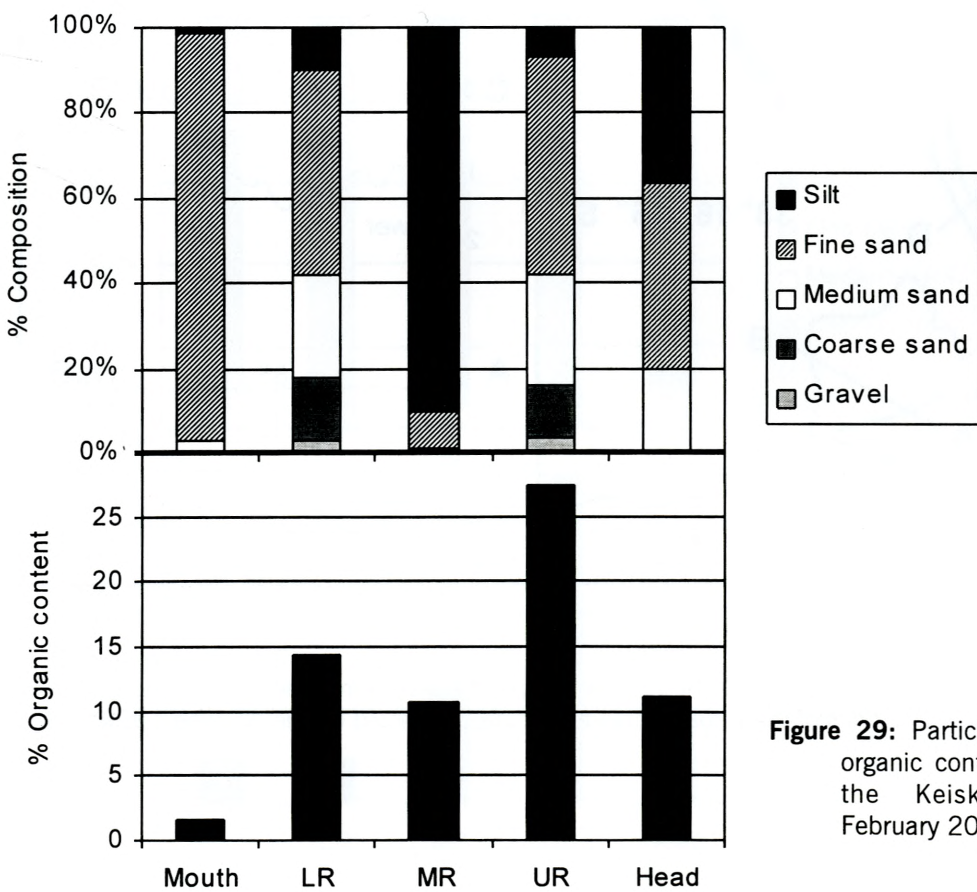

Figure 29: Particle size composition and organic content of the sediments in the Keiskamma Estuary (9th February 2000).

percentage organic content of the sediments did not show any general trends, with a peak of 27.4% in the upper reaches, a minimum of 1.7% at the mouth; the remaining samples contained between 10% and 15% organics (Figure 29).

Colloty (2000) found that the macrophyte vegetation of the estuary comprised mainly salt marsh, reed and sedge species, with a collective cover of approximately 112 hectares. In addition there are relatively small stands of submerged macrophytes (total area = 11 ha).

RESULTS

SPECIES COMPOSITION AND DIVERSITY

Species composition

A total of 75533 fish representing 57 species were captured using three gear types in all the estuaries during the study. Seasonal catches combining all the gear types for all the estuaries were similar, with summer and winter totals of 38211 individuals comprising 48 species and 37322 individuals of 47 species respectively (Table 4).

The number of species in each system ranged from eight in the Ngculura to 30 in the Keiskamma and Great Fish estuaries (Table 5). A total of 39 species were recorded during both summer and winter, with only 15 species being restricted to either season, most of which were rare taxa. *Gilchristella aestuaria* (average contribution = 37.8%) and *Atherina breviceps* (average contribution = 31.1%) numerically dominated the catches in all the estuaries (Table 5). Other important species included *Rhabdosargus holubi* (average contribution = 8.8%), *Liza richardsonii* (average contribution = 5.5%), *Glossogobius callidus* (average contribution = 5.1%), *Myxus capensis* (average contribution = 2.7%) and *Mugil cephalus* (average contribution = 1.3%).

Richness and diversity indices

The permanently open systems (Keiskamma and Great Fish) had the greatest richness index values in terms of seine netting (11.9 and 15.8 respectively) and a combination of seine and gill netting (14.3 and 16.4) (Table 6). In terms of gill netting, the Great Fish had the lowest richness (5.45), while the Keiskamma maintained a high richness (14.3). The Margalef index calculated for the communities correlated significantly with the linear length of each estuary when the gears were combined (r_s=0.91; p<0.001) and when analysing seine net results independently (r_s=0.91; p<0.001) (Figure 32). Other physical characteristics of each estuary that increased proportionally with richness (seine and gill net data combined) were the catchment size (r_s=0.71; p<0.02), mean annual run-off (r_s=0.79; p<0.02) and estuarine area (r_s=0.94; p<0.001). Similarly, the trends in richness from the seine net data correlated with these physical characteristics, except for a slightly higher correlation for the mean annual run-off (r_s=0.84; p<0.005).

The Shannon-Wiener index did not show any trends relative to the physical characteristics of the estuaries. The two open estuaries had very different diversities, with the Keiskamma having a much lower diversity (0.51). Nine species comprised 90% of the catch, of which *Gilchristella aestuaria* contributed 65% (Table 7). The Great Fish had the greatest diversity for the seine net data (0.80), with the smallest temporarily open/closed estuary, the Ngculura, having a similarly high diversity of 0.79. The remaining closed estuaries had relatively low diversity indices in the seine and combined gear results (Table 7). The gill net diversity was relatively high in all systems with only the Great Fish having an index value less than 0.75.

ESTUARINE ASSOCIATION

The permanently open estuaries had more marine and freshwater species than the temporarily closed systems (Figure 30), with the latter recording a higher number of marine species dependent on estuaries (category IIa). Neither the permanently open or temporarily open/closed estuaries conformed to the general trends in overall numbers of species from southern African systems. The estuaries in this study revealed a decrease in number of species from category IIa to III, compared with an increase across these categories in the southern African data (Figure 30).

The abundance of individuals in each estuarine dependence category illustrated different results from the number of species in each category. The estuarine resident species were dominant in all the systems except the small Ngculura Estuary (Figure 31) where the marine migrants *Rhabdosargus holubi, Liza richardsonii* and *Myxus capensis* comprised a major proportion of the total catch (Table 5). The permanently open estuaries had a greater abundance of marine migrants compared with the closed systems, although the large Bira and Mgwalana estuaries had equivalent proportions of marine migrants (Figure 31).

LONGITUDINAL DISTRIBUTION

Analysis on an individual estuary basis provided no strong evidence of longitudinal distributions using either gear type. However, analysis of the seine net composition data when all the estuaries were combined provided some indication of longitudinal trends in fish distribution within the estuaries (Figure 33 and 35). When using multidimensional scaling, a general gradient was apparent in the seine net data (Figure 34) but no trends were found in the gill net data set (Figure 36). The results from a Kruskal-Wallis ANOVA run on the fish densities in the different reaches similarly produced no significant difference from either the large (p=0.19) or small seine data set (p=0.92).

When the seine net fish composition data from the different reaches were tested using ANOSIM, the upper and lower reaches were found to differ significantly (p=0.01), while neither the upper nor lower were significantly different from the middle reaches. The SIMPER routine showed that 50% of the dissimilarity between the upper and lower reaches was accounted for by seven species. These included three estuarine spawning species; *Atherina breviceps*

Table 4. Number of individuals and species caught seasonally and overall by each gear type.

Gear type	Number of individuals	Number of species				
	Summer	Winter	Combined seasons	Summer	Winter	Combined seasons
Small seine	30292	31181	61473	8	13	14
Large seine	7311	5535	12846	35	30	42
Gill net	608	606	1214	20	20	23
Total	38211	37322	75533	48	47	57

(10.3%), *G. aestuaria* (8.8%), *Glossogobius callidus* (6.6%); and four marine species; *R. holubi* (6.8%), *L. richardsonii* (6.4%), *Liza dumerilii* (5.6%) and *M. capensis* (5.4%).

Although on a community basis the three reaches did not separate out, some species (when analysed individually) revealed specific range preferences. *A. breviceps* and *G. aestuaria* demonstrated opposite habitat preferences (Figure 37), with *A. breviceps* dominating the lower reaches and *G. aestuaria* becoming more abundant further upstream. The freshwater *Oreochromis mossambicus* exhibited a preference for the upper reaches with the majority (43%) of the individuals being captured in this region (Figure 38). The catch of *M. capensis*, a catadromous species, was also highest in the upper reaches (Figure 38). In contrast, the dominant marine migrant *R. holubi* showed a relatively uniform distribution throughout the three estuarine reaches (Figure 38).

LENGTH FREQUENCIES

Estuarine resident species

G. aestuaria comprised individuals from a range of size classes in both the permanently open and large closed estuaries (Figure 39). The modal size class in the large closed systems was 25-30 mm compared with 40-45 mm in the permanently open estuaries. The mean size range of 40 mm SL (±8.7 SD) in the open systems was significantly larger ($p<0.001$) than the mean size of 31 mm SL (±8.2 SD) in the closed estuaries. Conversely, the mean size class in each individual system within each estuary type (Figure 40) was similar, with the majority of individuals being approximately 1 year old in the large closed estuaries and 1 year or older in the permanently open estuaries (Figure 39).

The other pelagic estuarine resident, *A. breviceps*, produced a left skewed size class distribution in the large closed estuaries and a bimodal distribution in the permanently open estuaries (Figure 41). The modal size class in the large closed systems was 25-30 mm and in the permanently open estuaries the two peaks included the 30-35 mm and 55-60 mm size classes. There was very little mean size class variation between individual systems within each estuary type (Figure 42). When comparing estuary types, however, there were significant differences ($p<0.001$) with the permanently open estuaries having a mean size of 45 mm SL (±12.2 SD) and the large closed systems having a mean of 34 mm SL (±8.6 SD). There is consequently a large difference in the average age of this species within the different estuary types with the majority of captured individuals in the closed estuaries being less than 1 year and the majority of individuals sampled in the open systems being approximately 1 year or older (Figure 41).

G. callidus length frequency distribution revealed a left skewed distribution in the temporarily open/closed systems, with only six individuals from four size classes recorded in the permanently open estuaries (Figure 43). The modal size class of 35-40 mm in the large closed estuaries coincided with an age of 1 year with very few specimens being above two years of age (Figure 43). There was little variation in the mean length of fish within or between estuary types (Figure 44), with the mean length in the permanently open estuaries being 44 mm SL (±7.8 SD) and the mean for the temporarily open/closed systems being 41 mm SL (±13.8 SD).

A second gobiid species, *P. knysnaensis*, had a similar length frequency distribution in all the estuaries, with a slightly larger modal length in the permanently open systems (Figure 45). The majority of fish in both estuary types were approximately 1 year old. Figure 46 shows the limited differences in mean fish length between the individual systems, which is mirrored by the estuary types with an identical mean of 34 mm SL.

Marine migrant species

The length frequency distribution of *P. commersonnii* was similar in all the estuaries, with smaller size classes predominating (Figure 47). The majority of individuals were between 70 mm and 120 mm in both estuary types. There was a lack of variation in fish size in the individual systems (Figure 48) and between estuary types, with the permanently open systems having a mean fish length of 139 mm SL (±67.3 SD) and the large closed estuaries producing a mean of 145 mm SL (±85.1 SD). However the largest individuals were captured in the closed systems, with a maximum size of 562 mm, compared with 421 mm in the open estuaries.

R. holubi produced a left-skewed distribution in the large temporarily open/closed estuaries with the majority of individuals being under 1 year old (Figure

Table 5. The numerical contribution of each species caught by all three gear types in each of the study estuaries (values expressed as a % of total catch) (* = temporarily open/closed estuary; ** = permanently open estuary).

Family	Species	Common Name	Bira*	East Kleinemonde*	Gqutywa*	Great Fish**	Keiskamma**	Klein Palmiet*	Mgwalana*	Mpekweni*	Mtati*	Ngculura*
Ambassidae	*Ambassis natalensis*	Slender glassy				0.4						
Anguillidae	*Anguilla mossambica*	Longfin eel				0.1						
Ariidae	*Galeichthys feliceps*	White seacatfish				0.1	1.3		<0.1			
Atherinidae	*Atherina breviceps*	Cape silverside	42.0	38.8	79.3	0.2	1.3	56.5	18.5	14.6	43.3	16.1
Carangidae	*Caranx sexfasciatus*	Bigeye kingfish				0.5	0.1		<0.1	<0.1		
	Lichia amia	Leervis		<0.1	0.1		0.3		<0.1	<0.1	<0.1	
Cichlidae	*Oreochromis mossambicus*	Mozambique tilapia	0.4	1.5	<0.1	0.3			2.3	0.8	0.1	0.6
Clariidae	*Clarius gariepinus*	Sharptooth catfish				0.2						
Clinidae	*Clinus superciliosus*	Super klipfish					<0.1					
	Fucomimus mus	Mousey klipfish					<0.1					
Clupeidae	*Gilchristella aestuaria*	Estuarine roundherring	21.6	31.3	7.2	47.0	65.7	29.7	54.0	71.8	41.5	7.8
Cyprinidae	*Barbus aeneus*	Smallmouth yellowfish				0.2						
	Cyprinus carpio	Carp				0.1						
Elopidae	*Elops machnata*	Ladyfish	0.2				0.1		<0.1	<0.1	0.5	
Gerreidae	*Gerres acinaces*	Smallscale pursemouth			<0.1							
Gobiidae	*Caffrogobius gilchristi*	Prison goby				0.7	3.0					
	Caffrogobius natalensis	Baldy	<0.1									
	Caffrogobius nudiceps	Barehead goby	0.3				2.6		0.2			
	Glossogobius callidus	River goby	10.2	10.6	2.6	0.3	<0.1	8.7	4.3	2.2	1.7	10.7
	Oligolepis acutipennis	Sharptail goby				<0.1						
	Oligolepis keiensis	Speartail goby					0.1					
	Psammogobius knysnaensis	Speckled sandgoby	0.2	<0.1	0.2	2.6	0.8		<0.1	<0.1	<0.1	<0.1
Haemulidae	*Pomadasys commersonnii*	Spotted grunter	0.4	0.2	0.3	4.0	3.6		1.6	0.1	0.2	

Table 5. (continued)

Family	Species	Common Name	Bira*	East Kleinemonde*	Gqutywa*	Great Fish**	Keiskamma**	Klein Palmiet*	Mgwalana*	Mpekweni*	Mtati*	Ngculura*
Haemulidae	*Pomadasys olivaceum*	Piggy	0.1		0.3				<0.1			
Hemiramphidae	*Hemiramphus far*	Spotted halfbeak							<0.1			
	Hyporhamphus capensis	Cape halfbeak	<0.1							<0.1	<0.1	
Monodactylidae	*Monodactylus falciformis*	Oval moony	0.8	2.1	<0.1			0.2	0.2	0.7	0.5	0.9
Mugilidae	Juvenile Mugilidae	Juvenile mullet		0.7		0.2						
	Liza dumerilii	Groovy mullet	2.3	1.0	0.4	2.2	2.5		1.3	0.8	2.6	0.2
	Liza macrolepis	Largescale mullet	<0.1									
	Liza richardsonii	Southern mullet	1.9	1.3	1.0	19.1	5.5	0.9	1.2	0.2	2.2	21.4
	Liza tricuspidens	Striped mullet	<0.1	0.1	0.2	0.4	1.0		<0.1	0.2	<0.1	0.3
	Mugil cephalus	Flathead mullet	1.2	0.9	0.2	5.7	2.0	0.3	0.4	0.3	<0.1	2.3
	Myxus capensis	Freshwater mullet	0.5	3.6	<0.1	0.4	1.8		0.5	0.5	1.5	15.0
	Valamugil buchanani	Bluetail mullet					<0.1				<0.1	
	Valamugil cunnesius	Longarm mullet	0.2		<0.1	0.4					<0.1	
Notocheiridae	*Iso natalensis*	Surf sprite					0.3					
Pomatomidae	*Pomatomus saltatrix*	Elf	<0.1		0.9				<0.1	<0.1		
Sciaenidae	*Argyrosomus japonicus*	Dusky kob	0.2		0.1	1.3	3.4		0.4	0.1	0.2	
	Johnius dorsalis	Small kob					<0.1					
Serranidae	*Epinephelus andersoni*	Catface rockcod					<0.1					
Soleidae	*Heteromycteris capensis*	Cape sole		<0.1	0.4	1.0	<0.1		<0.1	<0.1	<0.1	<0.1
	Solea bleekeri	Blackhand sole	<0.1	<0.1	0.5	6.8	0.7		0.3	0.2	<0.1	
Sparidae	*Acanthopagrus berda*	Estuarine bream	<0.1			0.2	0.1			0.1		
	Diplodus cervinus	Zebra	<0.1									
	Diplodus sargus	Blacktail	<0.1									
	Lithognathus lithognathus	White steenbras		1.8	0.4	2.0	<0.1	2.2	0.2	0.3	0.1	0.1
	Rhabdosargus globiceps	White stumpnose	<0.1		<0.1							

Table 5. (continued)

Family	Species	Common Name	Bira*	East Kleinemonde*	Gqutywa*	Great Fish**	Keiskamma**	Klein Palmiet*	Mgwalana*	Mpekweni*	Mtati*	Ngculura*
Sparidae	*Rhabdosargus holubi*	Cape stumpnose	17.2	6.0	5.7	3.3	3.4	1.6	14.3	7.0	5.4	24.4
	Rhabdosargus sarba	Tropical stumpnose							<0.1	<0.1		
	Rhabdosargus thorpei	Bigeye stumpnose							<0.1			
	Sarpa salpa	Strepie	<0.1									
Syngnathidae	*Syngnathus acus*	Longsnout pipefish		<0.1	<0.1	<0.1	<0.1		<0.1	<0.1	<0.1	
	Syngnathus watermeyeri	Estuarine pipefish		0.1								
Teraponidae	*Terapon jarbua*	Thornfish			<0.1				<0.1		<0.1	
Tetraodontidae	*Amblyrhynchotes honckenii*	Evileye puffer				0.3						
Torpedinidae	*Torpedo fuscomaculata*	Blackspotted electric ray	<0.1									
		Total Individuals	10448	5615	7962	1257	2952	1534	10891	19768	12729	2377
		Total Species	29	20	25	30	30	8	29	25	24	14

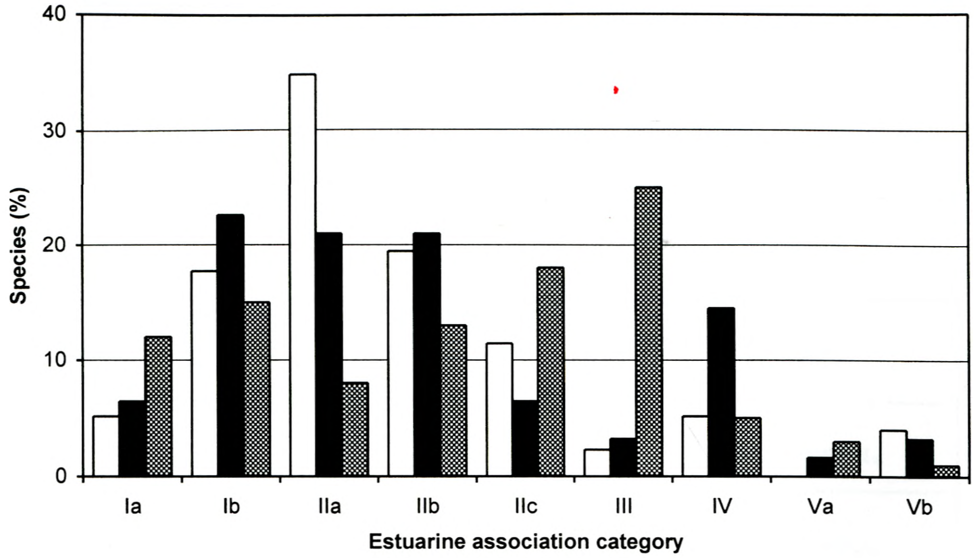

Figure 30: The percentage of species in each estuarine association category for temporarily open/closed estuaries in this study (clear bars), permanently open systems in this study (solid bars) and southern African estuaries in general (stippled bars). The southern African data was obtained from Whitfield (1998).

49). Similarly, in the open systems most fish were less than 1 year of age, with a slightly more condensed length frequency distribution of individuals recorded. Very little variation was evident in the mean *R. holubi* lengths between individual estuaries of the same type (Figure 50), yet a significant difference ($p<0.005$) between estuary types was calculated using the Kolmogorov-Smirnov test. The mean length in the open systems was 75 mm SL (±17.3 SD) and in the closed estuaries was 78 mm SL (±19.4 SD). The maximum sized individuals in the closed systems (222 mm SL) were considerably larger than those in the open estuaries (165 mm SL).

For *L. dumerilii* a slightly left-skewed distribution was evident in the large closed estuaries compared with a much stronger left-skewed plot in the permanently open systems (Figure 51). Thirty-three percent of the individuals in the closed estuaries were below 1 year of age compared with 70% of individuals in the permanently open systems. Minimal differences were evident when comparing individual systems within each estuary type (Figure 52). However, the length frequency of *L. dumerilii* in the permanently open estuaries was calculated to be significantly smaller ($p<0.001$) than those in the large closed systems. This was evident in the mean fish length of 105 mm SL (±44.9 SD) for open estuaries and 137 mm SL (±36.3 SD) in closed estuaries.

Similar length frequency distributions were produced for the other important mugilid species, *L. richardsonii* (Figure 53). In the large temporarily open/closed estuaries, most individuals were 1-2 years old, whereas in the permanently open systems most individuals were less than 1 year of age. The open systems contained significantly smaller individuals ($p<0.001$) with a mean size of 118 mm SL (±54.6 SD) compared with *L. richardsonii* in the closed estuaries with a mean of 142 mm SL (±42.0 SD). The variation between different systems within the large closed estuary type was relatively small, with the two open systems showing increased differences in both mean size and ranges (Figure 54).

DISCUSSION

SPECIES COMPOSITION AND DIVERSITY

Seasonal differentiation

The lack of seasonal differentiation in the number of individuals caught during this study is surprising, as several authors (e.g. Bennett, 1989; Harrison & Whitfield, 1995) have described large seasonal variations in estuarine ichthyofaunal densities. Similarly, the number of species in estuaries reportedly varies seasonally (Harrison & Whitfield, 1995), but this was not evident during this study. The lack of seasonal variation in temporarily closed estuaries may be due to the mouth status of these systems (predominantly closed during the study period), preventing large immigrations or emigrations of species. Conversely, the permanently open systems retained a connection to the sea for the duration of the study, allowing species to move freely.

Species composition

Two species, *G. aestuaria* and *A. breviceps*, numerically dominated the catches (more than 60% of the catch) in every estuary except the Ngculura and the Great Fish (Table 5). These planktivorous fishes are both estuarine residents, completing their entire lifecycles within estuaries (Whitfield, 1996). To avoid competition these species undergo spatial segregation (Harrison & Whitfield, 1995; Cowley & Whitfield, 2001), with *A. breviceps* densities dropping fourfold from the lower to the upper reaches and *G. aestuaria*

Table 6. Calculated Margalef's species richness index for fish data from seine netting, gill netting and a combination of these gears in each estuary (gill nets were not used in the Klein Palmiet).

System	Seine	Gill	Combined
Keiskamma	11.90	14.30	14.30
Ngculura	4.71	11.30	5.49
Gqutywa	6.99	11.20	8.04
Bira	8.41	12.40	9.22
Mgwalana	9.19	9.48	9.63
Mtati	7.02	12.10	8.15
Mpekweni	7.62	15.10	7.98
Great Fish	15.80	5.45	16.40
Klein Palmiet	2.43	N/A	N/A
East Kleinemonde	6.16	7.06	6.22

Table 7. The calculated Shannon-Wiener diversity index for fish data from seine netting, gill netting and a combination of these gears in each estuary (gill nets were not used in the Klein Palmiet).

System	Seine	Gill	Combined
Keiskamma	0.56	0.91	0.51
Ngculura	0.79	0.77	0.83
Gqutywa	0.38	0.95	0.33
Bira	0.62	0.91	0.57
Mgwalana	0.55	0.95	0.50
Mtati	0.55	0.82	0.49
Mpekweni	0.38	0.97	0.33
Great Fish	0.80	0.36	0.75
Klein Palmiet	0.48	N/A	N/A
East Kleinemonde	0.76	0.79	0.72

densities increasing twofold in the same direction (Figure 36). Cowley & Whitfield (2001) found an identical trend in the East Kleinemonde Estuary, with other authors identifying similar distribution patterns for *G. aestuaria* (Harrison & Whitfield, 1995). Whitfield (1980a) identified the converse distribution of *G. aestuaria* in the Mhlanga Estuary in Kwazulu-Natal, with the highest densities occurring in the lower reaches and the numbers decreasing further upstream. This may be due to the lack of *A. breviceps* in the Mhlanga Estuary, thus opening up the lower reaches to colonisation by *G. aestuaria*.

The third most dominant species was *R. holubi*, representing between 5% and 25% of the overall catch in all the estuaries except the permanently open systems and the Klein Palmiet (Table 5). The large *R. holubi* populations may be attributed to this species being able to recruit during marine overwash conditions (Cowley et al., 2001) and hence may have growing populations in closed estuaries. This species was unique in its universal distribution through the different reaches of the estuaries, with approximately 33% in each reach (Figure 38). These distributions are similar to those recorded by several authors for this species (Hanekom & Baird, 1984; Whitfield et al., 1989).

R. holubi has also been reported to associate with submerged macrophyte beds (Hanekom and Baird, 1984; Whitfield et al., 1989), yet in the three systems in this study where *R. holubi* predominated, the Mgwalana (14.3%), the Bira (17.2%) and the Ngculura (24.4%), very low macrophyte densities were reported

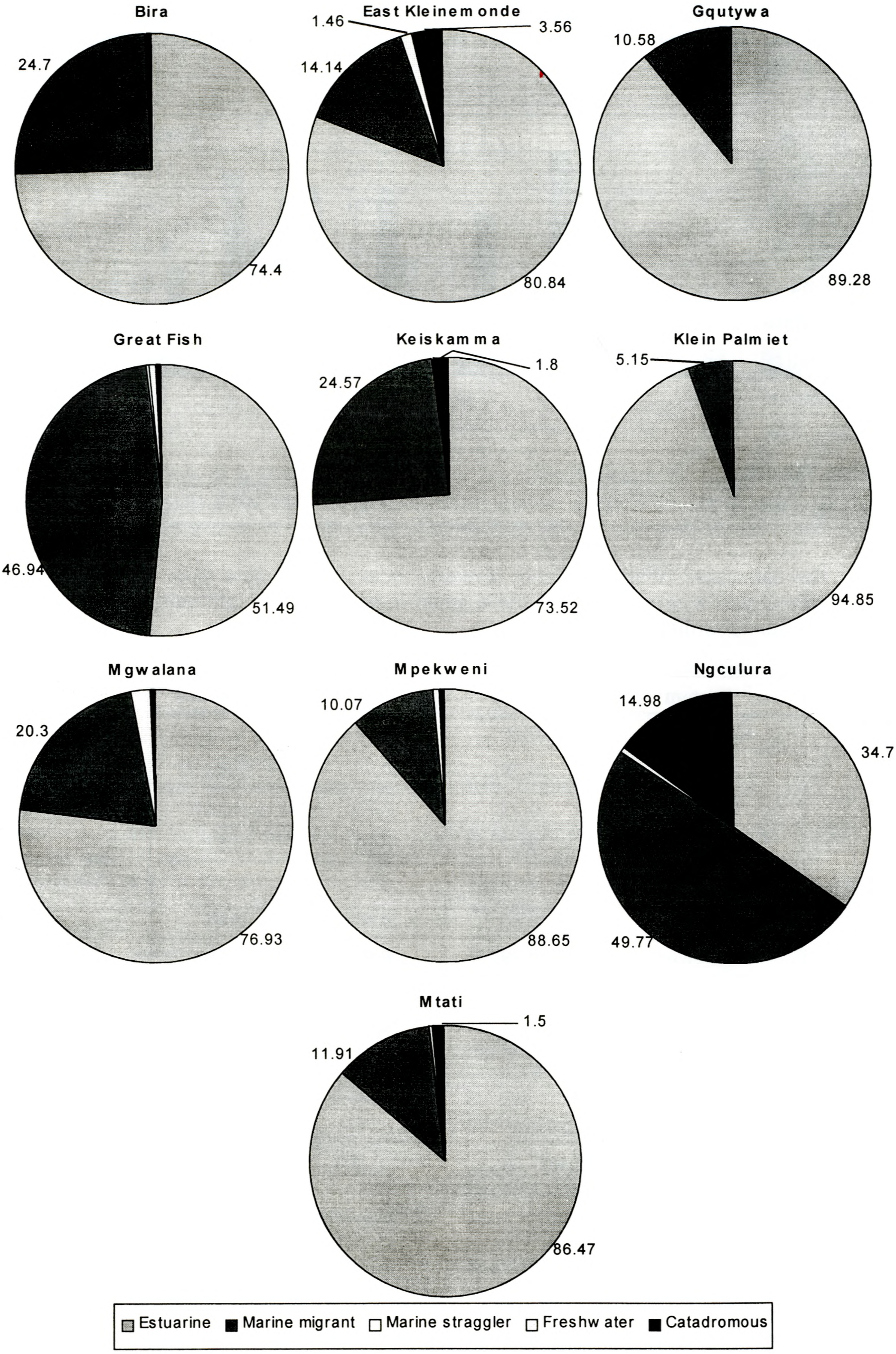

Figure 31: The percentage abundance of estuarine resident, marine migrant, marine straggler, freshwater migrant and catadromous migrant fish populations in each estuary.

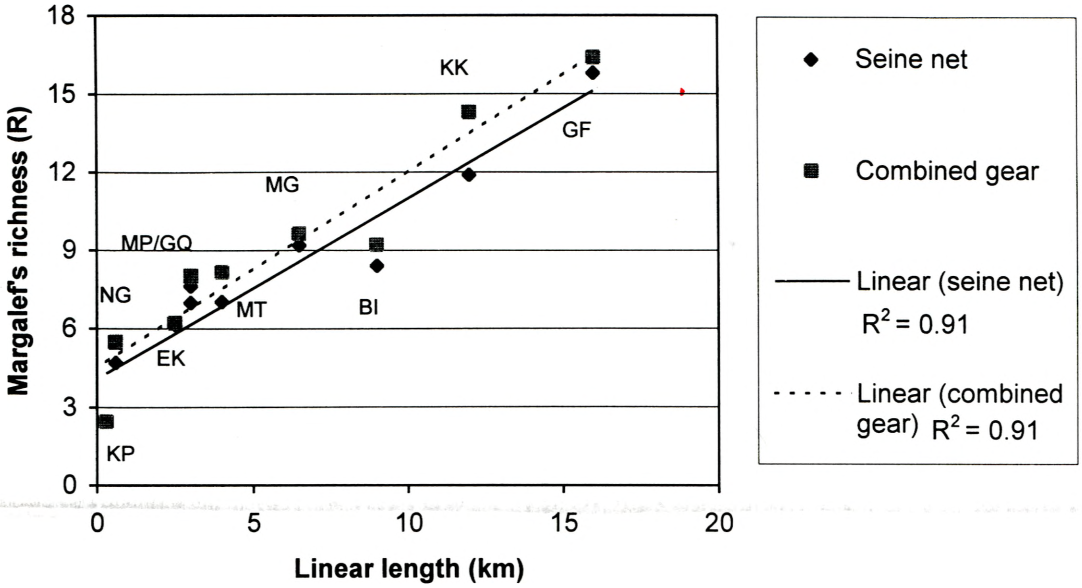

Figure 32: A plot of the linear length of the study estuaries versus the calculated Margalef's species richness index for each system. Each estuary is labelled using a two letter code (BI=Bira, EK=East Kleinemonde, GF=Great Fish, GQ=Gqutywa, KK=Keiskamma, KP=Klein Palmiet, MG=Mgwalana, MP=Mpekweni, MT=Mtati, NG=Ngculura).

(Colloty, 2000). Similar results have been recorded in the mouth area of the East Kleinemonde, where there were very low macrophyte densities but high *R. holubi* abundance (Cowley, 1998). However, where large catches of *R. holubi* were made away from macrophyte beds in the East Kleinemonde, Cowley & Whitfield (2001) noted the presence of thick filamentous algal mats.

Blaber (1985) commented that the mugilids are probably the most abundant family of marine fishes in south-east African estuaries. The mugilids were found to represent a minimum of 5% of the catch in all the systems except the Gqutywa, Klein Palmiet, Mgwalana and Mpekweni (Table 5). Of the eight mugilid species captured during this study *L. richardsonii* and *M. capensis* were the most common (Table 4). *M. capensis* is a catadromous fish whose overall distribution was highest in the upper reaches, with a decline in density in the middle reaches, and an increase again near the mouth (Figure 38). Most authors have reported a linear trend for this species, increasing from lower to upper reaches (Whitfield et al., 1994; Cowley & Whitfield, 2001). The relatively high numbers in the lower reaches of closed estuaries during this study may be due to some individuals awaiting an opportunity to migrate out to sea to breed.

The dominant freshwater species in the study area, *O. mossambicus*, demonstrated an increasing linear trend from the lower reaches to the upper reaches (Figure 37). Whitfield & Blaber (1979) related the distribution of this species within estuaries to several factors including salinity stability, slow water currents, suitable breeding areas, marginal vegetation and the absence of marine competitors and piscivores. These authors remarked that this species would occur where four of these factors were favourable, and be abundant if more than four factors were optimal. The increasing abundance of this species further upstream during this study, may be due to the increasing number of favourable factors, e.g. fewer piscivorous predators and marine competitors, slower water currents, more stable salinities and an increase in the marginal vegetation.

Richness and diversity

The dominance by a few species (e.g. *A. breviceps* and *G. aestuaria*) in the overall catch (all gear types), resulted in relatively low Shannon-Wiener diversity indices for the majority of estuaries (Table 7). Two of the closed systems, the Ngculura and East Kleinemonde, had higher diversities (0.83 and 0.72 respectively) as greater proportions of species contributed >5% of the catch. Although *G. aestuaria* accounted for nearly 50% of the catch in the Great Fish, eight other species contributed between 2% and 19%, thus accounting for a relatively high richness (0.75).

Similar trends were evident in the seine net fish diversity, with the Ngculura (0.79), East Kleinemonde (0.76) and Great Fish (0.80) having the highest overall diversities (Table 7). The fish diversity in the gill nets was high in most systems due to the relatively low densities and high species numbers normally caught by this gear. The low diversity in the Great Fish was possibly due to this estuary producing very poor gill net catches in terms of both fish densities and species numbers. These low species numbers in the Great Fish gill nets were reflected by the low species richness (5.45) for gill netting in this system (Table 6). The gill net catches in the remaining estuaries, except for the

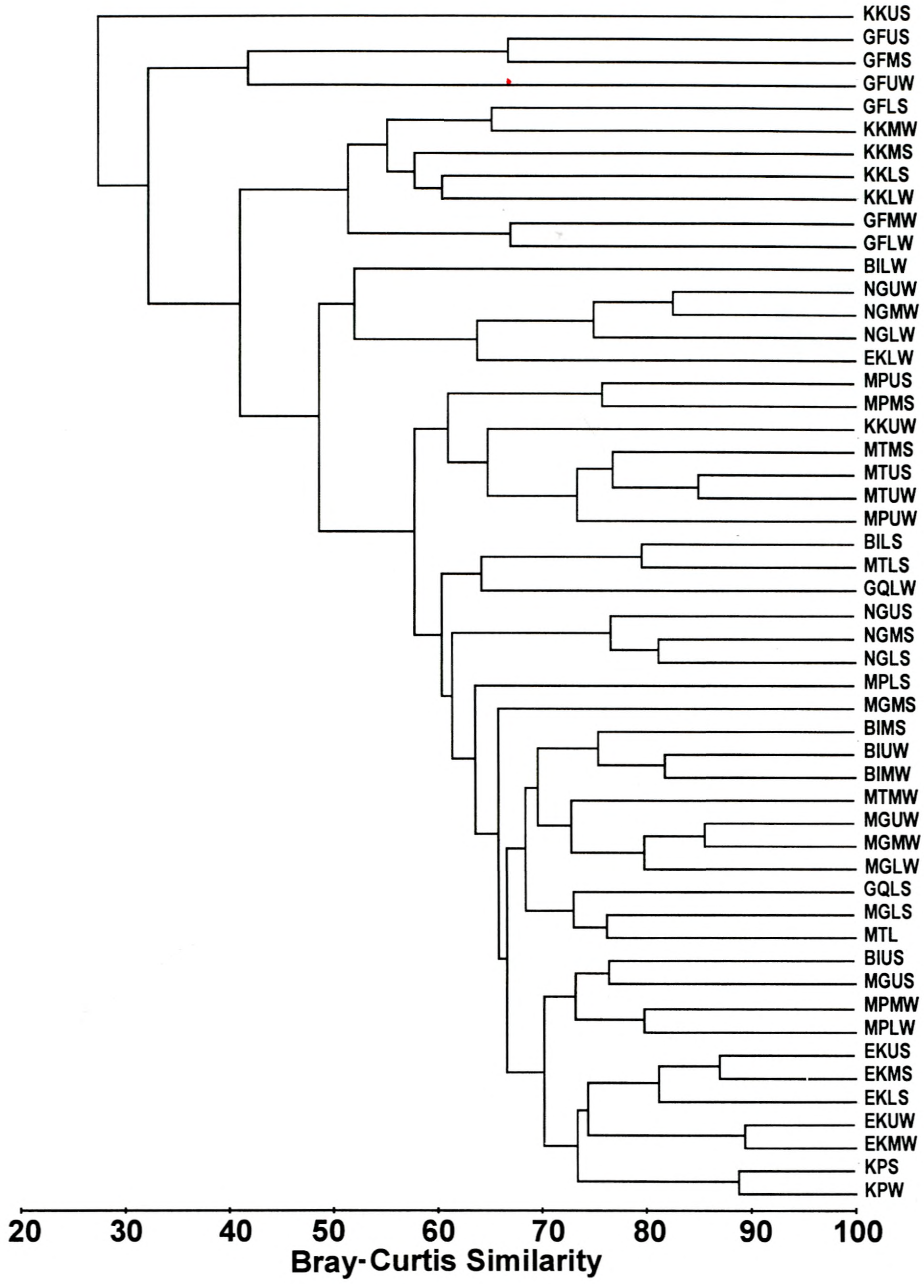

Figure 33: Similarity dendrogram of the combined small and large seine CPUE (catch per unit effort) based composition per reach per season. Each sample is represented by a four letter code; the first two letters are an estuary code (BI=Bira, EK=East Kleinemonde, GF=Great Fish, GQ=Gqutywa, KK=Keiskamma, KP=Klein Palmiet, MG=Mgwalana, MP=Mpekweni, MT=Mtati, NG=Ngculura), the third a reach code (L=Lower Reach, M=Middle Reach, U=Upper Reach) and the fourth a season code (S=Summer, W=Winter).

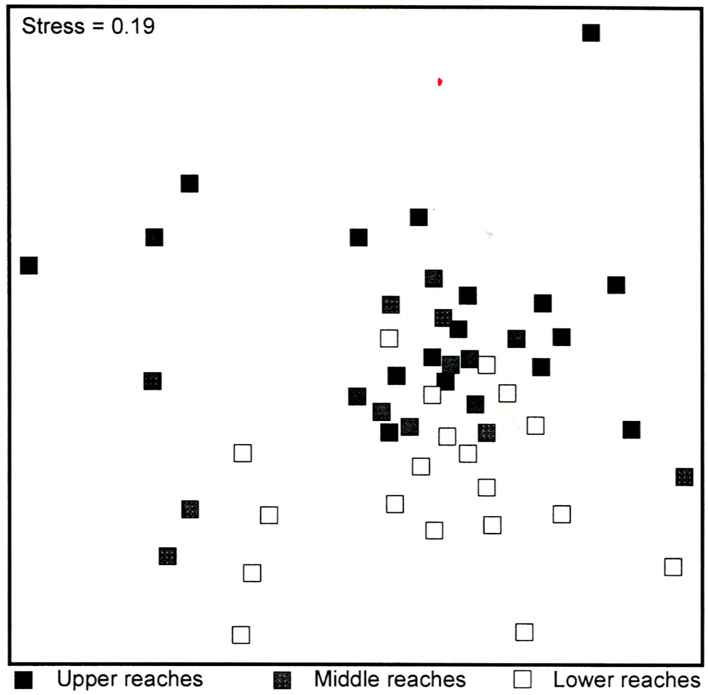

Figure 34: A two dimensional MDS plot of the seine net data points from Figure 33. The axes are arbitrary.

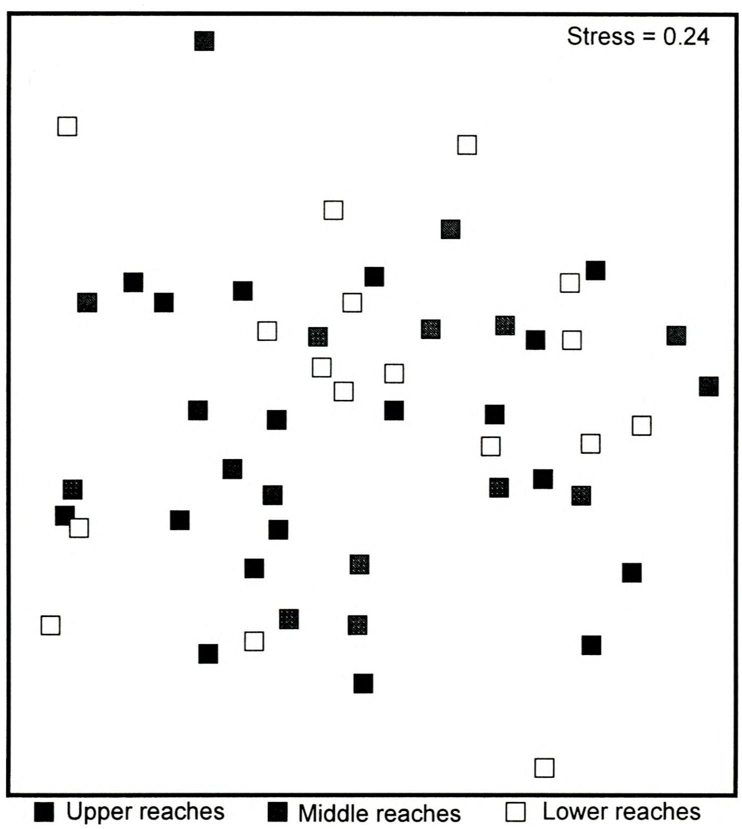

Figure 36: A two dimensional MDS plot of the gill net data points from Figure 35. The axes are arbitrary.

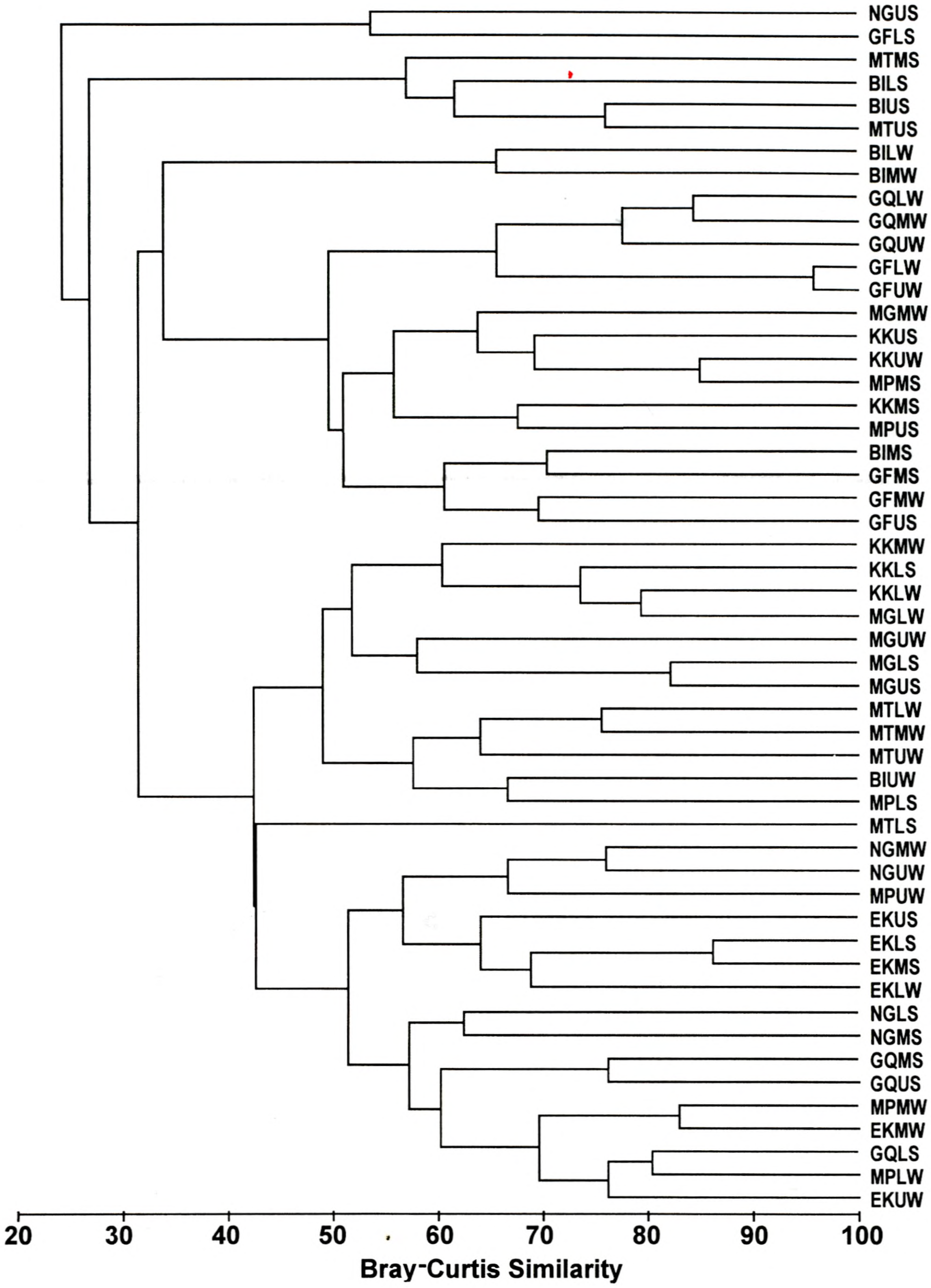

Figure 35: Similarity dendrogram of the gill net catch per unit effort (CPUE) based composition per reach per season. Each sample is represented by a four letter code, the first two letters are an estuary code (BI=Bira, EK=East Kleinemonde, GF=Great Fish, GQ=Gqutywa, KK=Keiskamma, KP=Klein Palmiet, MG=Mgwalana, MP=Mpekweni, MT=Mtati, NG=Ngculura), the third a reach code (L=Lower Reach, M=Middle Reach, U=Upper Reach) and the fourth a season code (S=Summer, W=Winter).

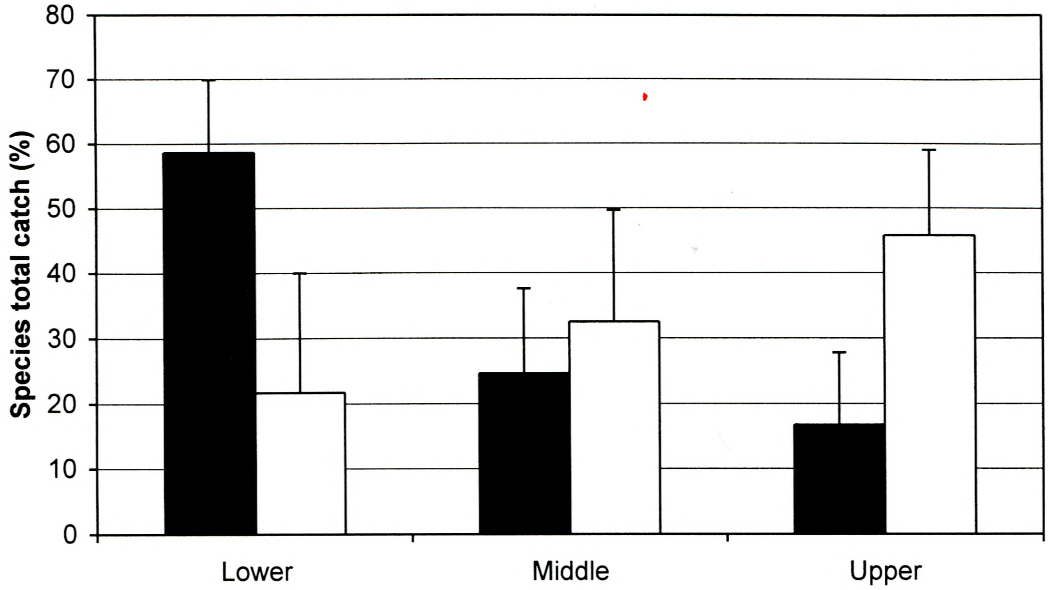

Figure 37: The longitudinal distribution (+SD) of *Atherina breviceps* (solid bars) and *Gilchristella aestuaria* (clear bars) from all the estuaries sampled, presented as a percentage of the total catch of each species for all estuaries combined.

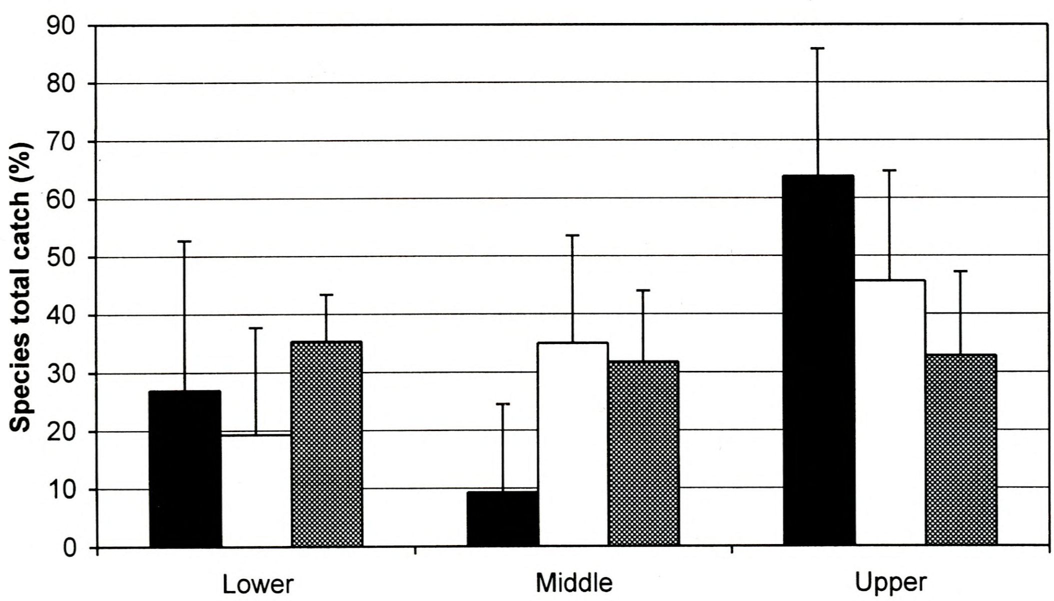

Figure 38: The longitudinal distribution (+SD) of *Myxus capensis* (solid bars), *Oreochromis mossambicus* (clear bars) and *Rhabdosargus holubi* (stippled bars) from all the estuaries sampled, presented as a percentage of the total catch of each species for all estuaries combined.

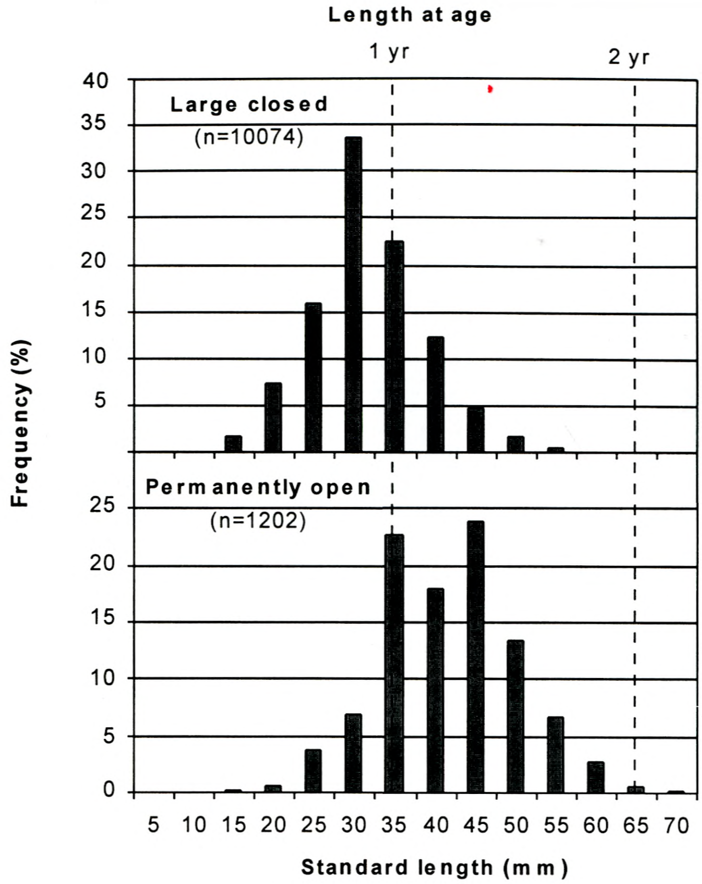

Figure 39: The length-frequency histograms for *Gilchristella aestuaria* in the large temporarily closed and permanently open systems. Length at age estimates after Talbot (1982).

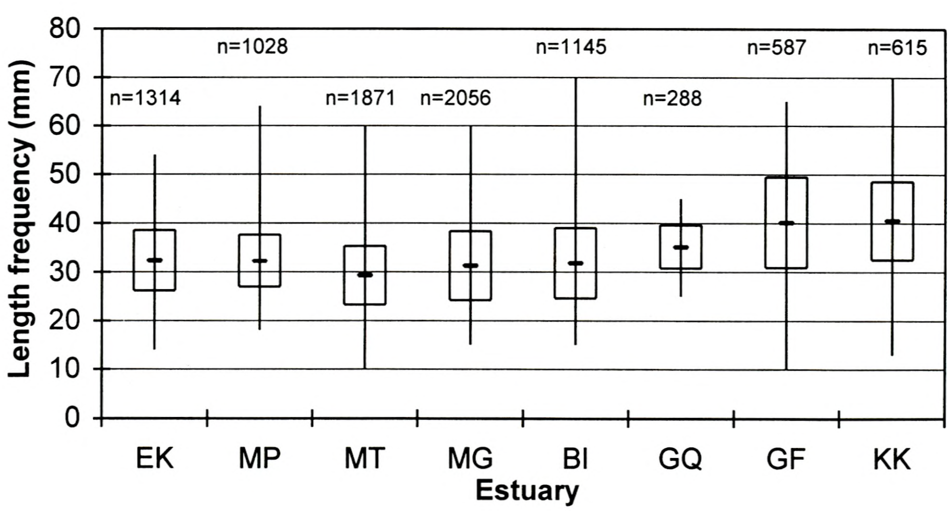

Figure 40: The mean (horizontal lines), standard deviation (clear bars) and range (vertical lines) of the lengths of *Gilchristella aestuaria* in each estuary. The number of fish measured (n) for each system is also shown. Each estuary is represented by a two letter code: EK=East Kleinemonde, MP=Mpekweni, MT=Mtati, MG=Mgwalana, BI=Bira, GQ=Gqutywa, GF=Great Fish and KK=Keiskamma.

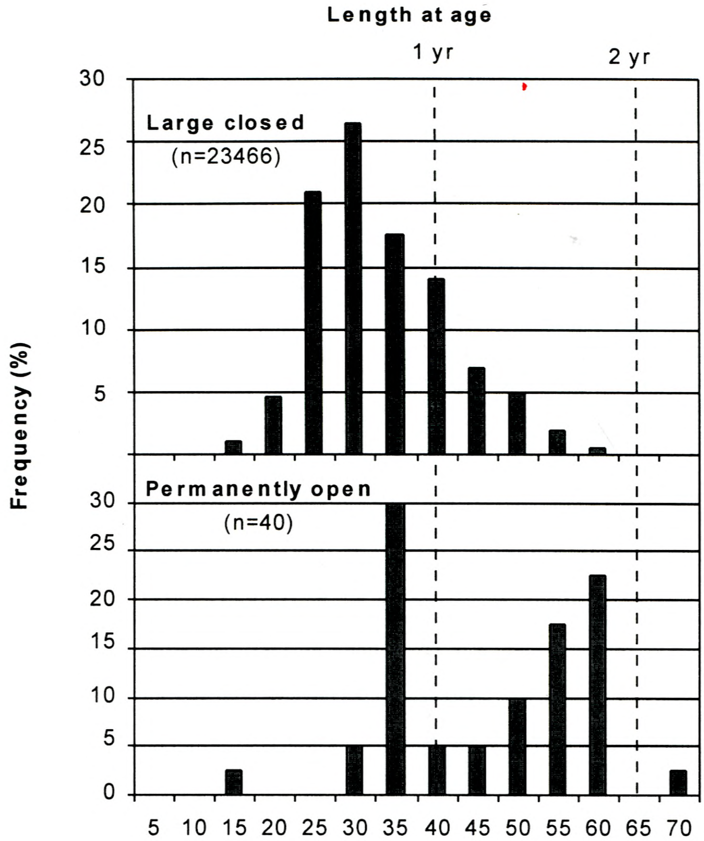

Figure 41: The length-frequency histograms for *Atherina breviceps* in the large temporarily closed and permanently open systems. Length at age estimates after Ratte (1989).

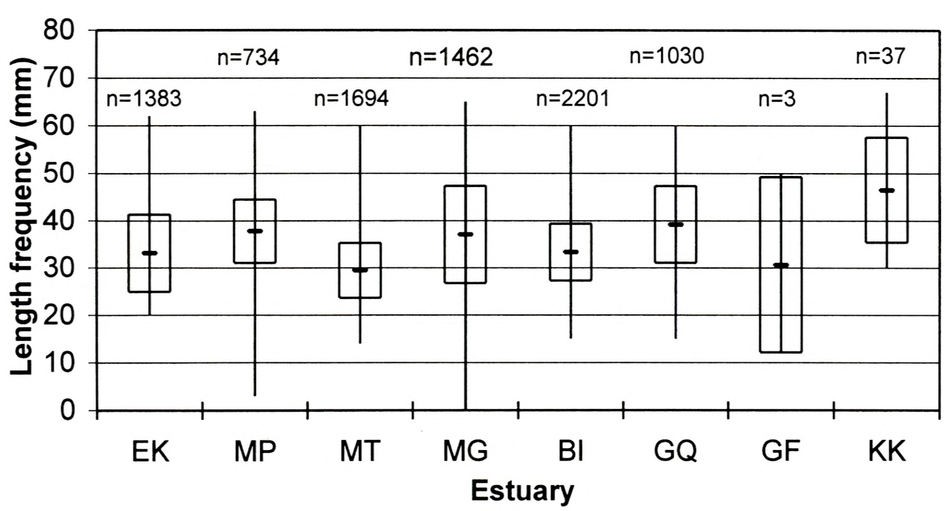

Figure 42: The mean (horizontal lines), standard deviation (clear bars) and range (vertical lines) of the lengths of *Atherina breviceps* in each estuary. The number of fish measured (n) for each system is also shown. Each estuary is represented by a two letter code: EK=East Kleinemonde, MP=Mpekweni, MT=Mtati, MG=Mgwalana, BI=Bira, GQ=Gqutywa, GF=Great Fish and KK=Keiskamma.

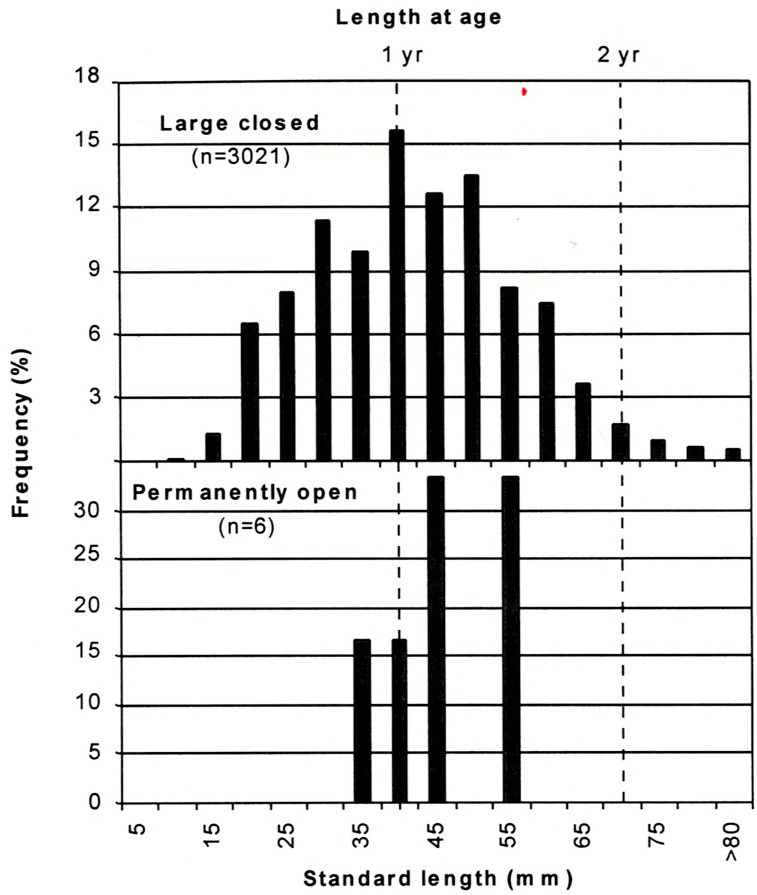

Figure 43: The length-frequency histograms for *Glossogobius callidus* in the large temporarily closed and permanently open systems. Length at age estimates after Boullé (1989).

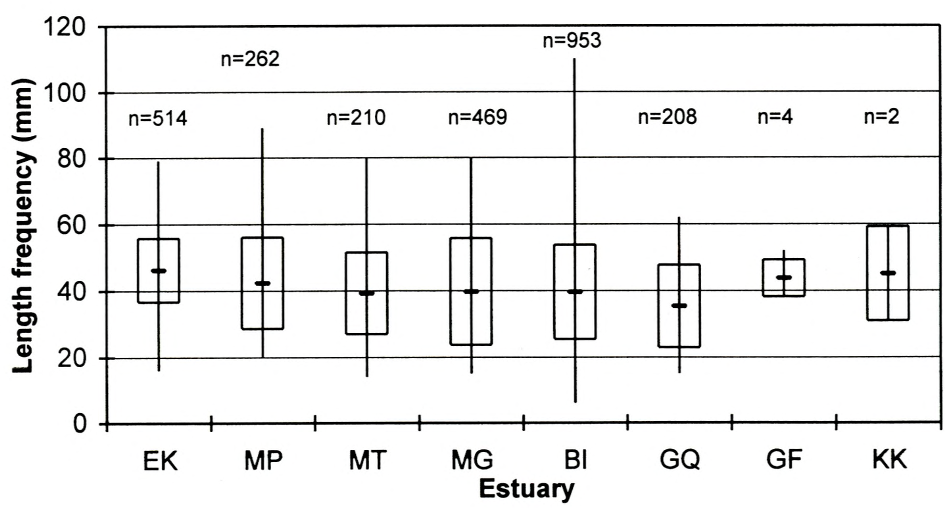

Figure 44: The mean (horizontal lines), standard deviation (clear bars) and range (vertical lines) of the lengths of *Glossogobius callidus* in each estuary. The number of fish measured (n) for each system is also shown. Each estuary is represented by a two letter code: EK=East Kleinemonde, MP=Mpekweni, MT=Mtati, MG=Mgwalana, BI=Bira, GQ=Gqutywa, GF=Great Fish and KK=Keiskamma.

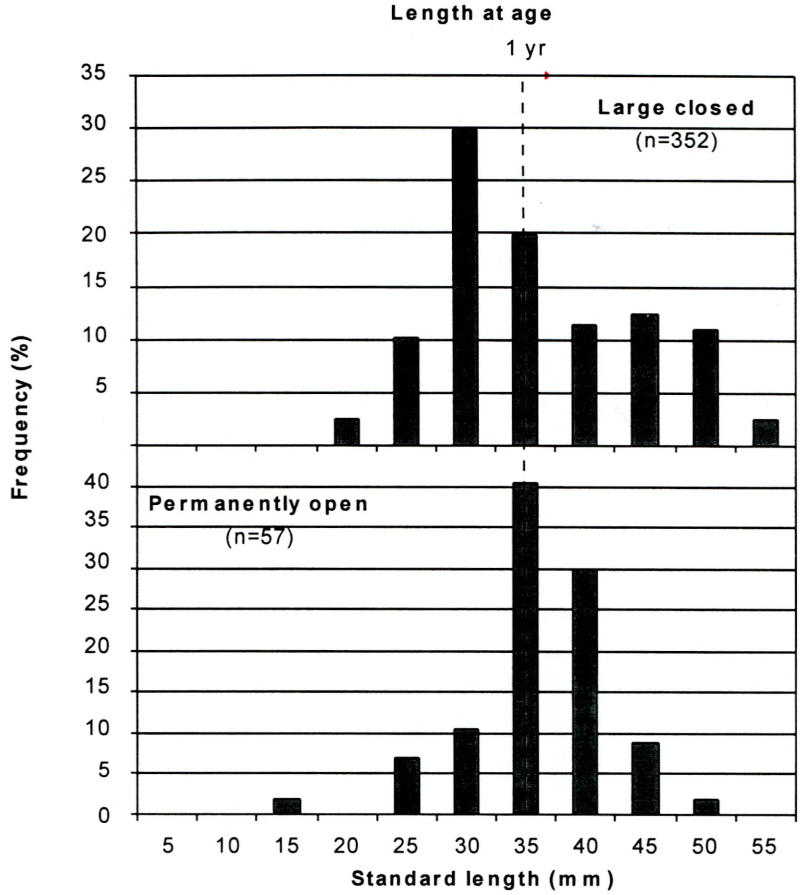

Figure 45: The length-frequency histograms for *Psammogobius knysnaensis* in the large temporarily closed and permanently open systems. Length at age estimates after Bennett (1989).

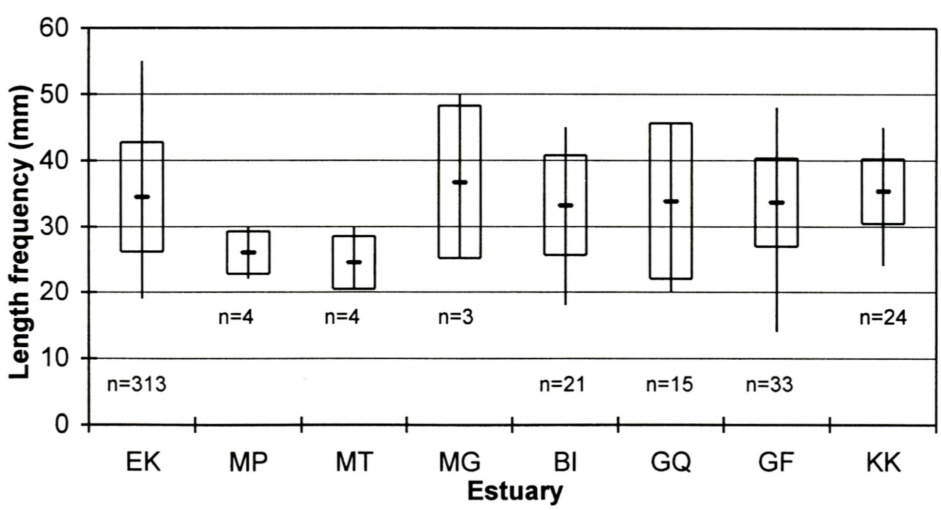

Figure 46: The mean (horizontal lines), standard deviation (clear bars) and range (vertical lines) of the lengths of *Psammogobius knysnaensis* in each estuary. The number of fish measured (n) for each system is also shown. Each estuary is represented by a two letter code: EK=East Kleinemonde, MP=Mpekweni, MT=Mtati, MG=Mgwalana, BI=Bira, GQ=Gqutywa, GF=Great Fish and KK=Keiskamma.

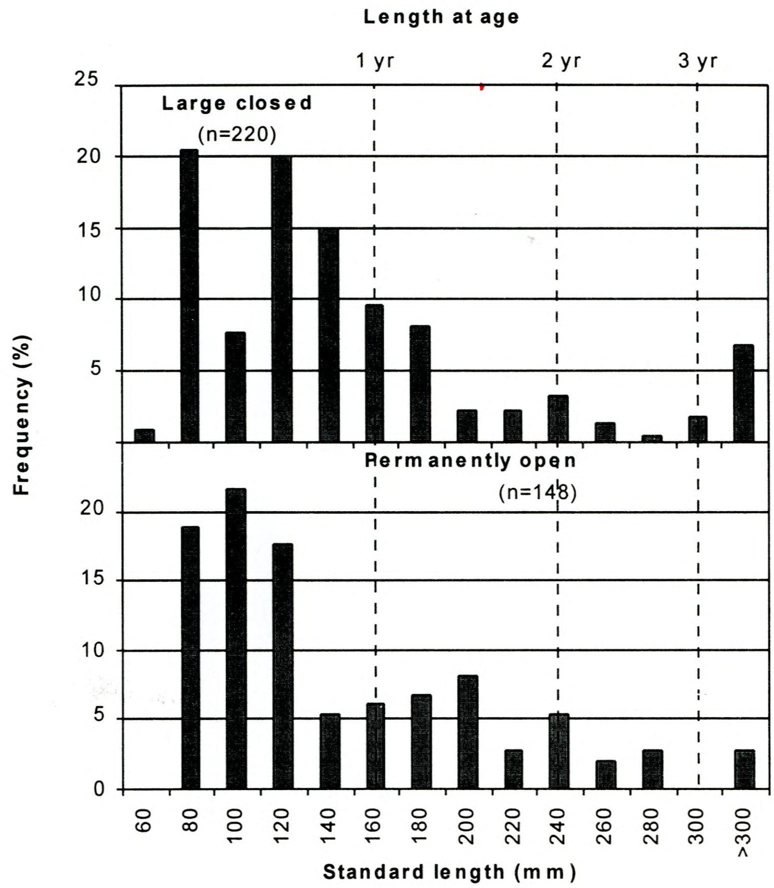

Figure 47: The length-frequency histograms for *Pomadasys commersonnii* in the large temporarily closed and permanently open systems. Length at age estimates after Wallace (1975b).

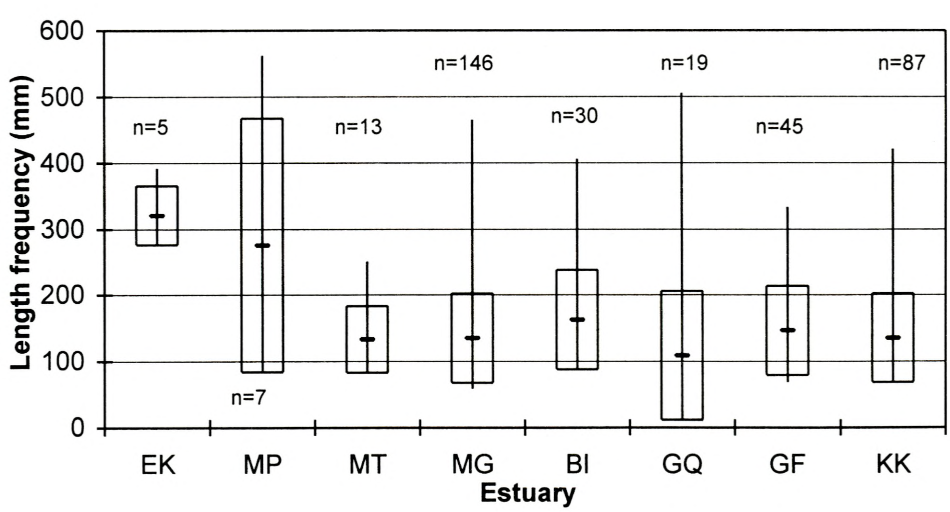

Figure 48: The mean (horizontal lines), standard deviation (clear bars) and range (vertical lines) of the lengths of *Pomadasys commersonnii* in each estuary. The number of fish measured (n) for each system is also shown. Each estuary is represented by a two letter code: EK=East Kleinemonde, MP=Mpekweni, MT=Mtati, MG=Mgwalana, BI=Bira, GQ=Gqutywa, GF=Great Fish and KK=Keiskamma.

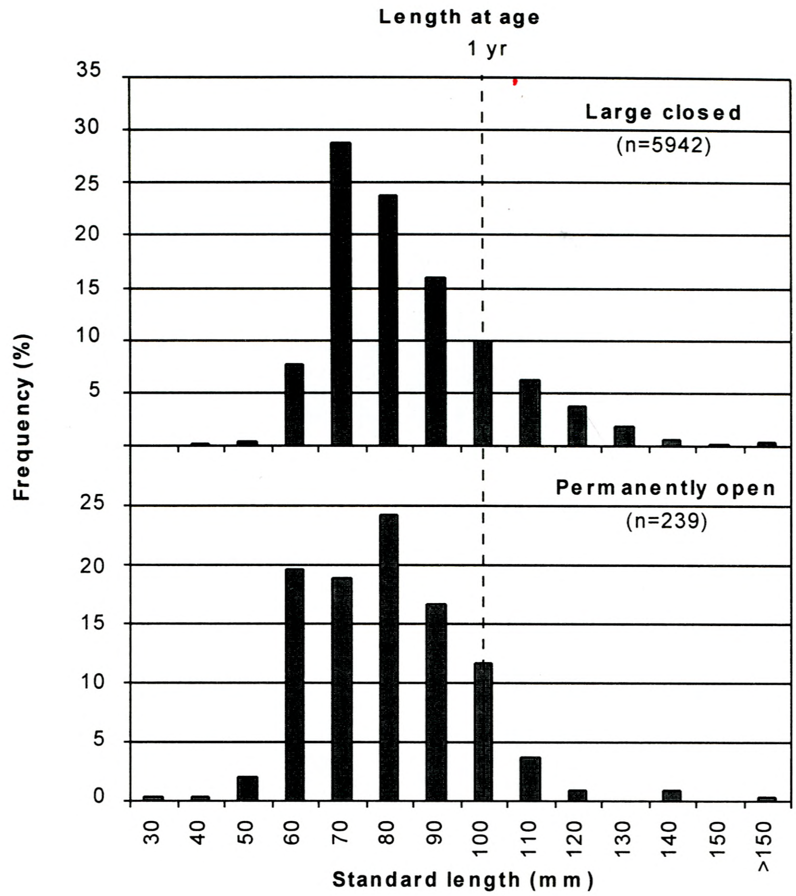

Figure 49: The length-frequency histograms for *Rhabdosargus holubi* in the large temporarily closed and permanently open systems. Length at age estimates after Blaber (1974).

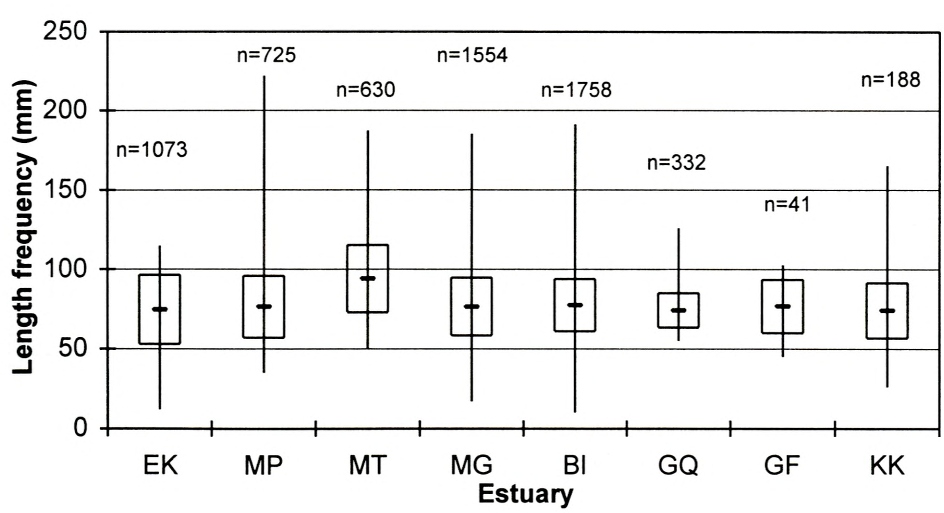

Figure 50: The mean (horizontal lines), standard deviation (clear bars) and range (vertical lines) of the lengths of *Rhabdosargus holubi* in each estuary. The number of fish measured (n) for each system is also shown. Each estuary is represented by a two letter code: EK=East Kleinemonde, MP=Mpekweni, MT=Mtati, MG=Mgwalana, BI=Bira, GQ=Gqutywa, GF=Great Fish and KK=Keiskamma.

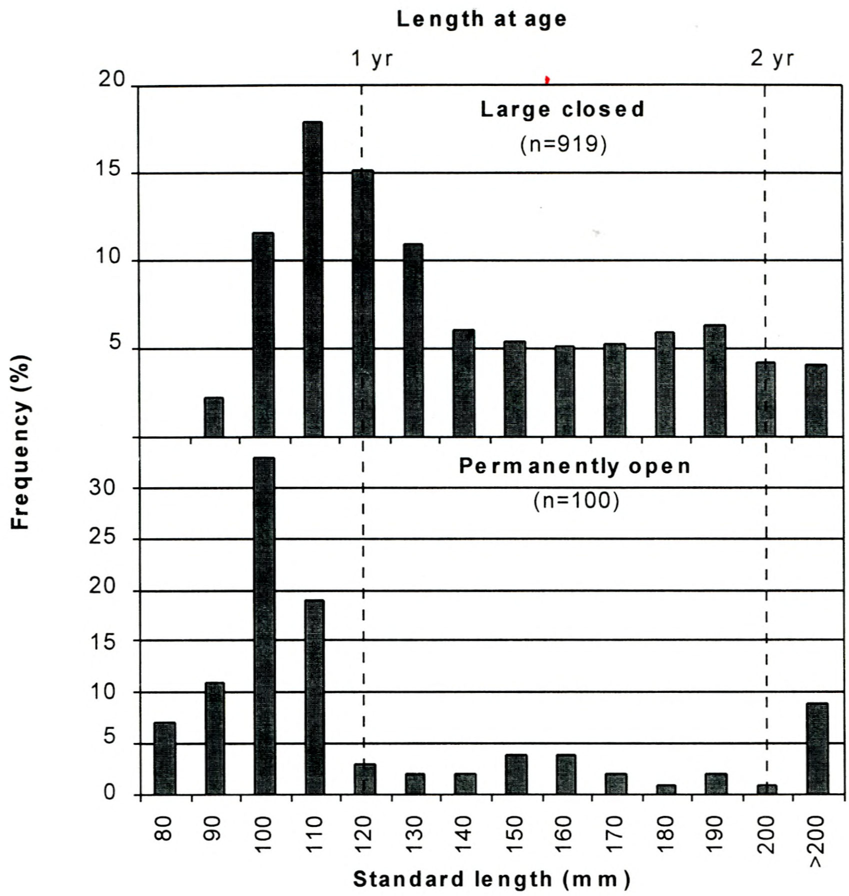

Figure 51: The length-frequency histograms for *Liza dumerilii* in the large temporarily closed and permanently open systems. Length at age estimates after van der Horst and Erasmus (1981).

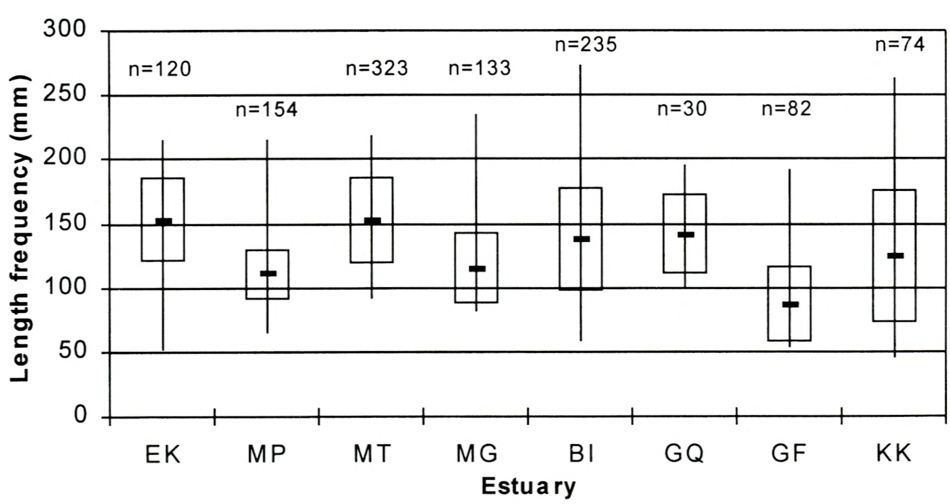

Figure 52: The mean (horizontal lines), standard deviation (clear bars) and range (vertical lines) of the lengths of *Liza dumerilii* in each estuary. The number of fish measured (n) for each system is also shown. Each estuary is represented by a two letter code: EK=East Kleinemonde, MP=Mpekweni, MT=Mtati, MG=Mgwalana, BI=Bira, GQ=Gqutywa, GF=Great Fish and KK=Keiskamma.

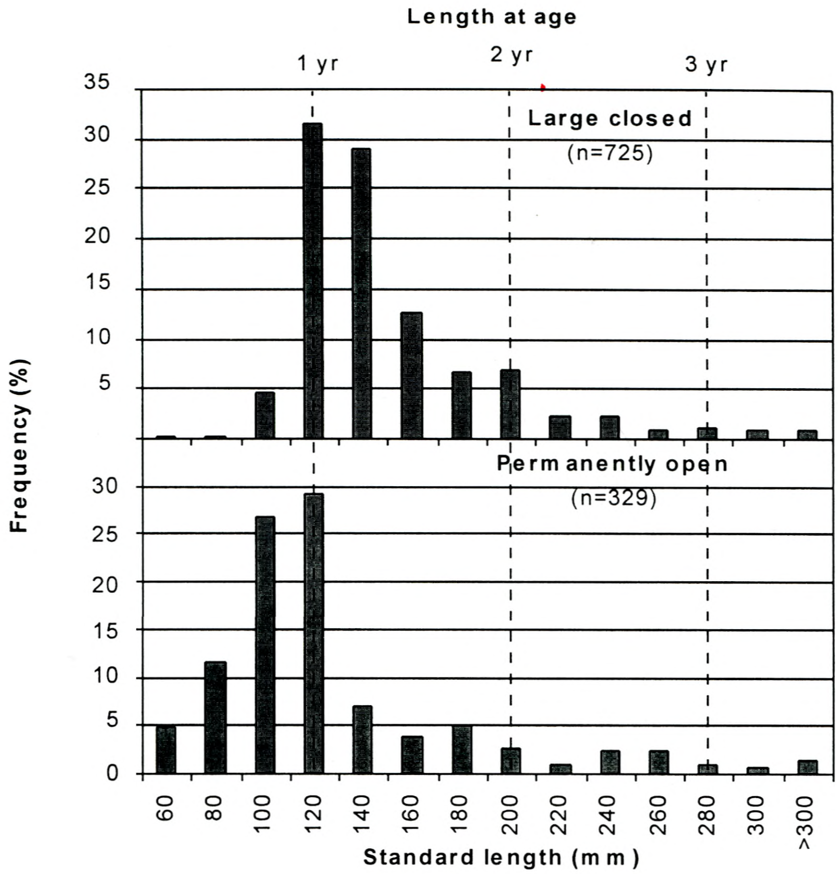

Figure 53: The length-frequency histograms for *Liza richardsonii* in the large temporarily closed and permanently open systems. Length at age estimates after de Villiers (1987).

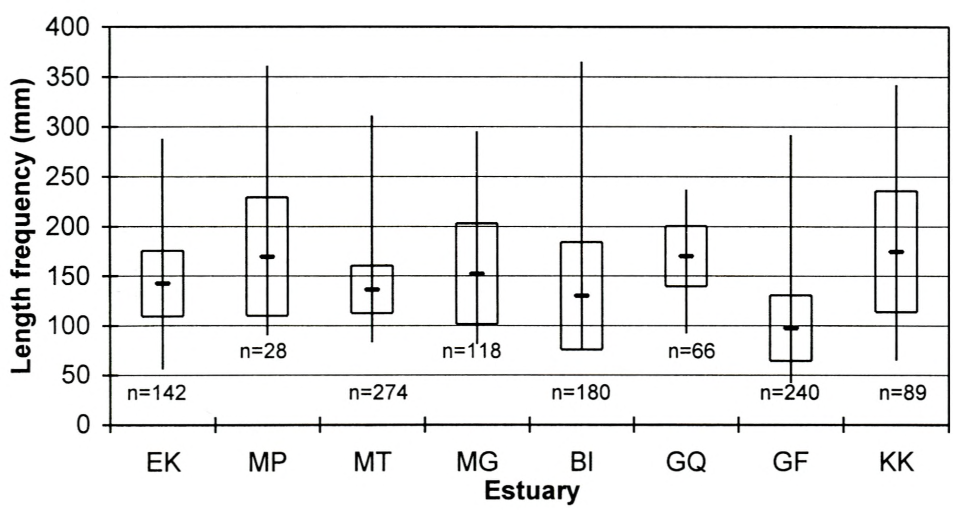

Figure 54: The mean (horizontal lines), standard deviation (clear bars) and range (vertical lines) of the lengths of *Liza richardsonii* in each estuary. The number of fish measured (n) for each system is also shown. Each estuary is represented by a two letter code: EK=East Kleinemonde, MP=Mpekweni, MT=Mtati, MG=Mgwalana, BI=Bira, GQ=Gqutywa, GF=Great Fish and KK=Keiskamma.

Mgwalana and East Kleinemonde, all produced Margalef's richness values >10. Once again, the seine net results controlled the resultant richness when both gear types were combined (Table 6).

The strong correlation between estuary size and fish species richness values (Table 6), is similar to trends highlighted by other authors. Whitfield (1980b) considered estuary size to be one of the major controlling factors of species richness in Maputaland estuaries. Similarly, Marais (1988) found that fish abundance and biomass in Eastern Cape estuaries could be correlated to catchment size ($r=0.46$, $p<0.001$; $r=0.59$, $p<0.001$ respectively). Suggestions have been made that it is not estuarine or catchment proportions that influence these trends, but more likely the hydrological consequences of the dimensions (Marais, 1988; Whitfield, 1996). Hydrological factors include increased nutrient input into systems with perennial freshwater inputs (Whitfield, 1996), positive salinity gradients and increased turbidity associated with larger systems (Marais, 1988). An important consideration is the effect of river flow and tidal prism on mouth status, with the smaller estuaries tending to close for longer periods. A prolonged closed phase reduces the recruitment potential of juvenile marine fish and prevents adult emigration back to the sea. Additionally, during the closed phase estuarine salinities may increase due to evaporation or decrease due to dilution with freshwater, resulting in only strongly euryhaline species surviving these conditions (Whitfield, 1983).

ESTUARINE ASSOCIATION

The relatively large proportion of category IIa and IIb species occurring in the temporarily open/closed systems may be explained by their strong attraction to estuaries. Cowley & Whitfield (2001) recorded that some of these species, *R. holubi* in particular, can recruit during overwash conditions. However, once they have entered these estuaries, there is no means of leaving until the following mouth opening event. The low number of marine straggler species (category III) in the temporarily open/closed estuaries may be related to their non-dependence on estuaries when compared with category II taxa.

The low proportion of category III species recorded in the permanently open estuaries during this study was surprising due to the accessibility of these systems to all marine species. An earlier study on the Great Fish reported four additional category III species (Whitfield et al., 1994), but this coincided with a greater marine influence in the middle reaches relative to this study (5-18‰ vs 0-3 ‰). The high proportion of species more dependent on estuaries (category II) in the two open estuaries is probably due to the increased opportunity for recruitment into these estuaries.

The high representation of freshwater species in the Great Fish and Keiskamma estuaries can be attributed to the strong perennial river flow, thus allowing these species to enter and retreat from estuarine waters as conditions changed. Additionally, two of the category IV species in the Great Fish were alien species (*Clarias gariepinus* and *Cyprinus carpio*) which added to the representation of this group (Laurenson & Hocutt, 1984; Laurenson et al., 1989).

The estuarine resident component of the communities dominated (>70%) in all the estuaries except the Ngculura (34.7%) and the Great Fish (51.5%) (Figure 31). The dominance by number of this group is not surprising as the species which contribute to the estuarine resident component are small and complete all or most of their life-cycles within estuaries (Whitfield, 1990). In contrast, the marine migrants spend only short periods in estuaries, either utilising these systems as a nursery area for juveniles or as a feeding ground when adult.

In a similar study of a temporarily open/closed estuary in Australia, the marine straggler and estuarine resident components of the Wilson Inlet community contributed a higher proportion of species (10% and 55% respectively) (Potter et al., 1993) compared to temporarily open/closed systems in this Eastern Cape study (2% and 23% respectively). The higher marine straggler representation in the Wilson Inlet may be due to the higher frequency of mouth opening during the Potter et al. (1993) study when compared with the temporarily open/closed systems in the Eastern Cape. In the permanently open Nornalup-Walpole Estuary, Potter & Hyndes (1994) identified a similar percentage (57%) of marine migrant species to that identified in the permanently open estuaries in the Eastern Cape (49%). The estuarine resident component in the Nornalupe-Walpole contributed a greater percentage of species (43%) relative to this Eastern Cape study (23%). The higher contribution of estuarine resident species in the Nornalup-Walpole estuary compared with permanently open Eastern Cape estuaries may be as a result of extensive lacustrine conditions in the former system.

LONGITUDINAL DISTRIBUTIONS

The lack of distinguishable fish assemblages in the different estuarine reaches is surprising, given reported (Cowley, 1998; Whitfield, 1980a) and observed (Figure 37; Figure 38) longitudinal density differences by the dominant species. The observed assemblage differences in the seine net results between the upper and lower reaches were due to some species (e.g. *O. mossambicus*, *M. capensis*, *G. aestuaria* and *A. breviceps*) being found at the longitudinal extremes. The species that accounted for the community differences were dominated by estuarine residents (category I), followed by marine species dependent on estuaries for their juvenile stages (category II).

LENGTH FREQUENCIES

The small sizes of estuarine resident species relative to marine migrant taxa is partly due to the estuarine residents having predominantly stenotopic traits and the marine migrants having mainly eurytopic traits (sensu Ribbink, 1994). Whitfield (1990) also suggests that a small body size is well suited to an estuarine life-history style, with most South African estuaries providing extensive littoral areas that small species can utilise very effectively.

The larger modal size of estuarine resident species in permanently open compared to closed systems may be indicative of a higher survival rate of smaller individuals in closed estuaries. The loss of larvae and early juveniles from open estuaries due to ebb tidal flushing is a distinct possibility. In contrast, all these size classes would be retained in closed estuaries, thus elevating their relative contribution to the overall population. Cyrus & Blaber (1987a; 1987b) have suggested that small fish undergo lower predation rates in turbid water environments. In this study, the open estuaries had higher turbidity levels than the closed systems, thus providing better protection to the larger (more visible) size cohorts of the small pelagic estuarine species.

In the permanently open estuaries the maximum size of the two goby species was smaller than in the closed systems, whereas the two planktivorous species (*A. breviceps* and *G. aestuaria*) revealed the opposite trend. These results may be due to the availability of food resources. Feeding studies on *G. aestuaria* and *A. breviceps* have shown that these species feed mainly on a variety of small crustaceans and insect larvae (Coetzee, 1982; White & Bruton, 1983; Cyrus et al., 1993). Blaber (1979) found that in turbid estuaries, *G. aestuaria* was a planktonic filter feeder, whereas in clear water systems this species was a visual predator (Blaber et al., 1981). The two goby species, *G. callidus* and *P. knysnaensis*, also feed on small crustaceans and insect larvae but are not planktivorous (Whitfield, 1988; Bennett & Branch, 1990). The trends of larger gobiid individuals in the closed estuaries and larger clupeid and atherinid individuals in the open systems may be due to differences in food resources in the different systems. The open estuaries are often plankton rich due to riverine and marine nutrient inputs (Froneman, 2000; Grange et al., 2000), while the closed systems have numerous small crustaceans associated with the extensive submerged and emergent macrophyte beds (Reavell & Cyrus, 1989; Whitfield, 1980c).

The length-frequency distributions of *G. aestuaria* in an earlier study of the closed Mhlanga Estuary (Harrison & Whitfield, 1995) showed similar trends and an identical modal size class of 30 mm when compared with the temporarily open/closed systems in this study. Kok & Whitfield (1986) reported almost identical size distributions for *A. breviceps* in the Swartvlei Estuary during the open and closed mouth stages. The current study identified significantly different *A. breviceps* length-frequency distributions, with the temporarily open/closed systems having a modal size class half that recorded in the Swartvlei system during closed mouth phases.

The gobiid species, *G. callidus* and *P. knysnaensis*, had similar length frequencies in temporarily open/ closed estuaries during this study when compared with an earlier investigation of the East Kleinemonde Estuary (Cowley & Whitfield, 2001). The modal size class of *G. callidus* in this study was higher than that recorded by Cowley & Whitfield (2001), while *P. knysnaensis* had an identical modal size class during both studies. The mean size of *G. callidus* during this study was the same as the earlier East Kleinemonde study, with means of 41.0±13.8 mm and 41.6±12.8 mm respectively. Also, the modal size class and length-frequency distributions of *G. callidus* in the closed estuaries during this study and in the closed Damba and Zotsha estuaries were similar (Harrison & Whitfield, 1995).

The age of estuarine species peaks at less than 1 year in the temporarily open/closed estuaries compared with 1 year or older in the permanently open systems. All these species commence breeding at approximately 7-9 months of age (Bennett, 1989; Boullé, 1989; Ratte, 1989; Talbot, 1982). As discussed earlier, the difference in dominant age classes is probably a feature of differential mortality or resource availability.

Three of the four marine migrant species, namely *P. commersonnii*, *L. dumerilii* and *L. richardsonii*, had different length-frequency distributions in the two estuary types. These species had a greater proportion of smaller individuals in the permanently open systems and fewer middle to large size class individuals compared with the temporarily open/closed estuaries. The modal size class for all four species was however similar in both estuary types. For example, *P. commersonnii* and *R. holubi* in the permanently open estuaries was one size class greater than in the closed systems, while *L. dumerilii* was one size class smaller in the open estuaries. *L. richardsonii* had an identical modal size class in both estuary types. The relatively similar modal distributions between these two estuary types may be linked to the opening of temporarily closed estuaries coinciding with peak recruitment of the postflexion larvae and 0+ juveniles of these species.

The larger maximum sized marine migrant individuals occurring in temporarily open/closed estuaries may be as a result of these species being trapped in closed estuaries for extended periods. In addition, the inability to reproduce in the estuarine environment means that surplus energy obtained from feeding is used for growth and not channelled into gonad development. The fish occupying permanently open systems are often 0+ juveniles that reside in these systems for 1-3 years before departing in time for the breeding season (Bennett, 1989; Whitfield, 1990). Adults of certain marine species are known to enter open systems to feed, but this is generally for short periods, hence the lower catches of these large individuals during this study.

SUMMARY AND CONCLUSIONS

This study describes the physical variability that occurred in 10 Eastern Cape estuaries, as well as discussing the fish community structure of these systems. The calculated Margalef's species richness index in the permanently open systems was higher than that calculated for the temporarily open/closed estuaries, although there were no trends identified when using the Shannon-Wiener diversity index. There were very minor longitudinal distribution trends in fish assemblages when all the estuaries were combined for analysis, with only the lower and upper reaches showing significant differences. When examined on an individual estuary basis no overall longitudinal distribution trends were evident although some fish species did reveal zonation patterns. The length frequency histograms for the different estuary types were varied for the estuarine resident species but similar for the marine migrant species. The length frequency differences in fish species between the permanently open and temporarily open/closed estuaries are probably be related to the variable access these species have to the marine environment, predation effects and the differences in foraging strategies by the various taxa.

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STYLE OF THE HOUSE

Hyphens: Certain substantive compounds are hyphenated: gill-raker, soft-ray, type-species, type-locality, type-series, type-specimen. Other words often used together are not hyphenated unless they are used in adjectival expressions before a noun: anal fin / anal-fin rays; lateral line / lateral-line scales; gill arch / gill-arch filaments, etc.

Word usage: Although the following word pairs are often used interchangeably, we believe that consistent use of the first word as a noun and the second as an adjective will improve the precision of our writing: mucus / mucous; maxilla / maxillary; opercle / opercular, operculum / opercular. The operculum (= gill cover) comprises (usually) four separate bones: opercle, subopercle, preopercle and interopercle. The words preoperculum, suboperculum and interoperculum are unnecessary substitutes and not to be used for preopercle, subopercle and interopercle. The plural of operculum is opercula.

Decimal comma versus decimal point: Contrary to most journals published in South Africa and some European countries, we will not use a comma in place of a decimal point. Most computers do not read a comma as a decimal point. In addition, it is common in ichthyological papers to give sequences of measurements that include decimal numbers, with each measurement separated by a comma. If the comma is used to separate items in a series, as well as being used to indicate a decimal number, it will cause considerable confusion.

Fin formulae: Fin formulae will be designated as follows: D XII,10-12 indicates on continuous fin with 12 spines and 10-12 soft (segmented) rays; DX/I,10-12 indicates a fin divided to the base in front of the last spine; and D X+I,12 indicates two separate dorsal fins, the first with 10 spines and the second with 1 spine and 12 soft rays. If it is necessary to differentiate branched and unbranched soft-rays, lower-case Roman numerals will be used for unbranched rays and Arabic numerals for branched rays, e.g. D iii,S. Principal caudal-fin rays are defined as those that touch the hypural bones. The number of principal caudal rays is usually the number of branched rays plus two. If the principal caudal rays are in two separate groups, the number of rays in the dorsal group is given first: thus, "principal caudal rays 8+7" means that there are 15 principal caudal rays, with 8 rays in the dorsal group and 7 in the ventral group.

Abbreviations: Abbreviations normally end with a full stop: et al., e.g., etc., n.b., (note: these commonly used abbreviations of Latin words are not italicized). Dr (Doctor) and Mr (Mister) and compass directions (north, west, northwest, etc.) are abbreviated using capital letters without full stops: N, W, NW. We recommend the following abbreviations for ichthyological terms: SL - standard length, TL - total length, FL - fork length, GR – gill-rakers, LL - lateral line.

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