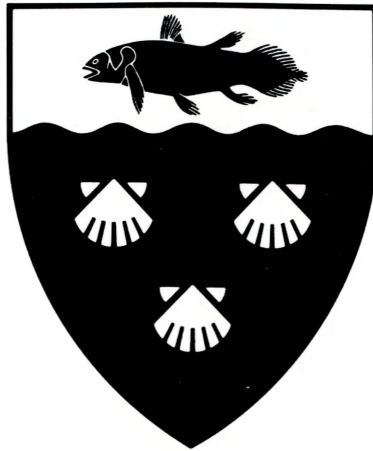


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**FISH COMMUNITY STRUCTURE IN THREE TEMPORARILY  
OPEN/CLOSED ESTUARIES ON THE NATAL COAST**

by

Trevor D. Harrison and Alan K. Whitfield

## ABSTRACT

Harrison, Trevor D. and Alan K. Whitfield. 1995. Fish community structure in three temporarily open/closed estuaries on the Natal coast. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology* No. 64, 80 pages, 50 figures, 3 appendices.

The fishes of three small Natal estuaries, the Mhlanga, Damba and Zotsha were sampled over a period of two years. A total of 68 fish taxa representing 24 families, 39 genera and 55 species were captured during this study. Forty seven fish taxa were recorded in the Mhlanga estuary of which *Gilchristella aestuaria*, *Oreochromis mossambicus*, *Valamugil cunnesius*, *Valamugil* sp. and juvenile mugilids numerically dominated. In terms of biomass, *O. mossambicus*, *V. cunnesius*, *Liza alata*, *Myxus capensis* and *Mugil cephalus* dominated the ichthyofauna of the Mhlanga system. In the Damba estuary, 24 fish taxa were recorded, the most abundant being *Glossogobius callidus*, *M. capensis* and *O. mossambicus*. *M. capensis*, *M. cephalus*, *O. mossambicus* and *G. callidus* dominated the fish biomass captured in the Damba system. A total of 56 fish taxa were recorded in the Zotsha estuary during this study, with the ichthyofauna numerically dominated by juvenile mugilids, *G. aestuaria*, *O. mossambicus*, *Rhabdosargus holubi*, *Terapon jarbua*, *Ambassis productus* and *G. callidus*. The species which dominated the fish biomass in the Zotsha system were *O. mossambicus*, *L. alata*, *Valamugil robustus*, *V. buchani*, *M. capensis*, *M. cephalus* and *V. cunnesius*.

Classifying the species according to whether they were resident estuarine, freshwater, estuarine-dependent marine or marine species revealed that the first three groups were all well represented in the systems. *Oreochromis mossambicus* was the dominant freshwater species in all three estuaries. *Gilchristella aestuaria* and *Glossogobius callidus* were the principal estuarine species in the Mhlanga and the Damba respectively, with *G. aestuaria*, *A. productus* and *G. callidus* being the dominant estuarine species captured in the Zotsha. The principal estuarine-dependent marine fishes captured in the Mhlanga were *V. cunnesius*, *Valamugil* sp., juvenile mugilids, *M. capensis*, *M. cephalus* and *L. alata*. In the Damba, *M. capensis* and *M. cephalus* were the dominant estuarine-dependent marine species and in the Zotsha juvenile mugilids, *R. holubi*, *T. jarbua*, *M. capensis*, *V. cunnesius*, *V. robustus*, *M. cephalus*, *L. alata* and *V. buchani* were the principal estuarine-dependent marine species.

The results of this study indicate that the estuaries are dominated at different periods by different assemblages of fishes. This is linked to the spawning and migration patterns of the various species as well as the hydrological regime of each estuary. During the winter these systems are normally closed with relatively deep waters and high food resource and habitat availability. Freshwater and estuarine species mainly inhabit the upper reaches of the systems while estuarine-dependent marine species, which dominate the fish community, mainly occupy the middle and lower reaches. When these estuaries open with the onset of the spring/summer rains, adult and sub-adult estuarine-dependent marine species emigrate to the marine environment and juveniles begin recruiting into the systems. Spring is also the peak breeding period of resident estuarine and freshwater species, resulting in an increase in the contribution of these fishes to the overall ichthyofauna during this period. When closed estuaries open the water level falls and this results in the fishes concentrating in the lower reaches of the system where moderate water depths are present, thus further contributing to an increase in the proportion of freshwater and estuarine species in this region.

The breaching of closed estuaries also results in a reduction in food resources and habitat availability. Competition and possible increased vulnerability to avian predation (due to the shallow nature of the systems), may contribute to a decrease in the proportion of estuarine and freshwater species in summer. The prolonged recruitment of 0+ juveniles of estuarine-dependent marine species results in an increase in the proportion of these fishes present in the estuaries during summer. In autumn, the systems normally close, water levels rise and available food resources and habitat increase. This allows the redistribution of freshwater and estuarine species upstream, leaving estuarine-dependent marine species to dominate the middle and lower reaches.

Although temporarily open/closed estuaries along the Natal coast may not be as diverse as permanently open estuaries in terms of their ichthyofauna, their importance must not be underestimated, since by providing a series of sheltered habitats along the coast they may contribute significantly to the viability of estuarine-dependent marine fish stocks.

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# FISH COMMUNITY STRUCTURE IN THREE TEMPORARILY OPEN/CLOSED ESTUARIES ON THE NATAL COAST

by

T.D. Harrison<sup>1</sup> and A.K. Whitfield<sup>2</sup>

## INTRODUCTION

The province of Natal is situated on the east coast of South Africa and its coastline extends 570 km SSW from Ponta do Ouro (26° 51'S; 32° 53'E) on the Mozambique border to the Mtamvuna estuary (31° 4'S; 30° 11'E) bordering the Eastern Cape Province. The coastline of Natal is relatively straight and is interrupted by 73 estuaries of varying sizes (Begg, 1978). The Tugela River (29° 13'S; 30° 30'E) forms a natural divide between southern and northern Natal. The Zululand segment of the Natal coast extends northward for 320 km from the Tugela, is backed by a low-lying sandy coastal plain, and due to the flatter topography, the rivers in this region are long and many drain into large coastal lakes rather than directly into the sea (Cooper, 1991). As a consequence, this area is characterised by a few large estuarine systems such as Richards Bay, Lake St Lucia and Kosi.

South of the Tugela the topography becomes steeper, and the remaining 250 km of coast is near-linear. The steep hinterland, and lack of a coastal plain has resulted in a large number of rivers that drain small catchments, each of which forms an independent outlet at the coast (Cooper, 1991). Within this area are some 62 estuarine systems (referred to as lagoons by Begg, 1978; 1984a; 1984b) that are cut off from the sea for much of the year by a sand bar across the mouth. These estuaries normally open for a few weeks during the summer rainy season when increased river discharge usually breaches the bar. The system then becomes tidal until the fluvial discharge rate falls and the mouth is then closed by longshore and onshore sand movement (Wallace, 1975a; Day, 1981a; Blaber, 1985).

The South African 3000 km long coastline has a total estuarine area of about 600 km<sup>2</sup>, 68% of which is in Natal (Begg, 1978). At least 80% of Natal's 408 km<sup>2</sup> estuarine area, however, is made up by the Lake St Lucia system, the largest estuarine system in South Africa (Begg, 1978). The 62 estuarine systems south of the Tugela together occupy only 1.6% of the total extent of estuarine waters in Natal (Begg, 1984a). After reviewing the state of knowledge of Natal's estuaries, Begg (1978) revealed that 51 out of the 73 estuaries along the Natal coast had virtually never been studied. Most of the work on Natal's estuaries had been conducted on large open systems such as St Lucia, Richards Bay and Kosi Bay (Begg, 1978).

An investigation into the comparative ecology of Natal's smaller estuaries by Begg (1984a; 1984b) suggested that of the 62 systems studied, only six made a significant contribution to the recruitment of estuarine-dependent

marine stocks. Begg (1984a) concluded that permanently open estuaries were supportive of immigrant species chiefly of marine origin, while seasonally closed estuaries supported resident species, often of freshwater origin. These conclusions, however, were drawn from collections sampled by only one gear type, namely a one metre beam trawl, and during relatively dry climatic conditions. Preliminary surveys of the fish community structure of differing estuaries on the Natal coast (Harrison, 1990), using a variety of sampling techniques and during more typical climatic conditions, revealed that although the fish faunas of temporarily closed estuarine systems were not as diverse as permanently open systems, estuarine-dependent marine species appeared to be an important component of the ichthyofauna. This has an important bearing on the management, conservation and exploitation of these coastal resources.

As the human population increases in South Africa, so will the pressure to utilise estuaries for a variety of activities. Since the majority of Natal's estuaries are characteristically small systems, they are particularly vulnerable to degradation and human impact (Begg, 1978). It is imperative therefore that the ecological significance of Natal's smaller estuaries and their importance to fish be understood prior to making recommendations about estuarine management, conservation and exploitation.

The aim of the present study was to investigate the ecology of the ichthyofauna of three temporarily open/closed estuaries along the coast of Natal. The key objectives of the study were:

- 1) To determine the fish community structure of the three estuaries.
- 2) To determine seasonal changes in the fish community structure in relation to physical and biological parameters.
- 3) To contribute to the overall understanding of three temporarily open/closed estuaries function and their importance to the fish community.

The ecology of the ichthyofauna of each system is presented separately, the fish community structure of the three systems is compared and some general conclusions are offered concerning the value of this type of estuary to estuarine-dependent marine fishes in particular.

## MATERIALS AND METHODS

Each of the three estuaries was sampled quarterly over the period August 1990 to May 1992.

### PHYSICOCHEMICAL CHARACTERISTICS

Selected physical and chemical parameters were recorded at fixed stations in each system at the beginning of each sampling survey (Figure 1). Water depths in the lower, middle and upper reaches of each estuary was measured using a weighted shotline graduated at 10 cm intervals.

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Surface and bottom salinities were measured in parts per thousand (‰) using a YSI model 33 S.C.T. meter. Surface and bottom temperatures (°C) and oxygen levels (mg l<sup>-1</sup>) were measured using a YSI model 57 oxygen meter. Surface and bottom water samples were also taken for turbidity. This was measured in Nephelometric Turbidity Units (NTU) in the laboratory, using a Hach model 2100A turbidimeter. Daily observations of the mouth condition of each system were recorded by local residents and the staff of the Natal Parks Board.

## ICHTHYOFAUNA

### Field Methods

Fishes were sampled using a variety of equipment, viz. a 1 metre beam trawl (1 m x 4 m x 14 mm bar mesh body, 7 mm bar mesh bag); a 2 metre otter trawl (2 m x 5 m x 18 mm bar mesh body, 6 mm bar mesh bag); a seine net (30 m x 1.7 m x 15 mm bar mesh fitted with a 5 mm bar mesh purse); and a fleet of gill nets. Each gill net comprised three 45 mm, 75 mm and 100 mm stretch mesh monofilament panels. Each panel was 3.3 m long and 1.7 m deep, producing a 10 m by 1.7 m gill net with a range of mesh sizes.

Trawling was carried out during daylight hours with the use of a 3.1 m semi-rigid inflatable boat equipped with an 8 hp outboard motor. The beam trawl was towed 10 m behind the boat and the otter trawl 20 m behind the boat. Trawl nets are easy to use and sample a great variety of habitats, over thick mud, along the edge of densely vegetated banks, over submerged vegetation or up narrow creeks (Gibbs & Matthews, 1981/1982; Begg, 1984a; Hartman & Herke, 1987). During the study period, an attempt was made to sample the same general areas within each system on each occasion using the trawl nets. All specimens collected by trawling were immediately placed in a 20 litre plastic bucket of water. A minimum of 25 specimens of the abundant species as well as those specimens that could not be identified in the field were immediately placed in labelled plastic bags and preserved in 10% formalin for transport to the laboratory. The remaining specimens were measured to the nearest mm standard length (SL) in the field, using vernier slide callipers or a measuring board, and returned to the system.

Seine netting was carried out during daylight hours and was limited to shallow (<1.5 m deep), unobstructed areas with gently sloping banks. One operator paid the net out from the bank while another operator encircled a given area with the net, either by wading the net into the water or with the aid of the boat. The net was then pulled onto the bank making sure that the foot rope was on the bottom, thus minimising the possibility of any fish escaping under the net. Although every attempt was made to select fixed seining sites in each system, the highly variable water level fluctuations within each system often precluded this. Seine netting was thus conducted at various sites within each system on each occasion depending on conditions at the time. Specimens collected by seine netting were treated like those collected by trawl.

Gill nets were deployed in the evening and lifted the following morning. Gill nets are one of the most efficient methods of sampling fish populations in deeper estuarine waters (Marais, 1985). They are, however, highly selective

and to overcome this, a range of mesh sizes (45 mm, 75 mm and 100 mm stretch mesh) was used. The gill nets were, where possible, deployed at fixed sites in open, mid-channel waters deeper than one metre. All specimens collected by gill netting were placed in labelled canvas cooler bags with ice for transport to the laboratory.

### Laboratory Methods

In the laboratory, specimens collected in the gill nets were identified by reference to Smith & Heemstra (1986). A minimum of 25 specimens of the abundant species were measured to the nearest mm standard length (SL) and weighed to the nearest 0.01g (wet mass). The remaining specimens were measured to the nearest mm (SL). Similarly a minimum of 25 specimens of the abundant species from the beam trawl, otter trawl and seine net collections were measured to the nearest mm (SL) and weighed to the nearest 0.01g (wet mass). The remaining specimens were then measured to the nearest mm (SL).

### Data Analyses

**Length/mass relationships:** To estimate the mass for fish that were measured but not weighed, the length-mass relationships of all species collected during this study were determined by the expression  $m = al^b$ , where  $m$  is the derived mass,  $l$  is the standard length,  $a$  is a constant (intercept of regression curve) and  $b$  an exponent (the regression coefficient) (Tesch, 1971). The parameters  $a$  (intercept) and  $b$  (slope) are most easily estimated by linear regression based on logarithms:  $\log(m) = \log(a) + b \log(l)$  (Cone, 1989). The length-mass relationships of all species collected during this study were determined by combining the data from the three systems and calculating the regressions by the method of least squares. These results are presented in Appendix 1.

**Species composition:** The total fish composition, both by number and by biomass, of the fish community within each system was calculated. The relative biomass contribution of each species was calculated using actual recorded masses and masses derived from length-mass relationships (Appendix 1).

**Sampling effectiveness:** In order to determine the effectiveness of the sampling methods employed during this study, the total species composition collected by each sampling method, both in terms of abundance and biomass, was calculated for each system. The fish communities captured by each sampling method were then compared with the total catch in each system using the following similarity indices:

Jaccard's (1928) index of similarity (IS<sub>J</sub>) (Mueller-Dombois & Ellenberg, 1974);

$$IS_J = \frac{c}{a + b + c} \times 100$$

where  $c$  is the number of species common to both samples,  $a$  is the number of species unique to the first collection and  $b$  is the number unique to the second. This index measures the ratio of common species to the total species in two samples (Mueller-Dombois & Ellenberg, 1974).

Sørensen's (1948) index of similarity (IS<sub>S</sub>) (Mueller-Dombois & Ellenberg, 1974);

$$IS_S = \frac{2c}{A + B} \times 100$$

where  $c$  is the number of species common to both samples,  $A$  is the total number of species in the first collection and  $B$  is the total number of species in the second. Sørensen's (ISs) index measures the ratio of the common to the average number of species in two samples, and by expressing the actually measured coinciding species occurrences against theoretically possible ones, this index includes a statistical probability term (Mueller-Dombois & Ellenberg, 1974).

**Seasonal species richness and diversity:** Temporal changes in the fish community within each system were determined by standardising the sampling effort for each occasion to two beam trawls, two otter trawls, two seine nets and two gill nets. The total number of species, the total number of individuals and the total fish biomass sampled on each occasion was then calculated for each system. The following ecological indices were also calculated:

Margalef's (1958) species richness index ( $D$ ) (Washington, 1984);

$$D = \frac{(S-1)}{\ln(N)}$$

where  $S$  is the total number of species and  $N$  is the total number of individuals. Species richness, as measured by the Margalef ( $D$ ) index, is a measure of diversity without considering the relative proportion of each species (Krebs, 1985).

The Shannon-Wiener (1949) diversity index ( $H'$ ) (Washington, 1984);

$$H' = -\sum_{i=1}^{i=n} \frac{n_i}{N} \times \ln \frac{n_i}{N}$$

where  $n_i$  is the number of individuals of each species and  $N$  is the total number of individuals. The Shannon-Wiener ( $H'$ ) index is influenced by both the number of species present and how evenly or unevenly the individuals are distributed (Krebs, 1985). The Shannon-Wiener index was also calculated using biomass as suggested by Wilhm (1968) (Washington, 1984);

$$H'w = -\sum_{i=1}^{i=w} \frac{w_i}{W} \times \ln \frac{w_i}{W}$$

where  $w_i$  is the biomass of each species and  $W$  is the total biomass.

The Pielou (1966) Equitability Index ( $J'$ ) (Washington, 1984);

$$J' = \frac{H'}{\ln S}$$

where  $S$  is the total number of species and  $H'$  is the Shannon-Wiener function. This index gives a measure of how evenly the individuals in a community are distributed.

The number of species, number of individuals, biomass and all the ecological indices were correlated with the various abiotic parameters using the Spearman rank test (Conover, 1980) where the coefficient ( $r$ ) ranges from -1 (perfect disagreement) to +1 (perfect agreement). Due to the small sample size (8), the correlations were treated as significant at the 85% confidence level ( $p$ ).

## Community Structure

Typically, estuarine fish communities are composed of a mixture of euryhaline marine species, estuarine species and euryhaline freshwater species (Wallace, 1975a; Odum, 1983; Blaber, 1985). A stenohaline marine component sometimes occurs in the mouth area of permanently open estuaries where the salinity does not fall below that of sea water but this is not generally considered part of the estuarine fauna (Wallace, 1975a). Using the estuary-association classification system of Whitfield (1994), the species collected in each system were divided into four categories: freshwater species, estuarine species, estuarine-dependent marine species and marine species. Estuarine species are capable of spending their entire life cycle within the estuarine environment, whereas estuarine-dependent marine species are inshore fishes which spawn at sea but mainly utilise estuaries as nursery areas during the juvenile phase of their life cycle (Wallace et al., 1984). The fish in each category are listed in Appendix 2.

The percent contribution made by each category to the total ichthyofaunal assemblage of each system, in number of specimens and in terms of biomass were calculated. Seasonal changes in the actual abundance and biomass of the various categories as well as the relative abundance and biomass were also determined, using a standard unit of effort.

## Comparative Ecology

To facilitate a comparison of the fish community structure of the three systems, the total sampling effort employed in each system was standardised to 10 beam trawls, 10 otter trawls, 10 seine nets and 10 gill nets. The total species composition of the fish community within each system was then calculated both by number and by biomass. Margalef's species richness index ( $D$ ) the Shannon-Wiener diversity index using numbers ( $H'$ ) and biomass ( $H'w$ ) and the Pielou Equitability Index ( $J'$ ) were also calculated for each system.

The fish communities of the three systems were compared using Jaccard's index of similarity ( $IS_J$ ) as well as Sørensen's index of similarity ( $IS_S$ ). Both these indices provide a qualitative measure of the similarity between two communities (Mueller-Dombois & Ellenberg, 1974). Since the similarity of two communities is a function not only of the number of shared and unique species, but also of the amount of each species present, the fish communities of the three systems were also compared quantitatively using Ellenberg's (1956) index of similarity ( $IS_E$ ) (Mueller-Dombois & Ellenberg, 1974):

$$IS_E = \frac{(\%c+2)}{\%a + \%b + (\%c+2)} \times 100$$

where  $\%c$  is the sum of the percent abundance or biomass values of the species common to both collections,  $\%a$  is the sum of the percent abundance or biomass values of the species restricted to the first collection and  $\%b$  is the sum of the percent abundance or biomass values of the species restricted to the second collection.

The contributions, both by number and by biomass, of freshwater species, estuarine species, estuarine-dependent marine species and marine species were calculated for each system using a standard total effort which incorporated all

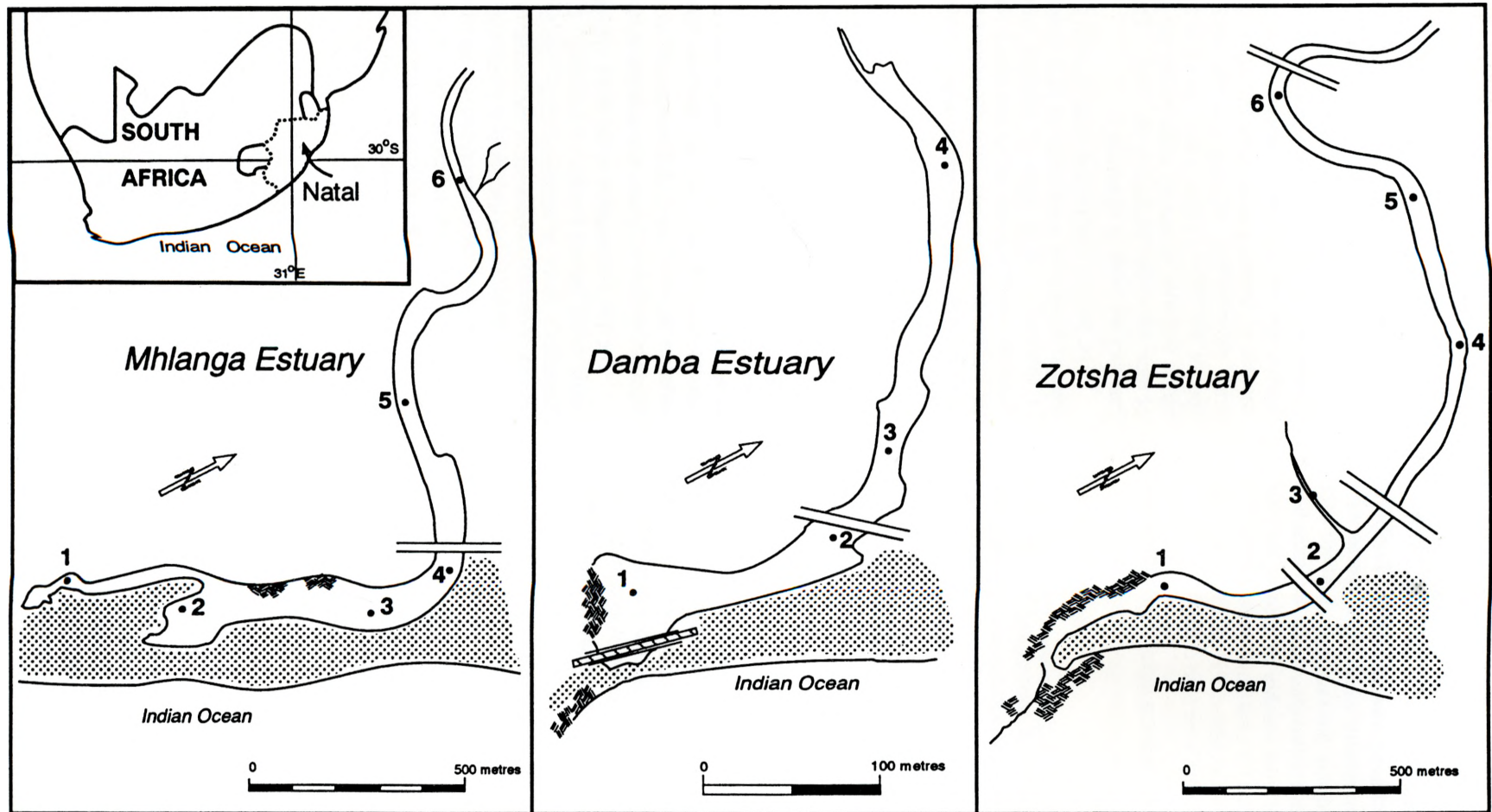


Figure 1. Map of the Mhlanga, Damba and Zotsha estuaries indicating abiotic sampling stations.

types of sampling gear. Seasonal changes in the actual abundance and biomass of the various categories of fishes as well as their relative abundance and biomass were compared by standardising the sampling effort for each occasion to two beam trawls, two otter trawls, two seine nets and two gill nets.

## MHLANGA ESTUARY

### STUDY AREA

The Mhlanga estuary (29° 42' S; 31° 05' E) lies 17 km north-east of Durban and forms part of a nature reserve administered by the Natal Parks Board. The river is 28 km long and has a catchment area of 118 km<sup>2</sup> (NRIO, 1986a). The catchment geology includes a mixture of Berea Red Sand, Dwyka Tillite, Ecca Shale, Natal Group Sandstone, Dolerite and some metamorphic rocks. The southern bank of the Mhlanga system is vegetated by reeds (*Phragmites*) and coastal forest vegetation while the northern bank is vegetated by *Phragmites* reeds (Appendix 3). The Mhlanga estuary has shown little morphological change over the past 50 years, suggesting that the system is in a state of dynamic equilibrium (Cooper, 1989).

### RESULTS

#### Physicochemical Characteristics

**Mouth condition:** Records of daily mouth condition of the Mhlanga estuary from June 1990 to May 1992 revealed that the mouth of the system opened frequently during the spring/summer months (September - March) but was closed during the winter (June - August). The period during which the mouth remained open ranged from 2 to 25 days (Figure 2).

**Depth:** The average water depth during the study period ranged from 220 cm (recorded in August 1990) to 40 cm (recorded in November 1991). The average depth of the system was greater during autumn and winter (May - August) than during spring and summer (November - February) (Figure 2).

**Temperature:** Water temperature in the Mhlanga followed a seasonal pattern with both surface and bottom temperature being warmer in the spring/summer (November - February) than during the autumn/winter (May - August). Average surface temperature in the Mhlanga ranged from a minimum of 16.2 °C in August 1991, to a maximum of 29.8 °C in February 1992. Average bottom temperatures ranged from 15.7 °C in August 1991 to 28.8 °C in February 1992. The average surface temperatures in the Mhlanga were generally higher than the average bottom temperatures with the exception of those in May 1991 where the average bottom temperature exceeded the average surface temperature (Figure 2).

**Salinity:** The average surface salinity in the Mhlanga ranged from 0.5‰ in May 1992 to 4.5‰ in November 1991. Average bottom salinities ranged from a minimum of 1‰ in August 1990 and May 1992, to a maximum of 10.7‰ in February 1991. Overall, bottom salinities in the Mhlanga were higher than surface salinities with the most marked stratification being recorded in November 1990, February 1991, May 1991 and August 1991 (Figure 2).

**Dissolved oxygen:** The monthly average dissolved oxygen in the surface waters ranged from 13.3 mg l<sup>-1</sup> recorded in August 1991 to 4.2 mg l<sup>-1</sup> recorded in May 1992. The average dissolved oxygen recorded in bottom waters were generally lower than those in surface waters and ranged from 9.0 mg l<sup>-1</sup> recorded in August 1991 to 3.7 mg l<sup>-1</sup> recorded in May 1992 (Figure 2).

**Turbidity:** Average surface turbidity ranged from 0.4 NTU recorded in November 1990 to 62 NTU recorded in November 1991. The average bottom turbidity in the Mhlanga were generally lower than those recorded at the surface and ranged from 0.3 NTU in November 1990 to 61 NTU in November 1991 (Figure 2).

#### Species Composition and Sampling Efficiency

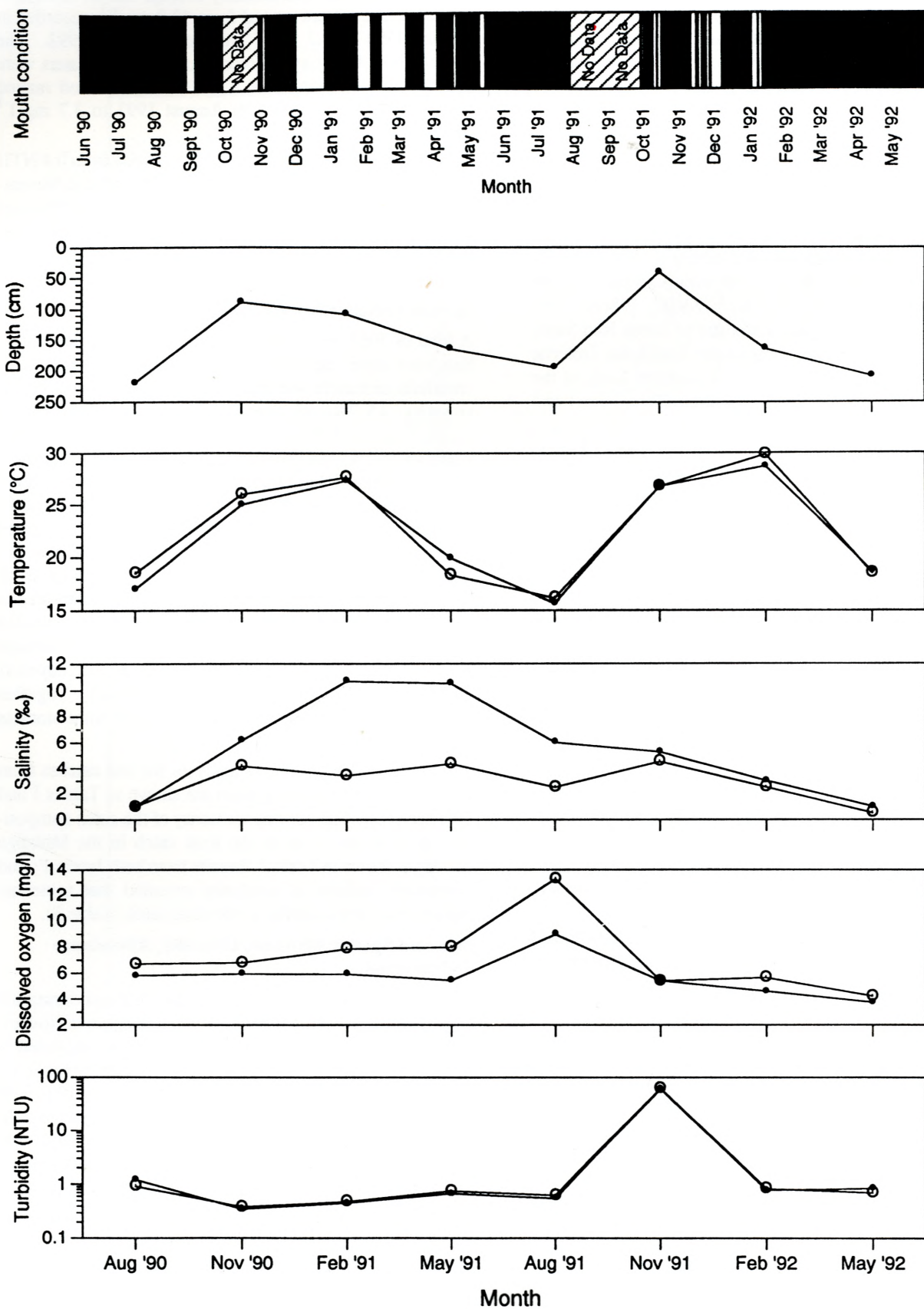
A total of 7961 specimens representing 19 families and 47 fish taxa were captured in the Mhlanga estuary. *Gilchristella aestuaria* was the most abundant species, representing 45.7% of the total catch. *Oreochromis mossambicus* (17.8%), *Valamugil cunnesius* (8.9%), *Valamugil* sp. (6.1%) and juvenile mugilids (4.7%) were the next most abundant fishes collected (Table 1). Together these fishes comprised over 83% of the specimens captured in the Mhlanga. The remaining 43 types of fishes each constituted less than 5% of the specimens caught and together accounted for less than 17% of the total ichthyofauna in the Mhlanga. A total fish biomass of 288.9 kg was captured in the Mhlanga estuary. *Oreochromis mossambicus* accounted for 46.6% of the total fish biomass, followed by *Valamugil cunnesius* (19.6%), *Liza alata* (9.6%) *Myxus capensis* (7.9%) and *Mugil cephalus* (7.5%) (Table 2). Together these five species accounted for 91% of the total biomass recorded in the Mhlanga.

Numerical and biomass analyses for fish catches from each of the four sampling gears are shown in Tables 1 and 2 respectively. The percent similarity of the catch composition of each gear type to the total catch in the Mhlanga estuary is shown in Table 3. Results from both Jaccard's and Sørensen's indices of similarity revealed that seine net catches were most similar to the total catch (Table 3).

#### Seasonal Species Richness, Diversity, Abundance and Biomass

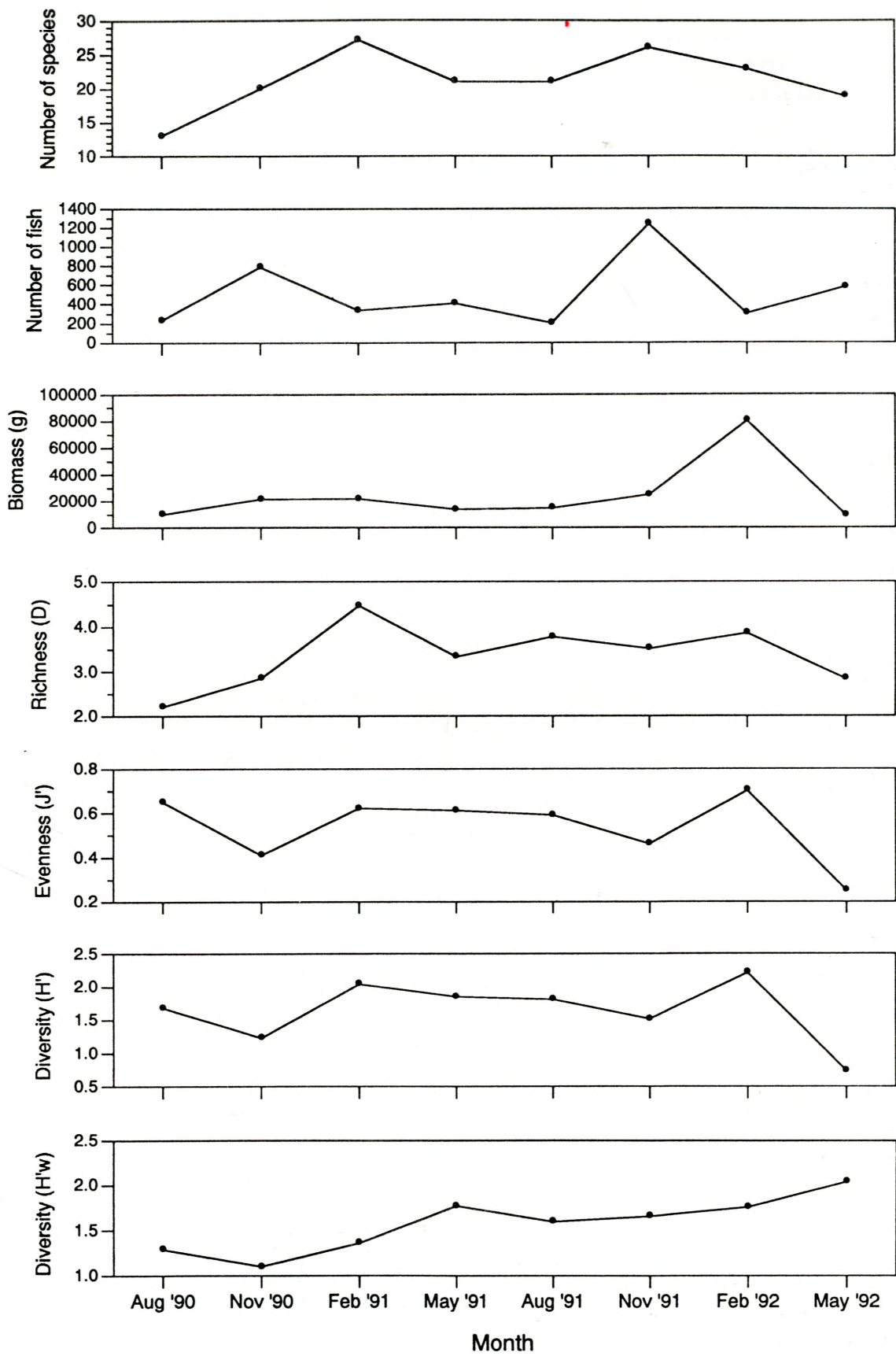
The number of species captured in the Mhlanga during the study period peaked in February 1991 and again in November 1991. The number of individuals captured increased in November 1990 and November 1991. Fish biomass increased slightly in November 1990 and February 1991 with a marked peak in February 1992. Margalef's species richness index (D) reached a maximum in February 1991 with two less pronounced peaks in August 1991 and February 1992. Pielou's evenness index (J') decreased in November 1990, November 1991 and May 1992. The Shannon-Wiener diversity index (H') exhibited two seasonal peaks, one in February 1991 and another in February 1992. The Shannon-Wiener index for biomass (H'w) reached a peak in May 1991 and rose again in May 1992 (Figure 3).

The number of species, the number of individuals and biomass in the Mhlanga were all inversely correlated with the average depth of the system. The number of species and biomass of fish captured was positively correlated with the



**Figure 2.** Daily mouth condition (□ open; ■ closed) and abiotic parameters measure in the surface (o) and bottom (●) waters of the Mhlanga estuary.





**Figure 3.** Seasonal changes in the number of species, number of individuals, biomass, species richness, species evenness, and species diversity in the Mhlanga estuary.

**Table 1.** Numerical composition of the fishes captured in the Mhlanga estuary using various sampling techniques. (August 1990 - May 1992).

Sampling Gear Fish Taxa	Beam Trawl x 34		Otter Trawl x 34		Seine Net x 37		Gill Nets x 38		Total	
	n	%	n	%	n	%	n	%	n	%
<i>Acanthopagrus berda</i>					2	0.04			2	0.03
<i>Ambassis productus</i>			2	0.12					2	0.03
<i>Ambassis</i> sp.					14	0.28			14	0.18
<i>Argyrosomus hololepidotus</i>			3	0.18			12	1.05	15	0.19
<i>Caranx ignobilis</i>							3	0.26	3	0.04
<i>Caranx sexfasciatus</i>							5	0.44	5	0.06
<i>Caranx</i> sp.			3	0.18	1	0.02			4	0.05
<i>Chelonodon laticeps</i>	1	0.57							1	0.01
<i>Crenimugil crenilabis</i>					2	0.04			2	0.03
<i>Eleotris</i> sp.	3	1.70	2	0.12					5	0.06
<i>Gerres rappi</i>	14	7.95	6	0.37	2	0.04			22	0.28
<i>Gerres</i> sp.			3	0.18	48	0.96			51	0.64
<i>Gilchristella aestuaria</i>	35	19.89	1021	62.33	2585	51.66			3641	45.74
<i>Glossogobius callidus</i>	20	11.36	68	4.15	8	0.16			96	1.21
<i>Glossogobius giuris</i>					1	0.02			1	0.01
<i>Goby</i> sp. I					1	0.02			1	0.01
<i>Herklotsichthys quadrimaculatus</i>					20	0.40			20	0.25
Juvenile mugilids					375	7.49			375	4.71
<i>Leiognathus equula</i>	1	0.57	8	0.49					9	0.11
<i>Lichia amia</i>					3	0.06	12	1.05	15	0.19
<i>Liza alata</i>			1	0.06			125	10.94	126	1.58
<i>Liza dumerilii</i>					136	2.72	3	0.26	139	1.75
<i>Liza macrolepis</i>			1	0.06	11	0.22	9	0.79	21	0.26
<i>Liza</i> sp.					79	1.58			79	0.99
<i>Liza tricuspidens</i>					11	0.22			11	0.14
<i>Micropterus salmoides</i>			1	0.06	1	0.02	2	0.17	4	0.05
<i>Monodactylus argenteus</i>							3	0.26	3	0.04
<i>Monodactylus falciformis</i>			3	0.18			10	0.87	13	0.16
<i>Mugil cephalus</i>	1	0.57			34	0.68	100	8.75	135	1.70
<i>Myxus capensis</i>			3	0.18	105	2.10	118	10.32	226	2.84
<i>Oligolepis acutipennis</i>			3	0.18	4	0.08			7	0.09
<i>Oligolepis keiensis</i>			20	1.22					20	0.25
<i>Oreochromis mossambicus</i>	85	48.30	435	26.56	627	12.53	273	23.88	1420	17.84
<i>Pomadasys commersonnii</i>	7	3.98	20	1.22	67	1.34	14	1.22	108	1.36
<i>Psammodobius knysnaensis</i>					1	0.02			1	0.01
<i>Pseudorhombus arsius</i>	1	0.57							1	0.01
<i>Rhabdosargus holubi</i>			23	1.40	46	0.92	1	0.09	70	0.88
<i>Rhabdosargus thorpei</i>			1	0.06					1	0.01
<i>Scomberoides</i> sp.					3	0.06			3	0.04
<i>Sillago sihama</i>					2	0.04			2	0.03
<i>Solea bleekeri</i>	1	0.57	2	0.12	1	0.02			4	0.05
<i>Terapon jarbua</i>	2	1.14	5	0.31	55	1.10	15	1.31	77	0.97
<i>Tilapia rendalli</i>			1	0.06					1	0.01
<i>Valamugil buchanani</i>					3	0.06	2	0.17	5	0.06
<i>Valamugil cunnesius</i>	5	2.84	3	0.18	265	5.30	436	38.15	709	8.91
<i>Valamugil robustus</i>					4	0.08			4	0.05
<i>Valamugil</i> sp.					487	9.73			487	6.12

average surface and bottom temperature of the system and the time that the mouth remained open during a particular season. The number of species recorded in the Mhlanga were also positively correlated with average surface and bottom salinity. The Shannon-Wiener diversity index ( $H'$ ) and Margalef's species richness index ( $D$ ) both showed a positive correlation with the time that the mouth of the Mhlanga was open during a particular season. The Shannon-Wiener index for biomass ( $H'w$ ) and Pielou's evenness index ( $J'$ ) did not exhibit any correlation with any of the abiotic variables measured (Table 4).

### Community Structure

**Overall abundance and biomass:** The fish community of the Mhlanga system was numerically dominated by estuarine species, which comprised 47.6% of the total ichthyo-

faunal assemblage. Estuarine-dependent marine species accounted for 34.2% of the total catch, and freshwater species accounted for 17.9%. Marine species comprised 0.3% of the total fish community in the Mhlanga estuary. In terms of biomass, estuarine-dependent marine species comprised 52.2% of the catch, freshwater species contributed 46.8% and estuarine species comprised 1%. The biomass of marine species in the Mhlanga was negligible (Figure 4).

**Seasonal changes in relative abundance and biomass:** During the study period, estuarine-dependent marine species numerically dominated the Mhlanga fish community in August 1990, February 1991, May 1991, August 1991 and February 1992, while estuarine species dominated in November 1990, November 1991 and May 1992. The contribution of freshwater species to the ichthyofauna in the

**Table 2.** Biomass composition of the fishes captured in the Mhlanga estuary using various sampling techniques (August 1990 - May 1992).

Sampling Gear Fish Taxa	Beam Trawl x 34		Otter Trawl x 34		Seine Net x 37		Gill Nets x 38		Total	
	g	%	g	%	g	%	g	%	g	%
<i>Acanthopagrus berda</i>					12.5	0.07			12.5	0.00
<i>Ambassis productus</i>			48.2	0.14					48.2	0.02
<i>Ambassis</i> sp.					0.4	0.00			0.4	0.00
<i>Argyrosomus hololepidotus</i>			599.2	1.68			4020.5	1.77	4619.7	1.60
<i>Caranx ignobilis</i>							354.8	0.16	354.8	0.12
<i>Caranx sexfasciatus</i>							578.7	0.25	578.7	0.20
<i>Caranx</i> sp.			29.2	0.08	3.8	0.02			33.0	0.01
<i>Chelonodon laticeps</i>	0.1	0.00							0.1	0.00
<i>Crenimugil crenilabis</i>					3.1	0.02			3.1	0.00
<i>Eleotris</i> sp.	6.0	0.08	2.0	0.00					8.0	0.00
<i>Gerres rappi</i>	253.6	3.32	48.4	0.14	49.0	0.27			351.0	0.12
<i>Gerres</i> sp.			0.5	0.00	2.7	0.01			3.2	0.00
<i>Gilchristella aestuaria</i>	75.7	0.99	956.4	2.69	1229.0	6.78			2261.1	0.78
<i>Glossogobius callidus</i>	135.6	1.78	294.2	0.83	18.3	0.10			448.2	0.16
<i>Glossogobius giuris</i>					0.7	0.00			0.7	0.00
<i>Goby</i> sp.1					0.1	0.00			0.1	0.00
<i>Herklotsichthys quadrimaculatus</i>					20.3	0.11			20.3	0.01
Juvenile mugilids					97.8	0.54			97.8	0.03
<i>Leiognathus equula</i>	1.1	0.01	13.1	0.04					14.2	0.00
<i>Lichia amia</i>					3.3	0.02	5434.1	2.39	5437.4	1.88
<i>Liza alata</i>			167.1	0.47			27608.2	12.13	27775.3	9.61
<i>Liza dumerilii</i>					1480.8	8.18	364.0	0.16	1844.8	0.64
<i>Liza macrolepis</i>			90.2	0.25	194.0	1.07	1149.8	0.51	1434.0	0.50
<i>Liza</i> sp.					107.4	0.59			107.4	0.04
<i>Liza tricuspidens</i>					26.7	0.15			26.7	0.01
<i>Micropterus salmoides</i>			79.7	0.22	0.1	0.00	435.5	0.19	515.3	0.18
<i>Monodactylus argenteus</i>							135.1	0.06	135.1	0.05
<i>Monodactylus falciformis</i>			93.9	0.26			517.9	0.23	611.8	0.21
<i>Mugil cephalus</i>	63.3	0.83			1600.9	8.84	19918.3	8.75	21582.4	7.47
<i>Myxus capensis</i>			217.7	0.61	1744.6	9.63	20788.3	9.13	22750.6	7.87
<i>Oligolepis acutipennis</i>			5.3	0.01	6.4	0.04			11.7	0.00
<i>Oligolepis keiensis</i>			23.4	0.07					23.4	0.01
<i>Oreochromis mossambicus</i>	6659.4	87.30	31614.4	88.85	8386.6	46.3	87885.9	38.61	134546.2	46.57
<i>Pomadasys commersonnii</i>	307.4	4.03	647.0	1.82	24.5	0.14	2170.7	0.95	3149.5	1.09
<i>Psammogobius knysnaensis</i>					1.3	0.01			1.3	0.00
<i>Pseudorhombus arsius</i>	22.4	0.29							22.4	0.01
<i>Rhabdosargus holubi</i>			265.6	0.75	193.7	1.07	48.1	0.02	507.4	0.18
<i>Rhabdosargus thorpei</i>			0.8	0.00					0.8	0.00
<i>Scomberoides</i> sp.					6.2	0.03			6.2	0.00
<i>Sillago sihama</i>					0.1	0.00			0.1	0.00
<i>Solea bleekeri</i>	3.1	0.04	1.7	0.02	4.2	0.02			8.9	0.00
<i>Terapon jarbua</i>	4.5	0.06	134.5	0.38	76.9	0.42	1004.9	0.44	1220.9	0.42
<i>Tilapia rendalli</i>			200.0	0.56					200.0	0.07
<i>Valamugil buchanani</i>					46.7	0.26	548.0	0.24	594.7	0.21
<i>Valamugil cunnesius</i>	102.0	1.34	52.6	0.15	1902.1	10.5	54653.4	24.01	56710.1	19.63
<i>Valamugil robustus</i>					71.6	0.40			71.6	0.02
<i>Valamugil</i> sp.					797.8	4.40			797.8	0.28

**Table 3.** Percent similarity of the catch composition of each gear type to the total catch in the Mhlanga estuary (IS<sub>J</sub> = Jaccard's index of similarity, IS<sub>S</sub> = Sørensen's index of similarity)

Gear	IS <sub>J</sub>	IS <sub>S</sub>	Similarity ranking
Beam trawl	27.66	43.33	4
Otter trawl	51.06	67.61	2
Seine net	70.21	82.50	1
Gill nets	38.30	55.38	3

Mhlanga was relatively high in November 1990, February 1991, November 1991 and February 1992. The numerical contribution of marine species increased in February 1992 (Figure 5).

In terms of biomass, freshwater species dominated the fishes collected in August 1990, November 1990 and February 1991. Although the fish community from May 1991 to May 1992 was dominated by estuarine-dependent marine species, the relative contribution of freshwater species to the total fish biomass was relatively high in November 1991 and February 1992. Estuarine species did not constitute a major component of the fish biomass captured throughout the study period, but their contribution did increase in November 1990, November 1991 and May 1992. The biomass

**Table 4.** Results of the Spearman rank correlation test between abiotic and biotic variables in the Mhlanga estuary (August 1990 - May 1992). Shaded areas denote significant ( $p < 0.15$ ) correlation values.

	Depth	Temperature		Salinity		Dissolved Oxygen		Turbidity		Mouth
		Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	% Open
<b>Number of species</b>	$r = -0.69$ $p = 0.07$	$r = 0.55$ $p = 0.14$	$r = 0.71$ $p = 0.06$	$r = 0.58$ $p = 0.12$	$r = 0.59$ $p = 0.12$	$r = 0.16$ $p = 0.68$	$r = 0.24$ $p = 0.95$	$r = 0.00$ $p = 1.00$	$r = -0.16$ $p = 0.68$	$r = 0.84$ $p = 0.03$
<b>Number of fish</b>	$r = -0.69$ $p = 0.08$	$r = 0.29$ $p = 0.45$	$r = 0.38$ $p = 0.31$	$r = 0.55$ $p = 0.15$	$r = 0.12$ $p = 0.75$	$r = -0.50$ $p = 0.19$	$r = -0.36$ $p = 0.34$	$r = 0.02$ $p = 0.95$	$r = 0.12$ $p = 0.75$	$r = 0.21$ $p = 0.57$
<b>Biomass</b>	$r = -0.73$ $p = 0.05$	$r = 0.75$ $p = 0.05$	$r = 0.81$ $p = 0.03$	$r = 0.53$ $p = 0.16$	$r = 0.32$ $p = 0.39$	$r = -0.02$ $p = 0.95$	$r = 0.02$ $p = 0.95$	$r = 0.09$ $p = 0.80$	$r = -0.12$ $p = 0.75$	$r = 0.62$ $p = 0.10$
<b>Richness (D)</b>	$r = -0.47$ $p = 0.22$	$r = 0.47$ $p = 0.22$	$r = 0.59$ $p = 0.12$	$r = 0.32$ $p = 0.39$	$r = 0.56$ $p = 0.13$	$r = 0.33$ $p = 0.38$	$r = 0.17$ $p = 0.66$	$r = -0.19$ $p = 0.61$	$r = -0.36$ $p = 0.34$	$r = 0.69$ $p = 0.07$
<b>Evenness (J')</b>	$r = 0.20$ $p = 0.59$	$r = 0.34$ $p = 0.38$	$r = 0.31$ $p = 0.41$	$r = -0.10$ $p = 0.80$	$r = 0.02$ $p = 0.95$	$r = 0.24$ $p = 0.53$	$r = 0.02$ $p = 0.95$	$r = 0.33$ $p = 0.38$	$r = 0.07$ $p = 0.85$	$r = 0.33$ $p = 0.38$
<b>Diversity (H')</b>	$r = -0.05$ $p = 0.90$	$r = 0.32$ $p = 0.39$	$r = 0.45$ $p = 0.23$	$r = 0.13$ $p = 0.73$	$r = 0.40$ $p = 0.30$	$r = 0.45$ $p = 0.23$	$r = 0.09$ $p = 0.80$	$r = 0.07$ $p = 0.85$	$r = -0.21$ $p = 0.57$	$r = 0.62$ $p = 0.10$
<b>Diversity (H'w)</b>	$r = 0.20$ $p = 0.59$	$r = -0.12$ $p = 0.75$	$r = 0.05$ $p = 0.90$	$r = -0.12$ $p = 0.75$	$r = -0.24$ $p = 0.53$	$r = 0.33$ $p = 0.38$	$r = -0.76$ $p = 0.04$	$r = 0.33$ $p = 0.38$	$r = 0.40$ $p = 0.28$	$r = -0.02$ $p = 0.95$

contribution of marine species to the Mhlanga fish community was low throughout the study period (Figure 6).

**Seasonal changes in actual abundance and biomass:** During this study, peak numbers of freshwater species occurred in November 1990 and November 1991. The biomass of freshwater species captured in the Mhlanga estuary was high in November 1990 and February 1991 with a peak occurring in February 1992. Both the abundance and biomass of estuarine species captured exhibited peaks in November 1990, November 1991 and May 1992. Estuarine-dependent marine species increased in abundance in May 1991 and in November 1991 and their biomass rose steadily throughout the study period with a peak in February 1992. Maximum numbers and biomass of marine species were captured in February 1992 (Figure 7).

#### Principal Species

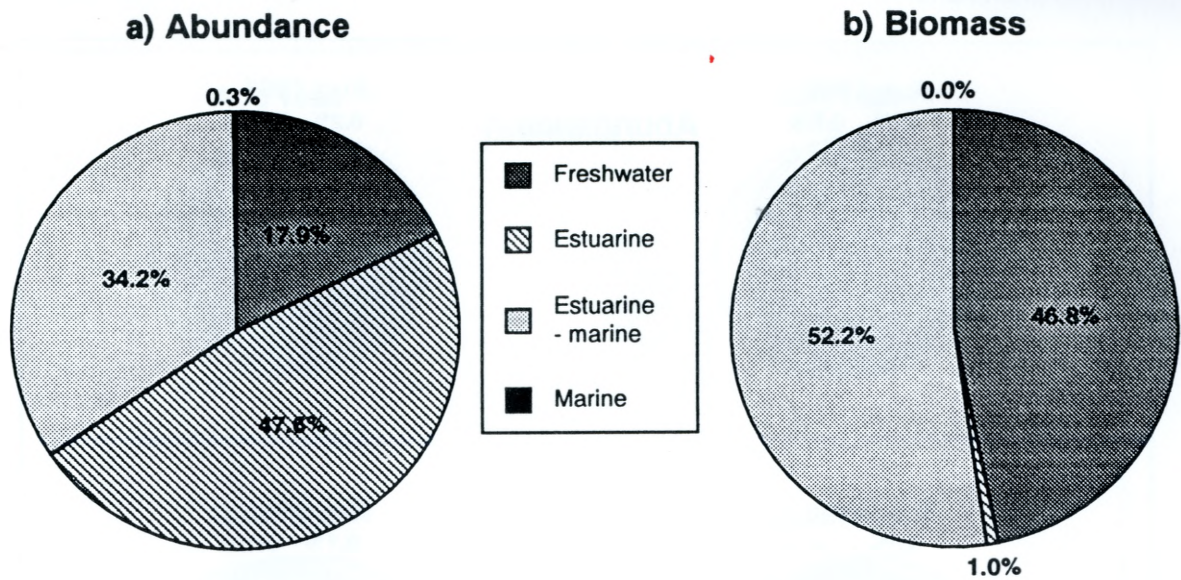
**Oreochromis mossambicus:** *O. mossambicus* exhibited peaks in abundance in November 1990 and November 1991. Biomass peaked in November 1990, February 1991 and February 1992 (Figure 8). *O. mossambicus* ranged in size from below 10 mm to 320 mm, with most specimens in the 10 - 30 mm size classes (Figure 8). Specimens captured in August 1990 were large individuals, mostly between 190 and 250 mm. In November 1990 and November 1991, the *O. mossambicus* captured were mostly below 30 mm. Specimens recorded in February 1991 ranged in size from 10 mm to 270 mm but were mostly juveniles below 60 mm. In May 1991, the 60 - 90 mm size classes predominated. Large specimens, 200 - 230 mm were captured in August 1991. *O. mossambicus* recorded in February 1992 and May 1992 were all larger than 100 mm (Harrison, 1993).

**Gilchristella aestuaria:** Peak numbers and biomass of *G. aestuaria* were recorded in November 1990, November

1991 and May 1992 (Figure 9). *G. aestuaria* was captured throughout the study period and were mostly 20 - 50 mm SL (Figure 9). Specimens captured in August 1990 were all in the 20 - 30 mm size class. *G. aestuaria* in November 1990 ranged in size from 10 - 60 mm but were mostly between 30 and 50 mm. A similar size range was recorded in February 1991 but the bulk of the specimens were in the 40 - 50 mm size class. In May 1991 all *G. aestuaria* were 40 - 60 mm. Specimens collected in August 1991 ranged in size from 20 - 60 mm, with 30 - 60 mm size classes predominating. *G. aestuaria* captured in November 1991 were mostly 20 - 50 mm. In February 1992 most specimens were in the 10 - 20 mm size class, while in May 1992 the 20 - 30 mm size class predominated (Harrison, 1993).

**Valamugil cunnesius:** Peak numbers of *V. cunnesius* were recorded in August 1991 and peak biomass in February 1992 (Figure 10). Size of *V. cunnesius* ranged from 30 - 230 mm, with most specimens in the 30 - 80 mm and 150 - 200 mm size classes (Figure 10). Specimens of 30 - 50 mm and those 150 - 180 mm predominated in August 1990. The *V. cunnesius* captured in November 1990, February 1991 and May 1991 were mostly 150 - 200 mm. In August 1991 the bimodal grouping was again evident and persisted through to May 1992 (Harrison, 1993).

**Myxus capensis:** High numbers and biomass of *M. capensis* were captured between August 1991 and February 1992 (Figure 11). Specimens ranged from 20 - 300 mm SL (Figure 11). Juveniles, predominantly in the 50 - 60 mm size class, and larger specimens 210 - 230 mm were recorded in August 1990. In November, *M. capensis* ranged from 30 - 210 mm, with specimens below 80 mm being well represented. Specimens 160 - 230 mm dominated the February, May and August 1991 collections. Juveniles below 40 mm



**Figure 4.** Percent numerical (a) and biomass (b) contribution of freshwater, estuarine, estuarine-dependent marine and marine species to the total ichthyofauna of the Mhlanga estuary.

predominated in November 1991 and February 1992 (Harrison, 1993).

***Mugil cephalus*:** High numbers of *M. cephalus* were captured in November 1990 but the peak in biomass was recorded in February 1992 (Figure 12). *M. cephalus* ranged from 30 - 320 mm, with most specimens 90 - 270 mm (Figure 12).

***Liza alata*:** The number of *L. alata* peaked in May 1991, with the biomass following a similar trend but peaking in February 1992 (Figure 13). *L. alata* ranged in size from 150 - 330 mm with most specimens in the 160 - 270 mm size classes (Figure 13).

## DISCUSSION

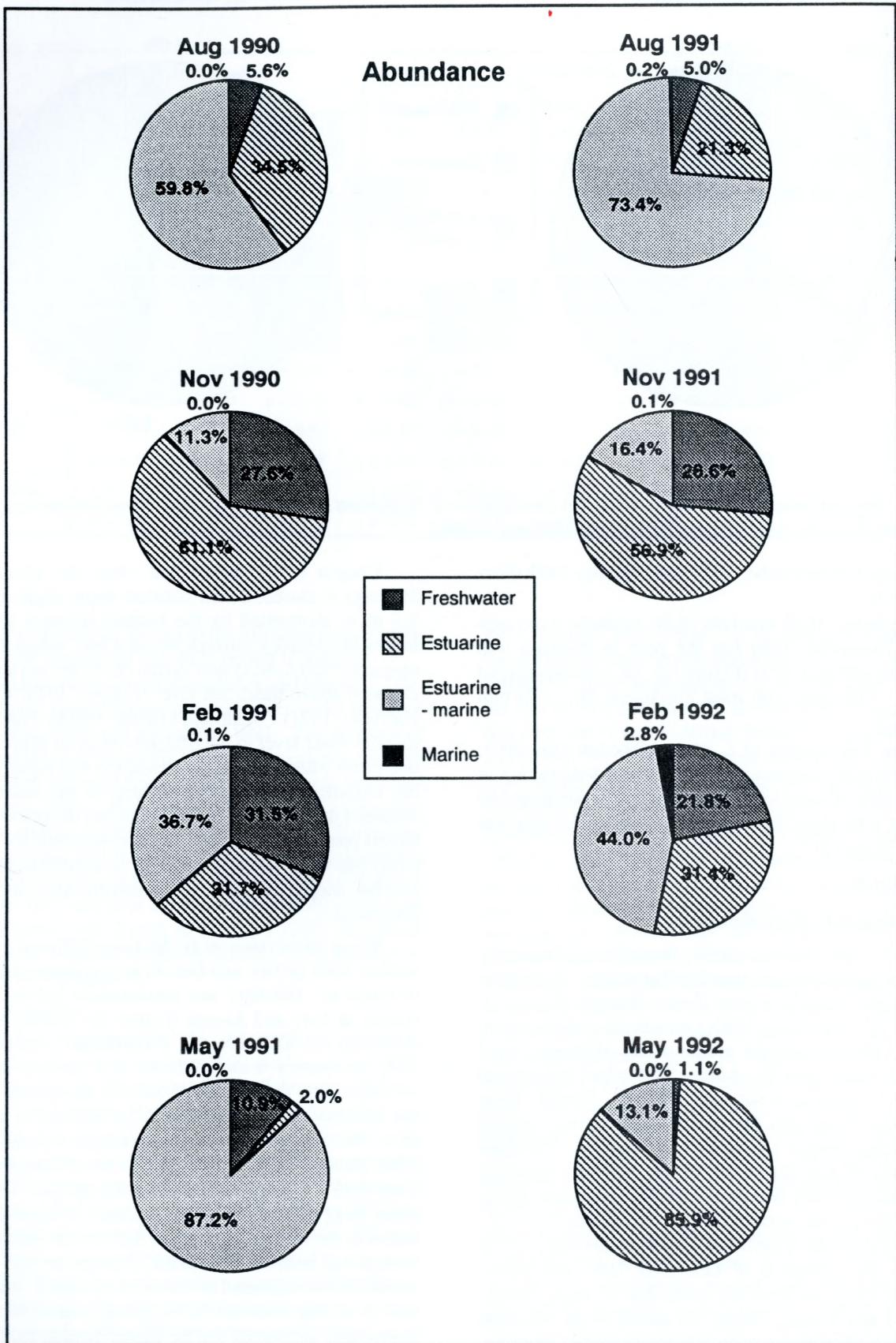
### Physicochemical Characteristics

The mouth of the Mhlanga estuary opened most frequently during the spring/summer months (September - February) but remained closed in winter (June - August) (Figure 2). Whitfield (1980a; 1980b; 1980c) recorded a similar pattern during his study where the mouth of the Mhlanga closed during the winter months (April - September) but opened following heavy rains in summer (October - March). Begg (1984b) also noted that the mouth of the system opened during spring/summer (November - February). Whitfield (1980b) found that the mouth of the Mhlanga generally closes within 10 days and Begg (1984b) found that during his study the system opened for periods ranging from 12 - 15 days. The mouth of the Mhlanga during this study period was, with the exception of December 1990 and February/March 1991, not open for more than 12 days, usually between 3 and 5 days. When the mouth of the Mhlanga opens against beachrock outcrops, the increased scour enables the mouth to remain open for up to 3 weeks (Cooper, 1991). This probably accounted for the long periods the mouth remained open in December 1990 and February/March 1991.

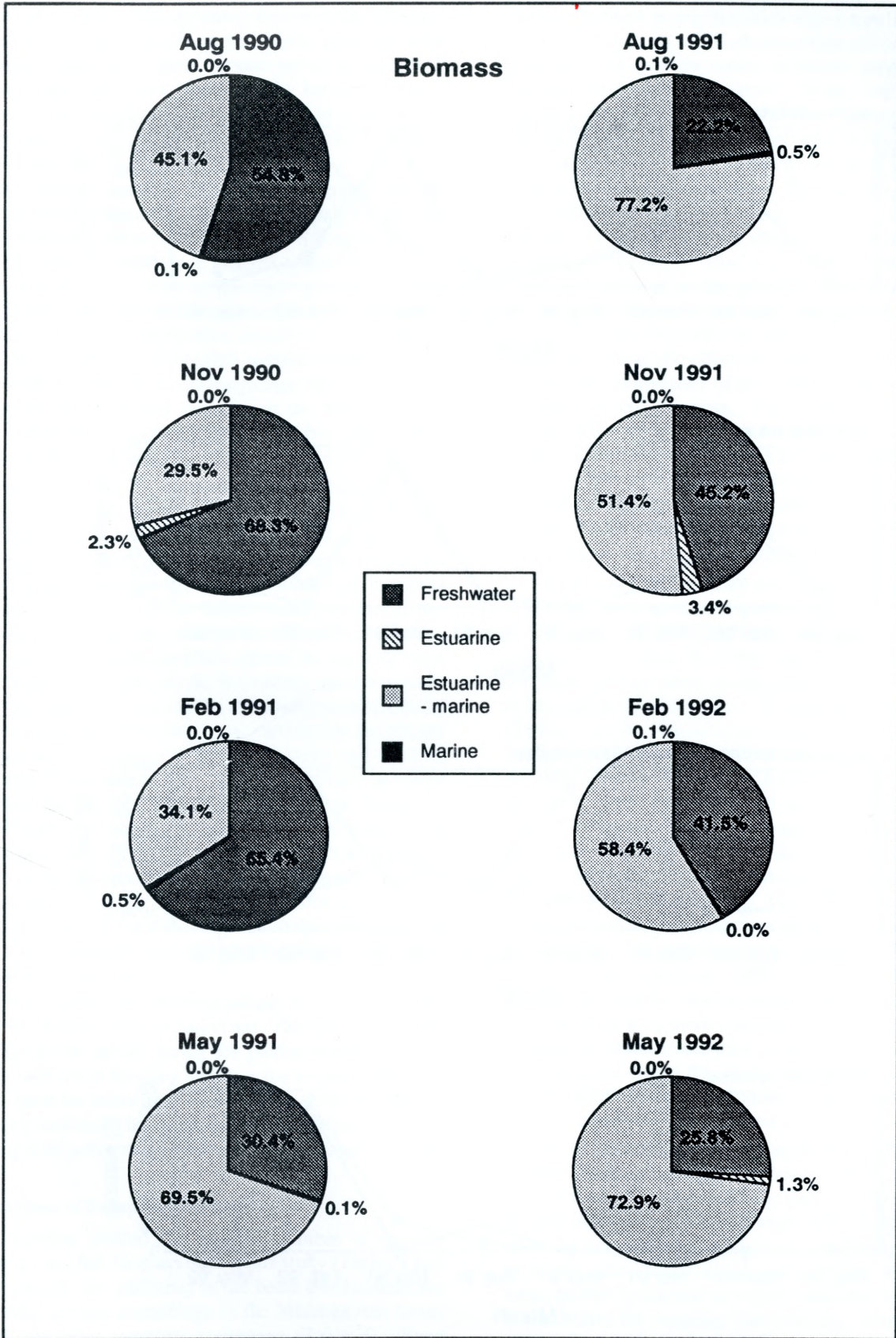
Cooper (1991) noted that when the mouth of the Mhlanga is closed, a near-constant water depth averaging 1.5 m is maintained by the balance between freshwater inflow and seepage through the sand bar. When the mouth opens, however, the system drains due to the bed level being elevated above mean sea level (Cooper, 1989; Cooper & Harrison, 1992). Whitfield (1980a; 1980b; 1980c) noted that the water level in the Mhlanga dropped approximately one metre when the estuary opened but rose rapidly following closure. The frequent opening of the mouth of the Mhlanga during spring and summer and the predominantly closed phase during winter probably accounts for the relatively low water levels recorded in November and February and the deeper nature of the system in May and August (Figure 2).

Water temperature in the Mhlanga followed a seasonal pattern, with surface and bottom temperatures above 27°C recorded in February and temperatures below 19°C recorded in May and August (Figure 2). During his study Whitfield (1980c) recorded a maximum temperature of 30°C in January a minimum of 14°C in July and Begg (1984b) found that the temperature of the surface water in the Mhlanga ranged from 28.5°C in February to 14.9°C in June. With the exception of temperatures recorded in May 1991, bottom water temperatures in the Mhlanga were not more than 1°C lower than those at the surface. During his study Begg (1984b) found no evidence of thermal stratification in the Mhlanga but noted that inverse thermal stratification had been recorded in the Mhlanga and was a feature commonly encountered in estuaries in winter, wherever a lack of mixing occurred due to salinity stratification. This is probably accounted for the higher bottom temperatures recorded in May 1991 (Figure 2).

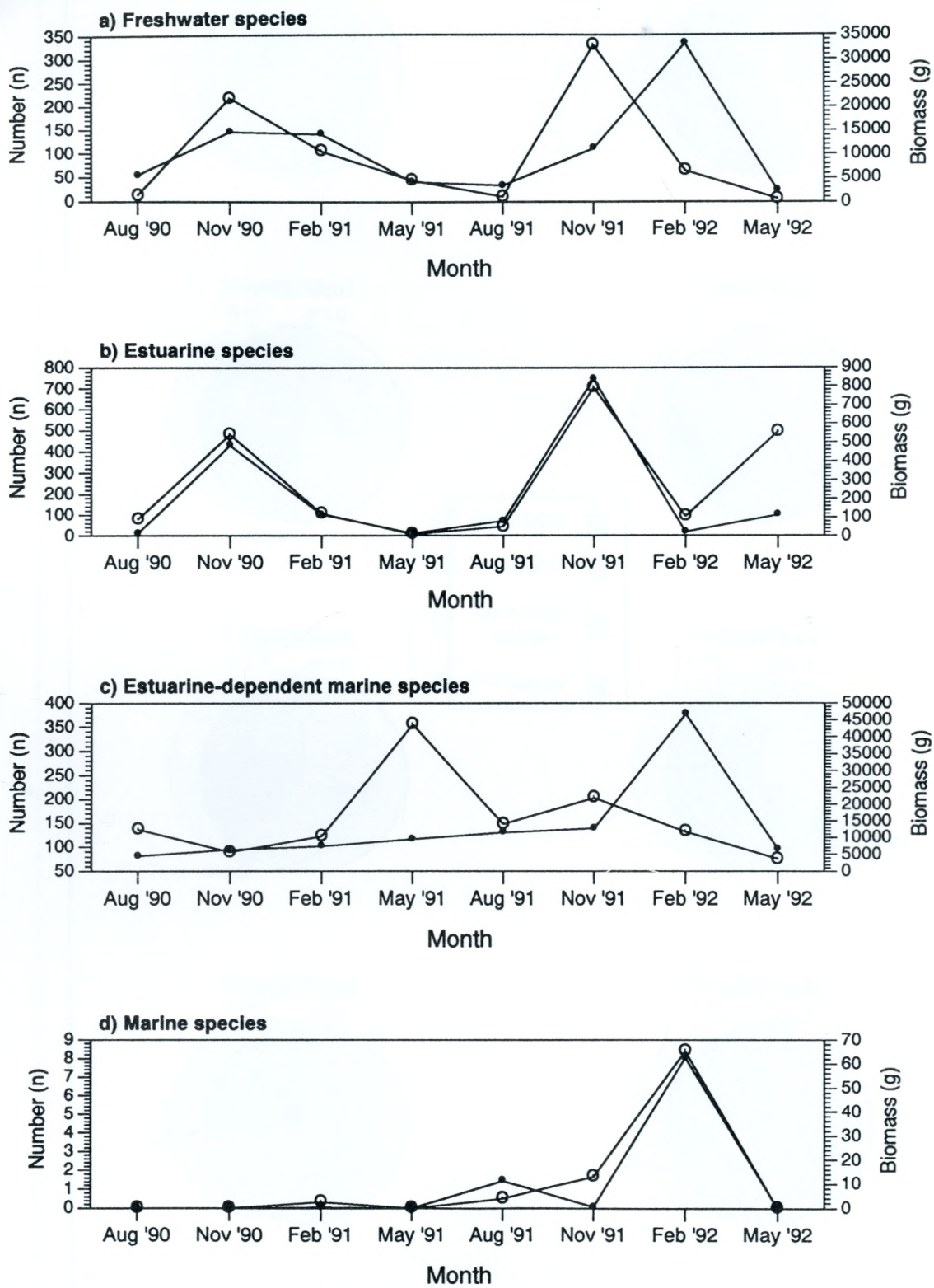
During this study surface salinities in the Mhlanga did not exceed 5‰ while bottom salinities ranged from 1 - 11‰ (Figure 2). Whitfield (1980a; 1980b; 1980c) found that



**Figure 5.** Seasonal numerical composition of freshwater, estuarine, estuarine-dependent marine and marine fish species in the Mhlanga estuary.



**Figure 6.** Seasonal biomass composition of freshwater, estuarine, estuarine-dependent marine and marine fish species in the Mhlanga estuary.



**Figure 7.** Seasonal fluctuations in the number (○) and biomass (●) of freshwater species (a), estuarine species (b), estuarine-dependent marine species (c) and marine species (d) in the Mhlanga estuary.



salinities in the Mhlanga ranged between 0‰ and 34‰ but were generally less than 10‰. Begg (1984b) also noted that low salinities were a distinguishing feature of the Mhlanga but that during open phases, much higher salinities were encountered and the system became vertically stratified. Sea water may also enter the estuary by barrier overwash (Cooper, 1989) and these two factors may have accounted for the relatively high bottom salinities recorded in February 1991 and May 1991 (Figure 2).

The average surface oxygen concentration in the Mhlanga ranged from 4.2 mg l<sup>-1</sup> to 13.3 mg l<sup>-1</sup> and the average bottom oxygen ranged from 3.7 - 8.9 mg l<sup>-1</sup> (Figure 2). Begg (1984b) noted that in general, bottom water in the Mhlanga tended to carry about 0.8 mg l<sup>-1</sup> less oxygen than at the surface and that the average surface oxygen ranged from 4.2 - 6.4 mg l<sup>-1</sup> while bottom dissolved oxygen ranged from 2.9 - 5.5 mg l<sup>-1</sup>. The higher oxygen values recorded in the surface waters of the Mhlanga may be a result of the decomposition of organic material in the bottom waters together with these waters being cut off from the surface circulation due to salinity stratification (Figure 2).

Except during November 1991, turbidity in the Mhlanga estuary was low (NTU) (Figure 2). Begg (1984b) noted that water in the Mhlanga was generally clear due to the system being relatively deep when closed and protected from the wind, making resuspension of the bottom materials difficult. Whitfield (1980a) linked water turbidity in the Mhlanga to river flow and estuary mouth condition. During the closed phase, sediment loads carried by the river were low and water transparency in the estuary relatively high. Following rains in the catchment, suspended sediment in the river increased and this material was carried into the estuary when the mouth opened, decreasing the water transparency in this area (Whitfield, 1980a). Heavy spring rains probably accounted for the high turbidities recorded in November 1991 (Figure 2). On one occasion during his study, Begg (1984a) recorded a plume of turbid river water in the upper reaches of the system extending over much clearer but more saline estuarine water. Surface turbidity during this study was slightly higher than that recorded in the bottom waters and this is probably due to slight salinity stratification within the system (Figure 2).

To summarise, the Mhlanga estuary is cut off from the sea for much of the year by a sand bar. The system normally opens for a few weeks during the predominantly summer rainy season when flooding breaches the barrier. When the mouth opens the water level in the system drops rapidly and the strong outflow of turbid water decreases after a few days allowing tidal penetration of seawater up the estuary (Figure 2).

### Comparison of Sampling Methods

Beam trawling yielded the smallest number of species, specimens and fish biomass during this study (Tables 1 and 2). As a result, the similarity of the beam trawl collections to the total species assemblage in the Mhlanga was lower than all the other sampling equipment (Table 3). Begg (1984a, 1984b) noted that water depth had a marked influence on the catch of the beam trawl in that during periods of high water, the fishes within a system become diluted thus increasing escape possibilities and reducing the vulnera-

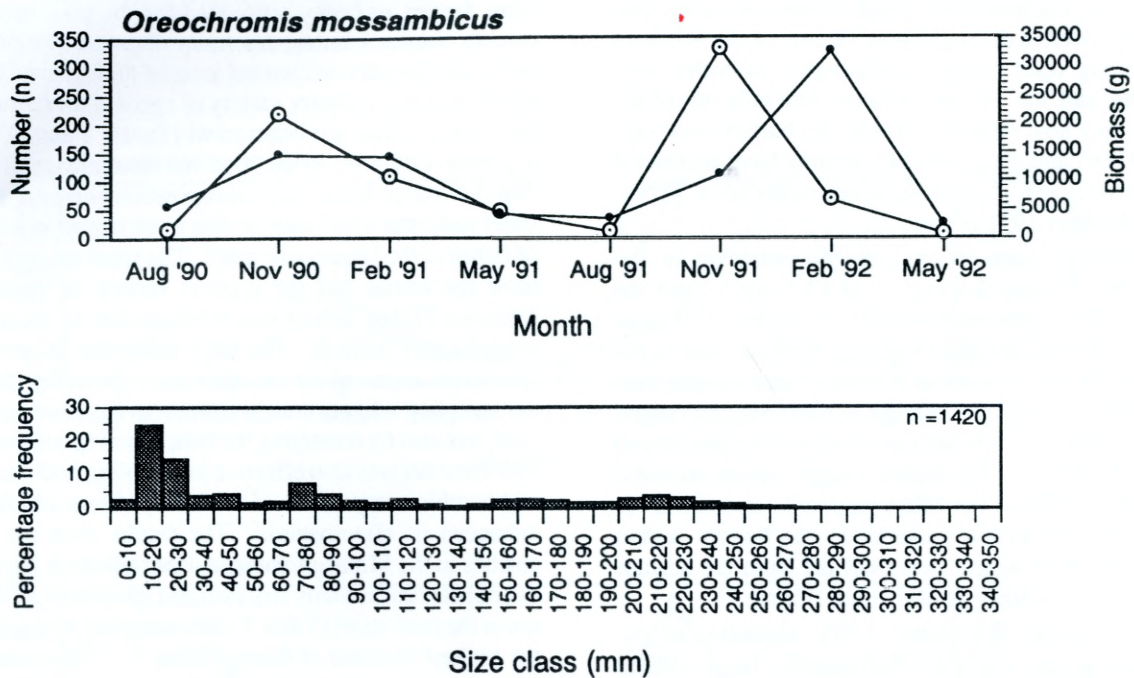
bility of both pelagic and demersal species to capture. The same factors probably accounted for the poor beam trawl catches obtained during this study where trawling was limited to the deeper mid channel areas of the estuary. The otter trawl captured a greater variety of species, more specimens and biomass than the beam trawl (Tables 1 and 2) and had a greater similarity to the total fish assemblage (Table 3). The difference in the catch composition between the beam trawl and otter trawl may be due to increased vulnerability of fishes to the larger otter trawl. The seine net captured the most specimens and the greatest variety of fishes in the Mhlanga (Table 1) and was most similar to the total fish assemblage (Table 3). The large collection of species and specimens captured by the seine net is probably due to the net sampling a larger area in relation to the other equipment used and also by encircling the fish, reducing net avoidance. The seine net was also effective in sampling both the pelagic and benthic components of the ichthyofauna which further enhanced its effectiveness. The results from the gill net catches in the Mhlanga, indicated that although the gill nets did not capture as many fish taxa and specimens as the seine net or the otter trawl (Table 1), this sampling method yielded the highest biomass of fishes (Table 2). This is due to the gill nets more effectively sampling larger, swifter fishes which are not effectively sampled using other gear.

Beam and otter trawls are effective for sampling bottom fishes and fishes of limited mobility (Lagler, 1971; Gibbs & Matthews, 1981/1982). This is reflected by the species composition of both the beam and otter trawls where the dominant species were mostly slow moving or demersal fishes such as *O. mossambicus*, *G. aestuaria* and *G. callidus* (Tables 1 and 2). The seine net collections were dominated by *G. aestuaria*, *O. mossambicus* and mugilids, particularly juveniles (Tables 1 and 2). Juvenile fishes in estuaries appear to prefer shallow littoral areas (Wallace & van der Elst, 1975; Blaber, 1985) and studies on relative gear selectivity and efficiency revealed that seine netting sampled littoral fish more effectively than other equipment (Hartman & Herke, 1987; Hayes, 1989). Gill nets, made of panels of different mesh sizes, are standard gears used by researchers for sampling fish populations in deeper estuarine waters (Marais, 1985; Craig et al., 1986). Hayes (1989) found that gill nets selected for large midwater fish, particularly adult and sub-adult grey mullet which, being strong swimmers, avoided the small seines used in his study. Similar results were obtained during this study where mugilids (*V. cunnesius*, *L. alata*, *M. capensis* and *M. cephalus*) dominated the gill net collections (Tables 1 and 2).

In the Mhlanga, each sampling technique differed in the number, biomass and type of fishes collected (Tables 1 and 2). Beam trawling appeared to be the least effective method of sampling the ichthyofauna while seine netting appeared to be the most effective method for sampling juvenile fish in littoral areas. Gill netting was effective for collecting large, mobile specimens in deeper waters and otter trawling was effective for sampling slow moving, demersal species in mid-channel areas.

### Community Structure

Of the 47 fish taxa captured in the Mhlanga estuary, *Gilchristella aestuaria*, *Oreochromis mossambicus*, *Vala-*



**Figure 8.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Oreochromis mossambicus* in the Mhlanga estuary.

*mugil cunnesius*, *Valamugil* sp. and juvenile mugilids were the most abundant (Table 1). Of the 21 fish species recorded by Whitfield (1980c), *O. mossambicus* (34.5%), *V. cunnesius* (17.6%) and *G. aestuaria* (10.8%) were the dominant species. Begg (1984a) recorded 16 species of fish in the Mhlanga and found that *V. cunnesius* (29.7%), *O. mossambicus* (21.6%), *Glossogobius giuris* (15.6%) and *G. aestuaria* (7%) were most abundant. Fifteen fish taxa were recorded by Ramm et al. (1986) and *V. cunnesius* (50.7%), juvenile mugilids (16.0%) and *Liza dumerilii* (8.6%) were the dominant taxa. Harrison (1990) captured 28 fish taxa in the Mhlanga and found that *G. aestuaria* (46.4%), *V. cunnesius* (14.5%), *L. alata* (8.0%), *O. mossambicus* (7.6%), *Myxus capensis* (6.0%) and *Mugil cephalus* (5.6%) were the dominant species.

In terms of biomass, *Oreochromis mossambicus*, *Valamugil cunnesius*, *Liza alata*, *Myxus capensis* and *Mugil cephalus* dominated the ichthyofauna in the Mhlanga (Table 2). Data from Whitfield (1980c) also revealed that *O. mossambicus* (26.4%), *V. cunnesius* (20.8%), *L. alata* (14.2%), *M. capensis* (12.5%) and *M. cephalus* (12.0%) dominated the fish biomass.

**Freshwater species:** Freshwater fishes in the Mhlanga estuary contributed 17.9% (46.8% by mass) to the ichthyofauna captured during this study (Figure 4). Data from Whitfield (1980c) revealed that this group of fishes comprised 34.5% by numbers and 26.4% by mass of the total ichthyofauna. Freshwater species contributed 21.6% to the total fish community captured by Begg (1984b), 3.7% of the fishes captured by Ramm et al. (1986) and 7.7% by Harrison (1990).

Freshwater species captured during this study were primarily *Oreochromis mossambicus* which comprised 17.8% numerically and 46.6% of the total fish biomass (Tables 1 and 2). Whitfield (1980c) found that in the Mhlanga, *O. mossambicus* numerically comprised 34.5% and 26.4% by mass of the total fishes captured. Begg (1984b) found that *O. mossambicus* numerically comprised 21.6% of the catch in the Mhlanga. *O. mossambicus* comprised 3.7% of the catch made by Ramm et al. (1986) and 7.6% by Harrison (1990). Differences in gear used probably account for the changes in *O. mossambicus* representation during the various studies.

*Oreochromis mossambicus* is a secondary freshwater cichlid (Skelton 1993) indigenous to southeast Africa. It is tolerant of a broad range of salinities and temperatures and occurs in widely differing habitats such as rivers, lakes and estuaries (Whitfield & Blaber, 1979; Bruton et al., 1982). Whitfield & Blaber (1979) found that *O. mossambicus* was common in seasonally closed estuaries and coastal lakes, but absent from permanently open tidal estuaries. Begg (1984a) also noted that *O. mossambicus* dominated the ichthyofauna in typically closed estuaries in Natal.

*O. mossambicus* breeds during spring and summer (September to February) when adult males move from deeper waters and congregate in shoals in shallow areas where they establish and defend their territories (Bruton & Bolt, 1975). The female broods the eggs and young in her mouth and when the fry have reached 9-10 mm they are released in shallow (0.1 m deep), calm, well vegetated areas (Bruton & Bolt, 1975). One female may produce three to four broods in a single season.

The peak numbers of predominantly juvenile (<30 mm) *O. mossambicus* recorded in November (Figure 8; Harrison, 1993) corresponds to the breeding cycle of this species. The high biomass recorded in February (Figure 8) is a result of predominantly larger specimens being captured (Harrison, 1993). During the cool winter months *O. mossambicus* usually inhabits deeper waters (Bruton & Bolt, 1975). This may be responsible for the low number and biomass of *O. mossambicus* recorded in May and August (Figure 8).

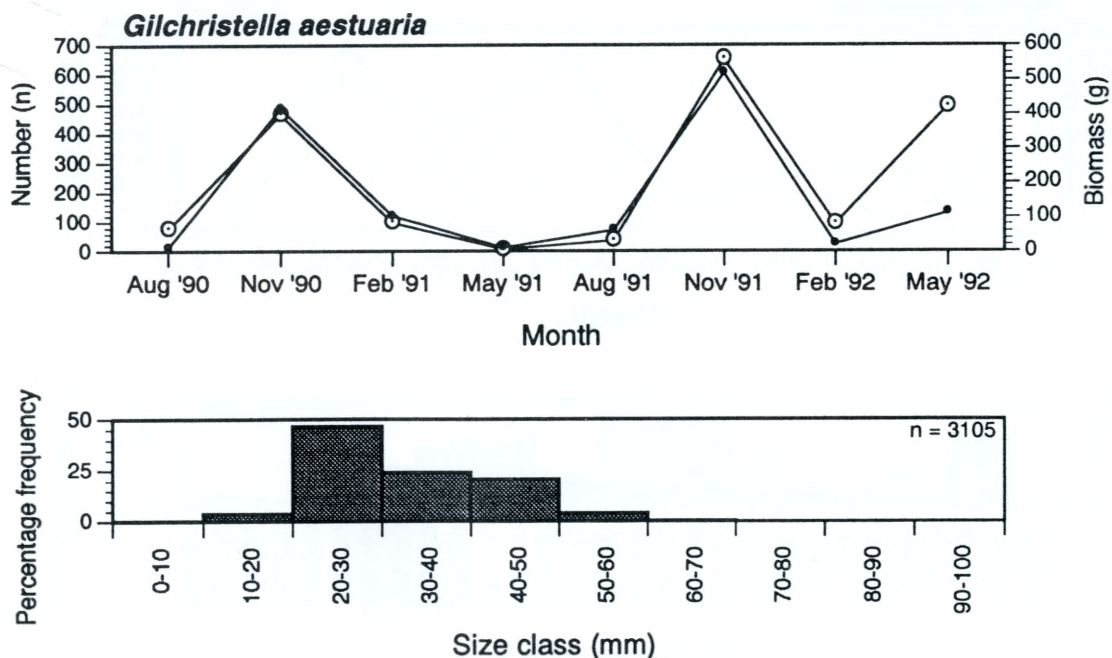
**Estuarine species:** This group of fishes numerically accounted for 47.6% of the ichthyofauna collected in the Mhlanga during this study (Figure 4). Data from other studies revealed that estuarine species comprised 19.1% of the fishes captured by Whitfield (1980c), 22.7% of the fishes collected by Begg (1984b), 0.9% of the fishes captured by Ramm et al. (1986) and 47.3% of the catch made by Harrison (1990). Differences in gear used probably account for the above differences in representation.

Species which can complete their entire life cycle within estuaries are usually small in size (Wallace et al., 1984) and as a consequence did not contribute significantly to the total fish biomass (Figure 4). This group of fishes comprised less than 1% of the fish biomass in the Mhlanga during this study and 2.2% of the fish biomass recorded by Whitfield (1980c).

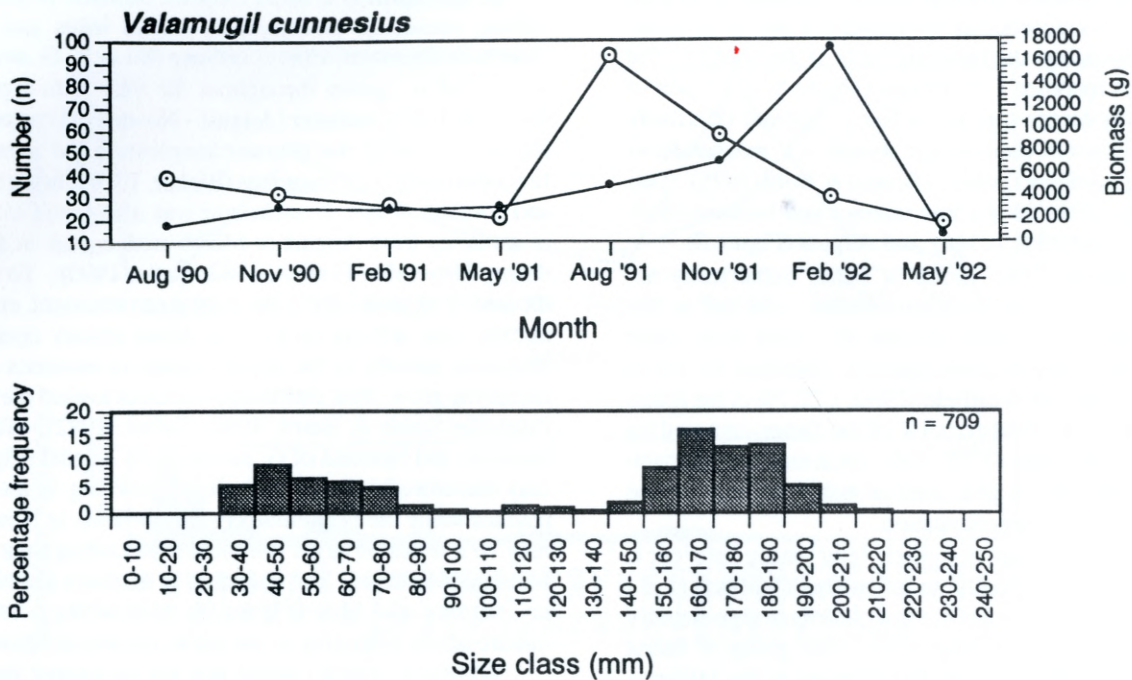
*Gilchristella aestuaria* was the dominant estuarine species captured in the Mhlanga and accounted for 45.7% by number and 0.8% by mass of the total fish fauna (Tables 1 and 2). During his study, Whitfield (1980c) found that *G. aestuaria* comprised 10.8% numerically and 0.2% by mass of the fish fauna captured in the Mhlanga. *G. aestuaria* accounted for 7.0% of the total fish fauna captured by Begg (1984b) and 46.4% of the catch made by Harrison (1990).

*G. aestuaria* is a small clupeid, endemic to southeast Africa, occurring in estuaries, coastal lakes and rivers (Smith & Heemstra, 1986). In Lake St Lucia, *G. aestuaria* was found to spawn throughout the year with a peak in spring and early summer (August - November) corresponding with a general rise in water temperature and an increase in zooplankton food resources (Blaber, 1979). In the eastern and southern Cape, *G. aestuaria* was also found to spawn in estuaries from August to March with a peak in activity during November (Talbot, 1982; Ratte, 1990). To reduce the loss of eggs and fry to the marine environment, either by normal tidal activity or when a closed estuary opens, *G. aestuaria* spawns in the upper reaches of estuaries and as the larvae grow, their distribution extends toward the mouth (Melville-Smith & Baird, 1980; Talbot, 1982). The low numbers and biomass of *G. aestuaria* in August (Figure 9) may therefore be due to the adults spawning in the upper reaches while the peak numbers and biomass in November may be a result of larger individuals extending their distribution downstream. The reduction in numbers and biomass in February and May (Figure 9) is possibly a result of mature adults migrating to the upper reaches to spawn.

Whitfield (1980b) stated that the prolonged breeding season of *G. aestuaria* is important in temporarily closed estuaries since breaching of the sand bar due to sudden thunderstorms and resultant fluctuation in physical conditions, can occur at any time of the year. He found that breeding of *G. aestuaria* in Mhlanga occurred during the closed phase of the estuary, enabling the fry to utilize a winter peak in zooplankton (Whitfield, 1980c). This may account for the high numbers and the occurrence of juvenile *G. aestuaria* in May 1992 (Figure 9; Harrison, 1993).



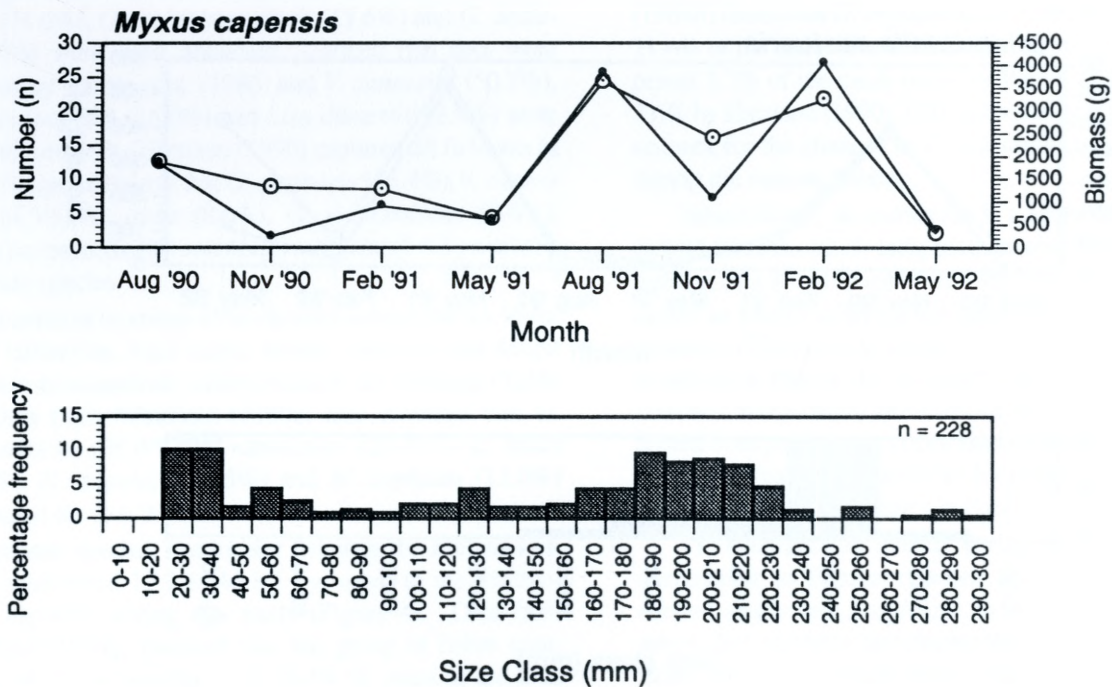
**Figure 9.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Gilchristella aestuaria* in the Mhlanga estuary.



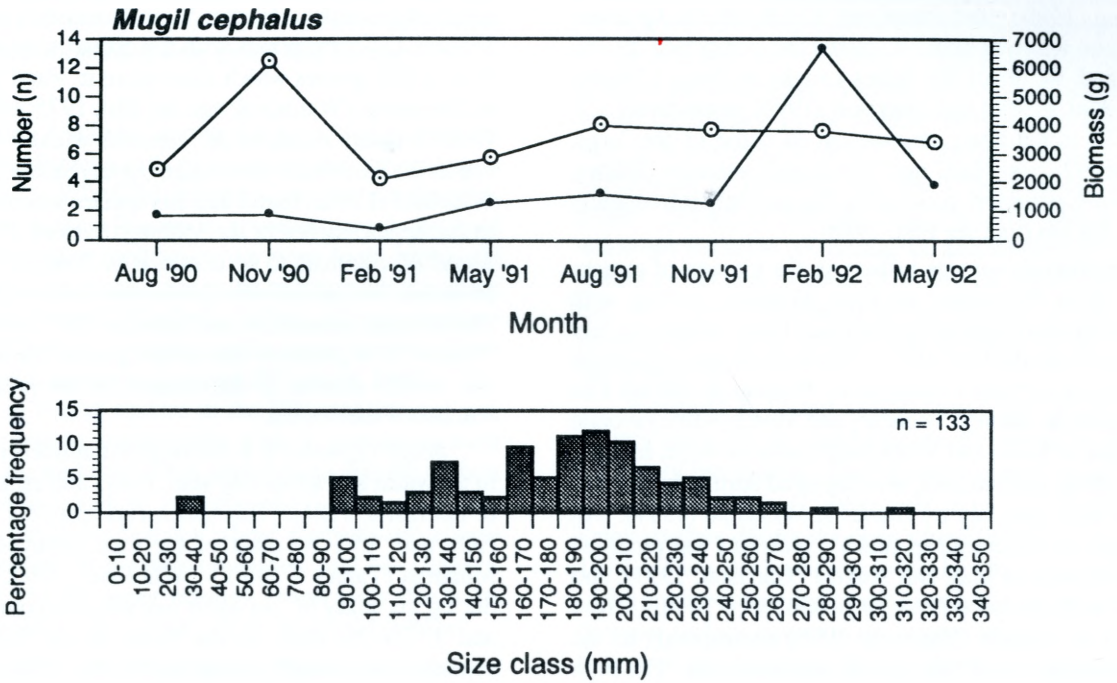
**Figure 10.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Valamugil cunnesius* in the Mhlanga estuary.

**Estuarine-dependent marine species:** This group of fishes comprised 34.2% (52.2% by mass) of the total ichthyofaunal assemblage captured in the Mhlanga during this study (Figure 4). Estuarine-dependent marine species comprised 46.3% by number and 71.4% by mass of the fish

fauna captured by Whitfield (1980c). This group of fishes numerically comprised 55.7%, 94.7% and 45.0% of the fishes collected by Begg (1984b), Ramm et al. (1986) and Harrison (1990) respectively.



**Figure 11.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Myxus capensis* in the Mhlanga estuary.

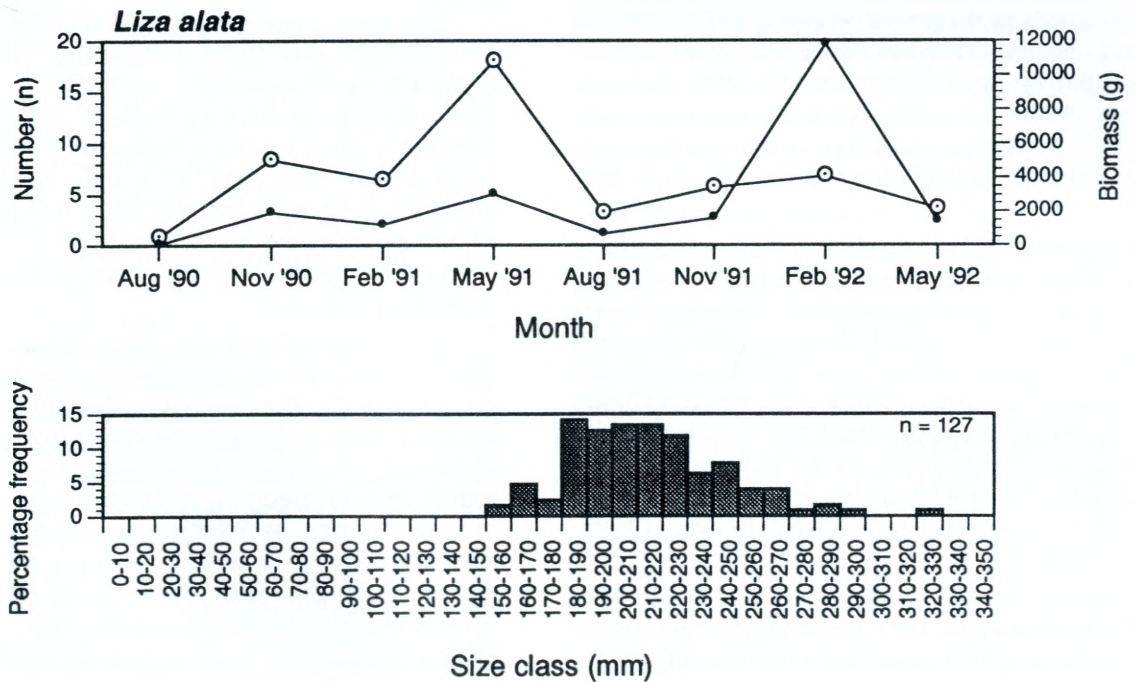


**Figure 12.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Mugil cephalus* in the Mhlanga estuary.

Estuarine-dependent marine species captured in the Mhlanga estuary during this study were dominated by mugilids, particularly *Valamugil cunnesius*, *Valamugil* sp., juvenile mugilids, *Myxus capensis*, *Mugil cephalus* and *Liza alata* (Tables 1 and 2). Together these mugilids comprised

25.9% numerically and 44.9% by mass of the total ichthyofaunal catch during this study.

*Valamugil cunnesius* was the dominant mullet species and comprised 8.9% numerically and 19.6% by mass of the total fishes captured (Tables 1 and 2). *V. cunnesius* was also



**Figure 13.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Liza alata* in the Mhlanga estuary.

the dominant mullet species captured in the Mhlanga by Whitfield (1980c) and comprised 17.6% (20.8% by mass) of the total ichthyofauna. *V. cunnesius* comprised 29.7%, 50.7% and 14.5% of the fishes caught by Begg (1984b), Ramm et al. (1986) and Harrison (1990) respectively. *V. cunnesius* is relatively uncommon in some of the large, permanently open Natal and Pondoland estuaries (Blaber, 1977) but is common in estuaries that are only infrequently open to the sea (van der Elst, 1988).

*V. cunnesius* spawns inshore in the vicinity of estuary mouths from November to June (Wallace, 1975b) with recruitment into estuaries taking place from January to July (Wallace & van der Elst, 1975). The best catches of juvenile *V. cunnesius* in Natal's estuaries by Wallace & van der Elst (1975) were in January, February and March; while juvenile *Valamugil* in Natal and Pondoland estuaries were, in addition to spring and summer, also captured during the months of May, June and July by Blaber & Whitfield (1977). An abundance of *Valamugil* sp. and *V. cunnesius* was recorded in the Mhlanga in May and August (Harrison, 1993), and together with the occurrence of juveniles (< 70 mm) from February to August (Harrison, 1993) corresponds to the recruitment period of this species into estuaries. The high biomass of *V. cunnesius* in February 1992 and subsequent decline in May 1992 (Figure 10) may be a result of emigration of mature specimens from the system to spawn at sea.

In Natal, estuarine-dependent marine species generally spawn inshore in the vicinity of estuary mouths during late autumn, winter and spring (May - November) (Wallace, 1975b). Recruitment of juveniles into estuaries takes place mainly during winter and spring (June - November) (Wallace & van der Elst, 1975). Blaber & Whitfield (1977) recorded juvenile mullet in Natal and Pondoland estuaries during spring and summer. A peak in juvenile mugilids was recorded in the Mhlanga in November (Harrison, 1993) and corresponds to the general spawning and recruitment pattern of estuarine-dependent marine fish. A peak in juvenile mugilids was also recorded in May 1991 (Harrison, 1993) and this may be a reflection of the later recruitment period of *V. cunnesius*, which recruits into estuaries from summer to winter (January - July) (Wallace & van der Elst, 1975).

*Myxus capensis* is a facultative catadromous mullet species which often spends parts of its life in freshwater, with 0+ juveniles ascending rivers and returning to the sea to spawn (Bok, 1979; Smith & Heemstra, 1986; Bruton et al., 1987). *M. capensis* accounted for 2.8% numerically and 7.9% by mass of the fishes captured in the Mhlanga (Tables 1 and 2). Whitfield (1980c) found that the above species contributed 4.12% numerically and 12.5% by mass towards the total ichthyofauna of the system. *M. capensis* comprised 1.6% of the fishes captured in the Mhlanga by Begg (1984b), 3.7% by Ramm et al. (1986) and 6.1% by Harrison (1990).

In Natal *M. capensis* spawns mainly from April to May (Wallace & van der Elst, 1975; Blaber, 1987). Bok (1979) and Bruton et al. (1987) found that in the eastern Cape this species spawns throughout the year with a peak in spring. High numbers and biomass of *M. capensis* were recorded in August and the subsequent reduction in November (Figure 11) may be a result of adults emigrating from the system to

spawn at sea. The high abundance, together with the occurrence of juveniles <60 mm SL in November and February (Figure 11) corresponds with the estuarine recruitment period of this species which takes place in Natal from August to December (Wallace & van der Elst, 1975; Blaber, 1987). Once it enters estuaries *M. capensis* usually migrates towards the freshwater dominated upper reaches (Bok, 1979). Whitfield (1980a) found that this species was most common in the upper reaches of the Mhlanga system. Blaber (1977) found *M. capensis* to be common in Pondoland and Natal estuaries, but had a distinct preference for low salinity areas. The decrease in numbers and biomass of *M. capensis* in May (Figure 11) is probably due to this species leaving the lower and middle reaches of the estuary for the preferred upper reaches of the system.

*Mugil cephalus* is a circumglobal mullet species found in all warm and temperate seas, rivers and estuaries (Smith & Heemstra, 1986). This species comprised 1.7% numerically and 7.5% by mass of the total ichthyofauna in the Mhlanga (Tables 1 and 2). Whitfield (1980c) found that during his study *M. cephalus* numerically comprised 3.7% and 12.0% by mass of the fishes in the Mhlanga. *M. cephalus* numerically comprised 3.8%, 5.5%, 5.6% of the fishes caught in the Mhlanga by Begg (1984b), Ramm et al. (1986) and Harrison (1990) respectively.

*M. cephalus* spawns in the shallow inshore marine environment between May and September (Wallace, 1975b), with recruitment of juveniles (<40 mm total length) into Natal estuaries occurring from June to October (Wallace & van der Elst, 1975; Blaber, 1987). The high numbers and low biomass of *M. cephalus* in November 1990 together with the occurrence of juveniles (<100 mm) in November and February (Figure 12; Harrison, 1993) may be a reflection of the successful recruitment of this species into the system.

*Liza alata* is one of the largest mugilids in the Indo-West Pacific region (Smith & Heemstra, 1986). *L. alata* comprised 1.6% numerically and 9.6% by mass of the ichthyofauna in the Mhlanga (Tables 1 and 2). Whitfield (1980c) found that *L. alata* accounted for 0.9% of the fishes caught in the Mhlanga and 14.2% of the total biomass. *L. alata* numerically accounted for 1.8% of the fishes captured by Ramm et al. (1986) and 8.0% by Harrison (1990). *Liza alata* was not captured by Begg (1984b), probably as a result of the trawl gear used.

All *L. alata* captured were above 150 mm (Figure 13) which accounts for the high biomass contribution of this species (Table 2). The abundance of *L. alata* increased from spring to autumn with numbers declining in August (winter) (Figure 13). *L. alata* biomass values followed a similar pattern. Peak numbers of *L. alata* were captured in October in Lake St Lucia by Whitfield & Blaber (1978a). The spawning period of *L. alata* is unknown but recruitment starts at 14 mm (SL) from July to January (Blaber, 1987). No juveniles were captured during this study.

**Marine species:** This group represented only 0.3% of the fishes captured (Figure 4), with a negligible contribution to biomass. Marine species were not captured in the Mhlanga by Whitfield (1980c), Begg (1984b), Ramm et al. (1986) or Harrison (1990). The occurrence of marine species in the

Mhlanga, particularly in February 1992 (Figure 7) is most likely a result of this group of fishes entering the system when the mouth opened during spring and summer.

### Seasonality

**Winter (June - August):** During the dry winter months the mouth of the Mhlanga estuary is closed and the system is deep (Figure 2). Whitfield (1980a) found that the distribution of fishes in the Mhlanga is governed largely by food availability and that food resources were high during the closed phase of the estuary due to the relative stability of the physical environment (Whitfield, 1980c). *O. mossambicus* was found to be most abundant in the upper reaches where benthic floc was most concentrated (Whitfield, 1980a). The distribution of mullet species in the Mhlanga estuary was related to substrate composition with *V. cunnesius* most abundant in the middle reaches where there was the highest proportion of fine sand, *M. cephalus* and *L. alata* were most common in the lower reaches where medium and coarse sand was present in greatest quantities, and *M. capensis* predominated in the upper reaches, presumably due to its catadromous life history (Bok, 1979; Whitfield, 1980a).

The relatively low numerical contribution of freshwater species (*O. mossambicus*) to the total winter ichthyofauna in the Mhlanga and the relatively high contribution of estuarine-dependent marine species (Mugilidae) (Figure 5) is probably a reflection of the distribution of these species in the system, where *O. mossambicus* occurs in the upper reaches of the estuary while mugilids occur in the middle and lower reaches. The relatively high biomass contribution of freshwater species to the total winter ichthyofauna in the Mhlanga (Figure 6) is a reflection of larger specimens of *O. mossambicus* being captured (Harrison, 1993). The relatively high numerical contribution of estuarine species (Figure 9) is a reflection of the spawning potential of *G. aestuaria* throughout the year.

The number of species, number of individuals and overall fish biomass in the Mhlanga were all negatively correlated with the average water depth of the system (Table 4). The relatively low number of species, number of individuals and fish biomass recorded in winter (Figure 3) may be a reflection of the deep nature of the system, resulting in the fishes becoming diluted and less susceptible to capture. Furthermore, during the closed mouth phase, marine fishes are unable to recruit into the Mhlanga which may also contribute to the low number of species, numbers and biomass. Species diversity indices are a reflection of both the number of species (richness) and the proportion of each species (evenness) (Krebs, 1985). The low richness (D) recorded in August is a reflection of the low number of species captured and this, coupled with the relatively high evenness, resulted in a moderate species diversity in the Mhlanga in winter (Figure 3).

**Spring (September - November):** During the spring rainfall months the Mhlanga estuary opens periodically (Figure 2). These open phases correspond to the peak recruitment period of juveniles of most estuarine-dependent marine species (Wallace & van der Elst, 1975). Whitfield (1980b) noted a marked increase in the number of marine species entering the Mhlanga estuary in spring (November). Although spring is the peak recruitment period of juveniles of

most estuarine-dependent marine species, the reduction in the relative contribution of these species to the ichthyofauna of the Mhlanga in November (Figures 5 and 6) may be a result of the emigration of adults from the system to spawn, which takes place in the vicinity of estuary mouths from May to November (Wallace, 1975b) and the limited initial recruitment of juveniles into the system during the open phase. Spring is also the peak breeding period for the dominant estuarine (*G. aestuaria*) and freshwater (*O. mossambicus*) species (Blaber, 1979; Bruton & Bolt, 1975) and this may have contributed to the increase in the relative proportions of these fishes in the Mhlanga during November (Figure 5).

Whitfield & Blaber (1979) found that when a closed estuary opens, *O. mossambicus* usually retreats to the upper reaches of the system. The Mhlanga estuary however was one system where *O. mossambicus* was recorded in the lower reaches during the open phase (Whitfield & Blaber, 1979). They attributed this to the fact that the shallowness of the upper reaches during the open phase and the reduction of water surface area over the estuary resulted in a redistribution of this species, with a proportion of the population utilising the lower reaches. The increase in the relative proportion of estuarine and freshwater species in the Mhlanga in spring may also be due to the redistribution and concentration of these fishes in the estuary when the water level is low.

Both the total number of species and the total number of individuals captured in the Mhlanga increased in spring (Figure 3). Since the number of species in the Mhlanga was positively correlated with the open mouth condition of the system (Table 4), it is probably a reflection of the influx of species into the system from the adjacent marine environment. The increase in the total number of individuals was most likely a reflection of the shallow nature of the system resulting in the fishes becoming concentrated and more susceptible to capture as well as the peak in breeding activity of estuarine and freshwater species. The low species diversity index in the Mhlanga during spring is probably a result of the low evenness due to the system being numerically dominated by estuarine species (*G. aestuaria*).

**Summer (December - February):** The extended spawning period of estuarine-dependent marine species is thought to prolong the period during which fry and juveniles occur in the inshore marine environment and act as a buffer against recruitment failure as a result of adverse marine or estuarine conditions (Wallace, 1975b). Recruitment of juveniles into permanently open estuaries takes place mainly during winter and spring (June - November) when river outflow is at a minimum (Wallace & van der Elst, 1975). In closed estuaries however, recruitment usually starts later and varies in accordance with the onset of the spring rains when increased river flow forces open estuary mouths (Wallace & van der Elst, 1975; Whitfield, 1980c). The relative contribution of estuarine-dependent marine species to the ichthyofauna in the Mhlanga increased in summer (February) (Figures 5 and 6) and may be a reflection of the steady recruitment of juveniles into the system when it opened during spring and summer (Figure 2).

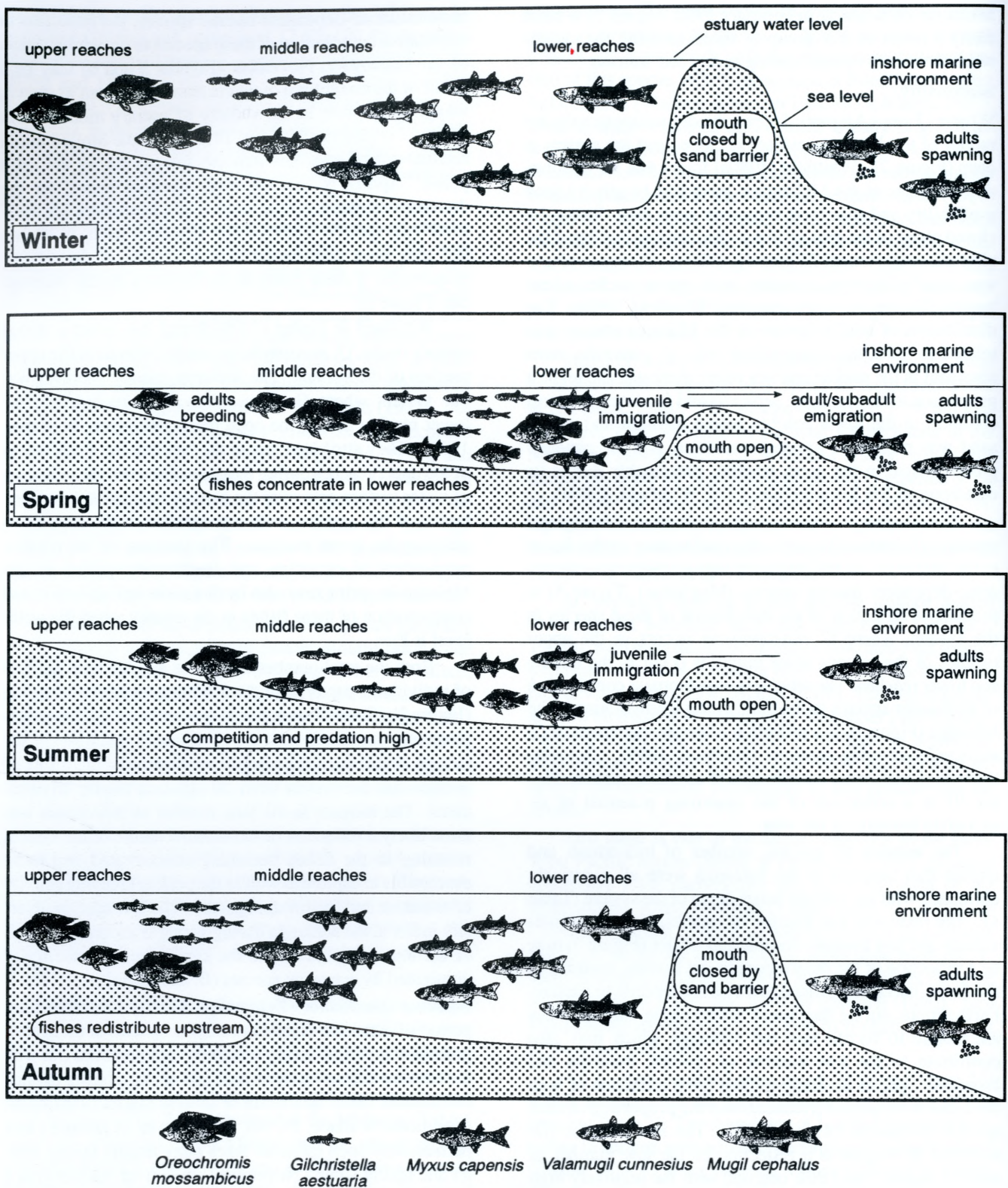


Figure 14. Diagrammatic representation of the seasonal fish community structure in the Mhlanga estuary.

During the open phase the Mhlanga becomes shallow and, although shallow waters may aid small fishes in avoiding fish predators (Whitfield & Blaber, 1978b), it renders them particularly vulnerable to bird predation (Whitfield & Blaber, 1978c; 1978d; 1978e). Bird predation may have contributed to the decrease in the relative proportions of

both estuarine and freshwater species to the ichthyofauna in the Mhlanga in summer when water levels were low (Figures 13 and 14). Whitfield (1980c) noted that during the open phases of the system, food resources in the Mhlanga are drastically reduced due to exposure of the non-channel areas and the scouring action of floodwaters. Competition



among the fishes both for habitat and food would therefore be expected to be high during the spring/summer and may also have contributed to the decline in the proportion of estuarine and freshwater species during summer.

The protracted immigration periods of estuarine-dependent marine species into the Mhlanga estuary when the system opened probably accounts for the increase in the number of species in summer. Mortality due to avian predation and competition may have accounted for the relatively low number of individuals. The high number of species and the low number of individuals contributed to the high species richness, high evenness and high species diversity in the estuary during summer (Figure 3).

**Autumn (March - May):** The extended opening of the mouth of the Mhlanga into the autumn of 1991 (Figure 2) together with the protracted recruitment period of estuarine-dependent marine species, particularly *Valamugil cunnesius*, may have contributed to the increased contribution of this group of fishes to the ichthyofauna in May 1991 (Figures 5 and 6). In autumn 1992 the mouth of the Mhlanga was closed (Figure 2) and estuarine species numerically dominated the ichthyofauna. This is possibly a reflection of summer breeding success of *Gilchristella aestuaria* and this species taking advantage of the relatively stable conditions during the closed phase (Whitfield, 1980b). The deep nature of the system in May 1992 (Figure 2) probably contributed to the decline in the contribution of freshwater species in the lower and middle reaches by allowing them to migrate and occupy the upper reaches of the system.

The decrease in the number of species in autumn is possibly due a reduction in the gear vulnerability of certain marine species in the enlarged and deeper system. The increase in the number of individuals in May 1991 is probably a reflection of the recruitment of mugilids into the system during summer, while the increase in May 1992 is due to increased *G. aestuaria* stocks during this period. This resulted in a decrease both in richness and evenness, particularly during May 1992. The net result was a lower species diversity in the Mhlanga during autumn.

## SUMMARY

A simplified diagrammatic representation of the community structure and utilisation of the Mhlanga estuary by selected species is presented in Figure 14. From the foregoing discussion it is apparent that the Mhlanga is dominated at different periods by various categories of fishes. During the winter the system is closed and food resources are relatively abundant. Freshwater species predominate in the upper reaches of the system while estuarine-dependent marine species mainly inhabit the middle and lower reaches. The fish community in winter tends to be dominated by estuarine-dependent marine species. When the system opens with the onset of spring/summer rains, adult and sub-adult estuarine-dependent marine species emigrate from the system to spawn at sea and 0+ juveniles begin recruiting into the system. Spring and summer is also the peak breeding period of resident estuarine and freshwater species and, because the system drains when it opens, these species are concentrated in the deeper lower reaches of the system and dominate the fish community. During the open phases, however, food resources and habitat in the Mhlanga are

drastically reduced and coupled with the influx of juvenile estuarine-dependent marine fishes, results in a decrease in the proportion of estuarine and freshwater species during summer. In autumn, reduced river flow is insufficient to maintain an open mouth and the system normally closes. Once closed the estuary quickly fills, inundating previously exposed habitats and food resources increase. This also results in the partial redistribution of freshwater species upstream and estuarine-dependent marine species again dominate the system.

## DAMBA ESTUARY

### STUDY AREA

The Damba estuary (30°40'S; 30°30'E) is situated 118 kilometres southwest of Durban. The river is 11 kilometres long and has a catchment area of 25 km<sup>2</sup> (NRIO, 1986a). The catchment geology comprises mainly Precambrian metamorphic rocks with some Natal Group Sandstone and Dolerite. The Damba is diverted near its mouth by a southerly-extending spit that is artificially stabilised to accommodate a railway alignment (Appendix 3). Hydrological studies suggest that the Damba estuary has shown considerable siltation since 1937 (NRIO, 1986b). The most important botanical feature of the Damba estuary is the swamp forest that fringes the lagoon (Begg, 1978).

### RESULTS

#### Physicochemical Characteristics

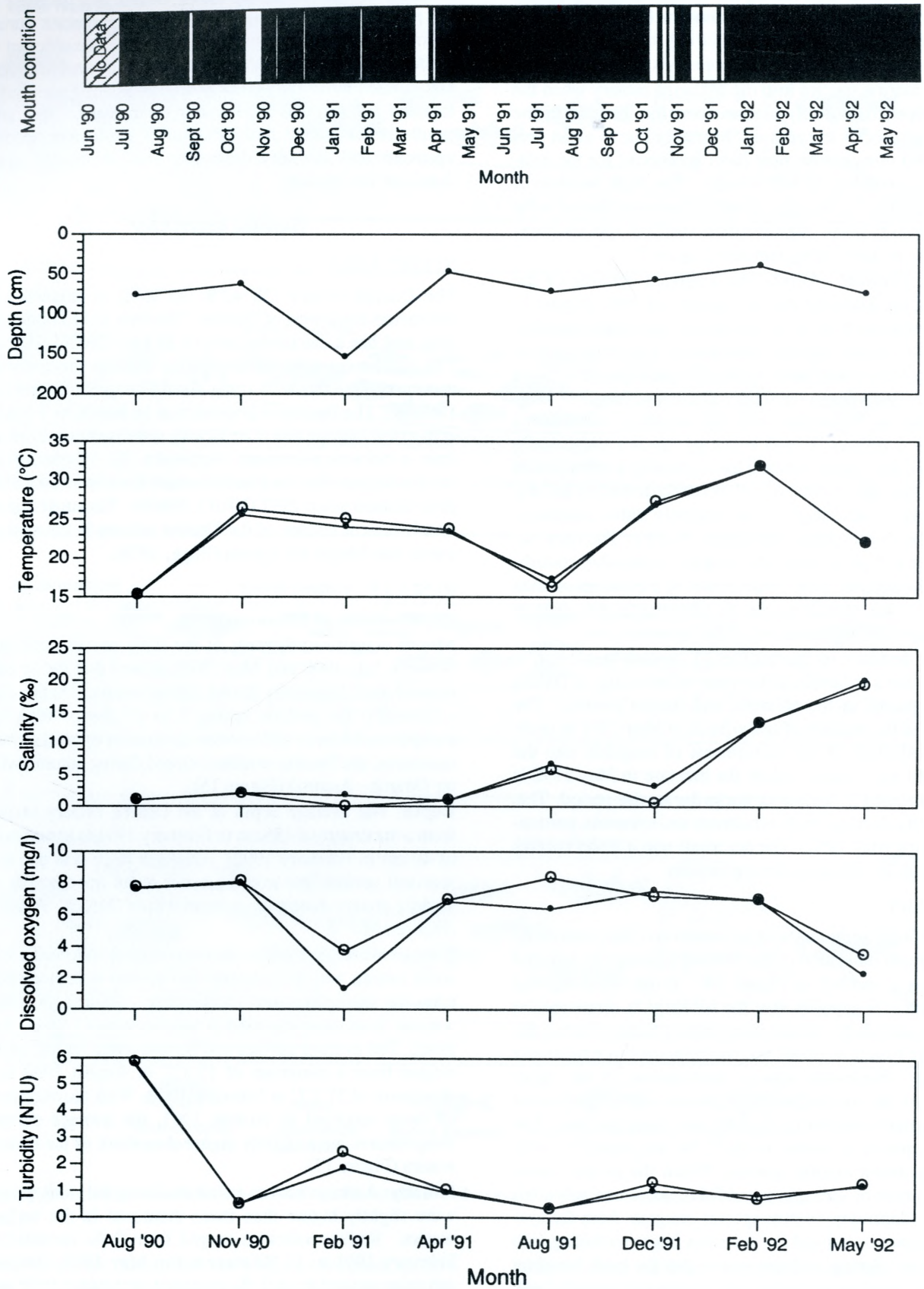
**Mouth condition:** Records of the daily mouth condition between July 1990 and May 1992 showed that the system opened most frequently during spring/summer (September - February) for periods lasting 2 to 15 days. With the exception of March 1991, when the system opened on two occasions, the Damba remained closed during autumn/winter (March - August) (Figure 15).

**Depth:** The average depth of the Damba estuary ranged from a maximum of 155 cm in February 1991 to a minimum of 40 cm in February 1992. Although there was no clear seasonal pattern, the average water depth appeared to be slightly greater during the autumn/winter (March - August) (Figure 15).

**Temperature:** Average water temperatures followed a seasonal pattern with both surface and bottom water temperatures in spring/summer (November - February) being warmer than those recorded in autumn/winter (April - August). The average surface and bottom water temperatures ranged from a minimum of 15.3°C in August 1990 to a maximum of 31.7°C in February 1992. With the exception of those recorded in August 1991, the average surface temperatures were slightly higher than those of the bottom waters (Figure 15).

**Salinity:** Average bottom salinities during the study period were slightly higher than those measured in the surface waters. Surface salinities ranged from 0 ‰ recorded in February 1991 to 19 ‰ recorded in May 1992. Bottom salinities ranged from 1 ‰ recorded in August 1990 and April 1991 to 20 ‰ recorded in May 1992 (Figure 15).

**Dissolved oxygen:** The average dissolved oxygen levels in the surface waters ranged from 8.3 mg l<sup>-1</sup> in August 1991 to 3.6 mg l<sup>-1</sup> in May 1992. With the exception of December



**Figure 15.** Daily mouth condition (□ open; ■ closed) and abiotic parameters measured in the surface (o) and bottom (●) waters of the Damba estuary.

**Table 5.** Numerical composition of the fishes captured in the Damba estuary using various sampling techniques (August 1990 - May 1992).

Sampling Gear Fish Taxa	Beam Trawl x 18		Otter Trawl x 18		Seine Net x 21		Gill Nets x 24		Total	
	n	%	n	%	n	%	n	%	n	%
<i>Ambassis productus</i>			6	1.01	38	1.86	1	0.78	45	1.54
<i>Awaous aeneofuscus</i>			1	0.17	4	0.20			5	0.17
<i>Crenimugil crenilabis</i>					3	0.15			3	0.10
<i>Elops machnata</i>							1	0.78	1	0.03
<i>Gerres</i> sp.					26	1.27			26	0.89
<i>Gilchristella aestuaria</i>			16	2.68	16	0.78			32	1.10
<i>Glossogobius callidus</i>	106	70.20	517	86.60	281	13.76			904	30.98
Goby sp. II			6	1.01					6	0.21
Juvenile mugilids					5	0.24			5	0.17
<i>Liza alata</i>					1	0.05	1	0.78	2	0.07
<i>Liza dumerilii</i>					2	0.10	6	4.69	8	0.27
<i>Liza macrolepis</i>							1	0.78	1	0.03
<i>Liza richardsonii</i>			1	0.17					1	0.03
<i>Monodactylus argenteus</i>							1	0.78	1	0.03
<i>Monodactylus falciformis</i>			1	0.17	5	0.24	1	0.78	7	0.24
<i>Mugil cephalus</i>			2	0.34	22	1.08	67	52.34	91	3.12
<i>Myxus capensis</i>					935	45.79	2	1.56	937	32.11
<i>Oreochromis mossambicus</i>	44	29.14	38	6.37	646	31.64	37	28.91	765	26.22
<i>Rhabdosargus holubi</i>			2	0.34	24	1.18	3	2.34	29	0.99
<i>Solea bleekeri</i>	1	0.66	5	0.84					6	0.21
<i>Tilapia rendalli</i>					1	0.05			1	0.03
<i>Valamugil cunnesius</i>					2	0.10	5	3.91	7	0.24
<i>Valamugil robustus</i>							2	1.56	2	0.07
<i>Valamugil</i> sp.			2	0.34	31	1.52			33	1.13

1991, the average dissolved oxygen in the bottom waters did not exceed levels in the surface waters. Dissolved oxygen in the bottom waters ranged from 8.0 mg l<sup>-1</sup> in November 1990 to 1.3 mg l<sup>-1</sup> in February 1991 (Figure 15).

**Turbidity:** Average surface turbidities during the study period ranged from 5.8 NTU recorded in August 1990 to 0.3 NTU recorded in August 1991. The average bottom turbidity ranged from 5.8 NTU recorded in August 1990 to 0.4 NTU recorded in August 1991 (Figure 15).

**Table 6.** Biomass composition of the fishes captured in the Damba estuary using various sampling techniques (August 1990 - May 1992).

Sampling Gear Fish Taxa	Beam Trawl x 18		Otter Trawl x 18		Seine Net x 21		Gill Nets x 24		Total	
	n	%	n	%	n	%	n	%	n	%
<i>Ambassis productus</i>			93.5	3.73	426.9	3.51	41.1	0.28	561.6	1.86
<i>Awaous aeneofuscus</i>			12.2	0.48	41.7	0.34			53.8	0.18
<i>Crenimugil crenilabis</i>					5.4	0.04			5.4	0.02
<i>Elops machnata</i>							170.0	1.15	170.0	0.56
<i>Gerres</i> sp.					10.2	0.08			10.2	0.03
<i>Gilchristella aestuaria</i>			13.3	0.53	8.5	0.07			21.7	0.07
<i>Glossogobius callidus</i>	369.5	47.55	1283.1	51.15	774.1	6.36			2426.7	8.04
Goby sp. II			1.7	0.07					1.7	0.01
Juvenile mugilids					1.2	0.01			1.2	0.00
<i>Liza alata</i>					19.1	0.16	339.2	2.30	358.3	1.19
<i>Liza dumerilii</i>					156.6	1.29	641.3	4.35	797.9	2.64
<i>Liza macrolepis</i>							69.0	0.47	69.0	0.23
<i>Liza richardsonii</i>			38.6	1.54					38.7	0.13
<i>Monodactylus argenteus</i>							18.6	0.13	18.6	0.06
<i>Monodactylus falciformis</i>			21.0	0.84	116.2	0.95	27.2	0.18	164.4	0.54
<i>Mugil cephalus</i>			206.2	8.22	165.6	1.36	8577.7	58.17	8949.5	29.63
<i>Myxus capensis</i>					9145.9	75.15	295.5	2.00	9441.4	31.26
<i>Oreochromis mossambicus</i>	405.3	52.16	781.3	31.14	954.6	7.84	3805.0	25.81	5946.2	19.69
<i>Rhabdosargus holubi</i>			39.1	1.56	211.8	1.74	144.7	0.98	395.6	1.31
<i>Solea bleekeri</i>	2.3	0.29	14.4	0.57					16.6	0.06
<i>Tilapia rendalli</i>					1.7	0.01			1.7	0.01
<i>Valamugil cunnesius</i>					51.9	0.43	428.0	2.90	479.9	1.59
<i>Valamugil robustus</i>							187.4	1.27	187.4	0.62
<i>Valamugil</i> sp.			4.4	0.17	79.4	0.65			83.8	0.28

**Table 7.** Percent similarity of the catch composition of each gear type to the total catch in the Damba estuary (IS<sub>J</sub> = Jaccard's index of similarity, IS<sub>S</sub> = Sørensen's index of similarity).

Gear	IS <sub>J</sub>	IS <sub>S</sub>	Similarity ranking
Beam trawl	12.50	22.22	4
Otter trawl	50.00	66.67	3
Seine net	70.83	82.93	1
Gill nets	54.17	70.27	2

### Species Composition and Sampling Efficiency

A total of 2918 specimens representing 10 families and 24 fish taxa were collected in the Damba system during this study. *Myxus capensis* was the most abundant species captured and accounted for 32.1% of the total catch. *Glossogobius callidus* and *Oreochromis mossambicus* were the next most abundant species and accounted for 31.0% and 26.2% of the total ichthyofauna respectively (Table 5). These three species together accounted for over 89% of the total catch. The remaining 21 fish taxa each contributed less than 4% to the total catch and together comprised only 10.7% of the total fish assemblage. A total fish biomass of 30.2 kg was caught in the Damba estuary. *Myxus capensis* and *Mugil cephalus* accounted for 31.3% and 29.6% of the

total biomass respectively. *Oreochromis mossambicus* accounted for 19.7% and *Glossogobius callidus* 8.0% (Table 6). Together these four species accounted for over 88% of the total biomass. The contribution of each of the remaining 16 types of fishes was less than 3% and together constituted 11.4% of the total fish biomass.

Numerical and biomass analyses for fish catches from each of the four sampling gears are shown in Tables 5 and 6 respectively. The percent similarity of the catch composition of each gear type to the total catch in the Damba estuary is shown in Table 7. Results from both Jaccard's and Sørensen's indices of similarity revealed that seine net catches were most similar to the total catch (Table 7).

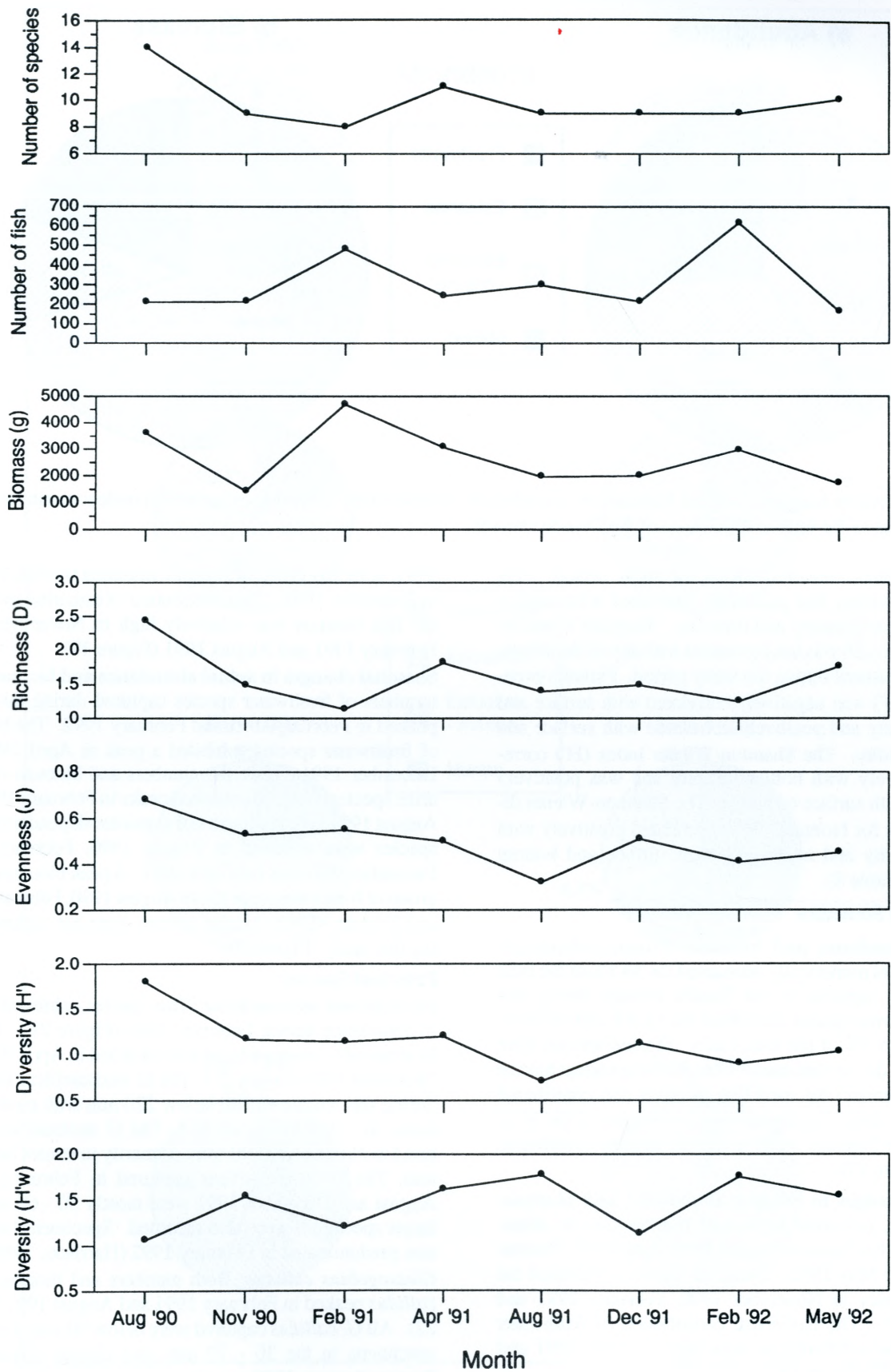
### Seasonal Species Richness, Diversity, Abundance and Biomass

A higher number of species was captured in the Damba during August 1990, April 1991 and May 1992 than on any of the other sampling occasions. The number of individuals captured showed a peak in February 1991 and again in February 1992. The fish biomass recorded peaked in August 1990, February 1991 and February 1992. Margalef's species richness index (D) showed peaks in August 1990, April 1991 and May 1992. Pielou's evenness index (J') was high in August 1990 with another peak occurring in December 1991. The Shannon-Wiener diversity index (H') showed a similar pattern with a high value in August 1990 and a slight peak in December 1991. The Shannon-Wiener diversity index for biomass (H'w) exhibited peaks in November 1990, August 1991 and February 1992 (Figure 16).

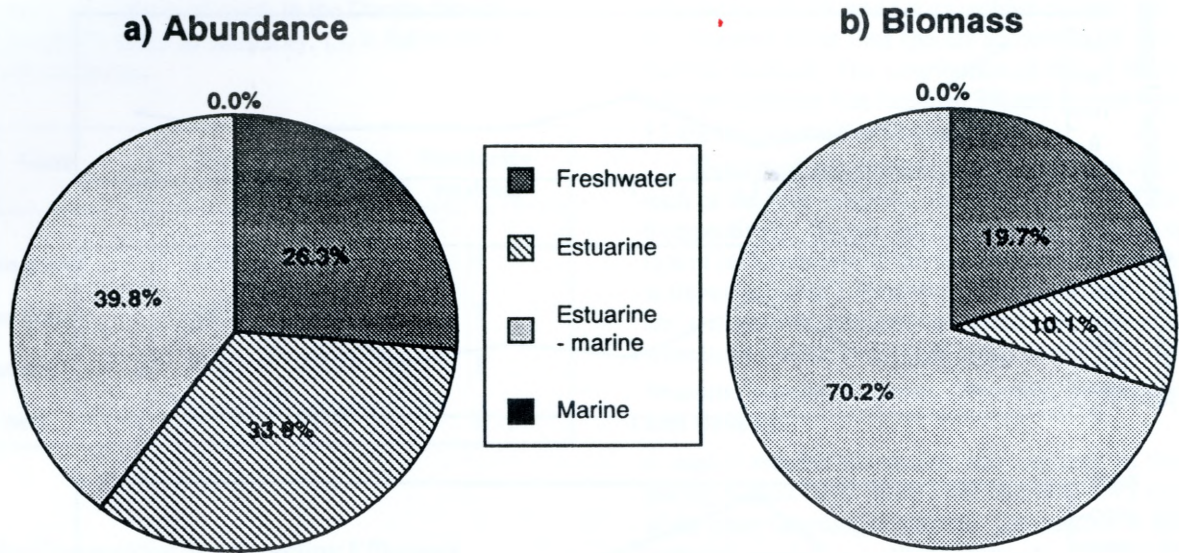
The number of species collected was inversely correlated with surface and bottom water temperatures. The number of individuals was not correlated with any of the

**Table 8.** Results of the Spearman rank correlation between abiotic and biotic variables in the Damba estuary (August 1990 - May 1992). Shaded areas denote significant ( $p < 0.15$ ) correlation values.

	Depth	Temperature		Salinity		Dissolved Oxygen		Turbidity		Mouth % Open
		Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	
<b>Number of species</b>	$r = -0.06$ $p = 0.87$	$r = -0.57$ $p = 0.13$	$r = -0.57$ $p = 0.13$	$r = 0.24$ $p = 0.52$	$r = -0.29$ $p = 0.44$	$r = -0.03$ $p = 0.95$	$r = 0.30$ $p = 0.42$	$r = 0.23$ $p = 0.54$	$r = 0.29$ $p = 0.44$	$r = -0.20$ $p = 0.60$
<b>Number of fish</b>	$r = 0.33$ $p = 0.38$	$r = 0.48$ $p = 0.21$	$r = 0.48$ $p = 0.21$	$r = -0.18$ $p = 0.63$	$r = 0.04$ $p = 0.92$	$r = 0.02$ $p = 0.95$	$r = -0.31$ $p = 0.41$	$r = -0.29$ $p = 0.45$	$r = -0.36$ $p = 0.34$	$r = 0.13$ $p = 0.73$
<b>Biomass</b>	$r = -0.26$ $p = 0.49$	$r = -0.12$ $p = 0.75$	$r = -0.12$ $p = 0.75$	$r = 0.63$ $p = 0.09$	$r = 0.61$ $p = 0.11$	$r = -0.31$ $p = 0.41$	$r = -0.26$ $p = 0.49$	$r = 0.67$ $p = 0.08$	$r = 0.62$ $p = 0.10$	$r = -0.04$ $p = 0.92$
<b>Richness (D)</b>	$r = -0.01$ $p = 0.97$	$r = -0.54$ $p = 0.15$	$r = -0.54$ $p = 0.15$	$r = 0.07$ $p = 0.84$	$r = -0.39$ $p = 0.31$	$r = 0.02$ $p = 0.95$	$r = 0.41$ $p = 0.28$	$r = 0.29$ $p = 0.45$	$r = 0.32$ $p = 0.39$	$r = -0.02$ $p = 0.95$
<b>Evenness (J')</b>	$r = 0.52$ $p = 0.17$	$r = -0.12$ $p = 0.75$	$r = -0.12$ $p = 0.75$	$r = -0.69$ $p = 0.07$	$r = -0.72$ $p = 0.06$	$r = -0.05$ $p = 0.90$	$r = 0.33$ $p = 0.38$	$r = 0.74$ $p = 0.05$	$r = 0.69$ $p = 0.07$	$r = 0.29$ $p = 0.45$
<b>Diversity (H')</b>	$r = -0.21$ $p = 0.57$	$r = -0.24$ $p = 0.53$	$r = -0.24$ $p = 0.53$	$r = -0.54$ $p = 0.15$	$r = -0.87$ $p = 0.02$	$r = -0.05$ $p = 0.90$	$r = 0.43$ $p = 0.26$	$r = 0.55$ $p = 0.15$	$r = 0.52$ $p = 0.17$	$r = 0.34$ $p = 0.38$
<b>Diversity (H'w)</b>	$r = 0.47$ $p = 0.21$	$r = 0.07$ $p = 0.85$	$r = 0.07$ $p = 0.85$	$r = 0.63$ $p = 0.09$	$r = 0.49$ $p = 0.19$	$r = 0.07$ $p = 0.85$	$r = -0.36$ $p = 0.34$	$r = -0.83$ $p = 0.03$	$r = -0.76$ $p = 0.04$	$r = -0.30$ $p = 0.43$



**Figure 16.** Seasonal changes in the number of species, number of individuals, biomass, species richness, species evenness, and species diversity in the Damba estuary.



**Figure 17.** Percent numerical (a) and biomass (b) contribution of freshwater, estuarine, estuarine-dependent marine and marine species to the total ichthyofauna of the Damba estuary.

abiotic variables measured during the study period. Fish biomass, however, was positively correlated with surface and bottom temperature and turbidity. Margalef's species richness index ( $D$ ) was not correlated with any of the abiotic variables measured during the study period. Pielou's evenness index ( $J'$ ) was negatively correlated with surface and bottom salinity and positively correlated with surface and bottom turbidity. The Shannon-Wiener index ( $H'$ ) correlated negatively with bottom salinity and was positively correlated with surface turbidity. The Shannon-Wiener diversity index for biomass ( $H'w$ ) correlated positively with surface salinity and negatively with surface and bottom turbidities (Table 8).

#### Community Structure

**Overall abundance and biomass:** Estuarine-dependent marine species numerically accounted for 39.8% of the total ichthyofauna captured in the Damba estuary during this study. Estuarine species accounted for 33.9% and freshwater species 26.3% of the total catch. Marine species were not recorded during this study. Estuarine-dependent marine species dominated the total fish biomass and contributed 70.2% to the total. Freshwater species comprised 19.7% of the total fish biomass while estuarine species contributed 10.1% (Figure 17).

**Seasonal changes in relative abundance and biomass:** Numerically, estuarine-dependent marine species dominated the ichthyofauna in August 1990, April 1991, December 1991 and May 1992. Estuarine species dominated the fish community in November 1990, February 1991 and August 1991. The numerical contribution of freshwater species to the ichthyofauna was high in April 1991 and February 1992 (Figure 18).

In terms of biomass, estuarine-dependent marine species dominated the ichthyofauna during most of the study period. The relative contribution of freshwater species to the total fish biomass was high in November 1990 and April

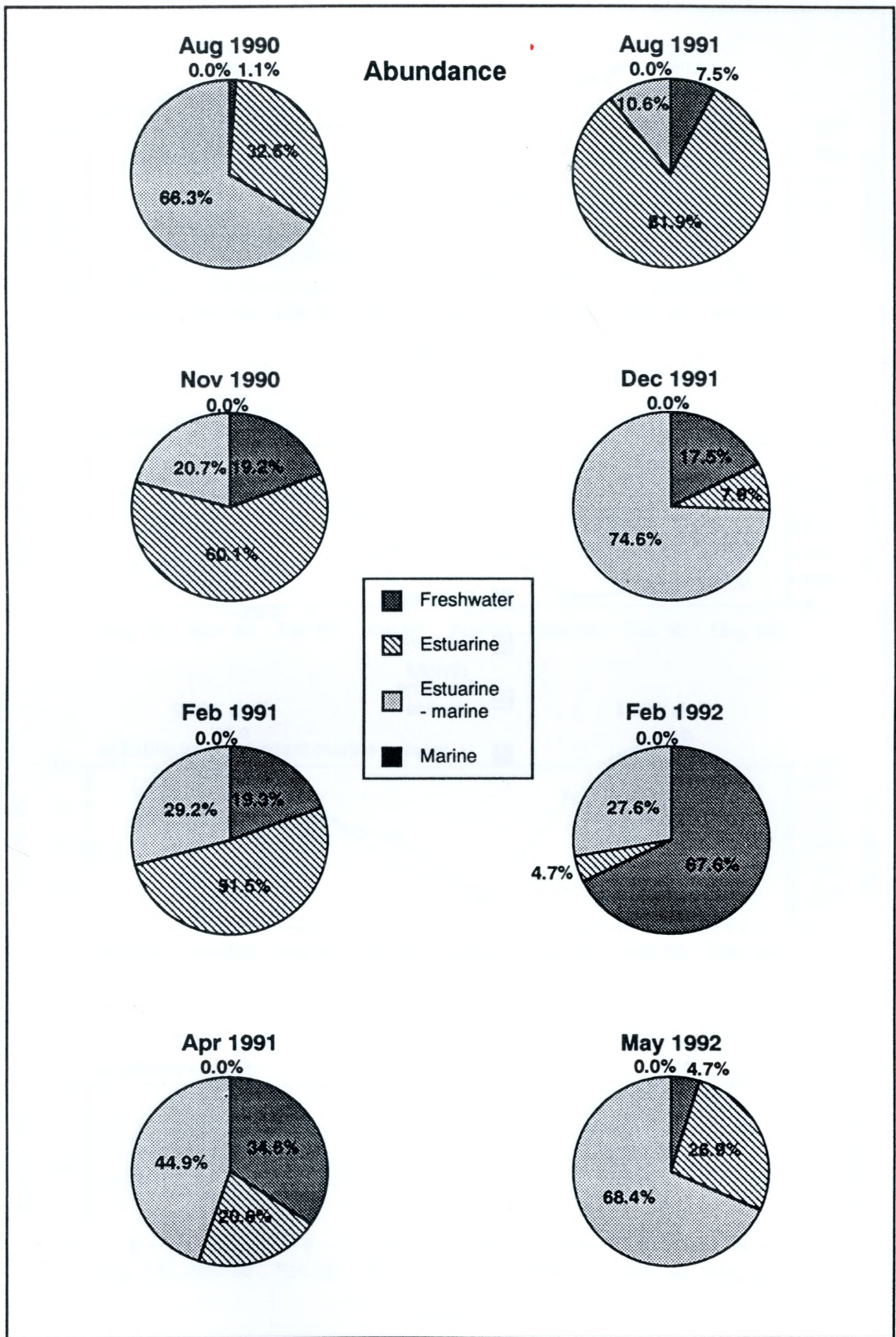
1991, with this group of fishes dominating the fish biomass in December 1991. The contribution of estuarine species to the fish biomass was relatively high in November 1990, February 1991 and August 1991 (Figure 19).

**Seasonal changes in actual abundance and biomass:** The numbers of freshwater species captured during this study peaked in February 1991 and February 1992. The biomass of freshwater species exhibited a peak in April 1991 and December 1991. Both the numbers and biomass of estuarine species captured exhibited peaks in February 1991 and August 1991. High numbers of estuarine-dependent marine species were captured in August 1990, February 1991, December 1991 and February 1992. A peak biomass of this group of fishes was recorded in August 1990, February 1991 and February 1992. Marine species were not captured during this study (Figure 20).

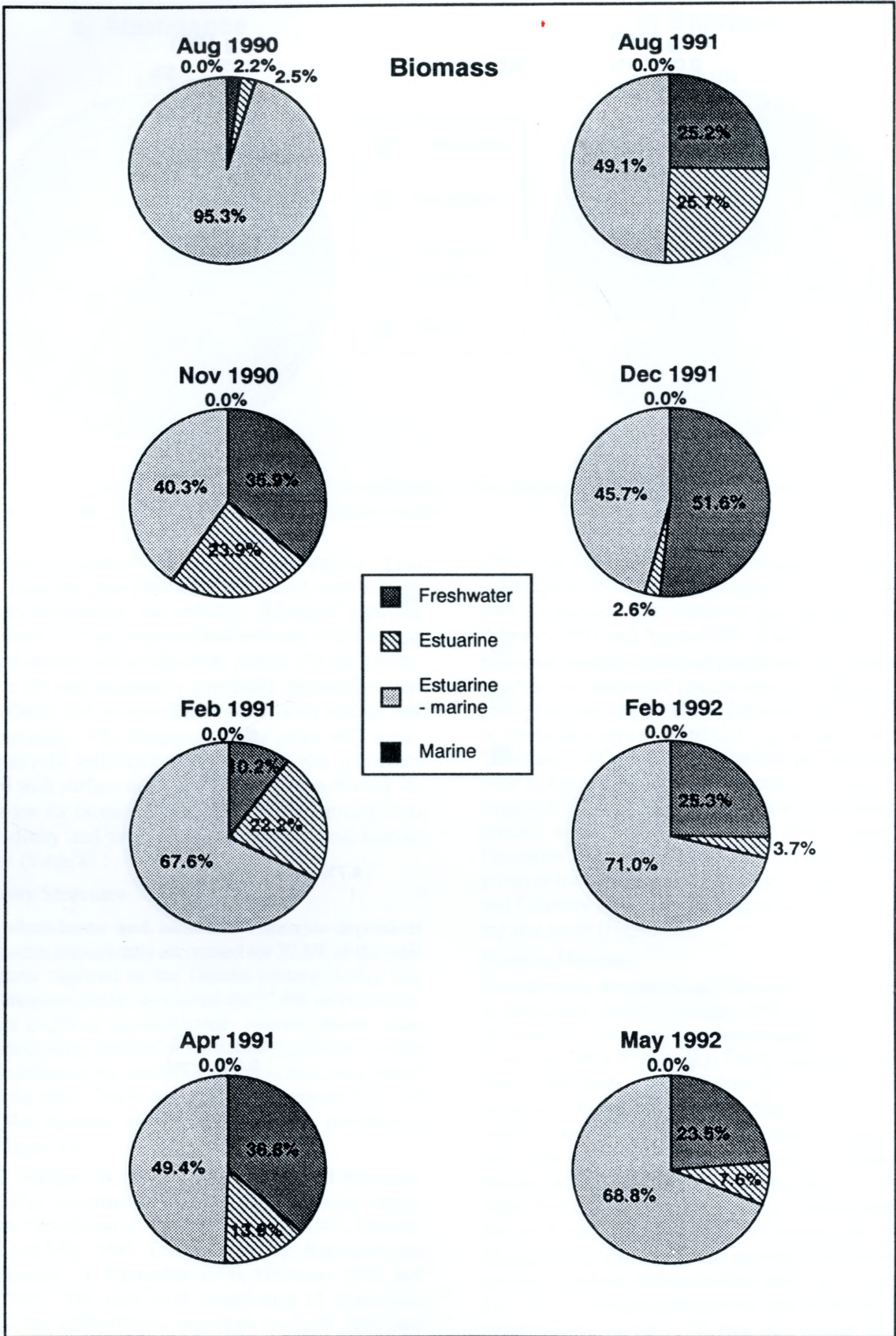
#### Principal Species

***Oreochromis mossambicus*:** This species exhibited a peak in abundance during February 1992 (Figure 21). A peak biomass of *O. mossambicus* was recorded in April 1991 and December 1991 (Figure 21). The *O. mossambicus* captured during this study were all below 220 mm with most specimens 10 - 50 mm (Figure 21). The *O. mossambicus* captured in November 1990 were primarily juveniles below 20 mm. The *O. mossambicus* captured in February, April, August and December 1991 were mostly 30 - 60 mm, but larger specimens were also recorded. Specimens below 30 mm predominated in February 1992 (Harrison, 1993).

***Glossogobius callidus*:** Both numbers and biomass of *G. callidus* peaked in February 1991 and August 1991 (Figure 22). All *G. callidus* captured were below 90 mm, with most specimens in the 30 - 70 mm size classes (Figure 22). During August 1990 a wide range in size classes were recorded (10 - 80 mm), with most specimens in the 20 - 30 mm group. *G. callidus* captured in November 1990 and February 1991 were mainly large specimens above 40 mm. Specimens in the 30 - 50 mm size classes predominated in

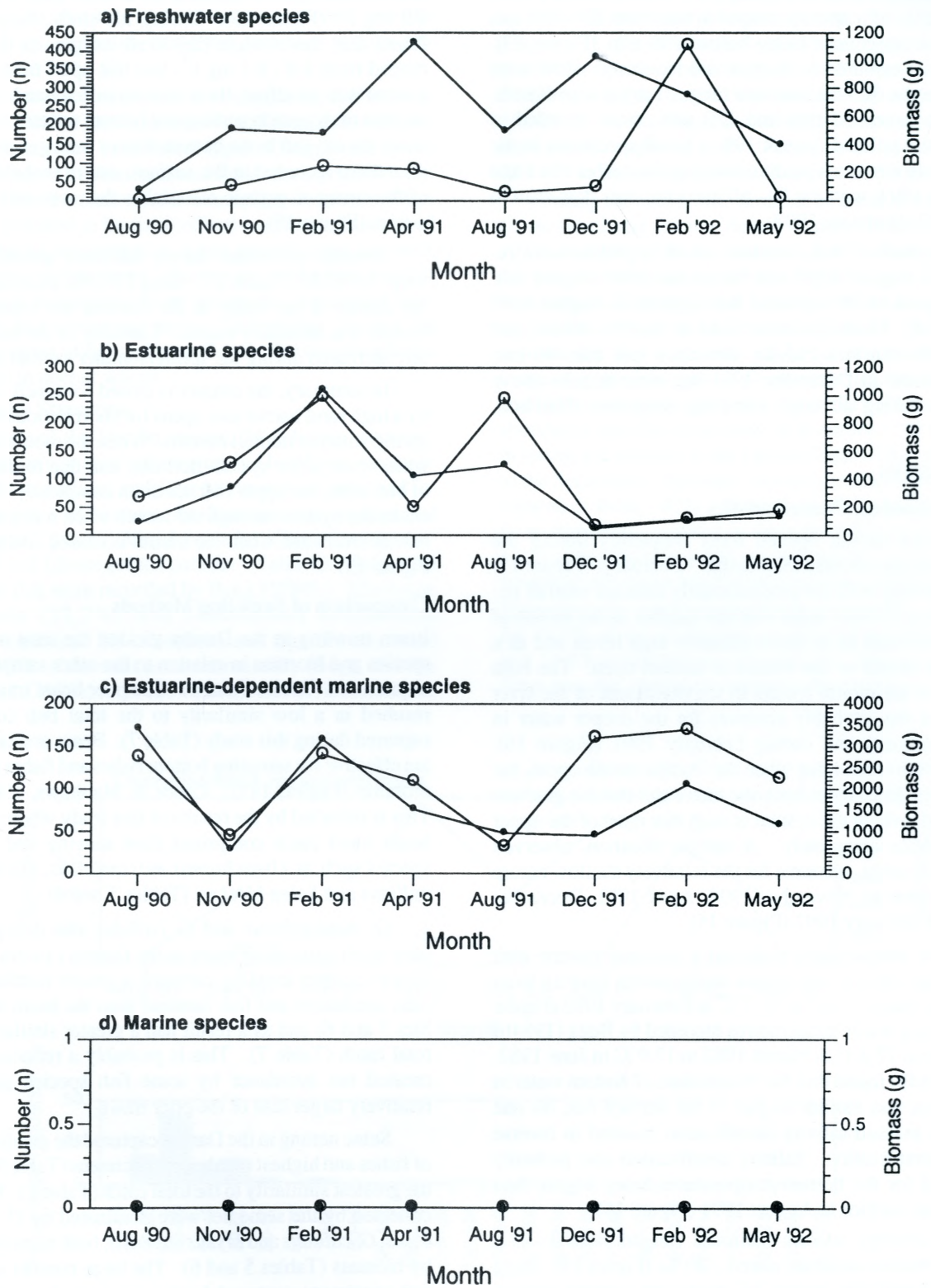


**Figure 18.** Seasonal numerical composition of freshwater, estuarine, estuarine-dependent marine and marine fish species in the Damba estuary.



**Figure 19.** Seasonal biomass composition of freshwater, estuarine, estuarine-dependent marine and marine fish species in the Damba estuary.





**Figure 20.** Seasonal fluctuations in the number (○) and biomass (●) of freshwater species (a), estuarine species (b), estuarine-dependent marine species (c) and marine species (d) in the Damba estuary.

April and August 1991. Specimens captured in December 1991, February 1992 and May 1992 were mostly 30 - 70 mm (Harrison, 1993).

***Myxus capensis***: Both the number and biomass of *M. capensis* reached a peak in February 1991 and February 1992 (Figure 23). *M. capensis* ranged in size from 20 - 250 mm with most specimens being below 100 mm (Figure 23). Individuals captured in August and November 1990 were mostly in the 30 - 60 mm size range. Larger size classes, mainly between 50 mm and 120 mm, were recorded in February, April and August 1991. Small specimens in the 30 - 40 mm size class predominated in December 1991 and February 1992, with the 50 - 60 mm size class dominant in May 1992 (Harrison, 1993).

***Mugil cephalus***: Peak numbers of *M. cephalus* were recorded in August 1990 and December 1991 (Figure 24). The biomass of *M. cephalus* was highest in August 1990 (Figure 24). Most specimens were in the 20 - 40 mm and 150 - 190 mm size classes. Juveniles less than 40 mm predominated in December 1991 but were usually above 150 mm during all other sampling occasions (Harrison, 1993).

## DISCUSSION

### Physicochemical Characteristics

The estuary mouth opened most frequently during the spring/summer months (September - February) (Figure 15) corresponding with the predominantly summer rainfall period. Begg (1984b) noted that the sandbar at the mouth of the Damba built up to extraordinarily high levels and as a result the mouth of the system is seldom open. The high sandbar at the mouth results in impoundment of the river water and this probably accounts for the deeper water in winter (August) and during February 1991 (Figure 15). Begg (1984b) found that when the Damba mouth opens, the water level drops by at least one metre and that the gradient of the bed level in the system is such that most of the upper reaches drain completely. A similar situation, observed during this study, accounts for the relatively shallow nature of the system in November 1990, April 1991, December 1991 and February 1992 (Figure 15).

Water temperatures followed a seasonal pattern with the average surface and bottom temperatures ranging from 15.3°C in August 1990 to 31.7°C in February 1992 (Figure 15). Surface water temperatures recorded by Begg (1984b) ranged from 27.8°C in March 1982 to 13.9°C in June 1982. Begg (1984b) found that the temperature of bottom water in the Damba was similar to that at the surface but, on one occasion, marked salinity stratification resulted in inverse thermal stratification. Salinity stratification also probably accounted for the bottom temperatures being higher than those at the surface in August 1991 (Figure 15).

The average surface salinities ranged from 0 - 19.3 ‰ while bottom salinities were 1 - 20 ‰ (Figure 15). Begg (1984b) found that during his study the average surface salinity in the Damba ranged from 0 - 7.6 ‰, and the average bottom salinity was 0 - 17.2 ‰. He suggested that the high salinities recorded in the system were due to overtopping of the sand bar during high spring tides, a factor which probably resulted in the relatively higher salinities

recorded in August 1991, February 1992 and May 1992 (Figure 15).

The average dissolved oxygen recorded in the surface waters ranged from 8.3 mg l<sup>-1</sup> to 3.6 mg l<sup>-1</sup>, and the average dissolved oxygen recorded in the bottom ranged from 8.0 - 1.3 mg l<sup>-1</sup> (Figure 15). During his study, Begg (1984b) found that the average dissolved oxygen in the Damba ranged from 4.8 - 8.7 mg l<sup>-1</sup>, and that apart from when the system was stratified, there was no difference between the amount of oxygen in surface and bottom waters. During this study the oxygen in the bottom waters were generally lower than those recorded in the surface, and is probably a result of the decay of organic material in the more saline bottom waters (Figure 15).

Average turbidities during the study period were always <6 NTU (Figure 15). Begg (1984b) noted that due to the clarity of the water in the Damba, the bottom of the system was generally visible. Turbidity in the estuary usually increased during the spring/summer rainfall period.

In summary, the estuary is closed for much of the year by a high sand barrier and opens for short periods during the spring/summer rainfall months. When the mouth opens, the water level in the system declines, and due to the gradient in bed level, the upper reaches drain completely. Sea water enters the system through the mouth when it is open and by barrier overwash when the mouth is closed (Begg, 1984b; Figure 15).

### Comparison of Sampling Methods

Beam trawling in the Damba yielded the least number of species and biomass in relation to the other sampling techniques used (Tables 5 and 6). The poor beam trawl catches resulted in a low similarity to the total fish community captured during this study (Table 7). Beam and otter trawls are effective for sampling bottom fishes and fishes of limited mobility (Lagler, 1971; Gibbs & Matthews, 1981/1982). This is reflected by the results of this study where the entire beam trawl catch comprised slow moving and demersal species such as *Oreochromis mossambicus*, *Glossogobius callidus* and *Solea bleekeri* (Tables 5 and 6).

*O. mossambicus* and *G. callidus* also dominated the otter trawl collections made in the Damba (Tables 5 and 6). However, otter trawling captured a greater number of species, specimens and fish biomass than the beam trawl (Tables 5 and 6) and as a result had a greater similarity to the total catch (Table 7). This is probably a reflection of decreased net avoidance by some fish species due to the relatively larger size of the otter trawl.

Seine netting in the Damba captured the greatest variety of fishes and highest number of specimens (Table 5) and had the greatest similarity to the total catch (Table 7). The fishes collected by the seine net were dominated by *O. mossambicus*, *G. callidus* and *Myxus capensis*, both numerically and by biomass (Tables 5 and 6). The large number of species and specimens captured by the seine net is most likely a reflection of (a) a greater number of collections taken with this equipment (b) the fact that the net samples a larger area in relation to the other equipment and (c) by encircling the fish and reducing net avoidance, particularly by the swifter mullet species such as *M. capensis*.

The catch from gill netting, although yielding the least number of specimens, produced the second highest number of species and the highest biomass of fishes in the Damba (Tables 5 and 6). Gill nets are effective for sampling larger, swifter fish in deep waters (Marais, 1985; Hayes, 1989). This accounts for the high biomass recorded and the mugilid, *Mugil cephalus*, being the dominant species collected (Tables 5 and 6).

The various techniques used to sample the fish fauna in the Damba yielded varying numbers and biomasses of fishes and were dominated by different types of fish. Beam trawls were dominated by demersal and slow moving species and appeared to be the least effective sampling technique. Otter trawling appeared to be more effective than the beam trawl in that, due to its larger size, more species were captured. Seine netting proved most effective in yielding the greatest variety of fishes and the most specimens, comprising both slow and fast swimming taxa. Gill netting yielded the highest biomass of fish and was effective for sampling larger specimens in deeper waters.

**Community Structure**

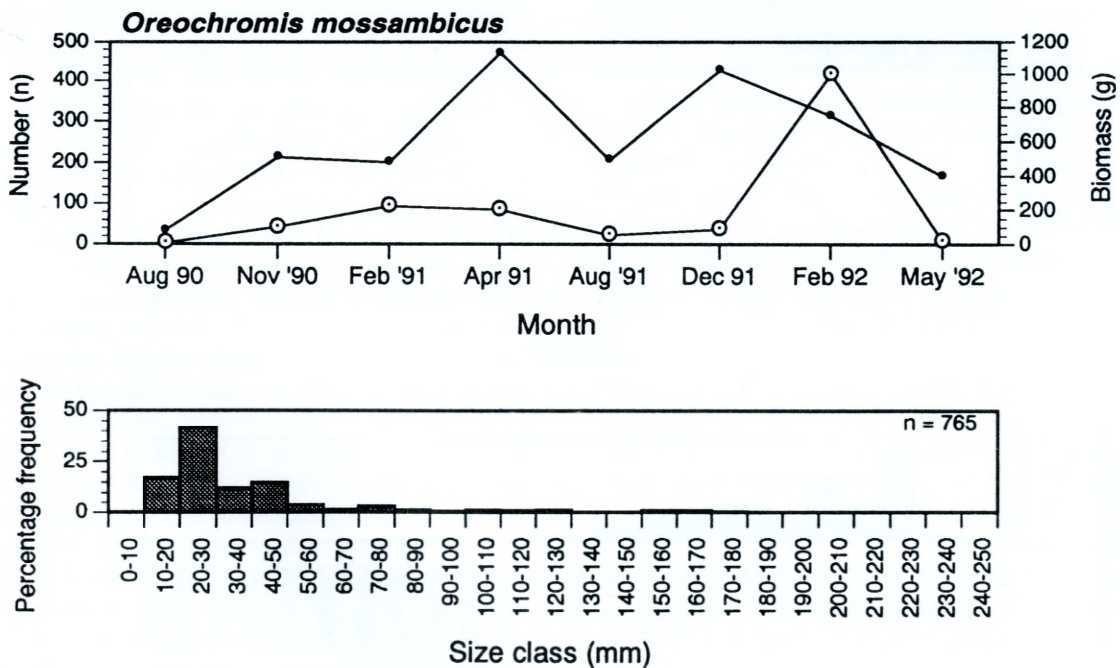
In this study of the Damba system, 24 fish taxa were collected and were numerically dominated by *Myxus capensis*, *Glossogobius callidus* and *Oreochromis mossambicus* (Table 5). In terms of biomass, the dominant species captured were *Myxus capensis*, *Mugil cephalus*, *Oreochromis mossambicus* and *Glossogobius callidus* (Table 6). Only three species of fish were recorded by Begg (1984b). *Glossogobius giuris* (52.7%) and *Oreochromis mossambicus* (46.5%) dominated his collections and together accounted for over 99% of the total catch numerically (Begg, 1984b). Ramm et al. (1985a) recorded eight species of fish and found

that *Glossogobius giuris* (44.3%), *Liza dumerilii* (12.5%), *O. mossambicus* (12.0%), *Ambassis productus* (11.6%) and *Gilchristella aestuaria* (9.0%) dominated their collections and numerically accounted for over 89% of the catch.

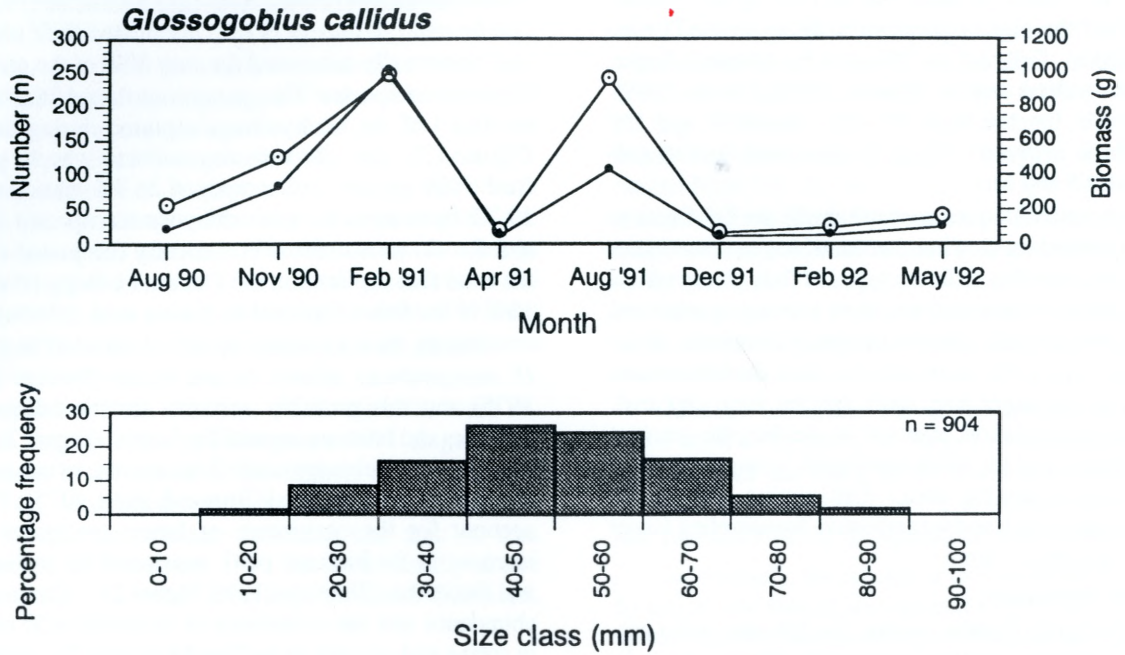
**Freshwater species:** This group contributed 26.3% (19.7% by mass) of the ichthyofauna captured during this study (Figure 17). *Oreochromis mossambicus* was the principal freshwater species and comprised 26.2% numerically and 19.7% by mass of the total ichthyofauna captured (Tables 5 and 6). *O. mossambicus* numerically comprised 46.5% of the total fish captured in the Damba by Begg (1984b) and 12% of the fishes captured by Ramm et al. (1985a).

During the cool winter months, both adult and juvenile *O. mossambicus* inhabit deeper waters (Bruton & Bolt, 1975) and this probably accounts for the relatively low numbers and biomass captured in August (Figure 21). From September to February adult *O. mossambicus* congregate in the shallow areas to breed (Bruton & Bolt, 1975). This may account for the occurrence of larger specimens and an increase in the biomass of *O. mossambicus* in November and December (Harrison, 1993; Figure 21). The increase in abundance and the occurrence of juveniles (<30 mm S.L.) in spring and summer in the Damba (Figure 21) corresponds to the September - February breeding season of this species (Bruton & Bolt, 1975). The high numbers and biomass of *O. mossambicus* captured in April 1991 (Figure 21) may be due to the shallow nature of the system at the time of sampling, which rendered them more susceptible to capture.

**Estuarine species:** Estuarine fishes numerically accounted for 33.9% of the ichthyofauna collected during this study and 10.1% of the biomass (Figure 17). *Glossogobius callidus* was the dominant estuarine dependent species cap-



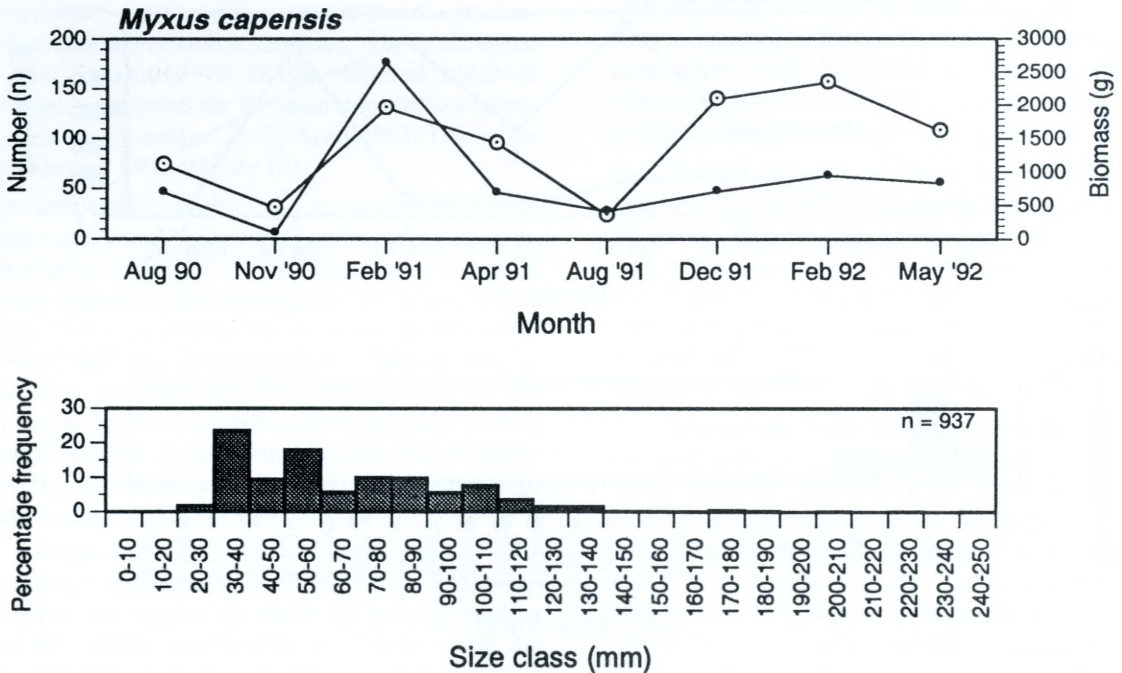
**Figure 21.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Oreochromis mossambicus* in the Damba estuary.



**Figure 22.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Glossogobius callidus* in the Mhlanga estuary.

tured and comprised 31% numerically and 8% by mass of the total ichthyofauna (Tables 5 and 6). *G. callidus*, is a tropical/subtropical species which is easily confused with *Glossogobius giuris*, a species which sometimes inhabits estuaries but is primarily freshwater (Smith & Heemstra, 1986). It is likely therefore that the *Glossogobius* species

captured by Begg (1984b) and Ramm et al. (1985a) in the Damba estuary were *G. callidus*. *Glossogobius* numerically comprised 52.7% of the ichthyofauna captured in the Damba by Begg (1984b) and 44.3% of the fishes captured by Ramm et al. (1985a).



**Figure 23.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Myxus capensis* in the Damba estuary.

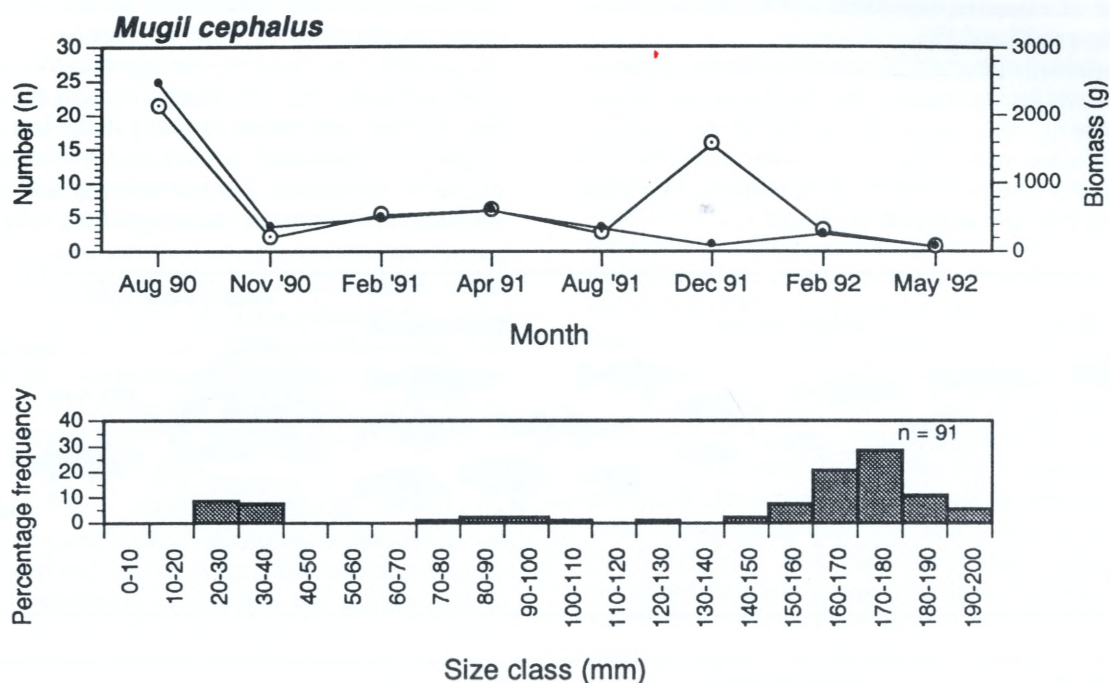


Figure 24. Seasonal abundance (○), biomass (●) and length frequency distribution of *Mugil cephalus* in the Damba estuary.

Little is known about the biology of *G. callidus* but it is thought to be similar to *G. giuris* (Coke, 1990). *G. giuris* breeds throughout the year with major spawning occurring in late spring and summer (November - February) (Crass, 1964; Bruton & Kok, 1980; Day *et al.*, 1981). The high numbers and biomass of *G. callidus* together with the occurrence of smaller size classes in February (Figure 22) suggests a predominantly spring/summer breeding period.

**Estuarine-dependent marine species:** This group comprised 39.8% (70.2% by mass) of the total ichthyofauna (Figure 17). Estuarine-dependent marine fishes numerically comprised only 0.4% of the total ichthyofauna captured in the Damba by Begg (1984b) and 22.7% by Ramm *et al.* (1985a).

*Myxus capensis* accounted for 32.1% numerically and 31.3% by mass of the total fishes captured during this study (Tables 5 and 6) and comprised 9.0% of the total ichthyofaunal catch made by Ramm *et al.* (1985a). *M. capensis* was not captured in the Damba estuary by Begg (1984b). *M. capensis* breeds throughout the year with a peak in spring (Wallace & van der Elst, 1975; Bok, 1979; Blaber, 1987). The biomass of *M. capensis* in the Damba declined in November 1990 and April 1991 (Figure 23), most likely as a result of larger specimens emigrating from the system when the mouth opened (Figure 15). High numbers of predominantly juvenile (<50 mm S.L.) *M. capensis* were captured in spring and summer (Figure 23). This is probably a reflection of the successful recruitment of juveniles of this species into the system which takes place during late winter and early summer (August - December) (Wallace & van der Elst, 1975; Blaber, 1987).

*Mugil cephalus* comprised 3.1% numerically and 29.6% by mass of the total ichthyofauna (Tables 5 and 6).

*M. cephalus* numerically comprised 0.8% of the ichthyofauna captured in the Damba by Ramm *et al.* (1985a) and was not recorded in this estuary by Begg (1984b). This species spawns in the inshore marine environment between May and September (Wallace, 1975b; Blaber, 1987) with recruitment of juveniles (<40 mm TL) into estuaries occurring from June to October (Wallace & van der Elst, 1975; Bok, 1979; Blaber, 1987). Successful recruitment probably accounted for the large number of juveniles (<40 mm SL) captured in December 1991 (Harrison, 1993). The reduction in the biomass of *M. cephalus* in spring (Figure 24) may be due to large individuals emigrating from the system once the mouth had opened.

**Marine species:** Marine species were not recorded in the Damba during this study (Figure 17) and is probably a result of its predominantly closed mouth condition. Species belonging to this group of fishes were also absent during the surveys by Begg (1984b) and Ramm *et al.* (1985a).

#### Seasonality

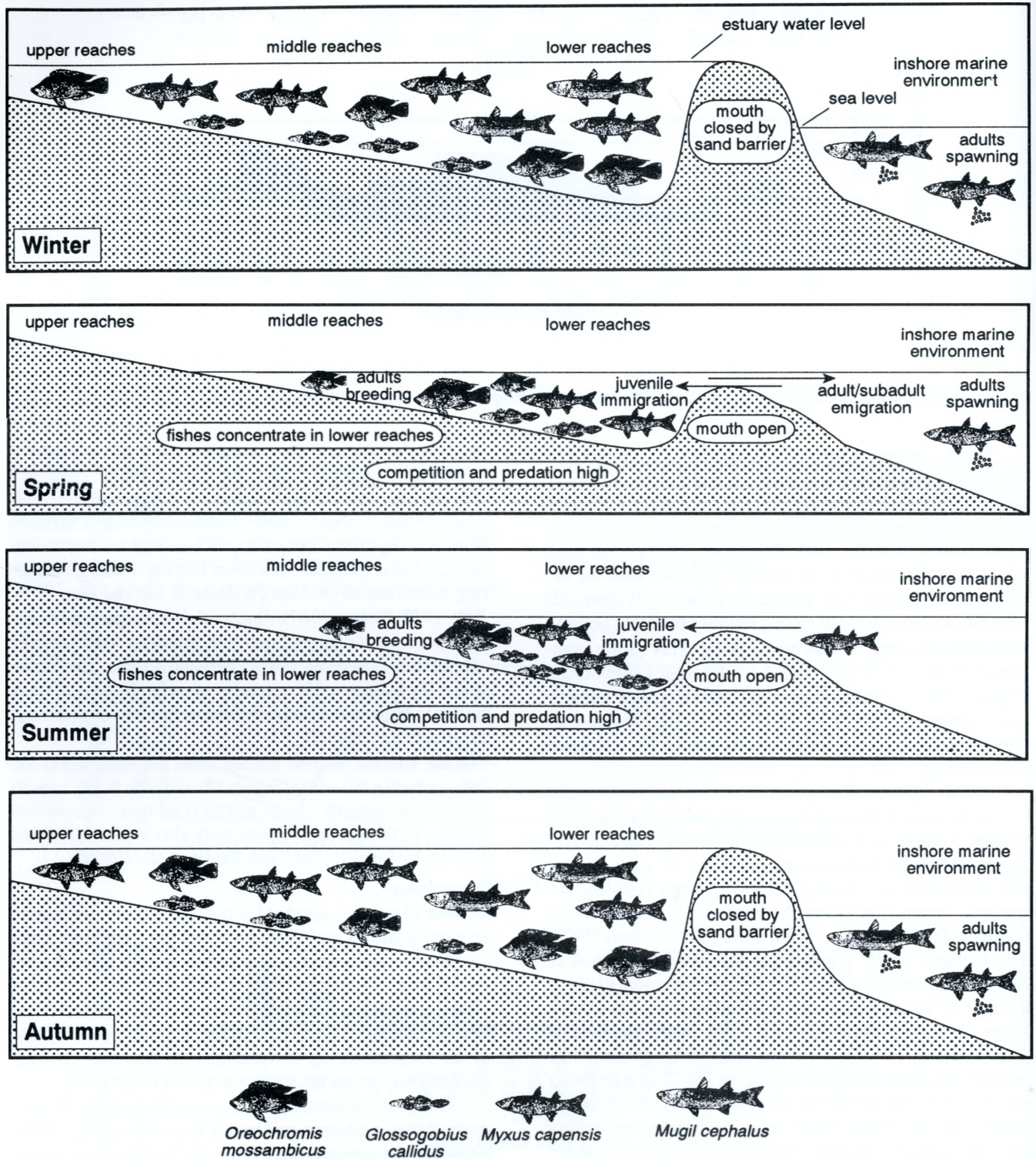
**Winter (June - August):** During the winter, the Damba estuary mouth closes (Figure 15) and the system is dominated by estuarine-dependent marine species (*Myxus capensis* and *Mugil cephalus*) and estuarine species (*Glossogobius callidus*) (Figures 18 and 19). The reproduction of *Glossogobius callidus* during the stable closed phase of the Damba may have contributed to the relatively high proportion of estuarine species in winter (Figure 18).

Due to its facultative catadromous life history, *M. capensis* shows a distinct preference for rivers (Bok, 1979). However, the elevated bed level in the Damba River results in this area being extremely shallow, especially during the dry winter season. *M. capensis* would therefore be restricted to the estuary thus contributing to the relatively high

proportion of estuarine-dependent marine species during winter (Figures 18 and 19).

The relatively low contribution of freshwater species to the total winter ichthyofauna in the Damba estuary (Figure 18) is probably a reflection of the fact that *O. mossambicus* probably inhabits deeper areas of the estuary during the cool winter months (Bruton & Bolt, 1975; Caulton, 1979) and are therefore not as susceptible to capture.

**Spring (September - November):** During spring the mouth of the Damba estuary opened for short periods and, due to the gradient of the bed level, the upper reaches become very shallow (Figure 15). The relative increase in the contribution of freshwater species in spring in the Damba (Figures 18 and 19) is most likely a result of *O. mossambicus* breeding within the system. The increase may also be due to the shallowness of the upper reaches resulting in the redistribu-



**Figure 25.** Diagrammatic representation of the seasonal fish community structure in the Damba estuary.

tion and concentration of *O. mossambicus* in the lower reaches of the system, as noted by Whitfield & Blaber (1979) in the Mhlanga estuary.

The reproduction, redistribution and concentration of *G. callidus* in the lower reaches of the Damba may also have accounted for the increase in the proportion of estuarine species in November 1990 (Figures 18 and 19). The exposure of the bed of the upper reaches of the Damba reduces the available habitat and food resources within the system, resulting in an increase in competition. The shallow nature of the system also increases the fishes vulnerability to bird predation (Whitfield & Blaber, 1978c; 1978d; 1978e). The decrease in the contribution of estuarine species to the ichthyofauna in December 1991 (Figures 18 and 19) may be a result of a combination of increased competition and/or bird predation of *G. callidus*.

In Natal, estuarine-dependent marine species generally spawn inshore in the vicinity of estuary mouths during late autumn, winter and spring (May - November) (Wallace, 1975b) with recruitment of juveniles into estuaries taking place mainly during winter and spring (June - November) (Wallace & van der Elst, 1975). Although spring is the peak recruitment period of juveniles of most estuarine-dependent marine species, the reduction in the relative contribution of these fishes to the ichthyofauna of the Damba estuary in November 1990 (Figures 18 and 19) may be a result of the emigration of large specimens of *M. capensis* and *M. cephalus* from the system when the mouth opened and poor recruitment of juveniles of these species into the estuary. Good recruitment in December 1991 resulted in the high contribution of estuarine-dependent marine species during this period (Figures 18 and 19).

**Summer (December - February):** The extended spawning period of estuarine-dependent marine species prolongs the period during which fry and juveniles occur in the inshore marine environment, and acts as a buffer against recruitment failure resulting from adverse environmental conditions (Wallace, 1975b). The mouth of the Damba opened periodically throughout the summer (Figure 15) and the high relative contribution of estuarine-dependent marine species (Figures 18 and 19) during this period is probably a result of the steady recruitment of 0+ juveniles into the system.

Successful spawning by *O. mossambicus* contributed to the increased numerical contribution of freshwater species in the estuary during summer (Figures 18 and 19). The high contribution of estuarine fishes in February 1991 (Figures 18 and 19) is probably also a result of *G. callidus* breeding during this period.

Both recruitment and concentration (due to reduced water levels) probably accounted for the relative increase in numbers of individuals and fish biomass in the Damba estuary during summer (Figure 16).

**Autumn (March - May):** The opening of the Damba estuary mouth in autumn 1991 (Figure 15), together with the prolonged spawning and recruitment period of *M. capensis* (Bok, 1979), probably contributed to the increased proportion of estuarine-dependent marine species in April 1991 (Figures 18 and 19). The shallow nature of the system in April 1991 (Figure 15) and the redistribution and concentration of *O. mossambicus* into the lower reaches probably

accounted for the increase in the proportion of freshwater species, while competition and predation probably accounted for the reduced contribution of small estuarine species such as *G. callidus* (Figures 18 and 19).

## SUMMARY

During the winter, the Damba estuary is closed by a high sand barrier. Due to the elevated bed level, the upper reaches of the Damba are very shallow and as a consequence the fishes in the system are restricted mainly to the lower and middle reaches. Freshwater species (*O. mossambicus*) inhabit the deeper pools in winter and estuarine-dependent marine species dominate the system.

When the estuary mouth opens in the spring, large individuals of estuarine-dependent marine species move out of the system, while 0+ juveniles begin migrating into the estuary. *O. mossambicus* moves into the shallow waters to breed during spring and their contribution to the ichthyofauna increases. With the more frequent opening of the mouth in spring and summer, the upper reaches drain completely and the fishes concentrate in the lower reaches, thus contributing to the increase in the proportion of freshwater and estuarine species.

Breeding of both freshwater and estuarine species continues during the summer, as does the recruitment of estuarine-dependent marine species. Draining of the upper reaches of the system when the mouth opens reduces the available aquatic habitat, food resources and increases competition. Susceptibility of small fishes to bird predation is increased and this contributes to a decrease in the relative contribution of estuarine species in summer. During autumn, *O. mossambicus* migrate to the deeper waters and as a result estuarine-dependent marine species dominate the littoral areas of the system (Figure 25).

## ZOTSHA ESTUARY

### STUDY AREA

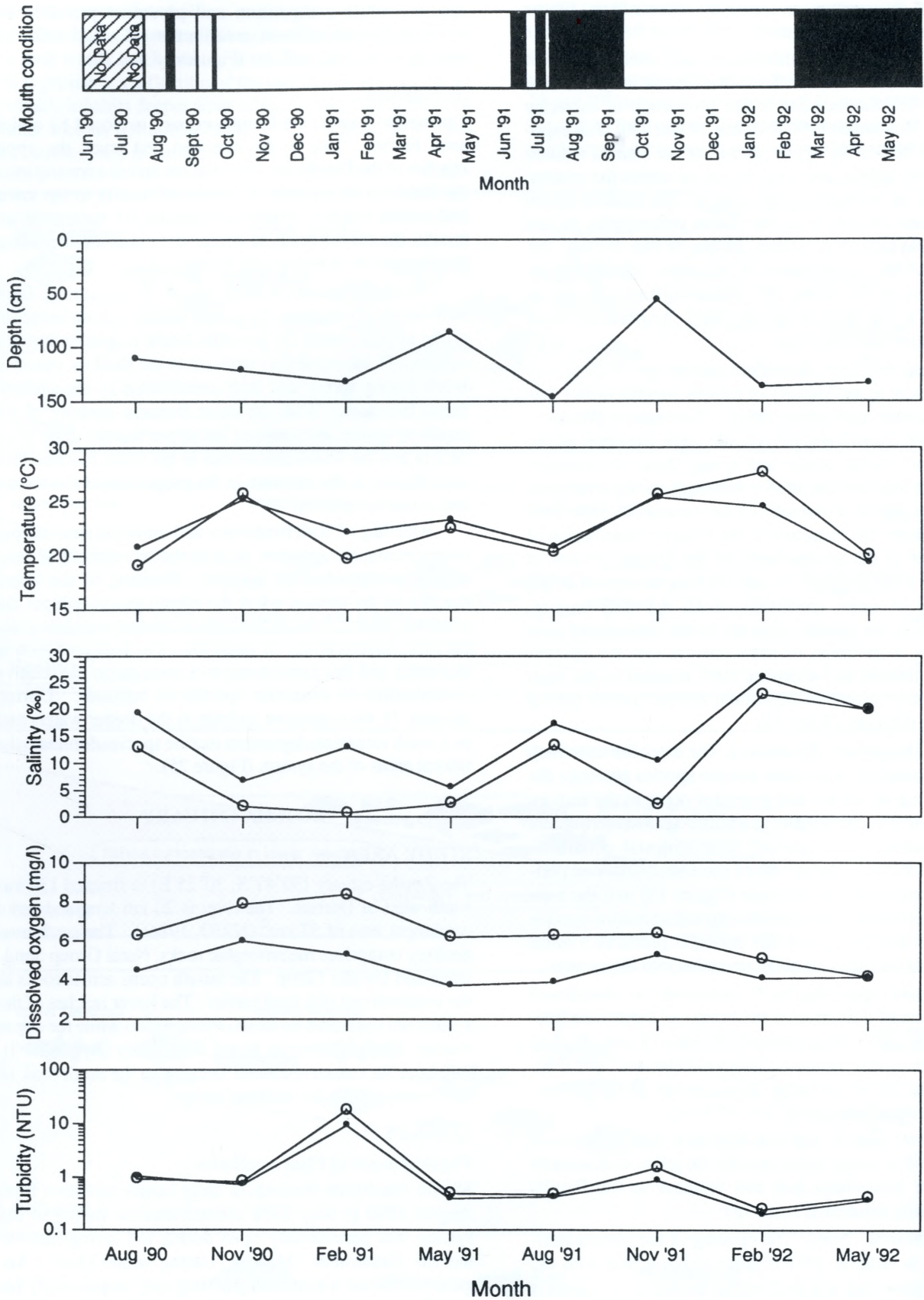
The Zotsha estuary (30° 47' S; 30° 25' E) is situated 134 km south west of Durban. The river is 20 km long and has a catchment area of 57 km<sup>2</sup> (NRIO, 1986a). The catchment geology comprises metamorphic rocks, Natal Group Sandstone and Dwyka Tillite. The mouth opens across rocks at the southern end of a sand barrier. The lower reaches of the system are vegetated by reeds (*Phragmites*) while the upper reaches support a riverine forest community (Appendix 3). The Ian Ellis nature reserve is situated on the north bank of the system, above the old road bridge.

### RESULTS

#### Physicochemical Characteristics

**Mouth condition:** Records of daily mouth condition from August 1990 to May 1992 showed that the mouth of the system was permanently open during the spring/summer months (September - March). During winter (June - August) the mouth was closed, opening only occasionally for periods of 4 to 19 days (Figure 26).

**Depth:** Average recorded water depths in the lower, middle and upper reaches of the estuary ranged from 147 cm in August 1991 to 57 cm in November 1991. The average depth was greater than 100 cm for much of the study period,



**Figure 26.** Daily mouth conditions (□ open; ■ closed) and abiotic parameters measured in the surface (o) and bottom (●) waters of the Zotsha estuary.



**Table 9.** Numerical composition of the fishes captured in the Zotsha estuary using various sampling techniques (August 1990 - May 1992).

Fish Taxa	Beam Trawl x 35		Otter Trawl x 35		Seine Net x 37		Gill Nets x 40		Total	
	n	%	n	%	n	%	n	%	n	%
<i>Acanthopagrus berda</i>							2	0.37	2	0.04
<i>Ambassis natalensis</i>					11	0.26			11	0.22
<i>Ambassis productus</i>	33	42.31	4	1.71	286	6.73	1	0.19	324	6.35
<i>Argyrosomus hololepidotus</i>	1	1.28					5	0.93	6	0.12
<i>Arothron immaculatus</i>					1	0.02			1	0.02
<i>Awaous aeneofuscus</i>							1	0.19	1	0.02
<i>Caranx papuensis</i>							9	1.67	9	0.18
<i>Caranx sexfasciatus</i>							2	0.37	2	0.04
<i>Caranx sp.</i>	1	1.28			31	0.73			32	0.63
<i>Crenimugil crenilabis</i>					225	5.29			225	4.41
<i>Croilia mossambica</i>			3	1.28	10	0.24			13	0.25
<i>Eleotris fusca</i>					1	0.02			1	0.02
<i>Eleotris mauritanus</i>					1	0.02			1	0.02
<i>Eleotris sp.</i>	1	1.28			1	0.02			2	0.04
<i>Favonigobius reichei</i>					1	0.02			1	0.02
<i>Gerres acinaces</i>					1	0.02			1	0.02
<i>Gerres rappi</i>	3	3.85	2	0.85	40	0.94	34	6.32	79	1.55
<i>Gerres sp.</i>					75	1.76			75	1.47
<i>Gilchristella aestuaria</i>			73	31.20	486	11.43			559	10.96
<i>Glossogobius biocellatus</i>					1	0.02			1	0.02
<i>Glossogobius callidus</i>	2	2.56	40	17.09	271	6.37			313	6.14
<i>Glossogobius giuris</i>			2	0.85	1	0.02			3	0.06
<i>Goby sp. III</i>					1	0.02			1	0.02
Juvenile mugilids					823	19.36			823	16.13
<i>Khulia mugil</i>					7	0.16			7	0.14
<i>Leiognathus equula</i>			4	1.71			7	1.30	11	0.22
<i>Lichia amia</i>					2	0.05	3	0.56	5	0.10
<i>Liza alata</i>					2	0.05	60	11.15	62	1.22
<i>Liza dumerilii</i>					40	0.94	7	1.30	47	0.92
<i>Liza macrolepis</i>					14	0.33	12	2.23	26	0.51
<i>Liza sp.</i>					129	3.03			129	2.53
<i>Liza tricuspidens</i>					25	0.59	2	0.37	27	0.53
<i>Lutjanus argentimaculatus</i>					1	0.02	6	1.12	7	0.14
<i>Lutjanus fulviflamma</i>					3	0.07			3	0.06
<i>Megalops cyprinoides</i>							1	0.19	1	0.02
<i>Monodactylus argenteus</i>							2	0.37	2	0.04
<i>Monodactylus falciformis</i>			1	0.43	5	0.12	1	0.19	7	0.14
<i>Monodactylus sp.</i>			1	0.43					1	0.02
<i>Mugil cephalus</i>					46	1.08	27	5.02	73	1.43
<i>Myxus capensis</i>					156	3.67	38	7.06	194	3.80
<i>Oligolepis keiensis</i>			4	1.71	4	0.09			8	0.16
<i>Oreochromis mossambicus</i>	5	6.41	13	5.56	431	10.14	95	17.66	544	10.66
<i>Pomadasys commersonnii</i>	2	2.56	19	8.12	9	0.21	4	0.74	34	0.67
<i>Pomadasys sp.</i>			1	0.43	3	0.07			4	0.08
<i>Pomatomus saltatrix</i>							1	0.19	1	0.02
<i>Pseudorhombus arsius</i>	1	1.28							1	0.02
<i>Rhabdosargus holubi</i>	2	2.56	27	11.54	496	11.67			525	10.29
<i>Rhabdosargus thorpei</i>			1	0.43	6	0.14			7	0.14
<i>Scomberoides sp.</i>					1	0.02			1	0.02
<i>Solea bleekeri</i>	27	34.62	37	15.81	7	0.16			71	1.39
<i>Terapon jarbua</i>			2	0.85	370	8.70	1	0.19	373	7.31
<i>Tilapia rendallii</i>					2	0.05			2	0.04
<i>Valamugil buchanani</i>							37	6.88	37	0.73
<i>Valamugil cunnesius</i>					55	1.29	86	15.99	141	2.76
<i>Valamugil robustus</i>					32	0.75	94	17.47	126	2.47
<i>Valamugil sp.</i>					138	3.25			138	2.71

with shallow water conditions (<90 cm) recorded on two occasions (Figure 26).

**Temperature:** Water temperature in the Zotsha appeared to follow a seasonal pattern with both surface and bottom waters being marginally warmer in the spring/summer (November - February) than those recorded during the autumn/winter (May - August). Average surface temperatures ranged from 19.0°C in August 1990 to 27.7°C in

February 1992, and bottom temperatures from 19.3°C in August 1991 to 25.4°C in November 1991. The average bottom temperature exceeded the average surface temperature on four occasions (August 1990, February 1991, May 1991 and August 1991). On all the other occasions surface water temperatures were higher than those recorded in the bottom waters (Figure 26).

**Salinity:** The average surface salinity ranged from 0.8‰ in February 1991 to 22.7‰ in February 1992. Average bot-

**Table 10.** Biomass composition of the fishes captured in the Zotsha estuary using various sampling techniques (August 1990 - May 1992).

Sampling Gear Fish Taxa	Beam Trawl x 35		Otter Trawl x 35		Seine Net x 37		Gill Nets x 40		Total	
	g	%	g	%	g	%	g	%	g	%
<i>Acanthopagrus berda</i>							639.5	0.38	639.5	0.34
<i>Ambassis natalensis</i>					67.0	0.49			67.0	0.04
<i>Ambassis productus</i>	208.3	18.74	36.6	0.86	1231.7	9.05	42.3	0.03	1518.9	0.82
<i>Argyrosomus hololepidous</i>	166.6	14.99					1439.1	0.86	1605.7	0.86
<i>Arothron immaculatus</i>					10.1	0.07			10.1	0.01
<i>Awaous aeneofuscus</i>							125.1	0.07	125.1	0.07
<i>Caranx papuensis</i>							1765.3	1.06	1765.3	0.95
<i>Caranx sexfasciatus</i>							268.5	0.16	268.5	0.14
<i>Caranx sp.</i>	4.3	0.38			82.1	0.60			86.4	0.05
<i>Crenimugil crenilabis</i>					656.7	4.82			656.7	0.35
<i>Croilia mossambica</i>			1.2	0.03	1.8	0.01			2.9	0.00
<i>Eleotris fusca</i>					2.2	0.02			2.2	0.00
<i>Eleotris mauritanus</i>					1.4	0.01			1.4	0.00
<i>Eleotris sp.</i>	1.0	0.09			1.0	0.01			2.0	0.00
<i>Favonigobius reichei</i>					0.3	0.00			0.3	0.00
<i>Gerres acinaces</i>					3.6	0.03			3.6	0.00
<i>Gerres rappi</i>	197.5	17.77	140.2	3.28	61.6	0.45	4529.8	2.71	4929.2	2.65
<i>Gerres sp.</i>					50.9	0.37			50.9	0.03
<i>Gilchristella aestuaria</i>			70.9	1.66	311.2	2.29			382.0	0.21
<i>Glossogobius biocellatus</i>					3.1	0.02			3.1	0.00
<i>Glossogobius callidus</i>	2.0	0.18	26.6	0.62	232.9	1.71			261.5	0.14
<i>Glossogobius giuris</i>			158.4	3.71	54.9	0.40			213.3	0.11
<i>Goby sp. III</i>					0.9	0.01			0.9	0.00
Juvenile mugilids					526.1	3.87			526.1	0.28
<i>Khulia mugil</i>					2.5	0.02			2.5	0.00
<i>Leiognathus equula</i>			116.7	2.73			454.9	0.27	571.6	0.31
<i>Lichia amia</i>					14.1	0.10	2802.2	1.68	2816.3	1.51
<i>Liza alata</i>					24.5	0.18	36630.3	21.90	36654.8	19.68
<i>Liza dumerilii</i>					561.9	4.13	1250.1	0.75	1812.0	0.97
<i>Liza macrolepis</i>					109.8	0.81	3393.6	2.03	3503.4	1.88
<i>Liza sp.</i>					193.8	1.42			193.8	0.10
<i>Liza tricuspidens</i>					108.2	0.79	893.5	0.53	1001.7	0.54
<i>Lutjanus argentimaculatus</i>					0.3	0.00	3514.6	2.10	3514.9	1.89
<i>Lutjanus fulviflamma</i>					6.2	0.05			6.2	0.00
<i>Megalops cyprinoides</i>							882.6	0.53	882.6	0.47
<i>Monodactylus argenteus</i>							115.4	0.07	115.4	0.06
<i>Monodactylus falciformis</i>			0.2	0.01	2.4	0.02	71.8	0.04	74.5	0.04
<i>Monodactylus sp.</i>			43.8	1.02					43.8	0.02
<i>Mugil cephalus</i>					474.4	3.49	10649.3	6.37	11123.7	5.97
<i>Myxus capensis</i>					996.6	7.32	14914.5	8.92	15911.1	8.54
<i>Oligolepis keiensis</i>			1.7	0.04	1.3	0.01			3.0	0.00
<i>Oreochromis mossambicus</i>	385.4	34.67	2129.3	49.81	2767.4	20.33	35190.3	21.04	40472.3	21.73
<i>Pomadasys commersonnii</i>	35.6	3.20	1020.6	23.88	88.8	0.65	941.8	0.56	2086.9	1.12
<i>Pomadasys sp.</i>			0.1	0.00	0.2	0.00			0.2	0.00
<i>Pomatomus saltatrix</i>							768.6	0.46	768.6	0.41
<i>Pseudorhombus arsius</i>	20.1	1.81							20.1	0.01
<i>Rhabdosargus holubi</i>	18.3	1.65	456.9	10.69	2200.2	16.17			2675.4	1.44
<i>Rhabdosargus thorpei</i>			0.7	0.02	35.1	0.26			35.9	0.02
<i>Scomberoides sp.</i>					0.6	0.00			0.6	0.00
<i>Solea bleekeri</i>	73.6	6.62	24.8	0.58	3.5	0.03			101.9	0.05
<i>Terapon jarbua</i>			46.0	1.08	915.8	6.73	57.4	0.03	1019.2	0.55
<i>Tilapia rendallii</i>					4.9	0.04			4.9	0.00
<i>Valamugil buchanani</i>							16205.1	9.69	16205.1	8.70
<i>Valamugil cunnesius</i>					312.9	2.30	10746.4	6.43	11059.4	5.94
<i>Valamugil robustus</i>					1347.6	9.90	18952.8	11.33	20300.4	10.90
<i>Valamugil sp.</i>					138.8	1.02			138.8	0.07

tom salinities ranged from 5.5 ‰ in May 1991 to 26.0 ‰ in February 1992. The waters in the Zotsha were stratified during the study period with bottom salinities being higher than those at the surface (Figure 26).

**Dissolved oxygen:** Average dissolved oxygen recorded in the surface waters ranged from 8.3 mg l<sup>-1</sup> in February 1991 to 4.2 mg l<sup>-1</sup> in May 1992. The average dissolved oxygen recorded in bottom water was lower than that in surface

water and ranged from 6.0 mg l<sup>-1</sup> recorded in November 1990 to 3.7 mg l<sup>-1</sup> recorded in May 1991 (Figure 26).

**Turbidity:** Average surface turbidity was generally higher than that recorded in bottom waters and ranged from 17.8 NTU recorded in February 1991 to 0.3 NTU recorded in February 1992. The average bottom turbidity in the Zotsha ranged from 9.2 NTU in February 1991 to 0.2 NTU in February 1992 (Figure 26).

**Table 11.** Percent similarity of the catch composition of each gear type to the total catch in the Zotsha estuary ( $IS_J$  = Jaccard's index of similarity,  $IS_S$  = Sørensen's index of similarity).

Gear	$IS_J$	$IS_S$	Similarity ranking
Beam trawl	19.64	32.84	4
Otter trawl	30.36	46.58	3
Seine net	78.57	88.00	1
Gill nets	46.43	63.41	2

### Species Composition and Sampling Efficiency

A total of 5101 specimens representing 22 families and 56 fish taxa were collected in the Zotsha system. The most abundant fishes collected were juvenile mugilids (16.1%), *Gilchristella aestuaria* (11.0%), *Oreochromis mossambicus* (10.7%), *Rhabdosargus holubi* (10.3%), *Terapon jarbua* (7.3%), *Ambassis productus* (6.4%) and *Glossogobius callidus* (6.1%) (Table 9). Together these fishes comprised over 67% of the fish fauna in the Zotsha lagoon. The remaining fishes each contributed less than 5% to the total catch and together comprised 32% of the catch. A total fish biomass of 186.2 kg was caught in the Zotsha estuary during this study. *Oreochromis mossambicus* dominated the fish biomass and accounted for 21.7% of the total. *Liza alata* (19.7%), *Valamugil robustus* (10.9%), *Valamugil buchanani* (8.7%), *Myxus capensis* (8.5%), *Mugil cephalus* (6.0%) and *Valamugil cunnesius* (5.9%) were the next

dominant species (Table 10) and together with *O. mossambicus* accounted for over 81% of the total fish biomass in the Zotsha. The remaining fishes each contributed less than 3% to the catch and together comprised 18.5% of the total biomass.

Numerical and biomass analyses for fish catches from each of the four sampling gears are shown in Tables 9 and 10 respectively. The percent similarity of the catch composition of each gear type to the total catch in the Zotsha estuary is shown in Table 11. Results from both Jaccard's and Sørensen's indices of similarity revealed that seine net catches were most similar to the total catch (Table 11).

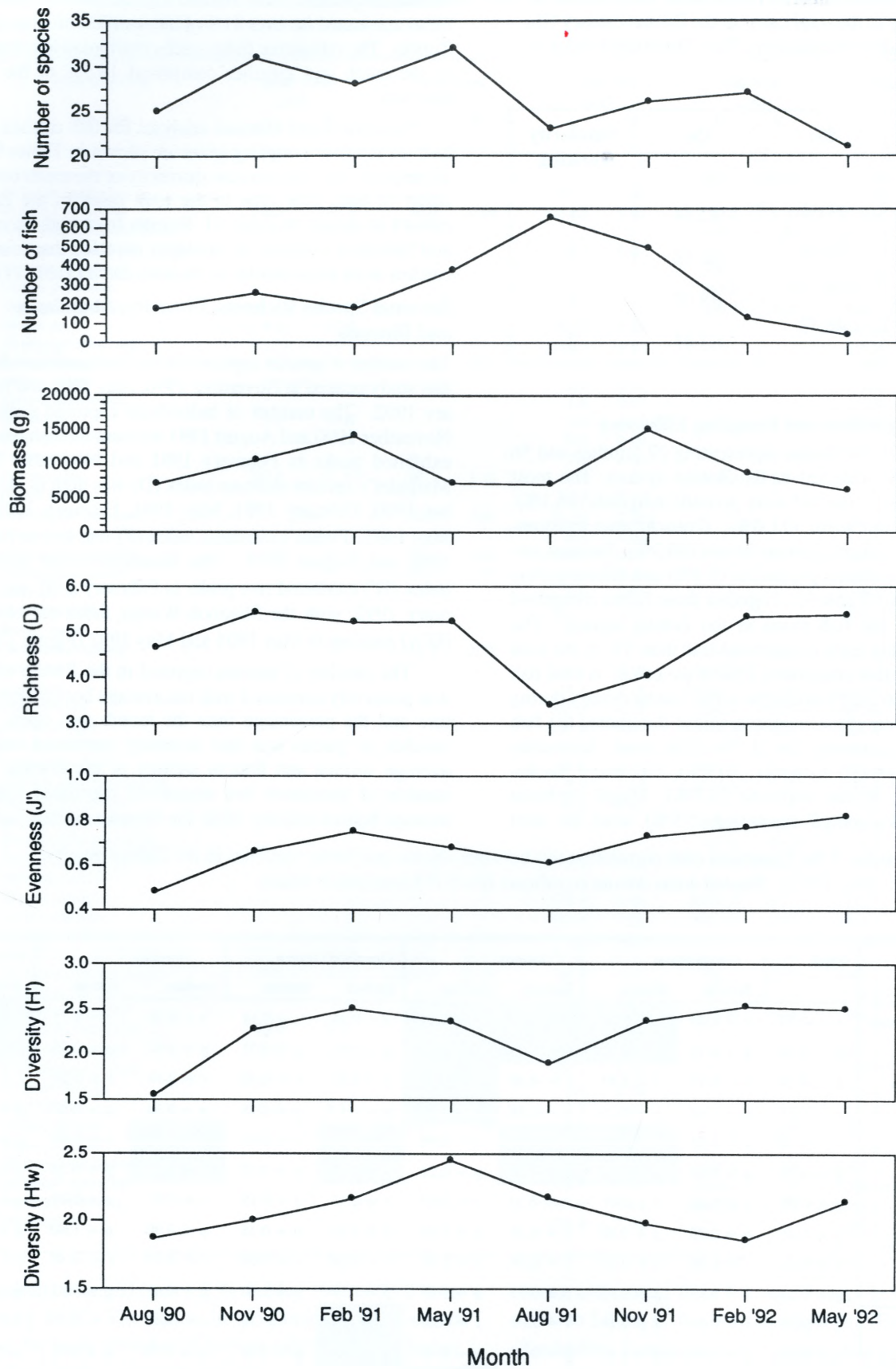
### Seasonal Species Richness, Diversity, Abundance and Biomass

The number of species captured in the Zotsha estuary during this study peaked in November 1990, May 1991 and February 1992. The number of individuals captured peaked in November 1990 and August 1991 whereas the fish biomass exhibited peaks in February 1991 and November 1991. Margalef's species richness index ( $D$ ) was high in November 1990, February 1991, May 1991, February 1992 and May 1992. Pielou's evenness index ( $J'$ ) was low in August 1990 and August 1991. The Shannon-Wiener diversity index ( $H'$ ) exhibited two peaks in February 1991 and February 1992, with the Shannon-Wiener index for biomass ( $H'w$ ) peaking in May 1991 and May 1992 (Figure 27).

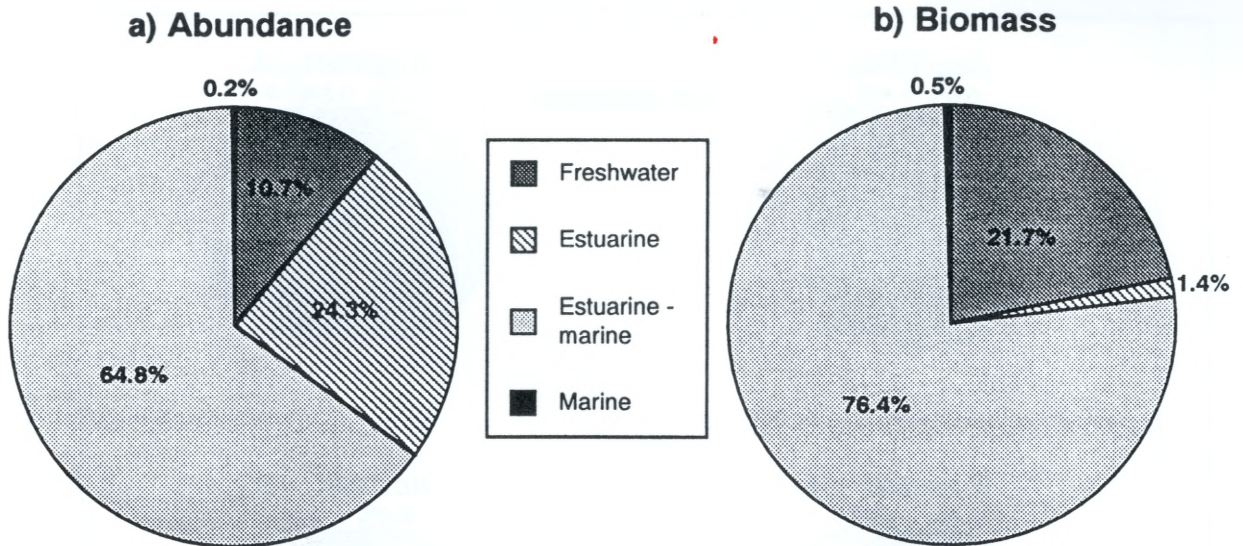
The number of species captured in the Zotsha estuary was positively correlated with the average bottom temperature and the percentage time the mouth was open. The number of species was also inversely correlated with the average surface and bottom salinity of the Zotsha. The number of specimens was negatively correlated with the average bottom salinity while the biomass of fish captured

**Table 12.** Results of the Spearman rank correlation test between abiotic and biotic variables in the Zotsha estuary. (August 1990 - May 1992). Shaded areas denote significant ( $p < 0.15$ ) correlation values.

	Depth	Temperature		Salinity		Dissolved Oxygen		Turbidity		Mouth % Open
		Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	
Number of species	$r = -0.43$	$r = 0.40$	$r = 0.61$	$r = -0.57$	$r = -0.69$	$r = 0.38$	$r = 0.14$	$r = 0.29$	$r = 0.12$	$r = 0.89$
	$p = 0.26$	$p = 0.28$	$p = 0.10$	$p = 0.13$	$p = 0.07$	$p = 0.31$	$p = 0.71$	$p = 0.45$	$p = 0.75$	$p = 0.02$
Number of fish	$r = -0.24$	$r = 0.17$	$r = 0.43$	$r = -0.40$	$r = -0.67$	$r = 0.52$	$r = -0.12$	$r = 0.33$	$r = 0.29$	$r = 0.10$
	$p = 0.53$	$p = 0.66$	$p = 0.26$	$p = 0.28$	$p = 0.08$	$p = 0.17$	$p = 0.75$	$p = 0.38$	$p = 0.45$	$p = 0.80$
Biomass	$r = -0.38$	$r = 0.45$	$r = 0.86$	$r = -0.67$	$r = -0.48$	$r = 0.71$	$r = 0.52$	$r = 0.57$	$r = 0.40$	$r = 0.42$
	$p = 0.31$	$p = 0.23$	$p = 0.02$	$p = 0.08$	$p = 0.21$	$p = 0.06$	$p = 0.17$	$p = 0.13$	$p = 0.28$	$p = 0.27$
Richness ( $D$ )	$r = 0.07$	$r = 0.12$	$r = 0.07$	$r = -0.33$	$r = -0.07$	$r = 0.17$	$r = 0.55$	$r = 0.05$	$r = 0.00$	$r = 0.42$
	$p = 0.85$	$p = 0.75$	$p = 0.85$	$p = 0.38$	$p = 0.85$	$p = 0.66$	$p = 0.15$	$p = 0.90$	$p = 1.00$	$p = 0.27$
Evenness ( $J'$ )	$r = 0.21$	$r = 0.24$	$r = 0.03$	$r = 0.24$	$r = 0.36$	$r = -0.36$	$r = 0.00$	$r = -0.31$	$r = -0.45$	$r = -0.22$
	$p = 0.57$	$p = 0.53$	$p = 0.95$	$p = 0.53$	$p = 0.34$	$p = 0.34$	$p = 1.00$	$p = 0.41$	$p = 0.23$	$p = 0.57$
Diversity ( $H'$ )	$r = 0.19$	$r = 0.26$	$r = 0.19$	$r = 0.04$	$r = 0.26$	$r = -0.96$	$r = 0.10$	$r = -0.11$	$r = -0.25$	$r = 0.05$
	$p = 0.61$	$p = 0.49$	$p = 0.61$	$p = 0.92$	$p = 0.49$	$p = 0.08$	$p = 0.80$	$p = 0.78$	$p = 0.51$	$p = 0.90$
Diversity ( $H'w$ )	$r = 0.01$	$r = -0.29$	$r = -0.23$	$r = -0.35$	$r = -0.56$	$r = 0.18$	$r = -0.30$	$r = 0.13$	$r = 0.07$	$r = 0.28$
	$p = 0.97$	$p = 0.45$	$p = 0.55$	$p = 0.36$	$p = 0.14$	$p = 0.63$	$p = 0.43$	$p = 0.73$	$p = 0.85$	$p = 0.45$



**Figure 27.** Seasonal changes in the number of species, number of individuals, biomass, species richness, species evenness, and species diversity in the Zotsha estuary.



**Figure 28.** Percent numerical (a) and biomass (b) contribution of freshwater, estuarine, estuarine-dependent marine and marine species to the total ichthofauna of the Zotsha estuary.

was positively correlated with the average bottom temperature, surface dissolved oxygen and surface turbidity. Fish biomass was negatively correlated with the average surface salinity of the system. Margalef's species richness index (D) and Pielou's evenness index (J') did not exhibit any correlation with any of the abiotic variables measured. The Shannon-Wiener diversity index (H') and the Shannon-Wiener index for biomass (H'w) were negatively correlated with surface dissolved oxygen and bottom salinity respectively (Table 12).

### Community Structure

**Overall abundance and biomass:** The total fish community captured in the Zotsha estuary during this study was numerically dominated by estuarine-dependent marine species. This group of fishes comprised 64.8% of the total fish assemblage, estuarine species 24.3%, freshwater species 10.7% and marine species 0.2%. In terms of biomass, estuarine-dependent marine species also dominated the ichthyofaunal assemblage and comprised 76.4% of the catch, whereas freshwater species contributed 21.7%. Marine and estuarine species contributed 0.5% and 1.4% to the total fish biomass respectively (Figure 28).

**Seasonal changes in relative abundance and biomass:** Estuarine-dependent marine species numerically dominated the fish community throughout most of the study period. The relative contribution of estuarine species to the ichthyofauna was high in November 1990, May 1991, August 1991 and May 1992. The percent contribution of freshwater species was relatively high in May 1991 and November 1991, with marine species well represented in February 1992 (Figure 29).

Estuarine-dependent marine species also dominated the fish biomass captured in the Zotsha throughout the study period. Freshwater species were a dominant component of the fish biomass in November 1990, May 1991, November

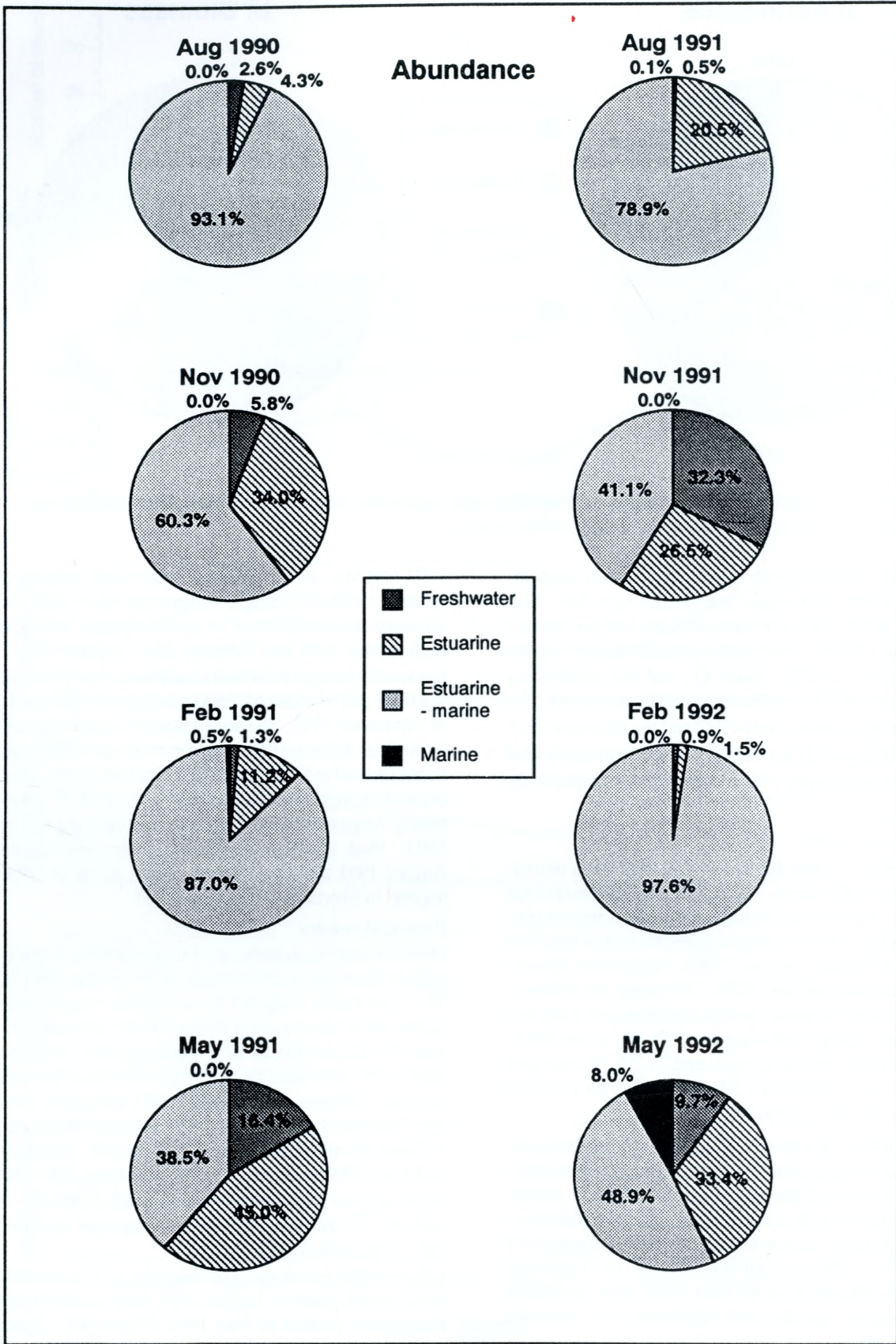
1991 and May 1992. Estuarine and marine species did not usually constitute a major component of the fish biomass, although the contribution of marine species was relatively high in May 1991 and February 1992 (Figure 30).

**Seasonal changes in actual abundance and biomass:** The numbers and biomass of freshwater species exhibited a peak in November 1991. The abundance of estuarine species was highest in August 1991, and the biomass of this group of fishes peaked in November 1990 and May 1991. Estuarine-dependent marine species exhibited a peak in abundance during August 1991, with the biomass peaking in February 1991. Peak numbers of marine species were captured in August 1991 and the biomass of this group of fishes was highest in February 1992 (Figure 31).

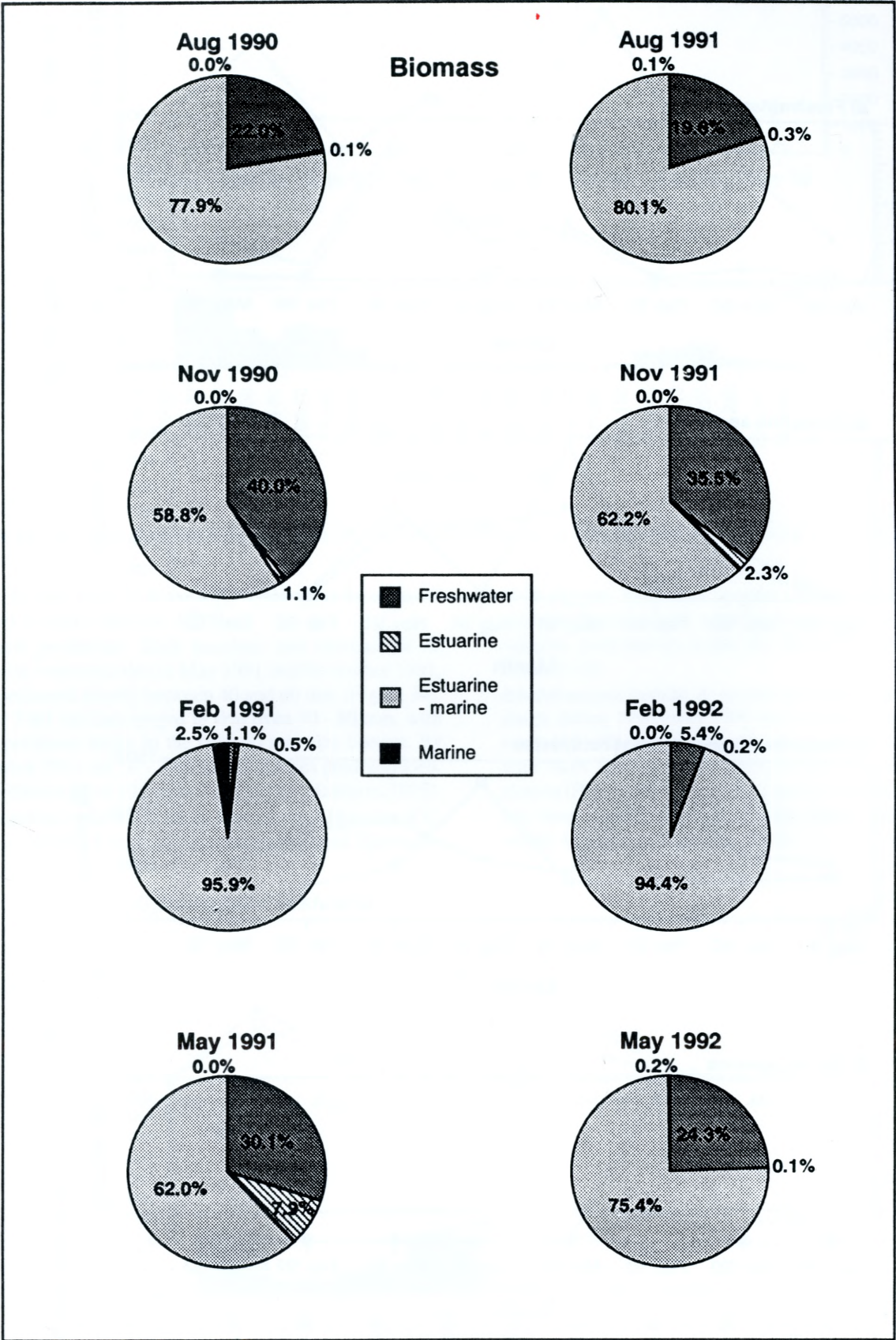
### Principal species

***Oreochromis mossambicus*:** *O. mossambicus* exhibited a peak in abundance and biomass in November 1991 (Figure 32). Specimens captured in the Zotsha estuary during the study period were mostly in the 20 - 80 mm and 190 - 220 mm size classes (Figure 32). Those captured in August and November 1990 were mostly large individuals between 190 mm and 230 mm. In February 1991 specimens below 30 mm dominated, and by May 1991 this cohort had grown to between 30 mm and 60 mm. In August 1991, February 1992 and May 1992, only large *O. mossambicus* 190 - 240 mm were captured. Specimens predominantly in the 20 - 40 mm and 60 - 80 mm size classes were captured in November 1991 (Harrison, 1993).

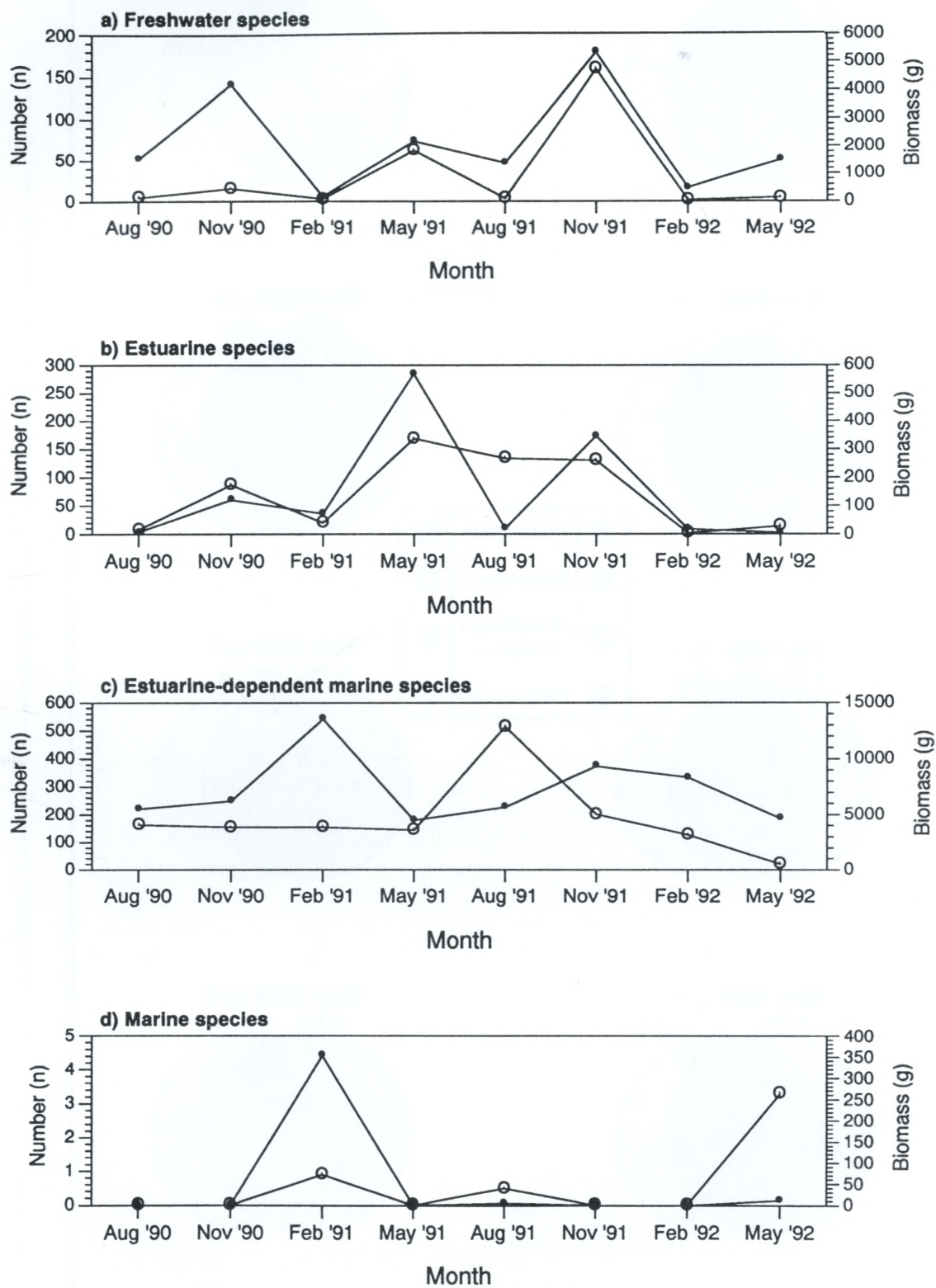
***Gilchristella aestuaria*:** The numbers of *G. aestuaria* captured were highest in August 1991, whereas the biomass of this species peaked in May 1991 (Figure 33). Specimens captured during this study were mostly in the 10 - 20 mm and 40 - 50 mm size classes (Figure 33). *G. aestuaria* captured in November 1990, February 1991 and May 1991 ranged from 10 - 60 mm and were mostly in the 30 - 50 mm size classes. Specimens captured in August 1991 were all



**Figure 29.** Seasonal numerical composition of freshwater, estuarine, estuarine-dependent marine and marine fish species in the Zotsha estuary.

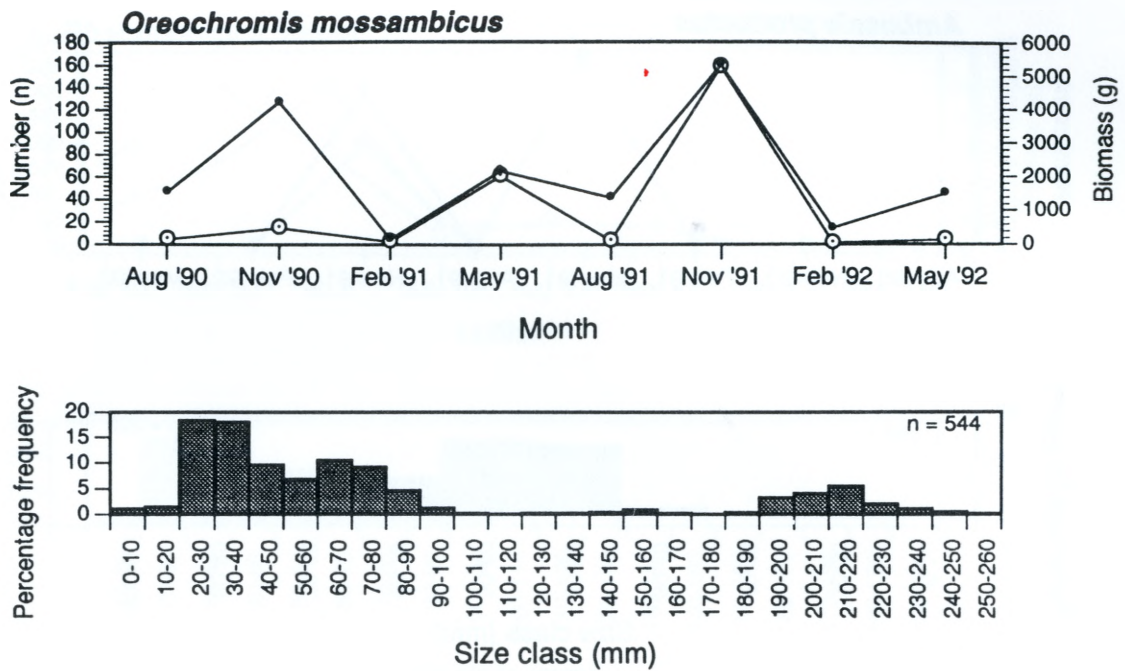


**Figure 30.** Seasonal biomass composition of freshwater, estuarine, estuarine-dependent marine and marine fish species in the Zotsha estuary.



**Figure 31.** Seasonal fluctuations in the number (○) and biomass (●) of freshwater species (a), estuarine species (b), estuarine-dependent marine species (c) and marine species (d) in the Zotsha estuary.





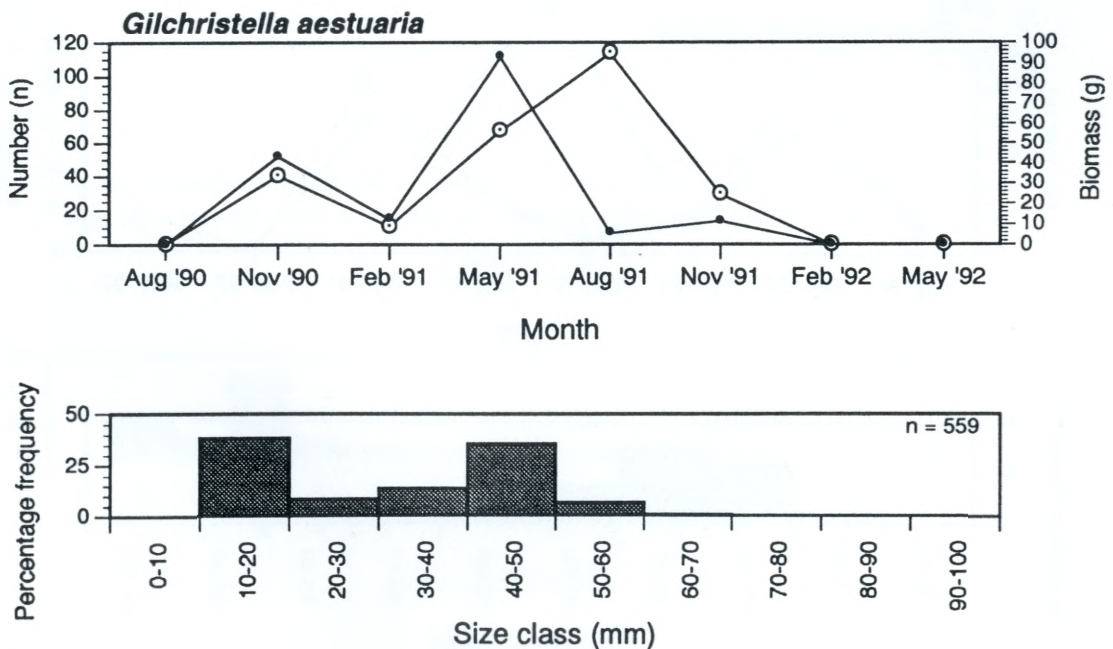
**Figure 32.** Seasonal abundance (○), biomass (●) and length frequency of *Oreochromis mossambicus* in the Zotsha estuary.

below 30 mm while in November 1991 were between 20 mm and 50 mm (Harrison, 1993).

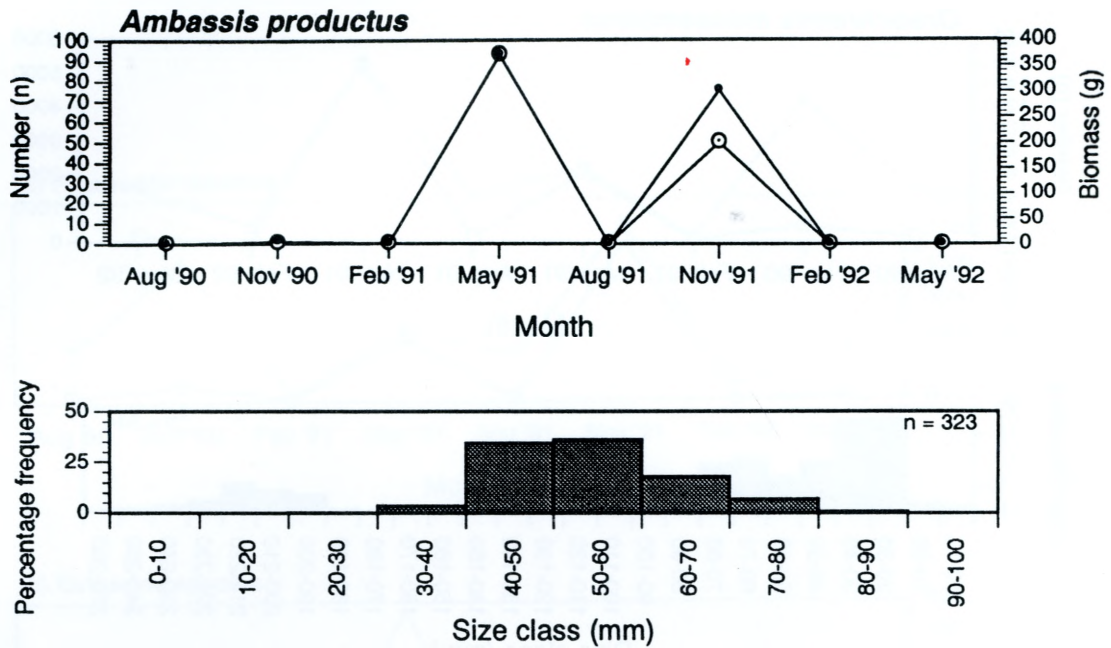
**Ambassis productus:** High numbers and biomass of *A. productus* were recorded in May 1991 and November 1991, with specimens mostly between 40 and 60 mm (Figure 34). In May 1991 the fish ranged in size from 30 - 80 mm, with most specimens being in the 40 - 60 mm size classes. By November 1991 the 50 - 70 mm size classes predominated, and specimens up to 90 mm were recorded (Harrison, 1993). **Glossogobius callidus:** Both the numbers and biomass of *G. callidus* exhibited peaks in November 1990 and November

1991 (Figure 35). This species was captured during the entire study period and, with the exception of the May 1992 samples, were mostly in the 20 - 50 mm size classes (Harrison, 1993).

**Rhabdosargus holubi:** *R. holubi* exhibited a peak in abundance during November 1990 and biomass peaked in February 1991 (Figure 36). Specimens were usually <100 mm, with most specimens occurring in the 20 - 60 mm size classes (Figure 36). Length frequency distributions suggest that new recruits enter the Zotsha estuary mainly during winter and spring (Harrison, 1993).



**Figure 33.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Gilchristella aestuaria* in the Zotsha estuary.

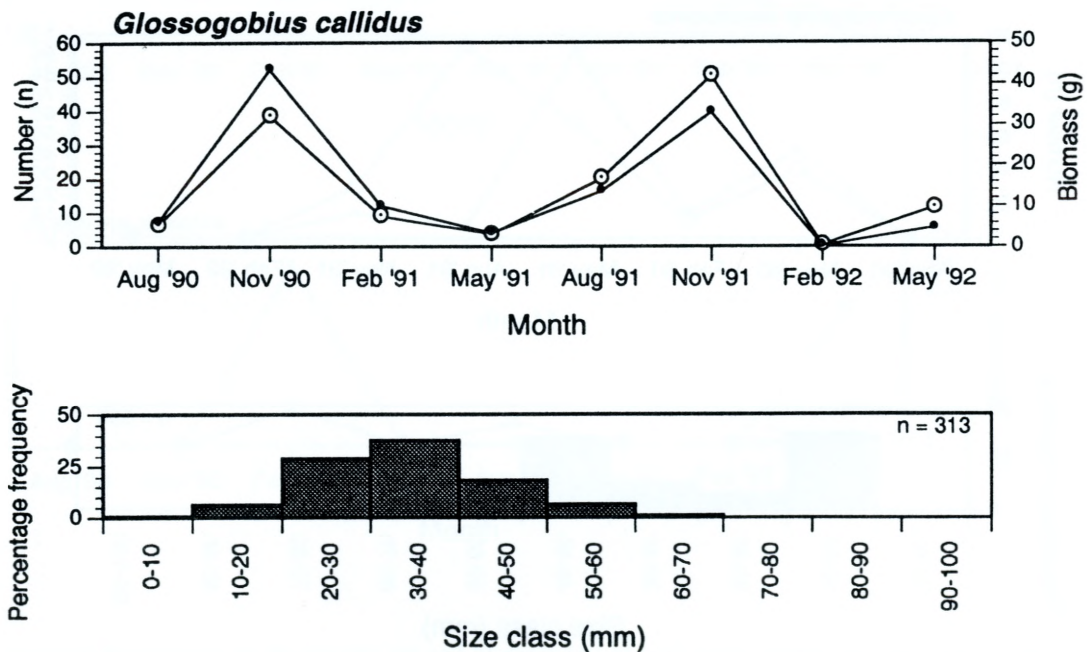


**Figure 34.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Ambassis productus* in the Zotsha estuary.

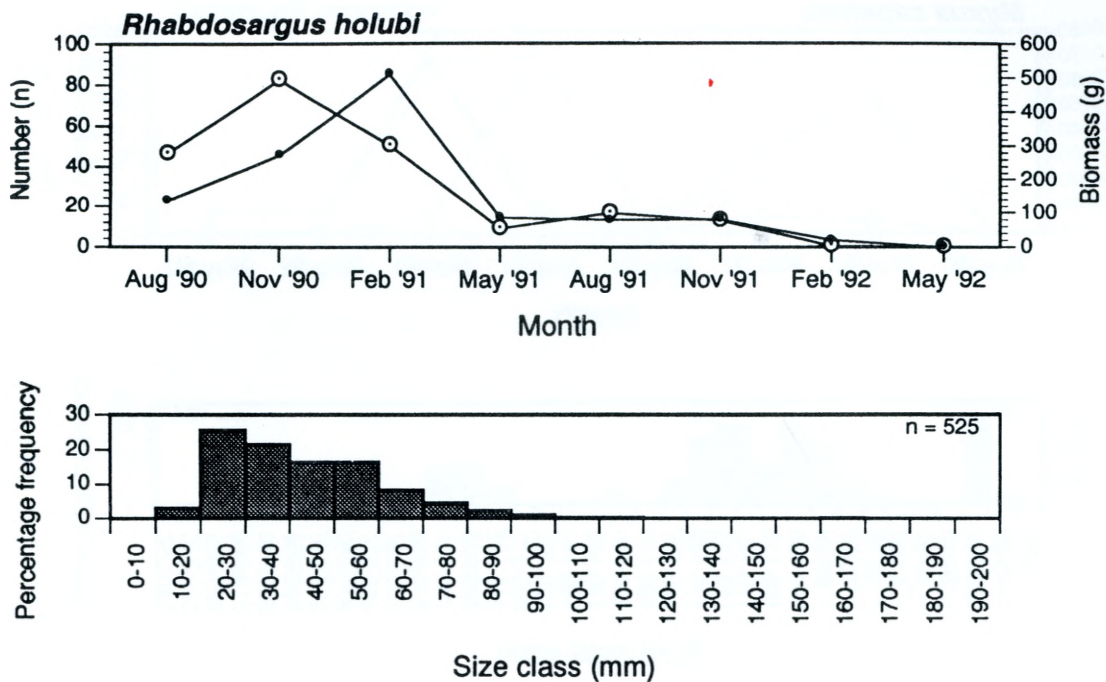
***Terapon jarbua*:** Both the numbers and biomass of *T. jarbua* peaked in August 1991 (Figure 37). *T. jarbua* ranged in size from <10 - 130 mm and were mostly in the 10 - 40 mm size classes (Figure 37).

***Myxus capensis*:** The numbers of *M. capensis* peaked in August 1991, while the biomass of this species peaked in November 1990 and November 1991 (Figure 38). *M. capensis* ranged from 10 - 340 mm, with the vast majority of specimens being in the 20 - 30 mm size class, primarily because of the abundance of this size class during August 1991 (Harrison, 1993).

***Valamugil cunnesius*:** The numbers of *V. cunnesius* peaked in February 1991 and November 1991, while the biomass of this species peaked in February 1991 (Figure 39). *V. cunnesius* captured during this study ranged in size from 30 - 230 mm, with most specimens occurring in the 40 - 80 mm and 160 - 190 mm size classes (Figure 39). The *V. cunnesius* captured in August 1990, November 1991 and February 1991 were mostly above 150 mm with small specimens <70 mm also being captured in November 1990 and February 1991. Similar size classes were also present in May 1991, November 1991 and February 1992 (Harrison, 1993).



**Figure 35.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Glossogobius callidus* in the Zotsha estuary.

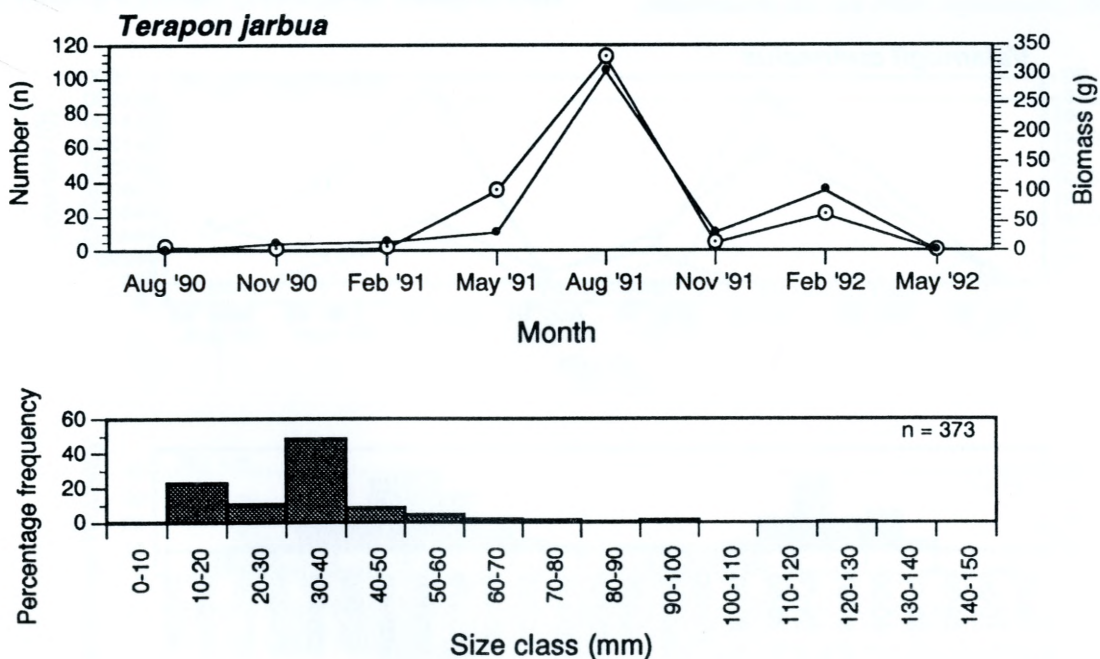


**Figure 36.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Rhabdosargus holubi* in the Zotsha estuary.

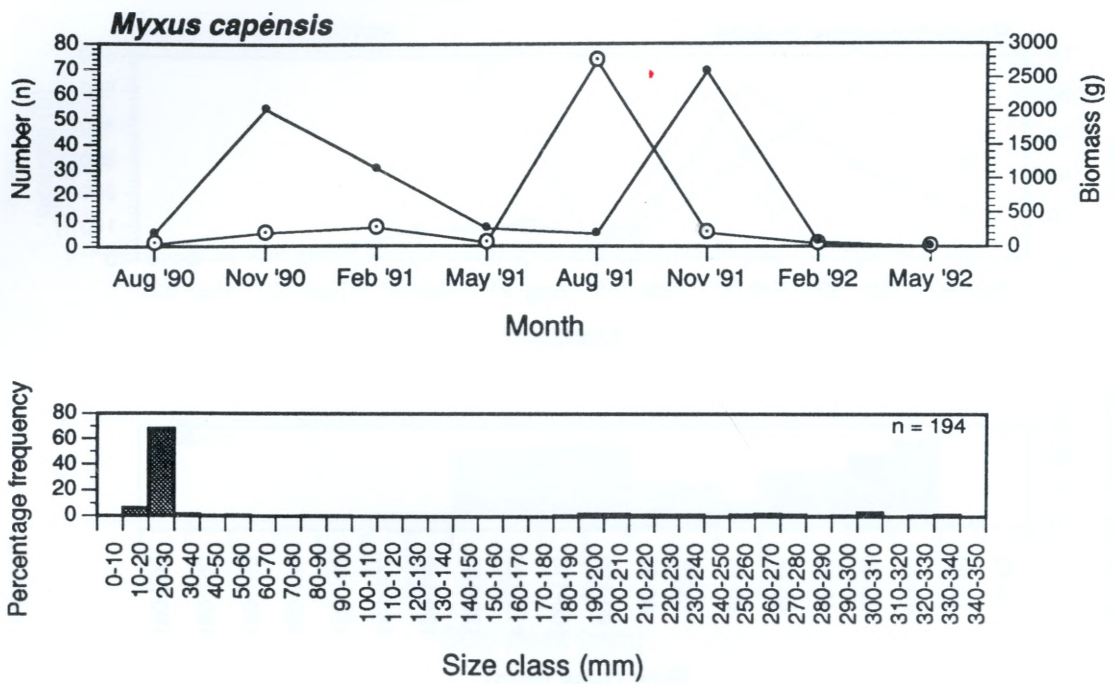
*Valamugil robustus*: High numbers of *V. robustus* were captured in February 1991 and February 1992, while the biomass of this species peaked in February 1991 (Figure 40). *V. robustus* captured in the Zotsha during this study ranged in size from 80 - 270 mm and were mostly in the 90 - 120 mm and 170 - 240 mm size classes (Figure 40). *V. robustus* was captured throughout the study period and were

generally above 180 mm. Specimens below 120 mm were only captured in February 1991, May 1991 and February 1992 (Harrison, 1993).

*Mugil cephalus*: Numbers of *M. cephalus* peaked in November 1991 while the biomass peaked in February 1991 (Figure 41). *M. cephalus* was captured throughout the study period and were mostly in the 20 - 50 mm and 210 - 270 mm



**Figure 37.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Terapon jarbua* in the Zotsha estuary.



**Figure 38.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Myxus capensis* in the Zotsha estuary.

size classes (Figure 41). Most of the specimens captured in November 1990 and November 1991 were between 20 mm and 50 mm. Immature *M. cephalus* 190 - 290 mm predominated during August 1990, February 1991, May 1991, August 1991 and May 1992 (Harrison, 1993).

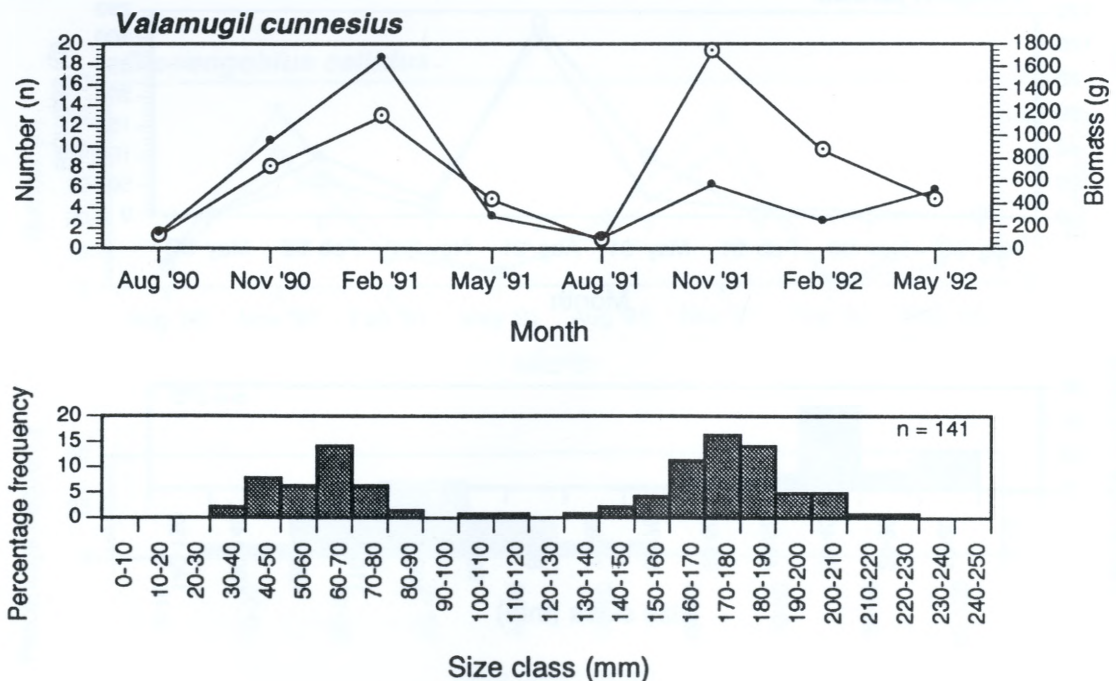
***Liza alata*:** Both the numbers and biomass of *L. alata* peaked in August 1990 and November 1991 (Figure 42). This species was captured throughout the study period and were mostly large specimens >210 mm (Figure 42). Small individuals <100 mm were only captured in November 1991 (Harrison, 1993).

***Valamugil buchanani*:** Both the abundance and biomass of *V. buchanani* peaked in February 1992 (Figure 43). *V. buchanani* captured in the Zotsha were between 180 and 330 mm, with most specimens occurring in the 250 - 300 mm size classes (Figure 43).

#### DISCUSSION

##### Physicochemical Characteristics

The mouth of the Zotsha estuary during this study was permanently open in the spring/summer (September - February). During winter (June - August) the mouth of the



**Figure 39.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Valamugil cunnesius* in the Zotsha estuary.

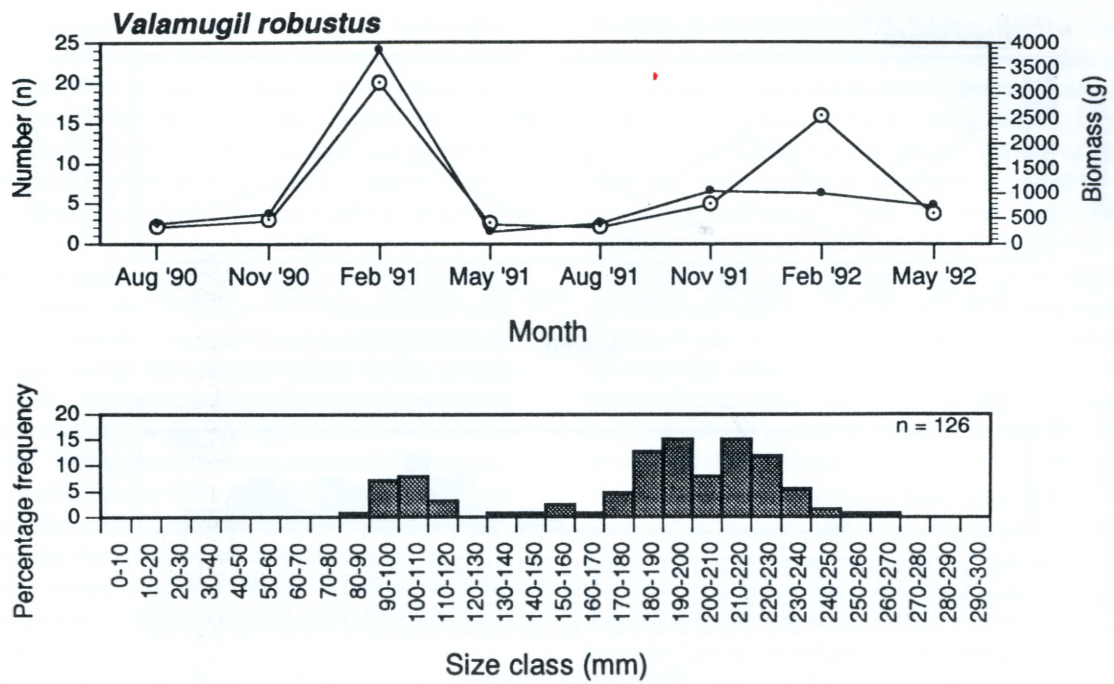


Figure 40. Seasonal abundance (○), biomass (●) and length frequency of *Valamugil robustus* in the Zotsha estuary.

system closed and only opened occasionally for short periods (Figure 26). Begg (1984b) noted that during the period June 1979 to August 1980, the mouth of the Zotsha was closed for 75% of the time. The mouth of the Zotsha opens across rocks at the southern end of a sand barrier. Cooper (1991) noted that the presence of rocks at the base or side of a channel enhances turbulence and assists in preserving an open mouth condition. This probably accounted for the predominantly open mouth condition of the Zotsha during this study. The rocky outcrop at the mouth also serves to dam outflowing water, and as a result, the system does not

drain when it opens (Cooper, 1991). This accounts for the relatively deep nature of the system during this study (Figure 26).

Water temperatures appeared to follow a seasonal pattern with both surface and bottom waters being warmer in the spring/summer (November - February) than those recorded during the autumn/winter (May - August) (Figure 26). During his studies Begg (1978; 1984b) found that the temperature of the surface water in the Zotsha ranged from 14°C in July to 27°C in February. He found that surface temperatures did not differ significantly from those at the

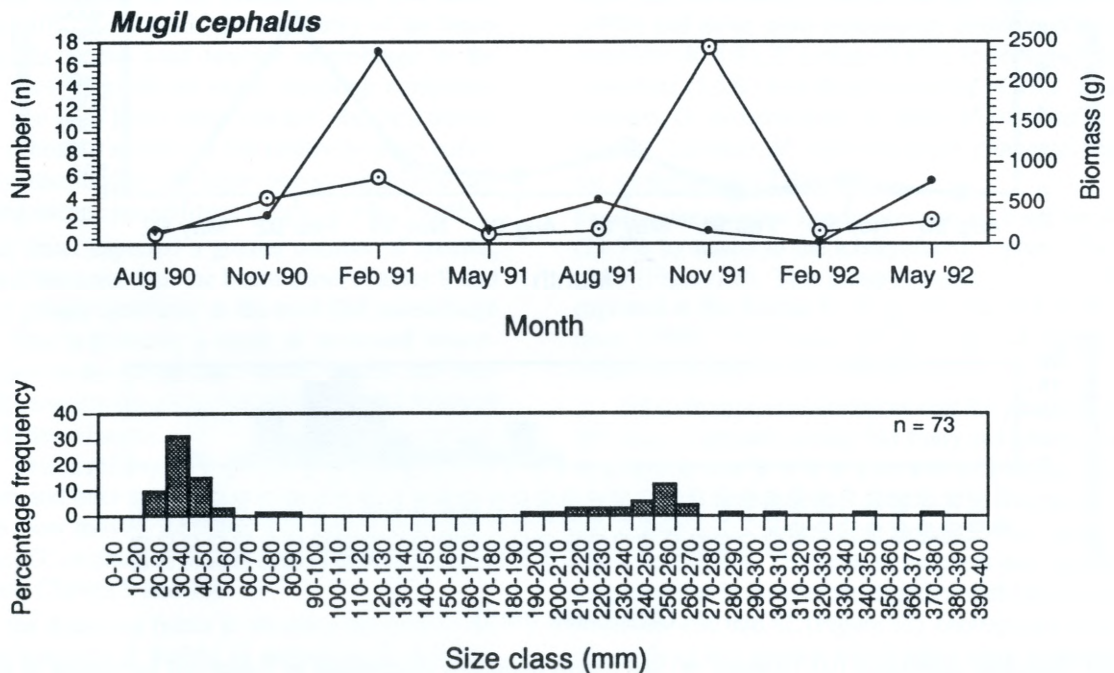
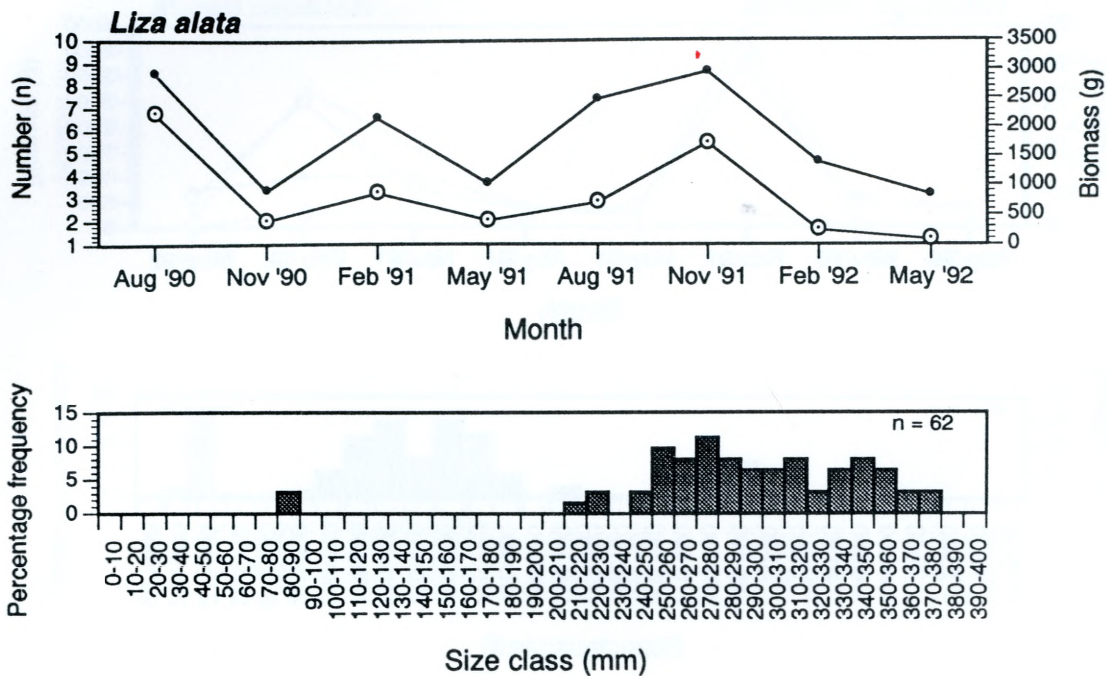


Figure 41. Seasonal abundance (○), biomass (●) and length frequency distribution of *Mugil cephalus* in the Zotsha estuary.



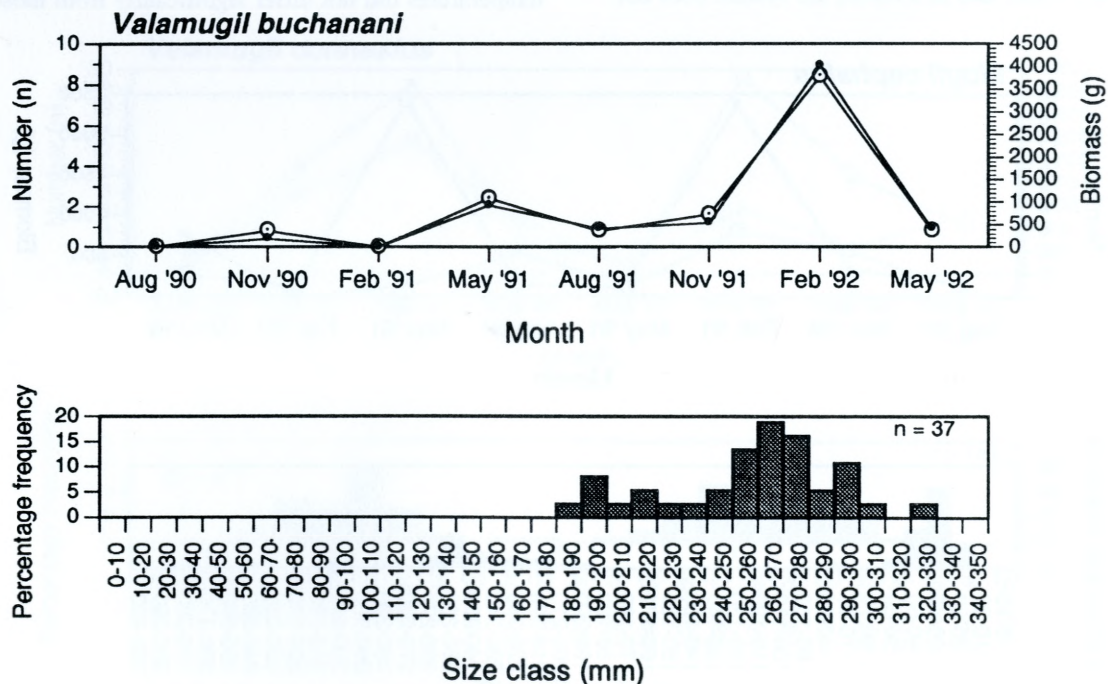
**Figure 42.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Liza alata* in the Zotsha estuary.

bottom when salinity layering was absent. However, when the system was stratified, bottom temperatures were higher than those at the surface (Begg, 1984b). Salinity stratification also accounted for the average bottom temperature exceeding that of the surface during this study, particularly during winter (Figure 26).

The waters of the Zotsha estuary were stratified during this study, with surface salinities ranging from 0.8 - 23 ‰ and bottom salinities from 5.5 - 26 ‰ (Figure 26). During

his study Begg (1984b) found that when the system was not stratified, salinity ranged from 2 - 8 ‰ but when the system was stratified, surface salinities ranged from 0 - 5 ‰ while those at the bottom ranged from 10 - 18 ‰. The relatively high salinities recorded during this study are a result of the predominantly open mouth condition of the system (Figure 26).

Begg (1984b) noted that the condition of the Zotsha estuary mouth was an important factor in determining the



**Figure 43.** Seasonal abundance (○), biomass (●) and length frequency distribution of *Valamugil buchanani* in the Zotsha estuary.

availability of oxygen in the water. The most favourable conditions occurred when the mouth was open, but suppressed oxygen levels occurred in bottom waters when the mouth closed because of a lack of mixing. During this study the average surface oxygen value was higher than that in the bottom waters and is probably a result of the bottom waters being cut off from the surface circulation due to stratification (Figure 26).

With the exception of turbidities recorded in February 1991 and November 1991, values in the Zotsha estuary were below 1 NTU (Figure 26). Begg (1984b) recorded relatively high (>100 cm) secchi disc measurements in the Zotsha during his study. On one occasion, however, a period of heavy rainfall reduced water transparency in the system (Begg, 1984b). The higher turbidities recorded during February 1991 and November 1991 probably reflects increased runoff during the spring/summer rainfall period. Surface turbidities during this study were higher than those recorded in the bottom waters and is probably a result of turbid riverine waters overlying the clearer more saline bottom waters (Figure 26).

To summarise, the mouth of the Zotsha opens across rocks at the southern end of a sand barrier during the spring/summer rainy season but closes during the dry winter months (Figure 26). The presence of rocks at the mouth assists in preserving an open mouth condition and acts to dam outflowing water at a specific level (Cooper, 1991). The predominantly open mouth condition allows tidal penetration of seawater up the estuary and results in the system becoming stratified (Figure 26). The bottom waters, being cut off from the surface circulation due to salinity stratification, results in lower dissolved oxygen levels and turbidities in the bottom waters and occasionally inverse thermal stratification (Figure 26).

### Comparison of Sampling Methods

Beam trawling yielded the least number of species, specimens and fish biomass in the Zotsha during this study (Tables 9 and 10). As a result, the similarity of the beam trawl collections to the total species assemblage in the Zotsha was lower than all the other sampling equipment (Table 11). The poor beam trawl catches obtained during this study is probably a result of the relatively deep nature of the estuary, resulting in the fishes becoming diluted and also increasing escape possibilities (Begg, 1984a; 1984b).

The otter trawl captured a greater number of species, specimens and biomass than the beam trawl (Tables 9 and 10) and had a greater similarity to the total fish assemblage (Table 11). This is probably a result of increased vulnerability of fishes to the larger otter trawl. Beam and otter trawls are effective for sampling bottom fishes and fishes of limited mobility (Lagler, 1971; Gibbs & Matthews, 1981/1982). This is reflected by the species composition of both the beam and otter trawls where, among the dominant species were slow moving or demersal species such as *O. mossambicus*, *G. aestuaria*, *G. callidus*, *S. bleekeri* and *P. commersonii* (Tables 9 and 10).

Among the dominant fishes in the seine net collections were juvenile mugilids, *R. holubi*, *G. aestuaria*, *O. mossambicus*, *T. jarbua* and *A. productus* (Tables 9 and 10). Juvenile fishes in estuaries appear to prefer shallow littoral areas

(Wallace & van der Elst, 1975; Blaber, 1985) and studies on relative gear selectivity and efficiency revealed that seine netting sampled littoral fish more representatively than other equipment (Hartman & Herke, 1987; Hayes, 1989). This probably accounted for the greater variety of fishes and relatively large number of specimens captured by the seine net during this study (Table 9), resulting in the highest similarity to the total fish assemblage (Table 11).

The gill net catches comprised the second highest number of species and specimens, and the highest fish biomass (Tables 9 and 10). The similarity of the gill net catches to the total fish community was the second highest measured for all the gear types (Table 3). The high biomass captured is due to the gill nets more effectively sampling larger, fast swimming fishes (Hayes, 1989).

Each sampling technique used in the Zotsha differed in the number, biomass and range of species collected (Tables 9 and 10). Beam trawling appeared to be the least effective method of sampling the ichthyofauna while seine netting appeared to be the most effective method for sampling juvenile fish in littoral areas. Gill netting was effective for collecting large, mobile specimens in deeper waters and otter trawling was effective for sampling slow moving, demersal species in mid-channel areas.

### Community Structure

Of the 58 fish taxa collected, the most abundant were juvenile mugilids, *Gilchristella aestuaria*, *Oreochromis mossambicus*, *Rhabdosargus holubi*, *Terapon jarbua*, *Ambassis productus* and *Glossogobius callidus* (Table 9). Begg (1984b) recorded 14 species of fish in the Zotsha estuary and found that *Glossogobius giuris* (75.8%), *Ambassis productus* (9.6%) and *Solea bleekeri* (6.1%) were the most abundant species. Of the 12 species recorded by Ramm *et al.* (1985b), *Valamugil cunnesius* (22.9%), *A. productus* (16.6%), *V. buchanani* (14.5%), *M. capensis* (12.5%) and *Liza macrolepis* (10.4%) dominated. Thirty eight fish taxa were collected in the Zotsha by Harrison (1990) and these were numerically dominated by juvenile mugilids (40.8%), *T. jarbua* (9.4%), *V. robustus* (6.6%), *V. cunnesius* (5.5%) and *Mugil cephalus* (4.9%). In terms of biomass, *O. mossambicus*, *L. alata*, *V. robustus*, *V. buchanani*, *M. capensis*, *M. cephalus* and *V. cunnesius* dominated the ichthyofauna (Table 10).

**Freshwater species:** Freshwater species contributed 10.7% (21.7% by mass) to the ichthyofauna captured during this study (Figure 28). This group comprised 1.6% of the fishes captured in the Zotsha by Begg (1984b) and 3.0% by Harrison (1990). Freshwater species were not captured in the Zotsha by Ramm *et al.* (1985b).

*Oreochromis mossambicus* was the principal freshwater species captured during this study and comprised 10.7% numerically and 21.7% of the total fish biomass (Tables 36 and 37). *O. mossambicus* numerically comprised 1.5% of the total fishes captured by Begg (1984a) and 2.9% by Harrison (1990). The peak in numbers and biomass of *O. mossambicus* in November, together with the occurrence of juveniles <30 mm SL (Figure 32), corresponds to the breeding cycle of this species which takes place in shallow areas during spring and summer (Bruton & Bolt, 1975). The increase in the number and biomass of *O. mossambicus* in

November may also be due to the shallow nature of the system during this period, resulting in the concentration of this species in the deeper lower reaches of the system (Whitfield & Blaber, 1979). This may also account for the increase in the number and biomass of *O. mossambicus* in May 1991 (Figure 32). The low numbers and biomass of *O. mossambicus* in February (Figure 32) may be a result of this species migrating to the preferred upper reaches of the system when the river became deeper and thus accessible to colonisation. During the cool season (May - June), both adult and juvenile *O. mossambicus* move into deeper waters (Bruton & Boltt, 1975), and this may account for the decline in the numbers and biomass of *O. mossambicus* in August (Figure 32).

**Estuarine species:** This group of fishes numerically accounted for 24.3% of the ichthyofauna collected and 1.4% of the biomass (Figure 28). Estuarine species numerically comprised 88.2% of the fishes collected in the Zotsha by Begg (1984b), 20.7% of the ichthyofauna captured by Ramm et al. (1985b) and 4.2% of the catch made by Harrison (1990).

The dominant estuarine species captured were *Gilchristella aestuaria*, *Ambassis productus* and *Glossogobius callidus*. *G. aestuaria* numerically comprised 11.0% of the fish community and 0.2% of the biomass, while *A. productus* contributed 9.6% numerically and 0.8% by mass. *G. callidus* comprised 6.1% numerically and 0.1% by mass (Tables 9 and 10).

*Glossogobius* was the dominant estuarine species (75.8%) captured in the Zotsha estuary by Begg (1984b), while *A. productus* and *G. aestuaria* contributed 9.6% and 2.1% to the ichthyofauna respectively. *A. productus* was the dominant estuarine species captured in the Zotsha by Ramm et al. (1985b) and comprised 16.6% of the catch. *Glossogobius* contributed 4.1% to the ichthyofauna (Ramm et al., 1985b). The dominant estuarine species captured in the Zotsha by Harrison (1990) was *G. aestuaria* (2.4% of the total catch), while *Glossogobius callidus* and *A. productus* contributed 0.8% and 0.3% respectively.

*Gilchristella aestuaria* spawns throughout the year, with a peak in spring and early summer (August - November) corresponding with a general rise in water temperature and an increase in zooplankton food resources (Blaber, 1979; Talbot, 1982; Ratte, 1990). To ensure that the eggs and fry are not lost to the marine environment either by normal tidal activity or when a closed estuary opens, *G. aestuaria* spawns in the upper reaches of estuaries and as the larvae grow, their distribution extends toward the mouth (Melville-Smith & Baird, 1980; Talbot, 1982). The increase in abundance, together with the occurrence of juveniles (<20 mm) in November 1990 and August 1991 (Figure 33), suggests that *G. aestuaria* probably breed in the upper reaches of the Zotsha estuary in late winter or early spring, corresponding to the spawning period of this species. Whitfield (1980c) found that in the Mhlanga estuary, *G. aestuaria* bred during the closed phase of the estuary, enabling the larvae to utilize the winter and spring peak in zooplankton abundance. The occurrence of juveniles 20-40 mm SL in the Zotsha estuary during November, together with an increase in biomass (Figure 33), is probably a reflection of

an expansion in their distribution downstream with growth. Three species of ambassids, which are similar in external morphology (Martin & Heemstra, 1988) and feeding ecology (Martin & Blaber, 1983), occur in south-east African estuaries. Martin (1983; 1988; 1989) found that the three species are usually separated spatially according to salinity and temperature preferences. *A. productus* is generally found in low-salinity areas (<10 ‰) and occurs most frequently in temporarily closed estuaries (Martin, 1988; 1989). Little is known about the breeding cycle of *A. productus* but it has been suggested that spawning occurs within estuarine systems (van der Elst, 1988). The occurrence of small (<40 mm) specimens, together with a peak in numbers and biomass in May 1991 and November 1991 (Figure 34), suggests a protracted breeding period with a possible peak in spring.

The occurrence of small (<20 mm) *Glossogobius callidus* from May to November indicates that this species has an extended breeding period, with the high numbers recorded in November (Figure 35) suggesting that recruitment attains a peak in spring. Whitfield (1980b) found that in the Mhlanga estuary *Glossogobius* bred during the stable closed phase. This prolonged breeding season of estuarine species is important in temporarily closed estuaries since fluctuations in physical conditions can occur at any time of the year (Whitfield, 1980b).

**Estuarine-dependent marine species:** This group of fishes comprised 64.8% (76.4% by mass) of the total ichthyofauna assemblage (Figure 28). Numerically they comprised 10.1% of the fishes collected in the Zotsha by Begg (1984a), 78.6% by Ramm et al. (1985b) and 90.7% by Harrison (1990). The dominant estuarine-dependent marine fishes captured during this study were juvenile mugilids, *Rhabdosargus holubi*, *Terapon jarbua*, *Myxus capensis*, *Valamugil cunnesius*, *Valamugil robustus*, *Mugil cephalus*, *Liza alata* and *Valamugil buchanani* (Tables 9 and 10). Altogether these fishes comprised 44.9% numerically and 61.7% by mass of the total catch made during this study.

*Rhabdosargus holubi* comprised 10.3% (1.4% by mass) of the total fishes captured during this study (Tables 9 and 10). *R. holubi* contributed 2% to the ichthyofauna captured in the Zotsha by Begg (1984b) and Ramm et al. (1985b) and 1.8% by Harrison (1990). In Natal, this species spawns in the marine environment mainly between May and August (Wallace, 1975b) with the peak recruitment period for 10 - 40 mm (TL) length classes from July to November (Wallace & van der Elst, 1975). A similar recruitment pattern was noted during this study where the abundance of *R. holubi* in the Zotsha increased in August and November due to the influx of juveniles (<40 mm SL (Figure 36). Blaber (1974) found that when the mouth of the West Kleinemonde estuary in the eastern Cape opened, the resident population of 1+ juvenile *R. holubi* emigrated from the system. Emigration of immature *R. holubi* from the Zotsha estuary appears to have taken place during summer and probably accounts for the low biomass recorded in May 1991 and May 1992 (Figure 36).

*Terapon jarbua* contributed 7.3% numerically and 0.6% by mass to the ichthyofauna captured (Tables 9 and 10). *T. jarbua* was not captured in the Zotsha by Begg



(1984b) or Ramm et al. (1985b), but comprised 9.4% of the catch made by Harrison (1990). This species spawns in Natal waters during the summer (Day et al., 1981) with juveniles 10 - 30 mm TL entering estuaries mainly between November and May (Wallace & van der Elst, 1975). A similar recruitment pattern of *T. jarbua* into the Zotsha estuary occurred during this study, where juveniles <30 mm were recorded from November to May (Figure 37).

Juvenile mugilids (<50 mm) comprised 16.1% (0.3% by mass) of the total ichthyofauna (Tables 9 and 10) and 40.8% of that captured by Harrison (1990). Fifteen species of mullet occur in south eastern Africa (Smith & Heemstra, 1986), of which 13 are commonly associated with southern African estuaries (Whitfield, 1994). The extended spawning season of mugilid species prolongs the period during which fry occur in the inshore marine environment and acts as a buffer against recruitment failure (Wallace, 1975b; Blaber, 1987). High numbers and biomass of juvenile mugilids were recorded in August during this study, corresponding to the general immigration pattern which occurs during winter and spring (June - November) in Natal waters (Wallace & van der Elst, 1975).

The freshwater mullet *Myxus capensis* accounted for 3.8% numerically and 8.5% by mass of the fishes captured (Tables 1 and 2). Begg (1984b) did not record any *M. capensis* in the Zotsha during his study and this species comprised 12.5% of the fishes captured in the above system by Ramm et al. (1985b) and 3.9% by Harrison (1990). In Natal, *M. capensis* spawns from April to May (Wallace & van der Elst, 1975; Blaber, 1987) and the high biomass of this species in November and subsequent reduction in February and May (Figure 38) may be a result of large individuals emigrating from the system to spawn at sea. The high numbers, together with the occurrence of juvenile (< 60 mm SL) *M. capensis* in February 1991 and August 1991 (Figure 38) is probably a reflection of the successful recruitment of this species which takes place in Natal from August to December (Wallace & van der Elst, 1975; Blaber, 1987). Once in estuaries *M. capensis* migrates into the upper reaches and enters riverine areas in some regions (Blaber, 1977; Bok, 1979; Whitfield, 1980a). The decrease in the numbers of juvenile *M. capensis* in May 1991 and November 1991 (Figure 38) may be due to an upstream migration away from the lower and middle reaches of the estuary.

The longarm mullet *Valamugil cunnesius* comprised 2.8% numerically and 5.9% by mass of the total fishes captured (Tables 9 and 10). This species contributed 0.3% towards the Zotsha ichthyofaunal community recorded by Begg (1984a), 22.9% by Ramm et al. (1986) and 5.5% by Harrison (1990). *V. cunnesius* spawns inshore in the vicinity of estuary mouths from November to June (Wallace, 1975b). The low numbers and biomass of *V. cunnesius* in August (Figure 39) may be a result of emigration of mature specimens from the system to spawn at sea. The occurrence of juveniles <70 mm SL from November to May (Figure 39) is probably a reflection of the successful recruitment of this species which takes place from January to July (Wallace & van der Elst, 1975).

*Valamugil robustus* comprised 2.5% numerically and 10.9% by mass of the total fishes captured during this study

(Tables 9 and 10). *V. robustus* was not captured in the Zotsha by Begg (1984a) or Ramm et al. (1986), but comprised 6.6% of the total ichthyofauna captured by Harrison (1990). Peak numbers and biomass of *V. robustus* were recorded during summer (Figure 40). Blaber (1977) found that *V. robustus* was the most common mullet species in the Kosi estuary and that it was more abundant in summer than in winter. He suggested that the species is mainly tropical, only moving south during the summer (Blaber, 1977). The spawning period of *V. robustus* is unknown but recruitment of juveniles (>10 mm SL) into estuaries occurs from September to May (Blaber, 1987). Juveniles <80 mm SL were not recorded in the Zotsha estuary and may be indicative of poor recruitment into this southern Natal system.

*Mugil cephalus* comprised 1.4% numerically and 6.0% by mass of the total ichthyofauna (Tables 9 and 10). This species was not captured by Begg (1984b) or Ramm et al. (1985b), but numerically comprised 4.9% of the ichthyofauna recorded in the Zotsha by Harrison (1990). *M. cephalus* spawns in the shallow inshore marine environment between May and September (Wallace, 1975b). The relatively low numbers and biomass of *M. cephalus* in May and August (Figure 41) may be due to the emigration of larger specimens from the system. The occurrence of juveniles <50 mm in November is probably a reflection of the successful recruitment of this species into the estuary during spring. *M. cephalus* recruits into Natal estuaries mainly from June to October (Wallace & van der Elst, 1975).

*Liza alata* comprised 1.2% numerically and 19.7% by mass of the ichthyofauna (Tables 9 and 10). This species numerically accounted for 4.1% of the fishes captured in the Zotsha by Ramm et al. (1985b) and 3.0% by Harrison (1990). *L. alata* was not captured by Begg (1984a), probably as a result of the trawl gear used. Blaber (1977) found this species to be relatively rare in some of the large, permanently open Natal and Pondoland estuaries. The abundance and biomass of *L. alata* in the Zotsha varied and was generally dominated by subadult fish with an almost complete absence of 0+ juveniles.

*Valamugil buchanani* comprised 0.7% numerically and 8.7% by mass of the total fishes captured during this study (Tables 9 and 10). This species comprised 0.6% of the fishes captured in the Zotsha by Begg (1984b), 14.5% by Ramm et al. (1985b) and 2.0% by Harrison (1990). The numbers and biomass of *V. buchanani* were generally low during this study (Figure 43) probably because this species is usually more abundant in the marine environment than estuaries (Whitfield 1994).

**Marine species:** This group numerically contributed 0.2% to the ichthyofauna during this study and 0.5% in terms of biomass (Figure 28). Marine species were not recorded in the Zotsha by Begg (1984b) or by Ramm et al. (1985b), but numerically comprised 2.1% to the ichthyofauna captured by Harrison (1990). The occurrence of this group of fishes in the Zotsha system is probably linked to the open mouth condition which allows marine species to enter the estuary.

#### Seasonality

**Winter (June - August):** During winter the Zotsha is dominated by estuarine-dependent marine species (Figures 29 and 30). These species generally spawn during late autumn,

winter and spring (May - November) (Wallace, 1975b), with recruitment of juveniles into estuaries taking place during winter and spring (June - November) when river flow is at a minimum (Wallace & van der Elst, 1975). The high numbers of estuarine-dependent marine species in the Zotsha during winter is probably a reflection of juvenile recruitment, particularly mugilids, into the system when it opened. Harrison & Cooper (1991) have reported juvenile mugilids actively migrating into the Zotsha during late winter.

The relatively low contribution of freshwater species to the total winter ichthyofauna (Figures 29 and 30) is probably a result of *O. mossambicus* inhabiting the deeper areas of the system during the cool winter months (Bruton & Boltt, 1975; Caulton, 1979). Whitfield (1980a; 1980c) found that in the Mhlanga estuary, food resources are high during the closed phase due to the relative stability of the physical environment. The high numerical contribution of estuarine species in the Zotsha estuary during winter may be a reflection of the extended breeding period of *G. aestuaria* and *G. callidus*, allowing them to make use of the more stable environmental conditions.

The low number of species recorded in winter (Figure 27) is a reflection of the predominantly closed nature of the system resulting in a limited influx of marine species. The low biomass of fishes is probably a reflection of the recruitment of mainly juveniles of estuarine-dependent marine species during periods when the mouth opened. Variable recruitment success and dilution due to higher water levels probably accounted for the variable numbers of individuals recorded in winter (Figure 27). Species diversity is a reflection of both the number of species (richness) and the proportion of each species (evenness) (Krebs, 1985). The low richness (D) recorded in winter is a reflection of the low number of species captured and this coupled with the relatively low evenness resulted in a low species diversity in the Zotsha during winter (Figure 27).

**Spring (September - November):** Spring is the peak recruitment period of juveniles of most estuarine-dependent marine species (Wallace & van der Elst, 1975). Although the numbers and biomass of this group of fishes was relatively high (Figure 31), the relative contribution of these species to the ichthyofauna of the Zotsha estuary decreased in November (Figures 29 and 30). This is probably a result of breeding by freshwater and estuarine species during spring (Figures 29 and 30). Furthermore, during November 1991 the Zotsha was particularly shallow (Figure 26) and this may have resulted in a redistribution of *O. mossambicus* into the lower reaches (Whitfield & Blaber, 1979), thus further increasing the relative proportion of freshwater species captured during this period (Figures 29 and 30).

Following spring rains, the Zotsha estuary opens (Figure 26), with both the total number of species and the total number of individuals increasing during this period (Figure 27). The positive correlation between the number of species and the open mouth condition (Table 39) is a reflection of the influx of marine species into the system from the sea. The increase in the total number of individuals may be attributed to the recruitment of estuarine-dependent marine species into the system as well as the breeding activity of estuarine and freshwater species. Overall, richness and

evenness in the Zotsha was high during spring and resulted in a high species diversity (Figure 27).

**Summer (December - February):** The extended recruitment period of estuarine-dependent marine species (Wallace, 1975b; Wallace & van der Elst, 1975), together with the open mouth condition, probably contributed to an increase in the proportion of this group of fishes during summer (Figures 29 and 30). The decrease in the proportion of both estuarine and freshwater species to the ichthyofauna in summer (Figures 29 and 30) may be a result of competition and predation. Juvenile fishes in estuaries appear to show a preference for shallow, calm, well vegetated areas (Wallace & van der Elst, 1975) which offers them protection from large piscivorous fishes (Whitfield & Blaber 1978b). Shallow water however, renders juvenile fish particularly vulnerable to bird predation (Whitfield & Blaber, 1978c; 1978d; 1978e). The movement of *O. mossambicus* into the preferred upper reaches, and *G. aestuaria* away from the lower and middle reaches during spawning, may also have contributed to the decrease in the proportion of freshwater and estuarine fishes in summer.

The continued migration of marine species into the Zotsha accounts for the increase in the number of species. Mortality due to competition and predation as well as the migration of fishes upstream, may have accounted for the relatively low number of individuals. The high number of species and the low number of individuals contributed to a high species richness, high evenness and high species diversity in the estuary during summer (Figure 27).

**Autumn (March - May):** The extended open mouth phase into the autumn of 1991, together with the protracted recruitment period of certain estuarine-dependent marine species (e.g. *Valamugil cunnesius*) into the system, may have contributed towards the high proportion of this group of fishes in the overall ichthyofaunal community in May 1991 (Figures 29 and 30). The shallow nature of the estuary in May 1991 may also have contributed to the increase in the proportion of freshwater species by concentrating *O. mossambicus* into the lower reaches of the system. The successful breeding of *Gilchristella aestuaria*, *Ambassis productus* and *Glossogobius callidus* during spring and summer (Figure 29) may account for the high numerical contribution of estuarine species in autumn.

The increase in the number of species and individuals in autumn 1991 was due to the immigration of marine species into the system when it was open. In contrast, closure of the mouth in May 1992 (Figure 26) resulted in a lower number of species and individuals during this month (Figure 27). Overall, the species diversity in the Zotsha in autumn was moderate (Figure 27).

## SUMMARY

A simplified diagrammatic representation of the seasonal community structure of selected species in the Zotsha estuary is presented in Figure 44. During the winter, freshwater species inhabit the upper reaches and deeper channel areas, while estuarine-dependent marine species inhabit the lower/middle reaches and dominate the fish community. When the system opens with the onset of spring/summer rains, juvenile estuarine-dependent marine species begin

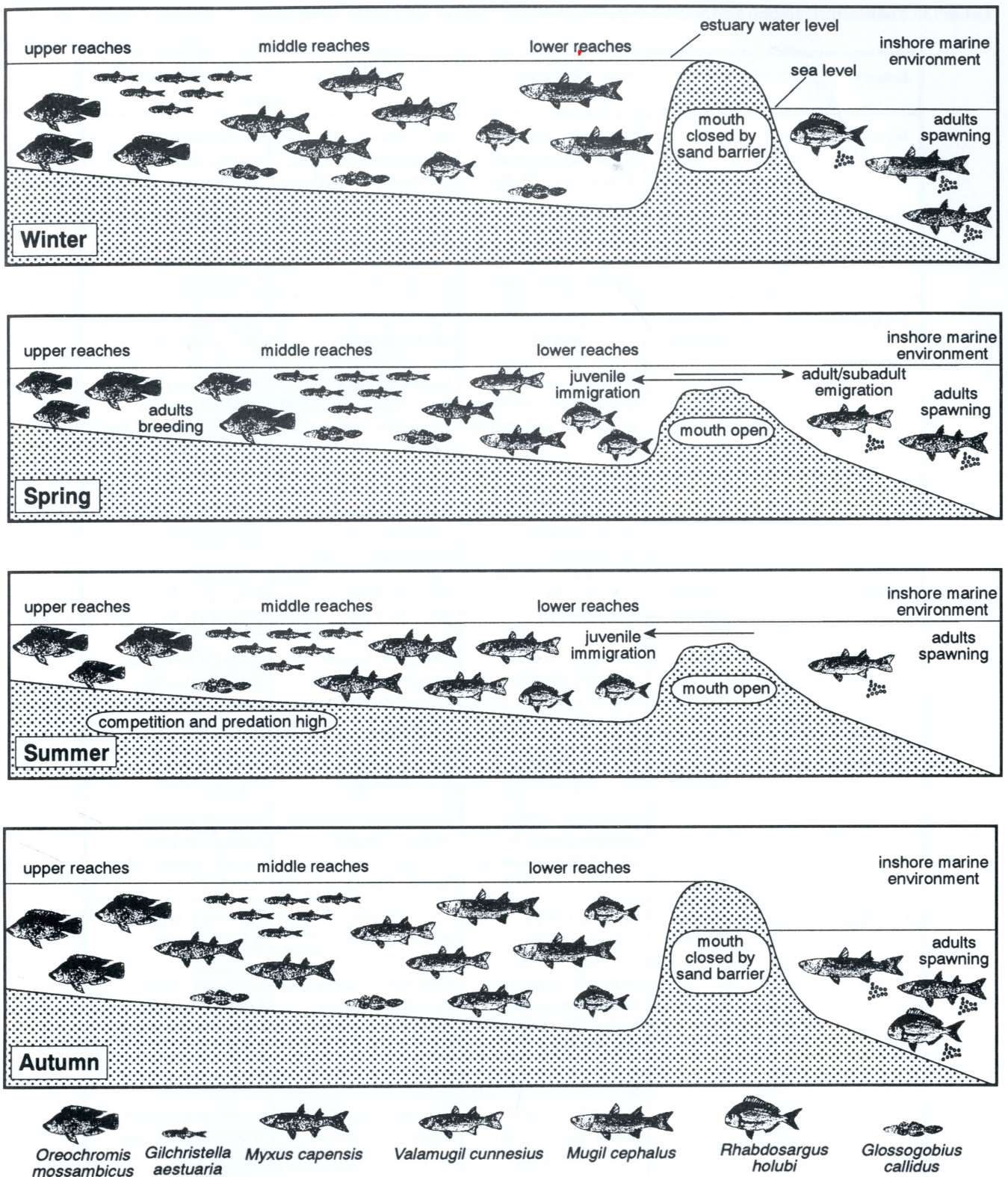


Figure 44. Diagrammatic representation of the seasonal fish community structure in the Zotsha estuary.

recruiting into the system. Spring is also the peak breeding period for resident estuarine and freshwater species, and the contribution of these fishes to the ichthyofauna increases during this period. Mortality due to competition and increased vulnerability to avian predation, as well as migration into the upper reaches, results in a decrease in the proportion of estuarine and freshwater species during summer. The

prolonged recruitment of estuarine-dependent marine species results in an increase in the proportion of this group of fishes during summer. In autumn the system normally closes, and during this period freshwater species redistribute upstream leaving estuarine-dependent marine species to dominate the lower and middle reaches.

**Table 13.** Summary of abiotic characteristics in the Mhlanga, Damba and Zotsha estuaries.

Estuary		Mhlanga	Damba	Zotsha
<b>Mouth condition</b>		Generally closed, frequently opens in summer (2 - 25 days).	Normally closed, occasionally opens in summer (2 - 15 days).	Normally open, system closes in winter.
<b>Depth</b>		40 - 220 cm shallow during summer when open.	40 - 155 cm normally shallow (< 100 cm).	57 - 147 cm generally deep (> 100 cm).
<b>Temperature</b>	Surface Bottom	16.2 - 29.8 °C 15.7 - 28.8 °C  Seasonal, water temperatures are warm in summer and cool in winter.  Stratified, surface temperatures generally exceed bottom temperatures.	15.3 - 31.7 °C 15.3 - 31.7 °C  Seasonal, water temperatures are warm in summer and cool in winter.  Occasionally stratified, surface temperatures sometimes exceed bottom temperatures.	19.0 - 27.7 °C 19.3 - 25.4 °C  Seasonal, water temperatures are warm in summer and cool in winter.  Exhibits both normal and inverse thermal stratification.
<b>Salinity</b>	Surface Bottom	0.5 - 4.5 ‰ 1.0 - 10.7 ‰  Stratified, bottom salinities generally exceed surface salinities.	0.0 - 19.3 ‰ 1.0 - 20.0 ‰  Stratified, bottom salinities generally exceed surface salinities.	0.8 - 22.7 ‰ 5.5 - 26.0 ‰  Strongly stratified, bottom salinities exceed surface salinities.
<b>Dissolved oxygen</b>	Surface Bottom	4.2 - 13.3 mg l <sup>-1</sup> 3.7 - 9.0 mg l <sup>-1</sup>  Stratified, surface oxygens generally exceed bottom values.	3.6 - 8.3 mg l <sup>-1</sup> 1.3 - 8.0 mg l <sup>-1</sup>  Occasionally stratified, surface oxygens sometimes exceed bottom values.	4.2 - 8.3 mg l <sup>-1</sup> 3.7 - 6.0 mg l <sup>-1</sup>  Strongly stratified, surface oxygens exceed bottom values.
<b>Turbidity</b>	Surface Bottom	0.4 - 62.0 NTU 0.3 - 61.0 NTU  Generally clear, turbidity increases during the summer rainy season.  Surface water turbidity is usually slightly higher than bottom water turbidity.	0.3 - 5.8 NTU 0.4 - 5.8 NTU  Generally clear, turbidity increases during the summer rainy season.  Surface water turbidity is usually slightly higher than bottom water turbidity.	0.3 - 17.8 NTU 0.2 - 9.2 NTU  Generally clear, turbidity increases during the summer rainy season.  Surface water turbidity is usually slightly higher than bottom water turbidity.

### THE COMPARATIVE ECOLOGY OF THREE SMALL NATAL ESTUARINE SYSTEMS

In this section the three case studies are compared. Differences are explained as far as possible and similarities are stressed. Finally a generalised conceptual model of the fish community structure in small Natal estuaries is presented.

### RESULTS

#### Physicochemical Characteristics

The abiotic parameters measured in the Mhlanga, Damba and Zotsha estuaries are summarised in Table 13.

#### Species composition, diversity and similarity

A total of 68 fish taxa representing 24 families, 39 genera and 56 species were captured in the three estuaries sampled

**Table 14.** Relative numerical composition of the fishes captured in the Mhlanga, Damba and Zotsha estuaries based on a standardised effort (August 1990 - May 1992).

Estuary	Mhlanga		Damba		Zotsha	
	n	%	n	%	n	%
<i>Acanthopagrus berda</i>	0.5	0.02			0.5	0.04
<i>Ambassis natalensis</i>					3.0	0.22
<i>Ambassis productus</i>	0.6	0.03	21.9	1.52	88.1	6.42
<i>Ambassis</i> sp.	3.8	0.17				
<i>Argyrosomus hololepidotus</i>	4.0	0.18			1.5	0.11
<i>Arothron immaculatus</i>					0.3	0.02
<i>Awaous aeneofuscus</i>			2.5	0.17	0.3	0.02
<i>Caranx ignobilis</i>	0.8	0.04				
<i>Caranx papuensis</i>					2.3	0.16
<i>Caranx sexfasciatus</i>	1.3	0.06			0.5	0.04
<i>Caranx</i> sp.	1.2	0.05			8.7	0.63
<i>Chelonodon laticeps</i>	0.3	0.01				
<i>Crenimugil crenilabis</i>	0.5	0.02	1.4	0.10	60.8	4.43
<i>Crotilia mossambica</i>					3.6	0.26
<i>Eleotris fusca</i>					0.3	0.02
<i>Eleotris mauritanus</i>					0.3	0.02
<i>Eleotris</i> sp.	1.5	0.07			0.6	0.04
<i>Elops machnata</i>			0.4	0.03		
<i>Favonigobius reichei</i>					0.3	0.02
<i>Gerres acinaces</i>					0.3	0.02
<i>Gerres rappi</i>	6.4	0.29			20.7	1.51
<i>Gerres</i> sp.	13.9	0.63	12.4	0.86	20.3	1.48
<i>Gilchristella aestuaria</i>	1009.2	46.15	16.5	1.15	152.2	11.09
<i>Glossogobius biocellatus</i>					0.3	0.02
<i>Glossogobius callidus</i>	28.0	1.28	479.9	33.30	85.2	6.21
<i>Glossogobius giuris</i>	0.3	0.01			0.8	0.06
<i>Goby</i> sp. I	0.3	0.01				
<i>Goby</i> sp. II			3.3	0.23		
<i>Goby</i> sp. III					0.3	0.02
<i>Herklotsichtys quadrimaculatus</i>	5.4	0.25				
Juvenile mugilids	101.4	4.63	2.4	0.17	222.4	16.21
<i>Khulia mugil</i>					1.9	0.14
<i>Leiognathus equula</i>	2.7	0.12			2.9	0.21
<i>Lichia amia</i>	4.0	0.18			1.3	0.09
<i>Liza alata</i>	33.2	1.52	0.9	0.06	15.5	1.13
<i>Liza dumerilii</i>	37.6	1.72	3.5	0.24	12.6	0.92
<i>Liza macrolepis</i>	5.6	0.26	0.4	0.03	6.8	0.49
<i>Liza richardsonii</i>			0.6	0.04		
<i>Liza</i> sp.	21.4	0.98			34.9	2.54
<i>Liza tricuspidens</i>	3.0	0.14			7.4	0.53
<i>Lutjanus argentimaculatus</i>					1.8	0.13
<i>Lutjanus fulviflamma</i>					0.8	0.06
<i>Megalops cyprinoides</i>					0.3	0.02
<i>Micropterus salmoides</i>	1.1	0.05				
<i>Monodactylus argenteus</i>	0.8	0.04	0.4	0.03	0.5	0.04
<i>Monodactylus falciformis</i>	3.5	0.16	3.4	0.23	1.9	0.14
<i>Monodactylus</i> sp.					0.3	0.02
<i>Mugil cephalus</i>	35.8	1.64	39.5	2.74	19.2	1.40
<i>Myxus capensis</i>	60.3	2.76	446.1	30.95	51.7	3.76
<i>Oligolepis acutipennis</i>	2.0	0.09				
<i>Oligolepis keiensis</i>	5.9	0.27			2.2	0.16
<i>Oreochromis mossambicus</i>	394.2	18.03	368.6	25.57	145.4	10.59
<i>Pomadasys commersonnii</i>	29.7	1.36			9.4	0.69
<i>Pomadasys</i> sp.					1.1	0.08
<i>Pomatomus saltatrix</i>					0.3	0.02
<i>Psammogobius knysnaensis</i>	0.3	0.01				
<i>Pseudorhombus arsius</i>	0.3	0.01			0.3	0.02
<i>Rhabdosargus holubi</i>	19.5	0.89	13.8	0.96	142.3	10.37
<i>Rhabdosargus thorpei</i>	0.3	0.01			1.9	0.14
<i>Scomberoides</i> sp.	0.8	0.04			0.3	0.02
<i>Sillago sihama</i>	0.5	0.02				
<i>Solea bleekeri</i>	1.2	0.05	3.3	0.23	20.2	1.47
<i>Terapon jarbua</i>	20.9	0.95			100.8	7.35
<i>Tilapia rendallii</i>	0.3	0.01	0.5	0.03	0.5	0.04
<i>Valamugil buchanani</i>	1.3	0.06			9.3	0.67
<i>Valamugil cunnesius</i>	188.7	8.63	3.0	0.21	36.4	2.65
<i>Valamugil robustus</i>	1.1	0.05	0.8	0.06	32.2	2.34
<i>Valamugil</i> sp.	131.6	6.02	15.9	1.10	37.3	2.72

**Table 15.** Relative biomass composition of the fishes captured in the Mhlanga, Damba and Zotsha estuaries based on a standardised effort (August 1990 - May 1992).

Estuary	Mhlanga		Damba		Zotsha	
	Fish Taxa	g	%	g	%	g
<i>Acanthopagrus berda</i>	3.4	0.00			159.9	0.34
<i>Ambassis natalensis</i>					18.1	0.04
<i>Ambassis productus</i>	14.2	0.02	272.4	1.98	413.4	0.88
<i>Ambassis</i> sp.	0.1	0.00				
<i>Argyrosomus hololepidotus</i>	1234.3	1.59			407.4	0.87
<i>Arothron immaculatus</i>					2.7	0.01
<i>Awaous aeneofuscus</i>			26.6	0.19	31.3	0.07
<i>Caranx ignobilis</i>	93.4	0.12				
<i>Caranx papuensis</i>					441.3	0.94
<i>Caranx sexfasciatus</i>	152.3	0.20			67.1	0.14
<i>Caranx</i> sp.	9.6	0.01			23.4	0.05
<i>Chelonodon laticeps</i>	0.1	0.00				
<i>Crenimugil crenilabis</i>	0.9	0.00	2.6	0.02	177.5	0.38
<i>Croilia mossambica</i>					0.8	0.00
<i>Eleotris fusca</i>					0.6	0.00
<i>Eleotris mauritanus</i>					0.4	0.00
<i>Eleotris</i> sp.	2.2	0.00			0.6	0.00
<i>Elops machnata</i>			70.8	0.51		
<i>Favonigobius reichei</i>					0.1	0.00
<i>Gerres acinaces</i>					1.0	0.00
<i>Gerres rappi</i>	102.1	0.13			1245.6	2.65
<i>Gerres</i> sp.	0.9	0.00	4.8	0.04	13.8	0.03
<i>Gilchristella aestuaria</i>	635.7	0.82	11.4	0.08	104.4	0.22
<i>Glossogobius biocellatus</i>					0.8	0.00
<i>Glossogobius callidus</i>	131.4	0.17	1286.7	9.35	71.1	0.15
<i>Glossogobius giuris</i>	0.2	0.00			60.1	0.13
Goby sp. I	0.1	0.00				
Goby sp. II			0.9	0.01		
Goby sp. III					0.2	0.00
<i>Herklotsichtys quadrimaculatus</i>	5.5	0.01				
Juvenile mugilids	26.4	0.03	0.6	0.00	142.2	0.30
<i>Khulia mugil</i>					0.7	0.00
<i>Leiognathus equula</i>	4.2	0.01			147.1	0.31
<i>Lichia amia</i>	1430.9	1.85			704.4	1.50
<i>Liza alata</i>	7314.5	9.44	150.4	1.09	9164.2	19.49
<i>Liza dumerilii</i>	496.0	0.64	341.8	2.48	464.4	0.99
<i>Liza macrolepis</i>	381.5	0.49	28.8	0.21	878.1	1.87
<i>Liza richardsonii</i>			21.5	0.16		
<i>Liza</i> sp.	29.0	0.04			52.4	0.11
<i>Liza tricuspidens</i>	7.2	0.01			252.6	0.54
<i>Lutjanus argentimaculatus</i>					878.7	1.87
<i>Lutjanus fulviflamma</i>					1.7	0.00
<i>Megalops cyprinoides</i>					220.7	0.47
<i>Micropterus salmoides</i>	138.1	0.18				
<i>Monodactylus argenteus</i>	35.6	0.05	7.8	0.06	28.9	0.06
<i>Monodactylus falciformis</i>	163.9	0.21	78.3	0.57	18.7	0.04
<i>Monodactylus</i> sp.					12.5	0.03
<i>Mugil cephalus</i>	5692.9	7.35	3767.4	27.37	2790.5	5.93
<i>Myxus capensis</i>	6006.2	7.75	4478.3	32.54	3998.0	8.50
<i>Oligolepis acutipennis</i>	3.3	0.00				
<i>Oligolepis keiensis</i>	6.9	0.01			0.8	0.00
<i>Oreochromis mossambicus</i>	36651.5	47.29	2699.2	19.61	10264.0	21.83
<i>Pomadasys commersonnii</i>	858.6	1.11			561.2	1.19
<i>Pomadasys</i> sp.					0.1	0.00
<i>Pomatomus saltatrix</i>					192.2	0.41
<i>Psammodobius knysnaensis</i>	0.3	0.00				
<i>Pseudorhombus arsius</i>	6.6	0.01			5.8	0.01
<i>Rhabdosargus holubi</i>	143.1	0.18	182.9	1.33	730.4	1.55
<i>Rhabdosargus thorpei</i>	0.2	0.00			9.7	0.02
<i>Scomberoides</i> sp.	1.7	0.00			0.2	0.00
<i>Sillago sihama</i>	0.1	0.00				
<i>Solea bleekeri</i>	2.5	0.00	9.2	0.07	29.1	0.06
<i>Terapon jarbua</i>	326.1	0.42			275.0	0.58
<i>Tilapia rendallii</i>	58.8	0.08	0.8	0.01	1.3	0.00
<i>Valamugil buchhanani</i>	156.8	0.20			4051.3	8.61
<i>Valamugil cunnesius</i>	14942.0	19.28	203.0	1.48	2771.2	5.89
<i>Valamugil robustus</i>	19.4	0.02	78.1	0.57	5102.4	10.85
<i>Valamugil</i> sp.	215.6	0.28	40.2	0.29	37.5	0.08

during this study. Based on a standardised sampling effort, *Gilchristella aestuaria* (46.2%), *Oreochromis mossambicus* (18.0%), *Valamugil cunnesius* (8.6%), *Valamugil* sp. (6.0%) and juvenile mugilids (4.6%) numerically dominated the ichthyofauna in the Mhlanga. In the Damba *Glossogobius callidus* (33.3%), *Myxus capensis* (31.0%) and *O. mossambicus* (25.6%) were the dominant fishes captured. The ichthyofauna of the Zotsha was numerically dominated by juvenile mugilids (16.2%), *G. aestuaria* (11.1%), *O. mossambicus* (10.6%), *Rhabdosargus holubi* (10.4%), *Terapon jarbua* (7.4%), *Ambassis productus* (6.4%) and *G. callidus* (6.2%) (Table 14).

In terms of biomass, *O. mossambicus* (47.3%), *V. cunnesius* (19.3%), *Liza alata* (9.4%), *Myxus capensis* (7.8%) and *Mugil cephalus* (7.4%) dominated the ichthyofauna of the Mhlanga. *M. capensis* (32.5%), *M. cephalus* (27.4%), *O. mossambicus* (19.6%) and *G. callidus* (9.4%) dominated the fish biomass captured in the Damba and *O. mossambicus* (21.8%), *L. alata* (19.5%), *Valamugil robustus* (10.9%), *Valamugil buehanani* (8.6%), *M. capensis* (8.5%), *M. cephalus* (5.9%) and *V. cunnesius* (5.9%) dominated the fish biomass in the Zotsha (Table 15).

Of the three systems surveyed during this study, the Damba had the lowest species richness (3.16), evenness (0.49) and diversity (1.55) while the Zotsha exhibited the highest richness (7.61) evenness (0.71) and diversity (2.85). The Mhlanga had a species richness of 5.98, an evenness value of 0.51 and a species diversity of 1.95. Species diversity calculated using biomass revealed that the Zotsha had an index value of 2.51, the Mhlanga 1.72 and the Damba 1.76 (Table 16).

According to Jaccard's index of similarity, the fish community in the Mhlanga and Zotsha showed the highest similarity (58.5%), while the Damba and the Zotsha exhibited the lowest similarity (35.6%). The Damba and the Mhlanga were 39.2% similar. Using Sørensen's index of similarity, the fish community in the Mhlanga and Zotsha were 73.8% similar, while the Zotsha and the Damba were 52.5% similar. The Mhlanga and the Damba were 56.3% similar. Ellenberg's index of similarity showed that by numerical species composition, the Mhlanga and the Zotsha were 98.1% similar, the Mhlanga and the Damba 94.2% similar and the Damba and the Zotsha 84.9% similar. In

**Table 16.** Margalef's species richness index (D), the Pielou Equitability Index (J'), the Shannon-Wiener diversity index (H') and the Shannon-Wiener diversity index using biomass (H'w) for the Mhlanga, Damba and Zotsha estuaries.

	Mhlanga	Damba	Zotsha
<b>Richness (D)</b>	5.98	3.16	7.61
<b>Evenness (J')</b>	0.51	0.49	0.71
<b>Diversity (H')</b>	1.95	1.55	2.85
<b>Diversity (H'w)</b>	1.72	1.76	2.51

**Table 17.** Percent similarity of the ichthyofauna of the Mhlanga, Damba and Zotsha estuaries (IS<sub>J</sub> = Jaccard's index of similarity, IS<sub>S</sub> = Sørensen's index of similarity, IS<sub>E</sub> = Ellenberg's index of similarity using numbers (n) and mass (g)).

	Mhlanga	Damba	Zotsha
<b>IS<sub>J</sub></b>			
Mhlanga	-	39.22	58.46
Damba	39.22	-	35.59
Zotsha	58.46	35.59	-
<b>IS<sub>S</sub></b>			
Mhlanga	-	56.34	73.79
Damba	56.34	-	52.50
Zotsha	73.79	52.50	-
<b>IS<sub>E</sub> (n)</b>			
Mhlanga	-	94.22	98.10
Damba	94.22	-	84.85
Zotsha	98.10	84.85	-
<b>IS<sub>E</sub> (g)</b>			
Mhlanga	-	93.45	95.93
Damba	93.45	-	80.58
Zotsha	95.93	80.58	-

terms of species biomass composition, the Mhlanga and the Zotsha were 95.9% similar, the Mhlanga and the Damba 93.5% similar and the Damba and the Zotsha 80.6% similar (Table 17).

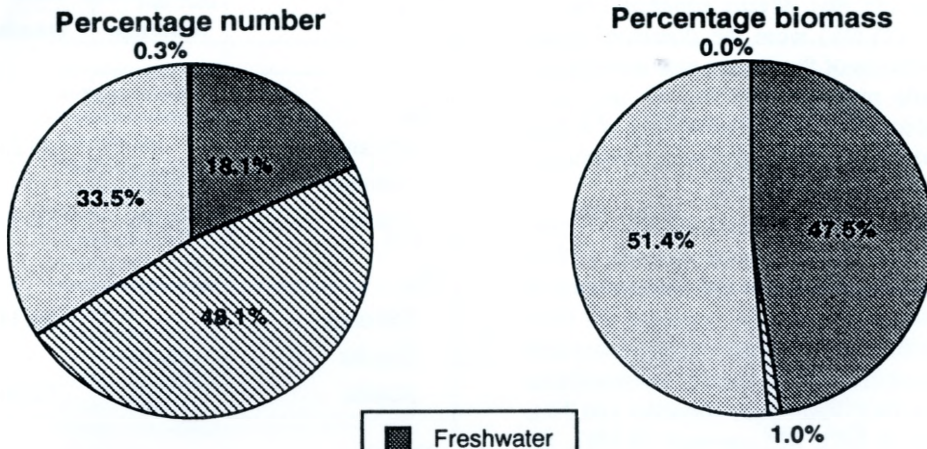
### Community Structure

Based on a standardised effort, estuarine species numerically comprised 48.1% of the ichthyofauna in the Mhlanga, followed by estuarine-dependent marine species (33.5%) and freshwater species (18.1%). Marine species numerically comprised 0.3% of the ichthyofauna captured. Estuarine-dependent marine species and freshwater species dominated the fish biomass in the Mhlanga and contributed 51.4% and 47.5% to the fish biomass respectively. Estuarine species comprised 1.0% of the total biomass and marine species comprised less than 0.1% (Figure 45).

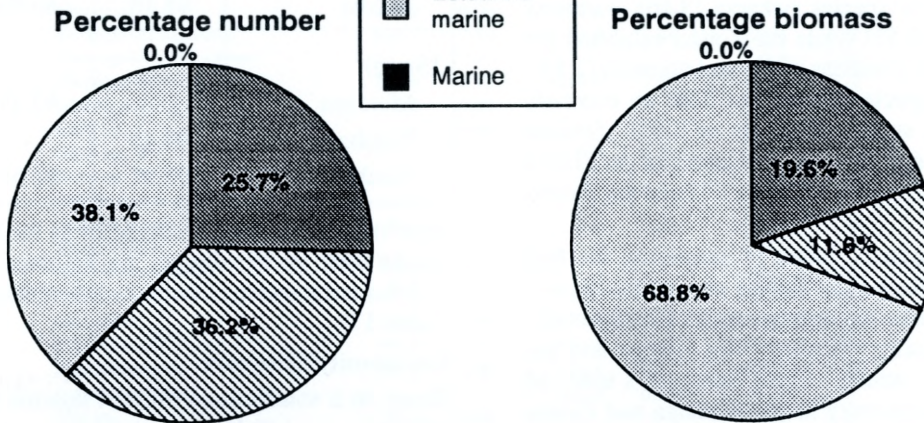
Estuarine-dependent marine species numerically dominated the fish fauna in the Damba and contributed 38.1% to the total. Estuarine species numerically comprised 36.2% of the total fishes and freshwater species comprised 25.7%. Marine species were not recorded in the Damba during this study. In terms of biomass, estuarine-dependent marine species dominated the ichthyofauna in the Damba and accounted for 68.8% of the total catch followed by freshwater species (19.6%) and estuarine species (11.6%) (Figure 45).

In the Zotsha, estuarine-dependent marine species dominated the fish community both by number and by mass. This group of fishes comprised 64.6% numerically and 76.2% by mass to the ichthyofauna. Estuarine species comprised 24.6% numerically and 1.5% by mass while freshwater species contributed 10.6% numerically and 21.8% by

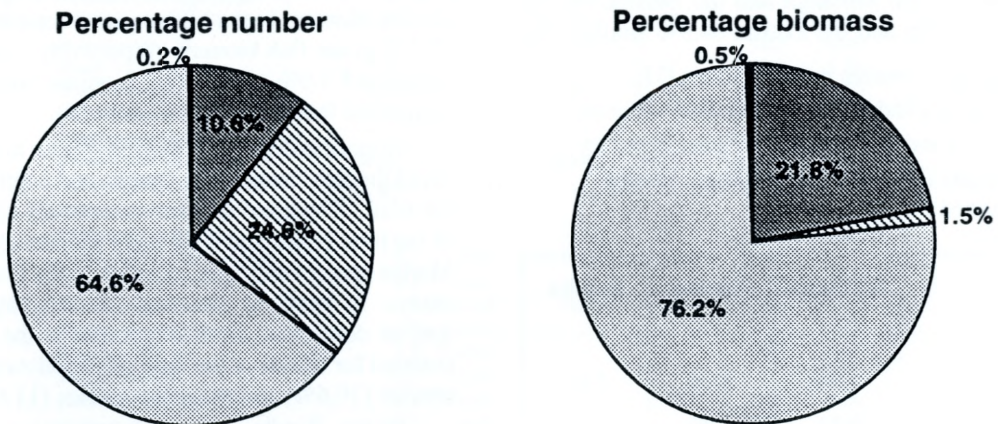
**a) Mhlanga estuary**



**b) Damba estuary**

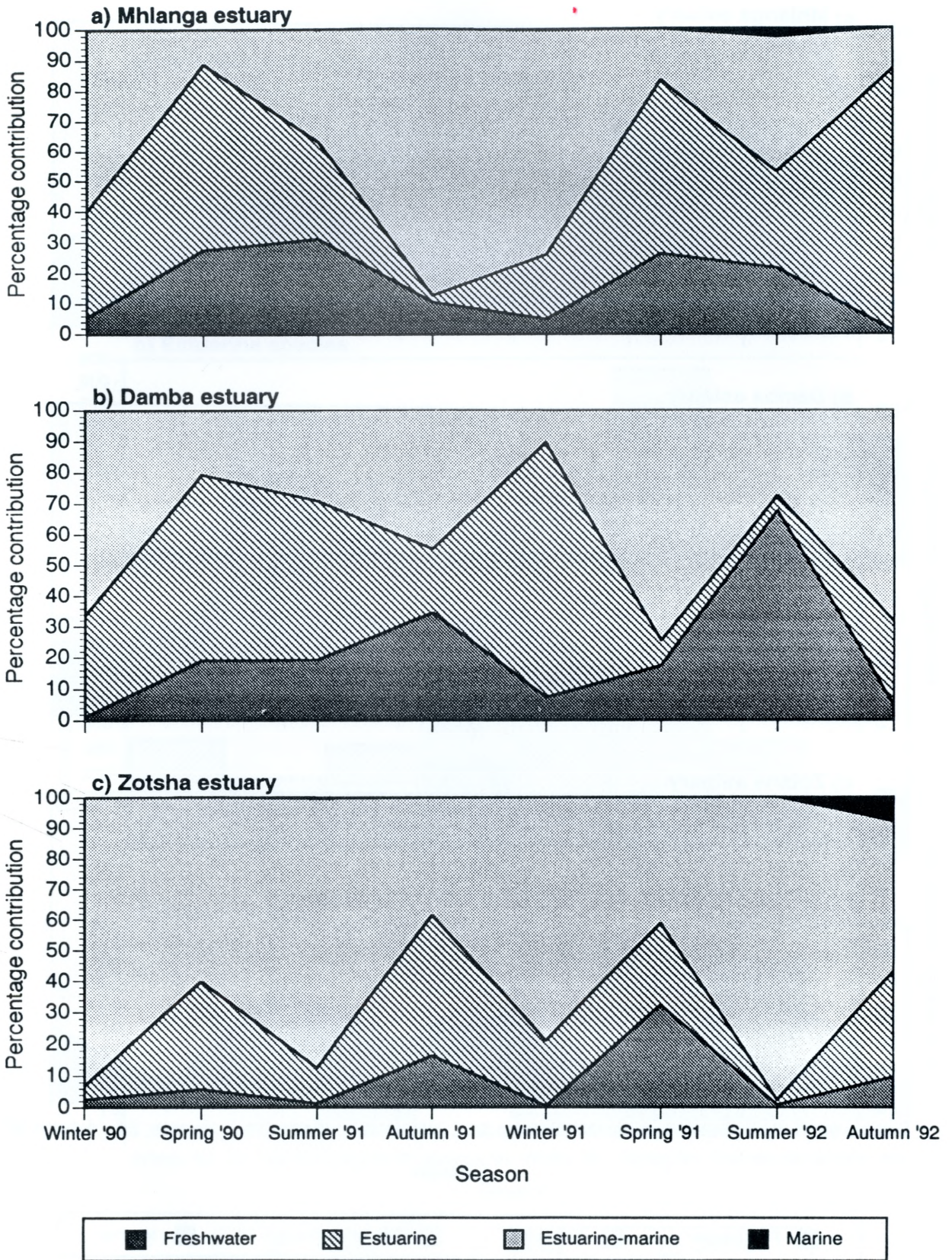


**c) Zotsha estuary**

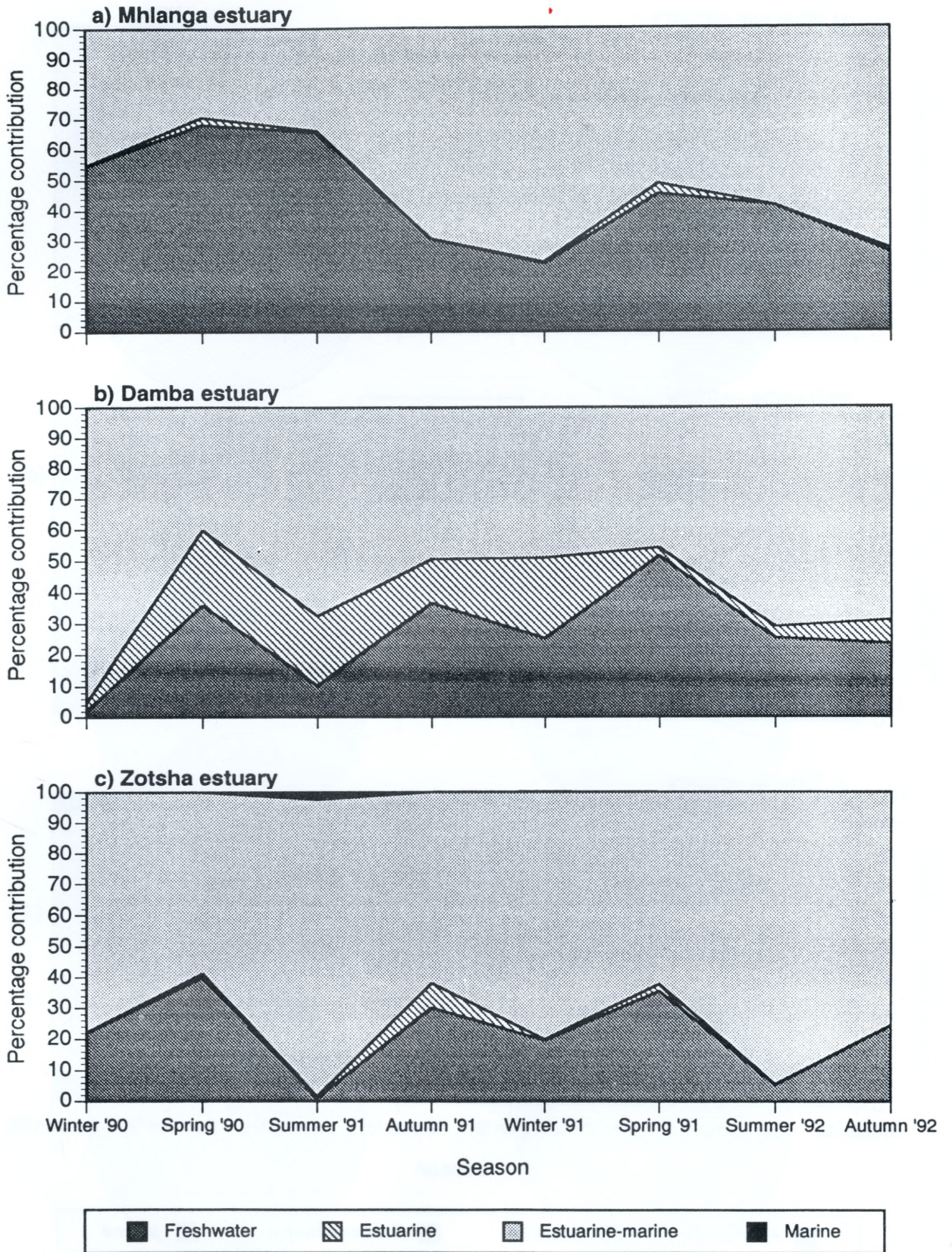


**Figure 45.** Percent numerical and biomass contribution of freshwater, estuarine, estuarine-dependent marine and marine species to the total ichthyofauna of the Mhlanga (a), Damba (b) and Zotsha (c) estuaries based on a standardised effort.

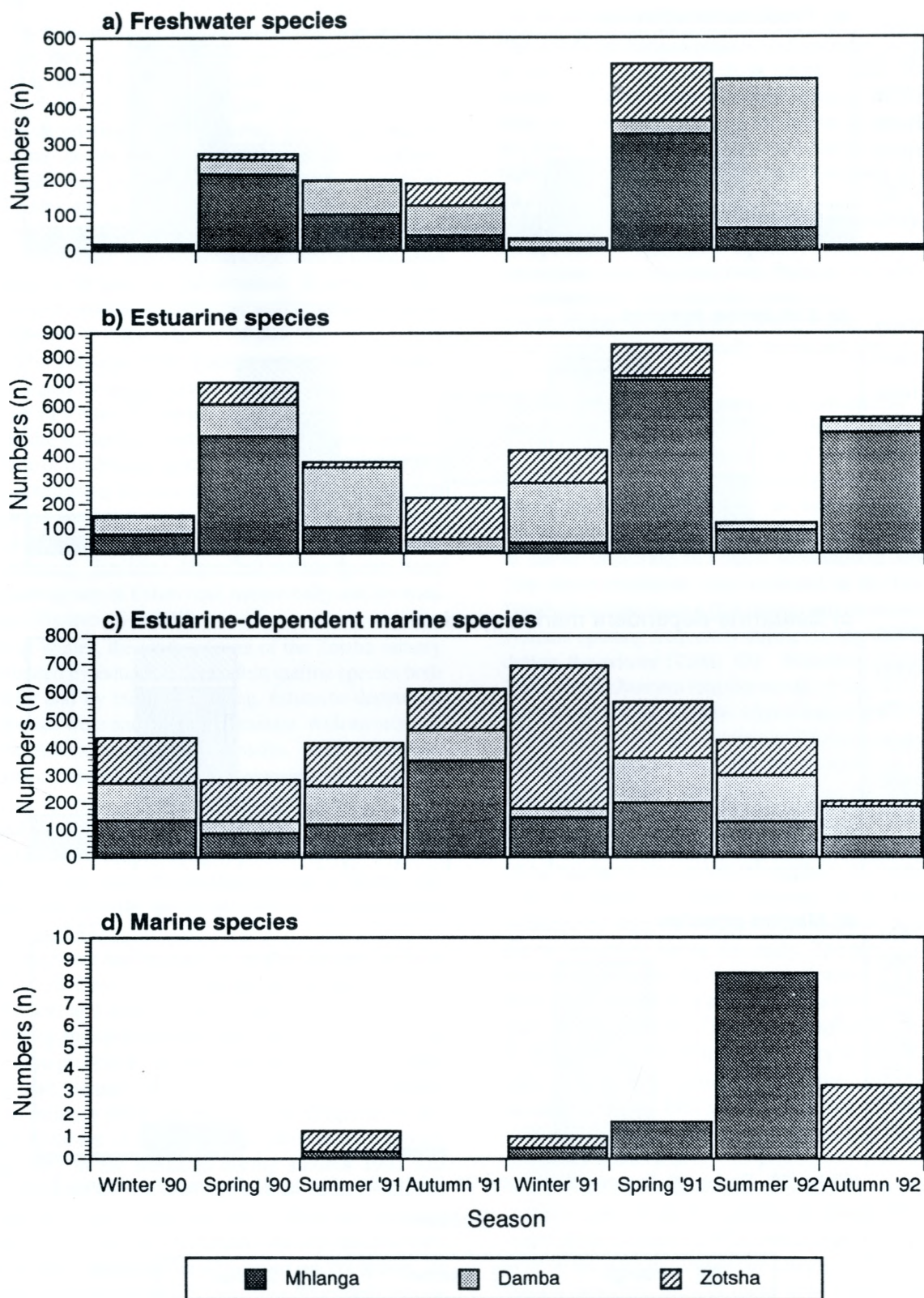




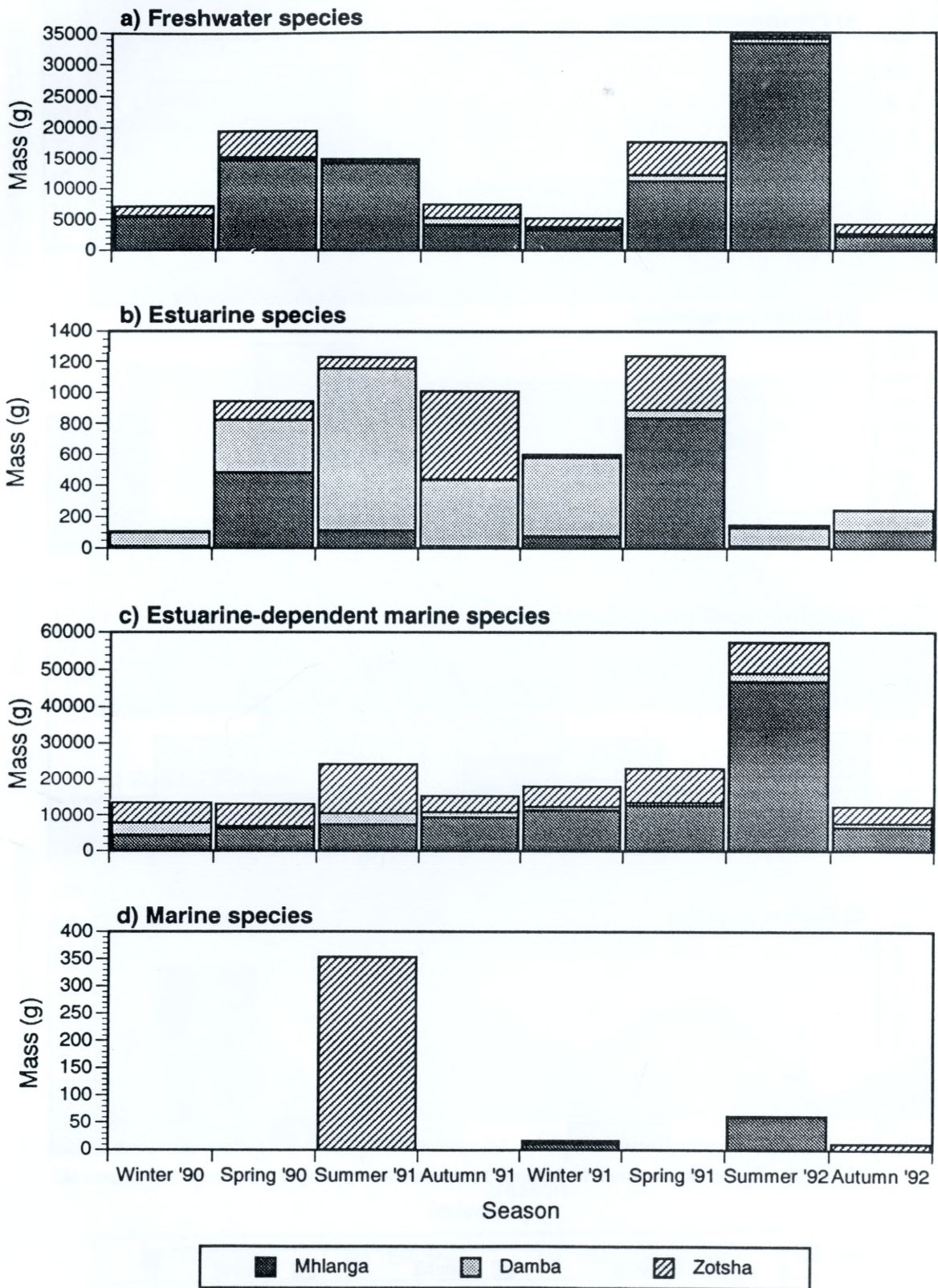
**Figure 46.** Seasonal numerical composition of freshwater, estuarine, estuarine-dependent marine and marine fish species in the Mhlanga (a), Damba (b) and Zotsha (c) estuaries.



**Figure 47.** Seasonal biomass composition of freshwater, estuarine, estuarine-dependent marine and marine fish species in the Mhlanga (a), Damba (b) and Zotsha (c) estuaries.



**Figure 48.** Seasonal fluctuations in the numbers of freshwater species (a), estuarine species (b), estuarine-dependent marine species (c) and marine species (d) in the Mhlanga, Damba and Zotsha estuaries.



**Figure 49.** Seasonal fluctuations in the biomass of freshwater species (a), estuarine species (b), estuarine-dependent marine species (c) and marine species (d) in the Mhlanga, Damba and Zotsha estuaries.

mass to the fishes captured. Marine species comprised 0.2% numerically and 0.5% by mass of the fishes captured in the Zotsha (Figure 45).

### Seasonality

During winter, the ichthyofauna of the Mhlanga estuary was numerically dominated by estuarine and estuarine-dependent marine species. In terms of biomass, estuarine-dependent marine species and freshwater species were the dominant fishes during winter. In spring, freshwater species and estuarine species numerically dominated the ichthyofauna. Freshwater species dominated the fish biomass in spring. Freshwater, estuarine and estuarine-dependent marine species were all well represented in the Mhlanga in summer. Freshwater and estuarine-dependent marine species dominated the summer fish biomass. In autumn, estuarine-dependent marine species were well represented, both numerically and by mass (Figures 46 and 48).

The ichthyofauna of the Damba estuary was numerically dominated by estuarine and estuarine-dependent marine species in winter. Estuarine-dependent marine species dominated the winter fish biomass. In spring the numerical contribution of freshwater species increased, with this group of fishes dominating the fish biomass. Freshwater species and estuarine species were numerically dominant in summer, while estuarine-dependent marine species dominated the fish biomass. Estuarine-dependent marine species were the dominant group of fishes both numerically and by mass in autumn (Figures 46 and 47).

During winter, the ichthyofauna of the Zotsha estuary was dominated by estuarine-dependent marine species both numerically and by mass. In spring, estuarine-dependent marine species were numerically dominant, with an increase in the contribution of freshwater species. Both freshwater and estuarine-dependent marine species dominated the fish biomass in spring. Estuarine-dependent marine species dominated the ichthyofauna in summer, both numerically and in terms of biomass. During autumn, estuarine-dependent marine species were the dominant group of fishes, with freshwater and estuarine species also being well represented (Figures 46 and 47).

High numbers and biomass of freshwater species were captured in all three systems during spring and summer. High numbers and biomass of estuarine species were recorded during spring in the Mhlanga and Zotsha, with large numbers also present in the Mhlanga during autumn 1992. Numbers and biomass of estuarine species in the Damba peaked in summer 1991 and winter 1991 (Figures 48 and 49). High numbers of estuarine-dependent marine species were recorded in the Mhlanga during autumn 1991 and spring 1991, whereas the peak in biomass of this group of fishes was recorded in summer 1992. Moderate numbers and biomass of estuarine-dependent marine species were recorded in the Damba during all seasons except spring. In the Zotsha, highest numbers of estuarine-dependent marine species were recorded during winter and spring, with the biomass peak occurring in summer 1991. Relatively high numbers of marine species were captured in the Zotsha estuary during most months, with a peak biomass occurring in summer 1992. Low numbers and biomass of marine

species were captured in the Mhlanga system and none were recorded in the Damba estuary (Figures 48 and 49).

## DISCUSSION

### Physicochemical Characteristics

The southeast African coast is well endowed with a variety of estuarine systems which, in terms of their shallow and sheltered waters, form a marked contrast to the adjacent deep and turbulent waters of the Indian Ocean (Wallace et al., 1984; Blaber, 1985). The three systems chosen for study represent the most abundant type of estuarine environment on the Natal coast (Cooper, 1991). They are essentially small water bodies which are fed by coastal catchments and do not receive significant inputs of fresh water. Fringing vegetation typically comprises *Phragmites* reeds, freshwater mangroves (*Barringtonia gymnorrhiza*) and lagoon hibiscus (*Hibiscus tiliaceus*) (Begg, 1984a; Cooper, 1991). True mangroves are generally absent and were not recorded in this study.

**Mouth condition:** Because their catchments are small, riverflow is generally insufficient during most months to prevent closure of the mouth by a barrier built up from longshore drift of sand. This closed phase is most apparent during the dry winter season. Increased fluvial discharge, particularly during the spring/summer rainy period, results in barrier breaching and outlet formation (Cooper, 1991). The above conditions were reflected in the Mhlanga and Damba estuaries during this study, with the mouths of these systems opening frequently during the summer but closing during the winter (Table 13). Whitfield (1980a; 1980b; 1980c) also observed that the mouth of the Mhlanga closed during the winter months (April-September) but opened following heavy rains in summer (October - March), while Blaber et al. (1984) noted that the mouth of the Mdloti was open intermittently throughout most of the year but completely closed from late May until late August.

Marine overwash-induced breaching, through lowering of the barrier to a point which enables rising water levels to form an outlet, has been observed in the Mnamfu and Mhlanga by Begg (1984a) and may also have accounted for barrier breaching during this study. The presence and duration of an open mouth is enhanced where rocky outcrops promote turbulent flow and scour (Cooper, 1991). Systems such as the Zolwane, Tongazi, Sandlundlu, Boboyi and Zotsha all have characteristically rocky outlets and maintain open mouths more commonly than other systems of a similar size (Cooper, 1991). This accounts for the predominantly open mouth condition of the Zotsha estuary during this study (Table 13).

**Depth:** During stable conditions when the mouths of small estuaries are closed, the systems are characterised by high water levels (Cooper, 1991), which often results in inundation of the adjacent floodplain (Begg, 1984a). When they breach, however, most of these small systems drain due to their elevated bed levels (Cooper, 1991). This accounts for the relatively shallow conditions encountered in the Mhlanga and Damba during spring and summer when the mouths of these systems frequently opened (Table 13). A rocky outcrop at the mouth of some systems prevents them

from draining (Cooper, 1991) and accounts for the relatively deep nature of the Zotsha estuary (Table 13).

**Temperature:** Temperatures recorded during this study followed a seasonal pattern where the systems were cooler during the winter and warmer in summer (Table 13). Thermal stratification was sometimes evident due to a lack of mixing and on some occasions the systems were inversely stratified where warmer saline water was overlain with cool fresh water.

**Salinity:** When generally closed systems open to the sea there is an initial strong outflow of fresh water, which after a while decreases, allowing tidal penetration of seawater into the estuary (Whitfield, 1990). During this tidal phase these systems may exhibit strong vertical and horizontal estuarine salinity gradients. Barrier overwash by the sea also enhances salinity gradients, as observed by Begg (1984a) in the Zinkwasi and Mvuzi systems. All the estuaries surveyed during this study were, on average, stratified with respect to salinity (Table 13). Begg (1984a) found that temporarily closed estuaries on the Natal coast often exhibited vertical salinity stratification, mainly due to the high degree of protection from wind activated wave action, which is the primary mixing mechanism in such systems.

**Dissolved oxygen:** The solubility of oxygen in water is a function of its partial pressure and the temperature and salinity of the water (Day, 1981b). Photosynthesis supplements the oxygen absorbed from the atmosphere while the gradual decay of organic material depletes the oxygen concentration. Deoxygenation may occur wherever bottom water is cut off from the surface circulation by haloclines or thermoclines (Day, 1981b). In estuaries where tidal currents are absent, oxygen concentrations in the bottom layers depend on the ratio of area to depth and the circulation due to the wind and inflow of river water. Begg (1984a) found that in the Mbango and Mdlotane estuaries the bottom water was lacking in oxygen because of poor circulation due to protection from the wind and the decomposition of organic material. Lack of mixing and stratification also accounted for depressed oxygen levels in the bottom waters of all three systems during this study (Table 13).

**Turbidity:** A number of factors interact to establish the turbidity regimes present in Natal's estuaries, including river flow, substratum type, wind and tides (Cyrus, 1988). The closure of small estuary mouths leads to the deposition of fine sediment on the substratum and an increase in water clarity. However, when these systems re-open during times of high river inflow, much sediment is brought down from the catchment and turbidities increase rapidly, reaching high levels (Cyrus, 1988). Begg (1984a) found that water transparency in Natal's estuaries declined during the rainy season while the rivers were flowing, but increased in the closed systems during winter due to reduced river inflow and settling of suspensoids. Turbidities in the systems during this study were generally higher in spring and summer than those recorded in autumn and winter (Table 13).

Cyrus (1988) noted that in the Tongati and Mdloti estuaries, lower turbidities occurred at the bottom of the water column than those at the surface and attributed this to the presence of a salt wedge in the two estuaries. Turbidities of the surface waters were generally greater than those

recorded at the bottom (Table 13) and is probably a result of the systems being stratified, resulting in turbid fresh waters overlying clearer, more saline waters, a feature Begg (1984b) noted in the Mhlanga.

In spite of a great morphological variation within Natal's small estuarine systems, similar processes appear to operate in all of them, although at different intensities (Cooper, 1991). A generalised model of these processes was described and illustrated by Cooper (1991). Many of Natal's small estuaries are typically small water bodies and do not receive significant inputs of fresh water. As a result their mouths are frequently closed by a sand barrier, particularly during the dry winter months. During this stable period the systems are typically deep, calm and clear. Overtopping of the bar by the sea enhances salinity and, due to a lack of wind induced mixing, they are often stratified both in terms of salinity and temperature. Stratification also results in depressed oxygen levels in the bottom waters. Following heavy rains, usually during the summer, these small estuaries often breach. Rocky outcrops at the mouths of some systems enhances the duration of an open mouth condition. Because the bed level of many of these estuaries is elevated relative to MSL, turbid riverine water quickly flows out of the systems following opening and they drain. When river flow decreases, sea water enters these systems on the flood tide and they may exhibit typical estuarine salinity gradients before longshore drift and/or onshore sediment transport eventually close their mouths (Cooper, 1991).

#### **Species Composition, Diversity and Similarity**

Natal estuaries have the highest fish species diversity in South Africa. Altogether, 133 species of fishes are associated with the subtropical estuaries on the Natal coast, of which 93 species (70%) may be regarded as having a relatively strong association with estuaries in the region (Whitfield, 1994). A total of 68 fish taxa (55 confirmed species) were collected during this study (Tables 14 and 15) and Begg (1984a; 1984b) recorded a total of 86 species of fish in the 62 Natal estuaries he studied.

The occurrence and diversity of fishes in south east African estuaries varies according to (a) latitude and (b) the individual characteristics of each estuary (Blaber, 1985). Marine species inhabiting southern African estuaries include tropical and subtropical Indo-Pacific species, endemic southern African species, temperate eastern-Atlantic species and cosmopolitan species (Wallace, 1975a; Wallace & van der Elst, 1975). As one moves from Natal around the Cape coast to the Atlantic west coast, estuarine fish diversity declines (Wallace & van der Elst, 1975, Whitfield et al., 1989) and is linked to the attenuation in the distribution of tropical and subtropical species in a southwesterly direction (Day et al., 1981).

**Mouth condition:** Superimposed upon the latitudinal change in diversity are variations caused by the nature of the estuary, particularly its degree of isolation from the sea (Blaber, 1985). Formation of a sand bar across the mouth of an estuary effectively blocks the migration of marine species into and out of the system, thereby directly influencing the composition of the fish community (Whitfield & Kok, 1992). Whitfield et al. (1989) noted that the species richness in the permanently open Knysna estuary was much

higher than that of the nearby Swartvlei estuary which is seasonally closed. Whitfield & Kok (1992) suggested that the relatively higher densities of most species in the Knysna system may be attributed to the deep, permanently open mouth condition and strong marine influence. Begg (1984a) found that open estuaries were species rich and were dominated by a wide variety of marine teleosts, especially Mugilidae and Sparidae. Systems which were normally closed were characterised by relatively few species and were commonly dominated by *Gilchristella aestuaria*, *Oreochromis mossambicus* and *Glossogobius* (Begg, 1984a).

Mouth condition may have also contributed to the species composition and diversity of the various systems during this study. The mouth of the Damba estuary remained closed for much of the study period and this system had the lowest species diversity (Table 16) with *Glossogobius callidus* and *O. mossambicus* being among the more common species captured (Tables 14 and 15). The mouth of the Mhlanga estuary opened more frequently than the Damba and had a higher species diversity (Table 16). *Gilchristella aestuaria* and *Oreochromis mossambicus* were among the dominant species captured along with a number of mugilids such as *Valamugil cunnesius*, *Myxus capensis*, *Mugil cephalus* and *Liza alata* (Tables 14 and 15). The Zotsha estuary remained open for most of the study period and, of the three systems, had the highest species diversity (Table 16). This estuary was dominated by a number of estuarine-dependent marine species such as *Rhabdosargus holubi*, *Terapon jarbua*, *M. capensis*, *V. cunnesius*, *V. robustus*, *M. cephalus* and *L. alata* (Tables 14 and 15).

**Depth:** Small fish in estuaries usually prefer relatively shallow waters which provide habitat types needed by juveniles, such as aquatic macrophyte beds, emergent reeds or mangroves (Wallace & van der Elst, 1975; Blaber, 1985). Shallow waters provide juveniles with a refuge from larger fish predators which are restricted to deeper waters (Whitfield and Blaber 1978b). This may account for the occurrence of fish predators such as *Argyrosomus hololepidotus*, *Pomatomus saltatrix*, *Platycephalus indicus*, *Lichia amia*, *Caranx* spp. *Scomberoides* spp. and *Lutjanus* spp. in the deeper Mhlanga and Zotsha systems, while in the relatively shallow Damba estuary piscivorous fishes were usually absent (Tables 14 and 15).

**Temperature:** Wallace (1975a) noted seasonal shifts in the distribution of fishes along the east and south coasts of South Africa which are associated with changes in water temperature. Subtropical east coast species extend into south coast waters in summer and warm temperate species such as *Lichia amia* enter east coast waters during winter (Wallace, 1975a). Branch & Grindley (1979) observed a similar seasonal change in the fishes of the Mngazana estuary in Transkei, where much of the ichthyofauna had affinities with the tropics in summer, while in winter many warm-temperate species increased in numbers. Cyrus & Blaber (1987a; 1987b) have shown that most of the abundant species present in Natal estuaries are able to tolerate the range of temperatures which occur in this region. Day et al. (1981) state that in tropical and subtropical estuaries, where there are small seasonal changes in temperature, the impor-

ance of temperature on fish distribution declines and the effect of salinity becomes more important.

**Salinity:** Fish which enter estuaries require an ability to adjust to changes in salinity. The change may be gradual, as normally occurs in a closed estuary, or sudden as often takes place in tidal estuaries (Whitfield, 1983). Furthermore, only strongly euryhaline species can survive in temporarily closed estuaries, during which period salinities rise above or fall below seawater concentrations (Whitfield, 1983). Begg (1984a) noted that in the temporarily closed Zinkwasi estuary, moderate salinities (>20‰) prevailed due to topping of the bar, resulting in a wide variety of species being present that are normally found in open, tidally influenced systems. The moderate salinities recorded in the Mhlanga and Zotsha may also have accounted for the occurrence of species such as *Arothron immaculatus*, *Chelonodon laticeps* and *Herklotsichthys quadrimaculatus* in these systems (Tables 14 and 15). These species were not captured in the Damba which was generally less saline (Figure 25).

**Dissolved oxygen:** High biological activity below the halocline of most stratified estuaries results in oxygen depletion and may be a factor limiting the distribution of estuarine fishes (De Sylva, 1985). Furthermore, in tropical estuaries the effects of dissolved oxygen may be more pronounced because of the generally high temperatures (McHugh, 1985). If additional oxygen-demanding substances are added to the water in the form of domestic or industrial pollution, this may further limit the occurrence and distribution of fishes and even result in fish mortalities. Begg (1984a) noted that organic pollution played a role in suppressing species richness in some Natal estuaries such as the Sezela, Tongati, Sipingo and Mbokodweni. Blaber et al. (1984) suggested that low oxygen tensions contributed to the impoverished fish fauna in the Tongati estuary. The Tongati was dominated by Mugilidae namely *Mugil cephalus*, *Myxus capensis* and *Valamugil cunnesius* (Blaber et al., 1984). Mullet are a group of fishes that are tolerant of low oxygen levels (<5 mg l<sup>-1</sup>) (Blaber, 1987). Low oxygen levels (<5 mg l<sup>-1</sup>) were recorded in both the surface and bottom waters in all three systems during this study (Table 13) and may have contributed to mugilids being among the dominant fishes captured (Tables 14 and 15).

**Turbidity:** Cyrus & Blaber (1987a; 1987b) suggest that turbidity, which is influenced by wind speed, substratum particle size and wave action may, to a large extent, determine the species composition of small estuarine systems. They divided some of the dominant fish species from Natal estuaries into groups according to their occurrence in various turbidities, viz. clear water species (<10 NTU), clear to partially turbid species (<50 NTU), intermediate turbidity species (10-80 NTU), turbid water species (>50 NTU) and species indifferent to turbidity.

Closure of the mouths of some estuaries leads to decreased water turbidity but when they re-open at times of high river inflow, turbidities increase rapidly (Cyrus, 1988). This may account for the occurrence of clear water and clear to partially turbid species such as *Gerres rappi*, *Monodactylus argenteus*, *Rhabdosargus holubi*, *Liza dumerilii*, *L. macrolepis*, *Valamugil buchanani* and *Caranx sexfasciatus* (Cyrus & Blaber, 1987a) as well as intermediate turbidity

and turbid water species such as *Valamugil cunnesius*, *Mugil cephalus*, *Leiognathus equula* and *Solea bleekeri* (Cyrus & Blaber, 1987a) in all three systems during this study (Tables 14 and 15). Species which are indifferent to turbidity such as *Pomadasy commersonnii*, *Acanthopagrus berda* and *Terapon jarbua* (Cyrus & Blaber, 1987a) were recorded in the Mhlanga and Zotsha estuaries (Tables 14 and 15).

**Other factors:** A factor frequently overlooked in the assessment of species diversity in estuaries is habitat variation. Estuaries with a wide range of habitats such as rocky reefs, seagrass beds, mangroves, salt marshes, sand flats, muddy creeks and littoral plant growth normally have a higher species diversity than more uniform estuaries (Whitfield, 1983; Blaber, 1985). In addition the size of an estuary may be important; small systems comprising a few hectares usually harbour fewer species than larger systems (Blaber, 1985). This was evident during this study where the Damba estuary, which has an area of 1.7 hectares (Begg, 1978), had a lower species richness and diversity than the Zotsha and Mhlanga systems (Table 16) which have areas of 7.3 and 11.4 hectares respectively (Begg, 1978).

Begg (1984a) concluded that the principal factor which determined the species composition and diversity of Natal's estuaries was the degree of contact each system had with the marine environment. This was probably a major factor which accounted for the species composition and qualitative similarity between the Mhlanga, Damba and Zotsha during this study. The greatest variety of fishes were captured in the normally open Zotsha, followed by the generally closed Mhlanga (Tables 13, 14 and 15). These two systems, which are furthest apart, exhibited the highest similarity in terms of the number of common fishes captured (Table 17). The lowest variety of fishes was captured in the normally closed Damba (Tables 13, 14 and 15) and exhibited a higher similarity to the species present in the Mhlanga than to those captured in the nearby Zotsha estuary (Table 17).

The similarity of two communities is not only a function of the number of common and unique species, but also of the amount of each species present (Mueller-Dombois & Ellenberg, 1974). A quantitative measure of the similarity between the fauna of the study systems revealed that they were more than 80% similar both numerically and in terms of biomass (Table 17). This indicates that temporarily closed estuaries on the Natal coast are dominated by similarly structured fish assemblages.

The dominant fishes captured in the Mhlanga, Damba and Zotsha estuaries during this study were mugilids (*Valamugil* spp., *Liza alata*, *Myxus capensis* and *Mugil cephalus*), *Oreochromis mossambicus*, *Gilchristella aestuaria* and *Glossogobius callidus* (Tables 14 and 15). Similar fish assemblages have been recorded in other small Natal estuaries where Mugilidae (*M. cephalus*, *M. capensis* and *V. cunnesius*) and *O. mossambicus* dominated the ichthyofauna of the Tongati and Mdloti systems (Blaber et al., 1984). *V. cunnesius*, *M. capensis* and *O. mossambicus* were also among the most abundant fishes recorded in the Sezela estuary by Ramm et al. (1987).

## Community structure

Freshwater, estuarine and estuarine-dependent marine species were numerically well represented in the fish communities of the Mhlanga, Damba and Zotsha. In terms of biomass, estuarine-dependent marine species dominated the ichthyofauna of all three systems (Figure 45). During the course of his study Begg (1984a) found that permanently open estuaries were dominated by migrant marine species, whereas in temporarily closed systems, resident estuarine and freshwater species predominated. A similar trend was observed during this study where estuarine-dependent marine species strongly dominated the ichthyofauna in the more frequently open Zotsha system when compared with the Mhlanga and Damba systems.

**Freshwater species:** With the exception of the cichlid *O. mossambicus*, freshwater fishes form only a small part of the estuarine fish community (Blaber, 1985). Few freshwater species tolerate a salinity of more than 10‰ and are therefore restricted in their utilisation of estuarine environments (Whitfield et al., 1981). *O. mossambicus* is extremely euryhaline and is a common component of the fauna of many south east African estuaries (Whitfield et al., 1981; Blaber, 1985). Generally they are common in closed estuaries and coastal lakes but absent from open, tidal estuaries (Whitfield & Blaber, 1979; Blaber, 1985). Begg (1984a) found that *O. mossambicus* was a dominant component of the ichthyofauna in typically closed estuaries in Natal.

*O. mossambicus* was the dominant freshwater species captured in all three systems sampled during this study. This species was also found to be common in the Tongati and Mdloti estuaries by Blaber et al. (1984). The distribution and occurrence of *O. mossambicus* in estuaries is governed by an interplay of factors, including salinity stability, water currents, suitable breeding sites, presence of marginal vegetation, marine competitors, and marine piscivorous fish (Whitfield & Blaber, 1979). As habitat suitability decreases, so the species becomes more and more restricted to the upper reaches of estuaries where factors such as slow water currents and sheltered breeding sites are present and the effects of marine predators and competitors are reduced (Blaber, 1985). Whitfield (1980a) and Blaber et al. (1984) found that in the Mhlanga and Mdloti systems respectively, *O. mossambicus* was most common in the middle and upper reaches. The low numbers and biomass of freshwater species captured in winter in the Mhlanga, Damba and Zotsha during this study (Figures 48 and 49) are probably a reflection of *O. mossambicus* concentrating in the preferred upper reaches of these systems.

The numbers and biomass of freshwater species in all three systems generally increased in spring and summer (Figures 48 and 49). This corresponds to the breeding cycle of *O. mossambicus* which takes place in shallow areas during spring and summer (September - February) (Bruton & Bolt, 1975). Spring and summer are also the periods when the mouths of closed systems frequently open. Whitfield & Blaber (1979) found that when the Mhlanga estuary opened, the shallowness of the upper reaches during the open phase and the reduction of water surface area over the estuary resulted in a forced redistribution of *O. mossambicus*, with a proportion of the population utilizing the lower



reaches of the system. The same factors probably also accounted for the increase in the number and biomass of freshwater fishes in the Mhlanga and the Damba in spring and summer during this study (Figures 48 and 49). Shallow waters also make *O. mossambicus* more susceptible to capture, thus further contributing to the increase in numbers and biomass.

Hall et al. (1987) found that 99% of the *O. mossambicus* in the Wilderness Lakes system were captured during the summer and autumn and that this species was rarely caught during winter and spring. During the cooler months, both adult and juvenile *O. mossambicus* inhabit deeper waters (Bruton & Bolt, 1975) and this, coupled with an upstream migration when the systems close, probably accounted for the decline in the numbers and biomass of freshwater species captured in autumn (Figures 48 and 49).

**Estuarine species:** There are relatively few fish species that can complete their entire life cycle within southern African estuaries and these are invariably small species (Whitfield, 1990). The most significant species which fall into this category in south east Africa are the clupeid *Gilchristella aestuaria* and a number of Gobiidae (Blaber, 1985). *G. aestuaria* was the dominant estuarine species in the Mhlanga, but in the Damba the gobiid *Glossogobius callidus* predominated. In the Zotsha estuary both *G. aestuaria* and *G. callidus* were well represented.

*G. aestuaria* is a pelagic shoaling zooplanktivore (Blaber, 1979). The poor contribution of *G. aestuaria* to the ichthyofauna of the Damba (Tables 14 and 15) may be a result of the generally shallow and restricted nature of the system. Shallow waters render pelagic fish species vulnerable to bird predation and *G. aestuaria* is an important prey item for birds (Day et al., 1981). *G. callidus* is a cryptic benthic species and its relatively high contribution in the Damba may be due to this species being less susceptible to avian predation.

The distribution and abundance of *G. callidus* in Natal's estuaries may be linked to substrate type. Whitfield (1988) found that in the Swartvlei estuary, estuarine species were concentrated in and around *Zostera* beds, with the exception of the goby *Psammogobius knysnaensis* which occurred mainly on sandy substrata. Pienaar (1978) found that the usual habitat of *Glossogobius giuris* are sandy-bottomed pools and backwashes of seasonal rivers or flood pans. *Glossogobius callidus* was an important component of the ichthyofauna of the Damba and Zotsha estuaries, both of which are characterised largely by a muddy sand substratum (Begg, 1984b), whereas the Mhlanga estuary is characterised by a sandy mud and silt substratum (Begg, 1984b) and *G. callidus* did not contribute significantly to the ichthyofauna (Tables 14 and 15).

Both *Gilchristella* and *Glossogobius* appear to prefer the upper reaches of estuaries. Branch & Grindley (1979) found that in the Mngazana estuary in the Transkei, *G. aestuaria* were limited to the upper reaches of the system while Talbot (1982) found that the juveniles and adults of this species were restricted to the upper and middle reaches of the Swartkops estuary in the eastern Cape. Beckley (1984) noted that *Glossogobius* was restricted to the upper reaches of the Sundays River estuary in the eastern Cape.

Whitfield (1980a) also recorded higher abundances and biomasses of *Glossogobius* in the upper reaches of the Mhlanga estuary. The low numbers and biomass of estuarine species during winter 1990 (Figures 48 and 49) may be due to *G. aestuaria* and *G. callidus* predominating in the upper reaches of these systems at the time of sampling.

Both *G. aestuaria* and *Glossogobius* breed throughout the year with a peak in late spring and summer (Crass, 1964; Blaber, 1979; Bruton & Kok, 1980) and this probably accounted for the high numbers and biomass of estuarine species captured in spring (Figures 48 and 49). To ensure that the eggs and fry are not lost to the marine environment either by normal tidal activity or when a closed estuary opens, *G. aestuaria* spawns in the upper reaches of estuaries and as the larvae grow, their distribution extends toward the mouth (Melville-Smith & Baird, 1980; Talbot, 1982). *Glossogobius* lays adhesive eggs on plants and submerged objects (Day et al., 1981; Bruton et al., 1982; van der Elst, 1988). The high numbers and biomass of estuarine species captured in spring and summer, particularly in the Mhlanga and Damba systems, may also be a result of the shallow nature of these estuaries after opening (Figures 2 and 15), resulting in a redistribution of these species towards the lower reaches.

Whitfield (1980b) states that the prolonged breeding season of estuarine species is important in closed estuaries since breaching of the sand bar due to sudden thunderstorms and resultant fluctuation in physical conditions, can occur at any time of the year. He found that *G. aestuaria* bred in the Mhlanga during the closed phase, enabling the fry to utilize a winter peak in zooplankton abundance (Whitfield, 1980c). The extended and successful breeding of *G. aestuaria* and *G. callidus* may account for the large numbers of estuarine species recorded in all three estuaries (Figure 48).

**Estuarine-dependent marine species:** This group comprises inshore species which spawn at sea but utilise estuaries as nursery areas during the juvenile phase of their life cycle (Wallace, 1975a; Wallace et al., 1984). The dominant estuarine-dependent marine group captured in all three systems during this study were mugilids (Tables 14 and 15). *Myxus capensis*, *Mugil cephalus* and *Valamugil cunnesius* were also among the dominant fishes recorded in the Mhlanga by Whitfield (1980c), the Tongati and Mdloti by Blaber et al. (1984), and the Sezela by Ramm et al. (1987). During the course of his study Begg (1984b) found that Mugilidae were undersampled because of the trawl gear used. Blaber (1985) suggested that the mugilids are probably the single most abundant group of fishes in all categories of estuary in southeast Africa. *Myxus capensis* is a catadromous mullet species which shows a distinct preference for freshwater areas in the eastern Cape (Bok, 1979). The shallow nature of the Damba may have restricted the distribution of *M. capensis* to the lower reaches of the system, thus accounting for their high contribution in this system.

In Natal, estuarine-dependent marine species generally spawn inshore in the vicinity of estuary mouths where the relatively stable marine environment is more suitable for the survival of egg and larval stages than estuaries (Wallace, 1975b). Spawning takes place during late autumn, winter

and spring (May - November) when the slow overall movement of the water mass between the Agulhas Current and the coast, frequent current reversals parallel with the shore, and the occurrence of onshore current components favours the retention of eggs and larvae inshore thus reducing the distance between breeding and nursery areas (Wallace, 1975b). The reduction in the numbers and biomass of estuarine-dependent marine species in the Mhlanga, Damba and Zotsha systems in spring 1990 (Figures 48 and 49) may be a result of adults of this group of fishes migrating to sea to spawn. Bennett et al. (1985) recorded a similar pattern in the Bot River estuary where the catches of large individuals of estuarine-dependent marine species declined after it had opened.

Blaber (1987) described a possible mechanism by which postlarval mullet locate and migrate into estuaries. In Natal, turbidity gradients exist from the mouths of estuaries into the sea, particularly during the rainy season (Cyrus, 1988). The fry, by following an increasing turbidity gradient would ultimately reach shallow, estuarine areas (Blaber, 1987). Movement into an open estuary can be achieved by fish passively drifting on the flood tide and then settling along the estuary margins during the ebb tide (Blaber, 1987). This is one of the mechanisms by which fish larvae and postlarvae were observed entering the Swartkops (Beckley, 1985) and Swartvlei (Whitfield, 1989) estuaries in the Cape. Wallace & van der Elst (1975), however, suggest that active estuarine immigration by 0+ juveniles is quantitatively much more important in South African east coast estuaries than passive, tidal recruitment. Harrison & Cooper (1991) have noted mullet actively swimming into the Zotsha estuary during strong outflows, suggesting that these fish can also gain access into temporarily open systems by active migration. Hall et al. (1987) found that tidal flow was not important in the migration of juvenile fishes within the Wilderness estuarine lakes system. Begg (1984a) has suggested that mugilids may gain access into closed systems by being washed into them at high tide when waves overtop the bar. Whitfield (1992) has recorded postlarval *Rhabdosargus holubi* and Mugilidae entering the Haga Haga estuary (32°46'S; 28°15'E) when the sand bar at the mouth was being overtopped.

The prolonged period of juvenile recruitment into South African estuaries, which is a function of the extended spawning season, is regarded as a strategy against (a) unseasonal floods which could open temporarily closed estuaries prematurely and (b) droughts which would delay the opening of these systems (Whitfield, 1990). In seasonally closed estuaries, recruitment usually starts later and varies in accordance with the onset of the spring rains when increased river flow forces open estuary mouths (Wallace & van der Elst, 1975; Whitfield, 1980c). Whitfield & Kok (1992) found that recruitment of most estuarine-dependent marine species into southern Cape estuaries reaches a peak during summer, which corresponds to the time when systems along this section of the coast are normally open to the sea. The higher numbers and biomass of estuarine-dependent marine species captured during spring 1991 and summer 1992, when compared to spring 1990 and summer 1991 (Figures 48 and 49), is probably a result of the more frequent mouth

openings in the Mhlanga and Damba systems during the former period.

**Marine species:** This group, which includes stenohaline species, comprises mainly inshore marine taxa which are not dependent on estuaries (Whitfield, 1994). These fishes did not contribute significantly to the ichthyofauna during this study. Probable reasons include the minimal tidal exchange with the sea, frequent mouth closure and relatively low salinities within these estuaries, thus reducing the potential for this group of fishes to utilise these systems.

#### Seasonality

**Winter:** During this period, estuarine-dependent marine species were a dominant component of the ichthyofauna of all three systems, both numerically and in terms of biomass (Figures 46 and 47). This is probably a reflection of the distribution of the various types of fishes, with freshwater and estuarine species mainly inhabiting the upper reaches (Branch & Grindley, 1979; Blaber et al., 1984; Beckley, 1984), leaving estuarine-dependent marine species to dominate the middle and lower reaches.

Whitfield (1980a; 1988) found that the distribution of fishes in the Mhlanga and Swartvlei estuaries was closely associated with their dominant food. In the Mhlanga, *O. mossambicus* was found to be most abundant in the upper reaches where benthic floc was most concentrated, while mugilids were distributed according to their preferred substrate particle size (Whitfield, 1980a). *V. cunnesius* was most abundant in the middle reaches, *M. cephalus* and *L. alata* were most common in the lower reaches and *M. capensis* was common in the upper reaches due to its attraction to freshwater areas (Bok, 1979; Whitfield, 1980a).

Whitfield (1980a; 1980c) also determined that in the Mhlanga estuary, food resources are high during the closed phase of the estuary due to the relative stability of the physical environment and increased habitat availability. Blaber et al. (1984) also recorded a peak in zooplankton and zoobenthos in the Mdloti estuary during winter when the mouth was closed. The relatively high numerical contribution of estuarine species in the Mhlanga system during spring 1990 and spring 1991 (Figure 48) is probably a reflection of the successful breeding of *G. aestuaria* and *G. callidus* during the relatively stable winter closed phase.

**Spring:** The relative proportions of freshwater and estuarine fishes increased in all three systems during spring, with freshwater fishes dominating the fish biomass (Figures 46 and 47). This corresponds with the peak breeding period for *G. aestuaria*, *Glossogobius* and *O. mossambicus* (Crass, 1964; Bruton & Bolt, 1975; Blaber 1979). The increase in the relative proportion of freshwater and estuarine species in spring particularly in the Mhlanga and Damba may also be due to the shallowness of the upper reaches of these systems after breaching, resulting in the redistribution and concentration of these fishes in the lower reaches. The reduction in the relative contribution of estuarine-dependent marine species to the ichthyofauna in spring (Figures 46 and 47) may be a result of the emigration of subadults and adults from the estuaries.

**Summer:** The extended spawning period of estuarine-dependent marine species prolongs the period during which larvae and juveniles occur in the inshore marine environ-

ment (Wallace, 1975b). Recruitment of juveniles into permanently open estuaries takes place mainly during winter and spring (June - November) when river outflow is at a minimum (Wallace & van der Elst, 1975). In temporarily closed estuaries recruitment usually starts later when increased river flow forces open estuary mouths (Wallace & van der Elst, 1975; Whitfield, 1980c). The increase in the proportional contribution of estuarine-dependent marine species in summer (Figures 46 and 47) is most likely a result of the extended spawning and successful recruitment of this group of fishes into the systems.

Following breaching, the Mhlanga and Damba estuaries are very shallow. Although shallow waters may aid small fishes in avoiding large piscivorous fish (Whitfield & Blaber, 1978b), it renders them vulnerable to bird predation, particularly by egrets, herons, cormorants and terns. In the West Kleinmond estuary, Blaber (1973) found that the numbers of juvenile *R. holubi* were reduced from 55000 individuals to 11000 within six months, due to heavy predation by piscivorous birds, chiefly herons and cormorants. Bird predation during this study may have contributed to the decrease in the relative proportions of both estuarine and freshwater species in summer (Figures 46 and 47). Another consequence of temporarily closed systems opening is that the available habitat and food resources are drastically reduced due to prolonged exposure of the benthos and the scouring action of floodwaters (Whitfield, 1980c; Blaber et al., 1984; Branch et al., 1985). Competition among fishes, both for suitable habitat and food, would therefore be expected to be high during spring/summer and may also have contributed to the decline in the proportion of estuarine and freshwater species in summer.

**Autumn:** Estuarine-dependent marine species were well represented in all systems during autumn, both numerically and by mass (Figures 46 and 47). The high proportion of this group in autumn is also a reflection of the increased water depth, allowing *O. mossambicus* to inhabit the preferred upper reaches (Whitfield & Blaber, 1979) and estuarine-dependent marine species to dominate the lower reaches.

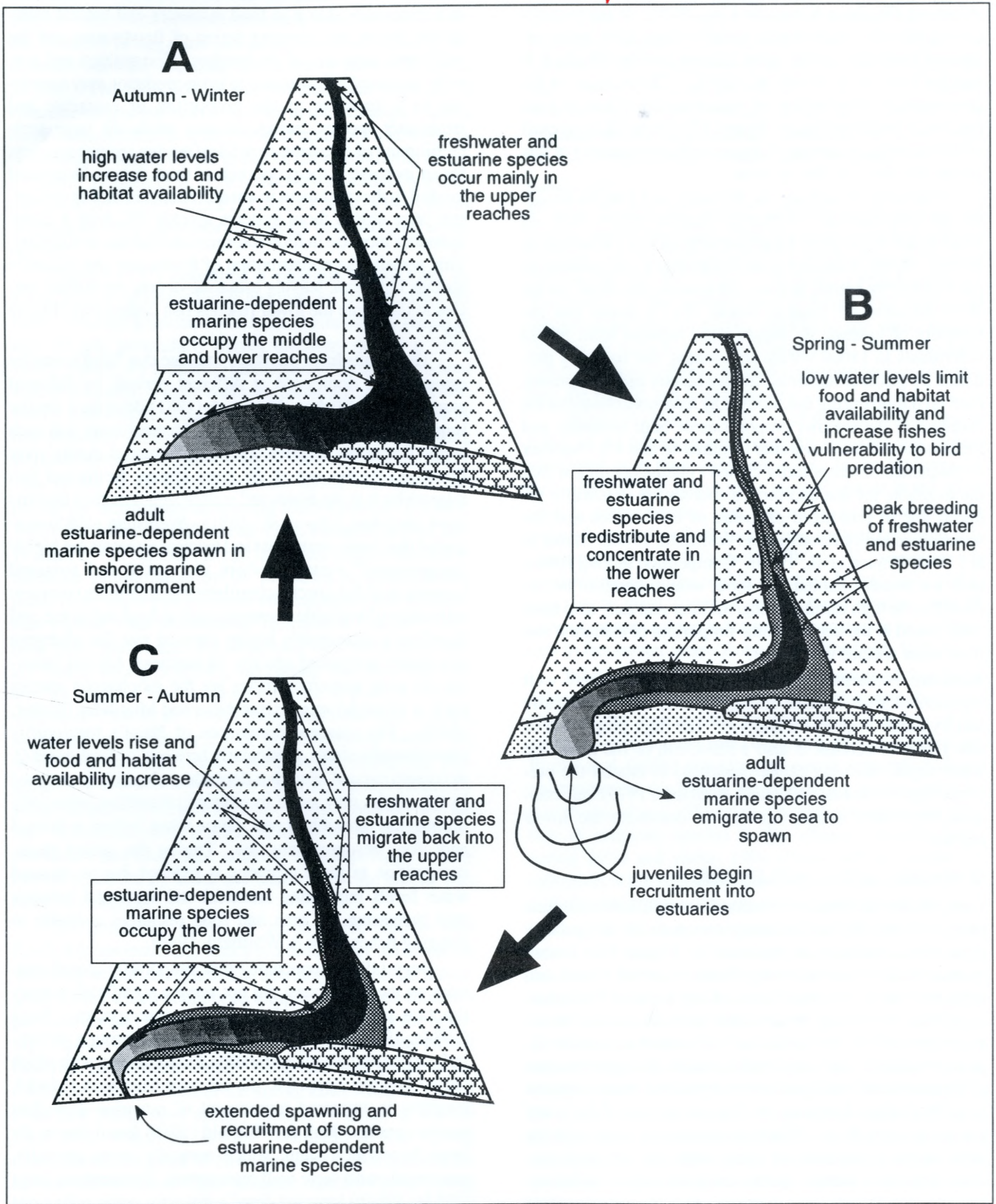
## SUMMARY AND CONCLUSIONS

Based on the information presented, a simplified conceptual model of the fish community structure of temporarily open/closed estuaries is presented in Figure 50. During winter, small estuaries on the Natal coast are closed and relatively deep, with inundation of the adjacent floodplain vegetation increasing the available food resources. Freshwater species (*O. mossambicus*) and estuarine species (*G. aestuaria* and *G. callidus*) tend to inhabit the upper reaches of these systems while estuarine-dependent marine species (e.g. Mugilidae) dominate the fish community of the lower reaches (Figure 50A). When these estuaries open with the onset of the spring/summer rains, adult and subadult estuarine-dependent marine species emigrate and juveniles immigrate into the estuaries. Spring is also the peak breeding period of resident estuarine (*G. aestuaria* and *G. callidus*) and freshwater (*O. mossambicus*) species, resulting in an increase in the proportion of these fishes during this period. Most of Natal's seasonally closed estuaries tend to drain when they open and this results in a redistribution of fresh-

water and estuarine species into the lower reaches, further contributing to the increase in the proportion of these fishes (Figure 50B). The breaching of closed estuaries also results in a temporary slump in food resources and habitat availability due to the scouring action of floodwaters and the prolonged exposure of the benthos. Competition and possible increased vulnerability to avian predation may contribute to a decrease in the proportion of estuarine and freshwater species during summer, while the large scale recruitment of estuarine-dependent marine species accounts for an increase in the proportion of these fishes. Decreased rainfall in the catchment in autumn results in mouth closure, and once closed these systems quickly fill, with a corresponding increase in food resources and habitat availability. This permits the redistribution of freshwater and estuarine species upstream, leaving estuarine-dependent marine species to dominate the lower reaches fish community (Figure 50C).

The results from this study indicate that Natal's smaller estuaries are dominated at different periods by different assemblages of fishes. Day et al. (1981) describe a similar sequence where there is a tendency for freshwater fish such as the Cichlidae to move down into estuaries during river flooding. At the end of the rainy season, freshwater fish migrate back to the rivers and marine migrants then become more abundant (Day et al., 1981). Weinstein (1985) suggested that warm-temperate and tropical estuaries are highly 'programmed' systems, where the spatial and temporal separation of fish species contribute toward a more complete utilisation of available resources such as food and space, and therefore a conceivably higher survival rate for otherwise potentially competing species. In southeast African estuaries the most numerous fishes are the iliophagous species such as *Oreochromis mossambicus* and Mugilidae (Blaber, 1985). The seasonal dominance of Natal's temporarily open/closed systems, particularly between the freshwater *O. mossambicus* and estuarine-dependent mugilids as outlined in this study, may serve to reduce competition, especially during the unstable open phase when habitat is limited and food resources are low. During the closed phase, competition in these estuaries is reduced due to elevated water levels inundating intertidal and supratidal habitats, thus increasing the area and food resources available to foraging fishes (Kok & Whitfield, 1986).

Begg (1984a) concluded that temporarily closed estuaries on the Natal coast did not serve a significant nursery function for estuarine-dependent marine species. Begg (1984a; 1984b) studied Natal's estuaries during a particularly dry period when the duration and frequency with which closed systems opened to the sea may have been reduced, resulting in impaired recruitment of estuarine-dependent marine species. Kok & Whitfield (1986) found that in the large Swartvlei system, which normally opens annually, marine migrants were well represented. Furthermore Begg (1984a; 1984b) sampled Natal's estuaries using only a one metre beam trawl which tended to undersample mugilids, a dominant estuarine-dependent marine group of fishes. The results of this study, using a variety of sampling techniques and during more typical climatic conditions, indicate that as a group, estuarine-dependent marine species are an



**Figure 50.** Schematic diagram illustrating cyclic fish community structure in small temporarily open/closed estuaries on the Natal coast.

important component of the ichthyofauna of Natal's smaller estuaries. Although the ichthyofauna of small temporarily open/closed estuaries may not be as diverse as large permanently open estuaries, their importance in maintaining estuarine-dependent fish stocks must not be underestimated. By providing a continuous sequence of sheltered environments over a long stretch of coast, it is likely that millions of juveniles of estuarine-dependent marine species make use of these estuarine nursery areas on an annual basis, and when they return to the sea, supplement the breeding populations of recreationally and commercially important fish taxa.

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**Appendix 1.** Length-mass relationship of selected fish species captured during this study (n = number of specimens, a = intercept, b = slope, r = sample correlation coefficient).

Fish species	n	a	b	r <sup>2</sup>
<i>Acanthopagrus berda</i>	4	0.0000107	3.263	1.00
<i>Ambassis natalensis</i>	11	0.0000447	2.878	0.97
<i>Ambassis productus</i>	167	0.0000186	3.081	0.96
<i>Argyrosomus hololepidotus</i>	19	0.0000352	2.884	0.96
<i>Awaous aeneofuscus</i>	5	0.0000059	3.299	1.00
<i>Caranx papuensis</i>	9	0.0000478	2.899	0.99
<i>Caranx sexfasciatus</i>	12	0.0000253	3.015	1.00
<i>Crenimugil crenilabis</i>	230	0.0000060	3.336	0.98
<i>Croilia mossambica</i>	9	0.0000001	4.329	0.83
<i>Gerres rappi</i>	79	0.0000089	3.294	1.00
<i>Gilchristella aestuaria</i>	677	0.0000015	3.581	0.97
<i>Glossogobius callidus</i>	647	0.0000102	3.129	0.97
<i>Glossogobius giuris</i>	4	0.0000078	3.154	1.00
<i>Herklotsichthys quadrimaculatus</i>	20	0.0000488	2.707	0.93
<i>Kuhlia mugil</i>	7	0.0000007	4.010	0.77
<i>Leiognathus equula</i>	15	0.0000668	2.871	0.99
<i>Lichia amia</i>	18	0.0000149	3.054	1.00
<i>Liza alata</i>	187	0.0000195	3.013	0.99
<i>Liza dumerilii</i>	148	0.0000260	2.948	0.99
<i>Liza macrolepis</i>	43	0.0000254	2.987	0.99
<i>Liza tricuspidens</i>	38	0.0000160	3.007	0.99
<i>Lutjanus argentimaculatus</i>	7	0.0000365	2.960	1.00
<i>Monodactylus argenteus</i>	5	0.0000029	3.601	0.97
<i>Monodactylus falciformis</i>	20	0.0000329	3.050	0.99
<i>Mugil cephalus</i>	255	0.0000294	2.951	0.99
<i>Myxus capensis</i>	753	0.0000158	3.038	0.99
<i>Oligolepis acutipennis</i>	7	0.0000083	3.194	0.93
<i>Oligolepis keiensis</i>	9	0.0000100	3.112	0.88
<i>Oreochromis mossambicus</i>	999	0.0000284	3.059	0.99
<i>Pomadasys commersonii</i>	95	0.0000139	3.112	1.00
<i>Rhabdosargus holubi</i>	240	0.0000137	3.225	0.99
<i>Rhabdosargus thorpei</i>	4	0.0000167	3.140	1.00
<i>Solea bleekeri</i>	47	0.0000135	3.075	0.88
<i>Terapon jarbua</i>	259	0.0000483	2.877	0.99
<i>Tilapia rendalli</i>	4	0.0000405	3.001	1.00
<i>Valamugil buchhanani</i>	40	0.0000245	2.997	0.99
<i>Valamugil cunnesius</i>	707	0.0000157	3.071	1.00
<i>Valamugil robustus</i>	106	0.0000227	2.992	0.99



**Appendix 2.** Fishes captured in the Mhlanga, Damba and Zotsha estuaries and their categorisation into freshwater, estuarine, estuarine-dependent marine and marine species.

Fish species	Common name	Category
<i>Acanthopagrus berda</i>	Riverbream	Estuarine-marine
<i>Ambassis natalensis</i>	Slender glassy	Estuarine
<i>Ambassis productus</i>	Longspine glassy	Estuarine
<i>Argyrosomus hololepidotus</i>	Kob	Estuarine-marine
<i>Arothron immaculatus</i>	Blackedged blaasop	Marine
<i>Awaous aeneofuscus</i>	Freshwater goby	Estuarine
<i>Caranx ignobilis</i>	Giant kingfish	Estuarine-marine
<i>Caranx papuensis</i>	Brassy kingfish	Estuarine-marine
<i>Caranx sexfasciatus</i>	Bigeye kingfish	Estuarine-marine
<i>Chelonodon laticeps</i>	Bluespotted blaasop	Marine
<i>Crenimugil crenilabis</i>	Fringelip mullet	Estuarine-marine
<i>Croilia mossambica</i>	Naked goby	Estuarine
<i>Eleotris fusca</i>	Dusky sleeper	Estuarine
<i>Eleotris mauritianus</i>	Widehead sleeper	Estuarine
<i>Elops machnata</i>	Ladyfish	Estuarine-marine
<i>Favonigobius reichei</i>	Tropical sand goby	Estuarine
<i>Gerres acinaces</i>	Smallscale pursemouth	Estuarine-marine
<i>Gerres rappi</i>	Evenfin pursemouth	Estuarine-marine
<i>Gilchristella aestuaria</i>	Estuarine roundherring	Estuarine
<i>Glossogobius biocellatus</i>	Sleepy goby	Estuarine
<i>Glossogobius callidus</i>	River goby	Estuarine
<i>Glossogobius giuris</i>	Tank goby	Estuarine
<i>Herklotsichthys quadrimaculatus</i>	Blueline herring	Marine
<i>Kuhlia mugil</i>	Rock flagtail	Marine
<i>Leiognathus equula</i>	Slimy	Estuarine-marine
<i>Lichia amia</i>	Garrick	Estuarine-marine
<i>Liza alata</i>	Diamond mullet	Estuarine-marine
<i>Liza dumerilii</i>	Groovy mullet	Estuarine-marine
<i>Liza macrolepis</i>	Large-scale mullet	Estuarine-marine
<i>Liza richardsonii</i>	Southern mullet	Estuarine-marine
<i>Liza tricuspidens</i>	Striped mullet	Estuarine-marine
<i>Lutjanus argentimaculatus</i>	River snapper	Estuarine-marine
<i>Lutjanus fulviflamma</i>	Dory snapper	Estuarine-marine
<i>Megalops cyprinoides</i>	Oxeye tarpon	Marine
<i>Micropterus salmoides</i>	Largemouth bass	Freshwater
<i>Monodactylus argenteus</i>	Natal moony	Estuarine-marine
<i>Monodactylus falciformis</i>	Cape moony	Estuarine-marine
<i>Mugil cephalus</i>	Flathead mullet	Estuarine-marine
<i>Myxus capensis</i>	Freshwater mullet	Estuarine-marine
<i>Oligolepis acutipennis</i>	Sharptail goby	Estuarine
<i>Oligolepis keiensis</i>	Kei goby	Estuarine
<i>Oreochromis mossambicus</i>	Mozambique tilapia	Freshwater
<i>Pomadasys commersonnii</i>	Spotted grunter	Estuarine-marine
<i>Pomatomus saltatrix</i>	Elf	Estuarine-marine
<i>Psammogobius knysnaensis</i>	Knysna sandgoby	Estuarine
<i>Pseudorhombus arsius</i>	Largetooth flounder	Marine
<i>Rhabdosargus holubi</i>	Cape stumpnose	Estuarine-marine
<i>Rhabdosargus thorpei</i>	Bigeye stumpnose	Estuarine-marine
<i>Sillago sihama</i>	Silver sillago	Estuarine-marine
<i>Solea bleekeri</i>	Blackhand sole	Estuarine-marine
<i>Terapon jarbua</i>	Thornfish	Estuarine-marine
<i>Tilapia rendalli</i>	Redbreast tilapia	Freshwater
<i>Valamugil buehanani</i>	Bluetail mullet	Estuarine-marine
<i>Valamugil cunnesius</i>	Longarm mullet	Estuarine-marine
<i>Valamugil robustus</i>	Robust mullet	Estuarine-marine

Appendix 3. Aerial views of the Mhlanga (upper left), Damba (lower left) and Zotsha estuaries (centre right).



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0 500 m



0 500 m

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### STYLE OF THE HOUSE

Hyphens: Certain substantive compounds are hyphenated: gill-raker, soft-ray, swim-bladder, 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 one continuous fin with 12 spines and 10-12 soft (segmented) rays; D X/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, 8. 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). Compass directions (north, west, northwest, etc.) are abbreviated using capital letters without the full stops: N, W, NW. Dr (Doctor) and Mr (Mister) will be used without a period. We recommend the following abbreviations for ichthyological terms: Standard length — SL, total length — TL, gill-rakers — GR, lateral line — LL.

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