ECOLOGY OF THE ICHTHYOFAUNA IN THREE TEMPORARILY OPEN/CLOSED ESTUARIES ON THE NATAL COAST

by

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ABSTRACT

The ichthyofauna of three small Natal estuaries, the Mhlanga, Damba and Zotsha was sampled over a period of two years. A total of 68 kinds of fishes representing 24 families, 39 genera and 56 species were captured during this study. Forty seven kinds of fishes were recorded in the Mhlanga 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. In the Damba, 24 kinds of fishes were recorded. The most abundant fishes captured were *Glossogobius callidus, M. capensis* and *O. mossambicus . M. capensis, M. cephalus, O. mossambicus* and *G. callidus* dominated the fish biomass captured in the Damba. A total of 56 kinds of fishes were recorded in the Zotsha during this study. The ichthyofauna of the Zotsha was 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 were *O. mossambicus , L. alata, Valamugil robustus, Valamugil buchanani , M. capensis, M. cephalus* and *V. cunnesius.*

Classifying the species captured according to whether they were resident estuarine species, freshwater species, estuarine-dependent marine species and marine species revealed that the first three groups were all well represented in the systems. The only system in which marine species made any significant contribution to the ichthyofauna was the Zotsha. *Oreochromis mossambicus* was the dominant freshwater species in all three estuaries during this study. *Gilchristella aestuaria* and *Glossogobius callidus* were the principal estuarine species in the Mhlanga and the Damba respectively. Both *G. aestuaria* and *G. callidus* were 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, A. productus, M. capensis, V. cunnesius, V. robustus, M. cephalus* and *L. alata* predominated.

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 mainly occupy the middle and lower reaches and

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dominate the fish community. When these systems 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 population during this period. When closed estuaries open many of them drain 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 slump 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 spawning and 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, these 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 continuous sequence of sheltered habitats along the coast they may contribute significantly to the viability of estuarine-dependent marine fish stocks.

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CHAPTER 1.
INTRODUCTION

In its broadest sense, an estuary is a place where a river meets the sea and forms a transition zone between freshwater and seawater (Pritchard, 1967; Day, 1981a). Estuaries may include a wide variety of aquatic coastal systems and range from small bodies of water which are only seasonally connected to the ocean (ephemeral inlets), to large permanently open systems (Day & Yáñez-Arancibia, 1985). As a consequence, many attempts have been made to define and classify estuaries (Pritchard, 1967; Day, 1981a; Begg, 1984a; Cooper, 1991). Estuaries are typically shallow systems, sheltered from major wave action; they have variable temperatures, salinities, turbidities and oxygen content. Estuaries are also among the most productive of ecosystems on earth (Odum, 1983; McHugh, 1985). In the open sea the number of grams of dry organic matter produced per m^2 per day is usually less than 1; in coastal waters and wild grasslands it is 0.5 - 3; in ordinary farmlands 3 - 10; in intensively cultivated farmland 10 - 25; and in estuaries 10 - 25 (Odum, 1983).

By providing abundant food and shelter, estuaries are utilised by many of the world's nektonic organisms (Odum, 1983; Day & Yáñez-Arancibia, 1985) of which about 99% comprise fish (Yáñez-Arancibia, 1985). Estuarine fish communities are typically composed of a mixture of species, some are restricted to the estuarine zone, some come in from the sea and some are freshwater species (Odum, 1983). From research conducted in estuaries, biologists have long maintained that the most important role of estuaries with regard to fish, is the provision of nursery grounds for juveniles of certain marine species, many of which are of direct or indirect commercial and recreational importance to man (Wallace *et al.*, 1984; Lenanton & Hodgkin, 1985). In the United States of America, 69% by weight of all the 1970 commercial landings consisted of estuarine-dependent species; while 62% by weight of the recreational fish catch (excluding invertebrates) was also of estuarine-dependent species (McHugh, 1976). Similarly in the State of New South Wales, Australia, 66% by weight of the total commercial catch was composed of estuarine-dependent species (Pollard, 1976; 1981).

About one-fifth of the 1500 species of fish recorded from the continental shelf of southern Africa occur in estuaries at some stage in their life cycle (Day *et al.*, 1981). Most of the marine fish which utilise estuaries are the juveniles of demersal feeders which when adult, live in nearshore areas along the coast (Day *et al.*, 1981). Commercial fishing in South African estuaries is limited and the percentage catch of estuarine dependent fish in the sea by commercial fishermen has not been determined (Day *et al.*, 1981; Wallace *et al.*, 1984). Sport fishing and the tourist attraction it provides are perhaps of much greater importance especially if one considers the monetary value of activities such as the manufacture of boats, sale of

outboard motors, fishing tackle, protective clothing and bait, the hire of accommodation, sale of local real estate etc. (Day *et al.*, 1981; Wallace *et al.*, 1984).

Apart from their contribution to various fishery resources, estuaries are part of the coastal environment and as a consequence are subject to human activities such as tourism, transportation, coastal development and industrialization, as well as pollution from domestic and industrial wastes (Begg, 1985; Day & Yáñez-Arancibia, 1985; Yáñez-Arancibia, 1985). The continuing economic growth of countries around the world and the subsequent development of their coastal zone may, under certain conditions, result in the deterioration of these coastal resources (McHugh, 1985; Yáñez-Arancibia, 1985).

The South African 3000 km long coastline has a total estuarine area of about 600 km^2, 68% of which is in Natal (Begg, 1978). At least 80% of Natal's 408 km^2 estuarine area, however, is made up by the Lake St Lucia system, the largest estuarine system in South Africa (Begg, 1978). Furthermore, 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 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 fauna of temporary 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 is to investigate the ecology of the ichthyofauna of Natal's temporarily open/closed estuaries. The key objectives of the study were:

1)   To determine the fish community structure of three temporarily open/closed estuaries on the Natal coast.

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 how Natal's small, temporarily open/closed estuaries function and their importance to fish.

In the following chapter the estuaries of Natal are described in terms of their setting including that of the hinterland and nearshore area and the three systems selected for this study described. The ecology of the ichthyofauna of each system is presented separately in chapters 4, 5 and 6. In the final chapter (chapter 7), the fish community structure of the three systems is compared and some general conclusions are reached.

CHAPTER 2.

STUDY AREA

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 (in the north) to the Mtamvuna estuary (31° 4'S; 30° 11'E) bordering Transkei (in the south) (Figure 1).

2.1. Topography

The terrain in Natal ranges from relatively flat coastal plains to exceedingly rugged mountain ranges but can be divided into four main geomorphological provinces: (1) Drakensberg escarpment (>2000 m); (2) highland plateau (1200 - 2000 m); (3) intermediate benchland (300 - 1200 m); and coastal lowlands (<300 m) (Goodlad, 1986; Figure 2).

The coastline of Natal is relatively straight and is interrupted by 73 estuaries of varying sizes (Begg, 1978) (Figure 2). The Tugela River forms a natural divide between southern and northern Natal. The Zululand segment of the Natal coast, which extends northward for 320 km from the Tugela, is backed by a low-lying sandy coastal plain which is 80 km wide in the north and narrows southward, tapering off just north of the Tugela estuary (Orme, 1974). Due to the flatter topography of the Zululand coastal plain, 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 relatively few, large estuarine systems such as Richards Bay, Lake St Lucia and Kosi Bay (Figure 2).

South of the Tugela the topography becomes steeper (the Drakensberg mountains attaining an altitude of 3385 m within 250 km of the coast) and the remaining 250 km of coast is near-linear comprising a mixed sandy rocky shore which, except in the immediate vicinity of Durban, lacks a coastal plain (Orme, 1974; Cooper, 1991). The steep hinterland, and lack of a coastal plain has resulted in a large number of rivers which drain small catchments, each of which forms an independent outlet at the coast (Cooper, 1991) (Figure 2). Within this area are some 62 estuarine systems which together occupy only 1.6% of the total extent of estuarine waters in Natal (Begg, 1984a).

According to King (1972) the steep relief south of the Tugela has developed through monoclinal tilting of the Province along a hinge located near the present coastline; thus elevating the interior, drowning the coast and continental shelf, and imparting a smooth profile to the coastal margin. Eustatic rise in sea level is also considered to have contributed to drowning of the coast (du Toit, 1954; Day, 1981a). During the major glaciations of the

Figure 1. Map of southern Africa indicating the province of Natal.

Figure 2. Map of Natal depicting the four main geomorphological provinces and river systems (after Orme, 1974).

Pleistocene, (16 000 - 30 000 years ago) over one third of the earth's surface was covered with ice one to two kilometres thick and the sea level was 100 m -150 m below the present level, corresponding approximately with the edge of the present continental shelf. The Pleistocene rivers eroded valleys to the edge of the continental shelf. With the rise in sea level during the last 15 000 years, the lower ends of these valleys were completely submerged. The upper valleys were only partly submerged and these drowned valleys now form the majority of Natal's estuaries (Day, 1981a). Since they formed they have acted as sites of sediment accumulation as the rivers adjusted to a new equilibrium (Cooper, 1991).

The vast majority of Natal's estuaries situated south of the Tugela are typically temporarily open/closed estuaries (referred to as lagoons by Begg, 1978; 1984a; 1984b) which are cut off from the sea for much of the year by a sand bar across the mouth. They 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).

2.2. Geology

The geological succession of Natal/Zululand may be subdivided into four principal sequences: Basement Complex, Natal Group Sandstone, Karoo Supergroup and the Cretaceous-Cainozoic sequence (Goodlad, 1986). These are shown in Figure 3.

The oldest rocks of Southern Africa, forming the foundation of the sub-continent are collectively referred to as the Basement Complex (Van der Eyk *et al.*, 1969). This complex of coarse-grained granites, granodiorites and gneisses is exposed in a narrow strip which tends roughly north-south and runs obliquely across Natal from a coastal position in the south to some 30 km inland in the north, corresponding to the Natal monocline and the intermediate benchland area (Van der Eyk *et al.*, 1969; Goodlad, 1986; Cooper, 1991). Overlying the Basement Complex is the Ordovician Natal Group Sandstone. This sequence of cross-bedded quartz arenites, arkoses and conglomerates are also distributed along the monocline axis (Kingsley, 1975; Goodlad, 1986).

Unconformably overlying the Natal Group Sandstone is the 1000 m-thick Karoo Supergroup. The lowermost unit in this group is the Dwyka Group which comprises mainly glacial diamictites. This formation outcrops along the monocline trend and in discontinuous bands parallel to the Basement Complex (Goodlad, 1986; Cooper, 1991). The Ecca Group conformably overlies the Dwyka Formation and comprises shales and sandstones (Cooper,

Figure 3. Simplified geological map of Natal (after Goodlad, 1986).

1991). On top of the Ecca Group are typically fine-grained sedimentary rocks of the Beaufort Group. The sandstones and shales of the Ecca and Beaufort Groups together are dominant in the highland plateau area (Goodlad, 1986). The high Drakensberg escarpment is formed of sandstones and shales of the Stormberg Group capped by a thick volcanic pile (Drakensberg basalt).

The final geological sequence includes relatively undeformed Cretaceous and Cainozoic sediments of aeolin, fluvial and marine origin. A very variable range of lithofacies underlies the Zululand coastal plain and to the south, outcrops along the coastal lowlands (Orme, 1974; Goodlad, 1986).

2.3. Soils

A simplified soil map of Natal is presented in Figure 4. The soils of the coastal lowlands largely comprise arenosols which are sands derived from aeolian and alluvial deposits (Brink, 1985). They are usually red in upland sites and dune ridges, yellow in flat areas, and grey in bottomland sites or in areas with impeded drainage. The intermediate benchland south of the Tugela is characterised by weakly developed shallow soils which are mainly reddish brown to yellow-brown sandy loams and clays derived from residual granite, gneiss or quartzite. North of the Tugela, black and red smectitic clays predominate. The smectitic clays are generally dark in colour and are commonly associated with low-relief landscapes on basic or ultrabasic igneous rocks or calcareous mudrocks of the Ecca Group and younger formations (Brink, 1985). The highland plateau and Drakensberg Escarpment are characterised by ferrallitic and fersiallitic soils. The ferrallitic soils are mainly red, yellow and grey sands and loams derived from residual granite, quartzite, sandstone and colluvial sands and usually occur in areas where the mean annual rainfall is above 800 mm (Brink, 1985). The fersiallitic soils are characteristically red, yellow and grey clays, sands and loams derived from residual intermediate, basic rocks, sandstones, shales and colluvium. Fersiallitic soils are usually found in a broad zone with an annual rainfall of 450 - 800 mm (Brink, 1985).

2.4. Climate

Situated approximately between latitudes 27° and 31°S, Natal's climate is typically subtropical. Air temperatures in Natal are at a maximum in February and a minimum in August (Schultze, 1965). Absolute maximum and minimum temperatures for Durban are 42.0 and 4.1°C and for Cape St Lucia 39.0 and 5.7 °C (Tinley, 1985).

Figure 4. Simplified soil map of Natal (after Brink, 1985).

Both thunderstorms and midlatitude cyclonic activity contribute to the weather pattern in Natal, the former in summer (October - March), the latter in winter (April - September) (Orme, 1974). In summer, a central high pressure system is typically located in the southeast and moist air flows into the interior from the Indian Ocean (Figure 5). The rapid altitudinal rise from the coast to the Drakensburg escarpment produces orographic rain in the upper hinterland catchment (Tinley, 1985; Goodlad, 1986). Summer rainfall of this type accounts for 80% of the annual precipitation in Natal (Tyson, 1987). Winter rainfall is typically associated with cyclonic depressions moving northwards from the Cape (Figure 5) and accounts for only a minor proportion of the total annual precipitation.

Natal receives a mean annual precipitation of 907 mm which is distributed unevenly throughout the province (Orme, 1974). Precipitation above 1250 mm occurs along the entire coastline, over the Drakensberg escarpment, and along the southern Zululand coast. The central interior regions receive average rainfall but values below the mean occur in the upper Tugela basin and a zone extending northward from central Zululand into Mozambique (Orme, 1974; Figure 6).

2.5. Vegetation

The vegetation in Natal may be broadly divided into four main veld types: bushveld, forest/scrubforest, sourveld and mixed grassveld (Acocks, 1975). Within each veld type however the vegetation and species composition can be very variable according to localised micro-climate, topography, soil type and moisture conditions.

The vegetation along the coastal belt ranges from dune pioneers on the seaward side through to dune scrub forest and typical coastal forest. The dune scrub forest is fairly uniform along the coast and is characterised by *Carissa macrocarpa*, *Ficus burtt-davyi*, *Eugenia capensis* and *Brachylaena discolor*. Much of the coastal forest has been replaced by sugar cane. Variations of the typical coastal forest include the Zululand palm veld, the mangrove forests and patches of swamp forest. The Zululand palm veld lies mostly north of the Tugela with small patches south of Durban. It typically consists of patchy tangled forest lying within grassveld and is dominated by lianas, palms and *Strelitzia nicolai*. Mangrove forests are located along several estuaries and are particularly well developed at Durban, Richards Bay, St Lucia and Kosi Bay. These forests are characterised by true mangrove species on the seaward side and species such as *Barringtonia racemosa* and *Hibiscus tiliaceous* in the riverine channel. Swamp forests occur in very small patches north of the Tugela and consist of elements of the typical coastal forest and indicator species such as *Macaranga capensis*.

Figure 5. Typical atmospheric circulation over southern Africa (after Goodlad, 1986),

Figure 6. Rainfall distribution in Natal (after Orme, 1974).

The hinterland of Natal is largely bushveld especially in the mid altitude regions with sourveld and mixed grassveld occurring at the higher altitudes. Bushveld consists chiefly of *Acacia* thornveld especially in the northern regions with abundant areas of forest and scrub forest of tropical affinity particularly in valleys inaccessible to grazing. The sourveld occurs mostly in the higher regions but extends much closer to the coast in the Pondoland area. This veld is typified by extremely dense grassland with subtropical forests occupying valleys and gorges. The higher altitude sourveld occurs on the eastern slopes and foothills of the Drakensberg. The vegetation is tall grassveld with sparse relics of forest/scrubforest with *Podocarpus latifolius* as the dominant tree species.

The remaining highland areas are characterised by mixed grassveld containing elements from both the sour and sweet grassveld. These areas are highly variable in species composition (grasses), with *Themeda triandra* being largely dominant. The vegetation on the summits of the Drakensberg consists of sparse typical montane flora containing elements of tropical affinity as well as outliers of the fynbos.

2.6. Ocean Currents

The main currents of the south-west Indian Ocean are shown in Figure 7. In the north-east the westward flowing Equatorial current divides into two branches, one branch flows northwards while the other branch flows southwards as the East Madagascar Current and the Mozambique Current. The former, after rounding the southern tip of Madagascar, flows in a westerly direction until it meets the African coastline at about 25°S. Here, it combines with the Mozambique Current to form the strong south-west flowing Agulhas Current.

In general the Agulhas Current follows the edge of the continental shelf. Along the Zululand coast this is very narrow and the current is consequentially a few kilometres off the shore. South of Port Durnford (28° 55'S; 31° 50'E) the shelf widens to a maximum width of 45 km in the vicinity of the Tugela River and the current is correspondingly far from the coast. South of the Tugela it again sweeps close inshore (Pearce, 1977; Schuman, 1987).

The inshore currents of the Natal coast are influenced by the Agulhas Current, the western edge of which generates eddies that are most pronounced where the continental shelf is wide. Most of the water movements are parallel to the shelf break and are characterised by current reversals at fairly regular intervals of one to three days. These reversals are directly related to the atmospheric low pressure systems that move along the coast in a north-easterly direction. As these are more pronounced during autumn and winter, there tends to be a more clearly defined north-going component (counter current) at this time of year (Pearce, 1977).

Figure 7. Ocean currents off southern Africa (after Pearce, 1977).

Mean surface temperatures in the Agulhas Current range between 23 - 28°C. The temperature of the inshore water is somewhat lower than that of the Agulhas Current and is associated with minor upwelling and the transportation of cooler water into the Natal region by the counter current (Pearce, 1977). Salinities of the inshore waters along the Natal coast, particularly in the immediate vicinity of estuary mouths are sometimes reduced by land runoff due to the many rivers which enter the sea in this region (Pearce, 1977). During the summer rainy season silt fans from most of the rivers extend kilometres out to sea and inshore currents distribute this turbid water along the coast. It is only north of St Lucia on the Zululand coast where there are no rivers that clear water conditions persist (Wallace, 1975a).

2.7. Study Sites

Three temporarily open/closed estuaries were chosen for study. These were the Mhlanga, the Damba and the Zotsha (Figure 8).

The Mhlanga estuary (29° 42'S; 31° 05'E) lies 17.5 kilometres north-east of Durban (Figure 8) and forms part of a nature reserve administered by the Natal Parks Board. The river is 28 kilometres long and has a catchment area of 118 km² (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. 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).

The Damba estuary (30° 40'S; 30° 30'E) is situated 118 kilometres south west of Durban (Figure 8). The river is 11 kilometres long and has a catchment area of 25 km² (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 which is artificially stabilised to accommodate a railway alignment. 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 which fringes the lagoon (Begg, 1978).

The Zotsha estuary (30° 47'S; 30° 25'E) is situated 134 kilometres south west of Durban (Figure 8). The river is 20 kilometres long and has a catchment area of 57 km² (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

Figure 8. Map of Natal indicating the systems sampled during this study, drawn at the same scale.

reaches of the system is vegetated by reeds (*Phragmites*) while the upper reaches supports a riverine forest community. The Ian Ellis nature reserve, which is administered by the Natal Parks Board, is situated on the north bank of the system, above the old road bridge.

CHAPTER 3.
MATERIALS AND METHODS

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

3.1. Abiotic characteristics

Selected physical and chemical parameters were recorded at fixed stations in each system at the beginning of each sampling survey (Figure 9). Water depth was measured using a weighted shotline graduated at 10 cm intervals. 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^{-1}) 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. The mean physical and chemical parameters measured on each sampling occasion were calculated for each system by summing and dividing.

Records of the daily mouth condition of each system was recorded on data sheets by local residents and the staff of the Natal Parks Board. Daily mouth condition data for each system was divided into four periods of three months: winter (June - August), spring (September - November), summer (December - February) and autumn (March - May) and the percent of the time for which the mouth was open during each period was calculated.

3.2. Ichthyofauna

3.2.1. Field methods

The ichthyofauna of the selected systems was sampled using a variety of sampling equipment. These included 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 30 m x 1.7 m x 15 mm bar mesh seine net 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

Figure 9. Abiotic sampling stations in Mhlanga, Damba and Zotsha estuaries.

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 (S.L.) 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 ground, thus minimising the possibility of any fish escaping from under the net. Beach seining is a common method for assessing abundance and species composition of littoral zone fish communities and has been used widely in freshwater, marine and estuarine studies. Seining combines several advantages over other assessment techniques in that the gear is simple and easy to deploy, a large area can be sampled and since sampling is active, should in principle, capture all species equally (Pierce *et al.*, 1990). However physical obstructions such as rocks, macrophytes, logs and tree branches may interfere with the seine and the process of snagging and unsnagging from obstructions can provide an escape route for enclosed fish, particularly benthic species (Pierce *et al.*, 1990).

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. As with the trawl collections, specimens collected by seine netting 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 (S.L.) in the field, using vernier slide callipers or a measuring board, and returned to the system.

Gill netting was carried out overnight with the nets being 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 30 mm x 60 mm x 30 mm canvas cooler bags with ice for transport to the laboratory.

3.2.2. Laboratory methods

In the laboratory, specimens collected in the gill nets were immediately identified by reference to Smith & Heemstra (1986). A minimum of 25 specimens of the abundant species were measured to the nearest mm (S.L.), using a measuring board, and weighed to the nearest 0.01g (wet mass) using a Mettler PJ 3000 balance. The remaining specimens were measured to the nearest mm (S.L.). 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 (S.L.) using vernier slide callipers or a measuring board and weighed to the nearest 0.01g (wet mass). The remaining specimens were then measured to the nearest mm standard length (S.L.).

3.2.3. Data analyses

The data collected for this study were entered into an Apple™ Macintosh™ Classic™ computer for analysis.

3.2.3.1. Length-mass relationships

In the study of fish populations, length - mass relationships serve two different but related functions. They are used (a) to describe mathematically the relationship between length and mass so that one may be derived from the other and (b) to compare the effect of biotic and abiotic factors on the health or well being of a population (Bolger & Connolly, 1989; Cone, 1989). The length of a fish is often more rapidly and easily measured than its mass and therefore it is convenient to be able to determine mass where length only is known.

Mass and length measurements made on specimens of a single species of fish have a relationship that is frequently very strong (Cone, 1989). It has been found that the length - mass relationship of most fish can adequately be described by the expression $m = al^b$, where m is the derived mass, l is the 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. A number of factors are known to affect changes in length - mass relationships. These include differences in growth stanzas, seasons, localities, degree of stomach fullness, gonad maturity stage, sex, gear type, the health and general condition of fish and preservation techniques (Tesch, 1971; Wysokiñski, 1985). These factors however have not been accounted for in the present study since the length - mass relationships of the species determined in this study were used merely to estimate the mass for fish that were measured but not weighed.

3.2.3.2. Species composition

The first task in characterising a biological community is the determination of what species live in that community. The relative proportions of different species in the community is a measure of relative abundance and linked with this is the concept of dominance. This refers to the fact that not all species in the community are equally important in determining the nature of the community (Krebs, 1985). Numerical abundance however, tends to over emphasise the importance of small individuals while composition by biomass tends to over emphasise the larger individuals (Odum, 1983).

In order to obtain a clearer picture of the nature of the fish community in each system the total species 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).

3.2.3.3. Sampling effectiveness

Studies of fish populations depend on equipment and methods which provide a representative sample of the community. Most techniques for sampling fishes are selective, among other things, with respect to species and size of individuals and can result in a catch that is not representative of the population as a whole (Lagler, 1971). Selectivity and gear efficiency are directly related. Selectivity is an expression of the difference in numbers or length frequency captured by a sampling gear from what is actually present in the water body, and efficiency is the percentage of organisms captured in the path of a gear (Hartman & Herke, 1987). Selectivity results from extrinsic factors (such as gear construction and its operation), from intrinsic factors (such as behavioural differences among or within species according to sex, size, habits, time and season) or from the interaction of both extrinsic and intrinsic factors

(Lagler, 1971). The diversity that characterises the fish communities, habitats and environmental conditions of most estuaries indicates that careful consideration must be given to gear choice and selectivity before estuarine fish populations can be accurately described.

In order to determine the effectiveness of each sampling method, 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 (1901, 1912, 1928) index of similarity (IS_J) (Mueller-Dombois & Ellenberg, 1974):

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

where c is the number of common species, 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_S) (Mueller-Dombois & Ellenberg, 1974):

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

where c is the number of common species, A is the total number of species in the first collection and B is the total number of species in the second. Sørensen's (IS_S) 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).

3.2.3.4. Seasonal species richness and diversity

The effects of physical and chemical factors such as temperature, oxygen, salinity, mouth condition and depth, and/or the interplay of biological factors such as spawning period and seasonal migrations, may lead to cyclical changes in the abundance and community structure of fish populations (Royce, 1972).

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):

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

where ni 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) where:

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

where wi 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<0.15).

3.2.3.5. Community structure

Typically, estuarine fish communities are composed of a mixture of euryhaline marine species, species restricted to estuaries and euryhaline freshwater species (Wallace, 1975a; Odum, 1983; Blaber, 1985). A stenohaline marine component usually occurs in the mouth area of most 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 information from Wallace (1975a), Wallace *et al.* (1984), Bruton *et al.* (1987), Bok (1988), Potter *et al.* (1990), Cyrus (1991) and in consultation with local experts, the species collected in each system were divided into four categories: freshwater species, estuarine species, estuarine-dependent marine species and marine species. 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, both numerically and in terms of biomass was calculated. Seasonal changes in the actual abundance and biomass of the various categories as well as the relative abundance and biomass was also determined, using a standard unit of effort.

3.2.3.6. Principal species

Monitoring the numerical changes which occur in a fish population through the course of time is essential to a basic understanding of the population dynamics and the rational management of this resource (Robson & Regier, 1971). Changes in abundance together with size frequency data can be related to aspects of a fish species' biology as well as to changes in environmental conditions (Wallace, 1975a).

The dominant species within each system were identified and temporal changes in abundance and biomass, using a standard unit of effort for each sampling occasion, calculated. Each species was also divided into 10 mm size classes and the percent frequency each size class made to the total catch on each sampling occasion, calculated.

3.2.3.7. 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 ten beam trawls, ten otter trawls, ten seine nets and ten 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 then 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 not only a function of the number of common 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 (Mueller-Dombois & Ellenberg, 1974):

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

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 contribution, both by number and by biomass, of freshwater species, estuarine species, estuarine-dependent marine species and marine species was calculated for each system using a standard total effort which incorporated all 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 was determined by standardising the sampling effort for each occasion to two beam trawls, two otter trawls, two seine nets and two gill nets.

CHAPTER 4.
THE MHLANGA ESTUARY

4.1. Results

4.1.1. Abiotic characteristics

4.1.1.1. 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 10).

4.1.1.2. Depth

The average water depth in the Mhlanga 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 10).

4.1.1.3. Temperature

Water temperature in the Mhlanga followed a seasonal pattern with both recorded 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 recorded in August 1991, to a maximum of 29.8 °C recorded 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 recorded in May 1991 where the average bottom temperature exceeded the average surface temperature (Figure 10).

4.1.1.4. Salinity

The average recorded 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 1.0 ‰ 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

Figure 10. Daily mouth condition (□ open; ■ closed) and abiotic parameters measured in the surface (⊙) and bottom (•) waters of the Mhlanga estuary, August 1990 - May 1992.

recorded in November 1990, February 1991, May 1991 and August 1991 (Figure 10).

4.1.1.5. Dissolved oxygen

The average dissolved oxygen in the surface waters of the Mhlanga ranged from 13.3 mg l^{-1} recorded in August 1991 to 4.2 mg l^{-1} 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^{-1} recorded in August 1991 to 3.7 mg l^{-1} recorded in May 1992 (Figure 10).

4.1.1.6. Turbidity

Average surface turbidity in the Mhlanga 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 10).

4.1.2. Species composition

A total of 7961 specimens representing 19 families and 47 kinds of fishes were captured in the Mhlanga system. *Gilchristella aestuaria* was the most abundant species captured 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 numerically comprised over 83% of the total assemblage captured in the Mhlanga during this study. The remaining 43 types of fishes each constituted less than 5% of the total catch and together accounted for less than 17% of the total ichthyofauna in the Mhlanga.

A total fish biomass of 288940.9 g 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. The remaining 43 types of fishes accounted for only 9% of the total biomass.

4.1.3. Sampling efficiency

4.1.3.1. Beam trawl

A total of 34 beam trawls conducted in the Mhlanga captured 176 specimens representing 13

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

Species	Beam Trawl x 34 (n)	(%)	Otter Trawl x 34 (n)	(%)	Seine Net x 37 (n)	(%)	Gill Nets x 38 (n)	(%)	Total (n)	(%)
Acanthopagrus berda					2	0.04			2	0.03
Ambassis productus			2	0.12					2	0.03
Ambassis sp.					14	0.28			14	0.18
Argyrosomus hololepidotus			3	0.18			12	1.05	15	0.19
Caranx ignobilis							3	0.26	3	0.04
Caranx sexfasciatus							5	0.44	5	0.06
Caranx sp.			3	0.18	1	0.02			4	0.05
Chelonodon laticeps	1	0.57							1	0.01
Crenimugil crenilabis					2	0.04			2	0.03
Eleotris sp.	3	1.70	2	0.12					5	0.06
Gerres rappi	14	7.95	6	0.37	2	0.04			22	0.28
Gerres sp.			3	0.18	48	0.96			51	0.64
Gilchristella aestuaria	35	19.89	1021	62.33	2585	51.66			3641	45.74
Glossogobius callidus	20	11.36	68	4.15	8	0.16			96	1.21
Glossogobius giuris					1	0.02			1	0.01
Goby sp.I					1	0.02			1	0.01
Herklotsichthys quadrimaculatus					20	0.40			20	0.25
Juvenile mugilids					375	7.49			375	4.71
Leiognathus equula	1	0.57	8	0.49					9	0.11
Lichia amia					3	0.06	12	1.05	15	0.19
Liza alata			1	0.06			125	10.94	126	1.58
Liza dumerilii					136	2.72	3	0.26	139	1.75
Liza macrolepis			1	0.06	11	0.22	9	0.79	21	0.26
Liza sp.					79	1.58			79	0.99
Liza tricuspidens					11	0.22			11	0.14
Micropterus salmoides			1	0.06	1	0.02	2	0.17	4	0.05
Monodactylus argentius							3	0.26	3	0.04
Monodactylus falciformis			3	0.18			10	0.87	13	0.16
Mugil cephalus	1	0.57			34	0.68	100	8.75	135	1.70
Myxus capensis			3	0.18	105	2.10	118	10.32	226	2.84
Oligolepis acutipennis			3	0.18	4	0.08			7	0.09
Oligolepis keiensis			20	1.22					20	0.25
Oreochromis mossambicus	85	48.30	435	26.56	627	12.53	273	23.88	1420	17.84
Pomadasys commersonnii	7	3.98	20	1.22	67	1.34	14	1.22	108	1.36
Psammogobius knysnaensis					1	0.02			1	0.01
Pseudorhombus arsius	1	0.57							1	0.01
Rhabdosargus holubi			23	1.40	46	0.92	1	0.09	70	0.88
Rhabdosargus thorpei			1	0.06					1	0.01
Scomberoides sp.					3	0.06			3	0.04
Sillago sihama					2	0.04			2	0.03
Solea bleekeri	1	0.57	2	0.12	1	0.02			4	0.05
Terapon jarbua	2	1.14	5	0.31	55	1.10	15	1.31	77	0.97
Tilapia rendalli			1	0.06					1	0.01
Valamugil buchanani					3	0.06	2	0.17	5	0.06
Valamugil cunnesius	5	2.84	3	0.18	265	5.30	436	38.15	709	8.91
Valamugil robustus					4	0.08			4	0.05
Valamugil sp.					487	9.73			487	6.12
Total number of specimens	176		1638		5004		1143		7961	
Total number of species	13		24		33		18		47	

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

Species	Beam Trawl x 34 (g)	(%)	Otter Trawl x 34 (g)	(%)	Seine Net x 37 (g)	(%)	Gill Nets x 38 (g)	(%)	Total (g)	(%)
Acanthopagrus berda					12.54	0.07			12.54	0.00
Ambassis productus			48.22	0.14					48.22	0.02
Ambassis sp.					0.44	0.00			0.44	0.00
Argyrosomus hololepidotus			599.18	1.68			4020.51	1.77	4619.69	1.60
Caranx ignobilis							354.80	0.16	354.80	0.12
Caranx sexfasciatus							578.70	0.25	578.70	0.20
Caranx sp.			29.23	0.08	3.79	0.02			33.02	0.01
Chelonodon laticeps	0.09	0.00							0.09	0.00
Crenimugil crenilabis					3.13	0.02			3.13	0.00
Eleotris sp.	0.00	0.00	0.00	0.00					0.00	0.00
Gerres rappi	253.60	3.32	48.44	0.14	48.95	0.27			350.99	0.12
Gerres sp.			0.53	0.00	2.68	0.01			3.21	0.00
Gilchristella aestuaria	75.69	0.99	956.44	2.69	1228.98	6.78			2261.11	0.78
Glossogobius callidus	135.63	1.78	294.22	0.83	18.30	0.10			448.15	0.16
Glossogobius giuris					0.68	0.00			0.68	0.00
Goby sp.I					0.08	0.00			0.08	0.00
Herklotsichthys quadrimaculatus					20.29	0.11			20.29	0.01
Juvenile mugilids					97.80	0.54			97.80	0.03
Leiognathus equula	1.08	0.01	13.13	0.04					14.21	0.00
Lichia amia					3.33	0.02	5434.10	2.39	5437.43	1.88
Liza alata			167.07	0.47			27608.20	12.13	27775.27	9.61
Liza dumerilii					1480.77	8.18	364.00	0.16	1844.77	0.64
Liza macrolepis			90.24	0.25	193.96	1.07	1149.80	0.51	1434.00	0.50
Liza sp.					107.44	0.59			107.44	0.04
Liza tricuspidens					26.65	0.15			26.65	0.01
Micropterus salmoides			79.73	0.22	0.06	0.00	435.50	0.19	515.29	0.18
Monodactylus argentius							135.13	0.06	135.13	0.05
Monodactylus falciformis			93.93	0.26			517.91	0.23	611.84	0.21
Mugil cephalus	63.29	0.83			1600.88	8.84	19918.25	8.75	21582.42	7.47
Myxus capensis			217.73	0.61	1744.56	9.63	20788.33	9.13	22750.62	7.87
Oligolepis acutipennis			5.31	0.01	6.38	0.04			11.69	0.00
Oligolepis keiensis			23.41	0.07					23.41	0.01
Oreochromis mossambicus	6659.38	87.30	31614.35	88.85	8386.58	46.30	87885.89	38.61	134546.20	46.57
Pomadasys commersonnii	307.39	4.03	646.99	1.82	24.49	0.14	2170.67	0.95	3149.54	1.09
Psammogobius knysnaensis					1.25	0.01			1.25	0.00
Pseudorhombus arsius	22.35	0.29							22.35	0.01
Rhabdosargus holubi			265.58	0.75	193.72	1.07	48.10	0.02	507.40	0.18
Rhabdosargus thorpei			0.81	0.00					0.81	0.00
Scomberoides sp.					6.16	0.03			6.16	0.00
Sillago sihama					0.12	0.00			0.12	0.00
Solea bleekeri	3.07	0.04	1.70	0.00	4.17	0.02			8.94	0.00
Terapon jarbua	4.53	0.06	134.53	0.38	76.94	0.42	1004.89	0.44	1220.89	0.42
Tilapia rendalli			200.00	0.56					200.00	0.07
Valamugil buchanani					46.66	0.26	548.00	0.24	594.66	0.21
Valamugil cunnesius	102.00	1.34	52.58	0.15	1902.11	10.50	54653.43	24.01	56710.12	19.63
Valamugil robustus					71.60	0.40			71.60	0.02
Valamugil sp.					797.79	4.40			797.79	0.28
Total biomass (g)	7628.10		35583.35		18113.28		227616.21		288940.94	
Total number of species	13		24		33		18		47	

species. Species which numerically dominated the beam trawl collections were *Oreochromis mossambicus* (48.3%), *Gilchristella aestuaria* (19.9%), *Glossogobius callidus* (11.4%) and *Gerres rappi* (8.0%) (Table 1). A total biomass of 7628.1 g was collected by beam trawling in the Mhlanga of which, *Oreochromis mossambicus* accounted for 87.3 % of the catch (Table 2).

According to Jaccard's index of similarity (IS$_J$) the beam trawl collections were 27.7% similar to the total catch. Sørensen's index of similarity (IS$_S$) revealed that the collections made by beam trawling were 43.3% similar to the total catch (Table 3).

4.1.3.2. Otter trawl

Thirty four otter trawls captured a total of 1638 specimens and 24 kinds of fishes. The otter trawl collections were dominated by *Gilchristella aestuaria* and *Oreochromis mossambicus* which accounted for 62.3% and 26.6% of the catch respectively (Table 1). Otter trawling yielded a total fish biomass of 35583.4 g. *O. mossambicus* dominated the total fish biomass captured by the otter trawl and comprised 88.9% of the catch (Table 2).

Jaccard's index of similarity (IS$_J$) revealed that the otter trawl collections were 54.1% similar to the total catch. The otter trawl collections were 67.6% similar to the total catch according to Sørensen's index of similarity (IS$_S$) (Table 3).

4.1.3.3. Seine net

Thirty seven seine net hauls collected 5004 specimens and 33 kinds of fishes. The seine net collections were dominated by *Gilchristella aestuaria* (51.7%), *Oreochromis mossambicus* (12.5%), *Valamugil* sp. (9.7%), juvenile mugilids (7.5%) and *Valamugil cunnesius* (5.3%) (Table 1). A total fish mass of 18113.3 g was collected by seine netting, these collections were dominated by *O. mossambicus* (46.3%), *V. cunnesius* (10.5%), *Myxus capensis* (9.6%), *Mugil cephalus* (8.8%), *Liza dumerilii* (8.2%) and *G. aestuaria* (6.8%) (Table 2).

Jaccard's index of similarity (IS$_J$) and Sørensen's index of similarity (IS$_S$) revealed that the collections made by seine netting were 70.2% and 82.5% similar to the total catch respectively (Table 3).

4.1.3.4. Gill nets

Gill netting yielded a total of 1143 specimens and 18 species. The 38 gill net collections were

dominated by *Valamugil cunnesius* (38.2%), *Oreochromis mossambicus* (23.9%), *Liza alata* (10.9%), *Myxus capensis* (10.3%) and *Mugil cephalus* (8.8%) (Table 1). Gill netting yielded a total fish biomass of 227616.2 g of which *O. mossambicus* (38.6%), *V. cunnesius* (24.0%), *L. alata* (12.1%), *M. capensis* (9.1%) and *M. cephalus* (8.8%) dominated (Table 2).

Jaccard's index of similarity (IS_J) revealed that the collections made by gill netting were 38.3% similar to the total catch. According to Sørensen's index of similarity (IS_S) the collections made by gill netting were 55.4% similar to the total catch (Table 3).

Table 3. Percent similarity of the catch composition of each gear type to the total catch in the Mhlanga estuary (IS_J = Jaccard's index of similarity, IS_S = Sørensen's index of similarity).

Gear	IS_J	IS_S	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

4.1.4. 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 in the Mhlanga increased in November 1990 and November 1991. Fish biomass in the Mhlanga increased slightly in November 1990 and February 1991 with a marked peak in February 1992 (Figure 11).

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 average surface and bottom temperature of the system and the percent 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 (Table 4).

Margalef's species richness index (D) reached a maximum in February 1991 with two less

Figure 11. Seasonal changes in the number of species, number of individuals, biomass, species richness, species evenness, and species diversity in the Mhlanga estuary, August 1990 - May 1992.

Table 4. Results of the Spearman rank correlation test between abiotic and biotic variables in the Mhlanga estuary (August 1990 - May 1992).

	Depth	Temperature		Salinity		Dissolved Oxygen		Turbidity		Mouth
		Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	% Open
Number of species	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
Number of fish	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
Biomass	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
Richness (D)	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
Evenness (J')	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
Diversity (H')	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
Diversity (H'w)	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

Shaded areas denote significant (p<0.15) correlation values.

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 11).

The Shannon-Wiener diversity index (H') and Margalef's species richness index (D) both showed a strong correlation with the percent 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).

4.1.5. Community structure

4.1.5.1. Overall abundance and biomass

Overall, the fish community captured in the Mhlanga system during this study was numerically dominated by fishes which spend their entire life cycle in the estuarine environment. This group of fishes comprised 47.4% of the total ichthyofaunal assemblage. Marine species dependent on estuaries during the juvenile stage of their life cycle, accounted for 33.9% of the total catch and freshwater species accounted for 17.9%. Marine species comprised less than 0.8% of the total fish community in the Mhlanga estuary (Figure 12).

In terms of biomass, marine species dependent on estuaries during the juvenile stage of their life cycle dominated the ichthyofaunal assemblage and comprised 50.3% of the catch. Freshwater species contributed 46.8% of the total fish biomass while estuarine species comprised less than 1%. Marine species comprised 2% of the total fish biomass in the Mhlanga (Figure 12).

4.1.5.2. Seasonal changes in relative abundance and biomass

During the study period, estuarine-dependent marine species numerically dominated the fish community captured in the Mhlanga in August 1990, February 1991, May 1991, August 1991 and February 1992. Estuarine species numerically dominated the ichthyofauna captured in November 1990, November 1991 and May 1992. The percent contribution of freshwater species to the ichthyofauna in the Mhlanga increased in November 1990, February 1991, November 1991 and February 1992. The numerical contribution of marine species although low, increased in February 1991 and February 1992 (Figure 13).

a) Abundance

b) Biomass

Figure 12. Percent numerical (a) and biomass (b) contribution of freshwater species, estuarine species, estuarine-dependent marine species and marine species to the total ichthyofauna of the Mhlanga estuary.

Figure 13. Seasonal numerical composition of freshwater species, estuarine species, estuarine-dependent marine species and marine species to the ichthyofauna of the Mhlanga estuary, August 1990 - May 1992.

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 increased in November 1991 and February 1992. Estuarine species did not constitute a major component of the fish biomass captured throughout the study period. The biomass contribution of marine species to the fish community in the Mhlanga increased in February 1991, May 1991 and August 1991 (Figure 14).

4.1.5.3. 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 increased in November 1990, February 1991 and February 1992 (Figure 15). Both the abundance and biomass estuarine species during this study increased in November 1990, November 1991 and May 1992 (Figure 15).

Marine species, dependent on estuaries during the juvenile stage of their life cycle, increased in abundance in May 1991 and in November 1991. The biomass of this group rose steadily throughout the study period with a peak in February 1992 (Figure 15). Maximum numbers of marine species were captured in February 1991 and February 1992. The biomass of this group of fishes peaked in May 1991 and February 1992 (Figure 15).

4.1.6. Principal species

4.1.6.1. *Oreochromis mossambicus*

Oreochromis mossambicus exhibited peaks in abundance in November 1990 and November 1991. Biomass peaked in November 1990, February 1991 and February 1992 (Figure 16). *Oreochromis mossambicus* captured in the Mhlanga during the study period ranged in size from below 10 mm to 320 mm (S.L.) (Figure 16). 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 small specimens below 30 mm. Specimens captured in February ranged in size from 10 mm to 270 mm but were mostly below 60 mm. In May 1991, the specimens collected were mostly in the 60 to 90 mm size classes. Large specimens, 200 to 230 mm were captured in August 1991. *O. mossambicus* captured in February 1992 and May 1992 were larger than 100 mm (Figure 16).

Biomass

Aug 1990
0.0%
45.1% 54.8%
0.1%

Aug 1991
2.1%
22.2%
0.5%
75.1%

Nov 1990
0.0%
29.6% 68.3%
2.1%

Nov 1991
0.9%
50.5% 45.2%
3.4%

Freshwater

Estuarine

Estuarine - marine

Marine

Feb 1991
3.3%
30.8% 65.4%
0.5%

Feb 1992
1.2%
57.3% 41.5%
0.0%

May 1991
7.4%
30.4%
62.1% 0.1%

May 1992
0.0%
25.8%
1.3%
72.9%

Figure 14. Seasonal biomass composition of freshwater species, estuarine species, estuarine-dependent marine species and marine species to the ichthyofauna of the Mhlanga estuary, August 1990 - May 1992.

Figure 15. 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, August 1990 -May 1992.

Oreochromis mossambicus

Size class (mm)

Figure 16. Seasonal abundance (O), biomass (•) and length frequency distribution of
Oreochromis mossambicus in the Mhlanga estuary, August 1990 - May 1992.

4.1.6.2. *Gilchristella aestuaria*

Peak numbers and biomass of *Gilchristella aestuaria* in the Mhlanga were recorded in November 1990, November 1991 and May 1992 (Figure 17). *Gilchristella aestuaria* was captured throughout the study period (Figure 17). Specimens captured in August 1990 were all in the 20 - 30 mm size class. *G. aestuaria* in November 1990 ranged in size from 10 mm to 60 mm but were mostly between 30 and 50 mm. A similar size range was collected in February 1991 but the bulk of the specimens were in the 40 - 50 mm size class. In May 1991 all the specimens were between 40 and 60 mm. Specimens collected in August 1991 ranged in size from 20 mm to 60 mm with specimens in the 30 - 40 mm and 50 - 60 mm size classes predominating. *G. aestuaria* captured in November 1991 were mostly between 20 and 50 mm. In February 1992 most of the specimens captured were in the 10 - 20 mm size class while in May the 20 - 30 mm size class predominated (Figure 17).

4.1.6.3. *Valamugil cunnesius*

Peak numbers of *Valamugil cunnesius* during this study were recorded in August 1990 and August 1991. The biomass of *V. cunnesius* increased throughout the study period with a peak occurring in February 1992 (Figure 18). *Valamugil cunnesius* captured in the Mhlanga during this study ranged in size from 30 to 230 mm (Figure 18). Specimens between 30 and 50 mm together with those between 150 and 180 mm predominated in August 1990. The *V. cunnesius* captured in November 1990, February 1991 and May 1991 were mostly between 150 mm and 200 mm. In August 1991, two size classes were captured; smaller specimens were mostly between 30 and 80 mm while the larger individuals were between 150 and 190 mm. Specimens captured in November 1991 were primarily between 160 mm and 200 mm but a few smaller specimens (80 to 100 mm) were also present. Small *V. cunnesius* in February 1992 were between 40 and 60 mm with larger specimens between 110 to 210 mm also present. Small individuals between 40 mm and 70 mm dominated the May 1992 sample (Figure 18).

4.1.6.4. *Valamugil* sp.

Both the abundance and biomass of *Valamugil* sp. showed distinct peaks in August 1990, May 1991 and February 1992 (Figure 19). *Valamugil* sp. (<60 mm S.L) in the Mhlanga were captured in August 1990, November 1990, February 1991, May 1991 and February 1992. No *Valamugil* sp. were captured in August 1991, November 1991 and May 1992 (Figure 19).

Gilchristella aestuaria

Figure 17. Seasonal abundance (O), biomass (•) and length frequency distribution of *Gilchristella aestuaria* in the Mhlanga estuary, August 1990 - May 1992.

Valamugil cunnesius

Figure 18. Seasonal abundance (O), biomass (•) and length frequency distribution of *Valamugil cunnesius* in the Mhlanga estuary, August 1990 - May 1992.

Valamugil sp.

Figure 19. Seasonal abundance (O), biomass (•) and length frequency distribution of *Valamugil* sp. in the Mhlanga estuary, August 1990 - May 1992.

4.1.6.5. Juvenile mugilids

The number of juvenile mugilids captured in the Mhlanga increased in November 1990, May 1991 and November 1991. The biomass of juvenile mugilids peaked in August 1990, May 1991 and November 1991 (Figure 20). Juvenile mugilids (<50 mm S.L.) were captured throughout the study period. Specimens captured in November 1990, February 1991, May 1991 and August 1991 were predominantly in the 10 - 20 mm size class. Juvenile mugilids captured in November 1991 and February 1992 were in the 20 - 30 mm size class and those captured in August 1990 and May 1992 were above 40 mm (Figure 20).

4.1.6.6. *Myxus capensis*

High numbers and biomass of *Myxus capensis* were captured in the Mhlanga in August 1990, August 1991, November 1991 and February 1992 (Figure 21). *Myxus capensis* specimens captured in the Mhlanga during the study period ranged from 20 to 300 mm (Figure 21). Juveniles, predominantly in the 50 - 60 mm size class, and larger specimens between 210 mm and 230 mm were captured in August 1990. In November *M. capensis* in the Mhlanga ranged from 30 mm to 210 mm with specimens below 80 mm being well represented. Specimens between 170 mm and 200 mm dominated the February 1991 collections. Larger specimens above 190 mm predominated in May 1991. *M. capensis* captured in August 1991 were mostly between 150 mm and 240 mm. Juveniles below 40 mm predominated in November 1991 and February 1992. Specimens captured in May 1992 were between 180 mm and 260 mm (Figure 21).

4.1.6.7. *Mugil cephalus*

High numbers of *Mugil cephalus* were captured in the Mhlanga in November 1990 with another slight peak in August 1991. A peak biomass of *M. cephalus* was recorded in the Mhlanga in February 1992 (Figure 22). *Mugil cephalus* specimens captured in the Mhlanga ranged from 30 mm to 320 mm (Figure 22). Specimens captured in August 1990 ranged in size from 140 mm to 250 mm. In November 1990, most of the *M. cephalus* captured were in the 120 to 160 mm, and 170 to 200 mm size ranges. Small specimens in the 30 - 40 mm size class were also captured in November 1990. *M. cephalus* captured in February 1991 were mostly between 150 mm and 200 mm. In May 1991, August 1991 and November 1991 most of the specimens collected were between 180 mm and 210 mm. Smaller specimens in the 110 - 120 mm size class were captured in May 1991 and specimens 130 -140 mm were also captured in November 1991. Three size groups were captured in February 1992. The smallest size group ranged from 90 to 110 mm while the other two size groups were 150 to 180 mm and

Juvenile mugilids

Figure 20. Seasonal abundance (O), biomass (•) and length frequency distribution of juvenile mugilids in the Mhlanga estuary, August 1990 - May 1992.

Figure 21. Seasonal abundance (O), biomass (•) and length frequency distribution of *Myxus capensis* in the Mhlanga estuary, August 1990 - May 1992.

Mugil cephalus

Figure 22. Seasonal abundance (O), biomass (•) and length frequency distribution of *Mugil cephalus* in the Mhlanga estuary, August 1990 - May 1992.

200 to 260 mm. All the specimens captured in May 1992 were between 170 mm and 270 mm (Figure 22).

4.1.6.8. *Liza alata*

The number of *Liza alata* captured in the Mhlanga peaked in November 1990, May 1991 and February 1992. The biomass of *L. alata* followed a similar trend with peaks occurring in November 1990, May 1991 and February 1992. Maximum numbers were recorded in May 1991 and a maximum biomass in February 1992 (Figure 23). *Liza alata* was captured throughout the study period and ranged in size from 150 mm to 330 mm (Figure 23). Two specimens between 150 and 170 mm were captured in August 1990. Specimens capt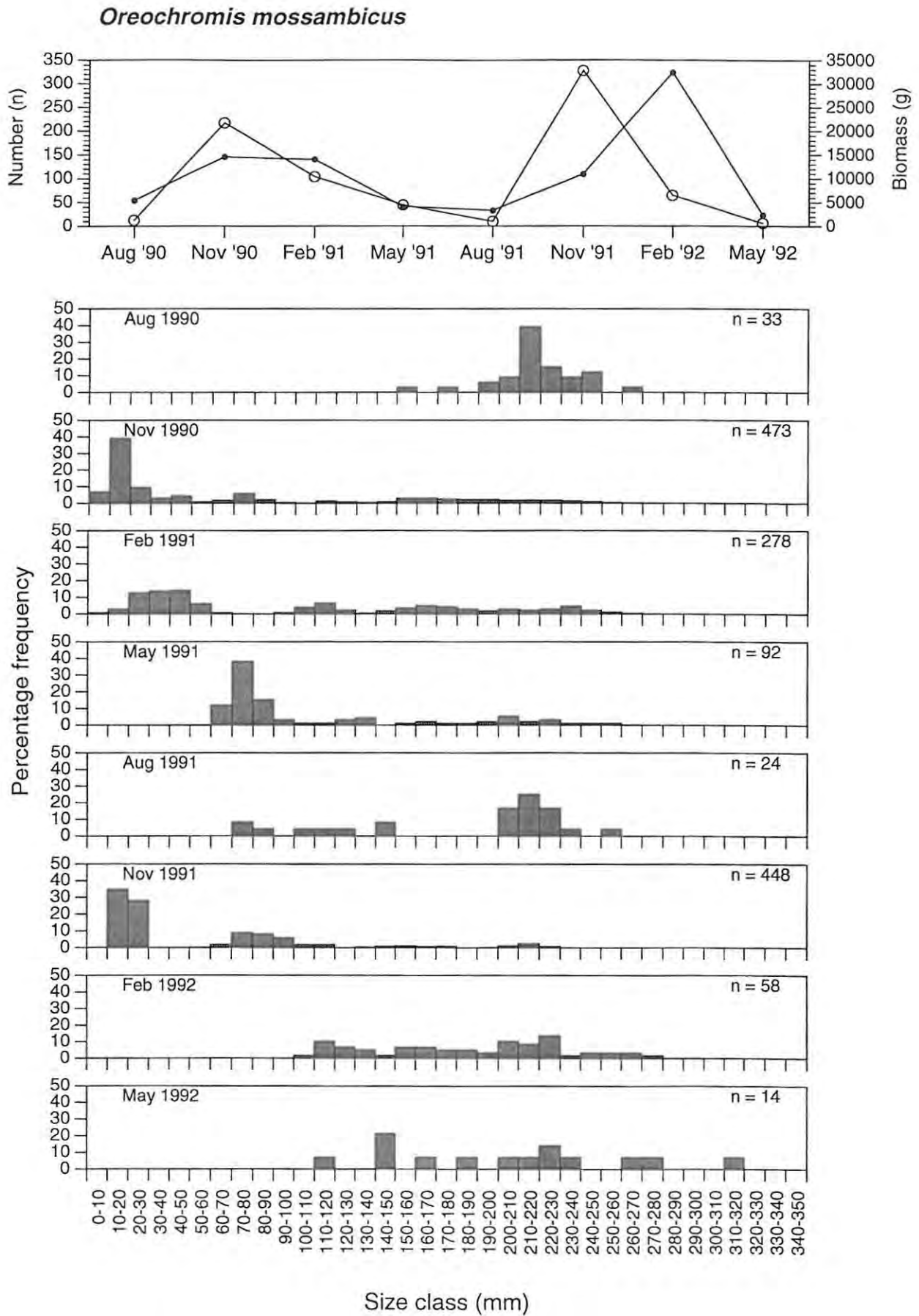ured in November 1990 were between 190 and 270 mm. *Liza alata* captured in February 1991 were between 160 and 270 mm. Specimens captured in May 1991 were mostly between 180 and 210 mm. In August 1991 *L. alata* ranged in size from 150 to 260 mm. In November 1991 specimens captured ranged in size from 190 to 300 mm. Specimens captured in February 1992 were between 190 and 280 mm in length. Larger specimens from 230 mm to 330 mm were captured in May 1992 (Figure 23).

4.2. Discussion

4.2.1. Abiotic 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 10). 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 to 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 of the Mhlanga 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
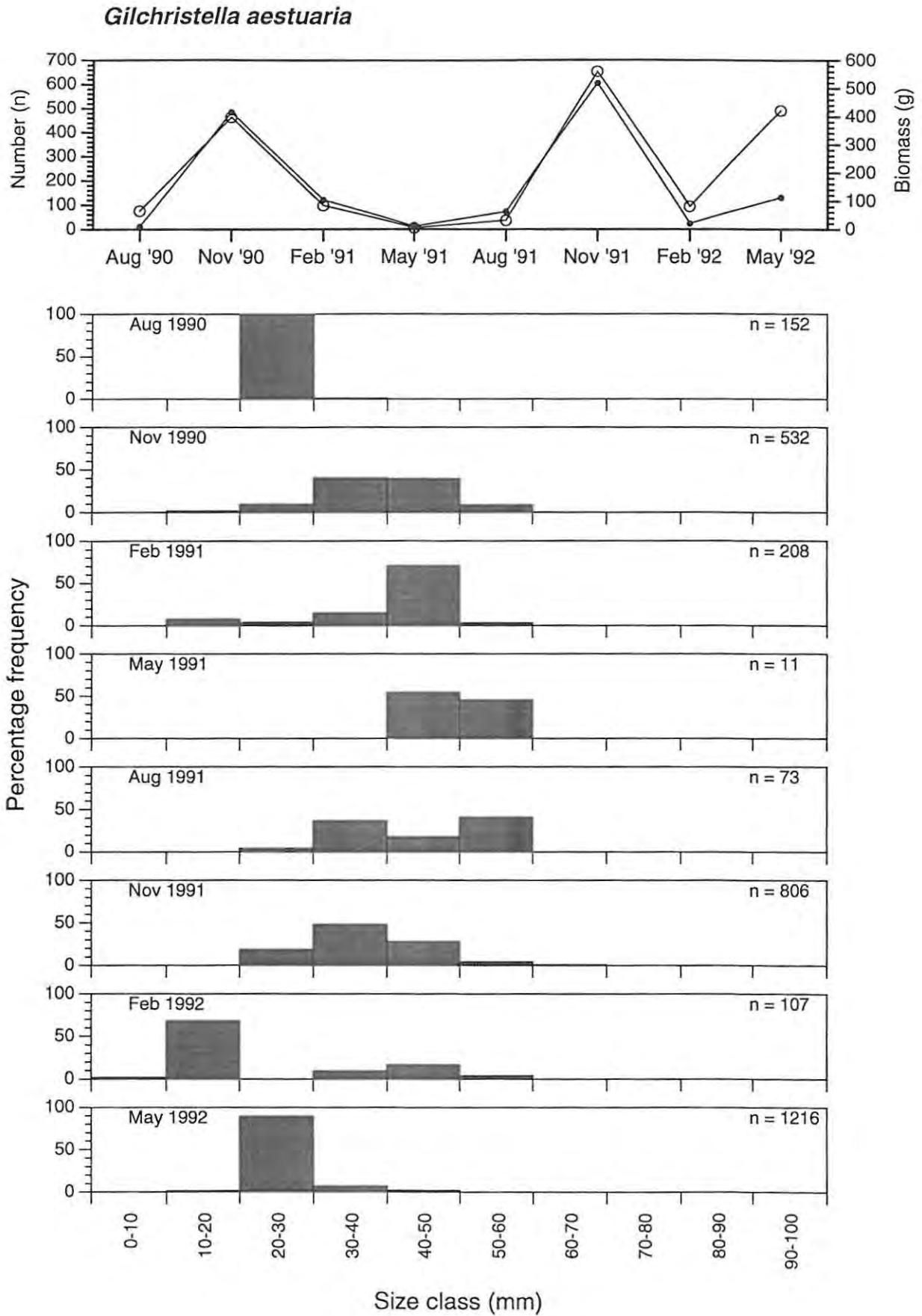
Liza alata

Figure 23. Seasonal abundance (O), biomass (•) and length frequency distribution of *Liza alata* in the Mhlanga estuary, August 1990 - May 1992.
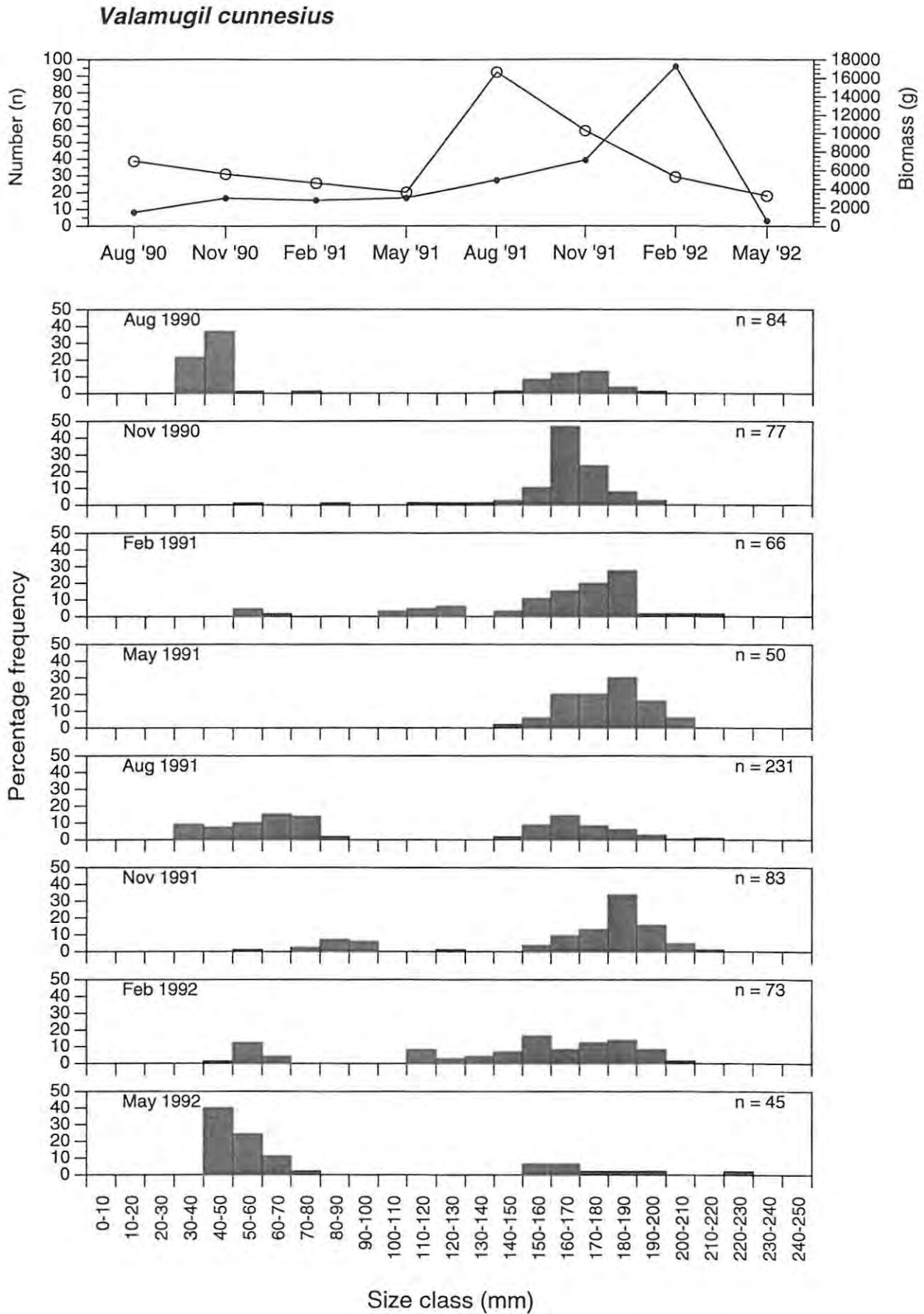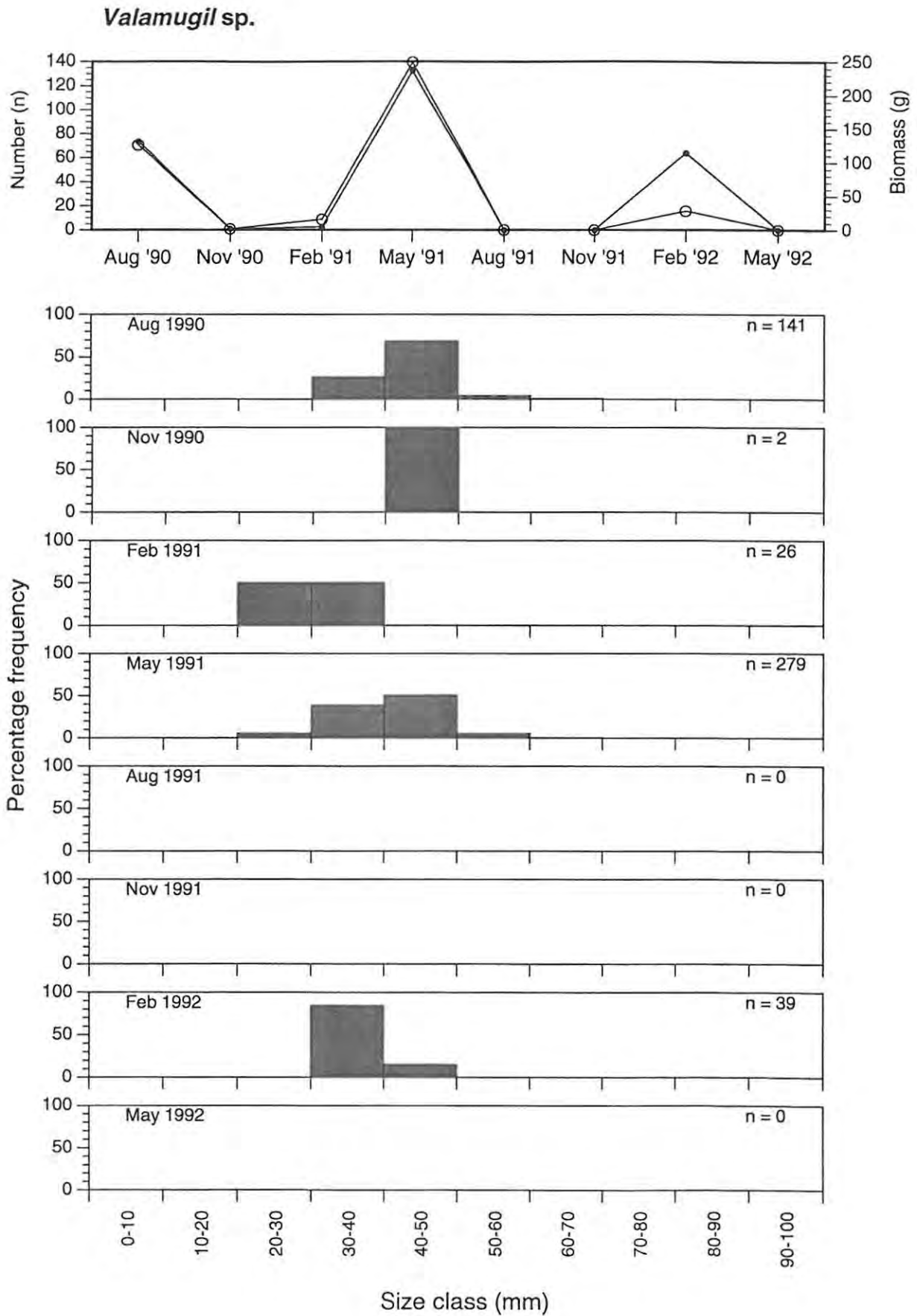
through the sand bar. When the mouth opens, however, the system drains due to the bed level being elevated above mean sea level (Cooper, 1989; Cooper & Harrison, 1992). Whitfield (1980a; 1980b; 1980c) noted that the water level in the Mhlanga dropped approximately one metre when the estuary opened but 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 10).

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 10). 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 10).

During this study surface salinities in the Mhlanga did not exceed 5‰ while bottom salinities ranged from 1‰ to 11‰ (Figure 10). Whitfield (1980a; 1980b; 1980c) found that salinities in the Mhlanga ranged between 0‰ and 34‰ but were generally less than 10‰. Begg (1984b) also noted that extremely 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 10).

The average surface oxygen concentration in the Mhlanga ranged from 4.2 mg l^{-1} to 13.3 mg l^{-1} and the average bottom oxygen ranged from 3.7 to 8.9 mg l^{-1} (Figure 10). Begg (1984b) noted that in general, bottom water in the Mhlanga tended to carry about 0.8 mg l^{-1} less oxygen than at the surface and that the average surface oxygen ranged from 4.2 mg l^{-1} to 6.4 mg l^{-1} while bottom dissolved oxygens ranged from 2.9 mg l^{-1} to 5.5 mg l^{-1}. 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 10).

Except during November 1991, turbidity in the Mhlanga estuary was low (<1.0 NTU) (Figure 10). 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 10). 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 10).

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 Mhlanga estuary mouth opens the water level in the system drops rapidly and the strong outflow of turbid water decreases after a few days thus allowing tidal penetration of seawater up the estuary (Figure 10).

4.2.2. Sampling efficiency

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 the vulnerability of both pelagic and demersal species to capture is reduced. 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 fishes, 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 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 fishes 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 kinds of fishes 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 specimens 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.

4.2.3. Species composition

Of the 48 kinds of fishes captured in the Mhlanga estuary, *Gilchristella aestuaria* , *Oreochromis mossambicus*, *Valamugil cunnesius* ,*Valamugil* sp. and juvenile mugilids were the most abundant (Table 1). This compares with previous collections made in the Mhlanga where, 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 the dominant species. Fifteen kinds of fishes 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 sorts of fishes 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* (5.56%) 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) revealed that *O. mossambicus* (26.4%), *V. cunnesius* (20.8%), *L. alata* (14.2%), *M. capensis* (12.5%) and *M. cephalus* (12.0%) also dominated the fish biomass in the Mhlanga.

4.2.4. Community structure

4.2.4.1. Freshwater species

Freshwater species in the Mhlanga estuary contributed 17.9% (46.8% by mass) to the ichthyofauna captured during this study (Figure 12). Data from Whitfield (1980c) revealed that this group of fishes numerically comprised 34.5% and 26.4% of the total fish biomass in the Mhlanga. Freshwater species contributed 21.6% to the total fish community captured in the Mhlanga 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 *O. mossambicus* which comprised 17.8% numerically and 46.6% of the total fish biomass in the Mhlanga (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).

Oreochromis mossambicus is a freshwater cichlid indigenous to south-east 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 open, tidal estuaries. Begg (1984a) also noted that *O.mossambicus* dominated the ichthyofauna in typically closed estuaries in Natal.

Oreochromis 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 & Boltt, 1975). The female broods the eggs and young in her mouth and when the fry have reached 9-10 mm (S.L.) they are released in shallow (< 0.1 m deep), calm, well vegetated areas (Bruton & Boltt, 1975). One female may produce three to four broods in a single season (Bruton & Boltt, 1975).

The peak numbers of predominantly juvenile (<30 mm S.L.) *O. mossambicus* in November (Figure 16) correspond to the breeding cycle of this species. The high biomass recorded in February is a result of predominantly larger specimens being captured. During the cool winter months *O. mossambicus* usually inhabits deeper waters (Bruton & Boltt, 1975). This may be responsible for the low number and biomass of *O. mossambicus* recorded in May and August (Figure 16).

4.2.2.2. Estuarine species

Estuarine species are a small group of fishes which spend their entire life cycle within the estuarine environment (Wallace *et al.*, 1984; Blaber, 1985). This group of fishes numerically accounted for 47.4% of the ichthyofauna collected in the Mhlanga during this study (Figure 12). Data from Whitfield (1980c) revealed that estuarine species comprised 15.3% of the fishes captured in the Mhlanga during his study. Estuarine species numerically comprised 22.7% of the fishes collected in the Mhlanga by Begg (1984b) and 47.1% of the catch made by Harrison (1990). Species which complete their entire life cycle within estuaries are small in size (Wallace *et al.*, 1984) and as a consequence did not contribute significantly to the total fish biomass (Figure 12). This group of fishes comprised less than 1% of the fish biomass in the Mhlanga both during this study and that of 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 ichthyofaunal community (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 in the Mhlanga by Begg (1984b) and 46.4% of the catch made by Harrison (1990). *G. aestuaria* was not captured in the Mhlanga by Ramm *et al.* (1986).

Gilchristella aestuaria is a small clupeid, endemic to south east Africa and occurs 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, *Gilchristella 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 17) 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 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 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 17).

4.2.4.3. Estuarine-dependent marine species

Estuarine-dependent marine species are inshore shallow-water species which spawn at sea but mainly utilise estuaries as nursery areas during the juvenile phase of their life cycle (Wallace, 1975a; Wallace *et al.*, 1984). This group of fishes comprised 33.9% (50.3% by mass) of the total ichthyofaunal assemblage captured in the Mhlanga during this study (Figure 12). Estuarine-dependent marine species comprised 49.1% by number and 72.2% by mass of the total ichthyofauna captured in the Mhlanga by Whitfield (1980c). This group of fishes numerically comprised 54%, 92% and 44.3% of the fishes collected by Begg (1984b), Ramm *et al.* (1986) and Harrison (1990) respectively.

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 made 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 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 total ichthyofaunal catch made in the Mhlanga 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).

Valamugil 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). The high abundance of *Valamugil* sp. and *V. cunnesius* in May and August together with the occurrence of juveniles (<70 mm S.L.) from February to August (Figures 18 and 19) 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 may be a result of emigration of mature specimens from the system to spawn at sea (Figure 18).

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. The peak in juvenile mugilids in November (Figure 11) corresponds to the general spawning and recruitment pattern of estuarine-dependent marine fish. The peak in juvenile mugilids in May 1991 (Figure 20) 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 most of its life

in freshwater, ascending the rivers as far as it can go 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 *Myxus capensis* comprised 4.12% numerically and 12.5% by mass of the total ichthyofauna in the Mhlanga. *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 from April to May (Wallace & van der Elst, 1975; Blaber, 1987). Bok (1979) and Bruton *et al.* (1987) found that in the eastern Cape, *M. capensis* spawns throughout the year with a peak in spring (March - November). The high numbers and biomass of *M. capensis* recorded in August and the subsequent reduction in November (Figure 21) may be a result of adults emigrating from the system to spawn at sea.

The high abundance together with the occurrence of juvenile (<60 mm S.L.) *M. capensis* in November and February (Figure 21) 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* migrates to the fresh water 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 freshwater areas. The decrease in numbers and biomass of *M. capensis* in May is probably due to this species leaving the estuary to the preferred freshwater upper reaches of the system (Figure 21).

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 *Mugil 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 ichthyofauna captured in the Mhlanga by Begg (1984b), Ramm *et al.* (1986) and Harrison (1990) respectively.

Mugil 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 22) may be a reflection of the successful recruitment of this species into the system.

Liza alata is one of the largest mugilids and occurs 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 during his study *L. alata* numerically accounted for 0.9% of the fishes in the Mhlanga and 14.2% of the total biomass. *Liza alata* numerically accounted for 1.8% of the fishes captured in the Mhlanga 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 S.L. 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 23). *L. alata* biomass values followed a similar pattern. Peak numbers of *L. alata* were captured in October in St Lucia by Whitfield & Blaber (1978a). The spawning period of *L. alata* is unknown but recruitment starts at 14 mm (S.L.) from July to January (Blaber, 1987). No juveniles were captured during this study.

4.2.4.4. Marine species

Eleven marine species were captured in the Mhlanga estuary during this study and contributed 0.8% numerically and 2.0% by mass to the total ichthyofauna (Figure 12). Marine species comprised 1.0% numerically and 0.6% by mass of the fishes captured in the Mhlanga by Whitfield (1980c) and 1.6 % of the fishes captured by Begg (1984b). Marine species numerically comprised 3.6% and 0.9% of the fishes captured in the Mhlanga by Ramm *et al.* (1986) and Harrison (1990) respectively.

The majority of the marine species captured in the Mhlanga estuary are species whose juveniles are found mainly at sea but are also abundant in estuaries. Although estuaries are not essential for the survival of these species, these areas make a contribution to the breeding stocks when the juveniles that grow up in estuaries migrate to sea to join the adult populations (Wallace *et al.*, 1984). The peak numbers and biomass of this group of fishes in February 1991, May 1991 and February 1992 (Figure 15) corresponds to the periods when the mouth of the Mhlanga frequently opened (Figure 10) and is most likely a result of this group of fishes opportunistically entering the system.

4.2.5. Seasonal community structure

4.2.5.1. Winter (June, July, August)

During the dry winter months (June - August) the mouth of the Mhlanga estuary is closed and the system is deep (Figure 10). 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 13) is probably a reflection of the distribution of these species in the system, where *O. mossambicus* occurs in the upper reaches of the system 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 14) is a reflection of larger specimens of *O. mossambicus* being captured (Figure 16). The relatively high numerical contribution of estuarine species is a reflection of the spawning potential of *G. aestuaria* throughout the year (Figure 17).

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 11) may be a reflection of the deep nature of the system, resulting in the fishes becoming diluted and less susceptible to capture. Furthermore, due to the closed nature of the system, 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 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 11).

4.2.5.2. Spring (September, October, November)

During the spring rainfall months the Mhlanga estuary opens periodically (Figure 10). 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 13 and 14) 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 in the Mhlanga estuary (Figures 16 and 17) and this may have contributed to the increase in the relative proportions of these fishes in the Mhlanga during November (Figure 13).

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 11). 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*).

4.2.5.3. Summer (December, January, 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 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 13 and 14) and may be a reflection of the steady recruitment of juveniles into the system when it opened during spring and summer (Figure 10).

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 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 11).

4.2.5.4. Autumn (March, April, May)

The extended opening of the mouth of the Mhlanga into the autumn of 1991 (Figure 1) 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 13 and 14). In autumn 1992 the mouth of the

Mhlanga was closed (Figure 10) and estuarine dependent 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 (Figure 17, Whitfield, 1980b). The deep nature of the system in May 1992 (Figure 10) 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 nett result was a lower species diversity in the Mhlanga during autumn.

4.3. Summary

A simplified diagrammatic representation of the community structure and utilisation of the Mhlanga estuary is presented in Figure 24. 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 system 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.

Figure 24. Diagramatic representation of the seasonal fish community structure in the Mhlanga estuary.

CHAPTER 5.
THE DAMBA ESTUARY

5.1. Results

5.1.1. Abiotic characteristics

5.1.1.1. Mouth condition

Records of the daily mouth condition of the Damba between July 1990 and May 1992 showed that the system opened most frequently during the 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 25).

5.1.1.2. Depth

The average depth of the Damba 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 of the Damba appeared to be slightly greater during the autumn/winter (March - August) (Figure 25).

5.1.1.3. Temperature

Average water temperatures recorded in the Damba 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 in the Damba 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 in the Damba were slightly higher than those of the bottom waters (Figure 25).

5.1.1.4. 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 19.3 ‰ recorded in May 1992. Bottom salinities ranged from 1 ‰ recorded in August 1990 and April 1991 to 20 ‰ recorded in May 1992 (Figure 25).

Figure 25. Daily mouth condition (□ open; ■ closed) and abiotic parameters measured in the surface (O) and bottom (•) waters of the Damba estuary, August 1990 - May 1992.

5.1.1.5. Dissolved oxygen

The average dissolved oxygen levels in the surface waters of the Damba system ranged from 8.3 mg l^{-1} in August 1991 to 3.6 mg l^{-1} in May 1992. With the exception of December 1991, the average dissolved oxygen in the bottom waters did not exceed those levels in the surface waters. Dissolved oxygen in the bottom waters of the Damba ranged from 8.0 mg l^{-1} in November 1990 to 1.3 mg l^{-1} in February 1991 (Figure 25).

5.1.1.6. Turbidity

Average surface turbidities in the Damba 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 25).

5.1.2. Species composition

A total of 2918 specimens representing 10 families and 24 kinds of fishes 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 types of fishes 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 30201.2 g 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.

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

Species	Beam Trawl x 18 (n)	(%)	Otter Trawl x 18 (n)	(%)	Seine Net x 21 (n)	(%)	Gill Nets x 24 (n)	(%)	Total (n)	(%)
Ambassis productus			6	1.01	38	1.86	1	0.78	45	1.54
Awaous aeneofuscus			1	0.17	4	0.20			5	0.17
Crenimugil crenilabis					3	0.15			3	0.10
Elops machnata							1	0.78	1	0.03
Gerres sp.					26	1.27			26	0.89
Gilchristella aestuaria			16	2.68	16	0.78			32	1.10
Glossogobius callidus	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
Liza alata					1	0.05	1	0.78	2	0.07
Liza dumerilii					2	0.10	6	4.69	8	0.27
Liza macrolepis							1	0.78	1	0.03
Liza richardsonii			1	0.17					1	0.03
Monodactylus argentius							1	0.78	1	0.03
Monodactylus falciformis			1	0.17	5	0.24	1	0.78	7	0.24
Mugil cephalus			2	0.34	22	1.08	67	52.34	91	3.12
Myxus capensis					935	45.79	2	1.56	937	32.11
Oreochromis mossambicus	44	29.14	38	6.37	646	31.64	37	28.91	765	26.22
Rhabdosargus holubi			2	0.34	24	1.18	3	2.34	29	0.99
Solea bleekeri	1	0.66	5	0.84					6	0.21
Tilapia rendalli					1	0.05			1	0.03
Valamugil cunnesius					2	0.10	5	3.91	7	0.24
Valamugil robustus							2	1.56	2	0.07
Valamugil sp.			2	0.34	31	1.52			33	1.13
Total number of specimens	151		597		2042		128		2918	
Total number of species	3		12		17		13		24	

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

Species	Beam Trawl x 18 (g)	(%)	Otter Trawl x 18 (g)	(%)	Seine Net x 21 (g)	(%)	Gill Nets x 24 (g)	(%)	Total (g)	(%)
Ambassis productus			93.53	3.73	426.94	3.51	41.10	0.28	561.57	1.86
Awaous aeneofuscus			12.15	0.48	41.66	0.34			53.81	0.18
Crenimugil crenilabis					5.39	0.04			5.39	0.02
Elops machnata							170.00	1.15	170.00	0.56
Gerres sp.					10.16	0.08			10.16	0.03
Gilchristella aestuaria			13.25	0.53	8.47	0.07			21.72	0.07
Glossogobius callidus	369.52	47.55	1283.07	51.15	774.14	6.36			2426.73	8.04
Goby sp. II			1.68	0.07					1.68	0.01
Juvenile mugilids					1.16	0.01			1.16	0.00
Liza alata					19.09	0.16	339.20	2.30	358.29	1.19
Liza dumerilii					156.62	1.29	641.30	4.35	797.92	2.64
Liza macrolepis							69.00	0.47	69.00	0.23
Liza richardsonii			38.65	1.54					38.65	0.13
Monodactylus argentius							18.63	0.13	18.63	0.06
Monodactylus falciformis			21.01	0.84	116.18	0.95	27.20	0.18	164.39	0.54
Mugil cephalus			206.16	8.22	165.58	1.36	8577.74	58.17	8949.48	29.63
Myxus capensis					9145.88	75.15	295.50	2.00	9441.38	31.26
Oreochromis mossambicus	405.29	52.16	781.31	31.14	954.61	7.84	3805.00	25.81	5946.21	19.69
Rhabdosargus holubi			39.09	1.56	211.81	1.74	144.70	0.98	395.60	1.31
Solea bleekeri	2.27	0.29	14.36	0.57					16.63	0.06
Tilapia rendalli					1.71	0.01			1.71	0.01
Valamugil cunnesius					51.88	0.43	428.00	2.90	479.88	1.59
Valamugil robustus							187.40	1.27	187.40	0.62
Valamugil sp.			4.39	0.17	79.37	0.65			83.76	0.28
Total biomass	777.08		2508.65		12170.65		14744.77		30201.15	
Total number of species	3		12		17		13		24	

5.1.3. Sampling efficiency

5.1.3.1. Beam trawl

A total of 18 beam trawls conducted in the Damba system during this study yielded 151 specimens representing three species. *Glossogobius callidus* (70.2%) and *Oreochromis mossambicus* (29.1%) numerically dominated the beam trawl collections in the Damba (Table 5). A total fish biomass of 777.1 g was collected by beam trawling in the Damba and was also dominated by *O. mossambicus* and *G. callidus* which comprised 52.2% and 47.6% of the total biomass respectively (Table 6).

The fishes collected by beam trawling in the Damba were, according to Jaccard's index of similarity, 12.5 % similar to the total fish assemblage captured during this study. Sørensen's index of similarity revealed that the beam trawl collections were 22.2% similar to the total catch (Table 7).

5.1.3.2. Otter trawl

Eighteen otter trawls, conducted in the Damba, yielded a total of 597 specimens and 12 kinds of fishes. *Glossogobius callidus* and *Oreochromis mossambicus* dominated the otter trawl collections and accounted for 86.6% and 6.4% of the catch respectively (Table 5). A total fish biomass of 2508.7 g was captured by otter trawling and this was dominated by *Glossogobius callidus* (51.2%), *Oreochromis mossambicus* (31.1%) and *Mugil cephalus* (8.2%) (Table 6).

Jaccard's index of similarity revealed that the otter trawl collections were 50.0% similar to the total fish assemblage while Sørensen's index of similarity showed a 66.7% similarity to the total catch (Table 7).

5.1.3.3. Seine net

Twenty one seine net hauls were conducted in the Damba during the study period and yielded 2042 specimens representing 17 kinds of fishes. *Myxus capensis* dominated the seine net collections and accounted for 45.8% of the total catch. The next most abundant species captured by seine netting in the Damba were *O. mossambicus* (31.6%) and *G. callidus* (13.8%) (Table 5). The total biomass of fishes captured by seine netting in the Damba was 12170.7 g and was dominated by *M. capensis* (75.2%), *O. mossambicus* (7.8%) and *G. callidus* (6.4%) (Table 6).

Jaccard's index of similarity and Sørensen's index of similarity revealed that fish collections made by seine netting in the Damba were 70.8% and 82.9% similar to the total fish assemblage respectively (Table 7).

5.1.3.4. Gill nets

Twenty four gill net collections yielded 128 specimens and 13 species in the Damba. The most abundant species collected by gill netting were *Mugil cephalus* (52.3%) and *O. mossambicus* (28.9%) (Table 5). A total fish biomass of 14744.8 g was captured in the Damba by gill netting and this was also dominated by *M. cephalus* (58.2%) and *O. mossambicus* (25.8%) (Table 6).

The fishes captured by gill netting were, according to Jaccard's index of similarity, 54.2% similar to the total fish community recorded in the Damba during this study. Sørensen's index of similarity showed that the gill net collections were 70.3% similar to the total catch (Table 7).

Table 7. Percent similarity of the catch composition of each gear type to the total catch in the Damba estuary (IS_J = Jaccard's index of similarity, IS_S = Sørensen's index of similarity).

Gear	IS_J	IS_S	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

5.1.4. 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 in the Damba peaked in August 1990, February 1991 and February 1992 (Figure 26).

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

Figure 26. Seasonal changes in the number of species, number of individuals, biomass, species richness, species evenness, and species diversity in the Damba estuary, August 1990 - May 1992.

abiotic variables measured during the study period. Fish biomass, however, was positively correlated with surface and bottom temperature and turbidity (Table 8).

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 and decreased steadily, reaching a low in August 1991. The Shannon-Wiener diversity index (H') showed a similar pattern with a high value in August 1990 and a low value in August 1991. The Shannon-Wiener diversity index for biomass (H'w) exhibited peaks in November 1990, August 1991 and February 1992 (Figure 26).

Margalef's species richness index (D) was not correlated with any of the abiotic variables measured in the Damba 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).

5.1.5. Community structure

5.1.5.1. Overall abundance and biomass

Marine species which depend on estuaries during the juvenile phase of their life cycle numerically accounted for 41.2% of the total ichthyofauna captured in the Damba estuary during this study. Species which spend their entire life cycle in the estuarine environment accounted for 32.1% and freshwater species 26.4% of the total catch. Marine species, not dependent on estuaries comprised 0.1% of the total fish fauna in the Damba (Figure 27).

Estuarine-dependent marine species also dominated the total fish biomass captured in the Damba estuary during this study and contributed 71.9% to the total. Freshwater species comprised 19.9% of the total fish biomass while estuarine species contributed 8.1% . Marine species comprised 0.2% of the total fish biomass in the Damba (Figure 27).

5.1.5.2. Seasonal changes in relative abundance and biomass

Numerically, estuarine-dependent marine species dominated the ichthyofauna of the Damba estuary in August 1990, April 1991, December 1991 and May 1992. Species which spend their entire life cycle in the estuarine environment dominated the fish community in November

Table 8. Results of the Spearman rank correlation test between abiotic and biotic variables in the Damba estuary (August 1990 - May 1992).

	Depth	Temperature		Salinity		Dissolved Oxygen		Turbidity		Mouth
		Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	% Open
Number of species	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
Number of fish	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
Biomass	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
Richness (D)	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
Evenness (J')	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
Diversity (H')	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
Diversity (H'w)	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

Shaded areas denote significant (p<0.15) correlation values.

a) Abundance

b) Biomass

Figure 27. Percent numerical (a) and biomass (b) contribution of freshwater species, estuarine species, estuarine-dependent marine species and marine species to the total ichthyofauna of the Damba estuary.

1990, February 1991 and August 1991. The numerical contribution of freshwater species to the ichthyofauna of the Damba was high in April 1991 and February 1992 (Figure 28).

In terms of biomass, estuarine-dependent marine species dominated the ichthyofauna of the Damba throughout the study period. The relative contribution of freshwater species to the total fish biomass in the Damba increased in November 1990, April 1991 and December 1991. The contribution of estuarine species to the fish biomass in the Damba was relatively high in November 1990, February 1991 and August 1991 (Figure 29).

5.1.5.3. Seasonal changes in actual abundance and biomass

The numbers of freshwater species captured in the Damba during this study peaked in February 1991 and February 1992. The biomass of freshwater species exhibited a peak in April 1991 and December 1991 (Figure 30). Both the numbers and biomass of estuarine species captured in the Damba increased in February 1991 and August 1991 (Figure 30).

High numbers of estuarine-dependent marine species were captured in the Damba in August 1990, February 1991, April 1991, December 1991 and February 1992 (Figure 30). A peak biomass of this group of fishes was recorded in August 1990, February 1991 and February 1992. Marine species were only captured in the Damba in August 1990 and May 1992 (Figure 30).

5.1.6. Principal species

5.1.6.1. *Oreochromis mossambicus*

Oreochromis mossambicus exhibited peaks in abundance in the Damba in February 1991 and February 1992. A peak biomass of *O. mossambicus* was recorded in April 1991 and December 1991 (Figure 31). The *O. mossambicus* captured in the Damba during this study were all below 220 mm (S.L.). Two size classes were captured in August 1990. The smaller size class was 30 to 40 mm while the larger specimens ranged between 100 mm and 130 mm. The *O. mossambicus* captured in November 1990 were mostly juveniles below 20 mm. In February 1991, larger specimens in the 30 to 50 mm size classes predominated. *O. mossambicus* captured in April 1991 were mostly between 30 mm and 60 mm. In August 1991 specimens in the 30 to 50 mm size classes predominated with some larger (>100 mm S.L.) individuals also being captured. The 30 to 50 mm size classes were well represented December 1991, but larger specimens in the 70 - 80 mm, 110 - 120 mm and 150 - 160 mm size classes were also captured. Specimens below 30 mm were predominant in February

Figure 28. Seasonal numerical composition of freshwater species, estuarine species, estuarine-dependent marine species and marine species to the ichthyofauna of the Damba estuary, August 1990 - May 1992.

Figure 29. Seasonal biomass composition of freshwater species, estuarine species, estuarine-dependent marine species and marine species to the ichthyofauna of the Damba estuary, August 1990 - May 1992.

Figure 30. Seasonal fluctuations in the number (O) and biomass (•) of freshwater species (a), estuarine species (b), estuarine-dependent marine species (c) and marine species (d) in the Damba estuary, August 1990 -May 1992.

Oreochromis mossambicus

Figure 31. Seasonal abundance (O), biomass (•) and length frequency distribution of *Oreochromis mossambicus* in the Damba estuary, August 1990 - May 1992.

1992. Three size classes (30 - 40 mm, 60 - 80 mm and 160 -180 mm) were present in May 1992 (Figure 31).

5.1.6.2. *Glossogobius callidus*

Both numbers and biomass of *Glossogobius callidus* in the Damba peaked in February 1991 and August 1991 (Figure 32). All *G. callidus* captured in the Damba during this study were below 90 mm (S.L.) (Figure 32). In August 1990 two size classes were captured, specimens in the one size class were mostly 20 - 30 mm while the remaining specimens were 40 - 50 mm and above. *G. callidus* captured in November 1990 were large specimens, mostly in the 40 to 60 mm size range. Two size classes, 20 to 40 mm and 50 to 70 mm, were captured in February 1991. Specimens in the 30 to 50 mm and 60 to 80 mm size classes predominated in April 1991. In August 1991 the *G. callidus* captured was mostly between 30 mm and 60 mm (S.L.). Specimens captured in December 1991 ranged from 30 to 70 mm and were mostly between 50 mm and 70 mm. In February 1992, two size classes were captured, the smaller specimens were mostly in the 20 - 30 mm size class while the larger specimens were predominantly in the 50 - 60 mm size class. *G. callidus* captured in May 1992 ranged from 30 to 70 mm with specimens in the 40 - 50 mm size class predominating (Figure 32).

5.1.6.3. *Myxus capensis*

Both the number and biomass of *Myxus capensis* reached a peak in February 1991 and February 1992 (Figure 33). *M. capensis* captured in the Damba ranged in size from 20 to 250 mm (S.L.) (Figure 33). Individuals captured in August 1990 were mostly in the 40 to 60 mm size range. In November 1990 smaller specimens in the 30 - 40 mm size class predominated with some larger specimens 60 to 80 mm also being captured. Two larger size classes, 70 to 90 mm and 100 to 120 mm, predominated in February 1991. In April 1991, smaller specimens, mostly 40 to 60 mm were captured together with larger individuals between 70 mm and 90 mm. *M. capensis* captured in August 1991 were between 50 mm and 110 mm. Small specimens in the 30 - 40 mm size class predominated in December 1991 and February 1992. In May, *M. capensis* were mostly between 30 mm and 60 mm (Figure 33).

5.1.6.4. *Mugil cephalus*

Peak numbers of *Mugil cephalus* were recorded in the Damba in August 1990 and December 1991 with a slight increase in abundance occurring in February 1991 and April 1991. The biomass of *M. cephalus* was high in August 1990 with a slight increase occurring in February 1991, April 1991 and February 1992 (Figure 34). All specimens captured in the Damba

Glossogobius callidus

Figure 32. Seasonal abundance (⊙), biomass (•) and length frequency distribution of *Glossogobius callidus* in the Damba estuary, August 1990 - May 1992.

Figure 33. Seasonal abundance (O), biomass (•) and length frequency distribution of *Myxus capensis* in the Damba estuary, August 1990 - May 1992.

Mugil cephalus

Figure 34. Seasonal abundance (O), biomass (•) and length frequency distribution of *Mugil cephalus* in the Damba estuary, August 1990 - May 1992.

during this study were below 200 mm (S.L.) (Figure 34). *M. cephalus* captured in August 1990 and November 1990 were mostly large specimens between 160 mm and 200 mm. Smaller specimens 80 to 100 mm were captured in February 1991 together with larger (> 140 mm) individuals. In April 1991 and August 1991 large specimens between 150 mm and 190 mm. Juveniles below 40 mm predominated in December 1991. In February 1992 and May 1992 the *M. cephalus* captured were all relatively large (>120 mm) specimens (Figure 34).

5.2   Discussion

5.2.1. Abiotic characteristics

The mouth of the Damba opened most frequently during the spring/summer months (September - February) (Figure 25) corresponding with the predominantly summer rainfall period. Begg (1984b) noted that the sandbar at the mouth of the Damba becomes built up to extraordinarily high levels and as a result the mouth of the system is seldom open. The high sandbar at the mouth of the Damba results in impoundment of the river water (Begg, 1984b) and this probably accounts for the deeper water in winter (August) and during February 1991 (Figure 25). Begg (1984b) found that when the mouth of the Damba 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 25).

Water temperatures recorded in the Damba 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 25).   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 the 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 25).

The average surface salinities in the Damba ranged from 0.0 ‰ to 19.3 ‰ while bottom salinities ranged from 1.0 ‰ to 20.0 ‰ (Figure 25). Begg (1984b) found that, during his study, the average surface salinity in the Damba ranged from 0.0 ‰ to 7.6‰ and the average bottom salinity ranged from 0.0 ‰ to 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 25).

The average dissolved oxygen recorded in the surface waters of the Damba system ranged from 8.3 mg l^{-1} to 3.6 mg l^{-1} and the average dissolved oxygen recorded in the bottom ranged from 8.0 mg l^{-1} to 1.3 mg l^{-1} (Figure 25). During his study, Begg (1984b) found that the average dissolved oxygen in the Damba ranged from 4.8 mg l^{-1} to 8.7 mg l^{-1} 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 25).

Average turbidities recorded in the Damba during the study period were always <6.0 NTU (Figure 25). Begg (1984b) noted that due to the clarity of the water in the Damba, the bottom of the system was generally visible. Apart from values recorded in August 1990, turbidity in the Damba also increased during the spring/summer rainfall period.

In summary, the Damba 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 of the 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 25).

5.2.2. Sampling efficiency

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.

5.2.3. Species composition

In this study of the Damba system, 24 kinds of fishes 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. 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.

5.2.4. Community structure

5.2.4.1. Freshwater species

Freshwater species contributed 26.4% (19.9% by mass) of the ichthyofauna captured during this study (Figure 27). *Oreochromis mossambicus* was the principal freshwater species captured 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 & Boltt, 1975) and this probably accounts for the relatively low numbers and biomass captured in August (Figure 31). From September to February adult *O. mossambicus* congregate in the shallow areas to breed (Bruton & Boltt, 1975). This may account for the occurrence of larger specimens and an increase in the biomass of *O. mossambicus* in November and December (Figure 31). The increase in abundance and the occurrence of juveniles (< 30 mm S.L.) in spring and summer in the Damba (Figure 31) corresponds to the September - February breeding season of this species (Bruton & Boltt, 1975). The high numbers and biomass of *O. mossambicus* captured in April 1991 may be due to the shallow nature of the system at the time of sampling, which rendered them more susceptible to capture.

5.2.4.2. Estuarine species

Species which spend their entire life-cycle within the estuarine environment numerically accounted for 32.1% of the ichthyofauna collected in the Damba estuary during this study and 8.1% of the biomass (Figure 27). *Glossogobius callidus* was the dominant estuarine dependent species captured and comprised 31% numerically and 8% by mass of the total fishes captured (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).

Little is known about the biology of *Glossogobius 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; Bruton *et al.*, 1982; van der Elst, 1988). The high numbers and biomass of *G. callidus* together with the occurrence of smaller size classes in February (Figure 32) suggests a predominantly spring/summer breeding period. Whitfield (1980b) found that, in the Mhlanga, *Glossogobius* bred during the stable closed phase and he captured juvenile (<2 cm S.L.) specimens in July. Small (< 30 mm S.L.) *G. callidus* specimens were also captured in the Damba during August 1990 (Figure 32).

This prolonged breeding season 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 (Whitfield, 1980b). To ensure that eggs and larvae are not lost to the marine environment either by normal tidal activity or when a closed estuary opens, *Glossogobius* lays adhesive eggs on plants and submerged objects (Crass, 1964; Bruton & Kok, 1980; Day *et al.*, 1981; Bruton *et al.*, 1982; van der Elst, 1988).

5.2.4.3. Estuarine-dependent marine species

Marine species which utilise estuaries as nursery areas during the juvenile phase of their life cycle comprised 41.2% (71.9% by mass) of the total ichthyofauna captured in the Damba estuary during this study (Figure 27). Estuarine-dependent marine species numerically comprised only 0.4% of the total ichthyofauna captured in the Damba by Begg (1984b) and 34.3% by Ramm *et al.* (1985a). Estuarine marine species captured during this study were dominated by mugilids namely *Myxus capensis* and *Mugil cephalus* .

Myxus capensis comprised 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* breeds throughout the year with a peak in spring (March - November) (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 33), most likely as a result of larger specimens emigrating from the system when the mouth opened (Figure 35). High numbers of predominantly juvenile (< 50 mm S.L.) *M. capensis* were captured in the Damba in spring and summer (Figure 33). 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 in the Damba during this study (Tables 5 and 6). *M. cephalus* numerically comprised 0.8% of the ichthyofauna captured in the Damba by Ramm *et al.* (1985a). This species spawns in the inshore marine environment between May and September (Wallace, 1975b; Blaber, 1987) with

recruitment of juveniles (<40 mm T.L.) 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 S.L.) captured in December 1991 (Figure 34). The reduction in the number and biomass of *M. cephalus* in spring may be due to large individuals emigrating from the system once the mouth had opened (Figure 34).

5.2.4.4. Marine species

Marine species contributed 0.14% numerically and 0.15% by mass to the ichthyofauna captured in the Damba during this study (Figure 27.). Marine species numerically comprised 0.41% of the fishes captured by Begg (1984b). Fishes belonging to this group of fishes were not captured by Ramm *et al.* (1985a).

Marine species only occurred in the Damba in August 1990 and May 1992 (Figure 30.) and because this group of fishes is not dependent upon estuaries, their occurrence is probably a result of these fishes straying into the system when it occasionally breached.

5.2.5. Seasonal community structure

5.2.5.1. Winter (June, July, August)

During the winter, the mouth of the Damba closes (Figure 25) and the system is dominated by estuarine-dependent marine species (*Myxus capensis* and *Mugil cephalus*) and estuarine species (*Glossogobius callidus*) (Figures 28 and 29). 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 28).

Due to its facultative catadromous life history, *M. capensis* shows a distinct preference for the freshwater upper reaches of estuaries (Bok, 1979; Whitfield, 1980a; Blaber, 1977). However, the elevated bed level in the upper reaches of the Damba estuary results in this area being extremely shallow (Begg, 1984b). *M. capensis* would therefore be restricted to the lower reaches of the estuary thus contributing to the relatively high proportion of estuarine-dependent marine species during winter (Figures 28 and 29).

The relatively low contribution of freshwater species to the total winter ichthyofauna in the Damba estuary (Figure 28) is probably a reflection of the fact that *O. mossambicus* usually inhabits deep pools in rivers during the cool winter months (Bruton & Boltt, 1975; Caulton, 1979) and was not as susceptible to capture.

A high number of species were captured in August 1990 and may be a reflection of a greater initial sampling effort employed at the beginning of the study. Due to the relatively small size of the Damba, the sampling effort was reduced on subsequent occasions. This, together with a relatively low numbers of individuals captured, resulted in a relatively high richness, evenness and diversity in August 1990 (Figure 26).

5.2.5.2. Spring (September, October, November)

During spring the mouth of the Damba opened for short periods and, due to the gradient of the bed level, the upper reaches drain completely and the system becomes shallow (Figure 25). The relative increase in the contribution of freshwater species in spring in the Damba (Figures 28 and 29) is most likely a result of *O. mossambicus* breeding within the system (Figure 31). The increase may also be due to the shallowness of the upper reaches resulting in the redistribution 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 28 and 29). The exposure of the bed of the upper reaches of the Damba reduces the available habitat and food resources within the system (Whitfield, 1980c), resulting in a subsequent 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 the Damba in December 1991 (Figures 28 and 29) 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 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 in November 1990 (Figures 28 and 29) 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 juvenile estuarine-dependent marine species into the estuary (Figures 33 and 34). Good recruitment in December 1991 (Figures 33 and 34) resulted in the high contribution of estuarine-dependent marine species during this period (Figures 28 and 29).

Species emigration from the system, together with a possible increase in mortality may have accounted for the decrease in the fish biomass and numbers in spring (Figure 26). The lower number of species and moderate number of individuals resulted in a moderate evenness, richness and diversity in spring (Figure 26).

5.2.5.3. Summer (December, January, 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 as a result of adverse environmental conditions (Wallace, 1975b). The mouth of the Damba opened periodically throughout the summer (Figure 25) and the high relative contribution of estuarine-dependent marine species (Figures 28 and 29) is probably a result of the steady recruitment of 0+ juvenile *M. capensis* into the system (Figure 33).

Successful spawning by *O. mossambicus* contributed to the increased numerical contribution of freshwater species in the Damba during summer (Figures 28 and 29). The high contribution of estuarine fishes in February 1991 (Figures 28 and 29) is probably a result of *G. callidus* breeding during this period (Figure 32). Although juvenile *G. callidus* were also captured in February 1992 (Figure 32) their minimal contribution to the total (Figures 28 and 29) is probably a reflection of the shallow nature of the system resulting in increased competition, bird predation and poor recruitment.

Both recruitment and concentration probably accounted for the increase in numbers of individuals and fish biomass in the Damba estuary during summer. The moderate number of species and high numbers of individuals resulted in a moderate richness, evenness and diversity indices in summer (Figure 26).

5.2.5.4. Autumn (March, April, May)

The opening of the Damba estuary mouth in autumn 1991 (Figure 25), together with the prolonged spawning and recruitment period of *M. capensis* (Figure 33; Bok, 1979), probably contributed to the increased proportion of estuarine-dependent marine species in April 1991 (Figures 28 and 29). The shallow nature of the system in April 1991 (Figure 25) 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 estuarine species (*G. callidus*) in April 1991 (Figures 28 and 29).

The deeper water, increased food and habitat availability, and successful breeding of *G. callidus* may have contributed to the increase in the proportion of estuarine species in May 1992 (Figures 28 and 29). The relatively low contribution of freshwater species to the ichthyofauna in the Damba in May 1992 (Figures 28 and 29) is most likely a reflection of *O. mossambicus* moving to deeper waters during the cooler months (Bruton & Boltt, 1975; Caulton, 1979). This results in estuarine-dependent marine species predominating the shallow areas and probably accounts for the high proportion of this group of fishes in May 1992 (Figures 28 and 29).

The number of individuals captured in autumn decreased due to a possible combination of increased competition and predation during periods of low water levels and dilution of individuals during periods of high water. The increase in the number of species and the decrease in the number of individuals resulted in a moderate evenness index which, together with a marginal increase in species richness, resulted in a moderate species diversity index in the Damba estuary during autumn (Figure 26).

5.3. 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 to the lower reaches. Freshwater species (*O. mossambicus*) inhabit the deeper pools in winter and estuarine-dependent marine species dominate the system.

When the mouth of the Damba opens in the spring, large individuals of estuarine-dependent marine species migrate out of the system while 0+ juveniles begin migrating into the system. *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 of the Damba in the spring and summer, the upper reaches of the system drains 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 (*G. callidus*) species continues in the summer as well as 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 as well as possible susceptibility to bird predation. 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 system (Figure 35).

Figure 35. Diagramatic representation of the seasonal fish community structure in the Damba estuary.

CHAPTER 6.
THE ZOTSHA ESTUARY

6.1. Results

6.1.1. Abiotic characteristics

6.1.1.1. Mouth condition

Records of daily mouth condition of the Zotsha estuary 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 36).

6.1.1.2. Depth

The average depth of the Zotsha estuary ranged from 147 cm recorded in August 1991 to 57 cm recorded in November 1991. The average depth of the Zotsha was greater than 100 cm for much of the study period. The system was shallow (< 90 cm) on two occasions, May 1991 and November 1991 (Figure 36).

6.1.1.3. 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. Average bottom temperatures ranged from 19.3 °C in August 1991 to 25.4 °C in November 1991. The average bottom temperature exceeded the average surface temperature in the Zotsha 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 36).

6.1.1.4. Salinity

The average surface salinity recorded in the Zotsha estuary ranged from 0.8 ‰ in February 1991 to 22.7 ‰ in February 1992. Average bottom 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 36).

Figure 36. Daily mouth condition (□ open; ■ closed) and abiotic parameters measured in the surface (O) and bottom (•) waters of the Zotsha estuary, August 1990 - May 1992.

6.1.1.5. Dissolved oxygen

Average dissolved oxygen recorded in the surface waters of the Zotsha ranged from 8.3 mg l⁻¹ in February 1991 to 4.2 mg l⁻¹ 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⁻¹ recorded in November 1990 to 3.7 mg l⁻¹ recorded in May 1991 (Figure 36).

6.1.1.6. Turbidity

Average surface turbidity in the Zotsha was generally higher that 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 36).

6.1.2. Species composition

A total of 5101 specimens representing 22 families and 56 kinds of fishes 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 32.2% of the catch.

A total fish biomass of 186241.0 g 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.

6.1.3. Sampling efficiency

6.1.3.1. Beam trawl

A total of 35 beam trawls, conducted in the Zotsha estuary, captured 78 specimens representing

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

Species	Beam Trawl x 35 (n)	(%)	Otter Trawl x 35 (n)	(%)	Seine Net x 37 (n)	(%)	Gill Nets x 40 (n)	(%)	Total (n)	(%)
Acanthopagrus berda							2	0.37	2	0.04
Ambassis natalensis					11	0.26			11	0.22
Ambassis productus	33	42.31	4	1.71	286	6.73	1	0.19	324	6.35
Argyrosomus hololepidotus	1	1.28					5	0.93	6	0.12
Arothron immaculatus					1	0.02			1	0.02
Awaous aeneofuscus							1	0.19	1	0.02
Caranx papuensis							9	1.67	9	0.18
Caranx sexfasciatus							2	0.37	2	0.04
Caranx sp.	1	1.28			31	0.73			32	0.63
Crenimugil crenilabis					225	5.29			225	4.41
Croilia mossambica			3	1.28	10	0.24			13	0.25
Eleotris fusca					1	0.02			1	0.02
Eleotris mauritianus					1	0.02			1	0.02
Eleotris sp.	1	1.28			1	0.02			2	0.04
Favonigobius rechei					1	0.02			1	0.02
Gerres acinaces					1	0.02			1	0.02
Gerres rappi	3	3.85	2	0.85	40	0.94	34	6.32	79	1.55
Gerres sp.					75	1.76			75	1.47
Gilchristella aestuaria			73	31.20	486	11.43			559	10.96
Glossogobius biocellatus					1	0.02			1	0.02
Glossogobius callidus	2	2.56	40	17.09	271	6.37			313	6.14
Glossogobius giuris			2	0.85	1	0.02			3	0.06
Goby sp. III					1	0.02			1	0.02
Juvenile mugilids					823	19.36			823	16.13
Khulia mugil					7	0.16			7	0.14
Leiognathus equula			4	1.71			7	1.30	11	0.22
Lichia amia					2	0.05	3	0.56	5	0.10
Liza alata					2	0.05	60	11.15	62	1.22
Liza dumerilii					40	0.94	7	1.30	47	0.92
Liza macrolepis					14	0.33	12	2.23	26	0.51
Liza sp.					129	3.03			129	2.53
Liza tricuspidens					25	0.59	2	0.37	27	0.53
Lutjanus argentimaculatus					1	0.02	6	1.12	7	0.14
Lutjanus fulviflamma					3	0.07			3	0.06
Megalops cyprinoides							1	0.19	1	0.02
Monodactylus argenteus							2	0.37	2	0.04
Monodactylus falciformis			1	0.43	5	0.12	1	0.19	7	0.14
Monodactylus sp.			1	0.43					1	0.02
Mugil cephalus					46	1.08	27	5.02	73	1.43
Myxus capensis					156	3.67	38	7.06	194	3.80
Oligolepis keiensis			4	1.71	4	0.09			8	0.16
Oreochromis mossambicus	5	6.41	13	5.56	431	10.14	95	17.66	544	10.66
Pomadasys commersonnii	2	2.56	19	8.12	9	0.21	4	0.74	34	0.67
Pomadasys sp.			1	0.43	3	0.07			4	0.08
Pomatomus saltatrix							1	0.19	1	0.02
Pseudorhombus arsius	1	1.28							1	0.02
Rhabdosargus holubi	2	2.56	27	11.54	496	11.67			525	10.29
Rhabdosargus thorpei			1	0.43	6	0.14			7	0.14
Scomberoides sp.					1	0.02			1	0.02
Solea bleekeri	27	34.62	37	15.81	7	0.16			71	1.39
Terapon jarbua			2	0.85	370	8.70	1	0.19	373	7.31
Tilapia rendallii					2	0.05			2	0.04
Valamugil buchanani							37	6.88	37	0.73
Valamugil cunnesius					55	1.29	86	15.99	141	2.76
Valamugil robustus					32	0.75	94	17.47	126	2.47
Valamugil sp.					138	3.25			138	2.71
Total biomass	**78**		**234**		**4251**		**538**		**5101**	
Total number of species	**11**		**17**		**44**		**26**		**56**	

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

Species	Beam Trawl x 35		Otter Trawl x 35		Seine Net x 37		Gill Nets x 40		Total	
	(g)	(%)	(g)	(%)	(g)	(%)	(g)	(%)	(n)	(%)
Acanthopagrus berda							639.50	0.38	639.50	0.34
Ambassis natalensis					67.02	0.49			67.02	0.04
Ambassis productus	208.29	18.74	36.64	0.86	1231.69	9.05	42.30	0.03	1518.92	0.82
Argyrosomus hololepidotus	166.60	14.99					1439.10	0.86	1605.70	0.86
Arothron immaculatus					10.12	0.07			10.12	0.01
Awaous aeneofuscus							125.10	0.07	125.10	0.07
Caranx papuensis							1765.30	1.06	1765.30	0.95
Caranx sexfasciatus							268.50	0.16	268.50	0.14
Caranx sp.	4.25	0.38			82.12	0.60			86.37	0.05
Crenimugil crenilabis					656.67	4.82			656.67	0.35
Croilia mossambica			1.17	0.03	1.77	0.01			2.94	0.00
Eleotris fusca					2.19	0.02			2.19	0.00
Eleotris mauritianus					1.42	0.01			1.42	0.00
Eleotris sp.	0.00	0.00			0.00	0.00			0.00	0.00
Favonigobius rechei					0.25	0.00			0.25	0.00
Gerres acinaces					3.58	0.03			3.58	0.00
Gerres rappi	197.54	17.77	140.22	3.28	61.64	0.45	4529.80	2.71	4929.20	2.65
Gerres sp.					50.87	0.37			50.87	0.03
Gilchristella aestuaria			70.86	1.66	311.17	2.29			382.03	0.21
Glossogobius biocellatus					3.10	0.02			3.10	0.00
Glossogobius callidus	1.98	0.18	26.62	0.62	232.86	1.71			261.46	0.14
Glossogobius giuris			158.41	3.71	54.85	0.40			213.26	0.11
Goby sp. III					0.85	0.01			0.85	0.00
Juvenile mugilids					526.07	3.87			526.07	0.28
Khulia mugil					2.48	0.02			2.48	0.00
Leiognathus equula			116.67	2.73			454.90	0.27	571.57	0.31
Lichia amia					14.09	0.10	2802.20	1.68	2816.29	1.51
Liza alata					24.51	0.18	36630.30	21.90	36654.81	19.68
Liza dumerilii					561.92	4.13	1250.10	0.75	1812.02	0.97
Liza macrolepis					109.78	0.81	3393.60	2.03	3503.38	1.88
Liza sp.					193.79	1.42			193.79	0.10
Liza tricuspidens					108.18	0.79	893.50	0.53	1001.68	0.54
Lutjanus argentimaculatus					0.34	0.00	3514.55	2.10	3514.89	1.89
Lutjanus fulviflamma					6.21	0.05			6.21	0.00
Megalops cyprinoides							882.60	0.53	882.60	0.47
Monodactylus argenteus							115.40	0.07	115.40	0.06
Monodactylus falciformis			0.24	0.01	2.44	0.02	71.80	0.04	74.48	0.04
Monodactylus sp.			43.78	1.02					43.78	0.02
Mugil cephalus					474.37	3.49	10649.30	6.37	11123.67	5.97
Myxus capensis					996.57	7.32	14914.50	8.92	15911.07	8.54
Oligolepis keiensis			1.70	0.04	1.25	0.01			2.95	0.00
Oreochromis mossambicus	385.36	34.67	2129.31	49.81	2767.37	20.33	35190.25	21.04	40472.29	21.73
Pomadasys commersonnii	35.62	3.20	1020.63	23.88	88.80	0.65	941.80	0.56	2086.85	1.12
Pomadasys sp.			0.03	0.00	0.17	0.00			0.20	0.00
Pomatomus saltatrix							768.60	0.46	768.60	0.41
Pseudorhombus arsius	20.13	1.81							20.13	0.01
Rhabdosargus holubi	18.34	1.65	456.91	10.69	2200.16	16.17			2675.41	1.44
Rhabdosargus thorpei			0.73	0.02	35.13	0.26			35.86	0.02
Scomberoides sp.					0.56	0.00			0.56	0.00
Solea bleekeri	73.55	6.62	24.78	0.58	3.54	0.03			101.87	0.05
Terapon jarbua			46.01	1.08	915.77	6.73	57.40	0.03	1019.18	0.55
Tilapia rendallii					4.88	0.04			4.88	0.00
Valamugil buchanani							16205.10	9.69	16205.10	8.70
Valamugil cunnesius					312.94	2.30	10746.41	6.43	11059.35	5.94
Valamugil robustus					1347.58	9.90	18952.82	11.33	20300.40	10.90
Valamugil sp.					138.83	1.02			138.83	0.07
Total biomass	1111.66		4274.71		13609.90		167244.73		186241.00	
Total number of species	11		17		44		26		56	

11 species. *Ambassis productus* (42.3%), *Solea bleekeri* (34.6%) and *Oreochromis mossambicus* (6.4%) numerically dominated the beam trawl collections (Table 9). A total fish biomass of 1111.7 g was collected by beam trawling in the Zotsha and was dominated by *Oreochromis mossambicus* (34.7%), *Ambassis productus* (18.7%), *Gerres rappi* (17.8%), *Argyrosomus hololepidotus* (15.0%) and *Solea bleekeri* (6.6%) (Table 10).

According to Jaccard's index of similarity (IS_J) the beam trawl collections were 19.6% similar to the total catch. Sørensen's index of similarity (IS_S) revealed that the collections made by beam trawling were 32.8% similar to the total fish assemblage captured in the Zotsha (Table 11).

6.1.3.2. Otter trawl

Thirty five otter trawls captured a total of 234 specimens and 17 kinds of fishes. The otter trawl collections were numerically dominated by *Gilchristella aestuaria* (31.2%), *Glossogobius callidus* (17.1%), *Solea bleekeri* (15.8%), *Rhabdosargus holubi* (11.5%), *Pomadasys commersonnii* (8.1%) and *Oreochromis mossambicus* (5.6%) (Table 9). Otter trawling yielded a total fish biomass of 4274.7 g. *O. mossambicus* (49.8%), *P. commersonnii* (23.9%) and *R. holubi* (10.7%) dominated the total fish biomass captured by the otter trawl (Table 10).

Jaccard's index of similarity (IS_J) revealed that the otter trawl collections were 30.4% similar to the total catch. The otter trawl collections were 46.6% similar to the total catch according to Sørensen's index of similarity (IS_S) (Table 11).

6.1.3.3. Seine net

Thirty seven seine net hauls collected 4251 specimens and 44 kinds of fishes. The seine net collections were dominated by juvenile mugilids (19.4%), *Rhabdosargus holubi* (11.7%), *Gilchristella aestuaria* (11.4%), *Oreochromis mossambicus* (10.1%), *Terapon jarbua* (8.7%), *Ambassis productus* (6.7%) and *Crenimugil crenilabis* (5.3%) (Table 9). A total fish mass of 167244.7 g was collected by seine netting and was dominated by *O. mossambicus* (20.3%), *R. holubi* (16.2%), *Valamugil robustus* (9.9%), *A. productus* (9.1%), *Myxus capensis* (7.3%) and *T. jarbua* (6.7%) (Table 10).

Jaccard's index of similarity (IS_J) and Sørensen's index of similarity (IS_S) revealed that the collections made by seine netting were 78.6% and 88.0% similar to the total catch respectively (Table 11).

6.1.3.4. Gill nets

Gill netting yielded a total of 538 specimens and 26 species. The 40 gill net collections were dominated by *Oreochromis mossambicus* (17.7%), *Valamugil robustus* (17.5%), *Valamugil cunnesius* (16.0%), *Liza alata* (11.2%), *Myxus capensis* (7.1%), *Gerres rappi* (6.3%) and *Mugil cephalus* (8.8%) (Table 9). Gill netting yielded a total fish biomass of 167244.7 g in the Zotsha. *L. alata* (21.9%), *O. mossambicus* (21.0%), *V. robustus* (11.3%), *V. buchanani* (9.7%), *M. capensis* (8.9%), *V. cunnesius* (6.4%) and *Mugil cephalus* (6.4%) dominated the biomass captured by gill netting in the Zotsha (Table 10).

Jaccard's index of similarity (IS_J) revealed that the collections made by gill netting were 46.4% similar to the total catch. According to Sørensen's index of similarity (IS_S) the collections made by gill netting were 63.4% similar to the total catch (Table 11).

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

6.1.4. 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. The fish biomass in the Zotsha exhibited peaks in February 1991 and November 1991 (Figure 37).

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

Figure 37. Seasonal changes in the number of species, number of individuals, biomass, species richness, species evenness, and species diversity in the Zotsha estuary, August 1990 - May 1992.

Zotsha. The number of specimens was negatively correlated with the average bottom salinity while the biomass of fish captured 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 (Table 12).

Margalef's species richness index (D) was high in November 1990, February 1991, February 1992 and March 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. The Shannon-Wiener index for biomass (H'w) peaked in May 1991 and May 1992 (Figure 37).

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).

6.1.5. Community structure

6.1.5.1. Overall abundance

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 65% of the total fish assemblage. Species dependent on estuaries for their entire life cycle, accounted for 17.6% of the total catch and freshwater species accounted for 10.8%. Marine species numerically comprised 6.6% of the total fish community in the Zotsha (Figure 38).

In terms of biomass, estuarine-dependent marine species also dominated the ichthyofaunal assemblage in the Zotsha and comprised 64.2% of the catch. Freshwater species contributed 21.9% of the total fish biomass and marine species 13.5%. Estuarine species only contributed less than 0.4% to the total fish biomass captured in the Zotsha (Figure 38).

6.1.5.2. Seasonal changes in relative abundance and biomass

Estuarine-dependent marine species numerically dominated the fish community captured in the Zotsha estuary throughout the study period. The relative contribution of estuarine species to the ichthyofauna captured in the Zotsha was high in November 1990, May 1991, August 1991 and May 1992. The percent contribution of freshwater species was high in May 1991 and November 1991. The numerical contribution of marine species increased in February 1991

Table 12. Results of the Spearman rank correlation test between abiotic and biotic variables in the Zotsha estuary (August 1990 - May 1992).

| | Depth | Temperature | | Salinity | | Dissolved Oxygen | | Turbidity | | Mouth |
		Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom	% Open
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 = 0.80	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

Shaded areas denote significant (p<0.15) correlation values.

Figure 38. Percent numerical (a) and biomass (b) contribution of freshwater species, estuarine species, estuarine-dependent marine species and marine species to the total ichthyofauna of the Zotsha estuary.

and February 1992 (Figure 39).

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 the Zotsha in November 1990 and November 1991. The biomass contribution of marine species to the fish community in the Zotsha was high in February 1992. Estuarine species did not constitute a major component of the fish biomass captured throughout the study period (Figure 40).

6.1.5.3. Seasonal changes in actual abundance and biomass

The numbers and biomass of freshwater species in the Zotsha exhibited peaks in November 1990, May 1991 and November 1991. A high biomass was also recorded in May 1992 (Figure 41). The abundance of estuarine species increased in November 1990 and August 1991 while the biomass of this group of fishes peaked in November 1990, May 1991 and November 1991 (Figure 41). Estuarine-dependent marine species exhibited peaks in abundance in August 1990 and August 1991. The biomass of estuarine-dependent marine species peaked in February 1991 and November 1991 (Figure 41). Peak numbers of marine species were captured in November 1991, August 1991 and February 1992. The biomass of this group of fishes was high in May 1991 and February 1992 (Figure 41).

6.1.6. Principal species

6.1.6.1. *Oreochromis mossambicus*

Oreochromis mossambicus exhibited peaks in abundance and biomass in November 1990, May 1991, November 1991 and May 1992 (Figure 42). *O. mossambicus* captured in the Zotsha during the study period ranged in size from below 10 mm to 240 mm (S.L.) (Figure 42). Specimens captured in August 1990 were mostly large individuals between 190 mm and 220 mm . As well as large specimens between 190 mm and 230 mm, small (< 30 mm) *O. mossambicus* were also captured in November 1990. In February 1991 specimens below 30 mm dominated. Larger specimens between 30 mm and 60 mm predominated in May 1991. In August 1991, large *O. mossambicus* 190 to 240 mm were captured. Specimens predominantly in the 20 to 40 mm and 60 to 80 mm size classes were captured in November 1991. Only large specimens above 190 mm were captured in February 1992 and May 1992 (Figure 42).

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Figure 39. Seasonal numerical composition of freshwater species, estuarine species, estuarine-dependent marine species and marine species to the ichthyofauna of the Zotsha estuary, August 1990 - May 1992.

Biomass

Aug 1990

5.8%

22.0%

0.1%

72.1%

Aug 1991

13.4%

19.6%

0.3%

66.7%

Nov 1990

4.1%

40.0%

55.0%

0.9%

Nov 1991

5.0%

35.5%

59.3%

0.3%

Legend:
- Freshwater
- Estuarine
- Estuarine - marine
- Marine

Feb 1991

8.9% 1.5% 0.2%

89.5%

Feb 1992

5.4% 0.0%

49.9%

44.7%

May 1991

21.1%

31.5%

46.0%

1.3%

May 1992

6.9%

24.3%

0.1%

68.7%

Figure 40. Seasonal biomass composition of freshwater species, estuarine species, estuarine-dependent marine species and marine species to the ichthyofauna of the Zotsha estuary, August 1990 - May 1992.

Figure 41. 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, August 1990 -May 1992.

Oreochromis mossambicus

Figure 42. Seasonal abundance (O), biomass (•) and length frequrncy distribution of *Oreochromis mossambicus* in the Zotsha estuary, August 1990 - May 1992.

6.1.6.2. *Gilchristella aestuaria*

The numbers of *Gilchristella aestuaria* captured in the Zotsha were high in November 1990 and August 1991. The biomass of *G. aestuaria* peaked in November 1990, May 1991 and November 1991 (Figure 43). *G. aestuaria* was only captured in the Zotsha from November 1990 to November 1991 (Figure 43). Specimens captured in November 1990 ranged from 20 to 60 mm and were mostly in the 30 to 50 mm size classes. *G. aestuaria* captured in February 1991 were in the 30 to 60 mm size classes while those in May 1991, were in the 40 to 60 mm size classes. Specimens captured in August 1990 were all below 30 mm while those captured in November 1991 were between 20 mm and 50 mm (Figure 43).

6.1.6.3. *Glossogobius callidus*

Both the numbers and biomass of *Glossogobius callidus* captured in the Zotsha exhibited peaks in November 1990 and November 1991 (Figure 44). *G. callidus* was captured in the Zotsha throughout the study period (Figure 44). Specimens captured in August 1990 ranged from 10 to 60 mm and were mostly in the 20 to 50 mm size classes. In November 1990 the specimens ranged from 10 to 70 mm and were also mostly between 20 mm and 50 mm. In February 1991 the 20 - 30 mm and 40 - 50 mm size classes were well represented. From May 1991 to November 1991 *G. callidus* captured in the Zotsha ranged in size from 10 to 60 mm and were mostly between 20 mm and 50 mm. One specimen in the 20 - 30 mm size class was captured in February 1992. In May 1992 specimens between 10 mm and 30 mm were well represented (Figure 44).

6.1.6.4. *Rhabdosargus holubi*

Rhabdosargus holubi exhibited a peak in abundance in the Zotsha in November 1990 and August 1991. The biomass of *R. holubi* peaked in February 1991 and November 1991 (Figure 45). The *R. holubi* captured in the Zotsha were largely below 100 mm (S.L.) (Figure 45). In August 1991 specimens in the 20 - 30 size class predominated. Larger specimens, 30 to 60 mm, dominated the November 1990 catch. In February 1991 specimens captured ranged from 40 to 100 mm but were mostly below 80 mm. Specimens in the 50 to 70 mm size classes were predominantly captured in May 1991. In August 1991 and November 1991 the *R. holubi* captured were mostly below 50 mm. One specimen in the 90 - 100 mm size class was captured in February 1992. No *R. holubi* were captured in May 1992 (Figure 45).

Gilchristella aestuaria

Figure 43. Seasonal abundance (O), biomass (•) and length frequency distribution of *Gilchristella aestuaria* in the Zotsha estuary, August 1990 - May 1992.

Figure 44. Seasonal abundance (⊙), biomass (•) and length frequency distribution of *Glossogobius callidus* in the Zotsha estuary, August 1990 - May 1992.

Figure 45. Seasonal abundance (⊙), biomass (•) and length frequency distribution of *Rhabdosargus holubi* in the Zotsha estuary, August 1990 - May 1992.

6.1.6.5. *Terapon jarbua*

Both the numbers and biomass of *Terapon jarbua* captured in the Zotsha peaked in August 1991 and February 1992 (Figure 46). *T. jarbua* captured during this study ranged in size from 10 mm to 130 mm (Figure 46). Specimens captured in August 1990 were all below 30 mm. A single specimen in the 90 - 100 mm size class was captured in November 1990. Three specimens in the 10 - 20 mm, 60 - 70 mm and 90 - 100 mm size classes were captured in February 1991. In May 1991 specimens in the 10 - 20 mm size class predominated. In August 1991, *T. jarbua* captured ranged from 20 to 60 mm but were mostly in the 30 - 40 mm size class. Specimens below 20 mm and 30 to 60 mm predominated in November 1991. In February 1992 *T. jarbua* captured ranged from 10 to 100 mm but were mostly below 70 mm. No *T. jarbua* were captured in May 1992 (Figure 46).

6.1.6.6. *Ambassis productus*

High numbers and biomass of *Ambassis productus* were captured in the Zotsha estuary in May 1991 and November 1991 (Figure 47). *A. productus* was only captured in the Zotsha in November 1990, May 1991 and November 1991. A single specimen in the 60 - 70 mm size class was captured in November 1990. *A. productus* captured in May 1991 ranged in size from 30 mm to 80 mm but were mostly between 40 mm and 60 mm. In November 1991 the specimens captured ranged in size from 20 mm to 90 mm with most of the specimens being in the 50 to 70 mm size classes (Figure 47).

6.1.6.7. Juvenile mugilids

The numbers and biomass of juvenile mugilids in the Zotsha estuary were high in August 1990 and August 1991 (Figure 48). Juvenile mugilids (<50 mm S.L.) were not captured in February 1991 and May 1992. Small specimens below 20 mm were predominantly captured in August 1990, November 1990 and May 1991. In August 1991 large specimens in the 30 - 40 mm size class predominated. Specimens in the 20 - 30 mm size class predominated in November 1991 and February 1992 (Figure 48).

6.1.6.8. *Myxus capensis*

The numbers of *Myxus capensis* in the Zotsha estuary increased in February 1991 and August 1991 while the biomass of this species peaked in November 1990 and November 1991 (Figure 49). *M. capensis* captured in the Zotsha during the study period ranged from 20 mm to 340 mm (Figure 49). Two specimens 180 - 190 mm and 250 - 260 mm were captured in August
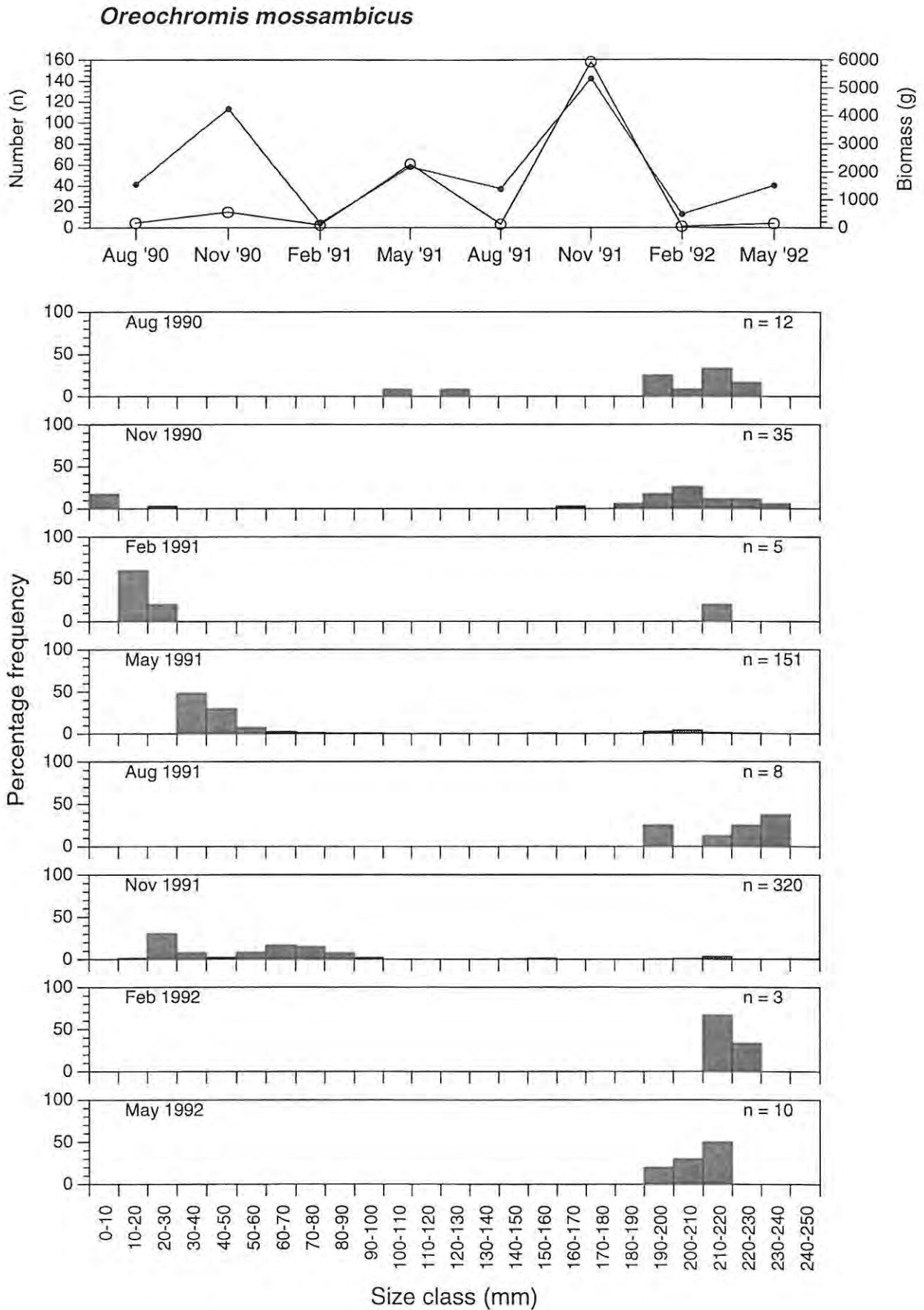
Figure 46. Seasonal abundance (O), biomass (•) and length frequency distribution of *Terapon jarbua* in the Zotsha estuary, August 1990 - May 1992.

Ambassis productus

Figure 47. Seasonal sbundance (○), biomass (•) and length frequency distribution of *Ambassis productus* in the Zotsha estuary, August 1990 - May 1992.

Figure 48. Seasonal abundance (O), biomass (•) and length frequency distribution of juvenile mugilids in the Zotsha estuary, August 1990 - May 1992.

Figure 49. Seasonal abundance (O), biomass (•) and length frequency distribution of *Myxus capensis* in the Zotsha, estuary August 1990 - May 1992.

1990. All *M. capensis* captured in November 1990 were above 200 mm. In February 1991, specimens 30 to 100 mm and 190 to 310 mm were captured in the Zotsha. Only three specimens between 190 mm and 230 mm were captured in May 1991. All *M. capensis* captured in August 1991 were below 30 mm while those captured in November were above 190 mm. Two specimens in the 50 - 60 mm and 180 - 190 mm size classes were captured in February 1992. No *M. capensis* were captured in May 1992 (Figure 49).

6.1.6.9. *Valamugil cunnesius*

Both the numbers and biomass of *Valamugil cunnesius* in the Zotsha estuary peaked in February 1991 and November 1991 (Figure 50). *V. cunnesius* captured during this study ranged in size from 30 to 230 mm (Figure 50). The *V. cunnesius* captured in August 1990, November 1991 and February 1991 were mostly above 150 mm with small specimens below 70 mm also being captured captured in November 1990 and February 1991. The *V. cunnesius* captured in May 1991 were mostly in the 50 to 70 mm and 140 to 160 mm size classes. Only two specimens 170 to 190 mm were captured in August 1991. Specimens captured in November 1991 were mostly between 50 mm and 80 mm and those captured in February 1992 were mostly between 30 mm and 50 mm. All the specimens captured in May 1992 were above 110 mm (Figure 50).

6.1.6.10. *Valamugil robustus*

High numbers of *Valamugil robustus* were captured in the Zotsha estuary in February 1991 and February 1992. The biomass of *V. robustus* peaked in February 1991 and November 1991 (Figure 51). *V. robustus* captured in the Zotsha during the study period ranged in size from 80 mm to 270 mm and were mostly between 170 mm and 250 mm (Figure 51). Smaller specimens below 120 mm were captured in February 1991, May 1991 and February 1992 (Figure 51).

6.1.6.11. *Mugil cephalus*

Numbers of *Mugil cephalus* in the Zotsha estuary peaked in February 1991 and November 1991 while the biomass peaked in February 1991, August 1991 and May 1992 (Figure 52). *M. cephalus* was captured throughout the study period and ranged in size from 20 to 390 mm (Figure 52). Only two specimens, 190 - 200 mm and 220 - 230 mm were captured in August 1990. Most of the specimens captured in November 1990 were between 30 mm and 60 mm. *M. cephalus* captured in February ranged in size from 80 to 390 mm but were mostly 240 to 260 mm in length. Two specimens 210 - 220 mm were captured in May 1991. In August
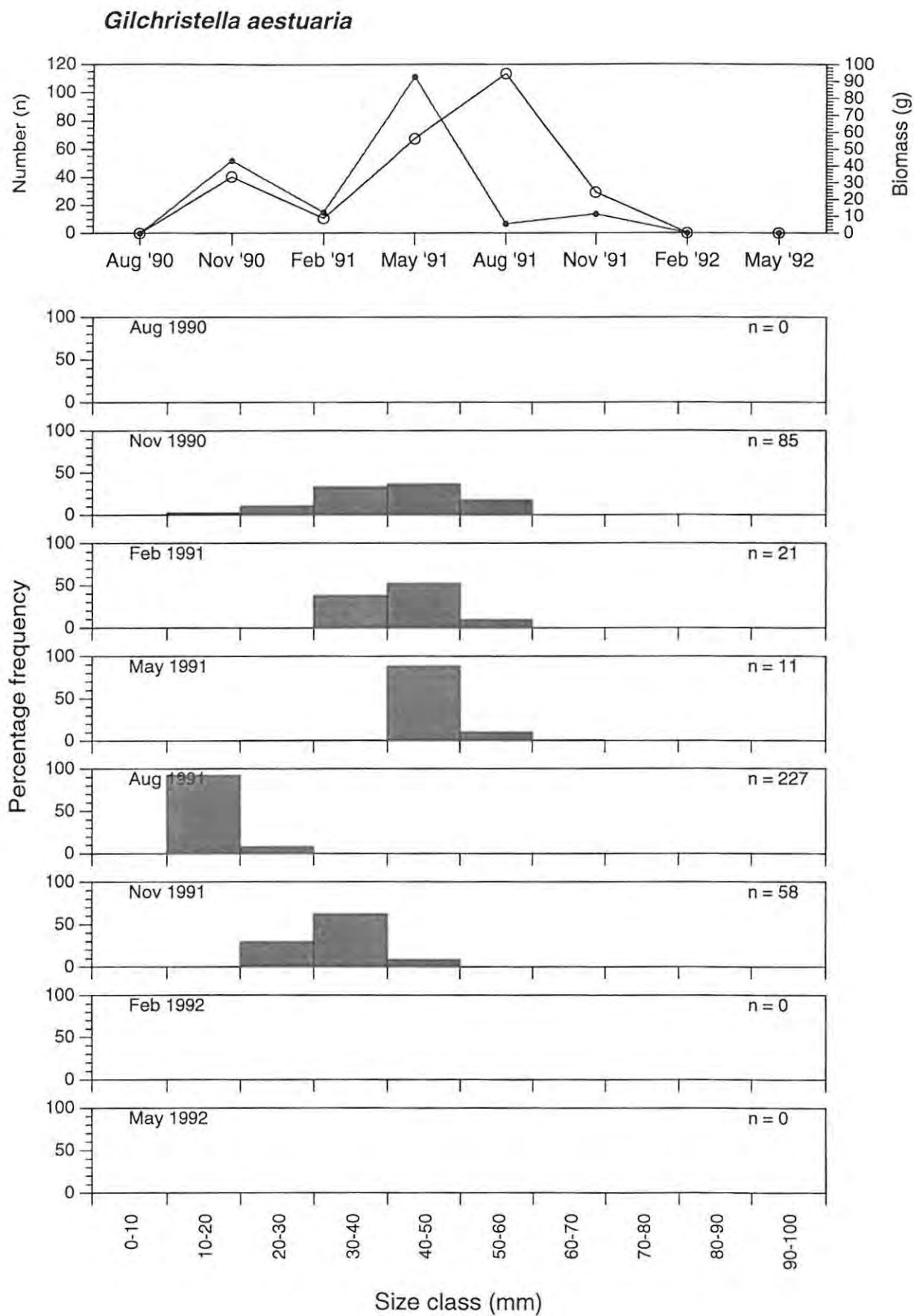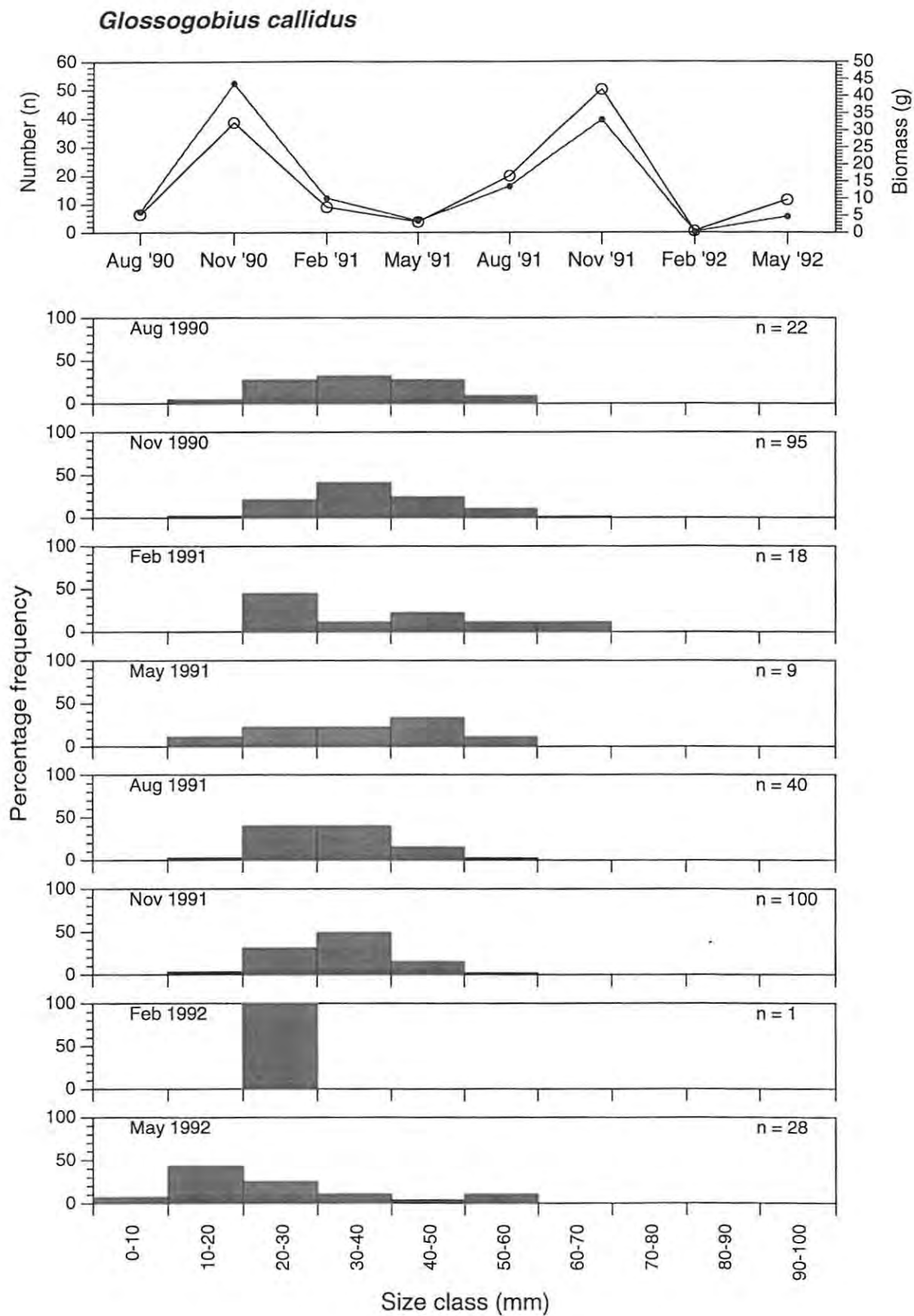
Figure 50. Seasonal abundance (O), biomass (•) and length frequency distribution of
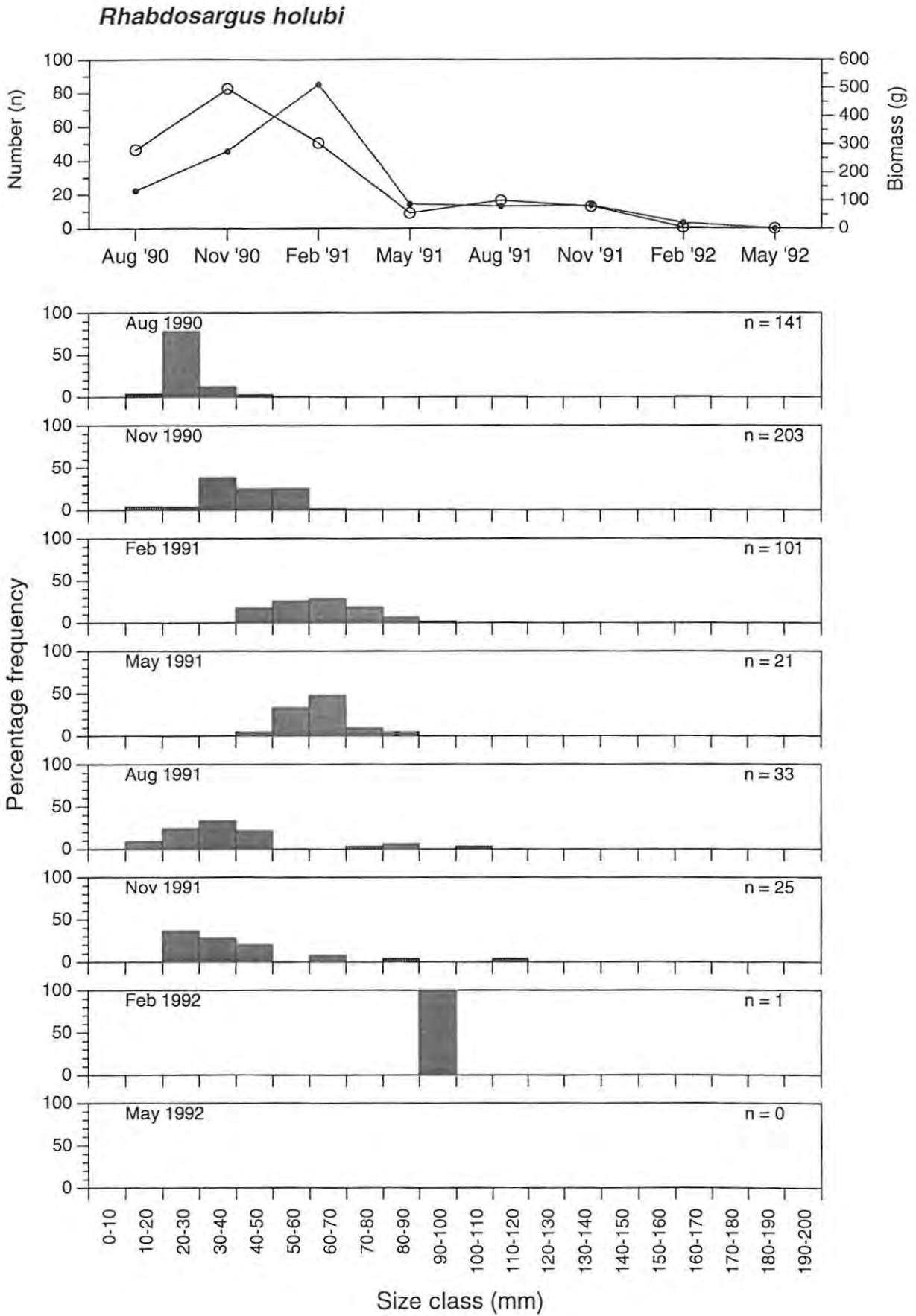*Valamugil cunnesius* in the Zotsha estuary, August 1990 - May 1992.

Figure 51. Seasonal abundance (⊙), biomass (•) and length frequency distribution of *Valamugil robustus* in the Zotsha estuary, August 1990 - May 1992.

Mugil cephalus

Figure 52. Seasonal abundance (O), biomass (•) and length distribution analysis of *Mugil cephalus* in the Zotsha estuary, August 1990 - May 1992.

1991 three specimens between 220 mm and 290 mm were captured. The majority of the specimens captured in November 1991 were between 20 mm and 50 mm. Only two specimens below 80 mm were captured in February 1992. *M. cephalus* captured in May 1992 were between 240 and 270 mm (Figure 52).

6.1.6.12. *Liza alata*

Both the numbers and biomass of *Liza alata* in the Zotsha estuary peaked in August 1990, February 1991 and November 1991 (Figure 53). *L. alata* captured throughout the study period were mostly large specimens above 210 mm (S.L.) Small individuals below 100 mm were only captured in November 1991 (Figure 53).

6.1.6.13. *Valamugil buchanani*

Both the abundance and biomass of *Valamugil buchanani* showed distinct peaks in November 1990, May 1991 and February 1992 (Figure 54). All the *V. buchanani* captured in the Zotsha were above 180 mm. No specimens were collected in August 1990 and February 1991 (Figure 54).

6.2. Discussion

6.2.1. Abiotic characteristics

The mouth of the Zotsha estuary during this study was permanently open in the spring/summer (September - February). In the winter (June - August) the mouth of the system closed and only opened occasionally for short periods (Figure 36). 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 of the Zotsha 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 (the average water depth generally exceeded one metre) (Figure 36).

Water temperatures in the Zotsha 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 36). During his study Begg (1984b) found
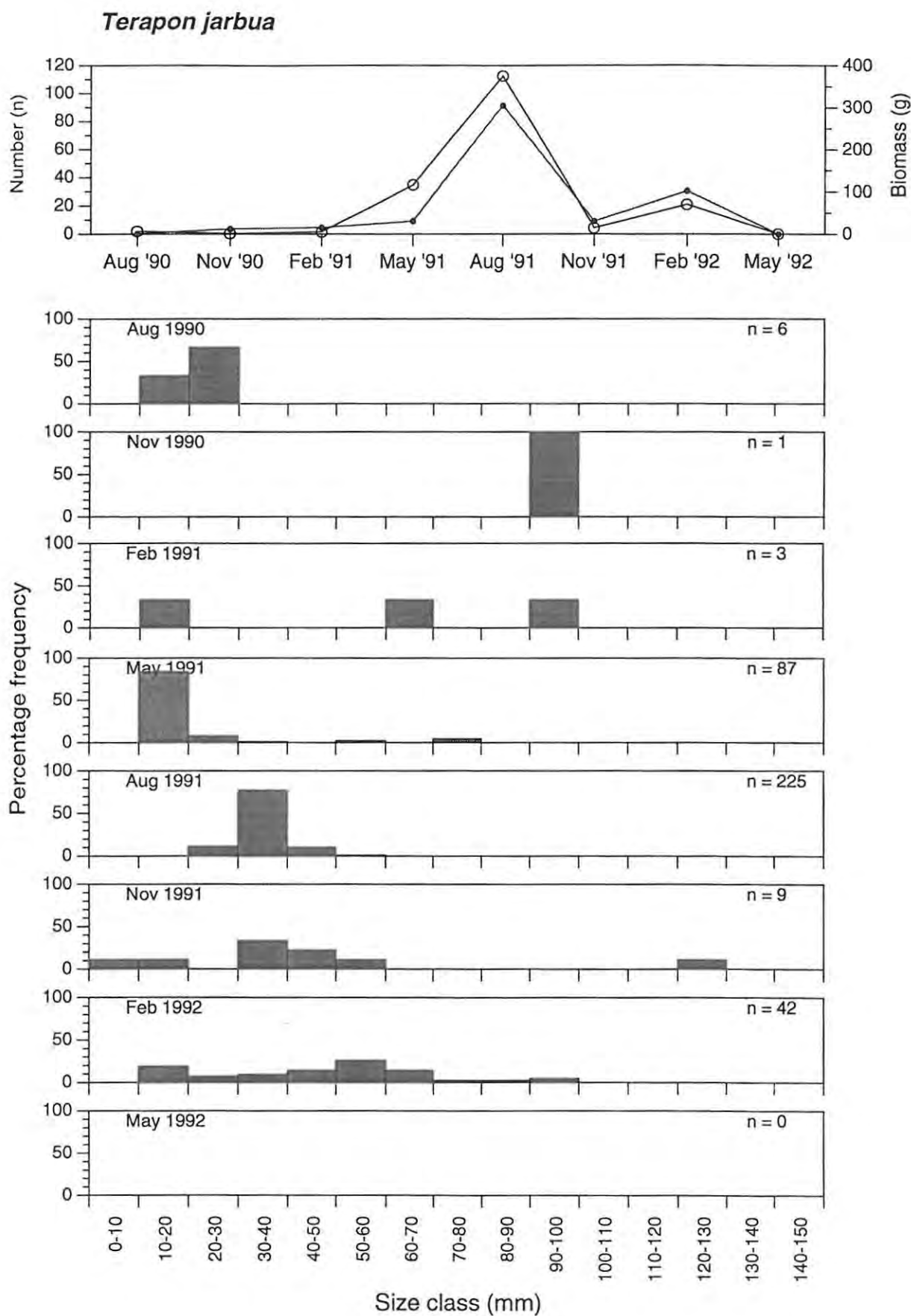
Liza alata

Figure 53. Seasonal abundance (O), biomass (•) and length frequency distribution of *Liza alata* in the Zotsha estuary, August 1990 - May 1992.
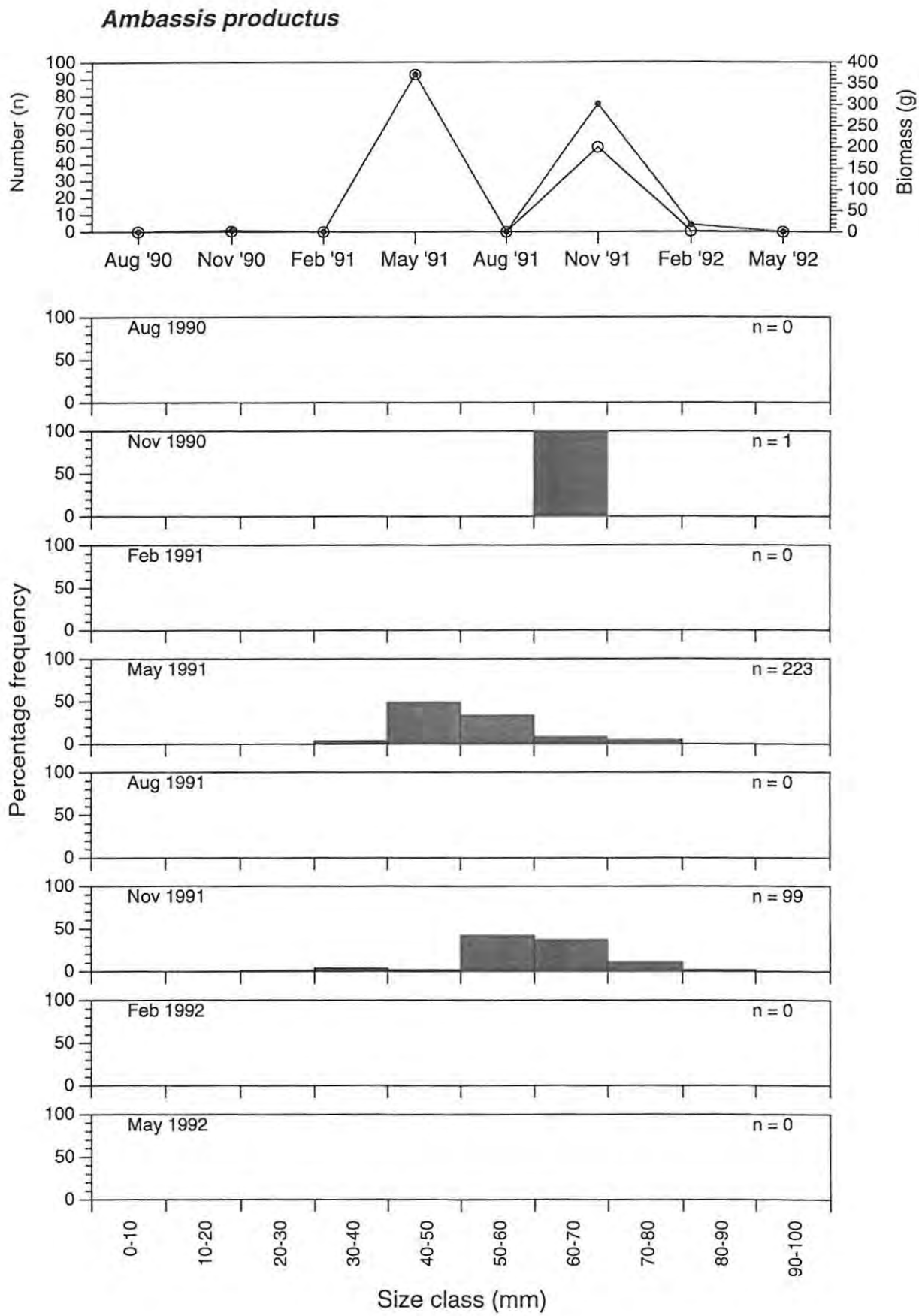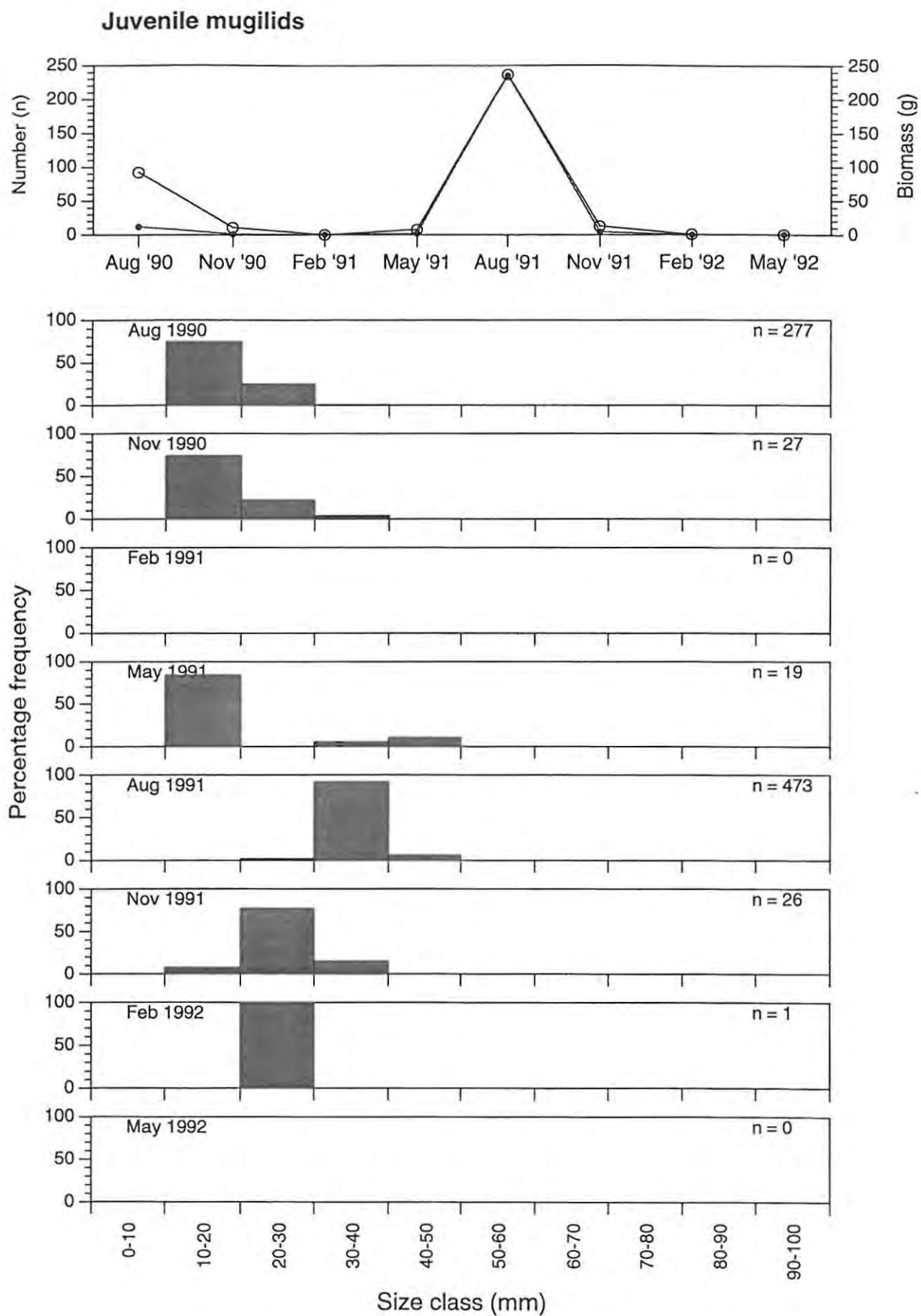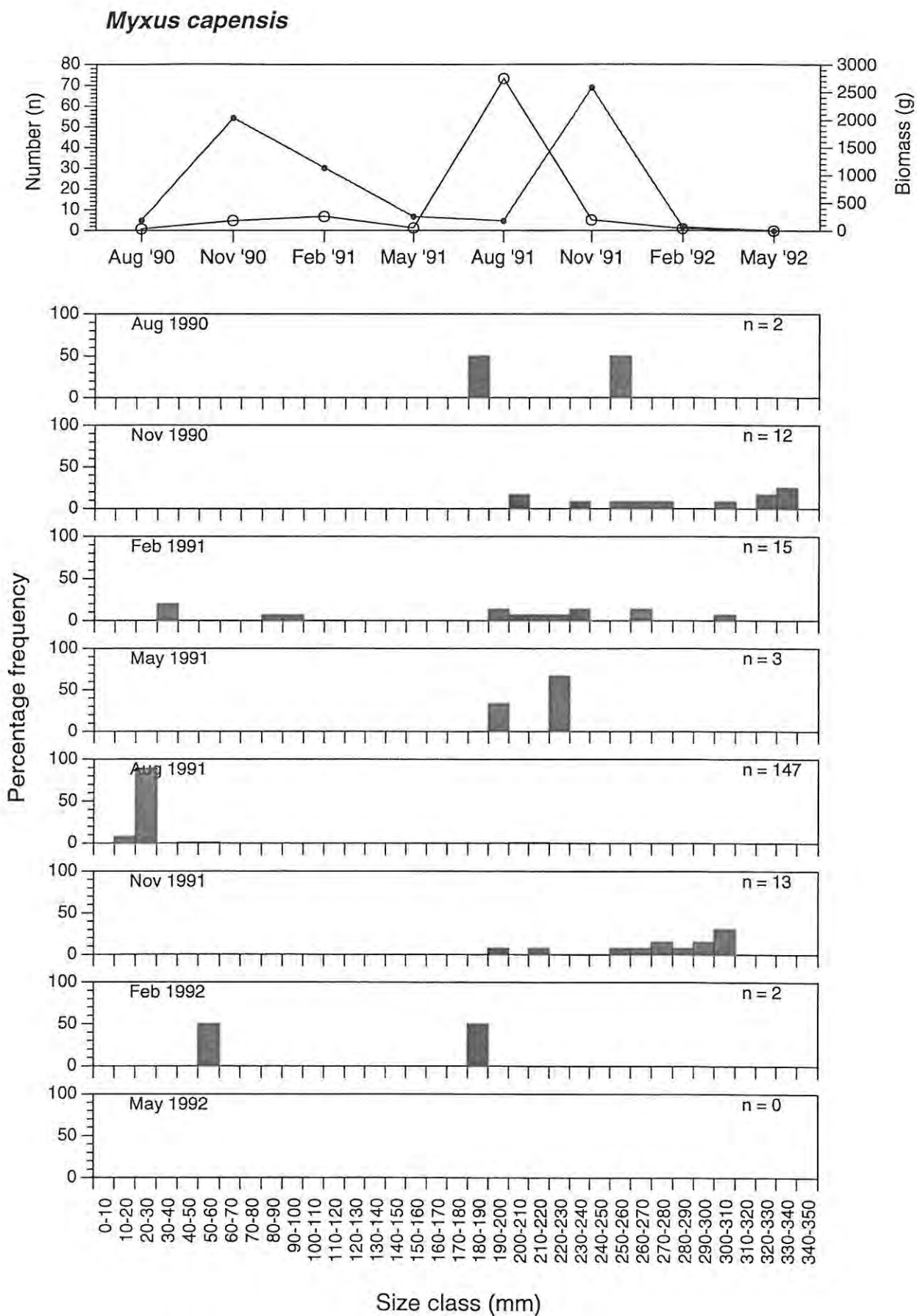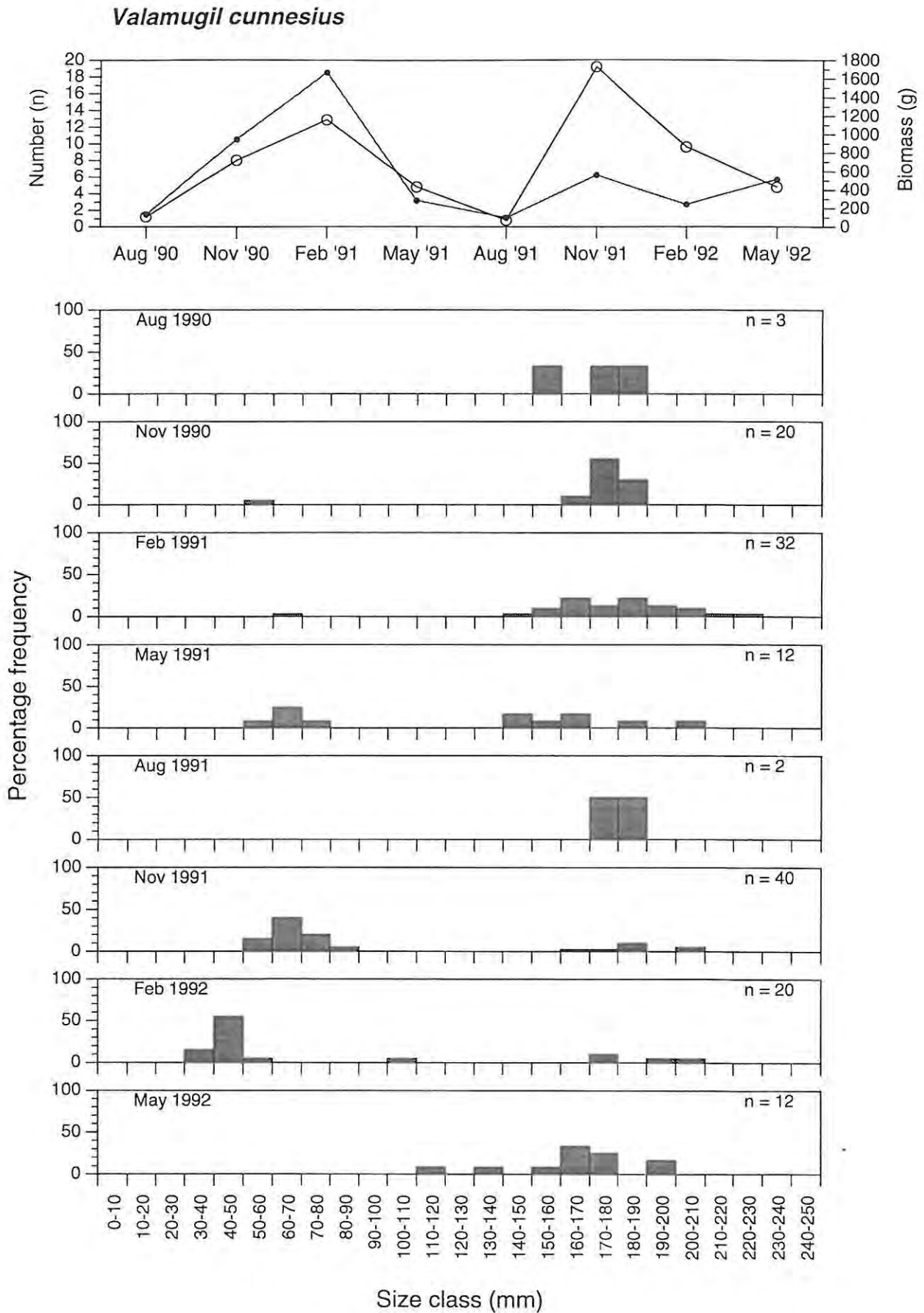
Valamugil buchanani

Figure 54. Seasonal abundance (O), biomass (•) and length frequency distribution of *Valamugil buchanani* in the Zotsha estuary, August 1990 - May 1992.
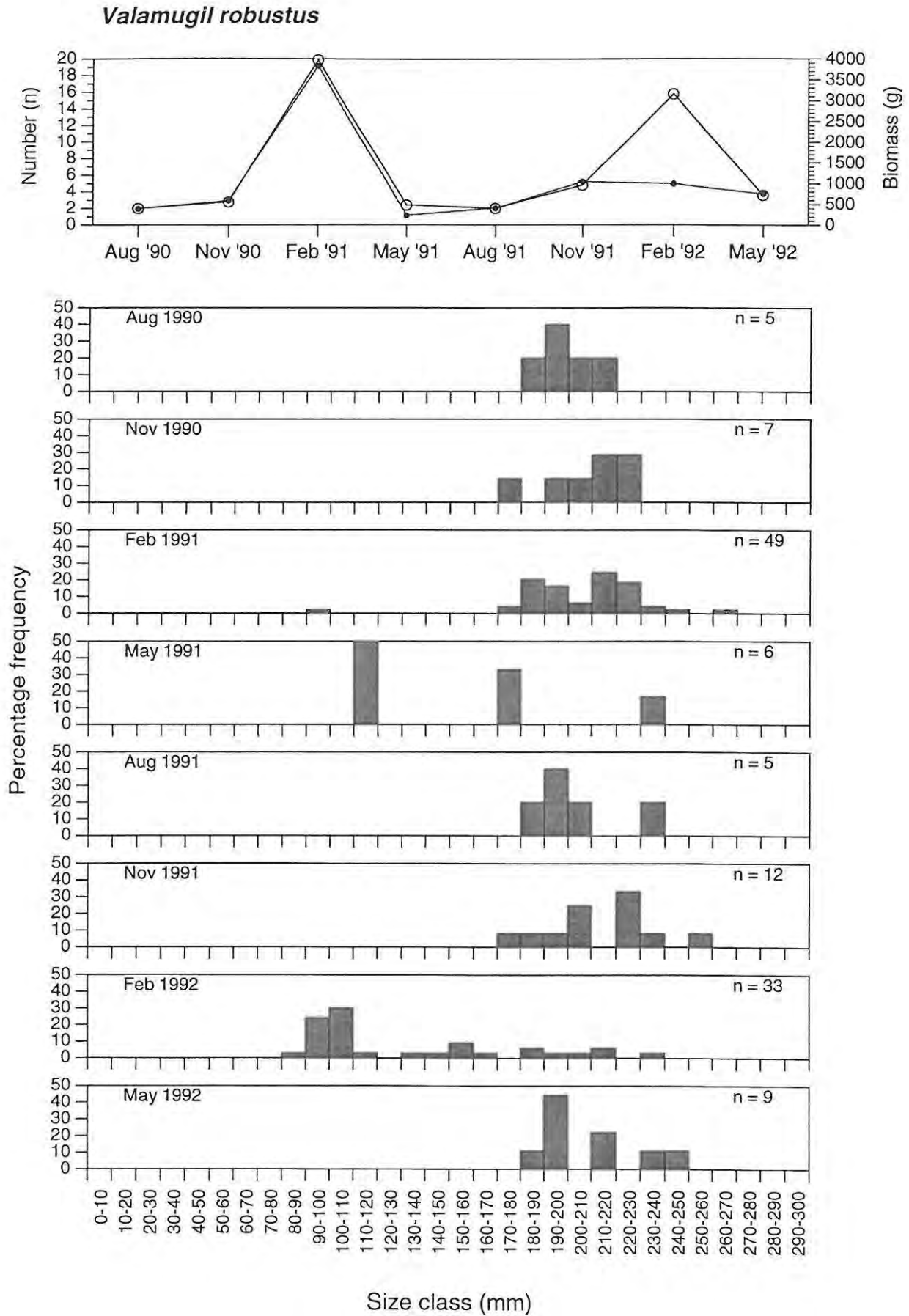
that the temperature of the surface water in the Zotsha ranged from 14.0 °C in July to 27.0 °C in September. He found that surface temperatures did not differ significantly from those at the bottom when salinity layering was absent. However, when the system was stratified, bottom temperatures were higher 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 36).

The waters in the Zotsha were stratified during the study period with surface salinities ranging from 0.8 ‰ to 23.0 ‰ and bottom salinities from 5.5 ‰ to 26.0 ‰ (Figure 36). During his study Begg (1984b) found that when the system was not stratified, salinity ranged from 2 ‰ to 8 ‰ but when the system was stratified, surface salinities ranged from 0 ‰ to 5 ‰ while those at the bottom ranged from 10 ‰ to 18 ‰. The relatively high salinities recorded during this study is a reflection of the predominantly open mouth condition of the system (Figure 36).

Begg (1984b) noted that the mouth condition of the Zotsha was an important factor in determining the 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 36).

With the exception of those recorded in February 1991 and November 1991, turbidities in the Zotsha were below 1 NTU (Figure 36). 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 high turbidities recorded during this study 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 fresh waters overlying the clearer more saline bottom waters (Figure 36).

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 36). 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 36). 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 36).

6.2.2. Sampling efficiency

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 thus 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 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. commersonnii* (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 in the Zotsha captured 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 used in the Zotsha (Table 3). The high biomass captured is due to the gill nets more effectively sampling larger, fast swimming specimens, particularly grey mullet, which are not effectively sampled using other gear (Hayes, 1989). Mugilids (*L. alata, V. robustus, V. buchanani, V. cunnesius, M. capensis* and *M. cephalus*) predominated in the gill net collections in the Zotsha (Tables 9 and 10).

Each sampling technique used in the Zotsha differed in the number, biomass and type 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 deep waters and otter trawling was effective for sampling slow moving, demersal species in mid-channel areas.

6.2.3. Species composition

Of the 58 kinds of fishes collected in the Zotsha estuary, the most abundant fishes collected 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 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 in the Zotsha 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 kinds of fishes 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 in the Zotsha (Table 10).

6.2.4. Community structure

6.2.4.1. Freshwater species

Freshwater species contributed 10.8% (21.9% by mass) to the ichthyofauna captured in the Zotsha estuary during this study (Figure 38). Freshwater species 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 in the Zotsha (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 the Zotsha in November together with the occurrence of juveniles (<30 mm S.L.) (Figure 42) corresponds to the breeding cycle of this species which takes place in shallow areas during spring and summer (September to February) (Bruton & Boltt, 1975). The increase in the number and biomass of *O. mossambicus* in November may also be due to the shallow nature

of the system causing this species become concentrated 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. The low numbers and biomass of *O. mossambicus* in February 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). This may account for the decline in the numbers and biomass of *O. mossambicus* in August (Figure 42).

6.2.4.2. Estuarine species

Estuarine species numerically accounted for 17.6% of the ichthyofauna collected during this study and 0.4% of the biomass (Figure 38). This group of fishes numerically comprised 78.6% of the fishes collected in the Zotsha by Begg (1984b), 4.1% of the ichthyofauna captured by Ramm *et al.* (1985b) and 3.8% of the catch made by Harrison (1990).

The dominant estuarine species captured in the Zotsha during this study were *Gilchristella aestuaria* and *Glossogobius callidus*. *G. aestuaria* numerically comprised 11.0% of the fishes captured in the Zotsha during this study and 0.2% of the biomass, while *G. callidus* contributed 6.1% numerically and 0.1% by mass (Tables 9 and 10). *Glossogobius* was the dominant estuarine species (75.8%) captured in the Zotsha by Begg (1984b) while *G. aestuaria* contributed 2.1% to the ichthyofauna. *Glossogobius* was also the dominant estuarine species captured in the Zotsha by Ramm *et al.* (1985b), comprising 4.1% of the catch. The dominant estuarine species captured in the Zotsha by Harrison (1990) was *G. aestuaria* (2.4% of the total catch) while *Glossogobius callidus* contributed 0.8%.

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 43) 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 fry to utilize a winter peak in zooplankton. The occurrence of larger *Gilchristella* specimens in the Zotsha estuary during

November, together with an increase in biomass, is probably a reflection of an extension of their distribution downstream with growth. The reduction in numbers and biomass in February may possibly be a result of the adults migrating upstream to spawn (Figure 43).

The occurrence of small (< 20 mm S.L.) *Glossogobius callidus* specimens from May to November indicates that this species has an extended breeding period, while the peak numbers and biomass in November suggests that recruitment attains a peak in spring (Figure 44). Whitfield (1980b) found that, in the Mhlanga estuary, *Glossogobius* bred during the stable closed phase and captured juvenile (<20 mm S.L.) specimens in July. 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).

6.2.4.3. Estuarine-dependent marine species

Marine species which utilise estuaries as nursery areas during the juvenile phase of their life cycle comprised 65.0% (64.2% by mass) of the total ichthyofauna assemblage captured in the Zotsha during this study (Figure 38). This group of fishes numerically comprised 19.2% of the fishes collected in the Zotsha by Begg (1984a), 78.7% by Ramm *et al.* (1985b) and 86.4% by Harrison (1990). The dominant estuarine-dependent marine fishes captured during this study were juvenile mugilids, *Rhabdosargus holubi*, *Terapon jarbua*, *Ambassis productus*, *Myxus capensis*, *Valamugil cunnesius*, *Valamugil robustus*, *Mugil cephalus* and *Liza alata* (Tables 9 and 10). Together these fishes comprised 51.8% numerically and 53.3% 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). *R. holubi* is endemic to the warm temperate waters of south east Africa, from the Cape of Good Hope to Zululand (Blaber 1973). 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 (T.L.) 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, corresponding with the occurrence of juveniles (<40 mm S.L.) in the system (Figure 45). Blaber (1974) found that when the mouth of the West Kleinemond estuary in the eastern Cape opened, the resident population of 1+ juvenile *R. holubi* emigrated from the system which was then re-colonised by 0+ juveniles. Emigration of larger individuals also appears to have taken place in the Zotsha in February and May and probably accounts for the low biomass in May and August (Figure 45).

Terapon jarbua contributed 7.3% numerically and 0.6% by mass to the ichthyofauna captured in the Zotsha during this study (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). *T. jarbua* is a widely distributed tropical Indo-Pacific species which extends south to Knysna (Smith & Heemstra, 1986). This species spawns in Natal waters during the summer (Day *et al*., 1981) with juveniles 10 - 30 mm T.L. entering estuaries between November and May (Wallace & van der Elst, 1975). A similar recruitment pattern of *T. jarbua* into the Zotsha occurred during this study, where juveniles below 30 mm were recorded from November to May. The high numbers and biomass recorded in August 1991 and February 1992 is probably a result of the larger size classes being more susceptible to capture (Figure 46).

Ambassis productus was the most abundant Ambassidae captured in the Zotsha and comprised 6.4% of the catch. *A. productus* comprised 9.6% of the fishes captured by Begg (1984b), 16.6% by Ramm *et al*. (1985b) and 0.3% by Harrison (1990). Ambassid fishes are common and widespread throughout shallow waters of the Indo-West Pacific region (Martin & Heemstra, 1988). Three species 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). It has been suggested that *A. productus* spawns at sea from late spring into autumn with maximum recruitment of fry (<10 mm S.L.) taking place from summer to autumn (Martin, 1983). High numbers and biomass of *A. productus* were captured in the Zotsha in May 1991 and November 1991 (Figure 47).

Juvenile mugilids (<50 mm S.L.) comprised 16.1% (0.3% by mass) of the total ichthyofauna in the Zotsha during this study (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, eight are considered to be dependent on estuaries during the juvenile phase of their life cycle (Wallace *et al*., 1984). Their extended spawning season, from late autumn to spring (May - November) (Wallace, 1975b; Blaber, 1987) prolongs the period during which fry occur in the inshore marine environment and acts as a buffer against recruitment failure (Wallace, 1975b; Blaber, 1987). The peak in juvenile mugilids in August during this study (Figure 48) corresponds to the general immigration pattern which takes place during winter and spring (June - November) (Wallace & van der Elst, 1975).

The endemic catadromous mullet, *M. capensis*, accounted for 3.8% numerically and 8.5% by

mass of the fishes captured in the Zotsha (Tables 1 and 2). Begg (1984b) did not record any *M. capensis* in the Zotsha during his study. *M. capensis* comprised 12.5% of the fishes captured in the Zotsha 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) while *M. capensis* in the eastern Cape spawns throughout the year with a peak in spring (March - November) (Bok, 1979; Bruton *et al.*, 1987). The high biomass of *M. capensis* in November and subsequent reduction in February and May, may be a result of large individuals emigrating from the system to spawn at sea (Figure 49). The high numbers together with the occurrence of juvenile (<60 mm S.L.) *M. capensis* in February 1991 and August 1991 (Figure 49) 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 may be due to this species leaving the estuary to the preferred freshwater reaches of the system (Figure 49).

The longarm mullet, *Valamugil cunnesius*, comprised 2.8% numerically and 5.9% by mass of the total fishes captured during this study (Tables 9 and 10). *V. cunnesius* comprised 0.3% of the total ichthyofaunal catch made in the Zotsha by Begg (1984a), 22.9% by Ramm *et al.* (1986) and 5.5% by Harrison (1990). *Valamugil 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 50) may be a result of emigration of mature specimens from the system to spawn at sea. The occurrence of juveniles (<70 mm S.L.) in the Zotsha from November to May (Figure 50) is probably a reflection of the successful recruitment of this species which takes place from January to July (Wallace & van der Elst, 1975). Juvenile *V. cunnesius* were, in addition to spring and summer, captured during the months of May, June and July in Natal and Pondoland estuaries by Blaber & Whitfield (1977).

Valamugil robustus comprised 2.5% numerically and 10.9% by mass of the total fishes captured in the Zotsha 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* was captured in the Zotsha in summer (Figure 51). Blaber (1977) found that *Valamugil 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). According to Smith & Heemstra (1986) *V. robustus* occurs from the Transkei to Madagascar and is common in southern Mozambique. The spawning period of *V. robustus* is unknown but recruitment of juvenile (>10 mm S.L.) into estuaries occurs from

September to May (Blaber, 1987). Juvenile *V. robustus* were recorded in Natal and Pondoland estuaries from spring to winter by Blaber & Whitfield (1977). The occurrence of smaller individuals in February and May in the Zotsha (Figure 51) is probably a reflection of the successful recruitment of this species into the system. The low numbers and biomass of *V. robustus* in May and August may be a result of the emigration of larger individuals from the system perhaps to spawn (Figure 51).

Mugil cephalus comprised 1.4% numerically and 6.0% by mass of the total ichthyofauna in the Zotsha estuary (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 captured 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 52) may be due to the emigration of larger specimens from the system. The occurrence of juveniles (< 50 mm) in November (Figure 52) is probably a reflection of the successful recruitment of this species into the estuary. *M. cephalus* recruits into Natal estuaries from June to October (Wallace & van der Elst, 1975).

Liza alata comprised 1.2% numerically and 19.7% by mass of the ichthyofauna in the Zotsha (Tables 9 and 10). *Liza alata* numerically accounted for 4.1% of the fishes captured in the Zotsha by Ramm *et al.* (1985b) and 3.0% by Harrison (1990). *Liza alata* was not captured by Begg (1984a) and is probably a result of the trawl gear used. Blaber (1977) found this species to be relatively rare in in some of the large, permanently open Natal and Pondoland estuaries. The abundance and biomass of *L. alata* in the Zotsha varied but was generally low in May (Figure 53) and may be a result of this species emigrating from the system. The spawning period of *L. alata* is unknown but recruitment starts at 14 mm (S.L.) from July to January (Blaber, 1987). Small specimens (< 90 mm S.L.) were captured in November 1991 (Figure 53).

6.2.4.4. Marine species

Marine species, not dependent on estuaries, numerically contributed 6.6% to the ichthyofauna in the Zotsha during this study and 13.5% in terms of biomass (Figure 38). Marine species comprised 0.62% of the fishes captured by Begg (1984b). This group of fishes numerically comprised 16.5% to the ichthyofauna captured by Ramm *et al.* (1985b) and 6.8% of the fishes captured by Harrison (1990).

Valamugil buchanani is an Indo-Pacific species, abundant along the shores of Mozambique and common as far as Durban, with few extending on to Knysna (Day *et al.*, 1981). This

species comprised 0.7% numerically and 8.7% by mass of the total fishes captured in the Zotsha during this study (Tables 9 and 10). *V. buchanani* 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* in the Zotsha varied throughout this study. According to Wallace (1975b), *V. buchanani* spawns between October and December in Natal waters with recruitment of fry < 50 mm T.L. occurring mainly from February to July (Wallace & van der Elst, 1975). Blaber & Whitfield (1977) recorded juvenile *V. buchanani* in Natal and Pondoland estuaries from spring to winter. Juveniles (<50 mm T.L.) were also found to abundant in the inshore environment while juveniles of other species of mullet have not been recorded in these areas (Wallace & van der Elst, 1975). *V. buchanani* is not considered dependent upon estuaries during the juvenile phase of its life cycle (Wallace *et al.*, 1984).

6.2.5. Seasonal community structure

6.2.5.1. Winter (June, July, August)

During winter the Zotsha is dominated by estuarine-dependent marine species (Figures 39 and 40). 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 numerical proportion of estuarine-dependent marine species in the Zotsha in 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 in late winter.

The relatively low contribution of freshwater species to the total winter ichthyofauna in the Zotsha (Figures 39 and 40) 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, food resources are high during the closed phase of the estuary due to the relative stability of the physical environment. The relatively high numerical contribution of estuarine species in the Zotsha estuary may be a reflection of the extended breeding period of *G. aestuaria* and *G.callidus* (Figures 43 and 44), allowing them to make use of the favourable, relatively stable winter conditions.

The low number of species recorded in winter (Figure 37) 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 32).

Species diversity is a reflection of both the 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 in winter (Figure 32).

6.2.5.2. Spring (September, October, 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 41), the relative contribution of these species to the ichthyofauna of the Zotsha estuary decreased in November (Figures 39 and 40). This is probably a result of peak breeding by *O. mossambicus* (Bruton & Boltt, 1975; Figure 42) and *G. callidus* (Figure 44) during spring. The relative proportions of freshwater and estuarine fishes in the Zotsha increased in November (Figures 39 and 40). In November 1991, the Zotsha was particularly shallow (Figure 36). The shallowness of the upper reaches system may have resulted in a redistribution of *O. mossambicus* into the lower reaches (Whitfield & Blaber, 1979) thus increasing the relative proportion of freshwater species captured during this period (Figures 39 and 40).

During the spring rainfall months the Zotsha estuary opens (Figure 36). Both the total number of species and the total number of individuals captured in the Zotsha increased in spring (Figure 37). The positive correlation between the number of species and the open mouth condition of the system (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 was most likely a reflection of the peak breeding activity of estuarine and freshwater species and the recruitment of estuarine-dependent marine species into the system. Overall, richness and evenness in the Zotsha was high in spring and resulted in a high species diversity (Figure 37).

6.2.5.3. Summer (December, January, February)

The open mouth condition of the Zotsha in summer resulted in an increase in the proportion of marine species entering the system (Figures 39 and 40). The increase in the proportion of estuarine-dependent marine species to the ichthyofauna in the Zotsha also increased in summer (Figures 39 and 40) and is a result of the extended spawning and recruitment period of this

group of fishes (Wallace, 1975b; Wallace & van der Elst, 1975).

The decrease in the proportion of both estuarine and freshwater species to the ichthyofauna in the Zotsha in summer (Figures 39 and 40) 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 migration of *O. mossambicus* to the preferred upper reaches and *G. aestuaria* to the upper reaches to spawn 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 Zotsha estuary during summer (Figure 37).

6.2.5.4. Autumn (March, April, May)

The extended opening of the mouth of the Zotsha into the autumn of 1991 together with the protracted recruitment period of estuarine-dependent marine species, particularly *Valamugil cunnesius*, may have contributed to the high contribution of this group of fishes to the ichthyofauna in May 1991 (Figures 39 and 40). The shallow nature of the system 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 protracted and successful breeding of *Gilchristella aestuaria* and *Glossogobius callidus* (Figures 43 and 44) may account for the high numerical contribution of estuarine species.

The increase in the number of species and individuals in autumn 1991 is due to the immigration of marine species into the system when it was open and the recruitment of *Valamugil* into the system. Closure of the mouth in May 1992 (Figure 36) resulted in a low number of species and individuals during this month (Figure 37). Overall, the species diversity in the Zotsha in autumn was moderate (Figure 37).

6.3. Summary

A simplified diagrammatic representation of the seasonal community structure of the Zotsha estuary is presented in Figure 55. During the winter, freshwater species inhabit the upper reaches and deeper pools in the system, while estuarine-dependent marine species inhabit the middle and lower reaches and dominate the fish community. When the system opens with the onset of spring/summer rains, juvenile estuarine-dependent marine species begin recruiting into the system. Spring is also the peak breeding period of resident estuarine (*G. aestuaria* and *G. callidus*) and freshwater (*O. mossambicus*) species and the contribution of these fishes to the ichthyofauna increases during this period. Mortality, due to competition and increased vulnerability to avian predation, and migration to the upper reaches results in a decrease in the proportion of estuarine and freshwater species in summer. The prolonged spawning and recruitment of estuarine dependent species results in an increase in the proportion of these species in summer. In autumn, the system normally closes and during this period, freshwater species redistribute upstream leaving estuarine-dependent marine species to dominate the middle and lower reaches.

Figure 55. Diagramatic representation of the seasonal fish community structure in the Zotsha estuary.

CHAPTER 7.

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 of small estuaries is presented.

7.1. Results

7.1.1. Abiotic characteristics

The abiotic parameters measured in each system are summarised in Table 13.

7.1.1.1. Mouth condition

The mouths of both the Mhlanga and the Damba were predominantly closed but opened frequently during the spring/summer rainfall months for periods ranging from 2 to 25 days. In contrast, the mouth of the Zotsha was permanently open during the spring/summer but closed during the dry winter period.

7.1.1.2. Depth

The average depth of the Mhlanga ranged from 40 cm to 220 cm with the system generally being shallower during the spring/summer. The Damba system also appeared to be shallower during the spring/summer. The average depth of the Damba ranged from 40 cm to 155 cm. The average depth of the Zotsha ranged from 57 cm to 147 cm but was generally greater than 100 cm throughout the study period.

7.1.1.3. Temperature

The average water temperatures of all three systems followed a seasonal pattern with high temperatures being recorded in spring/summer (November - February) and relatively low temperatures being recorded in autumn/winter (May - August). Surface temperatures in the Mhlanga ranged from 29.8°C to 16.2 °C and bottom temperatures ranged from 28.8°C to 15.7°C. Surface and bottom water temperatures in the Damba ranged from 31.7°C to 15.3°C. Surface water temperatures in the Zotsha ranged from 27.7°C to 19.0°C and bottom

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

		Mhlanga	Damba	Zotsha
Mouth condition		Generally closed, frequently opens in summer (2 - 25 days)	Normally closed, occasionally opens in summer (2 -15 days)	Normally open, system closes in winter.
Depth		40 - 220 cm shallow during summer when open.	40 - 155 cm normally shallow (< 100 cm).	57 - 147 cm generally deep (> 100 cm).
Temperature	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 stratification.
Salinity	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.
Dissolved oxygen	Surface Bottom	4.2 - 13.3 mgl^{-1} 3.7 - 9.0 mgl^{-1} Stratified, surface oxygens generally exceed bottom oxygens.	3.6 - 8.3 mgl^{-1} 1.3 - 8.0 mgl^{-1} Occasionally stratified, surface oxygens sometimes exceed bottom oxygens.	4.2 - 8.3 mgl^{-1} 3.7 - 6.0 mgl^{-1} Strongly stratified, surface oxygens exceed bottom oxygens.
Turbidity	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.

temperatures ranged from 25.4°C to 19.3°C. All the systems were thermally stratified with surface temperatures generally exceeding those at the bottom.

7.1.1.4. Salinity

Surface water salinities in the Mhlanga ranged from 0.5‰ to 4.5‰ while bottom salinities ranged from 1.0‰ to 10.7‰. Surface water salinities in the Damba ranged from 0.0‰ to 19.3‰ while bottom salinities ranged from 1.0‰ to 20.0‰. In the Zotsha, surface water salinities ranged from 0.8‰ to 22.7‰ while bottom salinities ranged from 5.5‰ to 26.0‰. All three systems were stratified with bottom salinities exceeding those of the surface waters.

7.1.1.5. Dissolved oxygen

Dissolved oxygen concentrations in the surface waters in the Mhlanga ranged from 13.3 mgl^{-1} to 4.2 mgl^{-1}. Dissolved oxygen concentrations in the bottom waters ranged from 9.0 mgl^{-1} to 3.7 mgl^{-1}. In the Damba, dissolved oxygen concentrations in the surface waters ranged from 8.3 mgl^{-1} to 3.6 mgl^{-1} while those in the bottom waters ranged from 8.0 mgl^{-1} to 1.3 mgl^{-1}. Dissolved oxygen concentrations in the surface waters in the Zotsha ranged from 8.3 mgl^{-1} to 4.2 mgl^{-1}. Dissolved oxygen in the bottom waters of the Zotsha ranged from 6.0 mgl^{-1} to 3.7 mgl^{-1}. Dissolved oxygen in surface waters generally exceeded those in bottom waters in all three systems.

7.1.1.6. Turbidity

Surface water turbidity in the Mhlanga ranged from 0.4 NTU to 62.0 NTU while the turbidity of the bottom waters ranged from 0.3 NTU to 61.0 NTU. Surface water turbidity in the Damba ranged from 0.3 NTU to 5.8 NTU. Bottom water turbidity in the Damba ranged from 0.4 NTU to 5.8 NTU. In the Zotsha, surface water turbidity ranged from 0.3 NTU to 17.8 NTU while the turbidity of the bottom waters ranged from 0.2 NTU to 9.2 NTU. Bottom waters were generally less turbid than those at the surface in all three systems. Overall, turbidities recorded in the Mhlanga, Damba and Zotsha during this study were generally higher in spring and summer than in autumn and winter.

7.1.2. Species composition, diversity and similarity

A total of 68 types of fishes representing 24 families, 39 genera and 56 species were captured in the three estuaries sampled during this study (Tables 14 and 15). Of the 47 kinds of fishes recorded in the Mhlanga, *Gilchristella aestuaria* (46.2%), *Oreochromis mossambicus* (18.0%),

Table 14. Numerical composition of the fishes captured in the Mhlanga, Damba and Zotsha estuaries (August 1990 - May 1992).

Species	Mhlanga (n)	(%)	Damba (n)	(%)	Zotsha (n)	(%)
Acanthopagrus berda	0.54	0.02			0.50	0.04
Ambassis natalensis					2.97	0.22
Ambassis productus	0.59	0.03	21.85	1.52	88.12	6.42
Ambassis sp.	3.78	0.17				
Argyrosomus hololepidotus	4.04	0.18			1.54	0.11
Arothron immaculatus					0.27	0.02
Awaous aeneofuscus			2.46	0.17	0.25	0.02
Caranx ignobilis	0.79	0.04				
Caranx papuensis					2.25	0.16
Caranx sexfasciatus	1.32	0.06			0.50	0.04
Caranx sp.	1.15	0.05			8.66	0.63
Chelonodon laticeps	0.29	0.01				
Crenimugil crenilabis	0.54	0.02	1.43	0.10	60.81	4.43
Croilia mossambica					3.56	0.26
Eleotris fusca					0.27	0.02
Eleotris mauritianus					0.27	0.02
Eleotris sp.	1.47	0.07			0.56	0.04
Elops machnata			0.42	0.03		
Favonigobius rechei					0.27	0.02
Gerres acinaces					0.27	0.02
Gerres rappi	6.42	0.29			20.74	1.51
Gerres sp.	13.86	0.63	12.38	0.86	20.27	1.48
Gilchristella aestuaria	1009.24	46.15	16.51	1.15	152.21	11.09
Glossogobius biocellatus					0.27	0.02
Glossogobius callidus	28.04	1.28	479.92	33.30	85.24	6.21
Glossogobius giuris	0.27	0.01			0.84	0.06
Goby sp. I	0.27	0.01				
Goby sp. II			3.33	0.23		
Goby sp. III					0.27	0.02
Herklotsichtys quadrimaculatus	5.41	0.25				
Juvenile mugilids	101.35	4.63	2.38	0.17	222.43	16.21
Khulia mugil					1.89	0.14
Leiognathus equula	2.65	0.12			2.89	0.21
Lichia amia	3.97	0.18			1.29	0.09
Liza alata	33.19	1.52	0.89	0.06	15.54	1.13
Liza dumerilii	37.55	1.72	3.45	0.24	12.56	0.92
Liza macrolepis	5.64	0.26	0.42	0.03	6.78	0.49
Liza richardsonii			0.56	0.04		
Liza sp.	21.35	0.98			34.86	2.54
Liza tricuspidens	2.97	0.14			7.26	0.53
Lutjanus argentimaculatus					1.77	0.13
Lutjanus fulviflamma					0.81	0.06
Megalops cyprinoides					0.25	0.02
Micropterus salmoides	1.09	0.05				
Monodactylus argenteus	0.79	0.04	0.42	0.03	0.50	0.04
Monodactylus falciformis	3.51	0.16	3.35	0.23	1.89	0.14
Monodactylus sp.					0.29	0.02
Mugil cephalus	35.8	1.64	39.5	2.74	19.18	1.40
Myxus capensis	60.31	2.76	446.07	30.95	51.66	3.76
Oligolepis acutipennis	1.96	0.09				
Oligolepis keiensis	5.88	0.27			2.22	0.16
Oreochromis mossambicus	394.24	18.03	368.59	25.57	145.38	10.59
Pomadasys commersonnii	29.73	1.36			9.43	0.69
Pomadasys sp.					1.10	0.08
Pomatomus saltatrix					0.25	0.02
Psammogobius knysnaensis	0.27	0.01				
Pseudorhombus arsius	0.29	0.01			0.29	0.02
Rhabdosargus holubi	19.46	0.89	13.79	0.96	142.34	10.37
Rhabdosargus thorpei	0.29	0.01			1.91	0.14
Scomberoides sp.	0.81	0.04			0.27	0.02
Sillago sihama	0.54	0.02				
Solea bleekeri	1.15	0.05	3.33	0.23	20.18	1.47
Terapon jarbua	20.87	0.95			100.82	7.35
Tilapia rendallii	0.29	0.01	0.48	0.03	0.54	0.04
Valamugil buchanani	1.34	0.06			9.25	0.67
Valamugil cunnesius	188.71	8.63	3.04	0.21	36.36	2.65
Valamugil robustus	1.08	0.05	0.83	0.06	32.15	2.34
Valamugil sp.	131.62	6.02	15.87	1.10	37.30	2.72
Total number of species	47		24		56	

Table 15. Biomass composition of the fishes captured in the Mhlanga, Damba and Zotsha estuaries (August 1990 - May 1992).

Species	Mhlanga (g)	(%)	Damba (g)	(%)	Zotsha (g)	(%)
Acanthopagrus berda	3.39	0.00			159.88	0.34
Ambassis natalensis					18.11	0.04
Ambassis productus	14.18	0.02	272.39	1.98	413.44	0.88
Ambassis sp.	0.12	0.00				
Argyrosomus hololepidotus	1234.26	1.59			407.38	0.87
Arothron immaculatus					2.74	0.01
Awaous aeneofuscus			26.59	0.19	31.28	0.07
Caranx ignobilis	93.37	0.12				
Caranx papuensis					441.33	0.94
Caranx sexfasciatus	152.29	0.20			67.13	0.14
Caranx sp.	9.62	0.01			23.41	0.05
Chelonodon laticeps	0.03	0.00				
Crenimugil crenilabis	0.85	0.00	2.57	0.02	177.48	0.38
Croilia mossambica					0.81	0.00
Eleotris fusca					0.59	0.00
Eleotris mauritianus					0.38	0.00
Eleotris sp.	0.00	0.00			0.00	0.00
Elops machnata			70.83	0.51		
Favonigobius rechei					0.07	0.00
Gerres acinaces					0.97	0.00
Gerres rappi	102.07	0.13			1245.61	2.65
Gerres sp.	0.88	0.00	4.84	0.04	13.75	0.03
Gilchristella aestuaria	635.72	0.82	11.39	0.08	104.35	0.22
Glossogobius biocellatus					0.84	0.00
Glossogobius callidus	131.37	0.17	1286.74	9.35	71.11	0.15
Glossogobius giuris	0.18	0.00			60.08	0.13
Goby sp. I	0.02	0.00				
Goby sp. II			0.93	0.01		
Goby sp. III					0.23	0.00
Herklotsichtys quadrimaculatus	5.48	0.01				
Juvenile mugilids	26.43	0.03	0.55	0.00	142.18	0.30
Khulia mugil					0.67	0.00
Leiognathus equula	4.18	0.01			147.06	0.31
Lichia amia	1430.93	1.85			704.36	1.50
Liza alata	7314.45	9.44	150.42	1.09	9164.20	19.49
Liza dumerilii	496.00	0.64	341.79	2.48	464.40	0.99
Liza macrolepis	381.54	0.49	28.75	0.21	878.07	1.87
Liza richardsonii			21.47	0.16		
Liza sp.	29.04	0.04			52.38	0.11
Liza tricuspidens	7.20	0.01			252.61	0.54
Lutjanus argentimaculatus					878.73	1.87
Lutjanus fulviflamma					1.68	0.00
Megalops cyprinoides					220.65	0.47
Micropterus salmoides	138.07	0.18				
Monodactylus argenteus	35.56	0.05	7.76	0.06	28.85	0.06
Monodactylus falciformis	163.92	0.21	78.33	0.57	18.68	0.04
Monodactylus sp.					12.51	0.03
Mugil cephalus	5692.93	7.35	3767.44	27.37	2790.53	5.93
Myxus capensis	6006.15	7.75	4478.31	32.54	3997.97	8.50
Oligolepis acutipennis	3.29	0.00				
Oligolepis keiensis	6.89	0.01			0.82	0.00
Oreochromis mossambicus	36651.49	47.29	2699.22	19.61	10263.98	21.83
Pomadasys commersonnii	858.55	1.11			561.24	1.19
Pomadasys sp.					0.05	0.00
Pomatomus saltatrix					192.15	0.41
Psammogobius knysnaensis	0.34	0.00				
Pseudorhombus arsius	6.57	0.01			5.75	0.01
Rhabdosargus holubi	143.13	0.18	182.87	1.33	730.42	1.55
Rhabdosargus thorpei	0.24	0.00			9.70	0.02
Scomberoides sp.	1.66	0.00			0.15	0.00
Sillago sihama	0.03	0.00				
Solea bleekeri	2.53	0.00	9.24	0.07	29.05	0.06
Terapon jarbua	326.14	0.42			275.00	0.58
Tilapia rendallii	58.82	0.08	0.81	0.01	1.32	0.00
Valamugil buchanani	156.82	0.20			4051.28	8.61
Valamugil cunnesius	14942.03	19.28	203.04	1.48	2771.18	5.89
Valamugil robustus	19.35	0.02	78.08	0.57	5102.42	10.85
Valamugil sp.	215.62	0.28	40.23	0.29	37.52	0.08
Total number of species	**47**		**24**		**56**	

Valamugil cunnesius (8.6%), *Valamugil* sp. (6.0%) and juvenile mugilids (4.6%) numerically dominated the ichthyofauna (Table 14). Together these fishes accounted for over 83% of the total catch. In the Damba, 24 kinds of fishes were recorded. The dominant fishes captured were *Glossogobius callidus* (33.3%), *Myxus capensis* (31.0%) and *O. mossambicus* (25.6%) (Table 14). These three species together accounted for over 89% of the catch numerically. A total of 56 kinds of fishes were recorded in the Zotsha during this study. 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). Together these fishes accounted for over 68% of the catch.

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 (Table 15). Together these species accounted for over 91% of the fish biomass captured in 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 comprised over 88% of the catch (Table 15). The species which dominated the fish biomass in the Zotsha were *O. mossambicus* (21.8%), *L. alata* (19.5%), *Valamugil robustus* (10.9%), *Valamugil buchanani* (8.6%), *M. capensis* (8.5%), *M. cephalus* (5.9%) and *V. cunnesius* (5.9%) (Table 15). Together these species contributed over 81% to the fish biomass captured in the Zotsha.

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 (Table 17).

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
Richness (D)	5.98	3.16	7.61
Evenness (J')	0.51	0.49	0.71
Diversity (H')	1.95	1.55	2.85
Diversity (H'w)	1.72	1.76	2.51

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 terms of species biomass composition, the Mhlanga and the Zotsha were 95.9% similar, the Mhlanga and the Damba 93.4% similar and the Damba and the Zotsha 80.1% similar (Table 17).

Table 17. Percent similarity of the ichthyofauna of the Mhlanga, Damba and Zotsha estuaries (IS_J = Jaccard's index of similarity, IS_S = Sørensen's index of similarity, IS_E = Ellenberg's index of similarity using numbers (n) and mass (g)).

	Mhlanga	Damba	Zotsha
IS_J			
Mhlanga	-	39.22	58.46
Damba	39.22	-	35.59
Zotsha	58.46	35.59	-
IS_S			
Mhlanga	-	56.34	73.79
Damba	56.34	-	52.50
Zotsha	73.79	52.50	-
IS_E (n)			
Mhlanga	-	94.22	98.10
Damba	94.22	-	84.85
Zotsha	98.10	84.85	-
IS_E (g)			
Mhlanga	-	93.45	95.93
Damba	93.45	-	80.58
Zotsha	95.93	80.58	-

7.1.3. Community structure

7.1.3.1. Overall abundance and biomass

Estuarine species comprised 47.9% of the ichthyofauna in the Mhlanga, numerically followed by estuarine-dependent marine species (33.2%) and freshwater species (18.1%). Marine species numerically comprised 0.8% of the ichthyofauna captured. Estuarine-dependent marine species and freshwater species dominated the fish biomass in the Mhlanga and contributed 49.5% and 47.5% to the fish biomass respectively. Estuarine species comprised 1.0% of the total biomass and marine species comprised 1.9% (Figure 56).

Estuarine-dependent marine species numerically dominated the fish fauna in the Damba and contributed 39.5% to the total. Estuarine species numerically comprised 34.5% of the total fishes and freshwater species comprised 25.8%. Marine species contributed 0.1% to the total catch. In terms of biomass, estuarine-dependent marine species dominated the ichthyofauna in the Damba and accounted for 70.6% of the total catch followed by freshwater species (19.8%) and estuarine species (9.4%). Marine species contributed 0.2% to the total biomass (Figure 56).

In the Zotsha, estuarine-dependent marine species dominated the fish community both by number and by mass. This group of fishes comprised 64.9% numerically and 64.2% by mass to the ichthyofauna. Estuarine species comprised 17.8% numerically and 0.4% by mass while freshwater species contributed 10.7% numerically and 22.0% by mass to the fishes captured. The Zotsha was the only system in which marine species contributed significantly to the ichthyofauna and comprised 6.5% numerically and 13.5% by mass of the fishes captured (Figure 56).

7.1.3.2. Seasonal changes in relative abundance and biomass.

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 in winter. In spring, freshwater species and estuarine species numerically dominated the ichthyofauna in the Mhlanga. 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 in the Mhlanga both numerically and by mass (Figures 57 and 58).

a) Mhlanga estuary

Percentage number

0.8%

18.1%

33.2%

47.9%

Percentage biomass

1.9%

49.5%

47.5%

1.0%

	Freshwater
	Estuarine
	Estuarine-marine
	Marine

b) Damba estuary

Percentage number

0.1%

25.8%

39.5%

34.5%

Percentage biomass

0.2%

19.8%

9.4%

70.6%

c) Zotsha estuary

Percentage number

6.5%

10.7%

17.8%

64.9%

Percentage biomass

13.5%

22.0%

0.4%

64.2%

Figure 56. Percent numerical and biomass contribution of freshwater species, estuarine species, estuarine-dependent marine species and marine species to the ichthyofauna of the Mhlanga (a), Damba (b) and Zotsha (c) estuaries.

Figure 57. Seasonal numerical contribution of freshwater species, estuarine species, estuarine-dependent marine species and marine species to the ichtyofauna of the of the Mhlanga (a), Damba (b) and Zotsha (c) estuaries, August 1990 - May 1992.

Figure 58. Seasonal biomass contribution of freshwater species, estuarine species, estuarine-dependent marine species and marine species to the ichthyofauna of the Mhlanga (a), Damba (b) and Zotsha (c) estuaries, August 1990 - May 1992.

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 the dominant fishes 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 the Damba in autumn (Figures 57 and 58).

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 numerically dominated the ichthyofauna with an increase in the contrib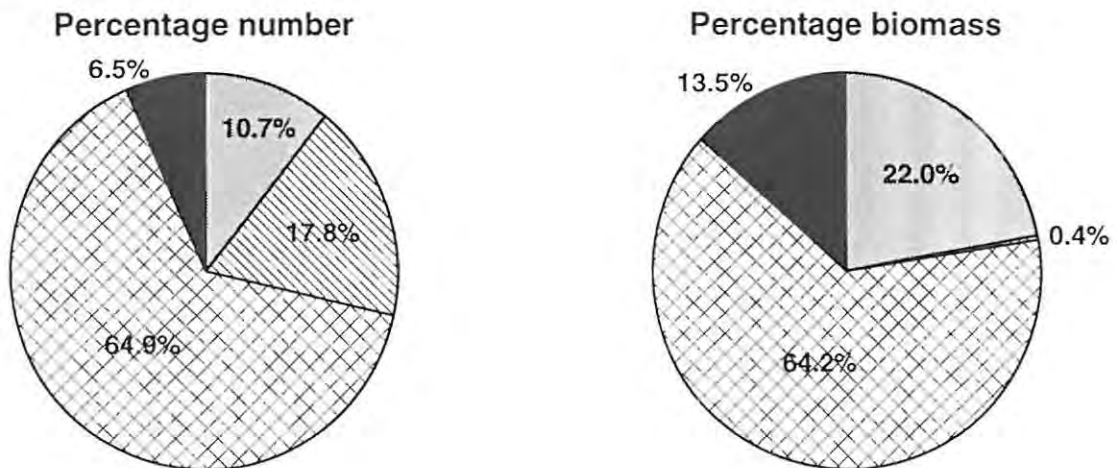ution of freshwater species. Both freshwater and estuarine-dependent marine species dominated the fish biomass in spring. Estuarine-dependent marine species dominated the ichthyofauna in the Zotsha in summer both numerically and in terms of biomass. In autumn estuarine-dependent marine species were the dominant group of fishes with freshwater and estuarine species also being well represented (Figures 57 and 58).

7.1.3.3. Seasonal changes in actual abundance and biomass

High numbers and biomass of freshwater species were captured in all three systems in spring and summer. High numbers and biomass of freshwater species were also recorded in the Damba and the Zotsha in autumn 1991 (Figures 59 and 60).

High numbers and biomass of estuarine species were recorded in spring in the Mhlanga and Zotsha. A peak in numbers of estuarine species was also recorded in the Mhlanga in autumn 1992 while in the Zotsha, high numbers were also recorded in autumn 1991 and winter 1991. A peak biomass of estuarine species was also recorded in the Zotsha in autumn 1991. Numbers and biomass of estuarine species in the Damba peaked in summer 1991 and winter 1991 (Figures 59 and 60).

High numbers of estuarine-dependent marine species were recorded in the Mhlanga in autumn 1991 and spring 1991. A peak biomass of this group of fishes was recorded in the Mhlanga in summer 1992. High numbers and biomass of estuarine-dependent marine species were recorded in the Damba in winter 1990, summer 1991 and summer 1992. In the Zotsha, high numbers of estuarine-dependent marine species were recorded in winter with a high biomass being recorded in summer 1991 and spring 1991 (Figures 59 and 60).

Figure 59. Seasonal fluctuation 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, August 1990 - May 1992.

Figure 60. Seasonal fluctuation 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, August 1990 - May 1992.

High numbers and biomass of marine species were captured in the Mhlanga in summer 1991, autumn 1991 and summer 1992. Marine species were recorded in the Damba in winter 1990 and autumn 1992. High numbers of marine species were captured in the Zotsha in winter 1991 and summer 1992 with a peak biomass occurring in summer 1992 (Figures 59 and 60).

7.2. Discussion

7.2.1. Abiotic characteristics

The south east 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 small 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.

7.2.1.1. 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). Similar conditions occurred during this study, particularly in the Mhlanga and Damba, where the mouths of these systems opened frequently during the summer but closed 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.

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).

7.2.1.2. 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 (Table 13).

7.2.1.3. Temperature

Temperatures recorded during this study followed a seasonal pattern where the systems were cooler during the winter and warmer during the summer (Table 13). Thermal stratification was also 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.

7.2.1.4. Salinity

When generally closed systems open to the sea, there is initially a strong outflow of fresh water, which after a while decreases, allowing tidal penetration of seawater (Whitfield, 1990). At this time these systems may exhibit vertical and horizontal estuarine salinity gradients. Barrier overwash of the sea also enhances salinity as observed by Begg (1984a) in the Zinkwasi and Mvuzi systems. All the systems surveyed during this study were, on average, stratified with respect to salinity (Table 13). Begg (1984a) found that closed systems often exhibited stratification where, due to over-protection from the wind (which is the primary mixing mechanism in such systems), the salinity of the bottom water was often found to be much greater than that at the surface.

7.2.1.5. 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).

7.2.1.6. Turbidity

A number of factors interact to establish the turbidity regimes present in Natal's estuaries, these are river flow, substratum type, wind and tides (Cyrus, 1988). The closure of the mouths of small estuaries, due to low inflow rates, leads to the deposition of fine sediment on the substratum and an increase in the clarity of estuarine waters. However when they re-open at 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 were clear, particularly in the closed systems during winter, due to the slow inflow of the river. 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 by Cooper (1991) and is reproduced in Figure 61. 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 period. During this stable period the systems are typically deep, calm and clear (Figure 61A). Overtopping of the bar by sea water enhances salinity and, due to a lack of wind induced mixing, they are often stratified both in terms of

Figure 61. Schematic diagram illustrating cyclic physical processes in small temporarliy open/closed estuaries on the Natal coast (after Cooper, 1991).

salinity and temperature. Stratification also results in depressed oxygen levels in the bottom waters. Following heavy rains, particularly 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 when they open and they drain (Figure 61B). When river flow decreases, sea water may enter the systems and they may exhibit typical estuarine salinity gradients before longshore drift and/or onshore sediment transport eventually closes their mouths (Figure 61C).

7.2.2. Species composition, diversity and similarity

Natal estuaries have the highest fish species diversity in southern Africa (Whitfield, 1983). Using data from Wallace et al. (1971), Wallace (1975), Whitfield (1980), Blaber & Cyrus (1981), Begg (1984a; 1984b), Junor (1990) and Coke (1990), some 347 species of fish have been recorded in Natal's estuaries. Over 67% (233) of these are stenohaline inshore marine species which are ecologically distinct from estuarine forms and as such are not considered part of the estuarine fauna (Wallace, 1975a). A further 33 species (10%) are inshore marine species whose juveniles are found mainly at sea but are also abundant in estuaries. Although estuaries are not essential for their survival, these areas do make a contribution to the adult stocks because juveniles that grow up in estuaries migrate to sea to join breeding populations (Wallace et al., 1984). Some 40 (12%) fish species are euryhaline marine species which are dependent on estuaries during the juvenile phase of their life cycles and whose survival is determined by ecologically viable estuaries along the Natal coast (Wallace et al., 1984; Cyrus, 1991). Nineteen fish species (5%) are species which are dependent upon estuaries for their entire life cycle (Cyrus, 1991). Included in this group are three species which are considered vulnerable and five species which are rare (Skelton, 1987; 1990). Of the remaining species recorded in Natal's estuaries, 18 (5%) are freshwater species which are able to penetrate the saline waters of estuaries to varying degrees (Junor, 1990; Coke, 1990). Included in these are four species of freshwater eels, whose small elvers pass through estuaries in their migration from the sea into South African rivers, and which again occur in estuaries as adults during their migration back to sea to spawn (Bruton et al., 1987). Additional to these indigenous species, four exotic freshwater species have also been recorded in Natal's estuaries. A total of 70 kinds of fishes (58 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,

temperate endemic South Coast 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, Day *et al.*, 1981; Whitfield *et al.*, 1989). This is linked to the attenuation in the distribution of tropical species where the fauna of estuaries in Transkei, Natal and Mozambique are dominated by subtropical and tropical Indo-Pacific species (Day *et al.*, 1981). South of Transkei there is a marked change and the percentage of tropical species decreases while that of endemic species increases. Most of the species from the southern Cape are either endemic or cold water forms from the south (Wallace, 1975a; Wallace & van der Elst, 1975; Blaber 1981; Day *et al.*, 1981; Whitfield, 1983).

7.2.2.1. 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 such as *Acanthopagrus berda*, *Argyrosomus hololepidotus*, *Rhabdosargus* spp., *Pomadasys* spp. and Mugilidae. 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. This system had the lowest species diversity (Table 16) with *Glossogobius callidus* and *O. mossambicus* being among the dominant 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*, *Valamugil* sp., juvenile mugilids, *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, Ambassis productus , M. capensis, V. cunnesius, V. robustus, M. cephalus* and *L. alata* (Tables 14 and 15).

7.2.2.2. Depth

The fish in estuaries appear to show a preference for relatively shallow waters which provide habitat types needed by juveniles, such as aquatic macrophyte beds and fringing vegetation of reeds or mangroves (Wallace & van der Elst, 1975; Blaber, 1985). Shallow waters also 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, apart from *Elops machnata*, piscivorous fishes were essentially absent (Tables 14 and 15).

7.2.2.3. 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. Sub-tropical 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 in 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 importance of temperature on fish distribution declines and the effects of salinity become more important.

7.2.2.4. Salinity

Essential to fish which enter estuaries is 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 Zinkwasi estuary, which was closed for 80% of the year, the system was sufficiently saline (21‰) due to topping of the bar,

to maintain a wide variety of species that are normally found in open, tidally influenced systems. The moderate salinities recorded in the Mhlanga and Zotsha may have accounted for the occurrence of species such as *Khulia mugil, Arothron immaculatus, Chelonodon laticeps, Herklotsichthys quadrimaculatus, Pseudorhombus arsius* and *Sillago sihama* in these systems during this study (Tables 14 and 15). These species were not captured in the Damba which was generally less saline (Figure 25).

7.2.2.5. 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 mgl^{-1}) (Blaber, 1987). Low oxygen levels (<5 mgl^{-1}) were recorded in both the surface and bottom waters in all three systems during this study (Table 13) and may account for mugilids being among the dominant fishes captured (Tables 14 and 15).

7.2.2.6. 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 entire species composition of small estuarine systems. They divided the fish fauna found in Natal estuaries into groups according to their occurrence in various turbidities. These were 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 reaching high levels (Cyrus, 1988). This may account for the occurrence of clear water and clear to partially turbid species such as *Gerres rappi, Monodactylus argentius, 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 *Pomadasys commersonnii, Acanthopagrus berda* and *Terapon jarbua* (Cyrus & Blaber, 1987a) were only recorded in the Mhlanga and Zotsha (Tables 14 and 15).

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, a wide range of substrates 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 of thousands of hectares (Blaber, 1985). This was evident during this study where the Damba which has an area of 1.7 hectares (Begg, 1978), had a lower species richness and diversity than the Zotsha and Mhlanga (Table 16) which have areas of 7.3 and 11.4 hectares respectively (Begg, 1978).

Begg (1984a) concluded that that the principal factor which determined the species composition and diversity of Natal's estuaries was the the degree of contact each system had with the sea. 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 ($IS_J = 58.5\%$, $IS_S = 73.8\%$) (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 ($IS_J = 39.2\%$, $IS_S = 56.3\%$) than to those captured in the nearby Zotsha ($IS_J = 35.6\%$, $IS_S = 52.5\%$) (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 the estuaries were dominated by similar fish assemblages. The Mhlanga was numerically dominated by *Gilchristella aestuaria, Oreochromis mossambicus, Valamugil cunnesius, Valamugil* sp. and juvenile mugilids (Table 14). In terms of biomass, *Oreochromis mossambicus, Valamugil cunnesius, Liza alata, Myxus capensis* and *Mugil cephalus* dominated the ichthyofauna in the Mhlanga (Table 15). This compares with previous collections made in the Mhlanga where the dominant fish species recorded by Whitfield (1980c) were *O.*

mossambicus, V. cunnesius, G. aestuaria, L. alata, M. capensis and *M. cephalus*. Begg (1984a) found that *V. cunnesius, O. mossambicus, Glossogobius giuris* and *G. aestuaria* were the dominant species in the Mhlanga. *V. cunnesius*, juvenile mugilids and *Liza dumerilii* were the dominant fishes captured in the Mhlanga by Ramm *et al.* (1986). Harrison (1990) found that *G. aestuaria,V. cunnesius, L. alata, O. mossambicus, Myxus capensis* and *Mugil cephalus* were the dominant species.

The Damba estuary was numerically dominated by *Glossogobius callidus, Myxus capensis* and *O. mossambicus* (Table 14). *M. capensis, M. cephalus, O. mossambicus* and *G. callidus* dominated the fish biomass captured in the Damba (Table 15). Begg (1984b) found that *Glossogobius giuris* and *Oreochromis mossambicus* were the dominant species in the Damba while Ramm *et al.* (1985a) found that *Glossogobius giuris, Liza dumerilii, O. mossambicus, Ambassis productus* and *Gilchristella aestuaria* dominated their collections.

The ichthyofauna of the Zotsha estuary was numerically dominated by juvenile mugilids, *G. aestuaria, O. mossambicus, Rhabdosargus holubi, Terapon jarbua, Ambassis productus* and *G. callidus* (Table 14). The species which dominated the fish biomass in the Zotsha were *O. mossambicus, L. alata, Valamugil robustus, Valamugil buchanani, M. capensis, M. cephalus* and *V. cunnesius* (Table 15). *Glossogobius giuris, Ambassis productus* and *Solea bleekeri* were the most abundant species captured in the Zotsha by Begg (1984b). Ramm *et al.* (1985b) found that *Valamugil cunnesius, A. productus, V. buchanani, M. capensis* and *Liza macrolepis* dominated their fish collections in the Zotsha while Harrison (1990) found that juvenile mugilids, *T. jarbua, V. robustus, V. cunnesius* and *Mugil cephalus* were the dominant fishes.

Overall, the dominant fishes captured in the Mhlanga, Damba and Zotsha during this study were mugilids (juveniles, *Valamugil* spp., *L. alata, M. capensis* and *M. cephalus*), *O. mossambicus, G. aestuaria* and *G. callidus* (Tables 14 and 15). Similar fish assemblages were 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 by Ramm *et al.* (1987). Mugilids were a group of fishes that were undersampled by Begg (1984a; 1984b) because of the trawl gear used.

7.2.3. 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

56). During the course of his study Begg (1984a) found that permanently open estuaries were dominated by immigrant marine species, whereas in temporarily closed systems the populations were dominated by resident estuarine and freshwater species. The high contribution of marine fishes to the ichthyofauna of the Zotsha, both numerically and by mass (Figure 56), is probably a result of the predominantly open condition of the mouth of the system.

7.2.3.1. Freshwater species

Freshwater species comprised 18.1% (47.5% by mass) of the fishes in the Mhlanga, 25.8% (19.8% by mass) of the ichthyofauna in the Damba and 10.7% (22.0% by mass) of the fishes in the Zotsha (Figure 56). 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 during this study and comprised 18.0% numerically and 47.3% by mass of the fishes captured in the Mhlanga. In the Damba, *O. mossambicus* numerically comprised 25.6% of the total catch and 19.6% of the total fish biomass. *O. mossambicus* comprised 10.6% numerically and 21.8% by mass of the fishes in the Zotsha (Tables 14 and 15). *O. mossambicus* was also found to be common in the Tongati and Mdloti estuaries by Blaber *et al.* (1984). The distribution and occurrence of *Oreochromis mossambicus* in estuaries is governed by an interplay of factors including salinity stability (although they can tolerate both high and low extremes); water currents (*O. mossambicus* avoids areas where high current speeds exist); 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 59 and 60) are probably a reflection of *O. mossambicus* inhabiting 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 59 and 60). This corresponds to the breeding cycle of *O. mossambicus* which takes place in shallow areas during spring and summer (September - February) (Bruton & Boltt, 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 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 59 and 60). Shallow waters also make *O. mossambicus* more susceptible to capture, thus further contributing to the increase in numbers and biomass. The particularly shallow nature of the Zotsha in autumn 1991 (Figure 36) probably also accounted for the high numbers and biomass of freshwater species captured during that period (Figures 59 and 60). 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 & Boltt, 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 59 and 60).

7.2.3.2. Estuarine species

Estuarine species numerically comprised 47.9% of the fishes captured in the Mhlanga estuary and 1.0% of the biomass. In the Damba system estuarine species comprised 34.5% of the total catch numerically and 9.4% by mass. Estuarine species captured in the Zotsha contributed 17.8% numerically and 0.4% to the biomass (Figure 56).

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 African estuaries are the clupeid *Gilchristella aestuaria* and a number of Gobiidae (Blaber, 1985). *G. aestuaria* was the dominant estuarine species in the Mhlanga and numerically comprised 46.2% and 0.8% by mass of the fishes captured (Tables 14 and 15). In the Damba, the gobiid *Glossogobius callidus* was the

dominant estuarine species and comprised 33.3% numerically and 9.4% by mass of the total catch (Tables 14 and 15). Both *G. aestuaria* and *G. callidus* were well represented in the Zotsha (Tables 14 and 15) and together constituted 17.3% numerically and 0.4% by biomass of the fishes in the Zotsha.

G. aestuaria is a pelagic shoaling zooplanktivore (Blaber, 1979) which occurs in open waters (Whitfield & Blaber, 1978b). The poor contribution of *G. aestuaria* to the ichthyofauna of the Damba (Tables 14 and 15) may be a result of the generally shallow nature of the system. Shallow waters also renders fish particularly vulnerable to bird predation (Whitfield & Blaber, 1978c; 1978d; 1978e). *G. aestuaria* is an important prey item for birds (Day *et al.*, 1981; Wallace *et al.*, 1984) and the shallowness of the Damba may have increased their susceptibility to bird predation thus further accounting for their low contribution. *G. callidus* on the other hand is a benthic species (Smith & Heemstra, 1986) 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; Cooper pers. comm.), while the Mhlanga estuary is characterised by a sandy mud and silt substratum (Begg, 1984b; Cooper pers. comm. 1993) 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. The low numbers and biomass of estuarine species during this study in winter 1990 (Figures 59 and 60) may be due to *G. aestuaria* and *G. callidus* predominating in the upper reaches of these systems.

Both *G. aestuaria* and *Glossogobius* breed throughout the year with a peak in late spring and summer (Crass, 1964; Blaber, 1979; Bruton & Kok, 1980; Day *et al.*, 1981; Bruton *et al.*, 1982; van der Elst, 1988) and this probably accounted for the high numbers and biomass of estuarine species captured in spring during this study (Figures 59 and 60). 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, *Gilchristella 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 (Crass, 1964; Bruton & Kok, 1980; 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 may also be a result of the shallow nature of these systems after they breached (Figures 10 and 25) resulting in a redistribution of these species to 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 high numbers and biomass of estuarine species recorded in the Mhlanga estuary in autumn 1992 and the high numbers and biomass in the Damba and Zotsha systems in winter 1991 (Figures 59 and 60).

7.2.3.3. Estuarine-dependent marine species

Estuarine-dependent marine species are inshore shallow-water 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). Estuarine-dependent marine species numerically comprised 33.2% of the fishes captured in the Mhlanga and 49.5% of the biomass (Figure 56). In the Damba, this group of fishes contributed 39.5% numerically and 70.6% by biomass to the total ichthyofauna (Figure 56). Estuarine-dependent marine species comprised 64.9% of the total fishes captured in the Zotsha numerically and 64.2% of the total biomass (Figure 56).

The dominant estuarine-dependent marine fishes captured in the Mhlanga during this study were *V. cunnesius*, *Valamugil* sp., juvenile mugilids, *M. capensis*, *M. cephalus* and *L. alata* and together these taxa comprised 25.2% of the fish fauna numerically and 44.1% by mass. In the Damba, *M. capensis* and *M. cephalus* were the dominant estuarine-dependent marine species. Together these two species comprised 33.7% numerically and 59.9% by mass of the ichthyofauna in the Damba. The dominant estuarine-dependent marine fishes captured in the

Zotsha were juvenile mugilids, *R. holubi*, *T. jarbua*, *A. productus*, *M. capensis*, *V. cunnesius*, *V. robustus*, *M. cephalus* and *L. alata*. Together these fishes numerically comprised 51.6% of the estuarine-dependent marine species and 54.0% of the biomass.

The dominant estuarine-dependent marine group captured in all three systems during this study were mugilids, namely juveniles, *Valamugil*, *L. alata*, *M. capensis* and *M. cephalus* (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 grey mullets (Mugilidae) are probably the single most abundant group of fishes in all categories of estuary in south east Africa.

Mullet are iliophagous or detritus feeders and interspecific competition is reduced by the various species selecting sand particles of different sizes (Blaber, 1976; 1977; Whitfield & Blaber, 1978a). *Liza alata* prefers coarse sand; *Mugil cephalus* medium sand; *Myxus capensis* fine and medium sand and *Valamugil* fine sand (Blaber, 1977). Blaber (1985) suggested that those species which prefer fine substrata may enter estuaries because such fine sediments accumulate in estuaries and are uncommon in the sea. This may account for the high contribution of *Valamugil* in the Mhlanga which has a finer sediment than the Damba and Zotsha.

Myxus capensis is a catadromous species which shows a distinct preference for the freshwater areas of eastern Cape estuaries (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. The relatively high contribution of *R. holubi*, *T. jarbua* and *A. productus* to the estuarine-dependent marine species captured in the Zotsha estuary is probably a result of the almost permanently open mouth of the system, allowing the juveniles of these species to recruit into the estuary once the adults have spawned at sea.

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 larva 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 59 and 60) 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 closed Bot River estuary where the catches of large individuals of estuarine-dependent marine species declined after it had opened.

Recruitment of juveniles into permanently open estuaries takes place during winter and spring (June - November) when river outflow is at a minimum (Wallace & van der Elst, 1975). This corresponds with the relatively high numbers of estuarine-dependent marine species captured in the predominantly open Zotsha estuary in winter 1991 (Figure 59).

Blaber (1987) described a possible mechanism by which postlarval mullet locate and migrate into estuaries by following a turbidity gradient and utilising tidal currents. In Natal, turbidity gradients exist from the mouths of estuaries into the sea, particularly during the rainy season (Cyrus, 1988) and the fry, by following an increasing turbidity gradient would ultimately reach shallow, estuarine areas (Blaber, 1987). Movement into the estuary was achieved by fish passively drifting on the flood tide and settling on 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 recruitment of larger fry 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 against strong outflowing water, suggesting that these fish can also gain access into closed systems by actively migrating into them when they open. Hall *et al.* (1987) found that tidal flow was not important in the migration of juvenile fish within the Wilderness 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 Hage Hage estuary 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 closed estuaries prematurely and (b) droughts which would delay the opening of these systems (Whitfield, 1990). In 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 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 high numbers of estuarine-dependent marine species captured in the Damba in summer and in the Mhlanga during summer, autumn and spring 1991 (Figure 59) is probably a result of the later recruitment of these fishes into the systems when they opened.

7.2.3.4. Marine species

Marine species which occurred in the estuaries during this study were largely inshore marine species whose juveniles are found mainly at sea but are also abundant in estuaries (Wallace *et al.*, 1984). This group of fishes comprised 0.8% numerically and 1.9% by mass of the ichthyofauna of the Mhlanga, 0.1% numerically and 0.2% by mass of the ichthyofauna of the Damba and 6.5% numerically and 13.5% by mass of the ichthyofauna of the Zotsha (Figure 56). Although estuaries are not essential for the survival of this group of fishes, these areas do make a contribution to the adult stocks because juveniles that grow up in estuaries migrate to sea to join breeding populations (Wallace *et al.*, 1984).

The high contribution of marine fishes to the ichthyofauna of the Zotsha is probably a result of the predominantly open condition of the mouth of the system. The relatively high numbers and biomass of marine species captured in the Mhlanga summer (Figures 59 and 60) is probably a result of these fishes straying into the system after it had opened.

7.2.4. Seasonal community structure

7.2.4.1. Winter

During winter, estuarine-dependent marine species were a dominant component of the ichthyofauna of all three systems, both numerically and in terms of biomass (Figures 57 and 58). This is is probably a reflection of the distribution of the various types of fishes, where freshwater (*O. mossambicus*) and estuarine species (*G. aestuaria* and *G. callidus*) inhabit the upper reaches (Branch & Grindley, 1979; Blaber *et al.*, 1984; Beckley, 1984), leaving estuarine-dependent marine species (mugilids) to dominate in the middle and lower reaches. *O. mossambicus* also inhabits deeper less accessible areas during the cool winter months (Bruton & Boltt, 1975; Caulton, 1979), further contributing to the low numerical contribution of freshwater species in winter. The relatively high biomass contribution of freshwater species to the winter ichthyofauna (Figure 58) is a result of large specimens of *O. mossambicus* being captured.

Whitfield (1980a; 1988) found that the distribution of fishes in the Mhlanga and the 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 predominantly catadromous life-history style (Bok, 1979; Whitfield, 1980a).

Whitfield (1980a; 1980c) found 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 zooplankon and zoobenthos in the Mdloti in winter when the mouth was closed. The relatively high numerical contribution of estuarine species in the Mhlanga and Damba systems in winter 1990 and 1991 respectively (Figure 57) is probably a reflection of the extended breeding period of *G. aestuaria* and *G. callidus*, allowing them to make use of the favourable, relatively stable winter conditions.

7.2.4.2. Spring

The relative proportions of freshwater and estuarine fishes increased in all three systems in spring, with freshwater fishes dominating the fish biomass (Figures 57 and 58). This corresponds with the peak breeding period for *G. aestuaria*, *Glossogobius* and *O. mossambicus* (Crass, 1964; Bruton & Boltt, 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 into 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 57 and 58) may be a result of the emigration of adults from the systems to spawn, which takes place in the vicinity of estuary mouths from May to November (Wallace, 1975b).

7.2.4.3. Summer

The extended spawning period of estuarine-dependent marine species prolongs the period during which larvae and juveniles occur in the inshore marine environment and acts as a buffer against recruitment failure as a result of adverse marine or estuarine conditions (Wallace, 1975b). Recruitment of juveniles into estuaries takes place 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

proportion of estuarine-dependent marine species to the ichthyofauna in summer (Figures 57 and 58) is most likely a result of the extended spawning and successful recruitment of this group of fishes into the systems (Wallace, 1975b; Wallace & van der Elst, 1975).

After breaching, the Mhlanga and Damba systems are very shallow. Although shallow waters may aid small fishes in avoiding large piscivorous fish (Whitfield & Blaber, 1978b), it renders them particularly vulnerable to bird predation including herons, cormorants and terns (Whitfield & Blaber, 1978c; 1978d; 1978e). Working in the West Klienemond 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 (Blaber, 1973; 1985). Bird predation during this study may have contributed to the decrease in the relative proportions of both estuarine and freshwater species in summer (Figures 57 and 58). Another consequence of temporarily closed systems opening is that available habitat and food resources are drastically reduced due to exposure of the tidal flats 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 the spring/summer and may also have contributed to the decline in the proportion of estuarine and freshwater species in summer.

7.2.4.4. Autumn

In autumn, estuarine-dependent marine species were well represented in all systems, both numerically and by mass (Figures 57 and 58). The high proportion of estuarine-dependent marine species in autumn is most likely a reflection of the deeper nature of the systems, allowing *O. mossambicus* to inhabit the preferred upper reaches (Bruton & Boltt, 1975; Caulton, 1979) and estuarine-dependent marine species to occupy and dominate the lower reaches. The successful summer breeding of *Gilchristella aestuaria* probably accounts for the high numerical contribution of estuarine species in the Mhlanga in autumn 1992 (Figures 57 and 58).

7.3. Summary & Conclusions

Based on the information presented, a simplified conceptual model of the fish community structure of temporarily open/closed estuaries is presented in Figure 62. During winter, small estuaries on the Natal coast are closed and deep, and due to inundation of the adjacent vegetated floodplain, food resources are high. 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

A

Autumn - Winter

high water levels increase food and habitat availability

freshwater and estuarine species occur mainly in the upper reaches

estuarine-dependent marine species occupy the middle and lower reaches

adult estuarine-dependent marine species spawn in inshore marine environment

B

Spring - Summer

low water levels limit food and habitat availability and increase fishes vulnerability to bird predation

peak breeding of freshwater and estuarine species

freshwater and estuarine species redistribute and concentrate in the lower reaches

adult estuarine-dependent marine species emigrate to sea to spawn

juveniles begin recruitment into estuaries

C

Summer - Autumn

water levels rise and food and habitat availability increase

freshwater and estuarine species migrate back into the upper reaches

estuarine-dependent marine species occupy the lower reaches

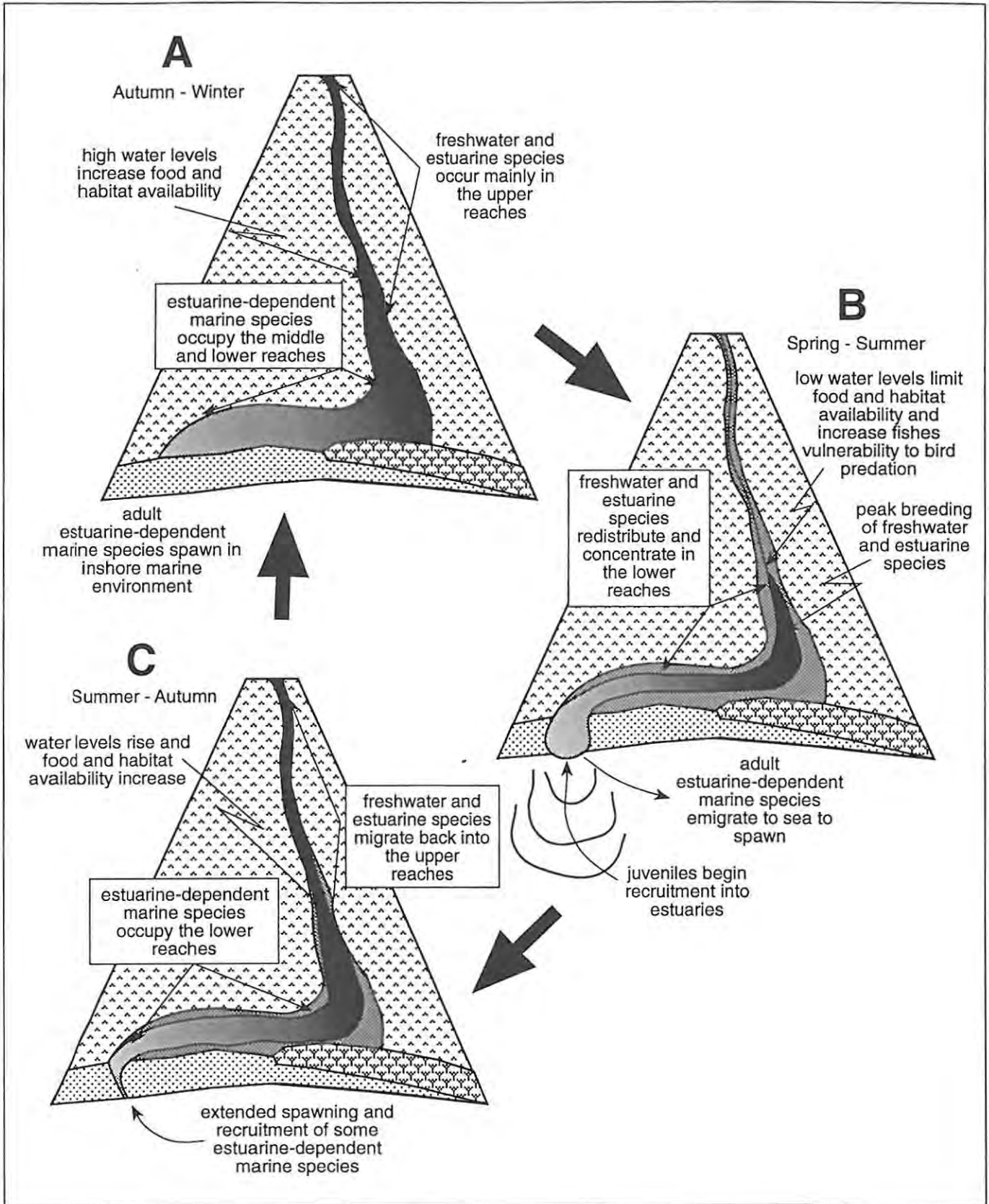extended spawning and recruitment of some estuarine-dependent marine species

Figure 62. Schematic diagram illustrating cyclical fish community structure in small temporarliy open/closed estuaries on the Natal coast.

reaches (Figure 62A). When these estuaries open with the onset of the spring/summer rains, adult estuarine-dependent marine species emigrate from these systems to spawn at sea and juveniles begin recruiting into the estuaries. Spring is also the peak breeding period of resident estuarine (*G. aestuaria* and *G. callidus*) and freshwater (*O. mossambicus*) species and results 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 freshwater and estuarine species into the lower reaches, further contributing to the increase in the proportion of these fishes (Figure 62B). 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 exposure of the bed subaerially. 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, while the prolonged spawning and 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 and food resources and habitat availability increase. This permits the redistribution of freshwater and estuarine species upstream, leaving estuarine-dependent marine species to occupy the lower reaches and dominate the fish community (Figure 62C).

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 sequence where there is a tendency for freshwater fish such as the Cichlidae to move down to the estuaries in the rainy season. 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). This is similar to the pattern described above for this study.

Weinstein (1985) found that warm-temperate and tropical estuaries were highly programmed systems, where the spatial and temporal separation of fish species contributed 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 south east 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 by freshwater species (*O. mossambicus*) and estuarine-dependent marine species (Mugilidae) as outlined in this study, may serve to reduce competition particularly during the unstable open phase when habitat is limited and food resources are low and thus optimise the nursery potential of these small estuaries. During the closed phase, the nursery function of temporarily open/closed estuaries is enhanced due to

elevated water levels inundating intertidal and supratidal habitats thus increasing shallow littoral habitats 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 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 the viability of estuarine-dependent resources must not be underestimated. By providing a continuous sequence of sheltered environments over a long stretch of coastline, it is likely that millions of juveniles of estuarine-dependent marine species make use of these estuarine nursery areas, and when they return to the sea, supplement the breeding populations of these recreationally and commercially important fish stocks.

Weinstein (1985) found it surprising just how little we actually know about the way in which estuaries 'work'. The Natal coast is characterised by a high frequency of estuaries, the vast majority of which are temporarily open/closed systems (Cooper, 1991). Although based on a limited number of samples and systems, this study may contribute toward a basic understanding of the ecology of the ichthyofauna of Natal's smaller estuaries.

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Appendix 1. Results of the length-mass relationship of selected species captured during this study (n = number of specimens, a = intercept, b = slope).

Species	Common name	n	a	b	r²
Acanthopagrus berda	Riverbream	4	0.00001066	3.263	1.000
Ambassis natalensis	Slender glassy	11	0.00004472	2.878	0.973
Ambassis productus	Longspine glassy	167	0.00001857	3.081	0.959
Argyrosomus hololepidotus	Kob	19	0.00003516	2.884	0.959
Awaous aeneofuscus	Freshwater goby	5	0.00000591	3.299	0.998
Caranx papuensis	Brassy kingfish	9	0.00004784	2.899	0.989
Caranx sexfasciatus	Bigeye kingfish	12	0.00002527	3.015	0.999
Crenimugil crenilabis	Fringelip mullet	230	0.00000595	3.336	0.976
Croilia mossambica	Naked goby	9	0.00000009	4.329	0.832
Gerres rappi	Evenfin pursemouth	79	0.00000890	3.294	0.998
Gilchristella aestuaria	Estuarine roundherring	677	0.00000145	3.581	0.971
Glossogobius callidus	River goby	647	0.00001019	3.129	0.970
Glossogobius giuris	Tank goby	4	0.00000784	3.154	0.999
Herklotsichthys quadrimaculatus	Blueline herring	20	0.00004879	2.707	0.925
Kuhlia mugil	Rock flagtail	7	0.00000065	4.010	0.773
Leiognathus equula	Slimy	15	0.00006676	2.871	0.988
Lichia amia	Garrick	18	0.00001491	3.054	0.998
Liza alata	Diamond mullet	187	0.00001951	3.013	0.989
Liza dumerilii	Groovy mullet	148	0.00002604	2.948	0.994
Liza macrolepis	Large-scale mullet	43	0.00002542	2.987	0.994
Liza tricuspidens	Striped mullet	38	0.00001597	3.007	0.986
Lutjanus arjentimaculatus	River snapper	7	0.00003649	2.960	1.000
Monodactylus argentius	Natal moony	5	0.00000289	3.601	0.974
Monodactylus falciformis	Cape moony	20	0.00003290	3.050	0.987
Mugil cephalus	Flathead mullet	255	0.00002942	2.951	0.989
Myxus capensis	Freshwater mullet	753	0.00001577	3.038	0.992
Oligolepis acutipennis	Sharptail goby	7	0.00000827	3.194	0.934
Oligolepis keiensis	Kei goby	9	0.00000998	3.112	0.885
Oreochromis mossambicus	Mocambique tilapia	999	0.00002843	3.059	0.994
Pomadasys commersonnii	Spotted grunter	95	0.00001389	3.112	0.997
Rhabdosargus holubi	Cape stumpnose	240	0.00001374	3.225	0.995
Rhabdosargus thorpei	Bigeye stumpnose	4	0.00001670	3.140	0.999
Solea bleekeri	Blackhand sole	47	0.00001350	3.075	0.884
Terapon jarbua	Thornfish	259	0.00004829	2.877	0.987
Tilapia rendalli	Readbreast tilapia	4	0.00004051	3.001	1.000
Valamugil buchanani	Bluetail mullet	40	0.00002452	2.997	0.995
Valamugil cunnesius	Longarm mullet	707	0.00001571	3.071	0.996
Valamugil robustus	Robust mullet	106	0.00002269	2.992	0.993

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

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