The ichthyofauna in a small temporarily open/closed Eastern Cape estuary, South Africa

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Declaration

The work presented in this thesis was conducted in the Department of Zoology and Entomology, Rhodes University, under the supervision of Professors P.W. Froneman and A.J. Booth. These studies represent original work by the author and have not been submitted in any form to another university.

Publications

Chapter 3:

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Chapter 5:

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Abstract

The ichthyofaunal community structure, population dynamics and movement patterns in the small temporarily open/closed (TOCE) Grant's Valley estuary, situated along the Eastern Cape coastline, were investigated over the period May 2004 to April 2005. Community structure in the littoral zone was assessed, while growth of selected ichthyofaunal species was investigated using the MULTIFAN model. Population size was assessed using mark recapture models and movement within the estuary using the Hilborn (1990) model. Total ichthyofaunal densities and biomass within the littoral zone ranged between 0.31 to 21.45 fish m^{-2} and 0.20 to 4.67 g wwt m^{-2}, with the highest values typically recorded during the summer. Results of the study indicated that the ichthyofaunal community structure within the estuary was closely linked to the mouth phase and the establishment of a link to the marine environment via overtopping events. In the absence of any link to the sea, the ichthyofaunal community was numerically dominated by estuarine resident species, mainly *Gilchristella aestuaria* and to a lesser extent, by the river goby, *Glossogobius callidus* which collectively comprised *ca*. 88% of all fish sampled. The establishment of the link to the marine environment contributed to an increased contribution of marine breeding species (e.g. *Rhabdosargus holubi*, *Myxus capensis* and *Atherina breviceps*) to the total ichthyofaunal abundances. In contrast, total ichthyofaunal biomass was almost always dominated by marine breeding species by virtue of their larger sizes. Results of hierarchical cluster analyses did not identify any spatial patterns in the ichthyofaunal community within the littoral zone. Results of MULTIFAN analysis indicated estuarine resident fish species bred over an extended period with peaks occurring in the summer months. Conversely, marine breeding fish were shown to recruit into the estuary following overtopping and breaching events. Results of the mark-recapture experiment indicated a population of *ca*. 12 000 (11 219 – 13 311) individuals greater than 50mm SL. Marine-breeding species (*R. holubi*, *Monodactylus falciformis,* and two mullet species) numerically dominated the ichthyofauna, possibly as a result of their effective use of overtopping events. The two mullet species, *M. capensis* and *Liza richardsonii,* and the Cape stumpnose*, R. holubi* moved extensively throughout the estuary, while the remaining species exhibited restricted movement patterns possibly due to the preference for refuge and foraging areas associated with reed beds. The observed movement patterns of individual fish species appeared to be associated with both foraging behaviour and habitat selection.

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I am forever grateful to Dr Jack Latrell for your influence when it was greatly needed. Thanks for everything.

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I would like to thank BP South Africa for providing funding to undertake this study and the Department of Zoology and Entomology, Rhodes University.

I would like to thank Tony Booth. Thanks to you, my knowledge of statistics and models has vastly increased. I truly enjoy the work we did together.

Finally I would like to thank William Froneman. I have appreciated all the support you have given, and I will miss our talks on the drive to Kenton-on-Sea.

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Chapter 1:

Introduction

The South African coastline stretches for *ca*. 3000km from the Orange River mouth on the west coast to Kosi Bay on the east coast. Based on the mean seawater temperatures and annual rainfall, the coastline can be broadly divided into three climatological regions; the subtropical region, the warm temperate region, and the cold temperate region (Allanson and Baird, 1999; Harrison *et al.*, 2000) (Figure 1.1). The two zones situated on the Indian Ocean, the subtropical region north of the Mbashe River, and the warm temperate region south of the Mbashe River to Cape Point near Cape Town, are influenced by the warm Agulhas Current (Figure 1.1). The Benguela Current influences the cool temperate region along the west coast (Allanson and Baird, 1999). Within these three climatic regions are 250 functional estuaries (Whitfield, 1995).

South African estuaries fall into many different classification system, with the simplest classification being those that are normally open or normally closed (Figure 1.2). Open estuaries can be further subdivided into barred (with sand accumulation at the mouth exposed above high tide) or non-barred (without the sand accumulation) estuaries. Open barred estuaries are further subdivided into river dominated and tidal dominated estuaries. Normally closed estuaries are subdivided into perched and non-perched estuaries (Harrison *et al.*, 2000) (Figure 1.2).

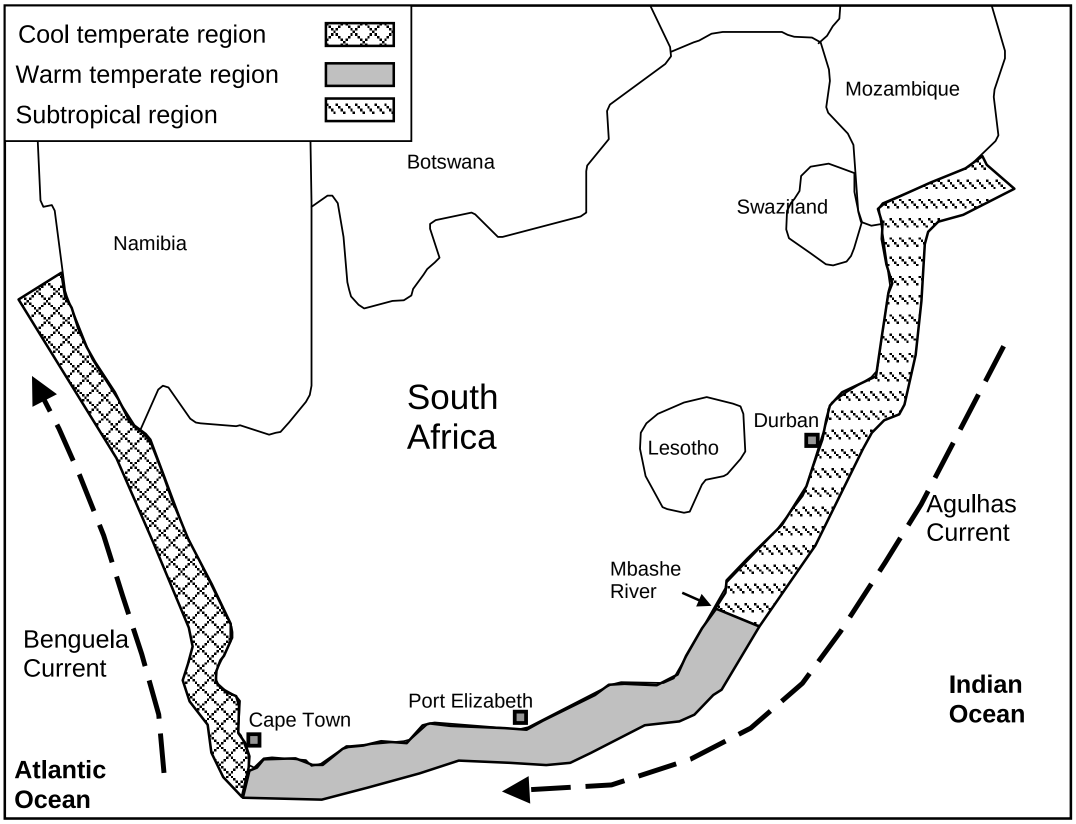

Figure 1.1: Biogeographical regions and predominant oceanic currents along the coast of South Africa. (After Allanson and Baird 1999).

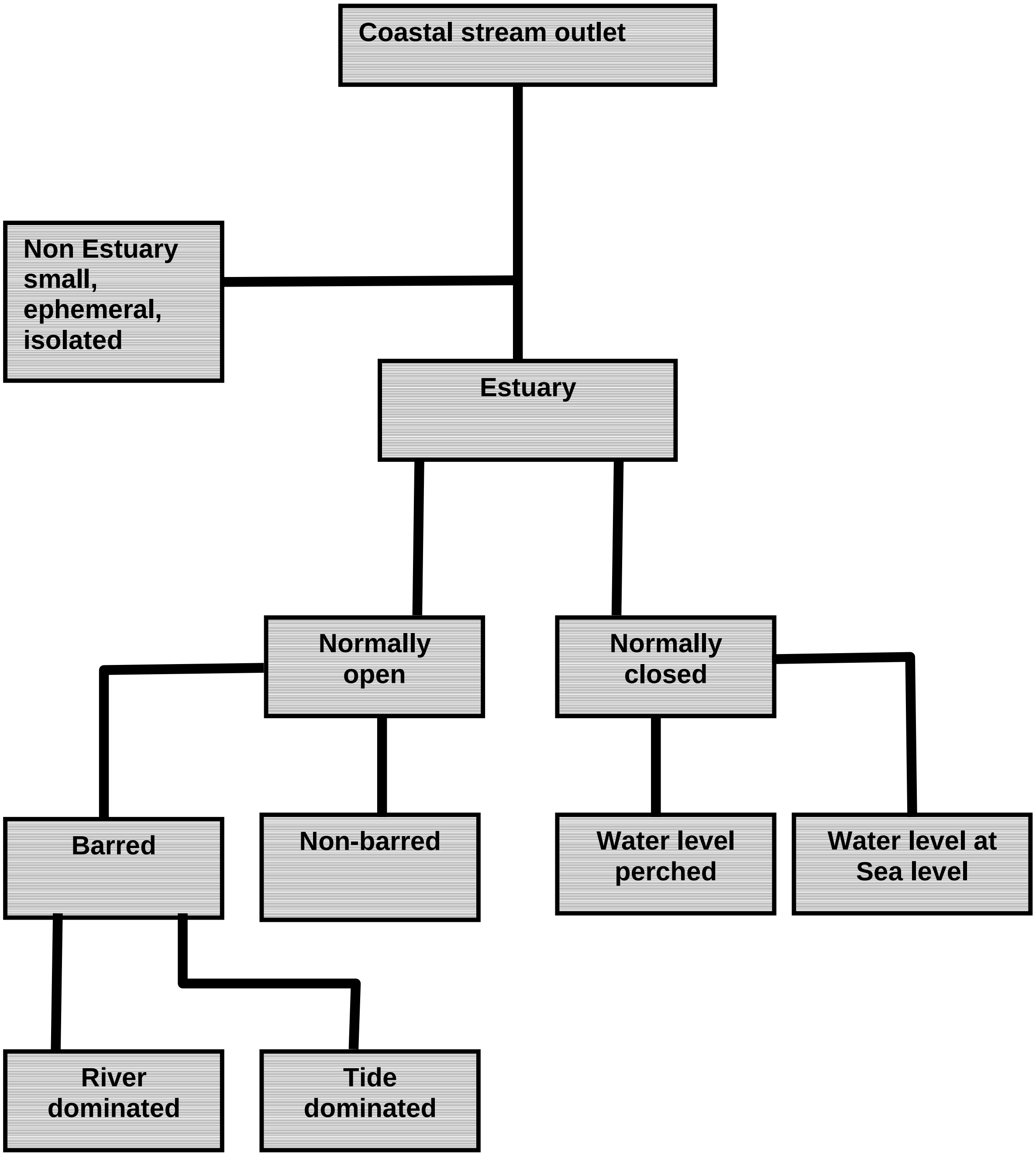

Figure 1.2: Conceptual hierarchical classification scheme for South African estuaries. (After Harrison et al. 2000).

1.1 Temporarily open/closed estuaries (TOCE)

TOCE account for *ca*. 70% of all functional estuaries along the South African coastline (Whitfield, 1992). These estuaries are characterised by a sandbar across the mouth that acts as a barrier between the marine and estuarine environment. TOCE are generally characterised by a virtual absence of horizontal temperature or salinity gradients. This is due to the small catchment size (generally < 500km^2), which limits freshwater inflow and strong persistent coastal winds which facilitate mixing of the water column (Froneman, 2002a). Physical and chemical variables within these systems are strongly influenced by seasonality and regional climate. Day (1981a) found that the annual water temperatures in cool temperate estuaries ranged between 11 and 24°C, while in the warm temperate zone, estuarine water temperatures ranged between 18 and 30°C. Finally, in the subtropical zone, annual temperatures varied between 19 and 28°C (Day, 1981a). Variations in salinity are generally associated with rainfall patterns with highest salinities generally recorded during the dry season and lowest during the rainy season (Day, 1981a; de Villiers *et al.*, 1999).

South African TOCE can be placed into two different geomorphic categories; perched and non-perched systems (Harrison *et al.*, 2000). Perched TOCE, which predominate along the southeastern coastline of southern Africa (KwaZulu-Natal), have an elevated berm barrier resulting in the water levels within the estuary being higher than the levels of most high tides (Figure 1.3). Breaching occurs in these systems when freshwater inflow exceed the outputs of evaporation, seepage, evapotranspiration and human use (Harrison *et al.*, 2000). The resulting breach coincides with a rapid cutting down of the berm barrier and outflow

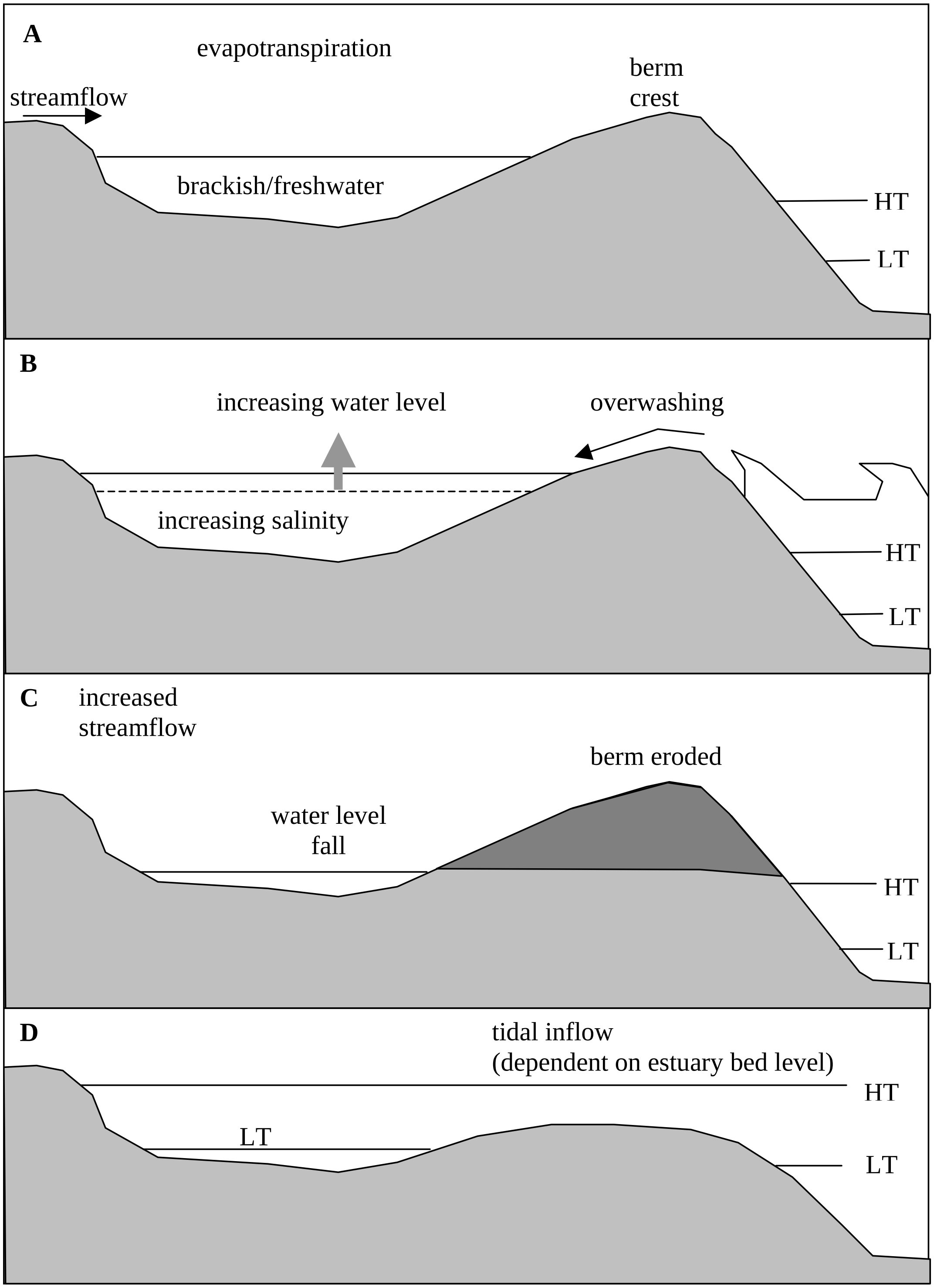

Figure 1.3: Cross-sectional diagram of perched temporarily open/closed estuary. Under balanced conditions (A), the stream flow is matched by evapotranspiration and seepage. Overwashing (B) may elevate water levels and salinity and increased streamflow (C) may promote breaching. When breached (D) the water levels are lowered and tidal flow may take place if the berm level is sufficiently low. (After Harrison *et al*. 2000).

of water, which can drain the system within a few hours. Due to the presence of the elevated sandbar at the mouth, overwash of marine waters across the sandbars seldom takes place. As a consequence, salinities within perched systems are typically mesohaline to oligohaline (< 10‰) (Harrison *et al.*, 2000).

In non-perched TOCE, water levels within the estuary are similar to that of the marine environment. These systems have a tendency to overtop with marine water during spring-high tides or during severe storms, particularly during winter (Figure 1.4). The establishment of frequent links to the marine environment via overtopping results in these systems having a relatively constant surface area and volume, and often provide a more stable habitat than perched estuaries (Harrison *et al.*, 2000). The increased frequency of overtopping events can contribute to the salinity in non-perched estuaries typically being >10‰ (Harrison *et al*. 2000). However, salinity values may be <5‰ during periods of high rainfall, while during periods of drought, hypersaline (>40‰) conditions may predominate throughout the system (Day, 1981a; Harrison *et al.*, 2000).

1.2 Sediments

Bottom sediments within the upper and middle reaches of TOCE are comprised mainly of clays, mud and organic matter of riverine origin, whereas in the lower reaches, coarse marine sediments prevail (Day 1981b; Vorwerk *et al*. 2001; Tweddle, 2003).

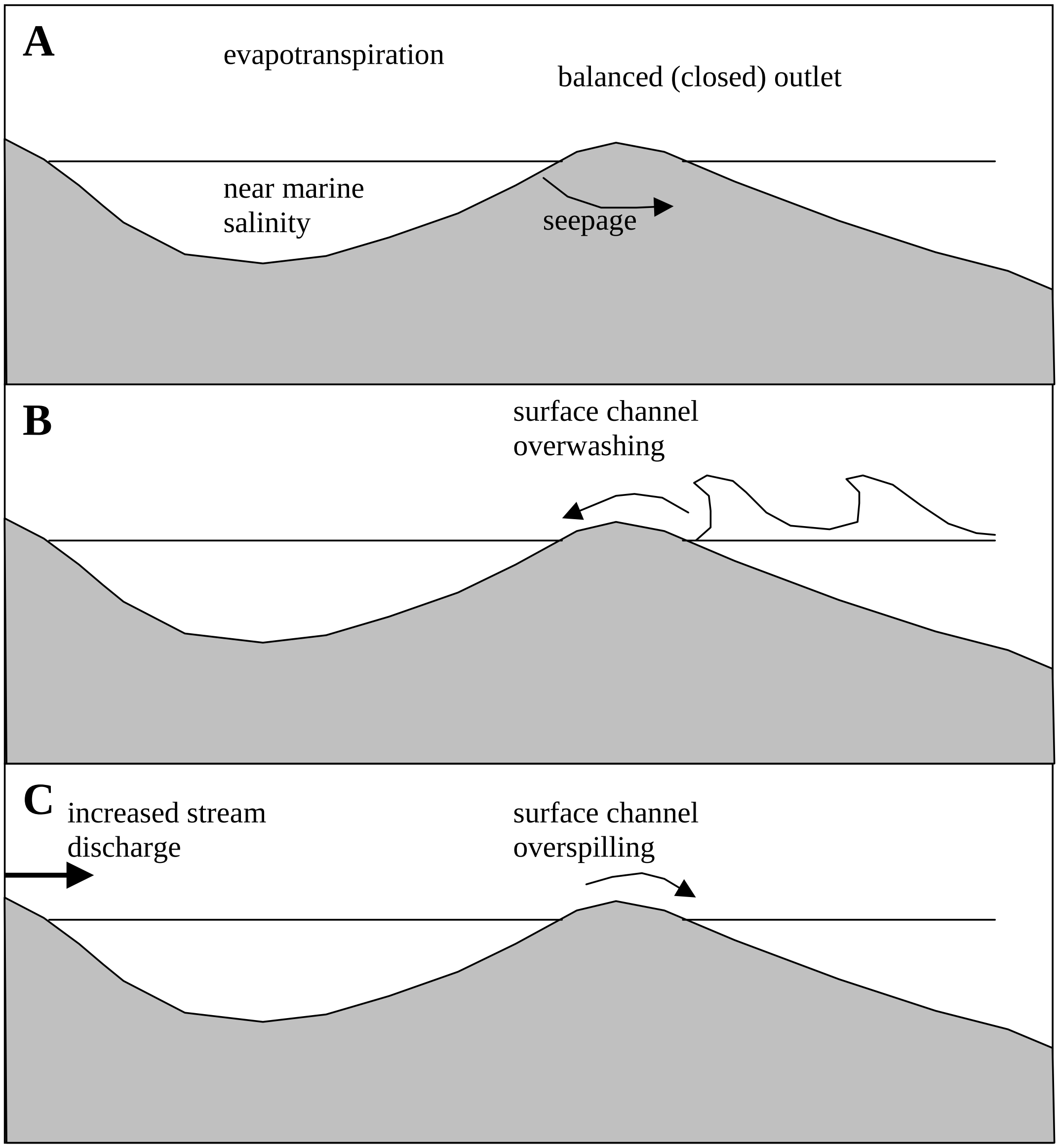

Figure 1.4: Cross-sectional diagram of a non-perched temporarily open/closed estuary. Under balanced conditions (A) stream flow is balanced by losses through evapotranspiration and seepage. Under high wave energy (B) overtopping introduces marine water into the system. Under improved inputs from overtopping (B) and stream flow (C) the system my breach. The depth of the channel is low since the estuary water level is close to sea level. (After Harrison *et al*. 2000).

1.3 Light Environment

Turbidity within TOCE is largely determined by mouth status and freshwater inflow into the estuary. During the open phase or following freshwater inflow into the estuary maximum turbidity values are recorded, which range between 30 and 90 NTUs. Conversely, when the estuary is closed, turbidity is reduced to <15 NTU (Froneman 2002a; 2002b).

1.4 Phytoplankton and zooplankton communities

Phytoplankton and microphytobenthic algae represent an important carbon source for both invertebrates and vertebrates in estuaries (Paterson and Whitfield, 1997; Froneman, 2001). In agreement with studies conducted in permanently open estuaries, phytoplankton biomass and production within TOCE have been shown to be positively correlated to freshwater input, which can be attributed to increased nutrient and macronutrient availability that promotes the growth of phytoplankton, particularly diatoms (Adams *et al*., 1999; Nozais *et al.*, 2001; Froneman, 2002a; Froneman, 2002c; Perissinotto *et al.*, 2002; Perissinotto *et al.*, 2003). During the closed phase when macronutrients concentrations are low, total phytoplankton biomass is generally low (<5 mg chl a m^{-3}) and is dominated by small picoplankton (< 2µm), reflecting reduced production resulting from nutrient limitation (Nozais *et al.*, 2001; Froneman, 2002a). During this phase, microphytobenthic algal concentrations attain their highest values (Perissinotto *et al.*, 2002; Froneman, 2002a; Froneman, 2002c). For example, during the closed phase, microphytobenthic algal biomass can be one to three orders of magnitude higher than the phytoplankton biomass (Nozais *et al.*, 2001). The large concentrations of microphytobenthic algae within TOCE can be linked to the favourable light environment and the virtual absence of currents which allows for the establishment of dense algal mats (Perissinotto *et al.*, 2002). The inflow of riverine water into the estuary coincides with a dramatic decrease in the microphytobenthic algae biomass resulting from increased turbidity and resuspension of sediment (Nozais *et al.*, 2001; Froneman, 2002c).

Zooplankton communities, within TOCE, are dominated, numerically and by biomass, by mesozooplankton (<2000µm). Copepods of the genera *Pseudodiaptomus* and *Acartia* contribute >95% of total abundance and biomass (Wooldridge, 1999; Froneman 2004). Total abundance and biomass of zooplankton in TOCE has been shown to vary in response to freshwater inflow, food availability and the establishment of a link to the marine environment via overtopping or breaching events (Froneman, 2004). Mesozooplankton abundance values are highly variable with abundances ranging from $<10^2$ to 10^5 individuals · m^{-3} and biomass from 10 to 10^3 mg dwt · m^{-3} (Perissinotto *et al.*, 2002; Froneman 2002a; 2004). The lowest abundance and biomass are typically found when the estuary has breached (Froneman 2004). The zooplankton diversity in TOCE has been shown to be lower than that recorded in permanently open estuaries within the same geographic region largely reflecting the reduce contribution of marine breeding species within these systems (Wooldridge, 1999; Froneman, 2001; 2002a; 2004). However, following breaching and overtopping events, diversity of the zooplankton within TOCE is similar to that recorded in the larger permanently open systems (Froneman 2004).

1.5 Aquatic vegetation communities

Areas of vegetation within estuaries provide structural complexity and habitat for estuarine fauna (Whitfield, 1983; Adams *et al*., 1999). Estuarine reed beds and submerged macrophytes have a diverse and abundant biota, with stems that provide surfaces for the attachment and growth of other important epifauna (Adams *et al*., 1999; Weis and Weis, 2003). Salt marshes are a prominant feature of TOCE found in warm temperate and cold regions, but are absent from estuaries in the subtropical zone. The macrophytes found in TOCE are generally tolerant to salinity changes (Adams *et al*. 1999). The common species found in TOCE in the Eastern Cape are *Phragmites australis*, *Ruppia cirrhosa* and *Potamogeton pectinatus* (Madsen and Adams, 1989; Adams *et al*., 1999; Colloty *et al.*, 2002).

1.6 Ichthyofaunal communities

Considerable research effort has been undertaken on the ichthyofaunal communities within permanently open estuaries along the southern African coast over the past three decades (Blaber, 1976; Whitfield, 1980a; Beckley, 1983; Beckley, 1984; Blaber, 1987; Whitfield and Kok, 1992; Ter Morshuizen and Whitfield, 1994; Baird *et al.*, 1996; Harris and Cyrus, 2000; Whitfield and Harrison, 2003). Worldwide, estuaries support a huge diversity of marine fish species (Gunter, 1938; Whitfield *et al.*, 1989; Neira and Potter, 1992a; Thiel and Potter, 2001; Jaureguizar *et al.*, 2004), many of which are present as juveniles highlighting the important role of estuaries as nursery areas.

Based on their estuarine dependence, Whitfield (1998) has classified the fish species in South African estuaries into five utilization categories (Table 1.1). This classification method is an updated, southern African approach, but is easily compared to the classification methods employed in Australia and indeed elsewhere in the world (Potter and Hyndes, 1999; Thiel and Potter, 2001).

Table 1.1: The five major categories of fishes that utilize southern African estuaries. (After Whitfield 1998).

Categories	Description of Categories
I	Estuarine species which breed in southern African estuaries. Further subdivided into: Ia. Resident species which have not been recorded spawning in marine or freshwater environments. Ib. Resident species which also have marine or freshwater breeding populations.
II	Euryhaline marine species which usually breed at sea with the juveniles showing varying degrees of dependence on southern African estuaries. Further subdivided into: IIa. Juveniles dependent on estuaries as nursery areas. IIb. Juveniles occur mainly in estuaries, but also found at sea. IIc. Juveniles occur in estuaries, but are usually more abundant at sea.
III	Marine species which occur in estuaries in small numbers, but are not dependent on these systems.
IV	Freshwater species, whose penetration into estuaries is determined primarily by salinity tolerance.
V	Catadromous species which use estuaries as a transit route between the marine and freshwater environments, but also may occupy estuaries in certain regions. Further subdivided into: Va. Obligate catadromous species which require a freshwater phasein their development Vb. Facultative catadromous species which do not require a freshwater phase in their development.

The five categories are: (I) estuarine residents, with *Atherina breviceps*, *Gilchristella aestuaria* and *Glossogobius callidus* commonly occurring in South African TOCEs; (II) marine migrants, with *Liza richarsonii*, *Mugil cephalus* and *Rhabdosargus holubi* often accounting for much of the ichthyofauna of South African TOCE; (III) marine stragglers, rarely found in TOCE; (IV) freshwater species, with *Oreochromis mossambicus*, often present in South African TOCE; and (V) catadromous fish, with the freshwater mullet, *Myxus capensis*, often found in great numbers in South African TOCEs (Whitfield, 1998; Vorwerk *et al.*, 2001).

1.7 Ichthyofauna in TOCE

The ichthyofaunal community structure and distribution in TOCE has over the past few years received considerable attention (Cowley *et al.*, 2001; Cowley and Whitfield, 2001; Vorwerk *et al.*, 2003; Tweedle, 2004). Results of these studies have shown that ichthofaunal community structure is linked to the mouth phase and the establishment of a link to the marine environment via overtopping (Cowley *et al*., 2001, Kemp and Froneman, 2004) (Figure 1.6). The presence of a sandbar at the mouth of the estuary which limits recruitment of marine breeding fish species into the estuary results in TOCE generally having lower species diversity than that recorded in permanently open systems within the same geographic region (Strydom *et al*. 2003). Fish species diversity within TOCE estuaries in South Africa has been shown to increase with overtopping and breaching events resulting from the recruitment of marine breeding species into the estuary (Bennett, 1989; Whitfield *et al.*, 1989; Griffiths and West, 1999; Tweedle, 2004). In the absence of a link, the ichthyofaunal community is largely represented by estuarine resident species (Gobiidae, Clupeidae and Atherinidae), which often numerically dominate samples (Vorwerk *et al.*, 2001;

2003; Kemp and Froneman, 2004; Tweedle, 2004). For example, Vorwerk *et al*. (2001) found that estuarine species accounted for *ca*. 95% of the catch in the small temporarily open/closed Klein Palmiet estuary along the Eastern Cape coast (Table 1.2). On the other hand, the ichthyofaunal biomass tends to be dominated by marine breeding species by the virtue of their larger sizes (Whitfield, 1989a; Cowley and Whitfield, 2002).

Overtopping and breaching events result in an increased contribution of marine breeding species within the estuary reflecting recruitment of juveniles from the marine environment into the estuary (Bell *et al*., 2001; Strydom, 2003; Kemp and Froneman, 2004) (Figure 1.5). Persistent links to the marine environment via overtopping also contributes to the build up of ichthyofaunal abundance within TOCE (Bell *et al*. 2001; Kemp and Froneman 2004). Within individual systems, shifts in the abundances and biomass of ichthyofauna are linked to recruitment of marine breeding species into the estuary, seasonal breeding patterns of estuarine resident species and habitat availability, including submerged macrophytes, reed beds and sediment type (Whitfield, 1983; Beckley, 1985; Marais, 1988; Strydom *et al.*, 2003). While the overtopping events contribute to the build up of ichthyofaunal abundance and biomass within TOCE, the breaching events coincide with a dramatic decline in total ichthyofaunal biomass as the biologically rich estuarine waters are exported into the marine environment (Griffiths, 1999). Of those estuarine species exported during the open periods, only the gobies have been shown to re-recruit into the estuaries, having passively been exported as preflexion larvae and actively re-recruiting as post-flexion larvae (Whitfield, 1989b; Neira and Potter, 1992b).

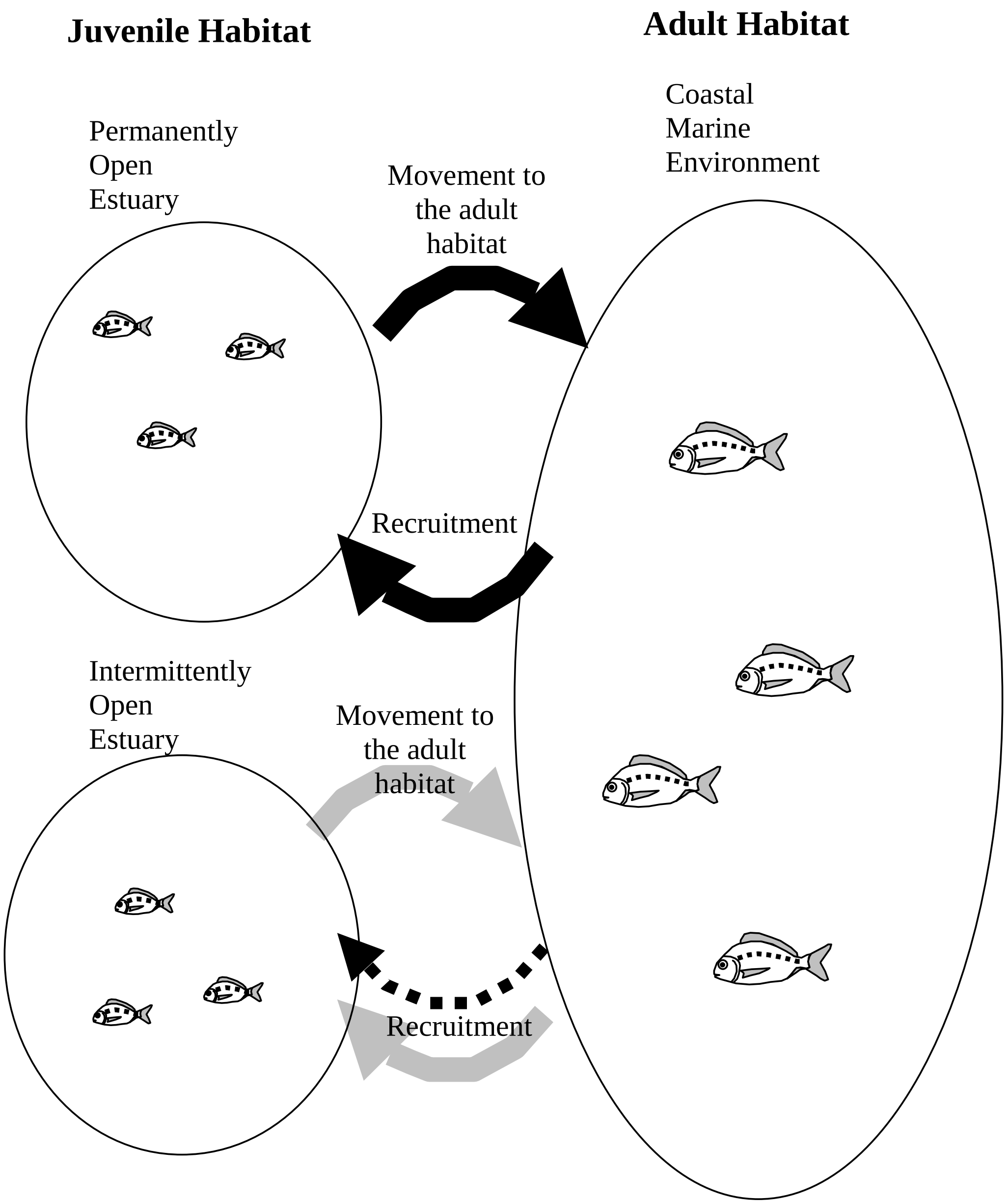

Figure 1.5: Representation of connections between the adult and juvenile populations for estuarine dependent marine breeding fish in permanently open and intermittently open estuaries. Black arrows represent permanent connection routes, grey arrows represent intermittently open connections and the dotted arrow represents a connection via overtopping.

1.8 Environmental influence on the fish communities

Environmental factors such as temperature and salinity have been shown to strongly influence fish communities within both permanently open and temporarily open/closed southern African estuaries (Day *et al.*, 1981; Whitfield, 1999a). Temperature has been shown to have a strong influence on abundance, while estuaries with salinities near seawater tend to have higher species richness and total biomass as they contain more marine fish species (Szedlmayer and Able, 1996; Marshall and Elliot, 1998). However, species most commonly occurring in South African estuaries have been shown to be tolerant to a range of salinities, especially to lower salinities (Whitfield *et al*. 1981) (Figure 1.6). Fish abundance, however, declines during periods of high freshwater inflow when salinities decrease, turbidity increases and there is a higher likelihood of being washed out to sea (Marais, 1983; Ter Morshuizen *et al.*, 1996; Whitfield and Harrison, 2003). There is the further effect of the scouring during increased riverine flow as detritus is removed from the estuary eliminated the food source for detritivores, such as the mullet (Marais, 1983). Due to the absence of any distinct horizontal gradients in temperature and salinity, ichthyofaunal community structure demonstrate virtually no horizontal patterns (Potter *et al.*, 1993; Vorwerk *et al*. 2001; Tweddle 2004). A notable exception is recorded at the mouth of these systems, which are typically characterised by an increased contribution of marine breeding species (Loneragan *et al.*, 1989; Neira and Potter, 1992a; Potter *et al.*, 1993; Tweddle 2004).

There is a lack of seasonal variation in the fish community structure of TOCE as there are fewer opportunities for recruitment into these estuaries (Griffiths, 2001a). Seasonal breeding patterns of the estuarine spawning species tend to lead to variations in fish populations, within estuaries, over a year, and often show distinct summer peaks in fish abundances (Gunter, 1938; Whitfield, 1999a). Furthermore, distribution patterns of fish species tend to vary seasonally with changes in salinity, temperature and with opening events (Morin *et al.*, 1992; Neira and Potter, 1992a)

1.7. Thesis aims

Within the Eastern Cape region, the research on ichthyofaunal community structure in TOCE has largely focussed on medium sized systems (surface area > 15ha), such as the East Kleinemonde (Blaber, 1973; Blaber, 1974a; Cowley and Whitfield, 2001; Cowley *et al.*, 2001; Bell *et al.*, 2001) and the Kasouga (Jubb, 1979; Froneman, 2002a; Froneman, 2002c; Tweedle, 2004). Information on the ichthyofaunal communities within the smaller (surface area < 5ha) TOCE within the region is thus lacking. The absence of this data is surprising given that small TOCE are the prevalent type of system recorded along the coastline (Harrison *et al.*, 2000). The main aims of this investigation are, therefore, to;

1. Investigate the seasonal and spatial patterns in the ichthyofauna within the littoral zone of a small Eastern Cape estuary,
2. Assess the population dynamics of the most common fish species within the estuary, and to
3. Examine fish population size and fish movement patterns within this small temporarilyopen/closed system.

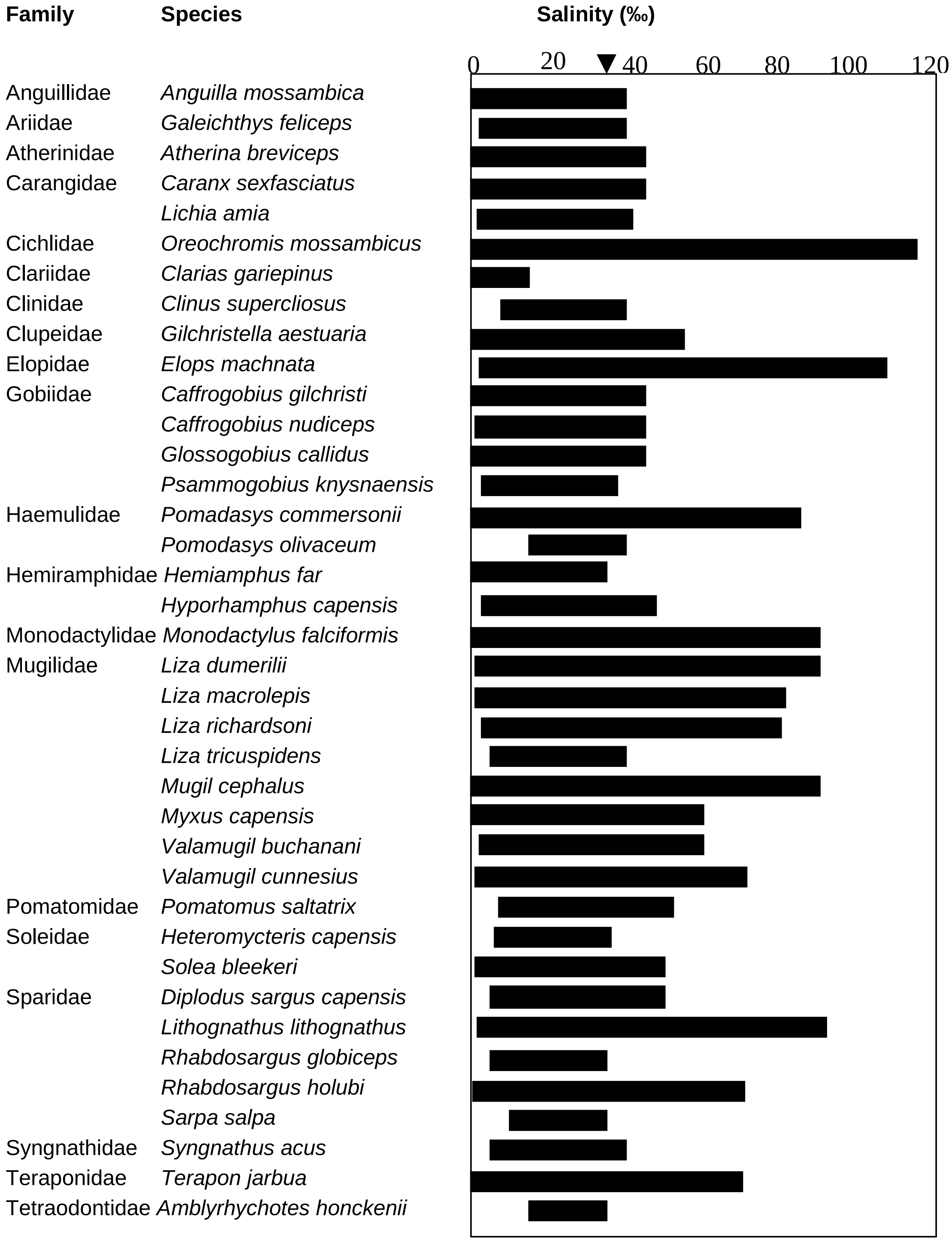

Figure 1.6: Salinity ranges of fish species commonly found in Eastern Cape estuaries. Arrow represents seawater. (After Whitfield *et al.* 1981, modified after Vorwerk *et al.* 2001 and Whitfield 1998).

Table 1.2: Fish species present in South African and worldwide temporarily open/closed (TOCE) and permanently open (PO) estuaries.

Estuary	Location	Size	Status	# of Fish Species	Marine species	Estuarine species	Freshwater species	Marine species % of total abundance	Reference
Grant's Valley	Eastern Cape	3ha	IO	15	9	5	1	8.6%	This Study
Klein Palmiet	Eastern Cape	1ha	IO	8	5	3	0	5.2%	Vorwerk et al 2001
East Kleinemonde	Eastern Cape	17.5ha	IO	19	12	6	1	17.7%	Vorwerk et al 2001
Mpekweni	Eastern Cape	57.6ha	IO	25	19	5	1	11.4%	Vorwerk et al 2001
Bira	Eastern Cape	122.3ha	IO	29	21	7	1	25.3%	Vorwerk et al 2001
Great Fish	Eastern Cape	192.7ha	PO	29	17	8	4	48.0%	Vorwerk et al 2001
Keiskamma	Eastern Cape	197ha	PO	30	20	10	0	26.5%	Vorwerk et al 2001
Bot	Western Cape	1360ha	IO	14	6	6	2	3.0%	Bennett et al 1985
Swan	Australia	5300ha	PO	71	53	14	4	78.4%	Loneragan et al 1989
Wellstead	Australia	250ha	IO	13	9	4	0	14.3%	Young and Potter 2002
Elbe	Germany	11700ha	PO	58	38	2	18	99.0%	Thiel and Potter 2001
Severn	UK	55700ha	PO	78	62	3	13	98.4%	Potter and Hyndes 1999

Chapter 2:

Study site

The Grant’s Valley Estuary (33˚40´12.1”S, 26˚42´12.6”E) is located approximately 5 km east of Kenton-on-Sea in the Eastern Cape, South Africa (Figure 2.1). This small estuary (length 900m; maximum width 14m) has a catchment area of about *ca.*13 km^2. The estuary is shallow (<1.5m) with a surface area of *ca.* 3 ha (Froneman 2002b). Clay sediments dominate the upper and middle regions of the estuary, while in the lower reaches the sediments comprise mainly coarse marine sands (P.W. Froneman, personal communication). Several farm dams impound the system, highly impacting fluvial input into the estuary. The catchment area of the estuary is mainly covered in coastal thicket, although in the upper reaches the estuary coastal grassland predominate (Figure 2.1). Reed beds, mainly *Phragmites australis*, occur on the east bank in the lower reaches and the west bank in the lower, middle and upper reaches of the estuary. The middle reaches of the estuary are also characterised by beds of the submerged macrophyte, *Potamogeton pectinatus*.

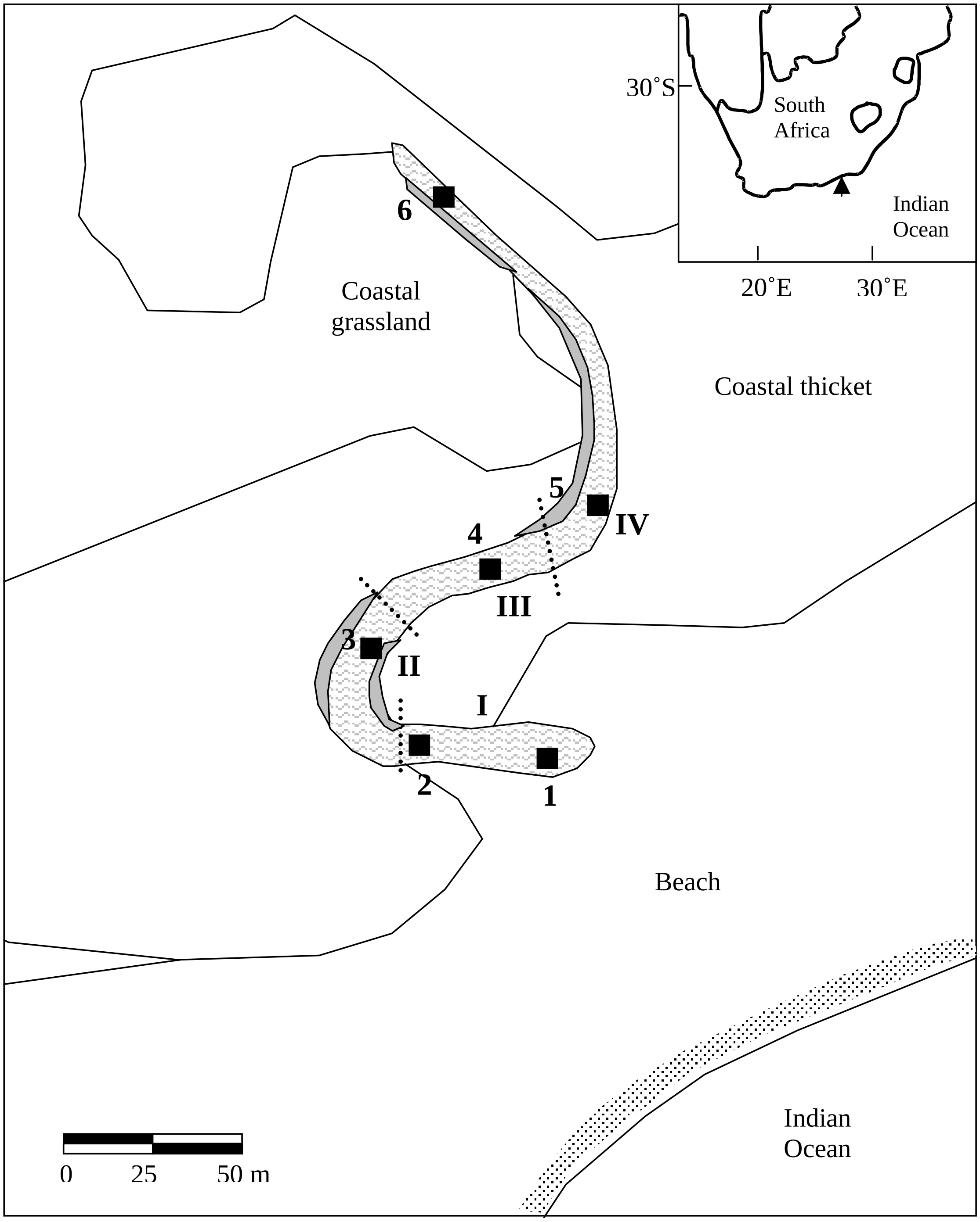

Figure 2.1: Map of Grant's Valley estuary, Eastern Cape, South Africa. The six sampling sites (■)(**1** to **6**), the four mark recapture regions (**I** to **IV**) separated by block nets (dotted lines) and reed beds (▒) are shown.

Figure 2.2: Aerial photographs of the lower reaches of Grant’s Valley estuary.

Figure 2.3: Aerial photographs of the middle and upper reaches of Grant's Valley estuary.

Chapter 3:

Spatial and temporal patterns in the ichthyofaunal community within the littoral zone of the intermittently open Grant's Valley estuary

3.1 Introduction

Studies indicate that the ichthyofaunal community structure of TOCEs is linked to the establishment of a link to the marine environment via breaching or overtopping events (Neira and Potter, 1992b; Vorwerk *et al.*, 2001; Cowley *et al.*, 2001; Vivier and Cyrus, 2002; Kemp and Froneman, 2004). In the absence of this link, TOCEs show a lower diversity and become dominated by estuarine resident species (Neira and Potter 1992b; Griffiths 1999; Griffiths and West 1999).

With the exception of the mouth region, fish communities within IO estuaries appear to be well-mixed with no clear spatial patterns in the distribution of species. This absence of any spatial patterns can be linked to the virtual absence of horizontal gradients in temperature and salinity within these systems (Vorwerk *et al.*, 2001; 2003; Froneman, 2002c).

The aim of this study was to investigate the spatial and temporal patterns in the ichhyofaunal community composition within the littoral zone of the small intermittently open Grant's Valley estuary.

3.2 Materials and Methods

3.2.1 Sampling procedure

Selected physico-chemical and biological variables were measured monthly at six sites along the length of the estuary over the period of May 2004 to April 2005.

3.2.2 Physico-chemical

Temperature and dissolved oxygen concentrations at each site were measured using a YSI 550DO dissolved oxygen and temperature meter. Salinity was measured using an Atago S-10 hand-held refractometer.

3.2.3 Water column chlorophyll-a (chl-a) and microphytobenthic chl-a concentrations

Water column chl-a concentrations at each station were measured from 200mL of water collected at 0.5 m depth that was filtered through a GF/C glass fibre filter (Schleicher & Schuell Microscience). The filters were then placed in 8 mL of 90% acetone and stored in a freezer at –20°C in the dark for 24 hours. Chl-a concentrations were then determined fluorometrically employing a 10-AU field fluorometer (Turner Designs). Chl-a concentrations were expressed as mg chl-a m^{-3}. Microphytobenthic algal concentrations were obtained from benthic cores (2 cm in diameter) that were extracted in 90% acetone and concentrations determined fluorometrically employing the method described above. Chl-a concentrations were expressed as mg m^{-3} of chl-*a*.

3.2.4 Submerged macrophyte cover

The percent cover of submerged macrophytes at each station was estimated visually.

3.2.5 Zooplankton

Net tows were conducted at night using a modified WP-2 net (nominal mouth size 0.05 m^2; mesh size 60 µm) towed at the surface (approx. 1 m depth). The net was fitted with a flowmeter (General Oceanics) to determine the amount of water filtered during each tow. The sample collected was immediately fixed in 10% buffered (hexamine) formalin for the analysis of zooplankton biomass in the laboratory. Total dry weight (Dwt) of zooplankton at each station was determined from ½ subsamples obtained using a Fulsom plankton splitter after oven drying at 60°C for 24h using a Sartorius microbalance. No correction factor for the loss of tissue for the sample preserved with formalin was applied. Data was expressed as mg Dwt m^{-3}.

3.2.6 Ichthyofauna

Fish were collected, at each site, with a seine-net (5 m × 1 m with a 500 µm mesh) that was pulled parallel along the shore of the estuary for a distance of 8m. This gave an effective sampling area of *ca*. 40 m^2. Fish collected were preserved in 10% buffered (hexamine) formalin solution and transported to the laboratory. In the laboratory, fish were identified to species level, standard length (SL) measured and weighed (g). Fish were identified to species as per Smith and Heemstra (1986). Fish abundance and biomass values were standardized and expressed as individuals · m^{-2} or g wwt · m^{-2}.

The fish collected were then classified according to the estuarine dependence categories given by Whitfield (1998) (Table 1.1). The catadromous (type V) freshwater mullet, *Myxus capensis*, was grouped with the type II, because dams restricted migration to the freshwater parts of the system (Vivier and Cyrus, 2002).

3.2.7 Numerical analysis

Multivariate statistical analysis of the fish abundance data was undertaken using the statistical package Plymouth Routines In Multivariate Ecological Research (PRIMER v5). Abundance data was logarithm transformed and hierarchical cluster analysis was employed to determine the temporal and spatial patterns in fish community composition. Groups were identified using hierarchical cluster analysis. Sources of dissimilarity between were tested using Similarity Percentage (SIMPER) programme and while significant differences between the groups were tested using Analysis of Similarities (ANOSIM) programme. Ichthyofaunal diversity during each month was calculated using three commonly used methods (Peet, 1974):

Shannon-Wiener Diversity Index

$$H = \sum - p_i \ln p_i$$

where p_i is the proportion of individuals in species i.

Simpson’s Index

$$D = 1 - \sum p_i{}^2$$

Margalef’s Richness Index

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

where S is the number of species present, and

N is the total number of fish.

3.2.8 Statistical analysis

Monthly fish abundances and salinity values were analysed for differences using ANOVA and significant values analysed with Newman-Keuls *post hoc* test. Comparisons between the biological and phyico-chemical variables were made using Pearson's correlation analysis. The analyses were conducted employing the statistical package, Statistica 6.1.

3.3 Results

3.3.1 Physical and chemical environment

A major breaching event occurred on the 22nd of December 2004, with a channel connecting the estuary to the sea for a period 17 days. A minor breaching event also occurred in April 2005 during which time the channel opened to the sea for *ca*. 1 day. Overtopping events occurred immediately prior to the onset of the survey, on 28 July and 25 October 2004, and on 10 January and 6 March 2005 (Figure 3.1.).

There were no significant spatial patterns in the temperature and salinity for each month ($p > 0.05$). As a consequence data for each month was pooled. Water temperatures exhibited a strong seasonal pattern with the minimum values recorded in winter (13°C) and the maximum values in summer (28.9°C). Intermediate temperatures were recorded in autumn and spring. Salinity values demonstrated a distinct temporal pattern. During the first five months of the survey (May – September 2004) mesohaline conditions prevailed throughout the estuary with salinities ranging between 13 and 17‰. The onset of the rainy season at the end of September contributed to oligohaline conditions persisting throughout the estuary for the rest of the study with salinities values ranging between 3 and 10‰ (October 2004

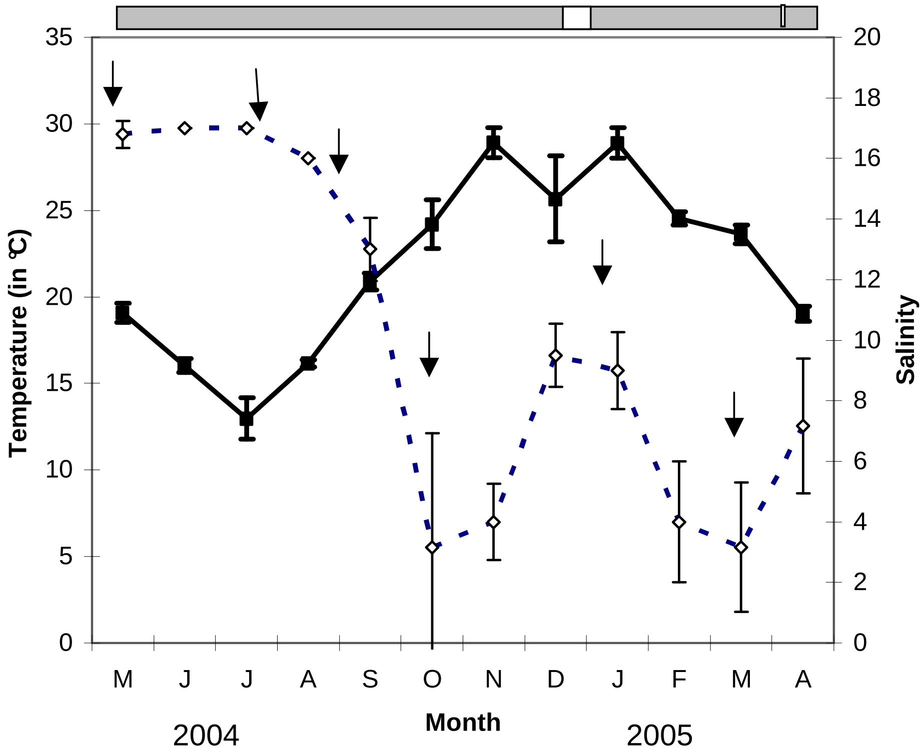

Figure 3.1: Monthly temperature (■) and salinity (◇) (± SD) from Grant's Valley estuary. Arrows indicate overtopping events and the bar indicates the mouth status as either open (☐) or closed (▨).

to April 2005). Variations in salinity during the study were linked to overtopping events and breaching events (Figure 3.1.).

3.3.2 Zooplankton and chl-a

The total water column chl-a concentration ranged between 0.42 and 8.32 mg · m^{-3} and zooplankton biomass between 29.7 and 152.6 mg Dwt · m^{-3}. Highest water column chl-a concentrations and zooplankton biomasses were recorded after the onset of the rainy season in September 2004. From September, the water column chl-a concentrations were always >4 mg chl-a · m^{-3} and zooplankton biomass >50mg Dwt · m^{-3}. Prior to September 2004, water column chl-a concentrations ranged from 0.42 to 2.51 mg · m^{-3} and zooplankton biomass between 29.7 and 43.9 mg Dwt · m^{-3} (Figure 3.2.). Total zooplankton biomass was significantly correlated to water column chl-a concentrations ($p<0.01$).

Microphytobenthic algae biomass ranged between 3.87 mg chl-a m^{-2} and 146.50 mg chl-a m^{-3} and demonstrated an inverse pattern to total water column chl-a concentrations with the highest values recorded at the beginning of the survey and the lowest after the estuary breached in September (Figure 3.2.). A significant negative relationship was found between water column chl-a and microphytobenthic algal concentrations ($p<0.001$).

3.3.3 Submerged macrophyte cover

The percentage cover of the submerged macrophytes increased during the study, largely reflecting the expansion of fennel pondweed, *Potamogeton pectinatus*, throughout the estuary. Overall vegetation cover increased from *ca*. 5% coverage at

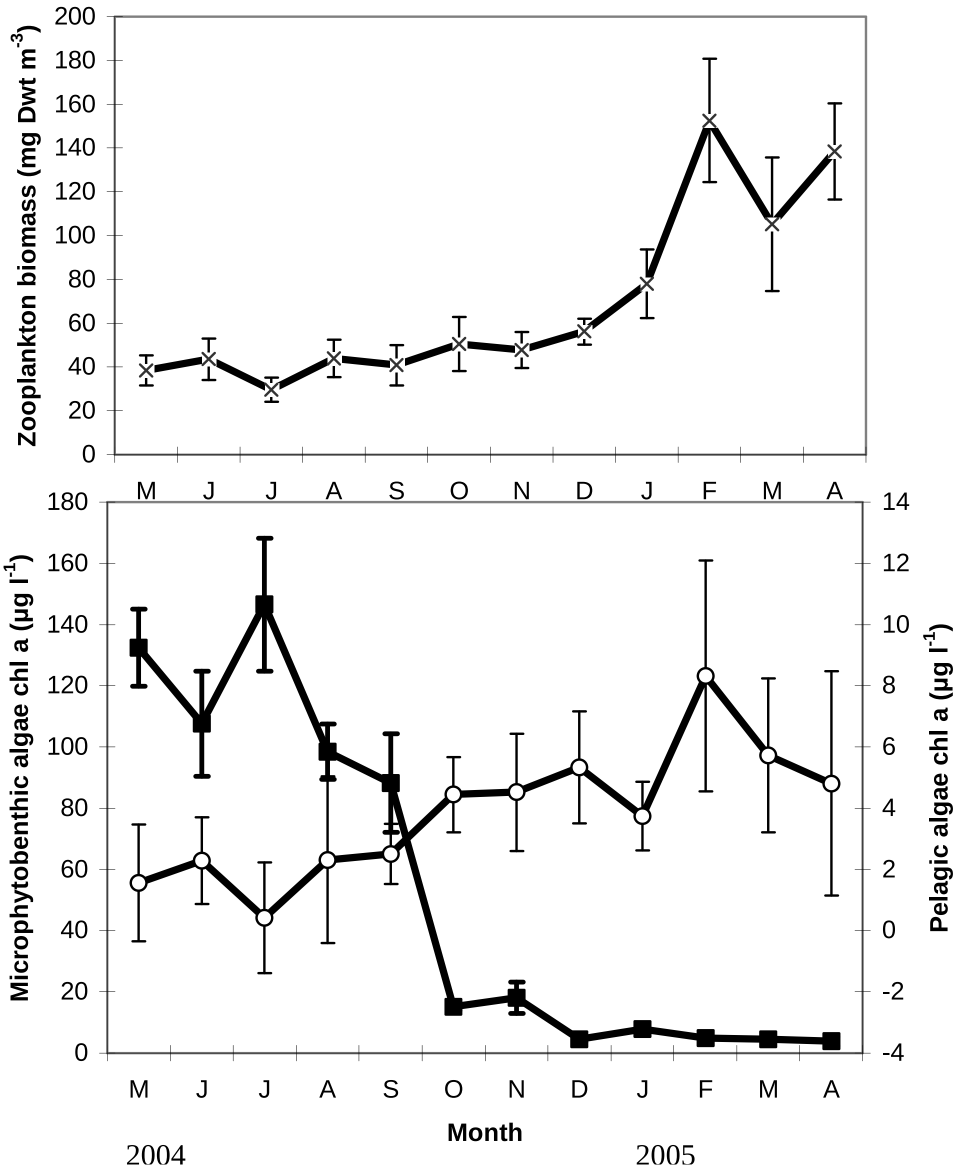

Figure 3.2: Mean monthly zooplankton biomass (a), microphytobenthic algae (■) and water column chl a (○) (b) in Grant's Valley estuary. Error bars represent one standard deviation.

the beginning of the study to *ca*. 46% at the end of the study (Figure 3.3.). The increase was particularly evident within the middle reaches of the estuary where it attained levels of up to 75% of the total area (stations 2, 3 and 4). In the lower and upper reaches of the estuary, submerged vegetation cover, although variable never exceeded 30% of the total surface area.

3.3.4 Ichthyofaunal abundance and biomass

During the study period, 14 469 fish were sampled representing nine families and 11 species. The mean fish abundance was 5.63 individuals · m^{-2}, with a high of 21.45 individuals · m^{-2} in December 2004 and a low of 0.31 individuals · m^{-2} in July 2004. The mean monthly fish biomass was calculated at 2.55 g · m^{-2}, with a high of 4.67 g · m^{-2} in January 2005, and a low of 0.20 g · m^{-2} in July 2004. A peak in abundance was seen in the summer months of November and December 2004, while a minor peak was also observed over the period February to April 2005 (Figure 3.4.). Total ichthyofaunal abundance was significantly correlated to percent cover of submerged macrophytes ($p<0.05$). Peaks in the abundance of marine breeding species occurred in May and August, while July and April had the lowest abundances of marine fish (Figure 3.5.).

Of the 11 species captured, the six most common species, *Gilchristella aestuaria*, *Myxus capensis*, *Oreochromis mossambicus*, *Rhabdosargus holubi*, *Atherina breviceps* and *Glossogobius callidus* accounted for *ca.* 98% of the small fish sampled. In particular, the estuarine roundherring, *G. aestuaria*, accounted for 86.9% of the total fish captured with peaks in abundances occurring over the periods

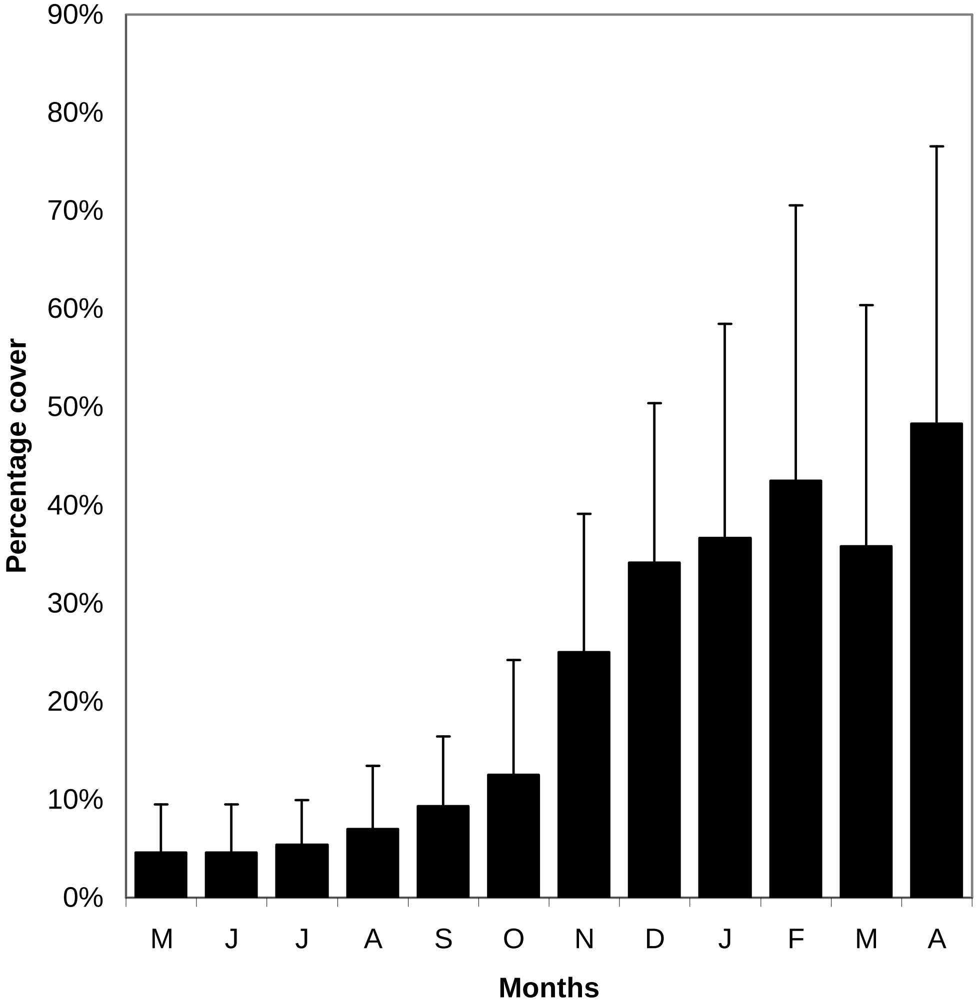

Figure 3.3: Average monthly vegetation cover (± SD) in Grant's Valley estuary.

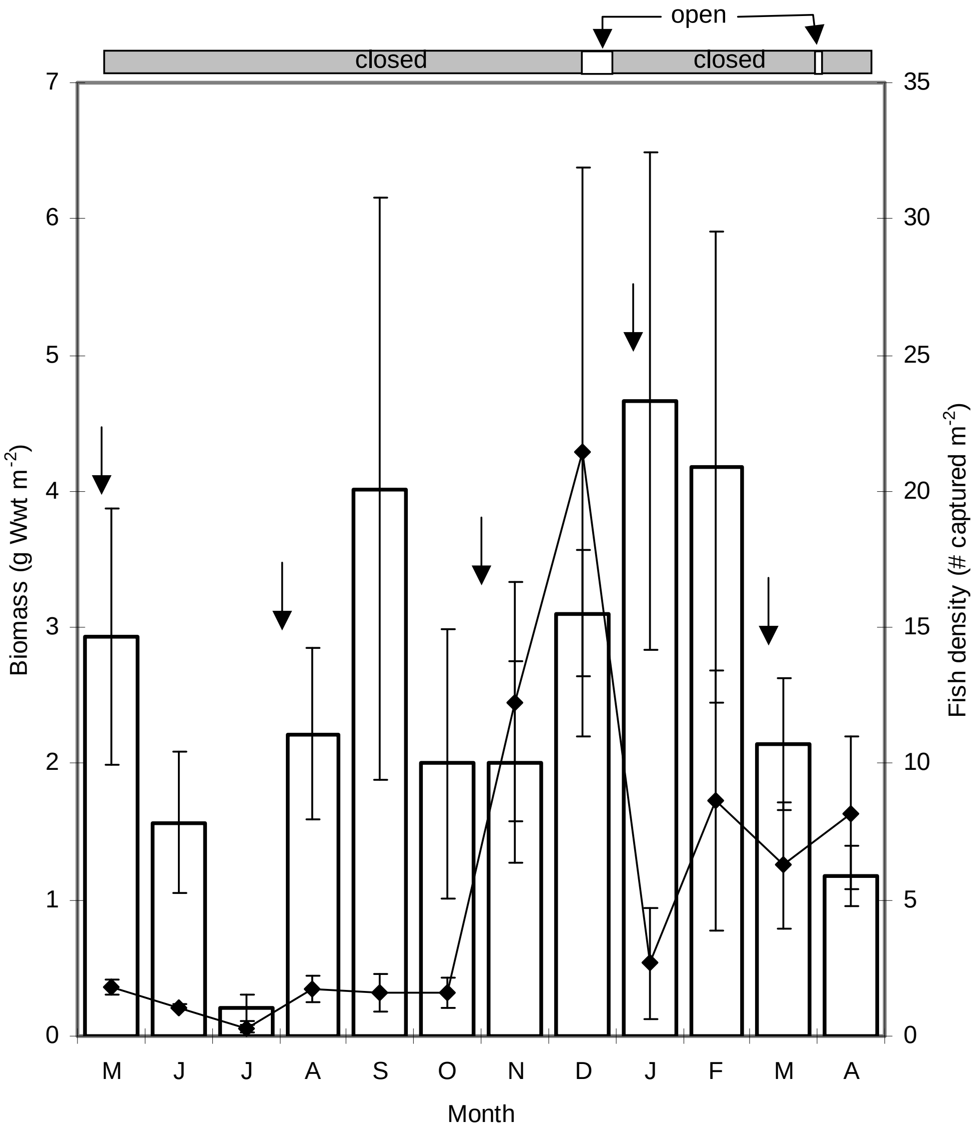

Figure 3.4: Mean monthly fish biomass (bars) and density (line) in Grant's Valley estuary (± SD). Arrows indicate the overtopping events and the bar indicates mouth status, either open or closed.

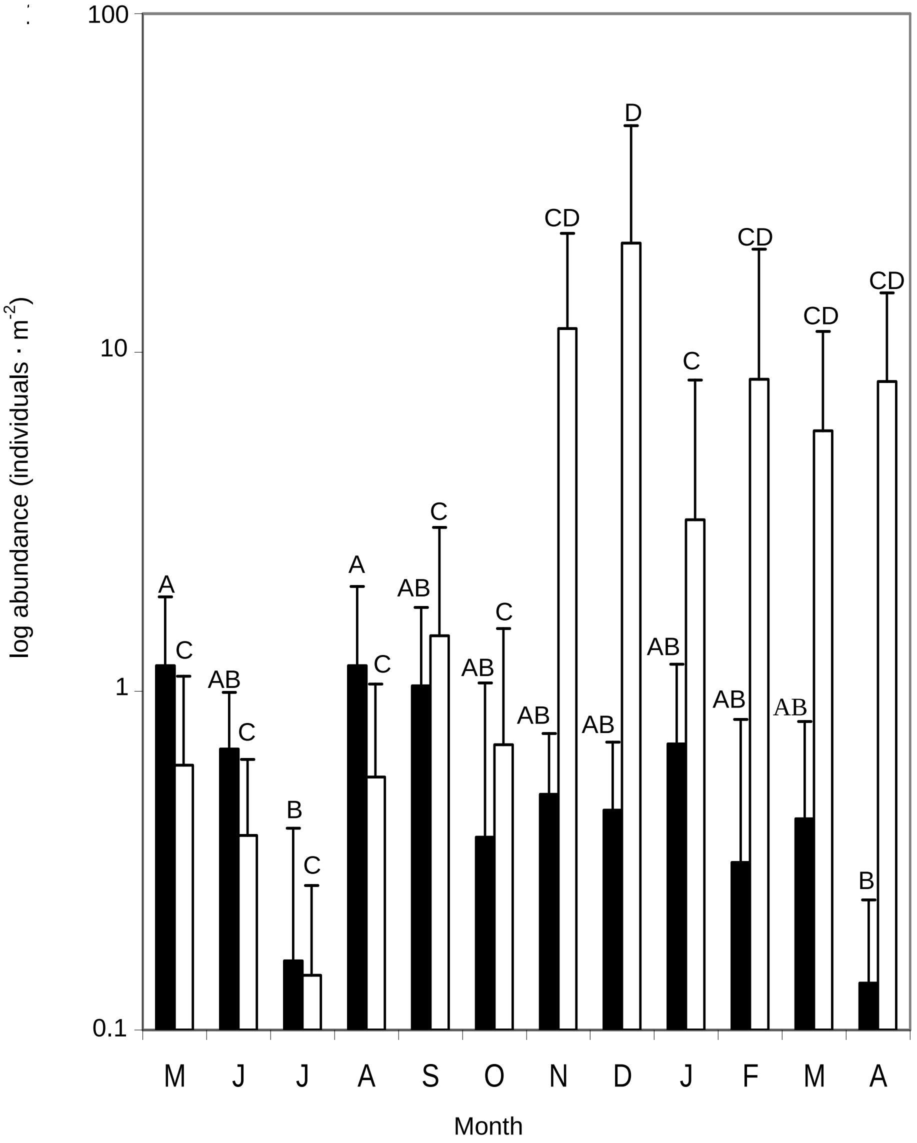

Figure 3.5: Natural logarithm transformed abundances of marine (■) and estuarine spawned (☐) fish in Grant's Valley estuary (± SD). Letters denote significance differences (ANOVA and Newman-Keuls; $p<0.05$).

November to December 2004, with densities of 11.3 and 20.6 individuals m^{-2} respectively, and February to April 2005, with densities of 7.9, 5.6 and 8.2 individuals m^{-2} respectively. *Gilchristella aestuaria* abundances ranged from 0.12 individuals m^{-2} in July to 20.60 individuals m^{-2} in December and SL ranged from 9mm to 54mm.

The freshwater mullet, *M. capensis*, comprised 5.9% of the total fish captured. Abundances of *M. capensis* ranged from 0.08 individuals m^{-2} in November to 0.98 individuals m^{-2} in August, and SL from 15mm to 115mm. Peaks in *M. capensis* abundances occurred in May and August 2004 and in January and March 2005, all corresponding to overtopping events, or the major breaching event in January 2005. Mozambique tilapia, *O. mossambicus,* contributed 2.8% of the total fish captured, with abundances ranging from 0.00 to 0.35 individuals m^{-2} and SL from 7mm to 66mm. Peaks in *O. mossambicus* abundances occurred at the onset of the study and during the period November 2004 to February 2005. Cape stumpnose, *R. holubi*, accounted for 1.4% of the total fish caught, with abundances ranging from 0.00 to 0.44 individuals m^{-2} (20mm to 96mm SL). Peak in the abundance of *R. holubi* was recorded in September 2004. Cape silversides, *A. breviceps*, contributed 1.3% of the total fish captured with abundances from <0.01 individuals m^{-2} to 0.44 individuals m^{-2} (11mm to 51mm SL). The peak in the abundance of *A. breviceps* was recorded in November 2004. River gobies, *G. callidus*, accounted for 1.1% of the total fish captured, abundances of 0 to 0.15 individuals m^{-2} (9mm to 98mm SL). Peaks in *G. callidus* abundance were recorded in December 2004 and January and February 2005. Southern mullet, *Liza richardsoni*, Cape moony, *Monodactylus falciformis*, white steenbras, *Lithognathus lithognathus*, Cape sole, *Heteromycteris capensis*, and thornfish, *Terapon jarbua* should be considered rare, as they contributed less than 2% of the total fish captured.

3.3.5 Estuarine Utilization categories

During the first five months of the survey, category II (marine breeding fish species) numerically dominated the catch contributing between 39.3% and 69.7% to the samples. Following the onset of the rainy season (September 2004), category I (estuarine residents) species were the most numerous contributing between 65.6% and 98.1% of the total catch (Figure 3.6.). On the other hand, marine breeding species always dominated the total biomass (Figure 3.6.). An exception was recorded during the final month of the survey where estuarine resident species contributed most of the total ichthyofaunal biomass (Figure 3.6.).

3.3.6 Ichthyofaunal diversity

The total number of species recorded ranged from a low of 5 in July and October 2004 to a high of 9 in November 2004 and March 2005. All indices, except Margalef's, showed a very similar diversity pattern (Figure 3.7). The diversity indicesvalues increased following the breaching event in late December 2004, while the minor increases were associated with the overtopping events in July and March (Figure 3.7). When analysed for heterogeneity, both the Shannon-Wiener index and the Simpson index are lowest in April 2005 ($H = 0.11$; $D = 0.04$) and highest in May 2004 ($H = 1.40$; $D = 0.65$). When analysed for species richness, the Margalef index showed a low in April 2005 ($R_{Mg} = 0.69$) and a high in September 2004 ($R_{Mg} = 1.18$) (Figure 3.7).

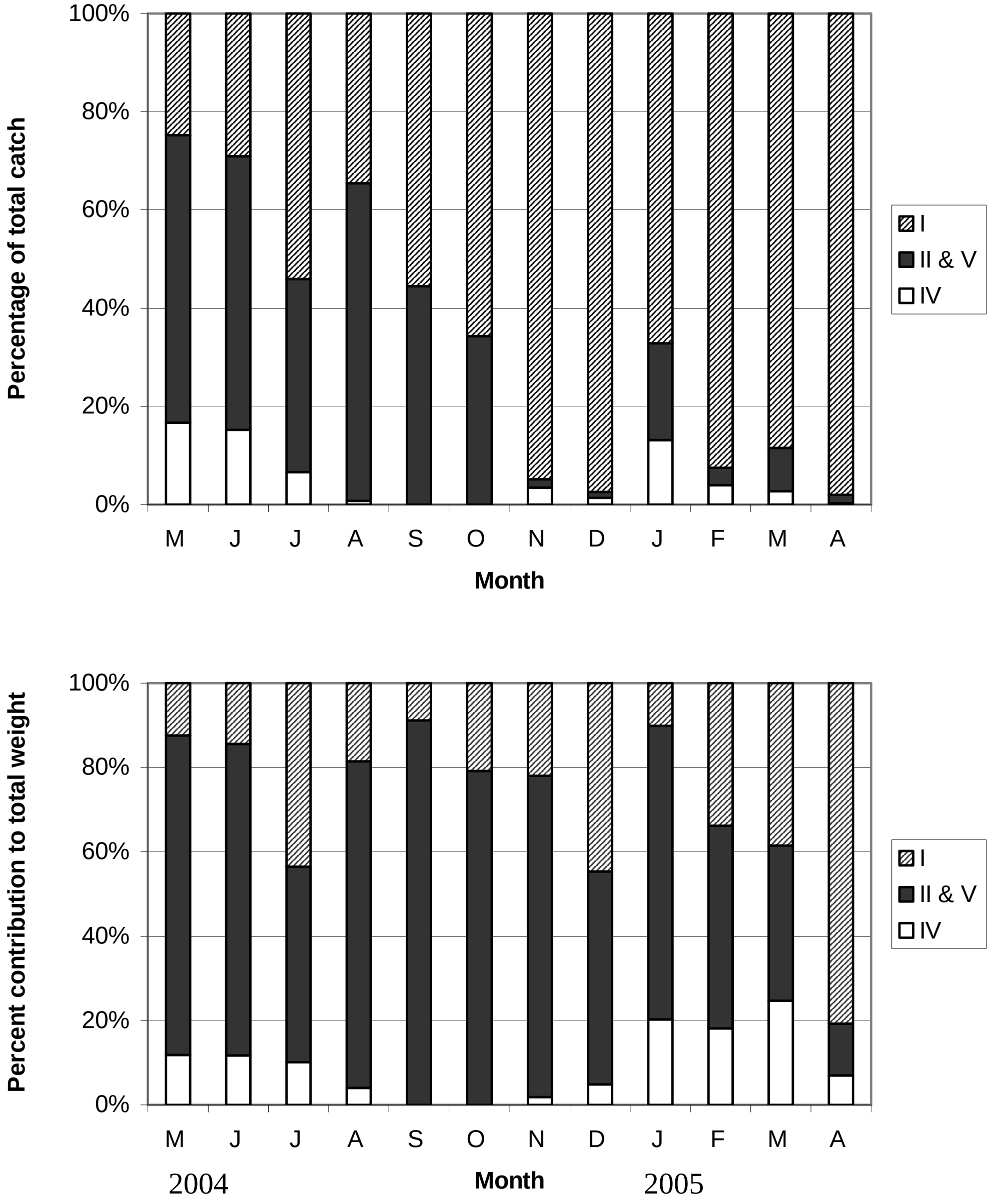

Figure 3.6: Monthly contributions to the ichthyofauna of the Grant's Valley Estuary by different fish estuarine utilization categories in (a) abundance and (b) biomass. Type I are estuarine resident fish, type II are marine spawned fish, type IV are freshwater fish and type V are catadromous fish.

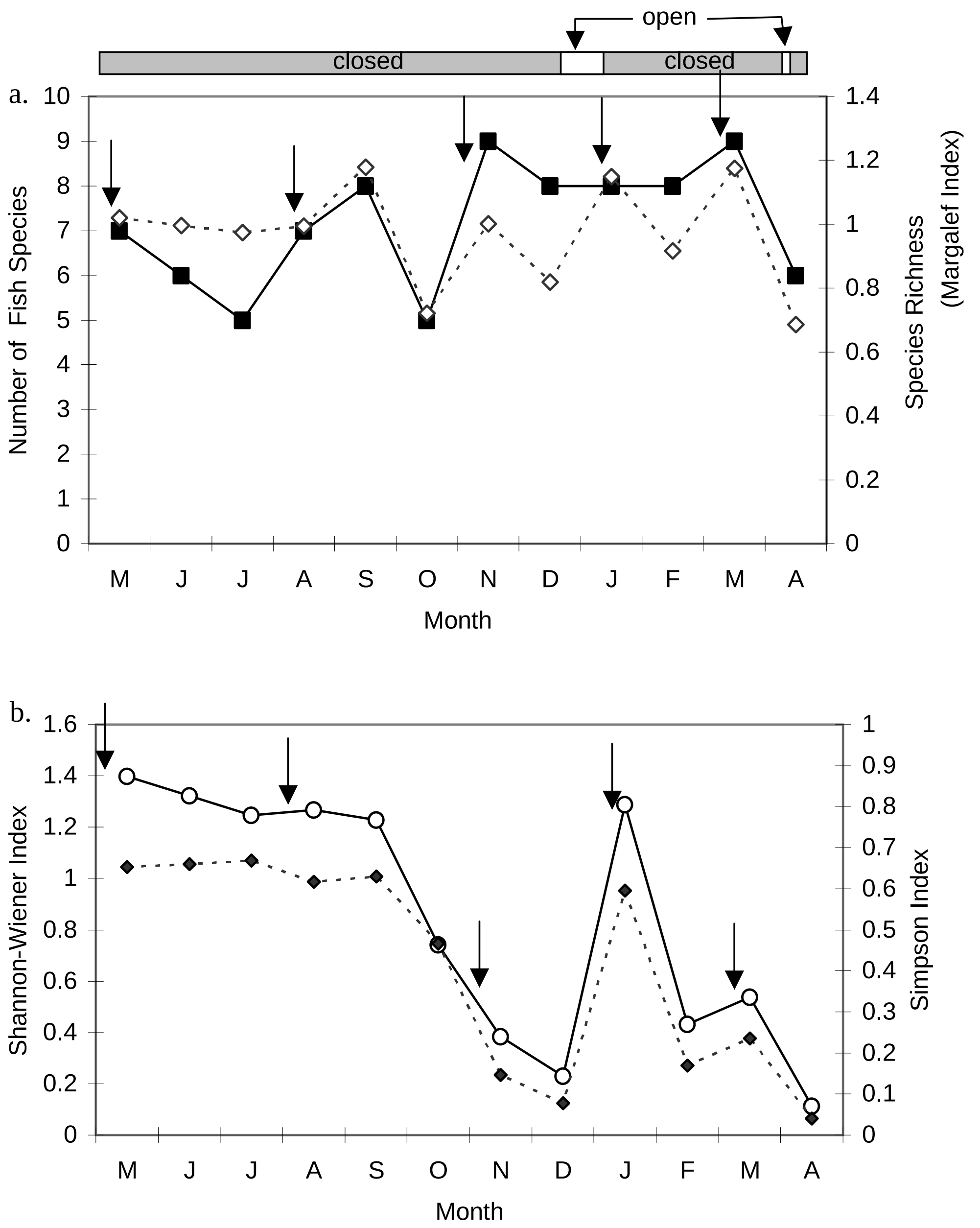

Figure 3.7: Estimates of monthly diversity in the Grant's Valley Estuary. Based on (a) number of fish species present (■), fish species richness, using the Margalef Index (◇), and (b) diversity using the Shannon-Wiener Index (○) and the Simpson Index. (◆). Arrows indicate overtopping events and the bar indicates mouth status.

3.3.7 Community analysis

The Bray-Curtis similarity of total ichthyofauna abundance showed no significant spatial patterns. As a consequence, data for each month was pooled. Three distinctive groupings, designated Groups 1 to 3, were identified with the hierarchical cluster analysis (Figure 3.8a) and multidimensional scaling (Figure 3.8b). SIMPER analysis showed differences between the groupings could largely be attributed to changes in the relative abundances of *G. aestuaria*, and to a lesser extent freshwater mullet, *M. capensis*, and Mozambique tilapia, *O. mossambicus*, to total ichthyofaunal abundance rather than the presence or absence of individual species. Group 1 consisted of those sampling months which were characterised by the numerical dominance of *G. aestuaria*. Group 2 comprising the months May, June, August, September, October and January, and was characterised by an increased contribution of marine breeding fish species to the total ichthyofaunal abundances. The final group, Group 3, was an outlier and comprised the July 2004 survey.

3.4 Discussion

Small IO estuaries are generally characterised by the absence of horizontal patterns in temperature and salinity, which can be linked to small catchment size which limits freshwater inflow into the estuary, shallow depth and strong coastal winds which facilitate the horizontal and vertical mixing of the water column (Potter *et al.*, 1993; Froneman, 2002a). The physico-chemical environment in IO estuaries can be highly variable over time, reflecting the influence of freshwater input via run-off and the establishment of a link to the marine environment via overtopping or breaching events (Kok and Whitfield, 1986; Vivier and Cyrus, 2002). During the present study, the inflow of marine water into the estuary following overtopping and

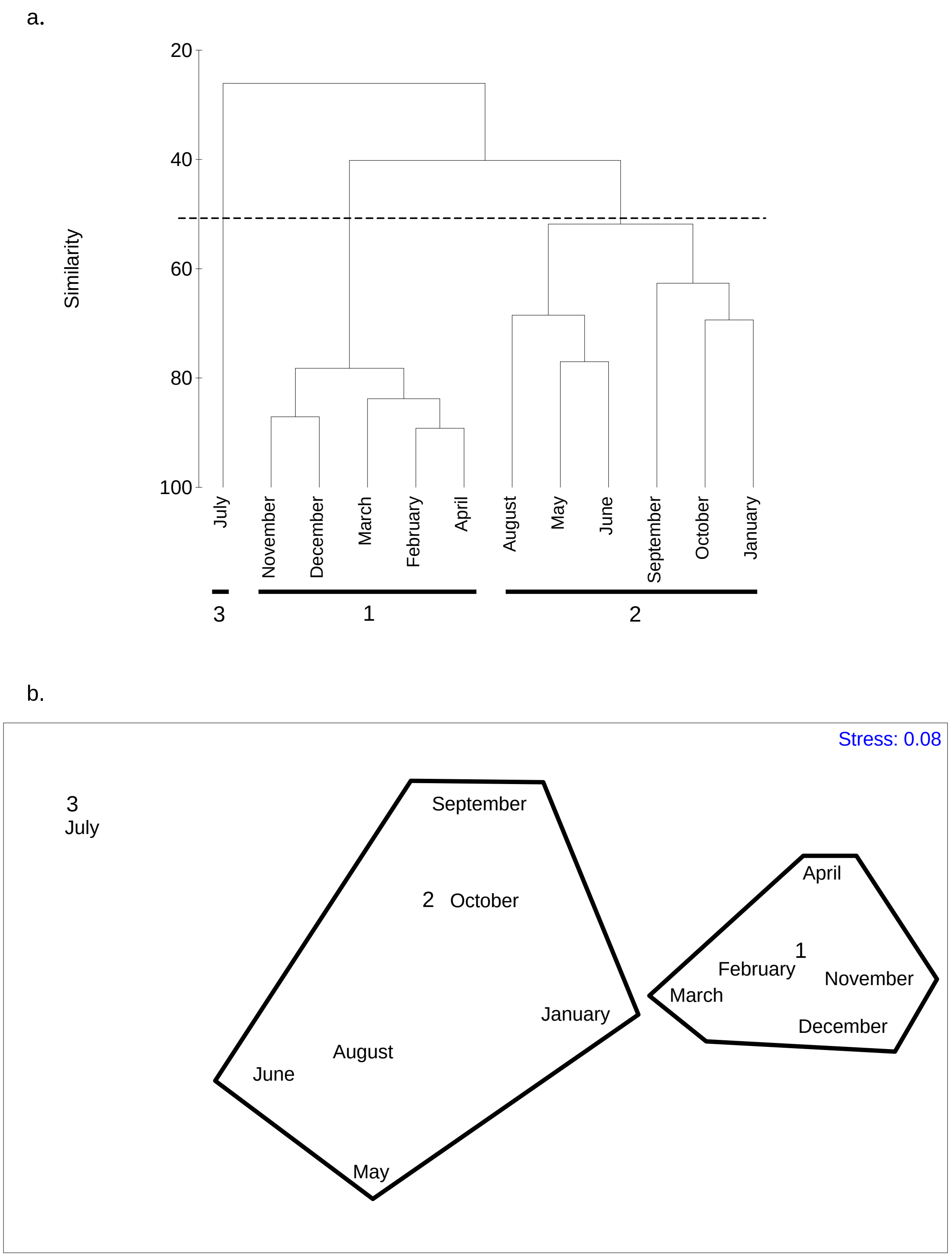

Figure 3.8: Similarity dendogram (a) and multidimensional scaling plot (b) of the fish community data for Grant's Valley estuary using Bray-Curtis hierarchical cluster analysis.

breaching events generally coincided with the increase in salinity.

Freshwater input has been shown to be a major factor controlling phytoplankton and zooplankton biomass in both permanently open and IO estuaries (Froneman, 2000; 2002a). The increase in total chl-a concentration following freshwater inflow into the estuary was associated with an increase in primary production which was sustained by the increase in macronutrient concentrations derived from the riverine inflow (Froneman, 2000; 2002c; Perissinotto *et al.*, 2002). The elevated zooplankton biomass during the latter half of the survey can likely be attributed to elevated chl-a concentrations (Froneman, 2002c). Total zooplankton biomass was significantly correlated to water column chl-a concentrations ($p < 0.05$). On the other hand, the onset of the rainy season in September 2004 coincided with a dramatic decline in microphytobenthic algal biomass (Figure 3). The observed pattern can likely be attributed to currents and to the change in light environment conferred by increased turbidity, which limits the growth of the microphytobenthic algae (Nozais *et al.*, 2001).

Permanently open estuaries are typically characterised by high ichthyofaunal diversity which can be linked to the permanent link to the marine environment allowing continuous recruitment of marine breeding species into the system (Whitfield, 1980b; 1983; Marais, 1988). Worldwide, permanently open estuaries are dominated in abundance and in biomass by marine spawning fish species (Loneragan *et al.*, 1989; Potter and Hyndes, 1999; Thiel and Potter, 2001; Vorwerk *et al.*, 2001). In southern African IO estuaries, estuarine spawning species numerically dominate in numbers which can be attributed to the sandbar at the mouth, which limits the recruitment of marine species into the system (Cowley and Whitfield, 2002). The relatively small size of estuarine resident species generally results in a relatively low contribution of these species to the total ichthyofaunal biomass in IO estuaries. For example in the East Kleinemonde Estuary, South Africa, although estuarine species contributed 84% of the total abundance, they comprised 12% of the total biomass (Cowley and Whitfield, 2002). Similarly, in the Moore River Estuary, Australia, estuarine species contributed 95% of the total abundance, but only 44% of the biomass (Young *et al.*, 1997) During this study, estuarine species contributed 89% of the total abundance and only 24% of total biomass.

The periodic contact with the marine environment is crucial for recruitment of marine breeding fish into IO systems (Kok and Whitfield, 1986; Vivier and Cyrus, 2002). Overtopping events during the first four months contributed to the relatively high contribution of marine spawning fish species to the total catch in the estuary (Figure 3.6). Although the overtopping events were associated with significant increases in ichthyofaunal abundances, they contributed less to the accumulation of fish biomass in the estuary. This is the consequence of overtopping events allowing mainly small larval and juvenile fish (< 50 mm SL) to recruit into the estuary (Kemp and Froneman, 2004).

During the present study, *G. aestuaria* was the major contributor to the total ichthyofaunal abundance during the closed phase and extreme dominance in abundance in this estuary, severely impacted heterogeneity of the system during the spring/summer period. Prolonged separation from the marine environment culminates in estuarine resident fish species numerically dominating the fish communities of IO systems in both South Africa and Australia. The observed pattern can be attributed to the decline in abundance of marine spawned fish species within these systems (Bennett *et al.*, 1985; Neira and Potter, 1992b; Potter *et al.*, 1993; Griffiths, 2001a; Vivier and Cyrus, 2002). The major breaching event that occurred between late December to early January coincided with a decrease in the abundance of *G. aestuaria*, coupled with an increased contribution of the marine breeding species to the total ichthyofauna (Vivier and Cyrus, 2002; Strydom, 2003). Previous studies have demonstrated that breaching events are associated with a dramatic decline in estuarine vertebrate biomass (Bennett *et al.*, 1985; Griffiths and West, 1999). On the other hand, the breaching events allow marine breeding fish to recruit into the estuary, which facilitates an increase in the ichthyofaunal diversity. The shift in the ichthyofaunal composition following the breaching event was evident from the results of the numerical analysis, which identified three main groupings, one numerically dominated by *G. aestuaria*, while the second group was characterised by an increased contribution of marine spawning fish species to the total ichthyofaunal abundance. The third group, the July sample, was characterised by both low fish abundance and biomass. These results indicate that breaching and overtopping events play an important role in structuring the ichthyofaunal abundances, biomass and species composition in the Grant's Valley estuary.

It is apparent, however, that seasonality may also partially contribute to temporal patterns in ichthyofaunal composition. The Mozambique tilapia, *O. mossambicus*, a freshwater species, attained maximum abundance during the spring/summer period while it was virtually absent during the winter months. The observed pattern is unlikely due to salinity changes as *O. mossambicus* is strongly euryhaline and has been found in salinities ranging from 0 to 100‰ (Morgan *et al.*, 1997; Whitfield, 1998). *Oreochromis mossambicus* are, however, strongly influenced by water temperatures, with optimal temperature from 20 to 35°C, and mass mortalities occurring at low temperatures, 10 to 13°C (Bruton and Taylor, 1979; Jubb, 1979). The temporal changes in the *O. mossambicus* population in Grant's Valley estuary is therefore related to seasonal patterns in temperature rather than marine access events.

In summary, the results of this study indicate that the ichthyofaunal community structure within the littoral zone of the Grant's Valley estuary was strongly linked to the establishment of a link to the marine environment through overtopping or breaching events. In the absence of these links, total ichthyofaunal abundance and biomass was dominated by estuarine resident species, mainly *G. aestuaria*.

Chapter 4

Growth patterns and population dynamics of selected fish species in the temporarily open/closed Grant's Valley estuary

4.1 Introduction

Recruitment of marine breeding species can only occur when the estuary floods and the mouth breaches or when rough seas cause waves to overtop the sandbar into the estuary (Cowley *et al.*, 2001; Bell *et al.*, 2001; Kemp and Froneman, 2004). These recruitment events allow larval and juvenile fish from the marine environment into TOCEs, which is imperative as marine breeding species often dominate these systems in species number, abundance and biomass (Cowley and Whitfield, 2001; Cowley and Whitfield, 2002; Lukey *et al.*, 2005). These marine fish species utilise estuaries as nursery grounds due to increased food availability and refuge from predation with recruitment of into TOCEs dependent on seasonal breeding patterns and the availability of larvae within the marine environment adjacent to the estuary (Neira and Potter, 1992b; Griffiths 2001b; Strydom *et al.*, 2002; Strydom 2003).

The growth and length of age of ichthyofauna in TOCEs can be accurately estimated because the time of recruitment, particularly during the closed phase, can be determined for marine breeding fish species (Griffiths, 2001b). This is in contrast to permanently open systems where continuous recruitment the estimation of these parameters more difficult.

To date, no studies have accessed the growth and length of age of ichthyofaunal communities within South African TOCEs. The aim of this study was to assess the growth patterns and population dynamics of the six most numerically abundant fish species, which account for *ca*. 98% of total ichthyofaunal abundance, within Grant’s Valley estuary.

4.2 Materials and Methods

The length-frequency distributions of the six most commonly captured fish species, *Gilchristella aestuaria*, *Glossogobius callidus*, *Myxus capensis*, *Atherina breviceps*, *Rhabdosargus holubi* and *Oreochromis mossambicus* were compiled by month. Those months where fewer than five individuals were sampled were not included in the analysis.

Growth curves were fitted to the monthly length-frequency distributions using MULTIFAN (Fournier *et al.*, 1990). This model analyses multiple length-frequency distributions simultaneously using robust maximum likelihood aproach to estimate the number of age classes represented by the data, the number of fish in each age class, and the von Bertalanffy growth parameters L_∞ and K.

The maximum likelihood function used the model is based on L_1 and L_{max} and the negative log-likelihood function ($\mathcal{L}$) to be minimised is:

$$\mathcal{L} = -1/2\sum_{\alpha=1}^{N_\mathrm{A}}\sum_{i=1}^{N_I}\log_e\left(2\pi(\xi_{i\alpha}+0.1/N_I\right)$$

$$-\sum_{\alpha=1}^{N_A} N_I \log_e(\delta)$$

$$+\sum_{\alpha=1}^{N_A}\sum_{i=1}^{N_I}\log_e\left[\exp\left\{\frac{-\left(\tilde{Q}_{i\alpha}-Q_{\alpha}\right)^2}{2(\xi_{i\alpha}+0.1/N_I)\delta^2}\right\}+0.01\right]$$

where N_A is the number of length frequency data sets,

N_I is the number of length intervals in each length frequency data set,

$\xi_{i\alpha}$ is the parameter determining relative variance of the sampling errors within the αth length frequency data set and is calculated as: $\xi_{i\alpha} = \tilde{Q}_{i\alpha}(1-\tilde{Q}_{i\alpha})$

δ is the parameter determining the overall variance of the sampling errors in the αth length frequency data set,

$\tilde{Q}_{i\alpha}$ is the observed proportion of fish in the αth length frequency data set having a length lying in the length interval *i*,

$Q_{i\alpha}$ is the predicted probability that a fish picked at random from those in the αth length frequency data set has a length lying in the length interval *i*.

The main assumptions of the MULTIFAN model are as follows:

1) Fish grow according to the von Bertalanffy growth model (VBGM),

$$\mu_j = L_\infty\left(1-e^{-Kt}\right) \text{(Ricker, 1975)}$$

where μ_j = the expected length at age *j*;

L_∞ = the asymptotic maximum length;

K = the rate at which the length approaches L_∞.

This growth function can be reparameterised as:

$$\mu_{j\alpha} = L_1 + (L_{\max} - L_1)\left[\frac{1-e^{-k(j-1)}}{1-e^{-k(N_j-1)}}\right] \text{(Schnute and Fournier, 1980)}$$

where L_1 is the mean length of the first age class in the sample,

L_{max} is the mean length of the last age class in the sample, and

N_j is the number of age classes present.

L_1 to L_{max} displays linear growth if K is very small, otherwise growth is curvilinear.

2) Proportions at age of the fish in each length class, x_i, are considered normally distributed about a mean length, $\mu_{j\alpha,}$ and a standard deviation, $\sigma_{j\alpha}$., such that

$$q_{ij\alpha} = \frac{1}{2\sqrt{2\pi}\sigma_{j\alpha}} \int_{x_i - w/2}^{x_i + w/2} \exp\left\{\frac{-(x_i - \mu_{j\alpha})^2}{2\sigma_{j\alpha}^2}\right\} dx$$

where w is the width of the length frequency intervals.

3) The standard deviations of the actual lengths about the mean length-at-age are a simple function of mean length at age, involving two parameters, λ_1 and λ_2, the standard deviation of the first age class and the age dependent increase in standard deviation, respectively (Fournier *et al.*, 1990). Such that:

$$\sigma_{j\alpha} = \lambda_1 \exp\left\{\lambda_2\left[-1 + 2\left(\frac{1-e^{-k(j-1)}}{1-e^{-k(N_j-1)}}\right)\right]\right\}$$

The most parsimonious models, with the fewest age classes and the most variability explained, were constructed by conducting a systematic search of plausible number of age classes. Each age class tested constituted a model fit and the maximum log-likelihood ($\mathcal{L}$) was calculated. Likelihood ratio tests were used to test for significant improvement in model fit. Twice the difference in the log-likelihood is χ^2 distributed with the respective degrees of freedom, *df*, equal to the difference in parameters. Following Fourier *et al*. (1990), if $p(\chi^2, df) < 0.10$, then a significant improvement in the statistical fit was gained by introducing an additional age class in the model.

4.3 Results

The Cape stumpnose, *R. holubi*, population (20 to 96mm SL) was shown to have eight age classes using the MULTIFAN model (Table 4.1). A peak in density was found in September 2004 (n = 105) (Figure 4.1) while minimal captures occurred in July (0), October (2), March (4) and April (1). VBGM resulted in a von Bertalanffy growth constant (K) of 0.313 and an asymptotic length (L_∞) of 9.14cm (Table 5.2).

Five age classes were noted in the *A. breviceps* population (11 to 51mm SL) (Table 4.1). A peak in density was found in November 2004 (n = 61) (Figure 4.2), while minimal captures occurred in October 2004 and February, March and April 2005 (all n = 1). VBGM resulted in a K of 0.190 and a L_∞ of 7.44cm (Table 5.2). The peak in density recorded in November 2004 occurred following an overtopping event and corresponded with the introduction of a new cohort into the estuary (Figure 4.2)

Six age classes of the *G. aestuaria* (9 to 54mm SL) were identified (Table 4.1). Small newly recruited fish (SL < 15mm) were sampled from October 2004 to April 2005 with a peak in density in December 2004 (n = 4945) (Figure 4.3). VBGM resulted in a *K* value of 0.342 and a L_∞ of 4.39cm (Table 4.2). Two new cohorts were followed from November 2004 (1) and February 2005 (2), with the first cohort showing a shift in size frequencies corresponding to the January breaching event.

Five age classes were noted for *M. capensis* (15 to 115mm SL) (Table 4.1) during the study, with a peak in abundance occurring in August 2004 (n = 61) (Figure 4.4). VBGM resulted in *K* and L_∞ values of <0.0001 and >30cm, respectively (Table 4.2). Recruitment into the estuary was seen to correspond to the overtopping events preceding the sampling trips in May, August, November and March and with the breaching event in late December 2004.

The river goby, *G. callidus*, population (9 to 98mm SL) had four age classes (Table 4.1). Peaks in abundance were recorded in May and December 2004 (n = 30; 29) and February and March (in both n = 30) (Figure 4.5). Minimal captures occurred in July and October 2004 (n = 1; 0) and April 2005 (n = 1). A *K* of 0.030 and a L_∞ of >20cm were recorded (Table 4.2).

Table 4.1: The log-likelihood function and number of parameters (in parenthesis) for the six most commonly captured fish species in Grant's Valley estuary as determined by the MULTIFAN model. Best-fit age-class model shown in bold and underlined.

Age classes	*Atherina breviceps*	*Gilchristella aestuaria*	*Glossogobius calidus*	*Myxus capensis*	*Oreochromis mossambicus*	*Rhabdosargus holubi*
3	141.65 (20)	-	74.12 (24)	-	-245.95 (18)	-
4	103.43 (27)	-	**<u>-14.59</u>** (33)	-468.12 (39)	**<u>-256.88</u>** (24)	-95.95 (27)
5	**<u>-60.77</u>** (34)	-656.64 (50)	-20.75 (42)	**<u>-693.13</u>** (50)	-256.70 (30)	-234.52 (34)
6	-72.27 (41)	**<u>-3229.53</u>** (61)	-21.93 (51)	-691.82 (61)	-21.93 (51)	-297.71 (41)
7	-69.68 (48)	-3231.94 (72)	-	-706.26 (72)	-	-353.08 (48)
8	-	-3231.22 (83)	-	-	-	**<u>-389.60</u>** (55)
9	-	-	-	-	-	-403.64 (62)

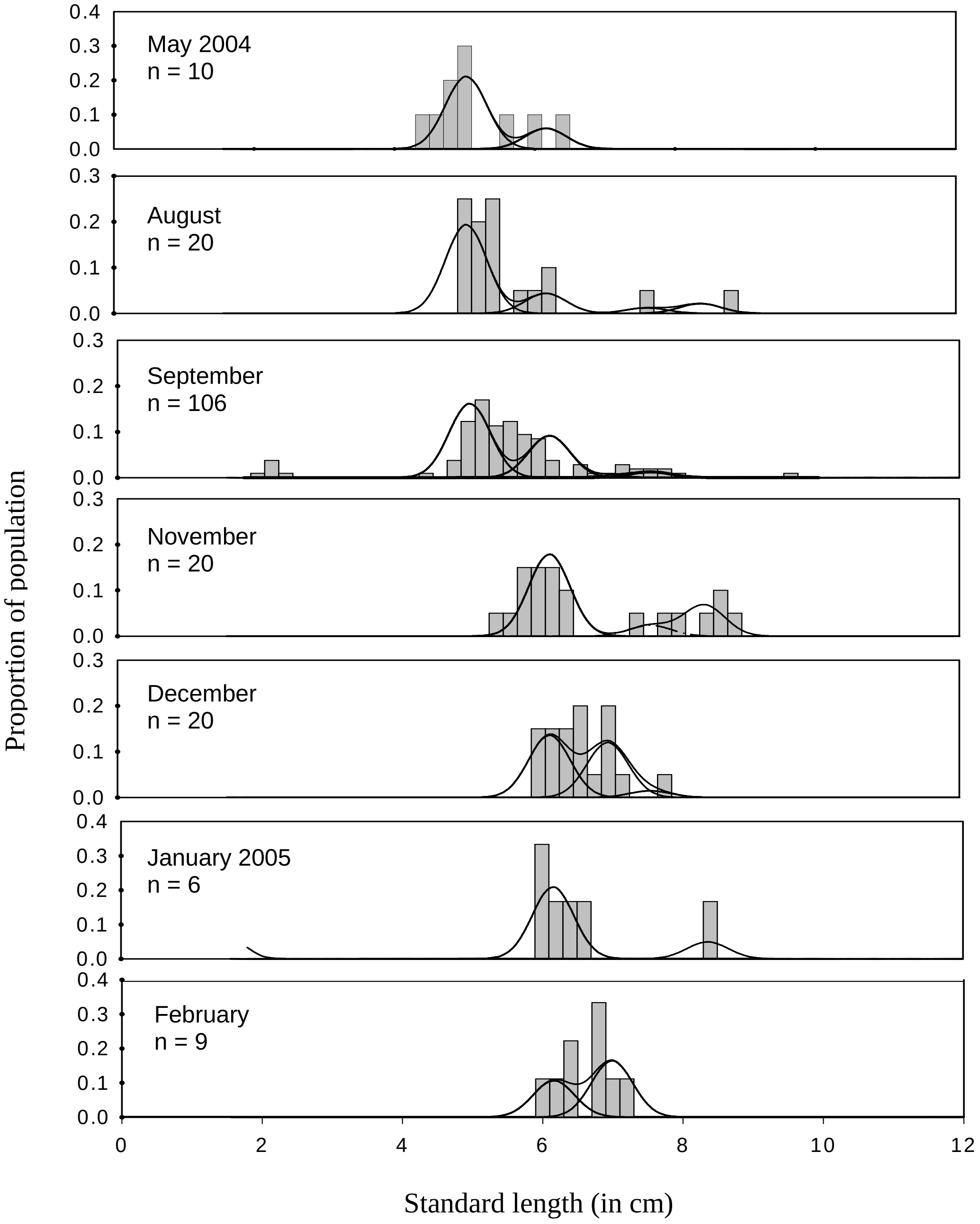

Figure 4.1: Monthly length-frequency distributions (SL) of *Rhabdosargus holubi* in Grant's Valley Estuary (bars). Curves represent the predicted length frequency distribution estimated using the MULTIFAN model.

Table 4.2: MULTIFAN parameter estimates for the six most commonly captured fish species in Grant's Valley estuary. L_1, L_{max} and L_∞ are the mean standard lengths of the first and maximum age classes and the asymptotic maximum length (in cm); K is the von Bertalanffy growth constant; λ_1 and λ_2 are the two parameters involved in determining the stardard deviations about the mean length-at-ages; and δ is the parameter determining the variance of the sampling errors in all the length frequency data sets (Fournier *et al.*, 1990).

	Atherina breviceps	*Gilchristella aestuaria*	*Glossogobius calidus*	*Myxus capensis*	*Oreochromis mossambicus*	*Rhabdosargus holubi*
Age classes	5	6	4	5	4	8
L_1 (cm)	1.61	1.53	1.95	1.95	1.39	1.24
L_{max} (cm)	4.71	3.87	8.89	7.20	5.10	8.26
K (cm•month^{-1})	0.190	0.342	0.030	1.75E-06	0.170	0.313
L_∞ (cm)	7.44	4.39	>>20	>>30	10.68	9.14
λ_1	0.209	0.249	0.713	0.459	0.439	0.289
λ_2	1.45E-06	3.60E-08	0.014	0.378	4.30E-07	6.80E-07
δ	0.217	0.147	0.228	0.139	0.116	0.145

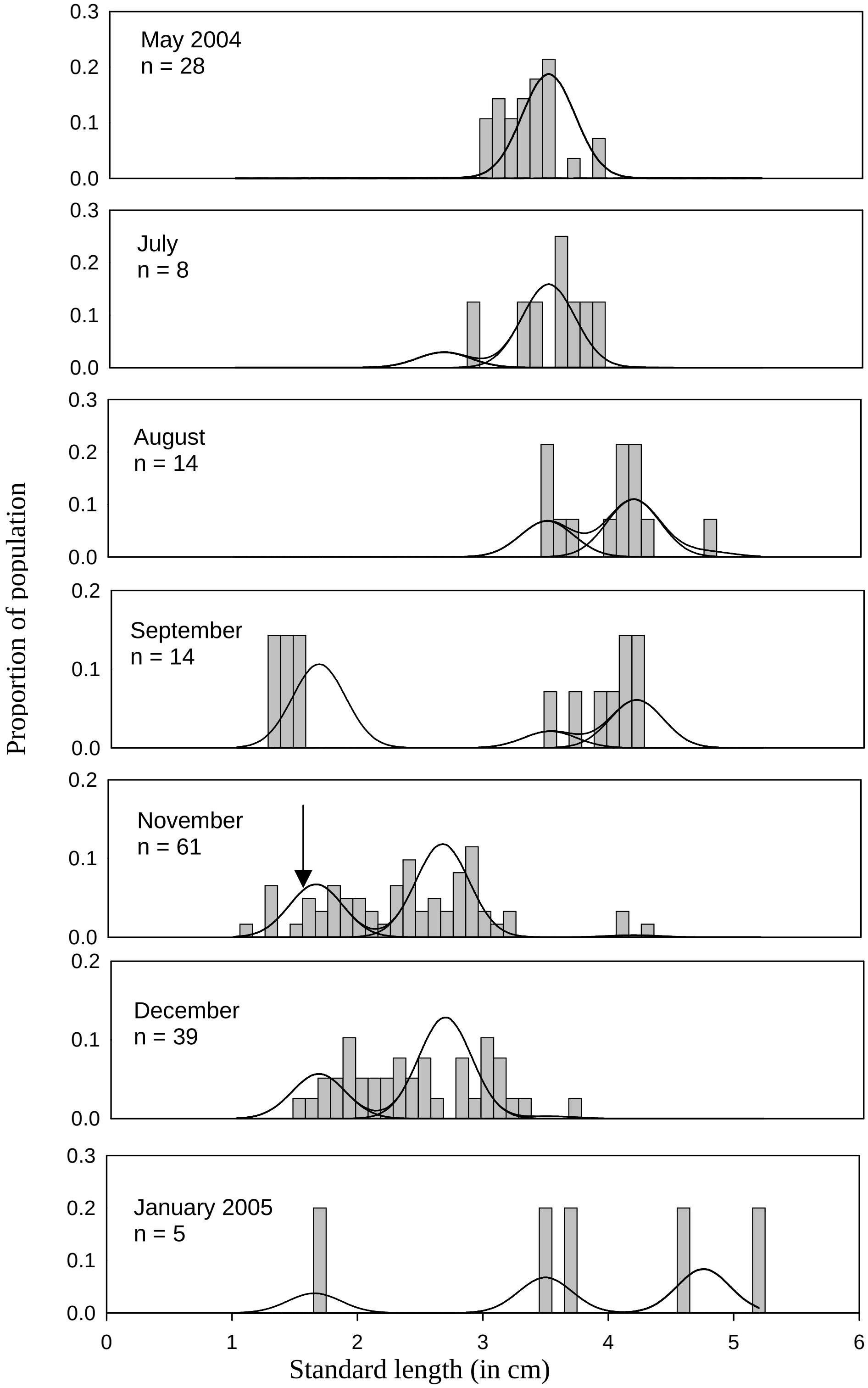

Figure 4.2: Monthly length-frequency distributions (SL) of *Atherina breviceps* in Grant's Valley Estuary (bars). Curves represent the predicted length frequency distribution estimated using the MULTIFAN model. Arrow indicates age-classe introduced by the November overtopping

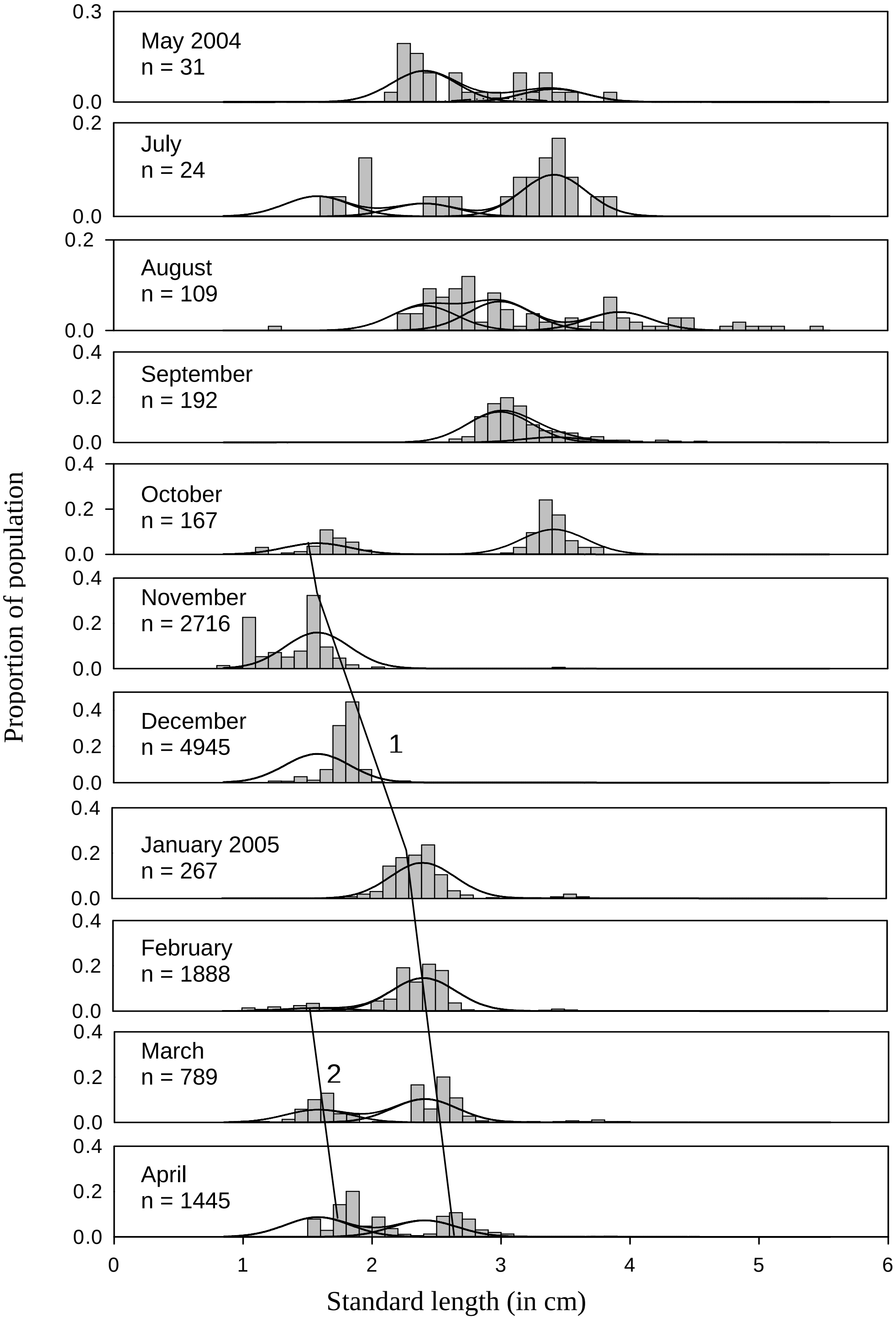

Figure 4.3: Monthly length-frequency distributions (SL) of *Gilchristella aestuaria* in Grant's Valley Estuary (bars). Curves represent the predicted length frequency distribution estimated using the MULTIFAN model. Straight lines represent newly recruited cohorts; 1 – from November with the size shift associated with the loss of smaller fish during the January breaching, and 2 – following the breaching event from February.

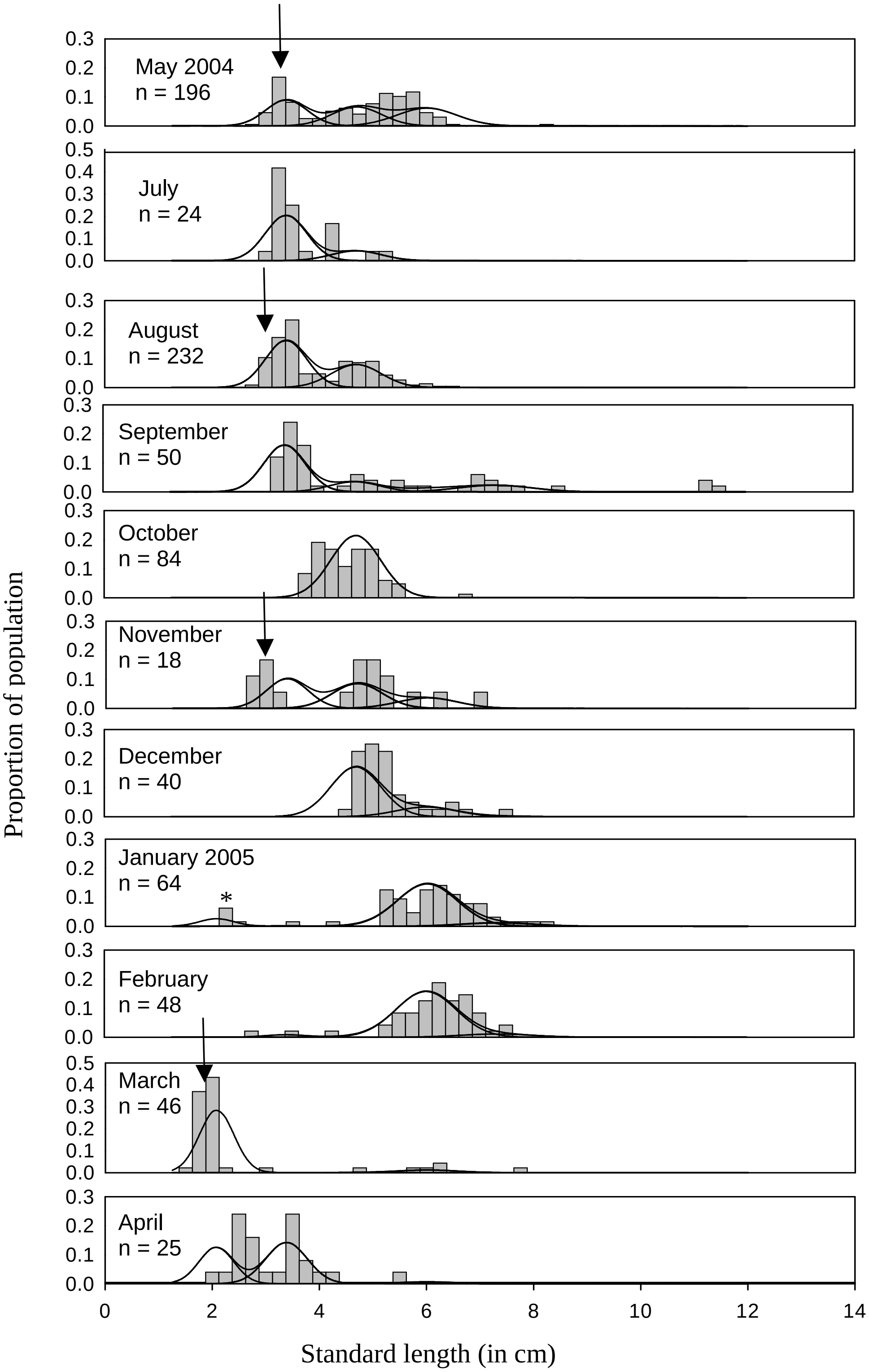

Figure 4.4: Monthly length-frequency distributions (SL) of *Myxus capensis* in Grant's Valley Estuary (bars). Curves represent modes assigned by length-frequency analysis (MULTIFAN). With arrows indicating recruitment via overtopping and the asterisk indicates the January breaching event.

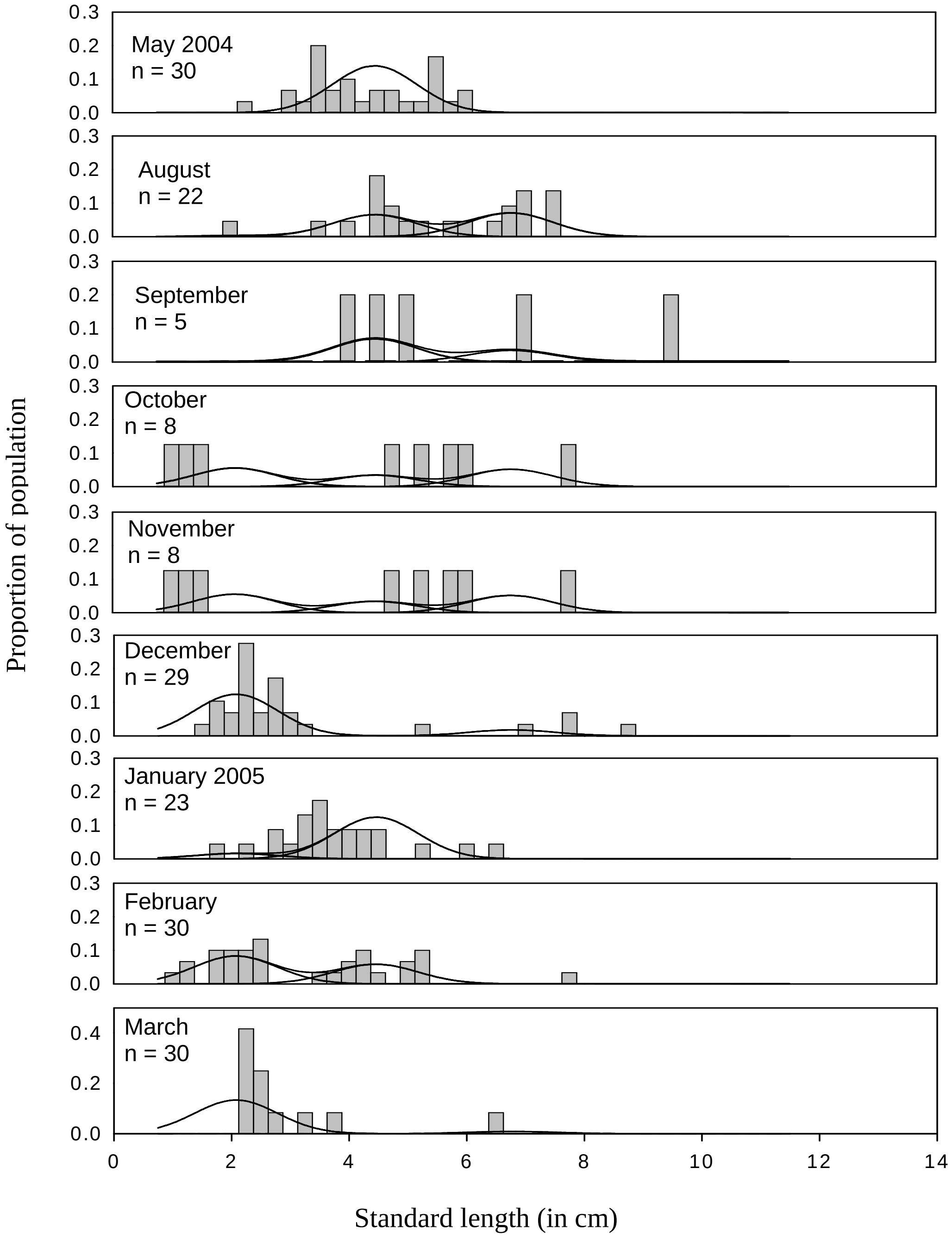

Figure 4.5: Monthly length-frequency distributions (SL) of *Glossogobius callidus* in Grant's Valley Estuary (bars). Curves represent the predicted length frequency distribution estimated using the MULTIFAN model.

Four age classes of the Mozambique tilapia, *O. mossambicus*, population (7 to 66mm SL) were identified (Table 4.1). A peak in abundance was recorded in February 2005 (n = 81) (Figure 4.6) while minimal captures occurred in July, August, September and October 2004 (n = 4; 3; 0; 0) and April 2005 (n = 3). After May 2004 the population declined dramatically. Recruitment of new cohorts occurred at the beginning of the summer in November and December (Figure 4.6). A K of 0.170 and a L_∞ of 10.68cm resulted from the best-fit model (Table 4.2).

4.4 Discussion

Within Grant's Valley Estuary the common estuarine breeding species, *G. aestuaria* and *G. callidus*, and the freshwater *O. mossambicus*, showed well-defined seasonal patterns in recruitment with peaks occuring during the warmer spring and summer months when the estuary was closed. As the recruitment of these species extended throughout this period multiple age-groups were evident. *Gilchristella aestuaria* recruit throughout the summer (Whitfield, 1998; Strydom *et al.*, 2002) and multiple, and abundant cohorts were established, with the peak recruitment period early in the summer. In contrast, *G. callidus* was shown to occur in much smaller abundances, with a peak in recruitment later in the summer. The Mozambique tilapia, *O. mossambicus*, population was greatly reduced in abundances during the winter months due to the species intolerance to low temperatures (Jubb, 1979). During the summer, when optimal water temperatures prevailed (Bruton and Taylor, 1979), two distinct cohorts recruited.

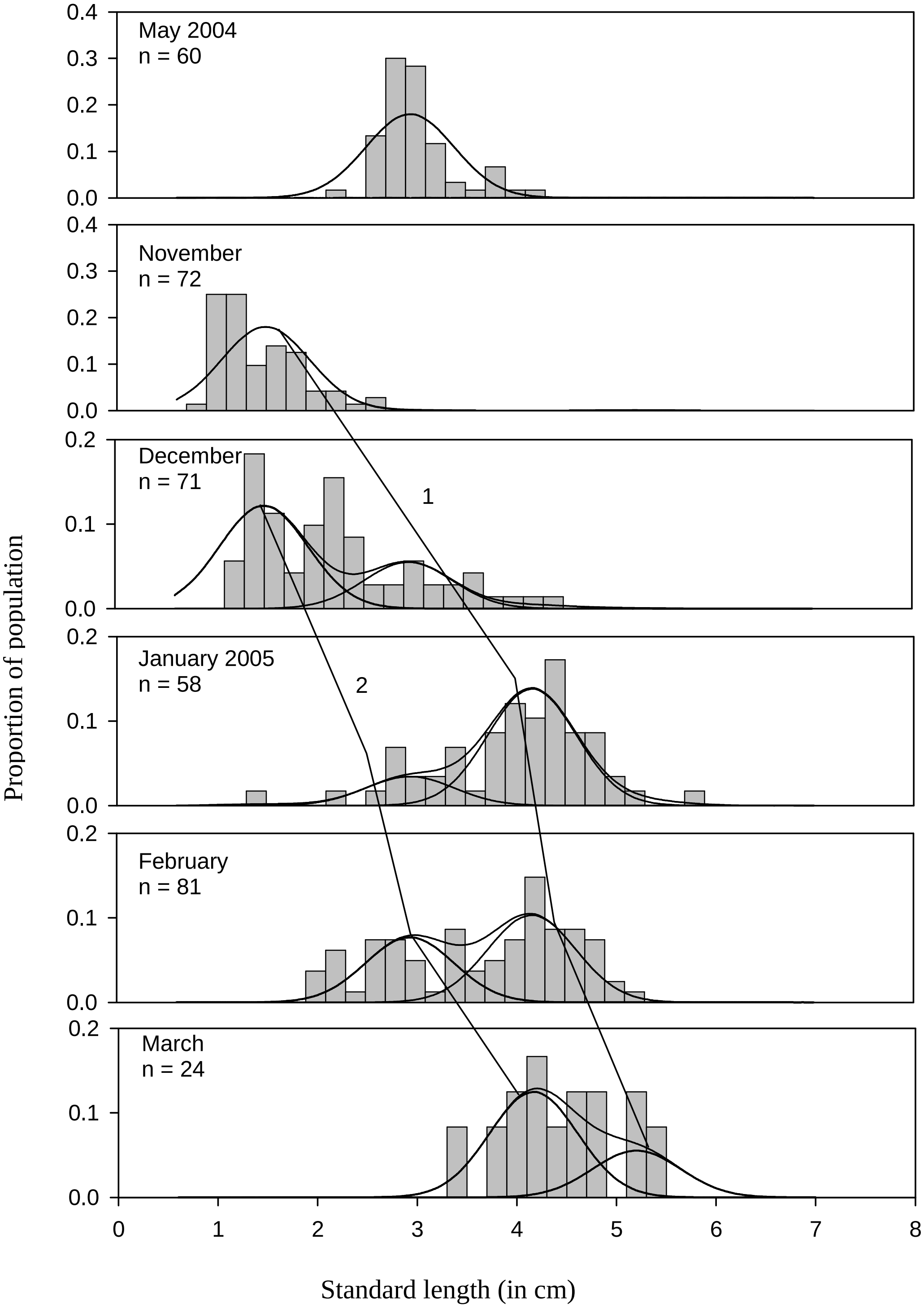

Figure 4.6: Monthly length-frequency distributions (SL) of *Oreochromis mossambicus* in Grant's Valley Estuary (bars Curves represent the predicted length frequency distribution estimated using the MULTIFAN model. Two cohorts beginning in November (1) and December (2) respectively are represented by two straight lines.

Previous studies have demonstrated that fish that reproduce within estuaries tend to be small, short lived species with high fecundities (Haedrich, 1983; Dando, 1984). *Gilchristella aestuaria* were shown to be fastest growing within Grant's Valley estuary, with an estimated von Bertalanffy *K* value of 0.342. *Gilchristella aestuaria* are highly productive, reaching their maximum sizes at relatively early ages and have been found to mature within seven months at approximately 28mm SL (Bigelow *et al.*, 1995; Whitfield, 1998). Within intermittently open estuaries, quick growth and early maturity allow *G. aestuaria* to be extremely productive and as a consequence they often numerically dominate the ichthyofaunal assemblages within TOCEs (Whitfield, 1998; Styrdom *et al*. 2002). During this study *G. aestuaria* accounted for 86.9% of the total fish sampled (see Chapter 3). *Oreochromis mossambicus* have been shown to attain sexual maturity within one year at 80 to 120mm SL (Whitfield, 1998). Maximum predicted size of this species is much smaller than in warmer regions, as the majority of individuals live for about one year due too temperature induced mortality (Bruton and Boltt, 1975; Bruton and Taylor, 1979; Jubb, 1979). The estimate growth rate of *G. callidus* was lowest amongst all estuarine fish species examined. This differs from previous reports, which suggest that *G. callidus* is a short lived, quick maturing, and highly productive species (Whitfield, 1998). The reduced estimated growth rate of *G. callidus* within the estuary suggests that other biological and physiological factors may be important. Field studies indicate that *G. callidus* preferentially inhabit muddy substrates with reduced vegetation cover (A.K. Whitfield, personal communication). During the course of this investigation percentage vegetation cover of submerged macrophytes increased from *ca*. 5% to *ca*. 45% (see Figure 3.3). After the breaching event, much of the *G. aestuaria* population was flushed out of the estuary. This is consistent with other research that showed increased river flow has a negative impact on *G. aestuaria* abundances (Strydom *et al.*, 2002). Re-recruitment did not occur as the population declined and no new recruits were recorded in January 2005.

The marine spawning fish species need a connection to form between the marine environment and the estuary in order to recruit into the system. *Myxsis capensis*, *R. holubi* and *A. breviceps* have all been demonstrated to utilize overtopping events to recruit into TOCEs (Kemp and Froneman, 2004; Tweedle, 2004). With an extended breeding season and peak recruitment periods coinciding with increased incidents of overtopping events, *M. capensis* is well suited to recruit in TOCEs (Bok, 1979; Kemp and Froneman, 2004). The analysis showed a good correlation between overtopping events recorded during the study and the establishment of new age classes of *M. capensis*. A similar but weaker pattern was observed for *A. breviceps*. There was a weak correlation between the establishment of new age classes and overtopping events for *R. holubi* within this estuary as recruitment during this sampling year was minimal. Recruitment during overtopping events is a passive process and recruitment into the estuary is dependent on the availability of larvae in surf zone adjacent to the estuary (Bell *et al.*, 2001; Strydom, 2003; Kemp and Froneman, 2004). Thus, seasonal breeding patterns of marine fish can highly influence the successful recruitment of the ichthofauna into TOCEs (Whitfield, 1998; Kemp and Froneman, 2004). Marine fish species, such as *M. capensis*, with extended breeding and recruitment periods are available in the surf zone to recruit into the estuary for much of the year, while species with more defined peaks in reproduction including *A. breviceps* and *R. holubi* may be less available for recruitment during these rare overtopping events (Whitfield, 1998).

Breaching events are regarded as the main source of recruitment for larval and juvenile marine fish in TOCEs (Neira and Potter, 1992b; Young *et al.*, 1997). During this study, the breaching event in late December coincided with the establishment of a new age class for *M. capensis*. The breaching events in TOCEs also provide the opportunity for large juvenile marine species in the estuary to join the adult populations in the marine environment.

The results of the analyses should be viewed with caution, as there are a number of potential sources of error. The use of the 5m seine net to sample fish within the littoral zone of the estuary may have resulted in the under-sampling of the larger individuals due to net avoidance. The absence of this data would undoubtedly result in changes in the estimates of growth parameters and asymptotic length. None the less, the analysis does provide evidence of the importance of overtopping events in the recruitment of marine breeding species into Grant's Valley estuary. The analysis does appear to have given reasonable growth estimates for *G.* aestuaria, *A.* breviceps, *O. mossambicus* and *R. holubi*. The population dynamics of fish species found within small TOCEs varies dependent on their lifestyles. Those spawned within the estuary show distinct cohorts and spring to summer peaks in abundance. While those spawned outside of the estuary show patchy cohorts related to marine access and peaks in recruitment occur in correlation with overtopping events.

Chapter 5:

Fish population size and movement patterns in the intermittently open Grant’s Valley estuary

5.1 Introduction

Information on fish population sizes within an estuary is crucial for the understanding the ecology of the system and relates directly to their management. Mark-recapture studies have shown that population size within TOCEs is highly variable (Cowley and Whitfield, 2001). This variability has been attributed to differences in recruitment opportunities (i.e., length of open phase, number of overtopping events, habitat availability) and biological factors such as predation (Blaber, 1973; Neira and Potter, 1992a; Cowley and Whitfield, 2001; Bell *et al*. 2001).

The movement and habitat selection of organisms within heterogeneous landscapes can be studied using ecological models that address population dynamics and spatial distributions (Lima and Zollner, 1996). Local fish movement can be seen as a measure of habitat selection and foraging behaviour in fish species with immigration rates as an indicator of habitat quality (Gilliam and Fraser, 1987; Bélanger and Rodríguez, 2002).

At present, very little is known about fish population sizes and movement within southern African intermittently open estuaries. The aim of this study was to examine the fish population size and fish movement patterns within this small intermittently open system.

5.2 Materials and methods

5.2.1 Sampling procedure

This study was conducted during the closed phase of the estuary between April 2004 and July 2004. Sampling occurred four times; in April, June and twice in July. Block nets (10 to 20 m long x 1.5 m, 50 mm mesh) were placed across the estuary at three different areas dividing the estuary into four distinct areas and preventing inter-area movement. Area 1 was the mouth region, closest to the ocean (Fig. 2.1). It is a shallow (0.5 m maximum depth) region characterised by the virtual absence of aquatic macrophytes. The mean salinity for this area was 16.75 ± 0.5‰, and water temperature ranged from 14.0˚C in July 2004 to 18.8˚C in May 2004. Area 2 is a deeper region of the estuary (1.5 m maximum depth) with a bed of the reed *Phragmites australis* located along the upper western bank. The mean salinity for this area was 16.5 ± 0.6‰, and water temperature ranged from 13.3˚C in July 2004 to 18.8˚C in May 2004. Area 3 was of medium depth (1 m maximum depth), and was devoid of reed beds, but with 5-10% cover of the submerged macrophyte *Potamogeton pectinatus*. The mean salinity for this area was 16.75 ± 0.5‰, and water temperature ranged from 13.5˚C in July 2004 to 18.5˚C in May 2004. The mean depth of Area 4 was approximately 1.5 m. An extensive reed bed was located on the upper, western bank. The mean salinity for this area was 16.75 ± 0.5‰, and water temperature ranged from 13.2˚C in July 2004 to 19.4˚C in May 2004.

Fish in the four areas were sampled during daylight hours (between 09h00 and 15h00) with a seine net (30m × 2m with a 15 mm mesh). The net was deployed in a semi-circle and hauled along the area by three to four people, ensuring the footrope was dragged along the bottom to minimise fish escape. Each haul across the complete width of the estuary encompassed ca. 300 m^2 in area 1 and ca. 400 m^2 for the other areas. Two to three net hauls were conducted within each area for each of the four sampling periods.

Fish captured were transferred to 200 L well aerated polycarbonate containers filled with estuarine water from the region sampled. All fish that were caught were identified, placed on a fish board, measured for standard length (SL) to the nearest millimetre, and marked by means of clipping a single fin depending on the region where the fish was originally sampled (Left pelvic fin for area 1, right pelvic fin for area 2, left pectoral fin for area 3, and right pectoral fin for area 4). The fin rays were clipped off in one straight cut using stainless steel scissors, leaving the base of the fin for regrowth. For sole, *Heteromycteris capensis*, there are no pectoral fins to clip; therefore, the fringing dorsal fin was clipped and only the total population size was estimated. If a fish was recaptured in an area different from where it was originally captured, it was returned to the recapture area. To minimize stress, all fish captured were returned to the estuary within 60 min of capture. To maximise survival only fish >50 mm SL were fin clipped. This size represents the length of fish that could not escape through the 15 mm mesh size of the seine net. No mortality from clipping and handling was recorded during the four surveys.

5.2.2 Data analysis

Population size estimates were determined using three different mark-recapture estimators. The first two, the Schnabel (1938) and derived (Cowley and Whitfield 2001) estimators, did not assume movement within the estuary, while the third, based on a Hilborn (1990) estimator, assumed that fish moved within the four demarcated areas.

In all models, the following assumptions were made: 1) there was no recruitment into, or emigration out of the population; 2) marked fish did not lose their marks and were easily recognisable on recapture; 3) marked and unmarked fish suffered the same mortality; 4) marked fish randomly mixed with unmarked fish; and 5) marked fish and unmarked fish are equally vulnerable to sampling.

5.2.3 Non-movement models

<u>5.2.3.1 Schnabel estimator</u>

The maximum likelihood estimate of the total number of fish, $\hat{N}$, from the Schnabel (1938) estimator is

$$\hat{N} = \frac{\sum_{t=2}^{T} m_t M_t}{\sum_{t=2}^{T} n_t} \quad \text{(Seber, 1982)}$$

where n_t is the number of fish sampled on the t^{th} occasion, m_t is the number of marked fish in the t^{th} sample, and M_t is the cumulative number of marked fish in the population, and T is the total number of time periods in the study. Variance estimates were obtained from the methods of Robson and Regier (1964).

5.2.3.2 Derived method

The derived method was used to obtain a population size estimate for those species where no recaptures or few recaptures were obtained. The percentage catch representation of these species was compared with a ‘control species’ from which calculated population size estimates were obtained (Cowley and Whitfield, 2001). The basic assumptions of the derived method were 1) that all species have an equal probability of capture, and 2) that the species under investigation have the same distribution as the ‘control species’ (Cowley and Whitfield, 2001). For example, if 50 individuals of a non-recaptured species were caught, 1000 individuals of the ‘control species’ (with a calculated population estimate of 2000) were caught during the same mark-recapture period, then the derived population size for the species with no recaptures would be 100 [i.e., 50/1000×2000] (Cowley and Whitfield, 2001). Multiple control species were considered for different species of fish, and the species with the highest recapture rate for that group was used. The use of multiple control species gave estimates closer to the modelled estimates for well-recaptured species. *Liza richardsonii* was used as the control species for all the mullet species, *Glossogobius callidus* was used as the control species for the benthic fish (gobies and the sole), and *Rhabdosargus holubi* was used as a control species for the remaining species (sparids, *Monodactylus* and *Oreochromis*).

5.2.4 Movement model

A modified Hilborn (1990) estimator was used to estimate both the number of fish in the estuary, and the probability of moving from one area to another. Species with good recapture rates (>10%) and the all the species combined were modelled and estimated using this method, while species with lower recapture rates were combined into families when possible for movement analysis.

5.2.4.1 Predicted number of marked fish

The predicted number of marked fish (with area-specific marks) that were marked in area *i* and moved to area *j* in the *t*th sampling occasion, $\hat{M}_{ij,t}$, is calculated from the surviving number of marks in that area and the newly marked fish introduced to all areas that move to or stay in area *i*. It is assumed that fish that were marked in each area move instantaneously according to the estimated movement matrix $\hat{\Phi}_{ij}$. Therefore,

$$\hat{M}_{ij,t+1} = \hat{M}_{ij,t} + \sum\nolimits_{j=1}^{A} M_{j,t} \hat{\Phi}_{ij}$$

5.2.4.2 Predicted recaptures

If there is a constant catchability over all areas, then the number of recaptures per area *j* that were originally marked in area *i* during the previous sampling occasion is

$$\hat{R}_{ij,t} = \hat{p}\hat{M}_{ji,t-1}$$

5.2.4.3 Total number of fish

The total number of fish in area *j* at time *t* is calculated from the total number of fish examined for marks at time *t* in area *i* and the estimate of catchability such that

$$\hat{N}_{j,t} = \frac{1}{\hat{p}} \sum_{i=1}^{A} n_{ij,t}$$

The average number of fish in the study area for the entire study is

$$\overline{N} = \frac{1}{T} \sum_{j=1}^{A} \sum_{t=2}^{T} \hat{N}_{j,t}$$

where T is the total number of time periods in the study.

5.2.4.4 Parameter estimation

The probability of capture, $\hat{p}$, and a movement matrix from area *i* to area *j*, $\hat{\Phi}_{ij}$, were estimated by minimising a Poisson likelihood of the form

$$-\ln L = -\prod_{t=1}^{T}\prod_{i=1}^{A}\hat{R}_{i,t} - R_{i,t}\ln\left(\hat{R}_{i,t}\right) - \ln\left(R_{i,t}!\right)$$

The movement matrix was simplified by noting that the last column vector is calculated from all the column vectors as

$$\Phi_{A,j} = 1 - \sum_{i=1}^{A-1}\Phi_{i,j}$$

It is assumed that the row vectors of the movement matrix sum to unity and that all parameters are positive.

5.2.4.5 Parameter variability

Parameter variability was estimated using parametric bootstrapping (Efron, 1979) as it is noted that the observed recaptures are Poisson-distributed. During each bootstrap iteration the observed number of fish marked in each area *i* that moved to area *j* were Poisson deviates drawn from the original observed number of recaptures that were marked in area *i* and moved to area *j*. The bootstrapping procedure was iterated 500 times, and the 100(1 – α) % confidence intervals calculated using the percentile method (Buckland and Garthwaite, 1991).

5.3 Results

5.3.1 Population estimates

A total of 3498 fish from six families and 12 species were marked during the study. In total, 448 recaptures were made, a recapture rate of 12.8%. While seven species were recaptured, most recaptures were from three species: *Rhabdosargus holubi*, *Monodactylus falciformis*, and *Glossogobius callidus* (Table 5.1). No recaptures were recorded for *Oreochromis mossambicus*, *Mugil cephalus*, *Diplodus sargus capensis*, *Caffrogobius gilchristi*, and *Psammogobius knysnaensis*. For those species where no recaptures were recorded, population size was estimated using the derived method. The estimated total number of fish using the Schnabel method (S) was 12262 (95% CI= 11219 – 12922; CV= 4.2%) individuals, and 12258 (95% CI= 11373 – 13311; CV= 4.2%) using the Hilborn method (H) (Table 5.2).

Rhabdosargus holubi (50 – 180 mm SL; mean = 74.9 mm) was the most abundant species captured in the estuary during the study and accounted for 40.6% of the captures. Population estimates for this species were 3970 (S), and 4162 (H).

The Cape moony (*Monodactylus falciformis*) (50 – 126 mm SL; mean = 66.1 mm) was the second-most-caught species in the study with 602 individuals, accounting for 17.2% of the fish captures. Population estimates were 1875 (S) and 1617 (H).

Table 5.1 Total fish captures in the Grant's Valley Estuary between April and July 2004. Sampling Effort (E) is represented by the number of seine hauls in each area. (EUC: Ib – estuarine species that breed manly in estuaries; IIa – marine species with juveniles dependent on estuaries as nurseries; IIb – marine species with juveniles occurring in estuaries; IIc – marine species with juveniles occasionally occuring estuaries; IV – freshwater species; Vb – facultative catadromous species)

Species	Number caught and marked					Percent recaptures (%)	Estuarine Utilization Category (EUC) (Whitfield 1998)
	1(E=8)	2(E=10)	3(E=9)	4(E=8)	Total		
SPARIDAE							
Rhabdosargus holubi	67	545	286	524	1422	17.2	IIa
Lithognathus lithognathus	3	26	60	30	110	13.6	IIa
Diplodus sargus capensis	0	4	0	0	4	0.0	IIc
MONODACTYLIDAE							
Monodactylus faliciformes	2	165	29	406	602	13.1	IIa
MUGILIDAE							
Myxus capensis	0	37	62	164	263	8.3	Vb
Liza richardsonii	0	49	50	53	152	8.5	IIc
Mugil cephalus	1	3	1	3	8	0.0	IIa
Juvenille Mugilidae	285	108	43	84	520	1.0	-
GOBIIDAE							
Glossogobius callidus	2	98	118	103	321	26.5	Ib
Caffrogobius gilchristi	0	1	0	1	2	0.0	Ib
Psammogobius knysnaensis	1	0	0	0	1	0.0	Ib
CICHLIDAE							
Oreochromis mossambicus	19	13	20	21	73	0.0	IV
SOLEIDAE							
Heteromycteris capensis	3	4	10	2	20	15.0	IIb
TOTAL	383	1053	679	1391	3498	12.8	

Table 5.2 Estimates of abundances for fish species in the Grant's Valley Estuary using three mark-recapture techniques, with 95% confidence intervals (CIs) and coefficients of variation (CV) in parentheses.

Species	Schnabel	(CIs; CV)	Hilborn	(CIs; CV)	Derived
SPARIDAE					
Rhabdosargus holubi	3970	(3602 – 4203; 4.3%)	4162	(3781 - 4659; 5.2%)	-
Lithognathus lithognathus	369	(250 - 724; 32.1%)	409	(285 – 671; 24.0%)	307
Diplodus sargus capensis	-		-		11
MONODACTYLIDAE					
Monodactylus faliciformes	1875	(1641 – 2216; 7.9%)	1617	(1355 - 1974; 10.0%)	1681
MUGILIDAE					
Myxus capensis	1113	(844 – 1790; 24.8%)	-		945
Liza richardsonii	546	(385 - 985; 50.2%)	-		-
Mugil cephalus	-		-		29
unidentified juvenile mullet	3276	(2180 - 6558; 32.3%)	-		1868
All mullet	7626	(5916 - 11496; 17.2%)	8042	(6151 - 11683; 17.0%)	-
GOBIIDAE					
Glossogobius callidus	660	(591 - 780; 7.7%)	655	(572 - 782; 8.2%)	-
Caffrogobius gilchristi	-		-		4
Psammogobius knysnaensis	-		-		2
CICHLIDAE					
Oreochromis mossambicus	-		-		207
SOLEIDAE					
Heteromycteris capensis	28	(21 - 111; 51.7%)	29	(15 - 67; 45.4%)	41
ALL SPECIES	12262	(11219 – 12922; 4.2%)	12258	(11373 - 13311; 4.2%)	-

Freshwater mullet (*Myxus capensis*) (52 – 270 mm SL; mean = 107.1 mm) was the most common mullet species in the estuary. Recaptures occurred on all the sampling trips, with 21 recaptures recorded. The population estimates for this species were 1113 (S).

The River goby (*G. callidus*) (50 – 133 mm SL; mean = 81.1 mm) was the third most abundant species of fish captured in the estuary with 321 captures, composing 9.2% of the overall abundance. *Glossogobius callidus* also had the highest recapture rate (26.5%) with 85 recaptures resulting in population estimates of 660 (S), and 655 (H).

Juvenile Mugilidae, those mullet too small and immature to identify accurately, were most likely juvenile *M. capensis* and *L. richardsonii* with occasional *M. cephalus*. A total of 511 juvenile mullet (50 –123 mm SL; mean = 62.9 mm) were caught and 5 recaptures were recorded throughout the study. The resulting estimate of total numbers was 3276 (S). The mullet were combined into the one group for increased accuracy of results. The total mullet population was estimated at 7626 (S), and 8042 (H).

The remaining species (*Liza richardsonii*, *Lithognathus lithognathus*, *H. capensis*, *Oreochromis mossambicus*, *Mugil cephalus*, *Diplodus sargus capensis*, *Caffrogobius gilchristi* and *Psammogobius knysnaensis*) captured accounted for ca. 10% of the total numbers with 371 captures and 29 recaptures. Of these, only *L. richardsonii*, *L. lithognathus* and *O. mossambicus* seem to have any significant contribution to the population. However, no conclusions can be made from the limited recaptures.

One longfin eel (*Anguilla mossambica*) was captured during the April sampling period. Occasional schools of estuarine roundherring (*Gilchristella aestuaria*) and Cape silverside (*Atherina breviceps*) were caught during this study, but these fish were considered too small to mark.

5.3.2 *Movement data.*

For the movement model, only two recaptures occurred in area 1 and both were fish marked from area 2. The other three areas all had many recaptures, from all the areas (area 2 = 147; area 3 = 183; area 4 = 116). Distinct patterns in movement were observed for the fish community sampled (Table 5.3). Of the 383 fish marked in area 1, 47 were recaptured with the model estimating 66% of their movement into area 3, with less movement into area 2 (28%) and minimal movement to area 4 (6%). No fish were predicted to remain in area 1, as no recaptures from this area were found in this area. Fish from area 2 (1053 marked, 212 recaptured) were equally estimated to remain in the area and move to area 3 (both 46%) with minimal movement to area 4 (8%) and area 1 (1%). Fish from area 3 (610 marked, 84 recaptured) remained in the area (39%), moved to area 4 (40%), while some movement to area 2 (19%), and no movement to area 1 was estimated. Fish marked in area 4 (1398 marked, 105 recaptured) tended to remain in the area (60%), while some movement was estimated into areas 2 and 3 (19% and 21%), and no movement was estimated into area 1.

The Mugilidae, a combined category of all species in the family, tended to move widely through the estuary (Table 5.4), but recapture rates were particularly low (1.8%). Mugilidae were caught throughout the estuary with some residency patterns shown for areas 2, 3 and 4. Area 1 had many captures in April (n = 279) and very few captures (n = 4) during the other sample periods. The benthic species, *G. callidus* was a particularly resident species (Table 5.5) with high proportions remaining in areas 3 and 4 (74% and 75%). Those marked in area 2 did show movement to areas 1 and 3 (10% and 52%), but none were found to move to area 4. *Monodactylus falciformis* also exhibited resident behaviour and was particularly dominant in vegetated areas (Table 5.6). Vegetated areas 2 (n = 165) and 4 (n = 406) had much higher captures then areas 1 (n = 2) and 3 (n = 29). Movement estimates also show *M. capensis* remained in area 2 (66%) and area 4 (67%). One the other hand those *M. capensis* marked in area 3 showed complete movement to area 4 (100%). Only one *M. capensis* marked in area 1 was recaptured, and it was recaptured in area 3. Cape stumpnose, *R. holubi*, were captured throughout the estuary, and recaptures occurred in all areas, except area 1. *Rhabdosargus holubi* showed some resident behaviour in area 2 (43%) and area 4 (41%), but movement from area 2 to area 3 (52%), and movement from area 4 to area 3 (36%) and area 2 (23%) was considerable. Those captured in area 1 were found to move to area 2 (33%) and area 3 (59%), while those captured in area 3 had a tendency to move to area 2 (48%), with significant numbers remaining in area 3 (26%) or moving to area 4 (26%) (Table 5.7). White steenbras, *L. lithognathus*, were captured in all areas. The majority of the captures occurred in area 3 (N = 65). All recaptures occurred on the final sampling date. Those fish captured in area 1 and area 2 showed a strong movement pattern to area 3 (100% and 80%), while fish captured in area 3 showed residency (33%) and movement to area 2

Table 5.3 Estimated movement probabilities for total fish population, using the Hilborn (1990) method, in the Grant's Valley Estuary with the 95% confidence intervals in parentheses. Probability of capture, $\hat{p}$ = 0.073 (CI = 0.066 – 0.080).

	Destination Area			
Source Area	Area 1	Area 2	Area 3	Area 4
Area 1	0.00 (0.00 - 0.01)	0.28 (0.15 - 0.40)	0.66 (0.52 - 0.78)	0.06 (0.02 - 0.14)
Area 2	0.01 (0.01 - 0.02)	0.46 (0.43 - 0.56)	0.46 (0.36 - 0.48)	0.08 (0.04 - 0.12)
Area 3	0.00 (0.00 - 0.01)	0.20 (0.13 - 0.30)	0.39 (0.27 - 0.48)	0.40 (0.29 - 0.52)
Area 4	0.00 (0.00 - 0.01)	0.19 (0.12 - 0.25)	0.21 (0.20 - 0.35)	0.60 (0.45 - 0.62)

Table 5.4 Estimated movement probabilities for the Mugilid population, using the Hilborn (1990) method, in the Grant's Valley Estuary with the 95% confidence intervals in parentheses. Probability of capture, $\hat{p}$ = 0.018 (CI = 0.012 – 0.025).

	Destination Area			
Source Area	Area 1	Area 2	Area 3	Area 4
Area 1	0.00 (0.00 - 0.50)	0.33 (0.00 - 1.00)	0.33 (0.00 - 1.00)	0.33 (0.00 - 1.00)
Area 2	0.00 (0.00 - 0.00)	0.62 (0.25 - 1.00)	0.25 (0.00 - 0.60)	0.12 (0.00 - 0.40)
Area 3	0.00 (0.00 - 0.00)	0.00 (0.00 - 0.00)	0.42 (0.14 - 0.75)	0.58 (0.25 - 0.86)
Area 4	0.00 (0.00 - 0.00)	0.17 (0.00 - 0.42)	0.25 (0.00 - 0.52)	0.58 (0.27 - 0.86)

Table 5.5 Estimated movement probabilities for the *Glossogobius callidus* population, using the Hilborn (1990) method, in the Grant's Valley Estuary with the 95% confidence intervals in parentheses. Probability of capture, $\hat{p}$= 0.156 (CI = 0.123 – 0.189).

	Destination Area			
Source Area	Area 1	Area 2	Area 3	Area 4
Area 1	0.00 (0.00 - 0.00)	0.67 (0.00 - 1.00)	0.33 (0.00 - 1.00)	0.00 (0.00 - 0.50)
Area 2	0.10 (0.00 - 0.24)	0.38 (0.16 - 0.62)	0.52 (0.31 - 0.77)	0.00 (0.00 - 0.00)
Area 3	0.00 (0.00 - 0.00)	0.00 (0.00 - 0.00)	0.74 (0.52 - 0.91)	0.26 (0.09 - 0.48)
Area 4	0.00 (0.00 - 0.00)	0.13 (0.03 - 0.25)	0.11 (0.02 - 0.21)	0.76 (0.63 - 0.89)

Table 5.6 Estimated movement probabilities for the *Monodactylus falciformis* population, using the Hilborn (1990) method, in the Grant's Valley Estuary with the 95% confidence intervals in parentheses. Probability of capture, $\hat{p} = 0.127$ (CI = 0.101 – 0.156).

	Destination Area			
Source Area	Area 1	Area 2	Area 3	Area 4
Area 1	0.00 (0.00 - 0.25)	0.00 (0.00 - 0.25)	1.00 (0.25 - 1.00)	0.00 (0.00 - 0.25)
Area 2	0.00 (0.00 - 0.00)	0.66 (0.51 - 0.79)	0.17 (0.07 - 0.29)	0.17 (0.06 - 0.30)
Area 3	0.00 (0.00 - 0.00)	0.00 (0.00 - 0.00)	0.00 (0.00 - 0.00)	1.00 (1.00 - 1.00)
Area 4	0.00 (0.00 - 0.00)	0.33 (0.16 - 0.52)	0.00 (0.00 - 0.00)	0.67 (0.48 - 0.84)

Table 5.7 Estimated movement probabilities for the *Rhabdosargus holubi* population, using the Hilborn (1990) method, in the Grant's Valley Estuary with the 95% confidence intervals in parentheses. Probability of capture, $\hat{p}$ = 0.095 (0.083 – 0.108).

	Destination Area			
Source Area	Area 1	Area 2	Area 3	Area 4
Area 1	0.00 (0.00 - 0.00)	0.33 (0.12 - 0.52)	0.59 (0.41 – 0.77)	0.07 (0.00 - 0.17)
Area 2	0.00 (0.00 - 0.00)	0.43 (0.36 - 0.51)	0.52 (0.43 - 0.59)	0.05 (0.02 - 0.09)
Area 3	0.00 (0.00 - 0.00)	0.48 (0.29 - 0.65)	0.26 (0.11 - 0.43)	0.26 (0.12 – 0.42)
Area 4	0.00 (0.00 - 0.00)	0.23 (0.11 - 0.37)	0.36 (0.20 - 0.51)	0.41 (0.26 - 0.57)

(67%). No *L. lithognathus* originally captured in area 4 were recaptured, so movement from this area cannot be estimated (Table 5.8).

5.4 Discussion

5.4.1 Population Estimates

Mark-recapture techniques are widely used to estimate animal population sizes. These techniques have been utilised for fish populations since the early 20th century, using various methods and resulting in estimates of survival, movement and population size (Schnabel, 1938; Darroch, 1958; 1961; Seber, 1965; Buckland, 1980; 1982). Closed populations, described as populations that remain unchanged during the period of investigation, tend to have simpler estimation models since the effects of the migration, mortality and recruitment are considered negligible (Seber, 1986). With immigration restricted by the mouth closure, and mortality minimized by the virtual absence of piscivorous fish and birds, recruitment was the only potential source of error for the mark-recapture population estimates. Recruitment of ichthyofauna into the estuary likely occurred during the overtopping events that occurred during the study (unpublished data). This recruitment is, however, unlikely to have introduced a high degree of error as we only considered fish >50 mm SL during the study and overtopping typically moves post-flexion larvae (SL < 10 mm) and juvenile fish (SL 10 – 40 mm) into the estuaries (Kemp and Froneman, 2004). Tag loss and fish mortality related to handling stress have also been identified as important sources of variability in mark-recapture studies (Hansen, 1988; Moffett *et al.*, 1997). Fin clipping probably reduced these problems as the study was conducted over a relatively short period of time and little or no fin regrowth was observed.

Table 5.8 Estimated movement probabilities for the *Lithognathus lithognathus* population, using the Hilborn (1990) method, in the Grant's Valley Estuary with the 95% confidence intervals in parentheses. Probability of capture, $\hat{p} = 0.077$ (CI = 0.039 – 0.116).

Source Area	Destination Area Area 1	Area 2	Area 3	Area 4
Area 1	0.00 (0.00 - 0.25)	0.00 (0.00 - 0.25)	1.00 (0.25 - 1.00)	0.00 (0.00 - 0.25)
Area 2	0.00 (0.00 - 0.00)	0.20 (0.00 - 0.67)	0.80 (0.33 - 1.00)	0.00 (0.00 - 0.00)
Area 3	0.00 (0.00 - 0.00)	0.67 (0.20 - 1.00)	0.33 (0.00 - 0.80)	0.00 (0.00 - 0.00)
Area 4	0.00 (0.00 - 0.00)	0.00 (0.00 - 0.00)	0.00 (0.00 - 0.00)	0.00 (0.00 - 0.00)

In the absence of any recaptures, the derived method used to estimate fish population sizes should be considered with caution (Cowley and Whitfield, 2001). Population estimates for those species; (*M. cephalus, D. capensis*, *C. gilchristi*, and *P. knysnaensis*) where no recaptures were made are therefore likely to be inaccurate. Many *O. mossambicus* were captured, but none were recaptured. Previous research has shown that adult *O. mossambicus* exhibit mass mortality in low temperature waters (e.g., during winter) (Jubb, 1979). As a consequence, the estimates of the population size of *O. mossambicus* are likely to be low. It is notable that a similar study conducted in IO estuaries within the same geographic region, *O. mossambicus* contributed < 2% of the total catch (Vorwerk *et al.*, 2001).

Species richness during this study was similar to that of Cowley and Whitfield (2001) in the nearby IO East Kleinemonde estuary, where 12 and 10 species were found in two different surveys, using similar gear and sampling strategy, compared to the 15 species found in this study. Larger IO estuaries and estuaries connected to the sea more often, such as the East Kleinemonde, should show a greater species richness than the smaller, isolated Grant's Valley estuary (Neira and Potter, 1992b; Vivier and Cyrus, 2002). Vorwerk *et al.* (2001) found 20 species of fish in the East Kleinemonde, including *A. breviceps*, *O. mossambicus, G. aestuaria, G. callidus, P. knysnaensis* and *H. capensis*. By contrast, in larger, permanently open systems within the same geographic region, up to 30 species may be recorded (Vorwerk *et al.*, 2001). Although that study employed both seine nets and gill nets, the use of the block nets with the small area of the Grant's Valley estuary probably increased the probability of this study capturing all species within the system. Australian studies (Griffiths and West, 1999; Griffiths, 2001c) found similar fish diversity (16 species) in the small (2 ha) Australian IO Shellharbour Lagoon with similar families dominating (sparids, mullets and gobies) while the smaller Bellambi Lagoon (1.4 ha) contained only five species. The lower fish species diversity in small IO estuaries in can be linked to limited recruitment and lower habitat availability (Bennett, 1989; Whitfield *et al.*, 1989; Griffiths and West, 1999). However, juvenile fish of economic importance are often amongst represented species (Griffiths and West, 1999).

Estuarine utilization categories divide fish species into groups based on their level of estuarine dependence (Wallace *et al.*, 1984; Whitfield, 1998). The two most numerically abundant fish species found in the Grant's Valley estuary (*R. holubi* and *M. falciformis*) are classified by Whitfield (1998) as category IIa fish, marine spawners dependent on estuaries for nursery areas. Of the 12 fish species sampled in this study, eight of the species spawn in the marine environment and have an obligate estuarine phase (type II or type V). The remaining four species, of which only the River Goby, *G. callidus*, makes a considerable contribution to overall numbers, are all species that can breed within the estuary (type I or type IV) (Whitfield, 1998). In small IO Australian estuaries, marine breeding fish do not appear to gain access to estuaries during overtopping events due to the general absence of marine fish larvae within the marine waters adjacent to the systems. As a consequence, estuarine breeding fish numerically dominate the ichthyofauna of those systems (Neira and Potter, 1992a; Potter *et al.*, 1993; Young *et al.*, 1997; Griffiths, 2001b). Marine spawned species have, however, been shown to enter these estuaries during opening events (Griffiths and West, 1999; Griffiths, 2001b; 2001c). In the Grant's Valley estuary, it is only overtopping that maintains the dominance of marine breeding species during the extended closed periods.

The numerically dominant fish species within the Grant's Valley estuary, namely *R. holubi*, *M. falciformis* and the mullet species, are all characterised by their ability to withstand a wide range in salinity conditions (Blaber, 1974b; Day *et al*., 1981; Bennett, 1985; Branch *et al.*, 1985), and demonstrate an extended breeding period (Wallace, 1975; Bok, 1979; van der Horst and Erasmus, 1981; Lasiak, 1984). These fish have also been shown to utilise overtopping events to recruit into the estuary during the extended closed phase (Kemp and Froneman, 2004). Another abundant species, *G. callidus*, which prefers freshwater but can breed in estuaries, is found over a wide range of salinities, but are almost never found breeding in the marine environment (Whitfield, 1998). *Glossogobius callidus* was found to be the dominant goby species, and abundant, in other nearby IO estuaries (Vorwerk *et al.*, 2001). Fish species highly tolerant to environmental changes may be the only species that can thrive in small IO estuaries as these systems have lower buffering capabilities and are more likely to experience rapid changes than larger systems (Griffiths and West, 1999).

There have been no similar population studies conducted in small IO estuaries. Studies conducted in the larger, IO East Kleinemonde estuary indicated a population estimate of ichthyofauna equivalent to 18 000 fish (*ca*. 0.10 fish · m^{-2}) in a study with a similar recapture rate and 133 000 (*ca*. 0.76 fish · m^{-2}) in a second study characterised by an increased frequency of overtopping events, but with a much lower recapture rate (Cowley and Whitfield, 2001). By contrast, during this study the mean fish density was estimated at *ca*. 0.41 fish m^{-2}. The higher densities in the Grant's Valley estuary, as compared to the first study, can be linked to extended mouth closure and the recruitment of fish into the estuary during overtopping events that leads to a build-up of fish biomass in the system. In contrast in the East Kleinemonde estuary, mouth-breaching events occur more frequently than in the Grant's Valley estuary (Cowley and Whitfield, 2001; Kemp and Froneman, 2004), resulting in emigration of fish from the estuary to the marine environment. During the second study, the increased overtopping could account for the larger fish abundance. Cowley and Whitfield's (2001) mullet numbers are more conservative since they included mullet >100 mm while this study included mullet >50 mm. In an Australian study (Young *et al.*, 1997), densities ranged from 0.53 to 11.87 fish m^{-2} in the much larger IO Moore River estuary. Densities in permanently open systems tend to be higher than IO estuaries as recruitment can constantly occur, but little quantification has been shown (Whitfield and Kok, 1992).

Rhabdosargus holubi, *M. falciformis*, and *M. capensis* are dominant species found in both the study by Cowley and Whitfield (2001) in the East Kleinemonde and in the current study on the Grant's Valley estuary. With respect to total estimated abundance, *R. holubi* were found to be less dominant in the present study, where they accounted for 30% of the total, than in the East Kleinemonde where they accounted for between 70 and 80% of the total ichthyofauna. The absence of *Pomadasys commersonnii* and the piscivorous *Lichia amia* in this study emphasized the differences between the two estuaries (Cowley and Whitfield, 2001). The presence of *R. holubi*, *L. lithognathus*, and the mullet show the importance of IO estuaries as significant fish habitats for a number of ecologically important fish (Bok, 1979; 1984; Bennett, 1993).

5.4.2 Fish movement studies

Habitat selection by fish species has been shown to be an important influence on fish assemblage structure in estuaries (Whitfield, 1999b). Channel depth, seagrass beds, rocky outcroppings, light penetration levels, sediment type, and the presence of aquatic macrophytes have all been shown to influence distribution of fish in estuaries worldwide (Connolly, 1994; Whitfield, 1999b; Griffiths, 2001a). Immigration rate has been shown to be a good indicator of habitat quality for those fish exhibiting exploratory behaviour (Bélanger and Rodríguez, 2002). Furthermore, estuary size also tends to structure fish assemblages (Anganuzzi *et al.*, 1994) as fish habitat preference and food source vary with size (Whitfield, 1998). Movement of the fish community within the estuary during the present study was seen to be minimal as the majority of fish were found to remain within the area of the estuary where they were captured although a slight upstream movement can been seen. This upstream movement may be a seasonal shift to deeper waters during the colder winter. Notable exceptions to this observation were the mullet, and Cape stumpnose, *R. holubi*, which appeared to demonstrate a high degree of inter-area movement.

For the mullet species, gut content analysis studies indicate that mullet consume mainly microphytobenthic algal and diatoms (Blaber, 1987). The mullet, as detritivores make an important link in overall fish production (Ray and Straškraba, 2001). Maximum biomass of microphytobenthic algae are generally recorded in the mouth region of the estuary where optimum conditions for growth prevail (Perissinotto *et al.*, 2003; Nozais *et al.*, 2005). The high degree of movement demonstrated by mullet may therefore be attributed to food availability and foraging behaviour. The most dominant mullet species in the estuary is the catadromous *M.*

capensis. Catadromous mullet have been shown to show a general upstream movement pattern in estuaries (Almeida, 1996), which may affect the movement of mullet even though they cannot reach freshwater due to impoundments and restricted fluvial flow. *Rhabdosargus holubi* did show some preference for areas with high densities of submerged vegetation, as large juveniles feed on epiphytic diatoms covering aquatic macrophytes (Whitfield, 1998). The absence of macrophytes in shallow mouth region during the study would make that area a less suitable habitat for these fish. The remaining species appeared to be restricted to specific areas, particularly those areas characterised by submerged macrophytes or reed beds. A number of previous studies have demonstrated that fish biomass is greatest in those regions of the estuary where reeds or submerged macrophytes persist (Weis and Weis, 2003; Adams *et al.*, 2004). The increase in biomass is thought to be a result of the reed beds providing refuge against predators coupled with their role as detritus traps providing improved foraging regions (Griffiths, 2001b; Weis and Weis, 2003; Nagelkerken and van der Velde, 2004).

Chapter 6:

General discussion

Results of this study indicate that the ichthyofaunal community structure within the littoral zone of Grant's Valley estuary was strongly linked to mouth phase and the establishment of a link to the marine environment via overtopping, and to a lesser extent, seasonality (Chapter 3). In the absence of these links, the ichthyofaunal community was numerically dominated by estuarine resident species, mainly *G. aestuaria* and *G. callidus* which could be attributed to the multiple recruitment events of these species during the closed phase (Chapter 4). The establishment of a link to the marine environment via breaching or overtopping resulted in an increased contribution of marine breeding species (e.g. *R. holubi*, *M. falciformis, M. capensis* and *L. richardsoni*) to the total ichthyofaunal assemblage within the estuary. This resulted in increased ichthyofaunal diversity.

Seasonal changes in water temperatures also appeared to contribute to the temporal change in the ichthyofaunal community due to the temperature induced mortality of Mozambique tilapia, *O. mossambicus* (Chapter 3). There were no spatial patterns in the ichthyofaunal community, which can be linked to the virtual absence of horizontal gradients in temperature and salinity within TOCEs (Froneman, 2002a). The observed pattern in ichthyofaunal community structure within the small intermittently open Grant's Valley estuary was in agreement with studies conducted in larger TOCEs (e.g. East Kleinemonde and Kasouga) (Cowley and Whtifield, 2001; Tweedle, 2004) within the same geographic region.

Overall, the ichthyofaunal diversity in the Grant's Valley estuary was much lower than that of the permanently open systems (e.g. Kariega and Great Fish) (Ter Morshuizen and Whitfield, 1994; Vorwerk *et al*. 2001). The reduced diversity can be ascribed to the presence of a sandbar at the mouth, which limited recruitment of marine breeding species into the system (Whitfield 1999b). Not all estuarine dependent marine fish species have been shown to equally utilize overtopping events to recruit into TOCE (Vivier and Cyrus, 2001; Kemp and Froneman, 2004). As a result, the estuarine dependent marine fish species found within TOCE is a subset of the community typically recorded in permanently open estuaries in the same region.

Results of the mark and recapture study indicate that the small Grant's Valley estuary sustained a population of approximately 12 000 individuals >50mm SL (Chapter 5). The large number of fish can likely be attributed to the accumulation in abundance due to the recruitment of marine breeding species into the estuary during overtopping events. It is worth noting that the estimates of abundance per unit area (0.41 fish · m^{-2}) exceeded those found in the larger East Kleinmonde estuary (0.10 fish · m^{-2}). The elevated values can likely be attributed to the reduced frequency of breaching events in the Grant's Valley estuary. Within TOCE movement of fish within these systems appears to be species specific and dependent on habitat selection and foraging behaviour (Whitfield, 1999b). Although the fish community did be enlarge, not show spatial patterns for the smaller sized fish, larger marine species showed some habitat preferences within the estuary.

This study has investigated spatial and temporal patterns; growth and recruitment; and movement and population size of the ichthyofauna in the littoral zone of the small temporarily open/closed Grant's Valley estuary using robust models and year long data. The study has highlighted a number of areas where future research is urgently required:

(1) Increased coastal development coupled with global climate change is likely to coincide with the dramatic reduction in freshwater inflow into these systems. The reduction in freshwater pulses in this semi-arid region is likely to be associated with a decreased frequency of breaching events (Reddering, 1988; Whitfield and Bruton, 1989). The impact of long-term separation of the estuary from the marine environment to South African TOCE is important to their biodiversity;

(2) Research on overtopping as a means of recruitment of fish from the marine environment into South African TOCE has been restricted to a single study in the subtropical region (Vivier and Cyrus, 2001) and two studies in the warm temperate zone (Bell *et al*., 2001; Kemp and Froneman, 2004). Results of these studies indicate that these events play an important role in structuring ichthyofaunal communities within TOCE. To date, no research has been undertaken to assess if marine species within TOCEs can utilize these events to return to the marine environment;

(3) Breaching events are associated with the export of marine breeding fish within TOCE into the marine environment (Harrison and Whitfield, 1995; Young *et al*., 1997). The large number of TOCE recorded along the southern African coastline suggests that these systems play an important role in the dynamics of the ichthyofauna within the near-shore environment.

(4) Food webs within TOCE are poorly understood. More research on the nutrient flow within these systems can be undertaken as food webs can show the community structure and trophic levels within estuaries. Furthermore, how the changing

environmental conditions (i.e. shifts in salinity and temperature) may result in shifts in the food web.

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