THE INFLUENCE OF OVERWASH AND BREACHING EVENTS ON THE SPATIAL AND TEMPORAL PATTERNS IN ICHTHYOFAUNA COMMUNITY COMPOSITION IN A TEMPORARILY OPEN/CLOSED SOUTHERN AFRICAN ESTUARY

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GAVIN PAUL TWEDDLE

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ABSTRACT

This study assessed the importance of overwash and breaching events on the ichthyofaunal community structure in the medium-sized temporarily open/closed Mpekweni Estuary located on the southeast coastline of southern Africa. The fish in the littoral zone of the estuary were sampled using a 5 m seine net while the channel region was sampled using two nets, a smaller meshed 30 m seine net to target the estuarine spawning species and the juvenile estuarine-dependant marine spawners, and a larger meshed 50 m seine net to target the larger marine and freshwater spawning species. Intensive monthly sampling over two years provided data on selected physico-chemical and biological parameters. During the two year sampling period from November 2005 to October 2007 the estuary breached in late July 2006 and remained open till the sandbar re-formed across the mouth in late December 2006. Thus, sampling encompassed three open/closed phases 1) initial closed period, 2) open period and 3) re-closed period after the berm was re-formed. The open period was divided into two phases 1) the out-flow phase and 2) the tidal phase.

A total of 36 fish species representing 19 families were sampled using the various seine nets employed during the investigation. In the littoral zone, the estuarine spawners (Estuarine Utilisation Category, [EUC] I), mainly the Gobiidae, *Glossogobius callidus*, dominated the samples numerically and by biomass. The smaller estuarine spawning species sampled in the channel were numerically dominated by *Gilchristella aestuaria* in conjunction with two other EUC I species, *Atherina breviceps* and *G. callidus*. The estuarine-dependant marine spawners (EUC II), however, dominated the ichthyofaunal biomass of the channel. The abundance and biomass of the larger species targeted were dominated by estuarine-dependant marine spawning species (EUC II), principally *Rhabdosargus holubi*.

During the closed periods of the estuary, total fish abundance and biomass displayed weak seasonal patterns. The breaching event and subsequent open period was associated with a decrease in the total abundances of fish in the littoral zone and channel of the estuary, reflecting the out-flow of estuarine biomass-rich water into the marine environment. The breaching event coincided with a shift in the community composition of the ichthyofauna, reflecting the recruitment of marine spawning species into the estuary.

Numerical analysis identified two distinct spatial fish communities within the estuary, a community associated with the mouth region and one comprising the rest of the estuary. The absence of any further spatial patterns in the ichthyofaunal community structure within the Mpekweni Estuary appear to be ascribed to the virtual absence of horizontal patterns in physico-chemical and biological parameters recorded in the system.

Cohort analyses were employed to determine possible recruitment events for selected estuarine and marine spawning species. The estuarine spawning species displayed continuous recruitment patterns throughout the study, which appeared to be unaffected by the breaching event. Conversely, the larger marine spawning species displayed multiple cohorts, indicating non-continuous recruitment. Subsequent retrospective analysis of cohorts for the different species identified summer recruitment peaks that coincided with the breaching event and open period. Minor recruitment of marine spawning species also occurred during overwash events.

The recruitment of ichthyofauna into the estuary was quantified during three distinct hydrological events: overwash, out-flow phase immediately after breaching and tidal phase during the period when the mouth was open. Estimates of fish recruitment were highest during the outflow phase immediately after the estuary breached and declined as the estuary became tidally inundated with marine water. Although not as high as the outflow and tidal phases, recruitment was evident during overwash events. Results of the current study highlight the importance of both breaching and overwashing events in structuring the ichthyofaunal community composition in a medium-sized southern African temporarily open/closed estuary. These results are broadly in agreement with similar studies conducted both locally and in other regions of the world.

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TABLE OF CONTENTS

LIST OF FIGURES

APPENDIX

LIST OF TABLES

APPENDIX

CHAPTER 1

GENERAL INTRODUCTION

1.1 INTRODUCTION

In 1967, Pritchard defined an estuary as, "a semi-enclosed body of water with a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage". While this definition may be acceptable to scientists working on estuaries in the northern hemisphere, in countries such as South Africa and Australia, many of the estuaries are characterised by the absence of a horizontal gradient in salinity. The absence of this gradient and freshwater abstraction can be attributed to amongst others, sporadic or reduced rainfall and small catchment areas which contribute to reduced freshwater inflow into these systems.

As a direct result of this inability to classify South African estuaries according to these guidelines, Day (1980) proposed that estuaries in South Africa be defined as, "a partially enclosed coastal body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixture of sea water with fresh water derived from land drainage". Elliott and McLusky's (2002) review of the estuarine definitions takes into account most definitions and the aspects of these estuarine definitions but fails to consider Day's (1980) definition for southern African estuaries.

More recently estuaries have been considered a component of transitional waters (Mclusky and Elliott, 2007). Alternatively, estuaries have been categorised according to their contribution as a filter of terrestrial run-off (rivers) into the world's oceans (Dürr *et al.*, 2011) or through modelling processes (Hume *et al.*, 2007). The latest definition of an estuary by Whitfield and Elliott (2012) and the one considered for this study is, "a semi-enclosed coastal body of water which is connected to the sea either permanently or periodically, has a salinity that is different from that of the adjacent open ocean due to freshwater inputs, and includes a characteristic biota".

The definition by Whitfield and Elliott (2012) is more concise than that proposed by Potter *et al.* (2010) which stated that "an estuary is a partially enclosed coastal body of water that is either permanently or periodically open to the sea and which receives at least periodic discharge from a river(s), and thus, while its salinity is typically less than that of natural sea water and varies temporally and along its length, it can become hypersaline in regions when evaporative water loss is high and freshwater and tidal inputs are negligible". However, the definition by Whitfield and Elliott (2012) is somewhat vague in regards to hypersalinity regimes; initial reading would suggest that systems exceeding marine salinities are not considered estuaries as there is limited influence of "freshwater inputs".

Whitfield (2000) identified ~ 258 functional estuaries along the ~ 3100 km of South African coastline, which ranges from the Orange River on the west coast to the Kosi River on the east coast (Whitfield, 1998). Harrison *et al.* (2000) suggested that only 67 % of South Africa's estuaries have been surveyed and that there are in fact ~ 370 outlets to the sea. Whitfield (1992) utilised Day's (1980) definition of a South African estuary, and separated the various estuarine environments into different categories based on a combination of physiographic, hydrographic and salinity characteristics. These characteristics identify five estuarine types along the South African coastline: estuarine bays, permanently open estuaries (POE), river mouths, estuarine lakes and temporarily closed estuaries (also known as intermittently open or temporarily open/closed estuaries or TOCEs).

The ecology of the South African estuaries is predominantly determined by geographic locality, where biological and environmental aspects are separated accordingly into three general biogeographic regions/zones (Figure 1.1) (Stephenson and Stephenson, 1972; Brown and Jarman, 1978; Emanuel *et al.*, 1992; Whitfield, 1994b; Turpie *et al.*, 2000; Harrison, 2002). These zones broadly correspond to the west coast, south coast and east coast of the country, which form the Cold/Cool Temperate Zone (CTZ), Warm Temperate Zone (WTZ) and the Sub-Tropical Zone (STZ), respectively (Stephenson and Stephenson, 1972; Brown and Jarman, 1978). The boundaries between these regions vary in different reports depending on the biological aspect being considered (Harrison, 2002).

Temporarily open/closed coastal systems account for the majority of estuaries found not only long the South African coastline (~71 %) (Whitfield 1992; 1998; 2000), but also along the south western (~ 82 %) (Potter and Hyndes, 1999) and south eastern (50 %) (Everett *et al.*, 2007) coastlines of Australia, respectively. These temporarily open/closed systems are not just limited to the South African and Australian coastlines but are also found in north (Kraus *et al.*, 2008), central (Raz-Guzman and Huidobro, 2002) and south America (Moscoso *et al.*, 2006; Dussaillant *et al.*, 2009), in New Zealand (Hume *et al.*, 2007) and the Mediterranean (Vizzini *et al.*, 2005). There are, however, very few peer-reviewed reports on similar estuarine types around the world, with the possible exception of Australia (Gobler *et al.*, 2005). Temporarily open/closed estuaries remain closed for extended periods of time due to the formation of a sand-bar or barrier that forms across the mouth of the estuary (Whitfield, 1992). The small catchment areas (< 500 km) of many South African TOCEs also contributes to the reduced freshwater inflow into these systems (Whitfield, 1992; 1998).

Despite the formation of a sandbar at the mouth of these estuaries, which may separate them from the marine environment for several years, these systems still remain ecologically viable and possess 'characteristic biota' (Whitfield, 1992; 1998; Moscoso *et al.*, 2006). Whitfield (1998) identified a multilayered system where both abiotic factors including physical and chemical parameters and biotic factors have an important direct and indirect influence on the biology within estuarine systems.

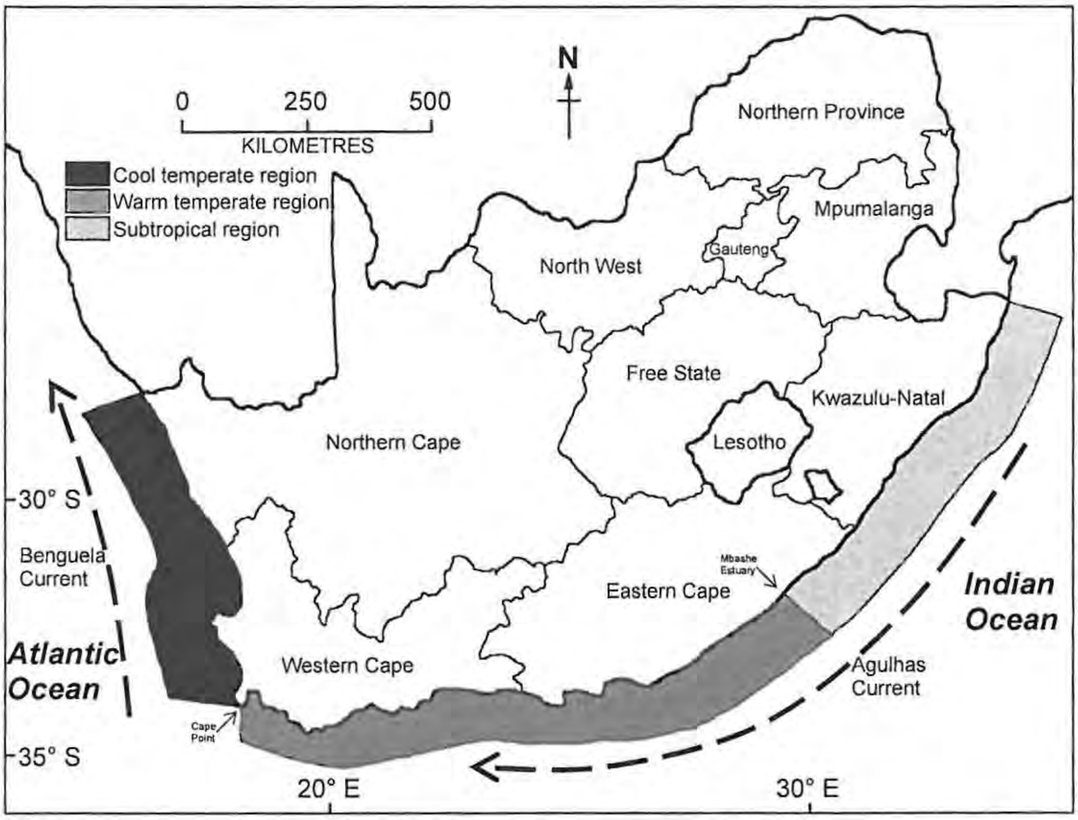

Figure 1.1: The geographic extent of the three biogeographical zones along the South African coastline (after Whitfield, 1994b).

During closed periods there are conditions under which water transfer can occur between the TOCEs and the marine system. Overwash occurs when marine waters wash over the sand bar at spring high tides or during severe storm events (Harrison *et al.*, 2000; Perissinotto *et al.*, 2000; Riddin and Adams, 2010). Overwash also provides a means of recruitment for fauna and flora (phytoplankton), either actively or passively (Whitfield, 1992; Cowley *et al.*, 2001; Vivier and Cyrus, 2001; Kemp and Froneman, 2004; Bernard and Froneman, 2005). Marine water entering a closed estuary is retained and subsequent evaporation combined with reduced freshwater flow can result in hypersalinity (> 40), particularly under drought conditions (Whitfield, 1992; 1998; Harrison *et al.*, 2000; Cooper, 2001).

Breaching events also create a connection between the estuary and the marine environment. Breaching occurs when an increase in water level exceeds the rate of natural seepage out of the system and a channel is formed due to scouring of the sand berm (Harrison *et al.*, 2000; Cooper, 2001). The build up of water in the system may be attributed to increased rainfall and flooding, reduction of water extraction up river or due to overwash events that raise the water levels in the estuary (Harrison *et al.*, 2000; Cooper, 2001). During a breaching event the water level in TOCEs can drop drastically (Harrison *et al.*, 2000; Cooper, 2001: Harrison, 2003; Whitfield *et al.*, 2008; 2012a).

Along the South African coastline there are two main types of TOCEs; non-perched, which predominate along the south coast (WTZ) and perched estuaries which are found along the east coast (STZ) (Harrison *et al.*, 2000; Cooper, 2001). Perched estuaries have an average surface water level exceeding that of the marine environment (Harrison *et al.*, 2000; Cooper, 2001). Non-perched are the more common systems with the average surface water level similar to that of the marine environment (Harrison *et al.*, 2000; Cooper, 2001). Primarily, lower salinities are observed in perched systems due to the reduced chance of overwashing with the dominant source of water being freshwater run-off (Harrison *et al.*, 2000; Cooper, 2001). When a perched system breaches it drains rapidly and won't experience tidal ebbing due to its height above the marine high water mark (Harrison *et al.*, 2000; Cooper, 2001: Harrison, 2003). Non-perched systems become tidally dominated until mouth closure (Harrison *et al.*, 2000; Cooper, 2001). The inland reach of the tidal surges depends on numerous factors, including tide height oscillation, estuarine flow rates and the morphology of the channel (Harrison *et al.*, 2000; Cooper, 2001).

Sediment distribution in TOCEs is similar to that of POEs, where the upper and middle reaches of TOCEs are comprised of mud/clay, silt and organic derived sediments and the mouth region is dominated by coarse to medium marine sand sediments (Day, 1981), which are deposited by washover (Cooper, 2001). Flood events that cause breaching scour large volumes of sediment from these estuaries (Reddering and Esterhuysen, 1987). Prior to closure marine sediments are deposited in the mouth and lower reaches of the estuaries (Badenhorst *et* al., 1989). When the estuaries are closed, the distribution patterns of various sediments remain the same, as the water currents in these closed systems are generally insufficient to allow sediment movement.

Temporarily open/closed systems are generally well mixed during the closed phase (Whitfield, 1992; 1998; Froneman, 2002a; 2002b). This homogeneity is attributed to their relatively large surface area, shallow water depths (< 2 m) and strong coastal winds which facilitate horizontal and vertical mixing of the water column (Whitfield, 1992; 1998; Froneman, 2002a; 2002b). The stable/homogenous nature of these closed systems is disrupted when subject to breaching, tidal influence while open, flooding due to overwash or terrestrial run-off and any combination thereof. Vertical stratification may occur during the closed phase following freshwater inflow but is more prominent during or immediately following a breaching event (Gama *et al.*, 2005; Whitfield *et al.*, 2008). Horizontal stratification tends to be more prominent during the open phase when tidal surges push marine water into the estuaries at depth and freshwater flows out along the surface (Whitfield, 1992; 1998; Harrison *et al.*, 2000; Whitfield *et al.*, 2008).

1.2 PHYSICAL AND CHEMICAL CHARACTERISTICS OF TEMPORARILY OPEN/CLOSED ESTUARIES

1.2.1 Water temperatures and salinity

During closed conditions, the water temperatures in TOCEs are predominantly determined by regional climate and season (Whitfield, 1992; 1998) Day (1981) and range between 18 °C and 30 °C for the WTZ (Day, 1981; Perissinotto *et al.*, 2000; 2002; Harrison, 2004). Under closed conditions salinities in TOCEs exhibits greater homogeneity/stability than POEs (Begg, 1984; Whitfield, 1992; 1998). Typically, the rate of change in salinity is slower in TOCEs, due to a lack of tidal influence, with changes occurring over weeks instead of hours or days. Changes may be by as much as 30 over the course of a few days or weeks depending on freshwater input and overwashing events. Mesohaline conditions (5 - 18) generally predominate during the closed phase although limnetic conditions (0.1 – 0.5) occur during periods of high rainfall (Nozais *et al.*, 2001) and hypersaline (> 40) conditions during periods of drought or high evaporation (Whitfield, 1992; 1998).

1.2.2 Dissolved oxygen concentrations

Dissolved oxygen concentrations in the water column are affected by the temperature and salinity of the water, higher temperature and/or salinity lowers the potential for dissolved oxygen in the water (Best *et al.*, 2007). In estuaries, benthic and/or pelagic oxygen levels are often much lower than the marine environment. This has been attributed to chemical action and biological uptake of the oxygen (Borsuk *et al.*, 2001). South African TOCEs, however, may be shallow enough that oxygen depletion is reduced by wind-generated mixing and are unlikely to experience hypoxic conditions. Hypoxic conditions have, however, been reported in the tropical Mpungwini Estuary and warm temperate Swartvlei Estuary situated on the east coast and south coast of South Africa, respectively (Allanson and Howard-Williams, 1984). These systems experienced anoxic conditions as a result of the high levels of hydrogen sulphide released from the sediments as a result of increased macronutrient concentrations derived from anthropogenic sources (Whitfield, 1995).

1.2.3 Light environment

Light penetration in TOCEs is highly variable, reflecting mouth status and the freshwater inflow into the estuary (Whitfield, 1998; Hecht and van der Lingen, 1992; Perissinotto *et al.*, 2000; 2002; Nozais *et al.*, 2001; Froneman, 2002b). Breaching and flooding events are typically associated with an increase in turbidity (75-90 Nephelometric Turbidity Units [NTU]) and the subsequent reduction in light penetration within the water column (Cooper *et al.*, 1993; Froneman, 2002b). When the mouth is closed, turbidity is much lower with readings of < 10 NTU not uncommon (Froneman, 2002a; 2002b).

1.2.4 Nutrient concentrations

Macronutrient input into TOCEs under natural conditions is attributed to terrestrial freshwater run-off contributing dissolved organic and inorganic compounds to the estuary, which in turn are cycled within the system via various biological pathways including plants (Pinet, 2000; Jennings, 2005) and bacterial assimilation (Calbet and Landry, 1999; Allan, 2007; Whitfield *et al.*, 2008). Limiting nutrients within estuaries include nitrogen and phosphates and the dynamics of these elements are strongly influenced by anthropogenic activities such as dairy/cattle/crop farming, garden fertilizers and household sewage within the catchment (Thomas *et al.*, 2005). Eutrophication can increase primary production and, through trophic cascading (Froneman, 2006b) affect subsequent trophic levels (Santangelo *et al.*, 2007).

1.3 BIOLOGY OF TEMPORARILY OPEN/CLOSED ESTUARIES

1.3.1 Phytoplankton biomass

The total chlorophyll-*a* (chl-*a*) concentrations and subsequently phytoplankton biomass in TOCEs (0.1 mg chl-*a*.m^{-3} and 15.4 mg chl-*a*.m^{-3}) are lower than reported for POEs (20 mg chl-*a*.m^{-3} and up to 100 mg chl-*a*.m^{-3}) along the South African coastline (Adams and Bate, 1999; Perissinotto *et al.*, 2000; 2003; Nozais *et al.*, 2001; Froneman, 2002a; 2002b). The reduced phytoplankton biomass recorded in TOCEs is thought to reflect reduced macronutrient concentrations due to limited freshwater inflow (Adams *et al.*, 1999; Froneman, 2002a; 2002b). Additionally, changes in the total chl-*a* concentration within TOCEs have been linked to seasonality and mouth phase (Campbell *et al.*, 1991; Perissinotto *et al.*, 2002; Froneman, 2002a). The total phytoplankton biomass during the breaching of the estuary decreases as a result of the out-flow of biologically rich estuarine waters into the marine environment (Whitfield *et al.*, 2008). In contrast to the water column, microphytobenthic algae concentrations in TOCEs are generally higher than those recorded in POEs within the same region (Adams and Bate, 1994; Nozais *et al.*, 2001; Froneman, 2002a). The microphytobenthic algae in TOCEs have been shown to attain levels two to three orders of magnitude higher than the water column phytoplankton biomass (Nozais *et al.*, 2001; Froneman, 2002a; Perissinotto *et al.*, 2003). Adams and Bate (1999) have suggested that low turbidity, high concentrations of macronutrients in the sediments and reduced current flow are the primary factors contributing to the high microphytobenthic algae biomass and the total primary production in TOCEs.

1.3.2 Macrophytes

The distribution and composition of the larger aquatic macrophytes in TOCEs is linked to geographic position of the system, salinity and mouth condition (Day, 1981; Riddin and Adams, 2008; 2010; Whitfield *et al.*, 2008; 2012b). Generally the macrophytes found in TOCEs are tolerant of larger salinity variations (Lubke and de Moor, 1998), an example of this being the salt marshes which are typically regions of high nutrient production (Paterson and Whitfield, 1996; 1997) and are prominent features of TOCEs in the WTZ and CTZ (Whitfield, 1994b). Spatial zonation of submerged macrophytes is evident in estuaries that experience salinity gradients. Typically marine and estuarine macrophytes dominate the lower reaches of POEs, while freshwater macrophytes are more evident closer to the head waters (Adams *et al.*, 1999). Salinity levels also contribute to the overall species diversity with highest diversity recorded in South African estuaries with salinity ranges of 25 to 30, while above 35 the diversity decreases rapidly (Whitfield *et al.*, 2012b). The decrease in water levels of TOCEs associated with breaching events and subsequent tidal phases often results in a loss of macrophytes and a delay in the recovery due to the littoral areas experiencing prolonged exposure (Riddin and Adams 2008; Whitfield *et al.*, 2008).

1.3.3 Zooplankton

The zooplankton abundance and biomass values recorded in TOCEs during the closed phase exceeds those levels recorded in the larger POEs within the same geographic region (Perissinotto *et al.*, 2000; Kibirige and Perissinotto, 2003a; 2003b; Froneman, 2004). Perissinotto *et al.* (2000) suggested that the elevated zooplankton biomass values during closed periods are sustained by the elevated microphytobenthic stocks of these systems. Conversely, due to the limited number of marine species recorded and the virtual absence of typical estuarine zooplankton in closed TOCEs (Wooldridge, 1999; Froneman, 2004), the zooplankton diversity is much lower than that of POEs, indicating the closed TOCEs zooplankton communities are dominated by a few highly abundant species (Grindley, 1981; Kibirige and Perissinotto, 2003a; 2003b).

Shifts in the zooplankton abundance, biomass and species composition within TOCEs have been linked to amongst others, mouth phase, freshwater inflow, seasonality and overwash events (Bate, 2007; Whitfield and Bate, 2007; Froneman, 2008; Whitfield, *et al.*, 2008; Perissinotto *et al.*, 2010a). Breaching events in TOCEs are typically associated with a reduction in the abundance and biomass of the zooplankton as estuarine rich waters are exported to the marine environment. The inflow of seawater into the estuary following the breaching event is, however, associated with an increase in the zooplankton diversity as marine spawning species recruit into the estuary. Similarly, the overwashing of marine waters across the sandbar during spring high tides and winter storms may also contribute to an increase in the zooplankton diversity within these systems (Froneman, 2004; Bernard and Froneman, 2005).

1.3.4 Ichthyofauna

The distribution of ichthyofauna in South African closed estuaries is typically associated with the three biogeographic regions (Figure 1.1). For the fish, these are the CTZ which ranges from the Orange River down the west coast to Cape Point, the WTZ from Cape Point to the Mbashe Estuary and the STZ, which extends from the Mbashe Estuary northwards to Kosi Bay (Whitfield, 1994b; Harrison, 2002). There is some debate in the literature as to the geographic position of the boundary between the WTZ and the STZ. The general consensus is that there is more of an extended transitional area between the two zones (Turpie *et al.*, 2000; Harrison, 2002) particularly in the marine environment (Sink *et al.*, 2004). Ichthyofaunal studies in estuaries suggest that the boundary is located south west of the Mngazana Estuary (Harrison, 2002). Whitfield (1994b) suggested the boundary should be in the vicinity of the Mbashe Estuary due to the presence of both mangroves, which favour subtropical conditions, and saltmarshes which are associated with the temperate zones. Harrison (2003) and Sink *et al.* (2004) concur that the Mbashe Estuary is the primary boundary between the WTZ and STZ for estuarine fish communities (Figure 1.1).

The South African coastline, unlike the Australian coastal region, does not have large areas of calmer coastal waters (Potter *et al.*, 1990) which contributes to South African estuaries being the main nursery areas for many marine fish species (Wallace *et al.*, 1984; Whitfield, 1999). Whitfield (1998), Harrison (1998) and Vorwerk *et al.* (2003) have discussed in great depth the necessity and importance of South African estuaries as nursery areas for many South African marine fish species, many of which are commercially and recreationally important (Lamberth and Turpie, 2003). Whitfield (1998) attributed the importance of estuaries as ichthyofaunal nursery areas to increased food availability, the sheltered nature of the TOCEs and the shallow water depth of the littoral zone providing a refuge for the larval and juvenile fish (Becker and Laurenson, 2008). Whitfield (1994b; 1998) categorised the different species of fish found in South African estuaries according to their level of estuarine utilisation and whether or not they spend their entire life-history in the estuarine environment (Table 1.1).

Table 1.1: The five major categories of estuarine associated fish species in southern African estuaries (after Whitfield, 1994b).

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 dependant on estuaries as nursery areas. IIb. Juveniles occur mainly in estuaries, but are 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. This category includes some species which may breed in both freshwater and estuarine systems.
V	Catadromous species which use estuaries as transit routes between the marine and freshwater environments but may also occupy estuaries in certain regions. Further subdivided into: Va. Obligate catadromous species which require a freshwater phase in their development. Vb. Facultative catadromous species which do not require a freshwater phase in their development.

The main categories of fish that utilise South African estuaries are estuarine spawners and marine spawners (Whitfield, 1994b; 1998). Due to the extended periods of mouth closure experienced by many South African TOCEs, recruitment of marine spawning species into the systems is limited by the status of the mouth of the estuary, primarily when the estuaries breach or during overwash events (Whitfield, 1992; 1998; Cowley, 1998; Bell *et al.*, 2001; Cowley *et al.*, 2001; Vivier and

Cyrus, 2001; Vorwerk, 2001; Kemp and Froneman, 2004; James, 2007; Whitfield *et al.*, 2008; 2012a).

The ichthyofaunal community structure, like the other components of the food web within southern African TOCEs appears to be determined by mouth status (Cowley, 1998; Vorwerk, 2001; Harrison, 2003; Tweddle, 2004; James, 2007; Whitfield *et al.*, 2008; 2012a). In the absence of any link to the marine environment, the ichthyofauna community within these systems are numerically and gravimetrically dominated by estuarine dependent species, including *Atherina breviceps, Glossogobius callidus* and *Gilchristella aestuaria* (Cowley, 1998; Vorwerk, 2001; Vorwerk *et al.*, 2003; Tweddle, 2004). Ichthyofaunal diversity and species richness during the closed phase of TOCEs has been demonstrated to be lower than those recorded in POEs within the same geographic region, due to the limited recruitment opportunities associated with mouth closure and reduced habitat availability (Vorwerk, 2001; Vorwerk *et al.*, 2003). There are relatively limited quantitative data on the density (ind.m^{-2} or n.m^{-2}) and biomass (g.m^{-2}) of fish species in South African estuaries (Bennett and Branch, 1990; Whitfield, 1993; Ter Morshuizen and Whitfield, 1994; Cowley, 1998). Findings by Bennett (1989a) and Whitfield and Kok (1992), and more recently James (2007) and James *et al.*, (2008b) indicate that abundance of selected ichthyofaunal species in TOCEs often exceeds that recorded in POEs within the same geographic region.

A link to the marine environment either through breaching or overwashing events has been shown to coincide with an increased contribution of marine spawning species including *Rhabdosargus holubi*, *Lithognathus lithognathus*, *Mugil cephalus*, *Liza richardsonii*, *Lichia amia* and *Pomadasys commersonnii* to the total ichthyofaunal community (Cowley, 1998; Vorwerk, 2001; Tweddle, 2004; James *et al.*, 2008b; Whitfield *et al.*, 2008; 2012a). This has the net effect of increasing the ichthyofaunal diversity within these systems (Cowley, 1998; Vorwerk, 2001; Tweddle, 2004). The magnitude of recruitment during the overwash events is, however, substantially lower than that recorded during the open phase (Kemp and Froneman 2006; Whitfield *et al.*, 2008). The ichthyofaunal assemblages in open TOCEs are broadly similar to those recorded in the larger POEs within the same geographic region (Vorwerk, 2001).

In the larger POEs in the northern hemisphere (Desmond *et al.*, 2002), Australia (Potter & Hyndes, 1999) and South Africa (Bok, 1979; Whitfield, 1998), spatial segregation and distribution of ichthyofaunal species occurs due to a variety of physico-chemical and biological factors including temperature, salinity, turbidity, vegetation cover/type and seasonal movement patterns of fish

(Whitfield, 1998; Attrill and Power, 2004). In South African and Australian TOCEs, no distinct spatial patterns in the ichthyofaunal community are evident, probably in response to the virtual absence of any spatial patterns in the physico-chemical variables within these systems (Whitfield, 1992; 1998; Cowley, 1998; Vorwerk, 2001; Froneman, 2002a; 2002b; Tweddle, 2004; Jones and West, 2005; Lukey, 2006; Whitfield *et al.*, 2012b). However, several authors (Hanekom and Baird, 1984; Potter *et al.*, 1990; Harrison and Whitfield, 1995; Whitfield, 1998) have suggested that in these smaller systems there is a potential for inter-species competition and resource partitioning which may contribute to spatial patterns in the distribution of ichthyofauna within these systems.

Salt marshes and the shallow littoral zones are important nursery areas for many fish species and subsequently provide good feeding grounds for predatory fish and other animals (Paterson and Whitfield, 1996; 1997; Connolly *et al.*, 1997; Becker and Laurenson, 2008; Whitfield *et al.*, 2012a). Habitat structure has a localised affect on spatial ichthyofaunal distribution; comparing the diversity, abundance and biomass values in vegetated and bare sand/mud regions of numerous estuaries have exhibited mixed results (Humphries *et al.*, 1992). In some estuaries diversity and biomass were higher over the bare sand/mud areas (Humphries *et al.*, 1992), while species present in the vegetation exhibited higher abundance values (Whitfield, 1988; Humphries *et al.*, 1992). Some estuaries did not demonstrate any variation (Hanekom and Baird, 1984) and different vegetation species revealed different results (Humphries *et al.*, 1992). There is also evidence of limited spatial variation in fish species within South African WTZ TOCEs which has been linked to a variation in sediment type between the middle and upper regions of the estuaries and the lower and mouth regions of the systems (Cowley, 1998; Vorwerk, 2001; Tweddle, 2004). Typically within the estuarine environment salinity appears to be a dominant component in determining diversity and distribution of ichthyofauna (Whitfield *et al.*, 2012b).

1.4 OBJECTIVES

Over the past decade, considerable biological research has been conducted in TOCEs in both the warm temperate and subtropical biogeographic zones along the southern African coastline (Harrison, 2002; 2003; 2004; Harrison and Whitfield, 2006; James, 2007; James *et al.*, 2007b; Whitfield, *et al.*, 2008; Perissinotto *et al.*, 2010a). The vast majority of the South African research has focussed on specific components of the biology, namely fish, plankton and to a lesser extent birds (Whitfield *et al.*, 2008; 2012b). Furthermore, many of the studies conducted in southern African TOCEs have limited temporal coverage, general once off surveys or surveys restricted to specific seasons. Few studies have attempted to link physico-chemical, plankton and ichthyofauna variables within these systems. The main aim of this investigation was to assess the impact of mouth status on the spatial and temporal patterns in the physico-chemical and biological variables (plankton and ichthyofauna) and the recruitment potential of ichthyofauna within the medium-sized TOC Mpekweni Estuary situated along the south-eastern coastline of southern Africa.

1.4.1 Thesis structure

The thesis is structured so that each aspect is independent and dealt with separately, however the findings in each of the working chapters all interlink to give a broader view and understanding of the ichthyofaunal community structure of the Mpekweni Estuary. The locality and description of the study estuary are presented in Chapter 2. In Chapter 3, the spatial and temporal patterns in selected physico-chemical and plankton dynamics in the system are presented. Chapter 4 presents the findings of a study that examined the spatial and temporal patterns in the ichthyofauna community composition, focussing particularly on the influence of mouth phase and overwashing events in determining the community structure. Chapter 5 concerns the growth and recruitment patterns of the numerically dominant fish species within the Mpekweni Estuary. In Chapter 6 the role of both overwashing and breaching events as a recruitment strategy for ichthyofauna is presented. Finally Chapter 7 synthesises and discusses the key interactions between the various chapters.

CHAPTER 2

STUDY SITE

This study was conducted in the Mpekweni Estuary (33° 26' 13" S, 27° 13' 57" E), which is located in the warm temperate biogeographic zone of South Africa (Stephenson and Stephenson, 1972; Brown and Jarman, 1978; Emanuel *et al*., 1992; Whitfield, 1994b; Turpie *et al*., 2000; Harrison, 2002). The Mpekweni Estuary (Figure 2.1) is classified as a medium-sized temporarily open/closed system (Whitfield, 1998; Vorwerk, 2001). Although the estuary is predominantly closed, heavy rains experienced in the Eastern Cape from the end of winter to the beginning of spring 2006, caused this estuary, along with many other TOCEs within the same geographic region, to breach after the July 2006 sampling session and remain open till after the December 2006 sampling session. Prior to the start of this study the estuary had breached and re-closed in the months of September and October 2005.

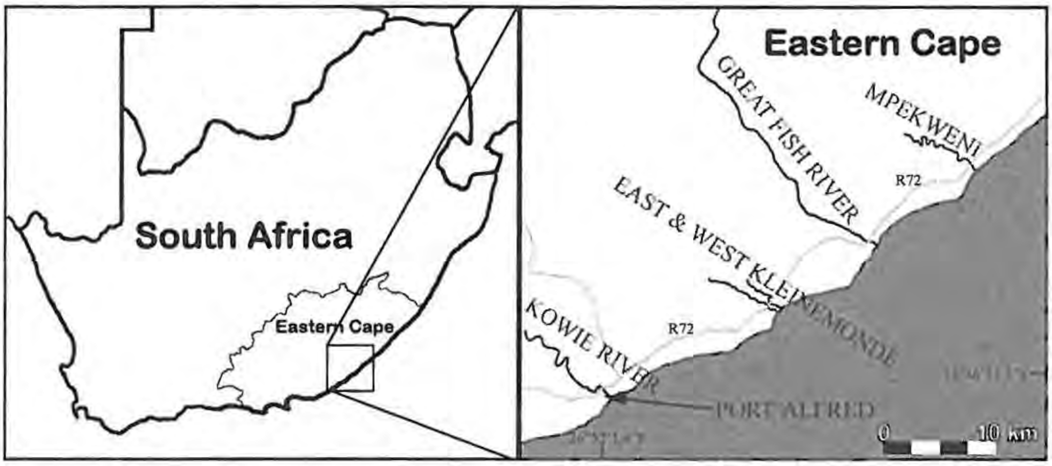

Figure 2.1: The study area shown in relation to the Eastern Cape and South African coastline.

Terrestrially, the Eastern Cape is described as being part of the subtropical region of southern Africa (Lubke, 1988; Lubke, 1998; Vorwerk, 2006). The position of the sub-region places it in the sub-tropical high pressure belt and north of the circumpolar belt of primarily westerly winds. A combination of these factors influences the climate within the region. In the summer months the sub-tropical high pressure belt is positioned south over the country reducing the effect of the circumpolar westerlies. In winter, the high pressure belt is positioned further north but high pressure events are more intense (Stone *et al*., 1998). The circumpolar westerlies are subsequently able to penetrate north and have a great influence on the weather patterns. The main influence on the climatic conditions experienced in the Southern and Eastern Cape are controlled by frontal conditions from the south and west of the country (Stone *et al.*, 1998; Vorwerk, 2006). There are other atmospheric conditions that influence the climatic conditions, such as extreme changes in temperature, from cold fronts to the hot berg winds and the warm subtropical air that also arrives from off the east coast of South Africa (Stone *et al.*, 1998).

The closest regional weather station to the study site is Port Alfred, located some 36 km southwest of the Mpekweni Estuary. According to the South African Weather Bureau, the minimum and maximum temperatures recorded at 08h00 during the period 1996 to 2005 ranged between 1.9°C and 38.5°C for the region (Vorwerk, 2001; 2006; South African Weather Bureau records in literature). These measurements are obviously extremes (Stone, 1988; Vorwerk, 2006) and the general pattern of weather for the region is seasonally cyclic (see Figure 2.2). Average air temperatures range from 9.5°C in winter to 26°C in summer. In comparison to the inland temperatures, the coastline is buffered by the marine environment, thus reducing large fluctuations in temperature. Rainfall has been described as having a bimodal pattern within the region, with maximum rainfall occurring in autumn and spring (Figure 2.3). The mean annual rainfall for the region is ~ 630 mm a year (Figure 2.3).

The rainfall patterns of southern Africa are influenced by the El Niño Southern Oscillation (ENSO), sea surface temperatures and land atmosphere feedback (Nicholson, 2000; Nicholson and Selato, 2000) and the south-eastern Cape of South Africa experiences wet and dry cycles of between 12 and 20 years in duration (Grange *et al.*, 2000). This study was conducted during a dry cycle under El Niño conditions in 2005 and 2007. Previous information on this system is limited and it was unknown if the frequency of overwash events and duration of open mouth conditions experienced (Chapter 3) were typical of this estuary, however, they were within the range of events reported for other similar TOCEs within the same region (Cowley, 1998; Tweddle, 2004; Lukey, 2006; James *et al.*, 2007b; Whitfield *et al.*, 2008).

The coastline along the Eastern Cape is predominantly rocky headlands and sandy dune fields. The dune fields are bordered by dune thicket and grasslands. The headlands often extend into the marine environment, creating reefs in the inshore area (Lubke, 1998).

The coastal hydrography within the region of study is dominated by the warm Agulhas Current which flows down the east coast of Africa and runs west along the south coast and as the shelf expands so the current moves off shore. Easterly winds periodically generate an upwelling of the colder bottom water on the Agulhas Bank as a result of offshore movement of the Agulhas Current (Schumann *et al.*, 1982; 1995; Walker, 1986; Lutjeharms *et al.*, 2000). When the current is pushed inland the warmer waters from the tropical and subtropical zone are transported into the region.

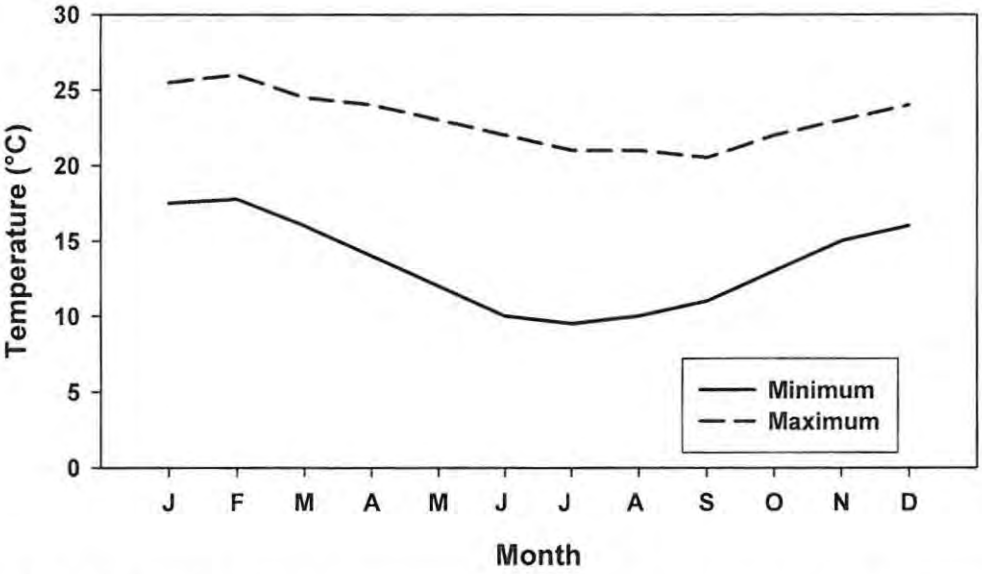

Figure 2.2: The average monthly minimum and maximum air temperatures (°C) recorded at Port Alfred between 1996 and 2005 (Henninger, 2008; South African Weather Bureau records – in literature).

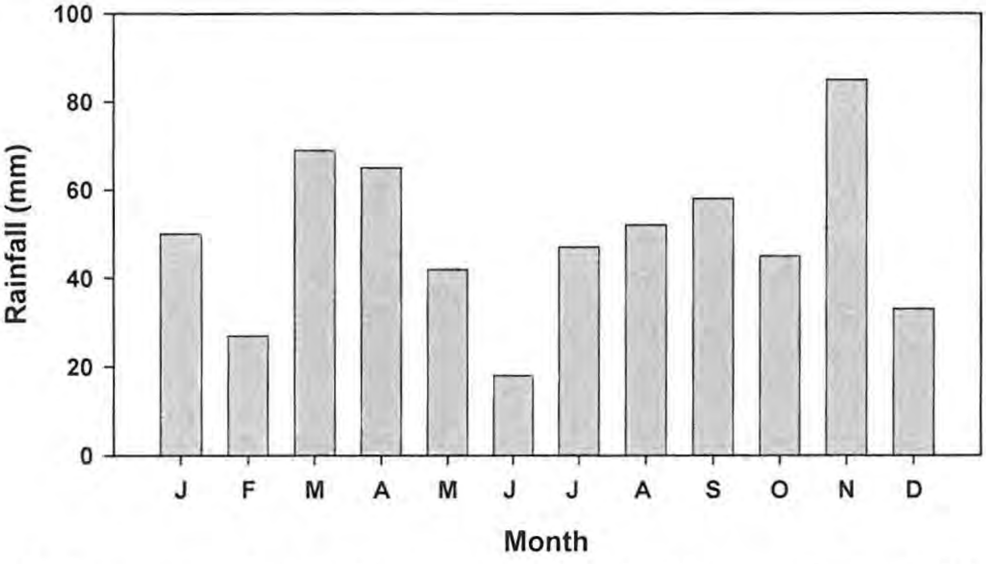

Figure 2.3: Average monthly rainfall recorded at Port Alfred between 1996 and 2005 (Henninger, 2008; South African Weather Bureau records – in literature).

Mpekweni Estuary:

The Mpekweni Estuary (Figures: 2.4 and 2.5) has been described as a virtually pristine estuary largely due to limited development in close proximity to the system and a catchment area that is mainly comprised of undisturbed coastal thicket (Vorwerk, 2001). Access to the estuary is restricted to the Mpekweni Beach resort on the east bank of the estuary or through private lands on the west bank. The mouth region of the estuary has a few holiday houses (< 10) along the west bank of the lower reaches of the estuary and the Mpekweni beach resort on the east bank (Figures: 2.4 and 2.5).

Vorwerk (2001) indicated that the estuary had a surface area of ~ 58 ha and a catchment size of ~ 65 km^2. The estuary is navigable for ~ 3 km and has an average depth of ~ 1.08 m and a maximum depth of 2.6 m (Vorwerk, 2001). The mouth region is dominated by marine sediments (Figure 2.5) and is shallow (< 1 m depth) with a single channel running along the west bank. The sediment in the middle and upper reaches is comprised of fine muddy sediments (Vorwerk, 2001). The banks of the estuary are predominantly covered by valley bushveld or grassland vegetation types and the width of the estuary ranges between < 30 m and ~ 150 m (Lubke and De Moor, 1998). Stability at the mouth of the estuary is enhanced by the presence of a rock formation as well as vegetated dunes. Aquatic macrophytes were limited to some *Phragmites australis* beds located in the lower and middle reaches of the estuary and under high water levels, the middle and upper stations were inundated and covered by submerged beds of *Juncus kraussii* and *Sarcocornia perennis* (Lubke and De Moor, 1998). Individual descriptions for the seine net sampling sites (Figure 2.4) are presented in the materials and methods section of Chapter 4.

When the mouth was open, due to the shallow nature of the estuary and the extensive exposed mudflats, seine net sampling was limited to the station in the mouth region (Figure 2.4) on the sea-ward side of the R72 road bridge; the implications of this limited sampling regime under open conditions are discussed in subsequent chapters.

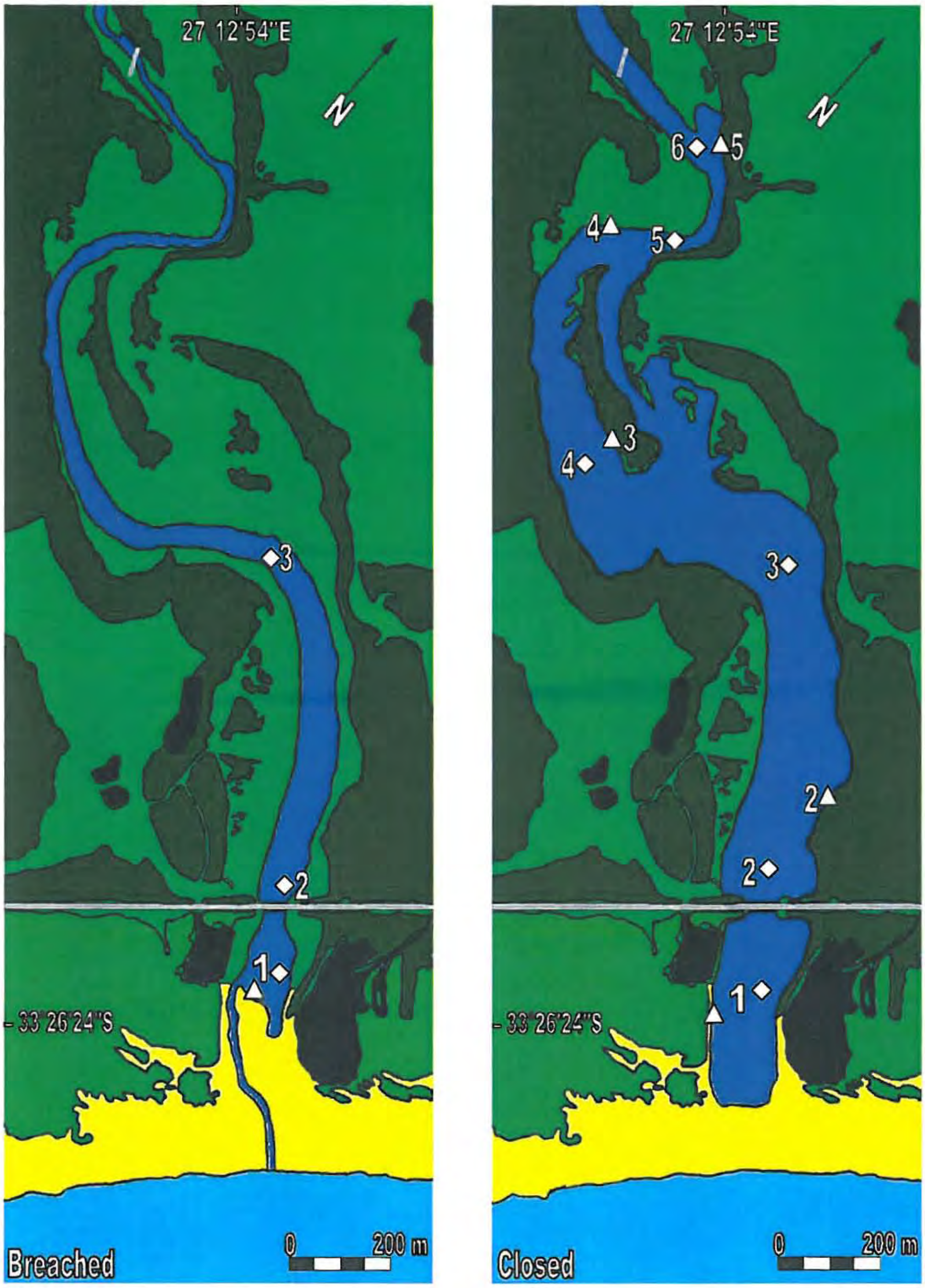

Figure 2.4: Map of the Mpekweni Estuary showing the observed low water level during open conditions and the observed high water levels during closed periods. Diamond shapes indicate physico-chemical, chlorophyll-*a* and zooplankton sampling stations (1 - 6), while the triangles indicate the locations where the 5 m, 30 m and 50 m seine nets were hauled. (Light green indicates grasslands, dark green indicates valley bushveld, the middle shade of green near the beach (yellow) indicates dune vegetation and black indicates built up areas. The R72 coastal road and the weir (at the top) are shown by the grey strips.

Figure 2.5: Images of the estuary under open conditions (a, b and c), closed conditions (d, e, and f) and the mouth of the estuary under open conditions (g, h and i).

CHAPTER 3

SPATIAL AND TEMPORAL VARIATIONS IN THE BASIC PHYSICO-CHEMICAL PARAMETERS, CHLOROPHYLL-*a* AND ZOOPLANKTON ABUNDANCE AND BIOMASS

3.1 INTRODUCTION

Temporarily open/closed estuaries (TOCEs) account for ~71% of the estuaries along the South African coastline. Numerous surveys have been conducted in TOCEs to assess the spatial and temporal patterns of the physico-chemical and biological variables within these systems (Harrison, 2002; Vorwerk, 2001; Gama *et al.*, 2005; Skinner *et al.*, 2006; Gama, 2008; Whitfield *et al.*, 2008; Perissinotto *et al.*, 2010a). Under closed conditions, TOCEs demonstrate strong seasonal patterns of the physico-chemical and biological variables which reflect the seasonal fluctuations in the prevailing climate (Campbell *et al.*, 1991; Whitfield, 1992; Adams and Bate, 1994; 1999; Froneman, 2002a; 2002b; 2004; Perissinotto *et al.*, 2002; Tweddle, 2004; Snow and Taljaard, 2007). The inflow of marine waters into TOCEs during overwash and breaching events contributes to dramatic changes in the physico-chemical (temperature, salinity and dissolved oxygen) and biological variables of the system (Whitfield, 1992; 1998; Cowley, 1998; Wooldridge, 1999; Froneman, 2002a; 2002b; 2004; Harrison, 2003; 2004; Lukey *et al.*, 2006; James *et al.*, 2007b; Snow and Taljaard, 2007). Additionally, these events represent important mechanisms for the recruitment of both marine spawning invertebrates and vertebrates into these estuaries (Whitfield, 1992; Bell *et al.*, 2001; Cowley *et al.*, 2001; Vivier and Cyrus, 2001; Froneman, 2004; Kemp and Froneman, 2004; Bernard and Froneman, 2005). As a consequence, both breaching and overwash events play an important role in structuring the plankton and nekton communities within TOCEs (Bennett *et al.*, 1985; Kok and Whitfield, 1986; Cowley *et al.*, 2001; Vorwerk, 2001).

The aim of this chapter was to assess the spatial and temporal patterns of selected physico-chemical and biological variables in the Mpekweni Estuary and provide a baseline for the study on the ichthyofaunal community composition within the estuary.

3.2 MATERIALS AND METHODS

Mouth phase (open, closed, overwash) was monitored daily by staff at the Mpekweni Holiday Resort. For the purpose of this study, seasons were defined as summer (November to February), autumn (March to April), winter (May to August) and spring (September to October). Sampling was conducted on a monthly basis from November 2005 to October 2007 at the 6 sites as indicated in Figure 2.4 (Chapter 2). No data were collected in the middle and upper reaches of the estuary during the open period of August 2006 to December 2006 due to logistical constraints attributed to the shallow water depth (< 30 cm) within these regions and the extensive mud flats that made the water inaccessible.

3.2.1 Physico-chemical sampling

Temperature (°C) and dissolved oxygen concentrations (mg.L^{-1}) were recorded at the surface and at the bottom of the water column at each sampling site using an YSI 610 probe. Salinity (expressed as practical salinity units: psu) was measured using an optical refractometer. Bottom water samples for salinity measurements were collected using an 8 L Niskin bottle. Nephelometric turbidity units (NTU) were extrapolated from the secchi disk depth measurements (cm) using the equation of Harrison (2003):

$$NTU = \exp\left(\frac{135.0 - \text{secchi depth(cm)}}{26.8}\right)$$

The water depth of the estuary at each sample site during each sampling trip was determined using a graduated weighted line.

Water samples for the determination of particulate organic matter concentration (POM) were collected from the surface and bottom waters at each sample site using the Niskin bottle. To determine POM concentrations, a 300 ml sample of water was vacuum filtered (<5 cm Hg) through a GF/F filter. Filters were subsequently dried at 60 °C for 24 hours and then weighed before being placed in a 500 °C oven for a further 24 hrs and re-weighed on a Sartorius microbalance. The POM concentration was calculated as the difference between the pre- and post- 500 °C readings and expressed as mg.L^{-1}.

3.2.2 Chlorophyll-*a* and zooplankton

Total chlorophyll-*a* concentration (chl-*a*) and zooplankton biomass were determined monthly at each station. For the determination of total chl-a concentration, a water sample collected from each depth was immediately placed in a cool, dark container for subsequent analysis in the laboratory. In the laboratory, 200 ml of water from each depth at each site was vacuum filtered (<5 cm Hg) through a GF/F filter. The filters were then extracted in 90 % acetone for a period of 24 hours in the dark at -20 °C. Chlorophyll-*a* concentrations were then determined fluorometrically (Turner 10AU fluorometer), before and after acidification according to the method of Holm-Hansen & Riemann (1978). Data were expressed as mg chl-*a*.m^{-3}.

Zooplankton tows ($n = 3$) were conducted at each station using a modified WP2 net (47 cm mouth diameter and a mesh size of 60 μm) fitted with a General Oceanics flow meter and a removable cod end. The net was towed at the surface (0.75 m depth) at idling speed. The volume of water filtered during each tow was determined from flow-meter readings. Samples collected were fixed in 10 % Formaldehyde buffered with hexamine (Froneman, 2004) for subsequent analysis in the laboratory. A Folsom plankton splitter was used to sub-sample ($^1/_2$, $^1/_4$, $^1/_8$, $^1/_{16}$, $^1/_{32}$ splits) the overly abundant zooplankton samples. The zooplankton samples were counted and abundance data were expressed as ind.m^{-3}. For the determination of the zooplankton biomass, the subsamples were gently filtered (vacuum < 5cm Hg) onto a pre-combusted, pre-weighed GF/F filter and dried at 60 °C for 24 hours and then re-weighed (Sartorius microbalance). The difference between the pre-weighed and the post-filtered weight provided the zooplankton dry weight biomass (expressed as mg Dwt.m^{-3}) for each sample and replicate. There are limitations to day versus night time sampling of zooplankton; abundance values are 1-3 magnitudes higher at night (Kibirige and Perissinotto, 2003b) and the community structure and dominant species also varies (Wooldridge, 1999; Kibirige and Perissinotto, 2003a; Froneman, 2004), all of which are attributed to diel vertical migration (Perissinotto *et al.*, 2000; Kibirige *et al.*, 2006). For the baseline provision of this chapter, day time samples were deemed sufficient, providing relative comparable species composition and abundances for the different temporal, spatial and mouth phase comparisons.

3.2.3 Indices and analysis

A Kolmogorov-Smirnov and Lillifors test for normality was conducted on all the physico-chemical and biological data using STATISTICA v.8. All data were normally distributed ($p < 0.05$). Subsequently, ANOVA's were conducted to determine differences in the data both spatially (vertically and horizontally) and temporally (monthly and seasonally). Three different phases, the initial closed period (November 2005 to July 2006), open period (August 2006 to December 2006) and re-closed period (January 2007 to October 2007) were also assessed using ANOVA. *Post-hoc* Tukey tests were conducted to identify sources of variation on the data identified to have significant differences by an ANOVA (STATISTICA v.8). Pearson correlation analysis (STATISTICA v.8) was then employed to determine the relationships between the selected physico-chemical (temperature, salinity, dissolved oxygen, turbidity, particulate organic matter) and biological parameters (phytoplankton [chl-*a*] and zooplankton abundance and biomass) over the duration of the investigation.

3.3 RESULTS

During the study, November 2005 to October 2007, the Mpekweni Estuary covered three distinct phases. For the first nine months of the study, the estuary remained closed (initial closed period). Following heavy rainfall within the catchment area in late June 2006, the estuary breached and remained open until the latter half of December 2006 (open period) after which time it closed again (re-closed period). The estuary remained closed for the remaining period of the investigation. Over the two year period, there were four major overwash events. These were recorded on 1st March 2006 (tidal amplitude 2.18 – 2.28 m), 19th February 2007 (tidal amplitude 2.14 – 2.23 m), 20th March 2007 (tidal amplitude 2.19 – 2.32 m) and 27th September 2007 (tidal amplitude 2.13 – 2.23 m). The tidal amplitudes were acquired from Mobile Geographics (www.mobilegeographics.com) using data from both Port Elizabeth and East London, South Africa.

3.3.1 Temperature

The surface water temperatures ranged from 13.3 °C to 28.4 °C and from 13.7 °C to 27.6 °C for the bottom waters (Figure 3.1). There were no significant differences between the two depths ($F_{(1, 256)} = 0.02$ $p > 0.05$). Distinct seasonal patterns ($F_{(3, 125)} = 206.85$ $p < 0.01$) were evident, with summer maxima (28.4 °C) and winter minima (13.3 °C). Intermediate values were recorded in the autumn and spring (Tukey $p < 0.05$). The temperatures recorded during the same winter months when the estuary was open and closed were not significantly different (Tukey $p > 0.05$). Spring and summer months, however, had a significantly lower temperatures during the open phase ($F_{(9, 50)} = 212.15$ $p < 0.05$). No significant spatial patterns of water temperature were evident during the investigation ($F_{(2, 126)} = 0.56$ $p > 0.05$).

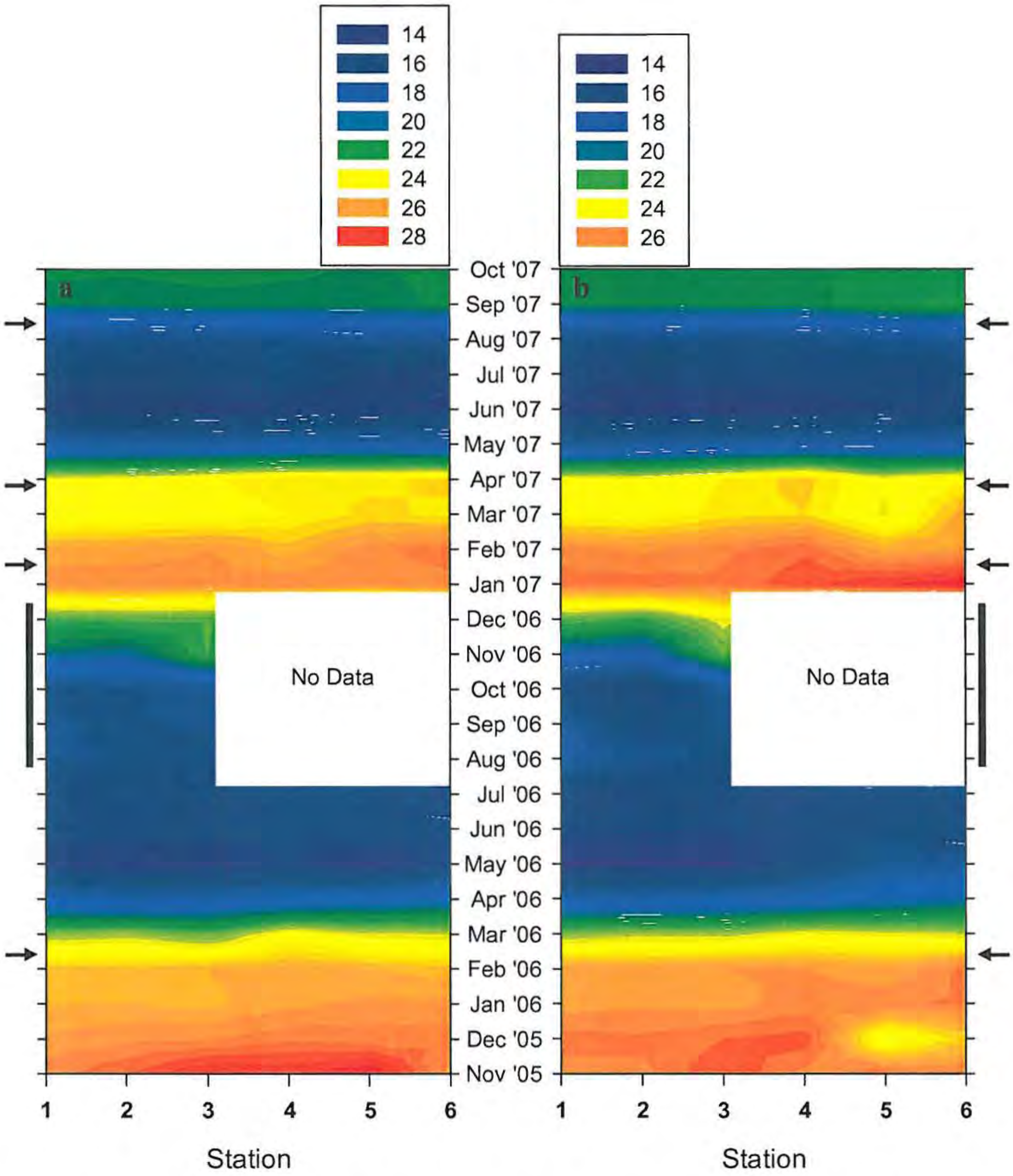

Figure 3.1: Spatial and temporal patterns of temperature (°C) recorded in the surface water (a) and at depth (b) for the Mpekweni Estuary over the period November 2005 to October 2007. The bar indicates the period when the mouth was open and the arrows, overwash events. No data were collected from the stations in the middle and upper reaches over the period August 2006 to December 2006 due to the shallow water depth.

3.3.2 Salinity

During the two years of the study, salinity values ranged from 3 to 39 (Figure 3.2). Salinity values were generally > 25 with the exception of the period August to October 2006 when the estuary breached and freshwater was flowing out of the system (salinity range 3 – 37, average 21). There were no significant vertical differences ($F_{(1, 256)} = 2.22$ $p > 0.05$) in salinity values. Seasonally, the salinity values in autumn were significantly higher than the winter and spring values ($F_{(3, 125)} = 5.40$ $p < 0.01$) (Tukey $p < 0.05$). With the exception of the first spring month during the open period ($F_{(9, 50)} = 11.19$ $p < 0.01$) (Tukey $p < 0.05$), there were no significant differences in salinity values between the open and closed phases for the remaining winter, spring and summer months. Spatially there was no significant horizontal stratification for both station ($F_{(5, 123)} = 0.91$ $p > 0.05$) or reach ($F_{(2, 126)} = 0.78$ $p > 0.05$). Salinity displayed a significantly positive correlation with temperature and negative correlation with dissolved oxygen concentrations ($p < 0.05$ in all cases, Appendix, Table I).

3.3.3 Particulate organic matter concentrations

The POM concentrations (Figure 3.3.b) in the bottom waters were significantly higher ($F_{(1, 256)} = 7.13$ $p < 0.01$) than in the surface waters (Figure 3.3.a) (Tukey $p < 0.05$). Surface POM concentrations ranged between 2.40 mg.L^{-1} and 21.60 mg.L^{-1} and between 3.00 mg.L^{-1} and 37.10 mg.L^{-1} in the bottom waters. Seasonally, the winter surface POM concentrations were significantly lower than during summer and autumn ($F_{(3, 125)} = 5.62$ $p < 0.01$) (Tukey $p < 0.05$). Surface water POM concentrations did display significantly higher values during the re-closed and open phases ($F_{(2, 126)} = 20.84$ $p < 0.01$) of the estuary (Tukey $p < 0.05$). The open period surface water POM concentration was significantly higher than the closed period ($F_{(1, 127)} = 76.37$ $p < 0.01$) (Tukey $p < 0.05$). Further post-hoc tests comparing the surface winter samples did not show any significant difference between the two closed periods and the open period, although there was a significant result with the re-closed period having higher POM values than the initial closed phase ($F_{(2, 21)} = 3.87$ $p < 0.05$). Similarly, post-hoc analysis comparing the summer data displayed no significant variation between the open and re-closed periods, although the initial closed period was significantly lower than the other periods ($F_{(2, 21)} = 8.14$ $p < 0.05$). A comparison of the autumn samples displayed significant higher POM values in the re-closed period versus the initial closed period ($F_{(1, 10)} = 135.79$ $p < 0.05$), while there were no significant differences for the spring months of the open and re-closed periods ($F_{(1, 10)} = 2.94$ $p > 0.05$).

Bottom water POM concentrations did not demonstrate any significant seasonal patterns ($F_{(3, 125)} = 2.05$ $p > 0.05$). Bottom water POM concentrations during the open phase were significantly higher than the re-closed and initial closed periods ($F_{(2, 126)} = 48.36$ $p < 0.01$) (Tukey $p < 0.05$). The open period had significantly higher bottom water POM concentrations than the closed phases ($F_{(1, 127)} = 76.37$ $p < 0.01$) (Tukey $p < 0.05$), further individual analysis of the seasons indicated that the POM values in the open period were significantly higher for all of the comparative seasons; summer ($F_{(2,21)} = 18.92$ $p < 0.05$), winter ($F_{(2,21)} = 6.07$ $p < 0.05$) and spring ($F_{(1,10)} = 6.73$ $p < 0.05$). Spatially there were no significant variations for either the stations or reaches for the surface water POM (station: $F_{(5,123)} = 0.99$ $p > 0.05$; reaches: $F_{(2,126)} = 0.23$ $p > 0.05$) and the bottom water POM (station: $F_{(5,123)} = 1.01$ $p > 0.05$; reaches: $F_{(2,126)} = 2.11$ $p > 0.05$).

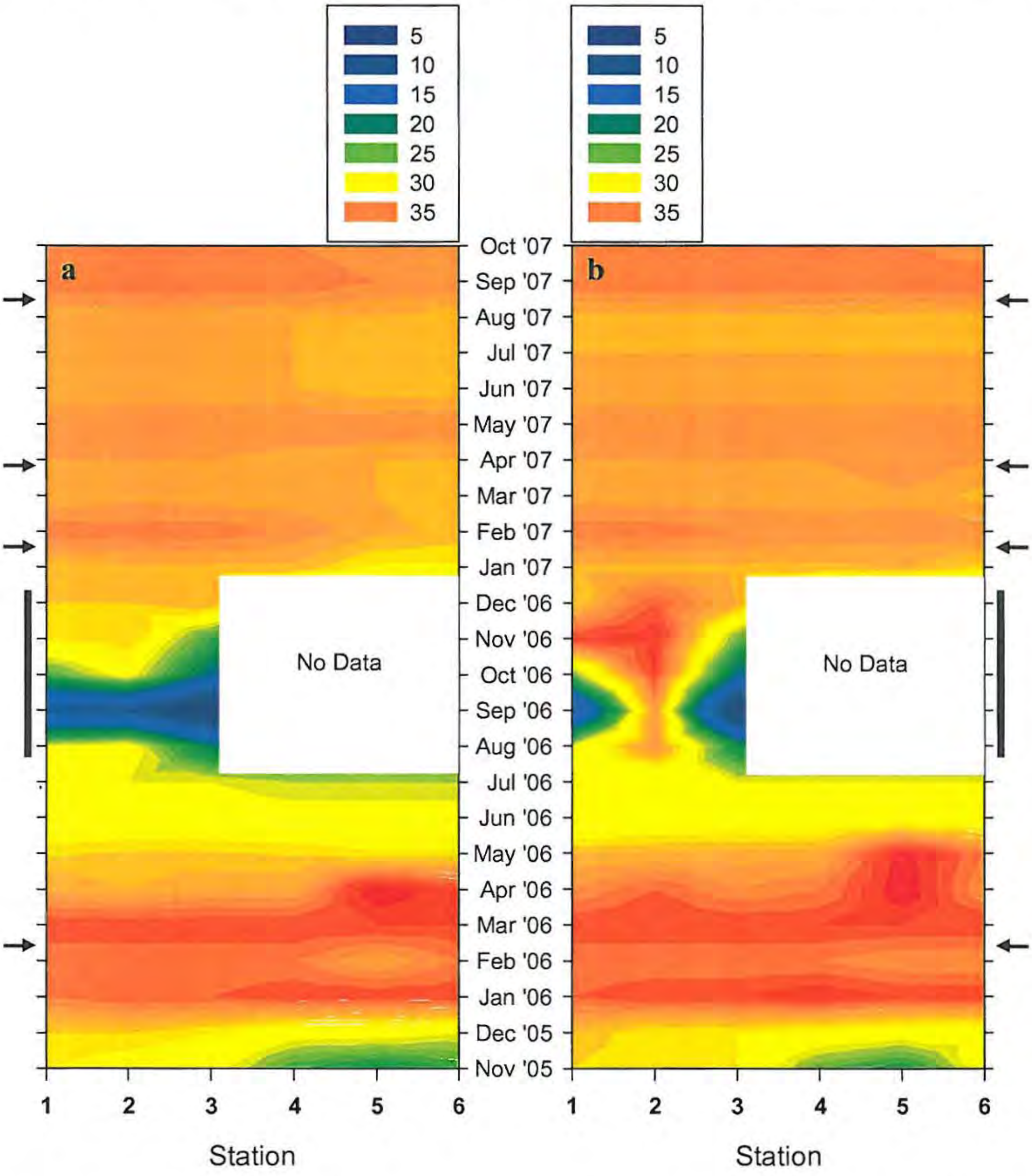

Figure 3.2: Spatial and temporal patterns of salinity recorded in the surface waters (a) and at depth (b) for the Mpekweni Estuary over the period November 2005 to October 2007. The bar indicates the period when the mouth was open and the arrows, overwash events. No data were collected from the stations in the middle and upper reaches over the period August 2006 to December 2006 due to the shallow water depth.

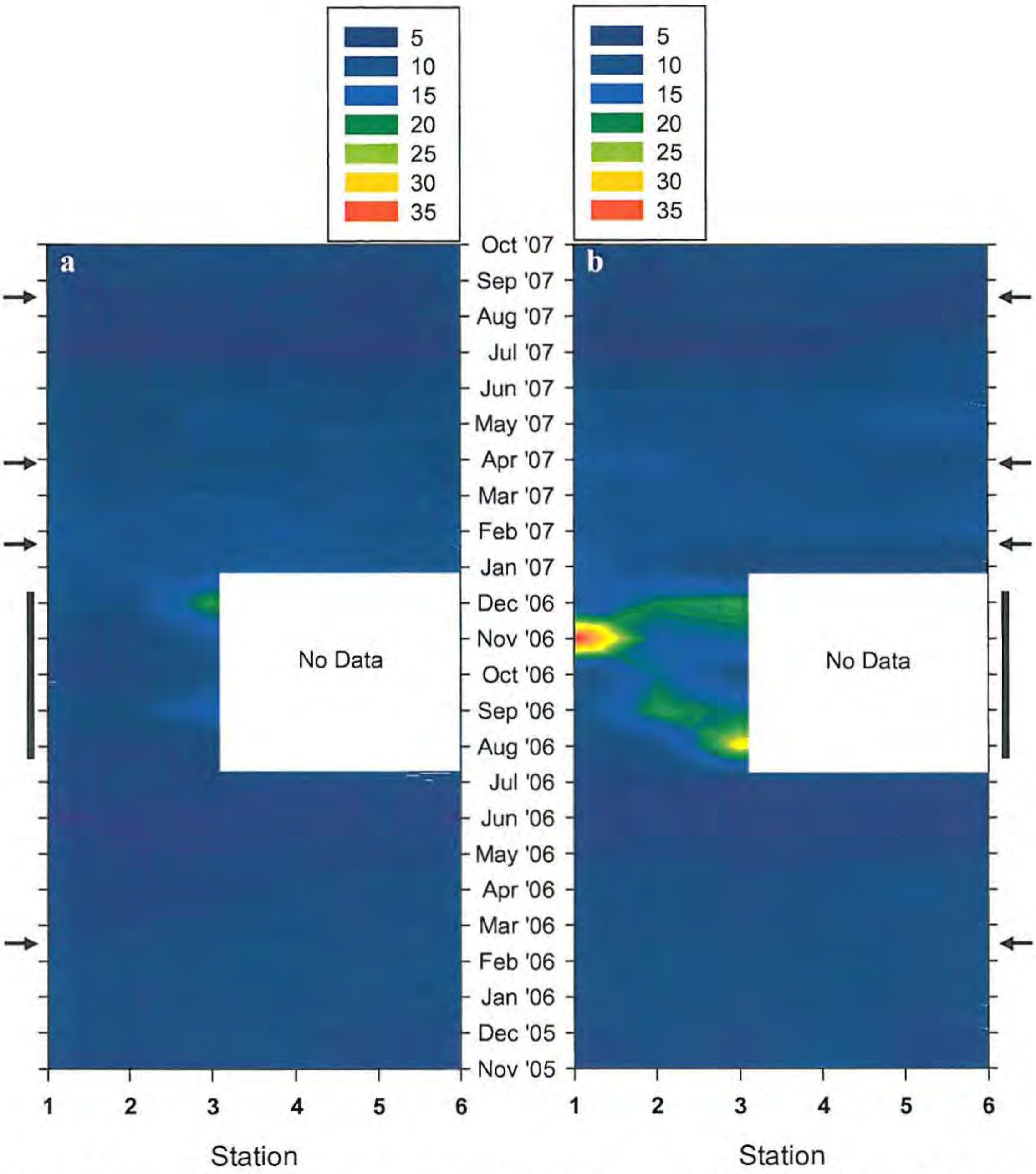

Figure 3.3: Spatial and temporal patterns of POM concentration (mg.L^{-1}) recorded in the surface waters (a) and at depth (b) for the Mpekweni Estuary over the period November 2005 to October 2007. The bar indicates the period when the mouth was open and the arrows, overwash events. No data were collected from the stations in the middle and upper reaches over the period August 2006 to December 2006 due to the shallow water depth.

3.3.4 Dissolved oxygen concentrations

Dissolved oxygen (DO) concentrations in the surface waters (Figure 3.4.a) were significantly higher than the bottom waters ($F_{(1,256)} = 51.77$ $p < 0.01$) (Figure 3.4.b) (Tukey $p < 0.05$). Surface DO concentrations ranged between 2.60 and 6.45 mg.L^{-1} and between 0.16 and 7.11 mg.L^{-1} for the bottom waters. Seasonally, the surface ($F_{(3, 125)} = 24.93$ $p < 0.01$) and bottom water ($F_{(3, 125)} = 18.33$ $p < 0.01$) DO concentrations in the winter months were significantly higher than in the remaining seasons (Tukey $p < 0.05$). During the winter months, however, the bottom DO concentrations of the open period were significantly lower than either of the closed phases ($F_{(2, 21)} = 6.89$ $p < 0.05$). In comparison to the closed periods, the surface water of the open period displayed significantly higher DO concentrations ($F_{(1, 127)} = 6.31$ $p < 0.05$) (Tukey $p < 0.05$). Further analysis of the comparable open and closed phases of the seasons indicated that higher open period surface DO concentrations were only significant during the spring months ($F_{(1, 10)} = 41.04$ $p < 0.05$).

3.3.5 Turbidity

The turbidity (NTU) values of the Mpekweni Estuary (Figure 3.5.b and 3.7) calculated from the secchi disk measurements (Figure 3.5.a and 3.6) ranged from 0.03 to 106.08 NTU (Figures 3.5 through 3.9). The autumn and winter NTU values were significantly lower than those of the summer months ($F_{(3, 125)} = 6.54$ $p < 0.01$) (Tukey $p < 0.05$). Although the turbidity values of the comparable months were slightly higher during the open period of the estuary, it was not significant ($F_{(9, 20)} = 1.57$ $p > 0.05$). Further analysis of all data showed the turbidity values during the initial closed period were significantly higher than during the re-closed period ($F_{(2, 126)} = 41.32$ $p < 0.01$) (Tukey $p < 0.05$). The turbidity values ranged from 0.10 to 65.31 NTU during the initial closed period, from 6.46 to 106.08 NTU during the open period and from 0.03 to 19.06 NTU during the re-closed period. Spatially the NTU values at Station 3 were significantly higher than at the remaining stations ($F_{(5, 123)} = 4.47$ $p < 0.01$) (Figure 3.9) (Tukey $p < 0.05$). Turbidity (NTU) was positively correlated with temperature and negatively correlated with dissolved oxygen concentrations (Appendix, Table I).

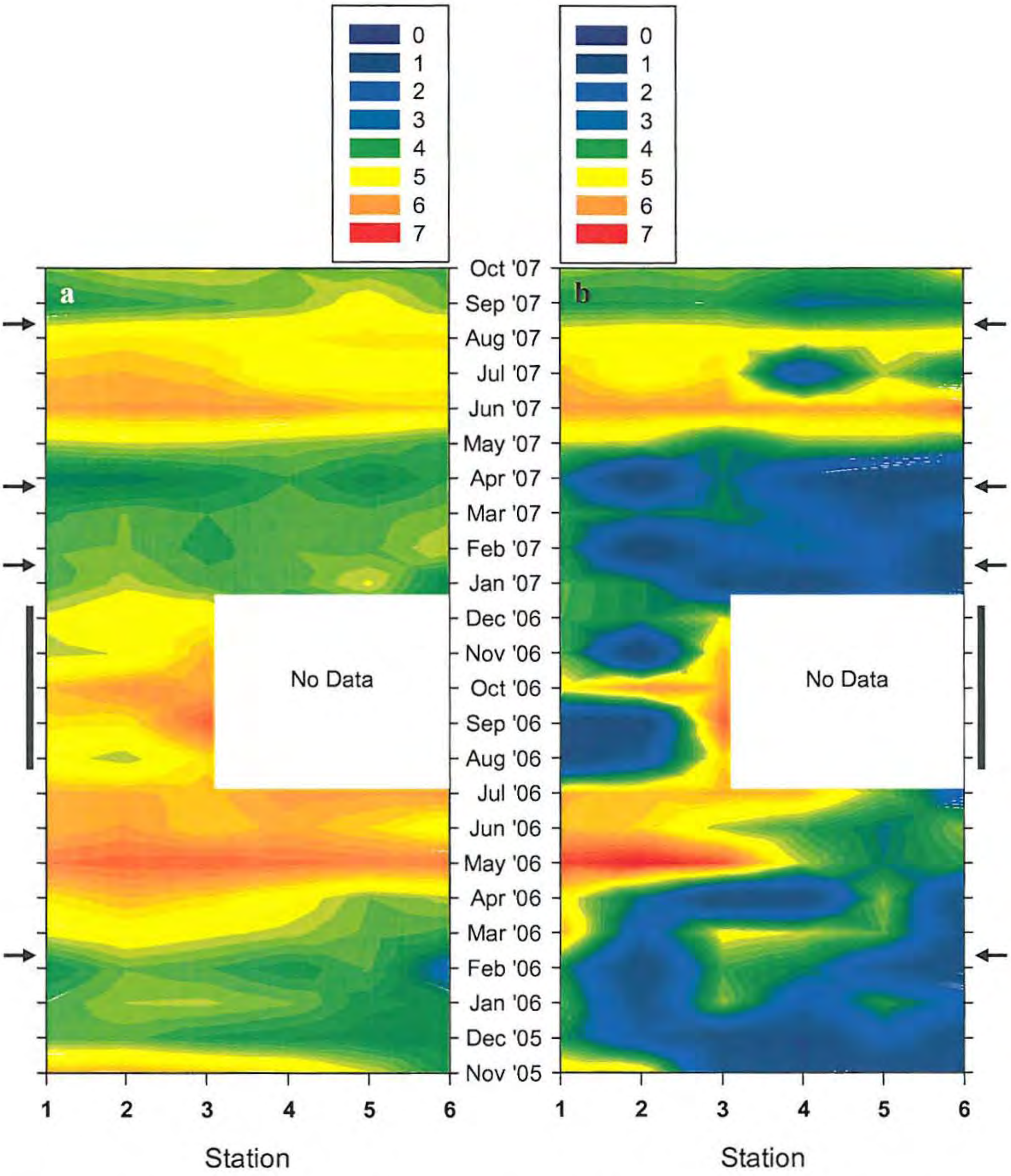

Figure 3.4: Spatial and temporal patterns of dissolved oxygen concentration (mg.L^{-1}) recorded in the surface waters (a) and at depth (b) for the Mpekweni Estuary over the period November 2005 to October 2007. The bar indicates the period when the mouth was open and the arrows, overwash events. No data were collected from the stations in the middle and upper reaches over the period August 2006 to December 2006 due to the shallow water depth.

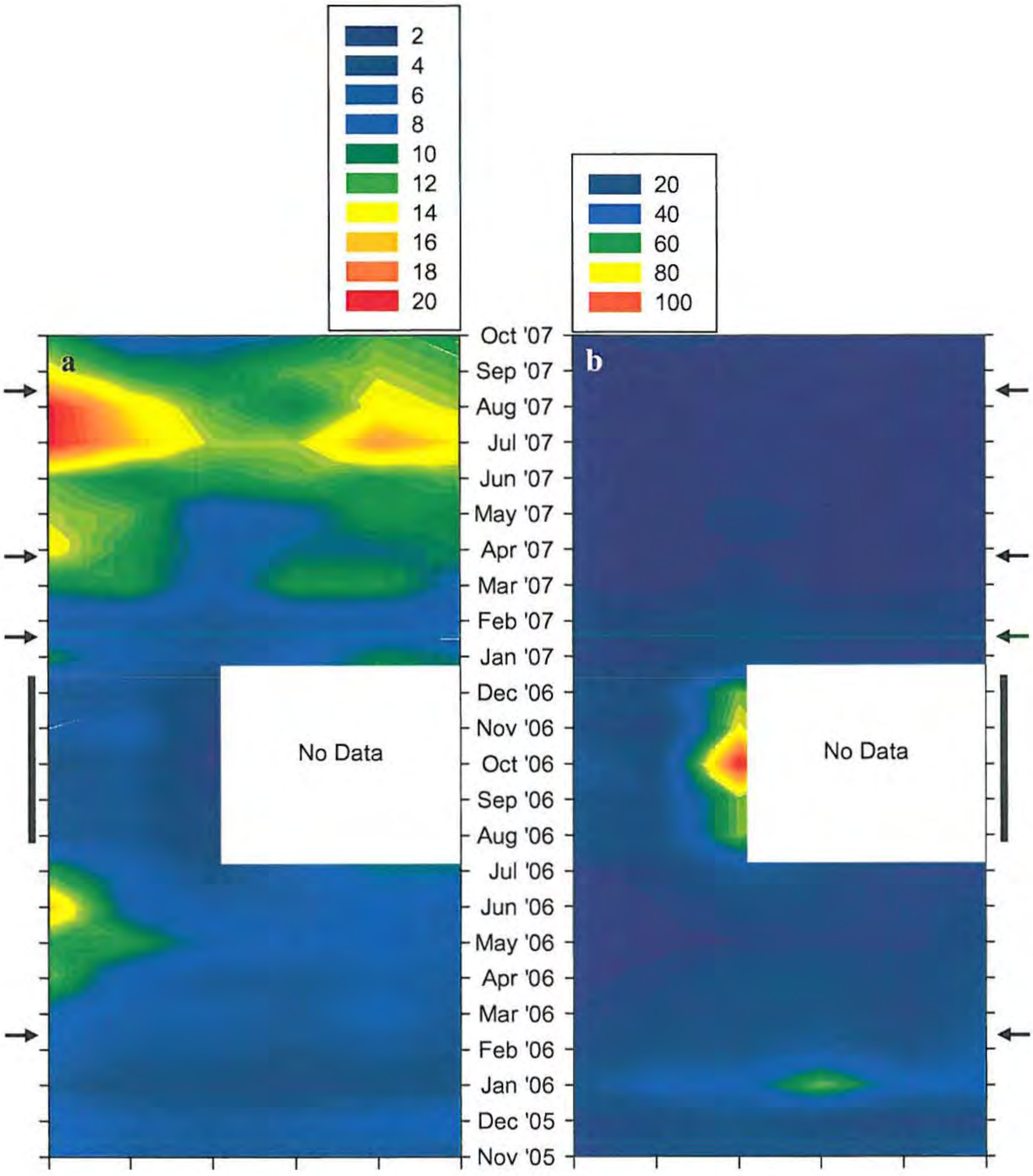

Figure 3.5: Spatial and temporal patterns of turbidity recorded by the secchi disk (depth in cm) (a) and calculated NTU values (b) for the Mpekweni Estuary over the period November 2005 to October 2007. Note: the scale is not the same for each graph. The bar indicates the period when the mouth was open and the arrows, overwash events. No data were collected from the stations in the middle and upper reaches over the period August 2006 to December 2006 due to the shallow water depth.

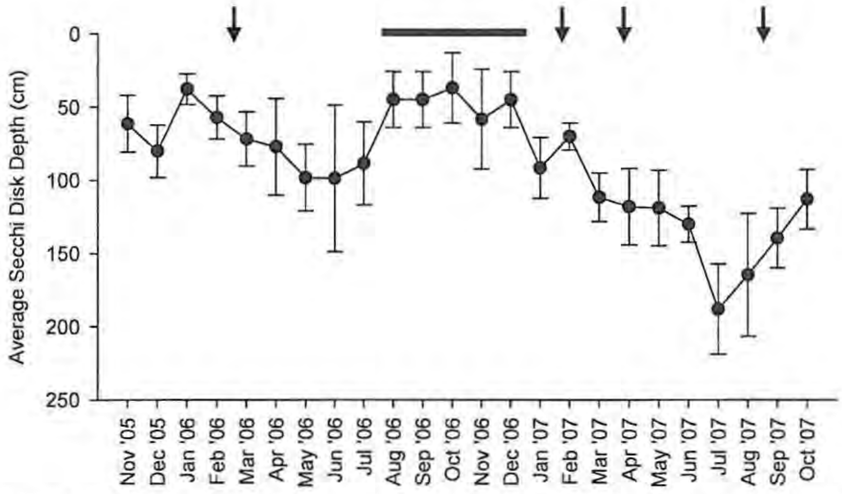

Figure 3.6: Average secchi disk depth measurements (cm) for each month for the duration of the study. Error bars indicate standard deviation. The bar indicates the period when the mouth was open and the arrows, overwash events.

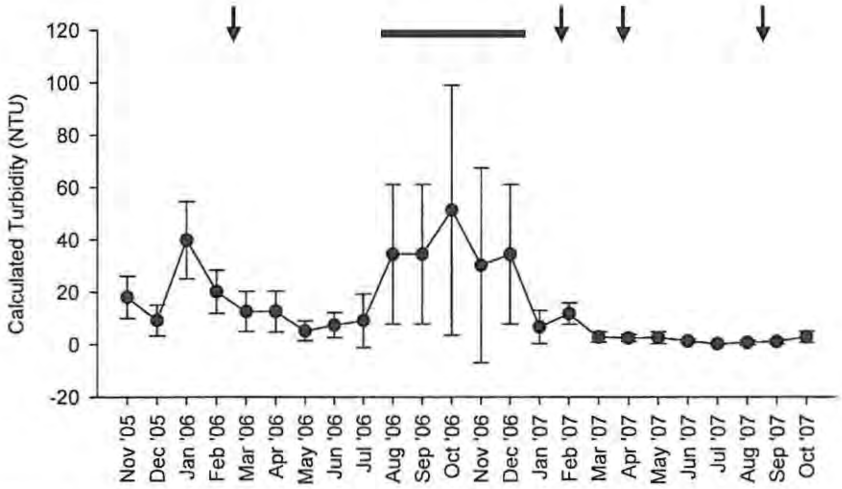

Figure 3.7: Average monthly turbidity (NTU) calculated from secchi disk readings (cm). Error bars indicate standard deviation. The bar indicates the period when the mouth was open and the arrows, overwash events.

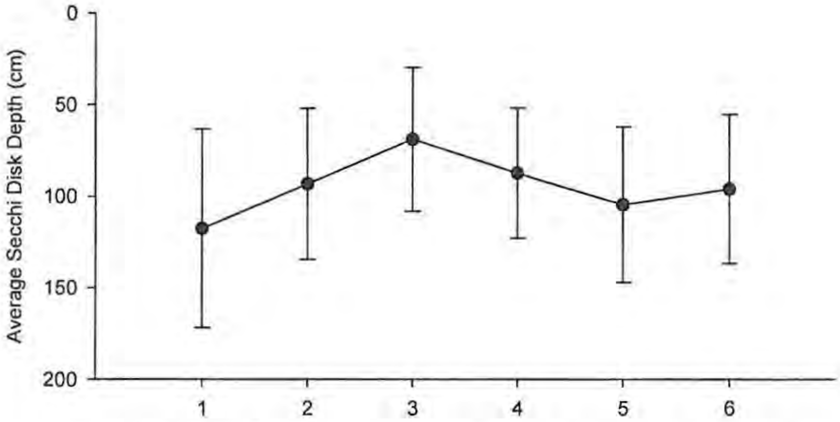

Figure 3.8: Average secchi disk depth measurements (cm) at each station for the duration of the study. Error bars indicate standard deviation.

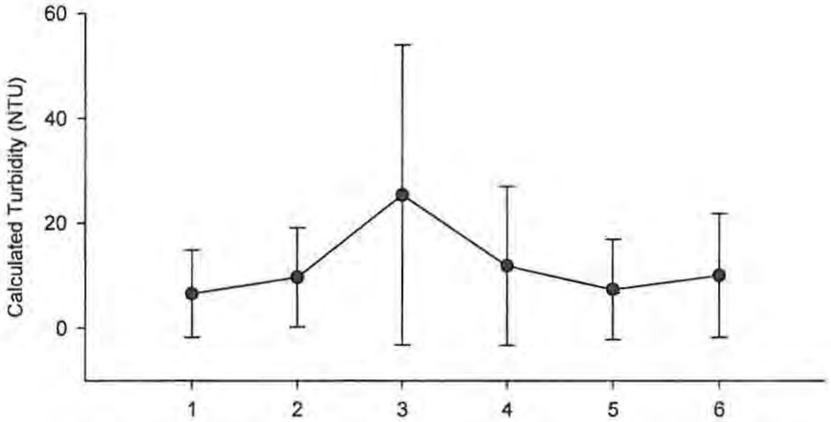

Figure 3.9: Average turbidity (NTU) for each station calculated from secchi disk readings (cm) from the duration of the study. Error bars indicate standard deviation.

3.3.6 Total chlorophyll-*a* concentration

The total chl-*a* concentrations over the duration of the study ranged between 0.14 and 3.74 mg chl-*a*.m^{-3} with an average of 1.54 mg chl-*a*.m^{-3} (± 0.74 SD). There were no significant spatial or vertical patterns of total chl-*a* concentration evident during the study (Figure 3.10). Also, there were no distinct seasonal patterns of total chl-*a* concentration (Figures: 3.10 and 3.11). In addition, mouth phase did not appear to have a significant impact on the total chl-*a* concentration within the estuary, although the initial two months of the open period displayed lower, non-significant values (Figure 3.11). The correlation analysis (Appendix, Table I) revealed that total chl-*a* concentration was significantly positively correlated with salinity and POM concentrations ($p < 0.05$ in both cases).

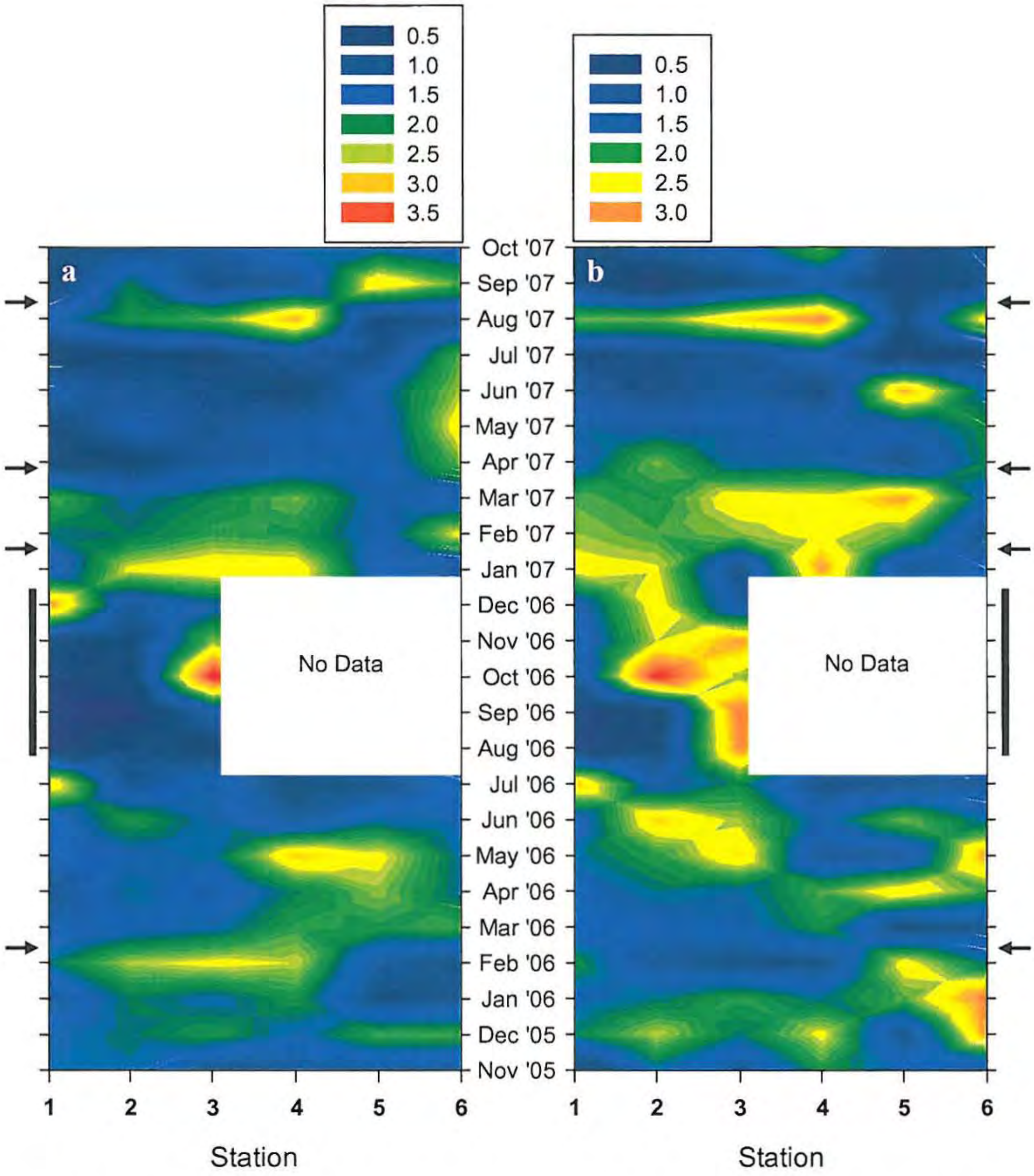

Figure 3.10: Spatial and temporal patterns of total chl-*a* concentration (mg chl-a.m^{-3}) in the surface (a) and bottom (b) waters for the Mpekweni Estuary over the period November 2005 to October 2007. Note: the scale is not the same for each graph. The bar indicates the period when the mouth was open and the arrows, overwash events. No data were collected from the stations in the middle and upper reaches over the period August 2006 to December 2006 due to the shallow water depth.

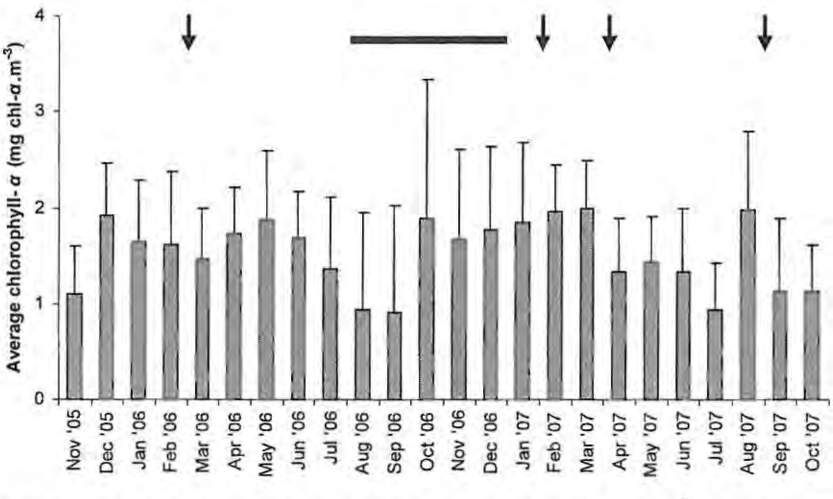

Figure 3.11: Average monthly total chl-*a* concentration (mg chl-*a*.m^{-3}) for the period November 2005 to October 2007 in the Mpekweni Estuary. Error bars indicate standard deviation. The bar indicates the period when the mouth was open and the arrows, overwash events.

3.3.7 Zooplankton

The total monthly zooplankton abundance ranged between 0.21 and 37584 ind.m^{-3} (average 2419.04 ind.m^{-3} ± 5290.63 SD) and the biomass between 0.13 and 588.79 mg Dwt.m^{-3} (average 14.87 mg Dwt.m^{-3} ± 40.08 SD). Seasonal patterns of the abundance values were evident, with the highest abundances during summer (2030.50 ind.m^{-3} ± 1430.70 SD) and autumn (2813.69 ind.m^{-3} ± 2755.21 SD) (Figure 3.12). The total zooplankton abundance in the spring (558.59 ind.m^{-3} ± 635.10 SD) were significantly lower than in the summer months ($F_{(3, 120)} = 7.23$ $p < 0.01$) (Tukey $p < 0.05$). Biomass values also demonstrated a seasonal pattern, with summer maxima (26.35 mg Dwt.m^{-3} ± 14.19 SD) and spring minima (4.58 mg Dwt.m^{-3} ± 1.80 SD) (Figure 3.13). Intermediate values were recorded in autumn (11.71 mg Dwt.m^{-3} ± 4.16 SD) and winter (17.59 mg Dwt.m^{-3} ± 36.71 SD). The winter and spring biomass values were significantly lower than the summer months ($F_{(3, 104)} = 7.57$ $p < 0.01$) (Tukey $p < 0.05$). Zooplankton abundance values during the re-closed period were significantly higher than the initial closed period ($F_{(2, 121)} = 5.74$ $p < 0.01$) (Tukey $p < 0.05$). There were no significant differences in total zooplankton abundance between the open and closed periods of the estuary ($F_{(1, 122)} = 0.61$ $p > 0.05$). The total zooplankton biomass also did not show any variation between the closed and open phases ($F_{(2, 105)} = 1.07$ $p > 0.05$). There were no significant spatial patterns of the total zooplankton abundance (station: $F_{(5, 118)} = 7.18$ $p > 0.05$; reaches: $F_{(2, 121)} = 1.59$ $p > 0.05$) and biomass (station: $F_{(3, 120)} = 7.23$ $p > 0.05$; reaches: $F_{(3, 120)} = 7.23$ $p > 0.05$) evident during the investigation.

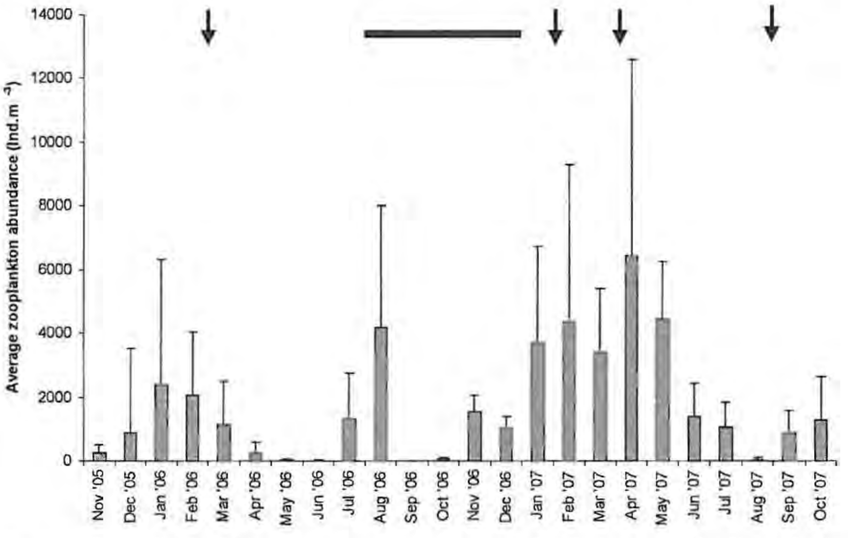

Figure 3.12: Average monthly daytime zooplankton abundance (ind.m^{-3}) for the period November 2005 to October 2007 in the Mpekweni Estuary. Error bars indicate standard deviation. The bar indicates the period when the mouth was open and the arrows, overwash events.

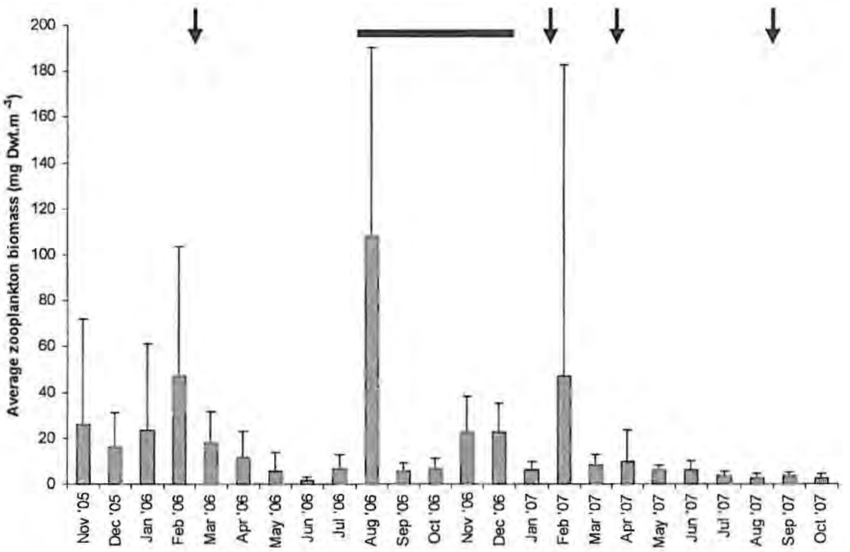

Figure 3.13: Average daytime monthly zooplankton biomass (mg Dwt.m^{-3}) for the period November 2005 to October 2007 in the Mpekweni Estuary. Error bars indicate standard deviation. The bar indicates the period when the mouth was open and the arrows, overwash events.

3.4 DISCUSSION

Temporarily open/closed southern African estuaries are characterised as homogenous well mixed systems with little evidence of vertical or horizontal stratification of physico-chemical and biological variables (Walker *et al.*, 2001; Froneman, 2002b; 2004). The absence of any vertical and horizontal gradients can be linked to, amongst others, small catchment size resulting in reduced freshwater inflow and strong coastal winds that are prominent along the coast and the shallow nature (< 1.5 m) of these systems (Froneman, 2002a; 2002b; 2004). The virtual absence of any horizontal and vertical patterns of the physico-chemical variables in the Mpekweni Estuary during this study is therefore, not unexpected. The strong seasonal patterns in temperature and oxygen observed during the closed phase of this study are consistent with the published literature (Cowley, 1998; Whitfield, 1998; Vorwerk, 2001; Froneman, 2002b; 2004; 2006a; Harrison, 2004; Lukey *et al.*, 2006) and can be related to the climatic regime of the region (Harrison, 2004).

The establishment of a link to the marine environment following the breaching event was associated with a significant drop in spring and summer water temperatures and spring salinity values were lower while there was an increase in the turbidity (NTU) and suspended POM concentrations. These changes in the physico-chemical variables were consistent with the literature and could be linked to the out-flow of estuarine water and the influence of the marine environment on the system (Whitfield *et al.*, 1994; Vorwerk, 2001; Harrison, 2004). Cowley (1998) and Whitfield (1998) suggested that breaching, overwash and overtopping events may contribute to the establishment of horizontal stratification in the lower reaches of TOCEs. During this investigation, the inflow of marine waters following the breaching of the estuary and during overwash events did not appear to contribute to any extended periods of vertical or horizontal stratification in the physico-chemical variables within the estuary. The absence of these patterns could be linked to limitations in the sampling strategy, the establishment of any stratification may have dissipated in the time period between overwash events and the monthly sampling trips.

A number of studies conducted both locally and internationally have demonstrated that spatial variations in the biology of estuaries can be related to horizontal patterns of physico-chemical variables within these systems (Wooldridge, 1999; Harrison, 2003; 2004; Froneman, 2004). Not surprisingly due to the virtual absence of any horizontal patterns of physico-chemical variables, no significant spatial patterns of the total chl-*a* concentration and the zooplankton abundance and biomass were evident within the Mpekweni Estuary (Figures: 3.10 and 3.14).

During the closed phases, the total chl-*a* concentrations and zooplankton abundance and biomass values demonstrated a seasonal pattern which can most probably be ascribed to the seasonal changes in water temperature and its effect on metabolic processes (Wooldridge, 1999; Marques *et al.*, 2006). Several authors (Anandraj *et al.*, 2007; 2008) have suggested that primary production rates within TOCEs are influenced by mouth status, with the highest values typically recorded during the closed phase. The decrease in total chl-*a* concentration during the open period of the estuary is therefore not unexpected and is thought to reflect the out-flow of biomass-rich estuarine waters into the marine environment (Perissinotto *et al*., 2000; Froneman, 2002a; 2004; Kibirige and Perissinotto, 2003b). The estimates of chl-*a* concentrations recorded in the Mpekweni Estuary during this study were within the range reported for other TOCEs in the same biogeographic region (Adams and Bate, 1999; Froneman, 2002a; 2002b; Gama *et al*., 2005; Skinner *et al*., 2006; Gama, 2008; Whitfield *et al*., 2008).

In contrast to the total chl-*a* concentration, the breaching event in late July 2006 coincided with an increase in zooplankton abundance (Figure 3.12). This result was in contrast to some studies conducted in TOCEs in both the STZ and WTZ along the southern African coastline (Kibirige *et al*., 2006). The increase in zooplankton abundance and *status quo* of the zooplankton biomass observed immediately following the opening of the estuary could be attributed to an increase in nauplii recorded, a higher contribution of *Pseudodiaptomus hessei* and an increase in the abundance of typically marine copepods; Oithonia spp. and Calanus spp. *Pseudodiaptomus hessei* populations are influenced by low salinities (Wooldridge, 1999; Adams *et al*., 2002) and the subsequent increased contribution (unpublished data) after the opening of the estuary could be associated with the lower salinity water flowing out of the system (Figure 3.2).

After the estuary re-closed the increased zooplankton abundance was attributed primarily to high nauplii abundances and an increased contribution of copepod species (primarily *Acartia longipatella* [unpublished data]) that typically dominate estuarine communities. This pattern of community change and dominance has also been recorded in similar systems (Kibirige and Perissinotto, 2003b; Froneman, 2004). Salinity changes in the Mpekweni Estuary after overwash events were slight (Figure 3.2) and this lack of extensive salinity variation could be attributed to the limited variation of subsequent plankton abundance and biomass samples. Expected changes in zooplankton community after overwash events were not in evidence. The predominant macrozooplankton species recorded during such events are the larger *Palaemon peringueyi* larvae and the mysid *Mesopodopsis wooldridgei* (Kemp and Froneman, 2004), however predation by the abundant zooplanktivorous fish (*Atherina breviceps* and *Gilchristella aestuaria*) could account for the lack of influence of these species on the community structure (Froneman, 2004). The zooplankton abundance and biomass recorded in the Mpekweni Estuary during the different hydrological phases fall within the range of values reported for other TOCEs in both the WTZ and STZ of southern Africa (Kibirige and Perissinotto, 2003b; Froneman, 2004; Perissinotto *et al*., 2004; Kibirige *et al*., 2006).

3.4.1 Summary

The Mpekweni Estuary demonstrates similar physical and chemical conditions to other TOCEs not only within the same geographic region but all along the South African coastline. The virtual absence of any horizontal and vertical patterns of the physico-chemical and biological variables during this study are in agreement with previous studies conducted in TOCEs both locally (Cowley, 1998; Vorwerk, 2001; Harrison, 2003; Tweddle, 2004; Vorwerk, 2004; 2006; Lukey, 2006; James, 2007) and in WTZ systems along the Australian coastline (Potter *et al.*, 1990). Seasonality in physico-chemical and biological variables was evident during the closed periods, which may be linked to seasonal variation in climate. The breaching event resulted in changes to physico-chemical and biological variables reflecting the initial out-flow of estuarine waters into the marine environment and the subsequent inflow and mixing of seawater during the tidal phase. These results highlight the important influence of mouth phase in determining the physico-chemical and biological aspects of TOCEs.

CHAPTER 4

SPECIES COMPOSITION AND THE SPATIAL AND TEMPORAL DISTRIBUTION OF THE ICHTHYOFAUNAL COMMUNITY IN THE MPEKWENI ESTUARY

4.1 INTRODUCTION

The study of the ichthyofaunal community structure in southern African TOCEs is often short-term (< 1 year) (Vorwerk, 2001; Tweddle, 2004; Lukey, 2006) or once-off surveys (Harrison, 2002; 2003; 2005). Notable exceptions are the studies by Cowley (1998) and James *et al.* (2007a), which were conducted over several seasons. Mouth phase/status has been identified as an important factor in determining the ichthyofaunal community structure within southern African TOCEs (Vorwerk *et al.*, 2003; James *et al.*, 2008b Whitfield *et al.*, 2008; 2012a; 2012b). The maximum abundances of ichthyofauna within these systems is generally attained during the closed phase (Bennett, 1989a; Whitfield and Kok, 1992; James *et al.*, 2008b), although diversity values are generally low (Vorwerk *et al.*, 2003). Ichthyofaunal abundance also displays a higher contribution of estuarine-dependant species in closed TOCEs compared to POEs within the same region (Cowley, 1998; Whitfield, 1998; Vorwerk, 2001; Harrison, 2003; Tweddle, 2004; James, 2007). Harrison (2004) identified temperature and salinity as the primary factors affecting spatial and temporal distribution of ichthyofauna within estuaries in the same geographic region. Other factors that affect spatial distribution of ichthyofauna within the TOCEs include estuary size, vegetation type/coverage, sediment type and geological structures (Hanekom and Baird, 1984; Harrison and Whitfield, 1995; Whitfield, 1998; Whitfield *et al.*, 2008; 2012a).

A previous study by Vorwerk (2001; Vorwerk *et al.*, 2003) conducted in the Mpekweni Estuary found no significant seasonal variation in abundance and composition of ichthyofauna within the estuary. The community composition of the ichthyofauna within the Mpekweni Estuary was found to be similar to that of other TOCEs within the same geographical region (Vorwerk, 2001; Vorwerk *et al.*, 2003). Abundance values (ind.m^{-2}) extrapolated from Vorwerk (2001) ranged between 0.23 ind.m^{-2} and 12.52 ind.m^{-2} and the total ichthyofaunal abundance and biomass were dominated by estuarine spawners. To the author's knowledge, there have been no further studies on the fish community structure within the estuary. The main aim of this chapter is to examine the spatial and temporal patterns in the ichthyofaunal community composition within the Mpekweni Estuary over a two year period. Shifts in the community composition were examined in relation to season and mouth status.

4.2 MATERIALS AND METHODS

4.2.1 Sampling

Sampling of the ichthyofauna within the Mpekweni Estuary was undertaken monthly over a two year period, from November 2005 to October 2007. Seine nets were used to sample fish because they have an efficiency of 80 % (Ratte, 1989; Heymans and Baird, 1995), are easy to use and have a limited influence on the mortality of the larger fish species typically associated with gill nets. Although there can be a high variability in sampling efficiency, seine nets have been used extensively throughout the literature to sample all types of estuarine environments, thus allowing for comparative sampling. By changing mesh size, length and depth of the nets they can be used to sample selectively (Rozas and Minello, 1997). Unfortunately due to the need for a fairly uniform substrate structure, these nets are inefficient in sampling fish in rocky areas, deep water and areas of high aquatic vegetation cover, including reed beds (Rozas and Minello, 1997).

Three seine nets (5 m, 30 m and 50 m) were deployed at each of five stations, resulting in 15 net hauls per month. During the open period (August 2006 to December 2006) due to the shallow nature (water depth < 0.3 m) and lack of access to the middle and upper reaches, sampling was restricted to only the mouth region of the estuary. Net hauls were conducted during the day, usually between the hours of 08h00 and 18h00. The Mpekweni Estuary was separated into three regions identified by Vorwerk (2001), the lower, middle and upper regions. Each region was sampled and sites (Figure 2.4) were selected to cover the length of the estuary and to encompass as many channel and littoral habitat types as was possible due to the limitation of substrate type that allowed for the pulling of seine nets. In the lower reaches, Station 1 was located on the west bank at the mouth of the estuary on sandy marine sediment, while Station 2 was situated on a rocky outcropping on the east bank where the bottom sediment was made up of mud and small rocks. In the middle reaches, Station 3 was on the east bank opposite some reed beds and the sediments consisted of fine mud. Station 4 in the upper reaches was situated in a fairly narrow part of the system which was fairly shallow and had muddy sediments. The bottom sediments at Station 5 also consisted of fine muddy sediments. During the lower water levels the sampling areas were largely devoid of vegetation, with the exception of some *Ruppia spp* blooms on some sampling occasions. During the high water levels, Stations 3 to 5 were inundated and the nets were hauled over submerged beds of *Juncus kraussii* and *Sarcocornia perennis*.

4.2.1.1 Juvenile and larval ichthyofauna in the littoral zone

The early developmental stages and small (Standard Length [SL] < 50 mm) fish were sampled using a 5 m beach seine net deployed in the littoral zone of the estuary according to the methods of Watt-Pringle and Strydom (2003) and Tweddle (2004). The net had dimensions of 5 m x 1 m and a mesh size of 500 μm. Two people pulled the net parallel to the bank for a pre-determined length of 5 m (kept consistent using a rope of 5 m laid out along the bank). The area sampled by the net during each haul was ~ 25 m^2. The bottom of the net was weighted with a steel chain to keep it in contact with the bottom. The fish sampled were immediately preserved in 10 % formaldehyde for later analysis in the laboratory. Fish were identified using Smith & Heemstra (1991) and standard length (SL) of individuals measured to the nearest 0.5 mm using either a fish measuring board or digital Vernier callipers. Abundances of each species was then determined for each station. Data were expressed as individuals per unit area ($ind.m^{-2}$). The biomass (grams wet weight per unit area [$g\ wwt.m^{-2}$]) of the fish (all nets) was then calculated using the length-weight relationship expressed by Tesch (1971) as:

$$w = al^b$$

Where w is the calculated weight (g), l is the length (mm Standard Length), a is the intercept of the regression curve and b the regression coefficient. The a and b parameters for each estuarine species were provided by Harrison (2001).

4.2.1.2 Larger estuarine, marine and freshwater spawning ichthyofauna

A 30 m and a 50 m seine net were used to sample the larger ichthyofauna (SL >50 mm) within the channel of the estuary. The study sites (see Chapter 2, Figure 2.4 for locations) were partly selected to limit the possibility of obstruction to the net during the retrieval process. The net was deployed by two to four individuals, ensuring the foot-rope was always kept in contact with the ground. The net was laid in a semi-circle from the bank by boat or wading and then pulled ashore. The 30 m seine net was used mainly to target the estuarine and smaller marine spawning species within the estuary and the 50 m seine net was employed to sample the larger fish, primarily the marine and freshwater spawning species (Cowley, 1998; Vorwerk, 2001). The area sampled for the 30 m was on average 146.26 m^2 and the 50 m seine net had an estimated coverage area of 400 m^2. The 30 m seine net measured 2 m deep with a stretched/bar mesh of 10 mm with a bag of 10 mm. The 50 m seine net was also 2 m deep but had a stretched mesh of 30 mm with the bag mesh also 30 mm.

Fish, were immediately removed from the bag and placed into plastic rectangular bins (on the bank of the estuary) that were filled with well aerated estuarine water. Fish were identified using Smith and Heemstra (1991), Branch *et al.* (1994) and Heemstra and Heemstra (2004), measured with a measuring board to the nearest mm SL and returned alive to the estuary. If field identification was not possible, one or two representative specimens were preserved and returned to the laboratory for later identification (Smith and Heemstra, 1991; Branch *et al.*, 1994; Heemstra and Heemstra, 2004).

4.2.2 Analysis

A complete list of all the fish species sampled and their estuarine utilisation categories (EUC – Table 1.1 from Chapter 1) was compiled from the literature (Table 4.1). Abundance and biomass data for each net were determined and the species composition and percentage contribution for each net was determined along with their mean Standard Length (SL) and mean wet weight (g wwt.m^{-2}), standard deviation (SD) and the size range for each species (See Tables: 4.2 and 4.3 for the juvenile and larval littoral zone species, Tables: 4.4 and 4.5 for the estuarine and smaller marine spawning species and Tables: 4.6 and 4.7 for the large marine and freshwater spawning species). The percentage contribution of each estuarine utilisation group (Chapter 1, Table 1.1) to the total abundance and biomass was calculated for each haul. The average monthly ichthyofaunal abundance and biomass sampled by each gear type was determined separately. The percentage contribution of each estuarine group to the monthly abundance and biomass for each ichthyofaunal group was also calculated. The temporal patterns in abundance and biomass were assessed for the closed and open phases and seasonally. Seasons were based primarily on water temperatures and defined as summer (November to February), autumn (March to April), winter (May to August) and spring (September to October).

The average species richness (Margalef's index) and the average diversity (Shannon-Wiener's index) of the ichthyofauna from each ichthyofaunal group were calculated both temporally and spatially using Plymouth Routines in Multivariate Ecological Research (PRIMER v.5.2.4) (Clarke and Warwick, 1998).

The species contributing > 90 % of each of the juvenile/larval, estuarine and smaller marine spawning species and the larger marine and freshwater spawning species were used to determine the presence of any spatial and temporal patterns in the ichthyofaunal community composition (Cowley, 1998; Vorwerk, 2001; Tweddle, 2004). Data in the form of average catch per unit effort (CPUE individuals per square metre – ind.m^{-2}) for each station were analysed using PRIMER (v.5.2.4). The data were first standardised and then log(x+1) transformed and a Bray-Curtis similarity matrix created (Vorwerk, 2001). Cluster analyses and multidimensional scale ordination plots were then calculated. To determine possible species accounting for the temporal and spatial patterns in community composition, the SIMPER procedure of PRIMER (v.5.2.4) was run to identify the main species contributing to the differences between the groups (Clarke and Warwick, 1994; 1998; Vorwerk, 2001; Tweddle, 2004).

4.3 RESULTS

In this study, a total of 51502 fish representing 19 families and 36 species were sampled (Table 4.1). Nine species of estuarine spawning fish (EUC Ia and Ib), 18 estuarine dependant marine spawning species (EUC IIa, IIb and IIc), four marine species that are not dependant on estuaries (EUC III) and one species for each of the freshwater (IV) and catadromous (V) categories were sampled during the investigation (Table 4.1).

4.3.1 Abundance and biomass

4.3.1.1 Littoral zone (juvenile and larval ichthyofauna)

A total of 6567 fish with an average abundance of 2.65 ind.m^{-2} (± 3.12 SD) were sampled in the shallow littoral zone of the Mpekweni Estuary using the 5 m seine net. The juvenile and larval ichthyofauna were represented by 16 species, covering nine families (Table 4.2). Numerically the six most abundant species were (values in brackets indicate percentage contribution to samples collected using the 5 m seine net): *Glossogobius callidus* (38.9 %), *Atherina breviceps* (25.5 %), *Gilchristella aestuaria* (16.7 %), *Rhabdosargus holubi* (6.7 %), *Myxus capensis* (6.0 %) and *Liza richardsonii* (4.7 %). These six species contributed to a combined monthly average of 95 % (± 13.5 SD) of the total number of fish sampled in the 5 m seine net for the period November 2005 to October 2007.

The abundance of the smaller juvenile and larval ichthyofauna sampled in the littoral zone displayed significant seasonal variability for CPUE ($F_{(3,\ 95)} = 2.91$ $p < 0.05$) and also when abundances were compared before the estuary opened, while it was open and after it closed again ($F_{(2,\ 95)} = 5.83$ $p < 0.01$). Abundances (Figure 4.3) varied between 0.66 ind.m^{-2} (± 0.43 SD) in July 2006 and 2.66 ind.m^{-2} (± 1.34 SD) in January 2006 prior to the breaching event. After the estuary breached and remained open (August 2006 to December 2006) the average abundance dropped to 0.44 ind.m^{-2} (± 0.01 SD) for both September and October 2006. The highest value recorded during the open phase was 5.20 ind.m^{-2}. After the estuary re-closed, the average abundance was highly variable, ranging between 0.22 ind.m^{-2} (± 0.31 SD) in the winter months and 7.70 ind.m^{-2} (± 4.91 SD) in the summer months. Abundance of the juvenile and larval ichthyofauna was significantly higher after the estuary had re-closed period in comparison to the initial closed period prior to breaching (Tukey $p < 0.005$).

Table 4.1: Ichthyofauna species sampled in the Mpekweni Estuary from the period November 2005 to October 2007 using a 5 m seine net (Small Seine – SS), 30 m seine (Medium Seine – MS) and a 50 m seine (Large Seine – LS). The expressed estuarine-dependence categories are after Whitfield (1992; 1998).

Family	Species	Common name	Estuarine-dependence category	Sample gear used	Number sampled
Antennariidae	*Antennarius striatus* (Shaw & Nodder, 1794)	Striped angler	III	SS	1
Atherinidae	*Atherina breviceps* Valenciennes, 1835	Cape silverside	Ib	SS,MS	6252
Blenniidae	*Omobranchus woodi* (Gilchrist & Thompson, 1908)	Kappie blenny	Ia	MS	1
Carangidae	*Lichia amia* (Linnaeus, 1758)	Garrick/Leervis	IIa	MS,LS	3
Cichlidae	*Oreochromis mossambicus* (Peters, 1852)	Mozambique tilapia	IV	SS,MS,LS	121
Clinidae	*Smithichthys fucorum* (Gilchrist & Thompson, 1908)	Leafy klipfish	III	MS	1
Clupeidae	*Gilchristella aestuaria* (Gilchrist, 1913)	Estuarine roundherring	Ia	SS,MS	13657
Elopidae	*Elops machnata* (Forsskål, 1775)	Lady fish/Springer	IIa	MS,LS	18
Gobiidae	*Caffrogobius gilchristi* (Boulenger, 1898)	Prison goby	Ib	SS,MS	28
	Caffrogobius nudiceps (Valenciennes, 1837)	Barehead goby	Ib	SS,MS,LS	20
	Glossogobius callidus (Smith, 1937)	River goby	Ib	SS,MS,LS	10284
	Psammogobius knysnaensis Smith, 1935	Speckled sandgoby	Ib?	SS,MS	82
Haemulidae	*Pomadasys commersonnii* (Lacepède, 1801)	Spotted Grunter	IIa	MS,LS	17
	Pomadasys olivaceum (Day, 1875)	Piggy	III	MS	33
Hemiramphidae	*Hyporhamphus capensis* (Thominot, 1886)	Cape halfbeak	Ia	MS	21
Monodactylidae	*Monodactylus argenteus* (Linnaeus, 1758)	Round moony	IIb	MS	1
	Monodactylus falciformis Lacepède, 1800	Oval moony	IIa	SS,MS,LS	98
Mugilidae	*Liza dumerilii* (Steindachner, 1869)	Groovy mullet	IIb	SS,MS,LS	1308
	Liza macrolepis (Smith, 1846)	Largescale mullet	IIa	MS,LS	9
	Liza richardsonii (Smith, 1846)	Southern mullet	IIc	SS,MS,LS	740
	Liza tricuspidens (Smith, 1935)	Striped mullet	IIb	SS,MS,LS	70
	Mugil cephalus Linnaeus, 1758	Flathead mullet	IIa	MS,LS	34
	Myxus capensis (Valenciennes, 1836)	Freshwater mullet	Vb	SS,MS,LS	2324
Paralichthyidae	*Pseudorhombus arsius* (Hamilton, 1822)	Largetooth flounder	III	MS	1
Platycephalidae	*Platycephalus indicus* (Linnaeus, 1758)	Bartail flathead	IIc	LS	1
Soleidae	*Heteromycteris capensis* Kaup, 1858	Cape sole	IIb	SS,MS,LS	79
	Solea turbynei Gilchrist, 1904	Blackhand sole	IIb	SS,MS,LS	805
	Solea fulvomarginata Gilchrist, 1904	Lemon sole	III	MS	1
Sparidae	*Diplodus sargus capensis* (Smith, 1844)	Blacktail	IIc	SS,MS,LS	53
	Lithognathus lithognathus (Cuvier, 1830)	White steenbras	IIa	MS,LS	109
	Rhabdosargus globiceps (Cuvier, 1830)	White stumpnose	IIc	MS	34
	Rhabdosargus holubi (Steindachner, 1881)	Cape stumpnose	IIa	SS,MS,LS	15273
	Rhabdosargus sarba (Forsskål, 1775)	Tropical/Natal stumpnose	IIb	MS,LS	9
	Sarpa salpa (Linnaeus, 1758)	Strepie	IIc	LS	5
Tetraodontidae	*Amblyrhynchotes honckenii* (Block, 1795)	Evil-eye blaasop/puffer	III	MS,LS	6
	Arothron hispidus Linnaeus, 1758	Whitespotted blaasop/puffer	III	MS	2

The majority of the juvenile/larval fish sampled in the littoral zone by the 5 m seine net consisted of EUC I species (Figure 4.2 – 81.44 %) followed by EUC II (12.33 %) and EUC V (6.00 %) species. The EUC III and IV contributed 0.02 % and 0.21 % to total fish abundances, respectively. Monthly abundances were dominated by EUC I species (Figure 4.5) with an increased contribution of the EUC II species during the open phase. Estuarine utilisation category I species were again well represented (range 40.24 % to 99.71 % of the monthly abundance) once the estuary closed.

The biomass of the juvenile/larval ichthyofauna sampled (Table 4.3) totalled 3962.18 g wwt, with an overall average biomass estimate of 1.60 g wwt.m^{-2} (± 2.28 SD) for the estuary. The dominant species contributing to >90 % of the total biomass were: *Glossogobius callidus* (55.97 %), *G. aestuaria* (8.92 %), *L. richardsonii* (7.76 %), *A. breviceps* (7.75 %), *R. holubi* (6.68 %) and *M. capensis* (5.58 %).

The average monthly biomass of the juvenile/larval ichthyofauna (Figure 4.4) ranged between 0.46 and 1.94 g wwt.m^{-2} for the period prior to breaching (November 2005 to July 2006). When the estuary was open (August 2006 to December 2006) the biomass gradually increased from 0.12 g wwt.m^{-2} to 2.58 g wwt.m^{-2}. Subsequent to the estuary closing, the average monthly biomass continued to increase to an average value of 6.61 g wwt.m^{-2} (± 5.37 SD) in March 2007. Biomass decreased after March 2007 during the autumn and winter months, reaching a low of 0.13 g wwt.m^{-2} in August 2007 before increasing again to a value of 3.44 g wwt.m^{-2} in October 2007 with the onset of spring (Figure 4.4). The biomass during the re-closed period displayed a significantly higher (Tukey $p < 0.01$) value than during the initial closed period ($F_{(2, 96)} = 4.85$ $p < 0.01$). Seasonally the winter biomass was significantly lower (Tukey $p < 0.005$) than the autumn biomass estimates ($F_{(3, 95)} = 4.94$ $p < 0.005$).

The total biomass of juvenile/larval fish sampled in the littoral zone (Figure 4.2) was dominated (74.21 %) by the EUC I species, while EUC II and V species contributed 16.51 % and 5.58 % to the total, respectively. The EUC III and IV species contributed 2.52 % and 1.17 % to the total biomass, respectively. Estuarine spawning species contributed most to the estimated monthly biomass on 21 out of the 24 sampling events. The larger marine and freshwater species demonstrated an increased contribution to the monthly average biomass during the open phase and during the summer and autumn months of the two year survey (Figure 4.6) (~ 30 % ± 26 SD versus ~ 5 % ± 6 SD average contributions). The first two months of the open phase were dominated by EUC II and EUC V species.

Spatially there was no significant variation in the distribution of the biomass of the juvenile/larval ichthyofauna (Figure 4.1). The lowest values were observed in the middle and upper reaches (Stations 3 and 4) of the estuary. The contribution of the different estuarine categories to the spatial distribution of biomass (Figure 4.1) showed that > 80 % of the total biomass was comprised of EUC I species at Stations 2 through 5. Estuarine species contributed only ~35 % of the biomass at Station 1, with 41 % attributed to EUC II species and 15 % attributed to EUC V species.

Glossogobius callidus was sampled throughout the estuary. While they appeared to be most abundant in the upper reaches of the estuary, CPUE analysis demonstrated that there was no significant difference between their abundances in the upper middle and lower reaches. For the other dominant juvenile/larval species in the littoral zone there was a trend of higher CPUEs sampled in the lower and upper reaches in comparison to the middle reaches. Other species sampled in the shallow littoral zone showed some spatial trends (Figure 4.7); *Psammogobius knysnaensis* was collected only from the sandy sediment at the mouth of the estuary, while juvenile *R. holubi* were found in higher numbers in the lower reaches of the estuary. A post-hoc test of the total ichthyofaunal abundance revealed significantly higher abundance (Tukey $p < 0.05$) at Station 1 than Station 2 ($F_{(4, 94)} = 2.99$ $p < 0.05$). A Pearson's correlation of these dominant species did not provide any significant correlation between spatial distribution and the abundance values of each species (Appendix, Table III).

The average biomass of *G. callidus* (Figure 4.7) was higher in the upper reaches, with a significant increase with distance from the mouth of the estuary (station: $F_{(4, 94)} = 3.08$ $p < 0.02$). A post-hoc test revealed a significantly higher contribution of *G. callidus* at Station 5 than Station 1 (Tukey $p < 0.05$), *G. aestuaria*, *A. breviceps* and *R. holubi* had lower biomass estimates in the middle reaches of the system but these were not significant (Figure 4.7).

4.3.1.2 Estuarine and smaller marine spawning ichthyofauna

A total of 41422 fish, with an average abundance of 2.92 ind.m^{-2} (± 4.45 SD) were sampled with the 30 m seine net that was used to target estuarine spawning species and the smaller marine spawning fish species (contributing > 95 % of the total abundance). Thirty three species of fish were sampled, representing 16 families (Table 4.4). Seven species contributed to a combined monthly average of 97 % (± 3.2 SD) of the total number of fish sampled between November 2005 and October 2007. *Gilchristella aestuaria* (30.33 %) was the most numerically dominant species followed by *R. holubi* (29.5 %), *G. callidus* (18.6 %), *A. breviceps* (11.1 %), *M. capensis* (4.5 %), *Solea turbynei* (1.9 %) and *L. dumerilii* (1.8 %).

The abundance of the estuarine and smaller marine spawning species (Figure 4.3) ranged between 0.91 ind.m^{-2} (± 1.45 SD July 2007) and 7.65 ind.m^{-2} (± 16.88 SD June 2007). Prior to breaching, the average abundance ranged between 1.72 ind.m^{-2} (± 1.50 SD) in June 2006 and 5.91 ind.m^{-2} (± 4.74 SD) in February 2006. After the estuary re-closed (December 2006 - January 2007), the average abundance was lower (2.25 ind.m^{-2} ± 5.49 SD) than the initial closed period (3.67 ind.m^{-2} ± 3.07 SD), with the exceptions of February 2007 and June 2007, with average abundances of 3.83 ind.m^{-2} (± 2.95 SD) and 7.65 ind.m^{-2} (± 16.88 SD), respectively. During the open period average abundances ranged between 0.93 ind.m^{-2} and 4.64 ind.m^{-2}.

Estuarine spawning species contributed to 60.32 % of the fish abundance sampled (Figure 4.2) while the EUC II species contributed 34.96 % and the catadromous species a further 4.48 %. Before the estuary breached, the majority (>60 %) of the species sampled fell into EUC I (Figure 4.5), with the EUC II species being the next dominant group. In May 2006 to July 2006 there was also a minor contribution (7.04 % to 9.02 %) by the EUC V species. During the first three months when the estuary was open EUC V and III species numerically dominated, dropping again in November and December 2006. After the estuary re-closed, with the exception of June 2007, the majority (>50 %) of the abundance was attributed to EUC II species, with the EUC V species also contributing between 11.27 % and 27.38 % in the months of January to March 2007 (Figure 4.5).

Spatial variation in the abundance of the smaller estuarine and marine spawning fish species sampled (Figure 4.1) showed an increase in abundance from Station 2 (1.33 ind.m^{-2} ± 1.72 SD) through to Station 5 (6.10 ind.m^{-2} ± 8.19 SD), with Station 1 having an average abundance value of 1.91 ind.m^{-2} (± 2.50 SD). Fish abundance at Station 5 was significantly higher (Tukey $p < 0.05$ and Tukey $p < 0.01$ respectively) than at Stations 1 and 2 ($F_{(4,94)} = 3.75$ $p < 0.01$). The abundances of fish in upper reaches (stations) were also significantly higher than in the lower reaches ($F_{(2,96)} = 40749.00$ $p < 0.02$) (Tukey $p < 0.02$). The estuarine spawners, EUC I (Figure 4.1), contributed the most, with values ranging between 55.18 % and 76.21 % of total abundance throughout the system, with the highest contribution at Station 2. Estuarine utilisation category II (22.02 % to 43.29 %) and to some extent EUC V species (1.41 % to 7.41 %) contributed to the rest of the abundance at each station (Figure 4.1).

The three dominant smaller estuarine and marine spawning ichthyofaunal species in terms of abundance (*G. aestuaria*, *R. holubi* and *G. callidus*) (Figure 4.7) all had distributional patterns that exhibited an increase in abundance with an increase in distance from the mouth of the estuary. *Atherina breviceps* had a higher distribution in the lower reaches while *M. capensis*, *S. turbynei* and *L. dumerilii* had higher abundances in the upper and middle reaches (Figure 4.7).

A combined total of 180073.05 grams of wet weight biomass for the smaller estuarine and marine spawning ichthyofauna was sampled (Table 4.5). The average fish biomass per unit area was 12.70 g wwt.m^{-2} (± 13.27 SD). Nine of the smaller estuarine and marine spawning ichthyofauna species sampled contributed 89.6 % of the total biomass; *Rhabdosargus holubi* (47.2 %), *L. dumerilii* (17.9 %), *M. capensis* (10.6 %), *G. callidus* (7.3 %), *G. aestuaria* (4.8 %), *Lithognathus lithognathus* (3.5 %), *A. breviceps* (2.5 %), *L. richardsonii* (2.0 %) and *S. turbynei* (0.9 %) (Table 4.5).

The lowest and highest average biomass of the smaller estuarine and marine spawning ichthyofauna were both onserved during the open period (Figure 4.4), with the lowest value in August 2006 (1.25 g wwt.m^{-2}) and the highest in October 2006 (34.31 g wwt.m^{-2}). In the initial closed period, the average fish biomass was 12.93 g wwt.m^{-2} (± 10.25 SD). Conversely, when the mouth was open the average fish biomass was 15.78 g wwt.m^{-2} (± 12.25 SD). After the estuary closed, the average biomass was 12.18 g wwt.m^{-2} (± 15.70 SD). The biomass in the first four months (November 2005 to February 2006) was significantly ($F_{(1, 42)} = 8.46$ $p < 0.01$) higher (Tukey $p < 0.05$) than the next five months (March 2006 to July 2006). In the 5 months during which the mouth remained open (August 2006 – December 2006), the fish biomass varied from month to month (1.25 g wwt.m^{-2} to 34.31 g wwt.m^{-2}). After the estuary closed the monthly biomass fluctuated (between 6.44 g wwt.m^{-2} and 21.77 g wwt.m^{-2}) till July 2007, after which there was a steady increase (from 6.84 g wwt.m^{-2} to 24.26 g wwt.m^{-2}) in biomass to October 2007. The spring biomass for the smaller estuarine and marine spawning fish were significantly higher than the winter values (Tukey $p < 0.05$) ($F_{(3, 95)} = 4.27$ $p < 0.02$). There were no significant temporal variations among fish biomass estimates during the initial closed, open and re-closed periods.

Biomass of the smaller estuarine and marine spawning ichthyofauna sampled showed significant variations with Station 5, having significantly higher values than Stations 1 (Tukey $p < 0.01$), 2 (Tukey $p < 0.001$) and 3 (Tukey $p < 0.005$) ($F_{(4, 94)} = 7.83$ $p < 0.0001$). The biomass in the upper reaches was significantly higher (Tukey $p < 0.05$) than the middle and lower reaches of the estuary ($F_{(2, 96)} = 8.56$ $p < 0.0005$) (Figure 4.1). Throughout the length of the estuary, the fish biomass was primarily comprised of the EUC II species, with the EUC I and V species being the next highest contributors (Figure 4.1). The biomass of the smaller estuarine and marine spawning ichthyofauna (Figure 4.2) was dominated by EUC II species (73.35 %) with the EUC I and V species contributing 14.93 % and 10.63 % respectively, the remaining 0.89 % and 0.20 % was attributed to EUC III and IV species respectively. The monthly biomass was dominated by the marine migrants whose juveniles depend on the estuaries (EUC II), with the exceptions of August 2006 and June 2007, where the EUC V and EUC I species, respectively, contributed the most to monthly biomass estimates (Figure 4.6). Estuarine utilisation category V species contributed more to the biomass during the months of May 2006 through to August 2007 and also January and February 2007.

The highest biomass contribution was by *R. holubi* which showed an increase from the lower to the upper reaches with almost double (1.87x) the biomass (although not significant) in the upper reaches (Figure 4.7). The biomass estimates of *Liza dumerilii*, *G. callidus*, *G. aestuaria* and *S. turbynei* also increased with distance from the mouth. The biomass of *M. capensis* was highest in the upper reaches, while *L. lithognathus* was more prominent in the lower reaches and *L. richardsonii* was sampled throughout the estuary.

4.3.1.3 Large marine and freshwater spawning species

A total of 3513 fish with an average abundance of 0.09 ind.m^{-2} (± 0.12 SD) were sampled by the 50 m seine net that was used to target the larger marine and freshwater spawning species. Twenty four species representing 11 families were sampled (Table 4.6). Numerically four species dominated (95 % (± 5.2 SD)) the abundance, the sparid, *R. holubi* (74.1 %) and the mullet, *L. dumerilii* (15.8 %), *L. richardsonii* (3.5 %) and *M. capensis* (2.2 %). The highest abundance of ichthyofauna (Figure 4.3) was during November in both 2005 and 2006 with average abundance values of 0.34 ind.m^{-2} (± 0.27 SD) and 0.34 ind.m^{-2} (± 0.00 SD), respectively. During the first month after the estuary breached (August 2006) no fish were sampled in the 50 m seine net (Figure 4.3).

There was a slight decrease in average abundance from the months before breaching through the open phase and into the subsequent closed phase (initial closed [0.12 ind.m^{-2} ± 0.13 SD]; open [0.09 ind.m^{-2} ± 0.14 SD]; re-closed [0.07 ind.m^{-2} ± 0.10 SD] periods). The summer months displayed a significantly higher abundance (Tukey $p < 0.001$) than the winter months ($F_{(3, 95)} = 6.11$ $p < 0.001$).

The total abundance of the larger marine and freshwater spawning fish species sampled was dominated by EUC II species (96.47 % [Figure 4.2]). The remaining 3.53 % of the abundance comprised the other four categories (Figure 4.2). During the initial closed period, the EUC III species contributed more than the EUC V species (Figure 4.5). However, after the estuary re-closed, the EUC V species were numerically more dominant than the EUC III species. The lowest average spatial abundance value (Figure 4.1) for the larger fish species was at Station 2 (0.04 ind.m^{-2} ± 0.06 SD), while the highest average value was at Station 5 (0.13 ind.m^{-2} ± 0.19 SD), indicating a general trend of increasing abundance towards the upper reaches of the estuary. A significant difference in the abundance between the three reaches was identified using an ANOVA ($F_{(2, 96)} = 3.33$ $p < 0.05$), however, multiple post-hoc tests could not identify the specific significant variations between the reaches, although there was a general increase in abundance values with an increase in distance from the mouth of the estuary. The contribution of each estuarine utilisation category to the spatial distribution (Figure 4.1) was dominated by EUC II species (>92 % for all stations).

Six species contributed to 95.8 % of the total calculated biomass (128 087.35 g wwt, average 3.25 g wwt.m^{-2} (± 4.30 SD)). The species were: *R. holubi* (41.7 %), *L. dumerilii* (33.9 %), *M. capensis* (9.9 %), *L. richardsonii* (7.0 %), *L. lithognathus* (1.8 %) and *P. commersonnii* (1.5 %) (Table 4.7). Biomass of the larger species (Figure 4.4) showed a cyclic change in monthly biomass in the second half of the study period, with the highest and the lowest monthly biomass sampled during the open phase of the estuary. During the initial closed period prior to breaching (July/August 2006) November 2005 had an average value of 8.54 g wwt.m^{-2} (± 4.19 SD) and the next four months of the study (December 2005 to March 2006) varied between 3.38 g wwt.m^{-2} (± 2.47 SD) and 5.21 g wwt.m^{-2} (± 3.24 SD). From March 2006 the biomass decreased monthly to July (2006) 0.84 g wwt.m^{-2} (± 0.69 SD).

The total biomass of the larger marine and freshwater spawning fish sampled was dominated by EUC II species (87.34 %) (Figure 4.2), with EUC V and remaining groups contributing 9.88 % and 2.78 %, respectively. In the remaining groups, EUC I species contributed the smallest biomass estimate (0.08 %). Monthly biomass (Figure 4.6) was dominated by EUC II species, followed by EUC V species, except in the first month (November 2005), when EUC III and IV species contributed ~ 17 % to the biomass. The biomass from each station showed a similar average for each of Stations 1 (3.86 g wwt.m^{-2} ± 4.55 SD), 3 (4.44 g wwt.m^{-2} ± 4.58 SD) and 5 (3.72 g wwt.m^{-2} ± 6.13 SD) (Figure 4.1), while Station 2 had the lowest average biomass (1.37 g wwt.m^{-2} (± 2.00 SD)). The overall biomass at each station (Figure 4.1) was dominated by EUC II species, with category V species contributing just less than 25 % to Station 1, while in Stations 3 to 5 EUC III and IV species contributed slightly to the biomass.

The larger *R. holubi* showed a significantly higher abundance ($F_{(2, 96)} = 3.72$ $p < 0.05$) in the upper versus lower reaches (Tukey $p < 0.05$), while of the three dominant mullet species, *L. richardsonii* and *M. capensis* decreased in abundance with an increase in distance from the mouth. *Liza dumerilii* had significantly higher abundance values in the middle reaches ($F_{(2, 96)} = 6.00$ $p < 0.005$) in comparison to the upper (Tukey $p < 0.05$) and lower reaches (Tukey $p < 0.005$) (Figure 4.7).

The biomass of *R. holubi* increased from the lower to the upper reaches (Figure 4.7). The highest biomass for *L. dumerilii* was sampled in the middle reaches (Figure 4.7). The biomass of *Myxus capensis* and *L. richardsonii* was highest in the lower reaches, with a decline to the upper reaches. The lowest biomass estimates of *Lithognathus lithognathus* were in the middle reaches, while the highest biomass estimates of *Pomadasys commersonnii* were in the upper reaches (Figure 4.7).

Table 4.2: The sample composition, abundance, rank and size composition (mean standard length (mm), standard deviation and length range) of the juvenile/larval fish sampled by the 5 m seine net in the littoral zone of the Mpekweni Estuary between November 2005 and October 2007. A total of 6567 fish were sampled.

Species	Number sampled	% sample composition	Rank	Mean SL (mm)	Standard deviation	Length range (mm)
Antennariidae						
Antennarius striatus	1	0.02	17	139.00	-	-
Atherinidae						
Atherina breviceps	1674	25.49	2	21.56	± 9.01	2 – 54
Cichlidae						
Oreochromis mossambicus	14	0.21	10	33.55	± 21.81	10 – 83
Clupeidae						
Gilchristella aestuaria	1095	16.67	3	25.96	± 4.98	5 – 43
Gobiidae						
Caffrogobius gilchristi	3	0.05	15	61.00	± 5.29	55 – 65
Caffrogobius nudiceps	2	0.03	16	55.00	± 5.66	51 – 59
Glossogobius callidus	2555	38.91	1	34.20	± 11.66	7 – 77
Psammogobius knysnaensis	19	0.29	8	45.21	± 9.95	21 – 57
Monodactylidae						
Monodactylus falciformis	11	0.17	11	21.13	± 5.43	11 – 28
Mugilidae						
Liza dumerilii	21	0.33	7	40.62	± 6.01	27 – 52
Liza richardsonii	307	4.67	6	35.19	± 9.68	11 – 48
Liza tricuspidens	4	0.06	13	40.00	± 6.38	34 – 49
Myxus capensis	394	6.00	5	29.24	± 8.65	11 – 60
Soleidae						
Heteromycteris capensis	15	0.23	9	36.40	± 7.23	16 – 45
Solea turbynei	11	0.17	12	48.82	± 10.42	25 – 59
Sparidae						
Diplodus sargus capensis	4	0.06	14	37.00	± 8.37	26 – 44
Rhabdosargus holubi	437	6.65	4	19.48	± 12.42	8 – 72

Table 4.3: The sample composition, biomass, rank and size composition (mean weight (g wwt), standard deviation and weight range) of the juvenile/larval fish sampled in the littoral zone of the Mpekweni Estuary between November 2005 and October 2007. A total of 3962.18 g wwt was estimated.

Species	Total biomass (g)	% sample composition	Rank	Mean biomass (g)	Standard deviation	Weight range (g)
Antennariidae						
Antennarius striatus	100.00	2.52	7	-	-	-
Atherinidae						
Atherina breviceps	306.94	7.75	4	0.18	± 0.26	0.00 – 1.96
Cichlidae						
Oreochromis mossambicus	46.34	1.17	8	3.31	± 6.47	0.03 – 20.19
Clupeidae						
Gilchristella aestuaria	353.50	8.92	2	0.32	± 0.18	0.00 – 1.43
Gobiidae						
Caffrogobius gilchristi	16.47	0.42	12	5.49	± 1.43	3.89 – 6.61
Caffrogobius nudiceps	7.57	0.19	14	3.78	± 1.24	2.91 – 4.66
Glossogobius callidus	2217.77	55.97	1	0.87	± 0.87	0.01 – 7.46
Psammogobius knysnaensis	38.17	0.96	9	2.01	± 1.07	0.16 – 3.62
Monodactylidae						
Monodactylus falciformis	4.90	0.12	17	0.45	± 0.28	0.06 – 0.88
Mugilidae						
Liza dumerilii	32.65	0.82	10	1.55	± 0.58	0.46 – 2.99
Liza richardsonii	307.47	7.76	3	1.00	± 0.55	0.03 – 2.10
Liza tricuspidens	5.30	0.13	16	1.33	± 0.66	0.78 – 2.28
Myxus capensis	221.17	5.58	6	0.56	± 0.44	0.02 – 3.94
Soleidae						
Heteromycteris capensis	9.07	0.23	13	0.60	± 0.27	0.04 – 1.50
Solea turbynei	23.23	0.59	11	2.11	± 1.06	0.24 – 3.37
Sparidae						
Diplodus sargus capensis	6.95	0.18	15	1.74	± 1.00	0.52 – 2.65
Rhabdosargus holubi	264.67	6.68	5	0.61	± 1.57	0.01 – 12.05

Table 4.4: The sample composition, abundance, rank and size composition (mean standard length (mm), standard deviation and length range) of the estuarine and smaller marine spawning fish species sampled by the 30 m seine net in the Mpekweni Estuary between November 2005 and October 2007. A total of 41422 fish were sampled.

Species	Number sampled	% sample composition	Rank	Mean SL (mm)	Standard deviation	Length range (mm)
Atherinidae						
Atherina breviceps	4578	11.05	4	41.68	± 8.22	4 – 65
Blenniidae						
Omobranchus woodi	1	< 0.01	29	58.00	-	-
Carangidae						
Lichia amia	2	< 0.01	27	294.00	± 76.37	240 – 348
Cichlidae						
Oreochromis mossambicus	77	0.19	9	43.52	± 18.80	21 – 100
Clinidae						
Smithichthys fucorum	1	< 0.01	30	44.00	-	-
Clupeidae						
Gilchristella aestuaria	12562	30.33	1	33.33	± 5.04	3 – 67
Elopidae						
Elops machnata	16	0.04	22	93.50	± 31.94	48 – 165
Gobiidae						
Caffrogobius gilchristi	23	0.06	18	66.52	± 15.07	33 – 105
Caffrogobius nudiceps	17	0.04	21	63.18	± 14.44	48 – 97
Glossogobius callidus	7719	18.64	3	44.41	± 11.34	12 – 152
Psammogobius knysnaensis	63	0.15	13	49.97	± 8.36	26 – 72
Haemulidae						
Pomadasys commersonnii	13	0.03	23	147.54	± 66.85	54 – 300
Pomadasys olivaceum	33	0.08	16	44.58	± 12.87	26 – 67
Hemiramphidae						
Hyporhamphus capensis	21	0.05	20	128.90	± 24.04	75 – 171
Monodactylidae						
Monodactylus argenteus	1	< 0.01	31	16.00	-	-
Monodactylus falciformis	69	0.17	11	41.65	± 20.78	21 – 124
Mugilidae						
Liza dumerilii	732	1.77	7	120.96	± 41.13	33 – 260
Liza macrolepis	8	0.02	24	62.38	± 35.90	38 – 122
Liza richardsonii	310	0.75	8	69.72	± 33.53	22 – 207
Liza tricuspidens	65	0.16	12	43.65	± 24.78	27 – 165
Mugil cephalus	22	0.05	19	104.32	± 50.81	34 – 245
Myxus capensis	1854	4.48	5	67.21	± 32.72	11 – 246
Paralichthyidae						
Pseudorhombus arsius	1	< 0.01	32	164	-	-
Soleidae						
Heteromycteris capensis	63	0.15	14	53.75	± 18.99	9 – 134
Solea turbynei	770	1.86	6	48.91	± 9.46	21 – 103
Solea fulvomarginata	1	< 0.01	33	53	-	-
Sparidae						
Diplodus sargus capensis	40	0.10	15	48.68	± 19.73	23 – 99
Lithognathus lithognathus	77	0.19	10	138.77	± 45.89	32 – 227
Rhabdosargus globiceps	33	0.08	17	42.27	± 5.87	26 – 54
Rhabdosargus holubi	12234	29.54	2	53.04	± 19.03	11 – 159
Rhabdosargus sarba	8	0.02	25	73.75	± 15.80	45 – 100
Tetraodontidae						
Amblyrhynchotes honckenii	5	0.01	26	69.20	± 15.02	52 – 93
Arothron hispidus	2	< 0.01	28	60.00	± 12.73	51 – 69

Table 4.5: The sample composition, biomass, rank and size composition (mean weight (g wwt), standard deviation and weight range) of the estuarine and smaller marine spawning ichthyofauna sampled by the 30 m seine net in the Mpekweni Estuary between November 2005 and October 2007. A total of 180,073.05 g wwt was estimated.

Species	Total biomass (g)	% sample composition	Rank	Mean biomass (g)	Standard deviation	Weight range (g)
Atherinidae						
Atherina breviceps	4483.48	2.49	7	0.98	± 0.51	0.00 – 3.51
Blenniidae						
Omobranchus woodi	12.00	0.01	31	-	-	-
Carangidae						
Lichia amia	966.60	0.54	12	483.30	± 335.74	245.90 – 720.70
Cichlidae						
Oreochromis mossambicus	365.65	0.20	14	4.75	± 6.92	0.31 – 35.50
Clinidae						
Smithichthys fucorum	7.00	< 0.01	32	-	-	-
Clupeidae						
Gilchristella aestuaria	8669.45	4.81	5	0.69	± 0.36	0.00 – 5.88
Elopidae						
Elops machnata	118.95	0.07	21	7.43	± 8.91	0.60 – 32.23
Gobiidae						
Caffrogobius gilchristi	191.35	0.11	17	8.32	± 5.9572	0.77 – 30.31
Caffrogobius nudiceps	152.97	0.08	20	9.00	± 5.99	2.39 – 23.34
Glossogobius callidus	13095.97	7.27	4	1.7	± 1.59	0.03 – 59.17
Psammogobius knysnaensis	165.35	0.09	19	2.62	± 1.39	0.31 – 7.50
Haemulidae						
Pomadasys commersonnii	1434.80	0.80	10	110.37	± 153.75	3.30 – 567.53
Pomadasys olivaceum	81.52	0.05	26	2.47	± 1.97	0.33 – 7.20
Hemiramphidae						
Hyporhamphus capensis	112.51	0.06	22	5.36	± 3.12	0.67 – 12.83
Monodactylidae						
Monodactylus argenteus	0.50	< 0.01	33	-	-	-
Monodactylus falciformis	383.23	0.21	13	5.55	± 11.20	0.37 – 73.99
Mugilidae						
Liza dumerilii	32251.10	17.91	2	44.06	± 44.26	0.82 – 297.41
Liza macrolepis	90.19	0.05	23	11.27	± 17.23	1.31 – 41.04
Liza richardsonii	3512.72	1.95	8	11.33	± 17.49	0.21 – 162.80
Liza tricuspidens	266.63	0.15	15	4.10	± 13.56	0.39 – 81.23
Mugil cephalus	1027.19	0.57	11	46.69	± 88.41	0.89 – 320.47
Myxus capensis	19144.57	10.63	3	10.33	± 18.65	0.02 – 286.75
Paralichthyidae						
Pseudorhombus arsius	20.00	0.01	30	-	-	-
Soleidae						
Heteromycteris capensis	169.69	0.09	18	2.69	± 4.39	0.01 – 31.12
Solea turbynei	1643.12	0.91	9	2.00	± 1.54	0.14 – 18.60
Solea fulvomarginata	25.00	0.01	29	-	-	-
Sparidae						
Diplodus sargus capensis	229.05	0.13	16	5.73	± 7.45	0.36 – 32.21
Lithognathus lithognathus	6232.21	3.46	6	80.94	± 66.57	0.77 – 282.22
Rhabdosargus globiceps	66.46	0.04	27	2.01	± 0.81	0.40 – 4.12
Rhabdosargus holubi	84652.58	47.19	1	6.92	± 9.60	0.00 – 139.07
Rhabdosargus sarba	85.91	0.05	25	10.74	± 6.37	2.17 – 24.00
Tetraodontidae						
Amblyrhynchotes honckenii	86.61	0.05	24	17.32	± 11.79	6.65 – 37.38
Arothron hispidus	28.67	0.02	28	14.33	± 8.00	8.67 – 19.99

Table 4.6: The sample composition, abundance, rank and size composition (mean standard length (mm), standard deviation and length range) of the larger marine and freshwater spawning fish sampled by the 50 m seine net in the Mpekweni Estuary between November 2005 and October 2007. A total of 3513 fish were sampled.

Species	Number sampled	% sample composition	Rank	Mean SL (mm)	Standard deviation	Length range (mm)
Carangidae						
Lichia amia	1	0.03	16	245.00	-	-
Cichlidae						
Oreochromis mossambicus	30	0.85	6	87.33	± 42.66	37 – 287
Elopidae						
Elops machnata	2	0.06	14	336.00	± 45.25	304 – 368
Gobiidae						
Caffrogobius gilchristi	2	0.06	15	98.50	± 9.19	92 – 105
Caffrogobius nudiceps	1	0.03	17	90.00	-	-
Glossogobius callidus	10	0.28	10	50.70	± 24.98	18 – 88
Haemulidae						
Pomadasys commersonnii	4	0.11	13	270.50	± 75.92	160 – 325
Monodactylidae						
Monodactylus falciformis	18	0.51	8	78.11	± 26.38	45 – 122
Mugilidae						
Liza dumerilii	555	15.80	2	154.23	± 38.10	22 – 300
Liza macrolepis	1	0.03	18	220.00	-	-
Liza richardsonii	123	3.50	3	146.24	± 39.34	70 – 315
Liza tricuspidens	1	0.03	19	95.00	-	-
Mugil cephalus	12	0.34	9	170.67	± 58.33	102 – 255
Myxus capensis	76	2.16	4	194.70	± 47.62	79 – 315
Platycephalidae						
Platycephalus indicus	1	0.03	20	143.00	-	-
Soleidae						
Heteromycteris capensis	1	0.03	21	70.00	-	-
Solea turbynei	24	0.68	7	74.83	± 9.11	55 – 89
Sparidae						
Diplodus sargus capensis	9	0.26	11	65.00	± 2.87	62 – 69
Lithognathus lithognathus	32	0.91	5	126.63	± 49.45	80 – 235
Rhabdosargus globiceps	1	0.03	24	72	-	-
Rhabdosargus holubi	2602	74.09	1	81.69	± 17.28	10 – 212
Rhabdosargus sarba	1	0.03	22	80.00	-	-
Sarpa salpa	5	0.14	12	88.40	± 10.01	80 – 105
Tetraodontidae						
Amblyrhynchotes honckenii	1	0.03	23	77.00	-	-

Table 4.7: The sample composition, biomass, rank and size composition (mean weight, standard deviation and weight range) of the larger marine and freshwater spawning fish sampled by the 50 m seine net in the Mpekweni Estuary between November 2005 and October 2007. A total of 128,087.35 g wwt was estimated.

Species	Total biomass (g)	% sample composition	Rank	Mean biomass (g)	Standard deviation	Weight range (g)
Carangidae						
Lichia amia	261.02	0.20	11	-	-	-
Cichlidae						
Oreochromis mossambicus	1502.69	1.17	8	50.09	± 155.06	1.75 – 865.22
Elopidae						
Elops machnata	659.06	0.51	9	329.53	± 139.15	231.13 – 427.93
Gobiidae						
Caffrogobius gilchristi	50.23	0.04	16	25.12	± 7.35	19.92 – 30.31
Caffrogobius nudiceps	18.31	0.01	20	-	-	-
Glossogobius callidus	35.98	0.03	17	3.60	± 4.29	0.09 – 11.20
Haemulidae						
Pomadasys commersonnii	1936.03	1.51	6	484.01	± 285.73	86.04 – 721.62
Monodactylidae						
Monodactylus falciformis	448.50	0.35	10	24.92	± 23.39	3.62 – 70.50
Mugilidae						
Liza dumerilii	43433.65	33.91	2	78.26	± 61.18	0.26 – 447.68
Liza macrolepis	233.81	0.18	12	-	-	-
Liza richardsonii	8904.68	6.95	4	72.40	± 85.56	6.46 – 597.92
Liza tricuspidens	16.00	0.01	21	-	-	-
Mugil cephalus	1732.29	1.35	7	144.36	± 126.63	23.55 – 361.03
Myxus capensis	12651.84	9.88	3	166.47	± 113.90	9.09 – 607.88
Platycephalidae						
Platycephalus indicus	30.00	0.02	18	-	-	-
Soleidae						
Heteromycteris capensis	4.15	< 0.01	24	-	-	-
Solea turbynei	174.91	0.14	13	7.29	± 2.52	2.71 – 11.88
Sparidae						
Diplodus sargus capensis	79.75	0.06	15	8.36	± 1.22	7.62 – 10.59
Lithognathus lithognathus	2352.71	1.84	5	73.52	± 91.23	12.21 – 313.25
Rhabdosargus globiceps	10.29	0.01	23	10.29	-	-
Rhabdosargus holubi	53423.39	41.71	1	20.53	± 16.93	0.03 – 338.01
Rhabdosargus sarba	12.26	0.01	22	-	-	-
Sarpa salpa	94.47	0.07	14	18.89	± 7.37	13.27 – 31.47
Tetraodontidae						
Amblyrhynchotes honckenii	21.34	0.02	19	-	-	-

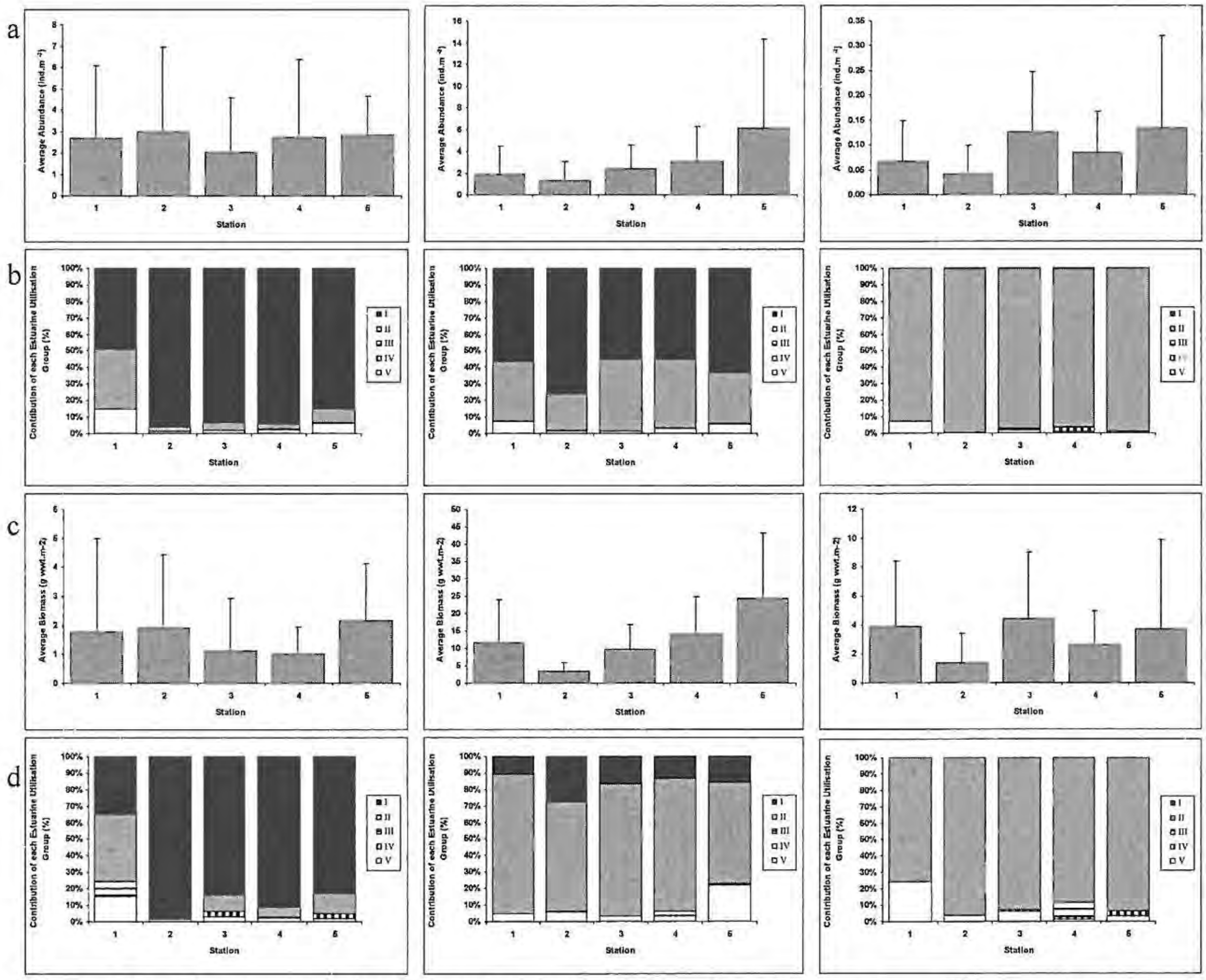

Figure 4.1: The average abundance (a), contribution of each estuarine utilisation group to the abundance (b), average biomass (c) and contribution of each estuarine utilisation group to the biomass (d) for juvenile/larval ichthyofauna (left column), estuarine and smaller marine spawning species (middle column) and larger marine and freshwater spawning species (right column) sampled at each station in the Mpekweni Estuary (error bars indicate standard deviation).

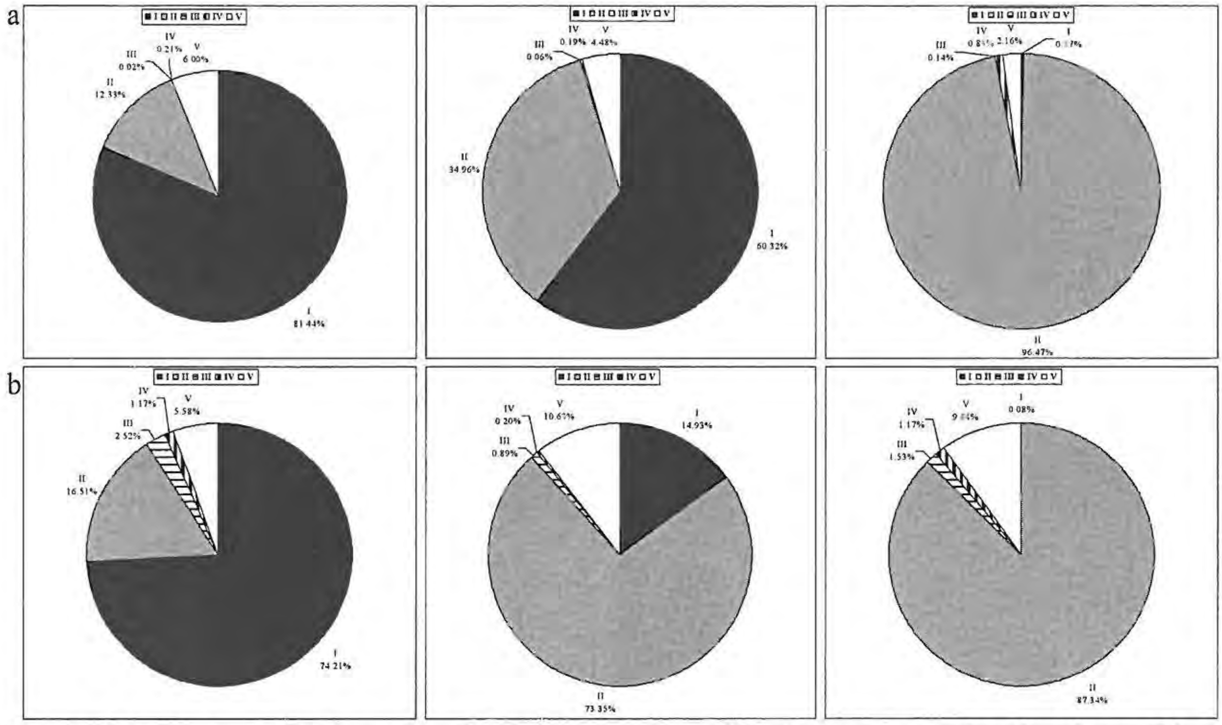

Figure 4.2: The contribution of each of the estuarine utilisation group to the abundance (a) and biomass (b) of larval/juvenile ichthyofauna (left column), estuarine and smaller marine spawning species (middle column) and larger marine and freshwater spawning ichthyofauna (right column).

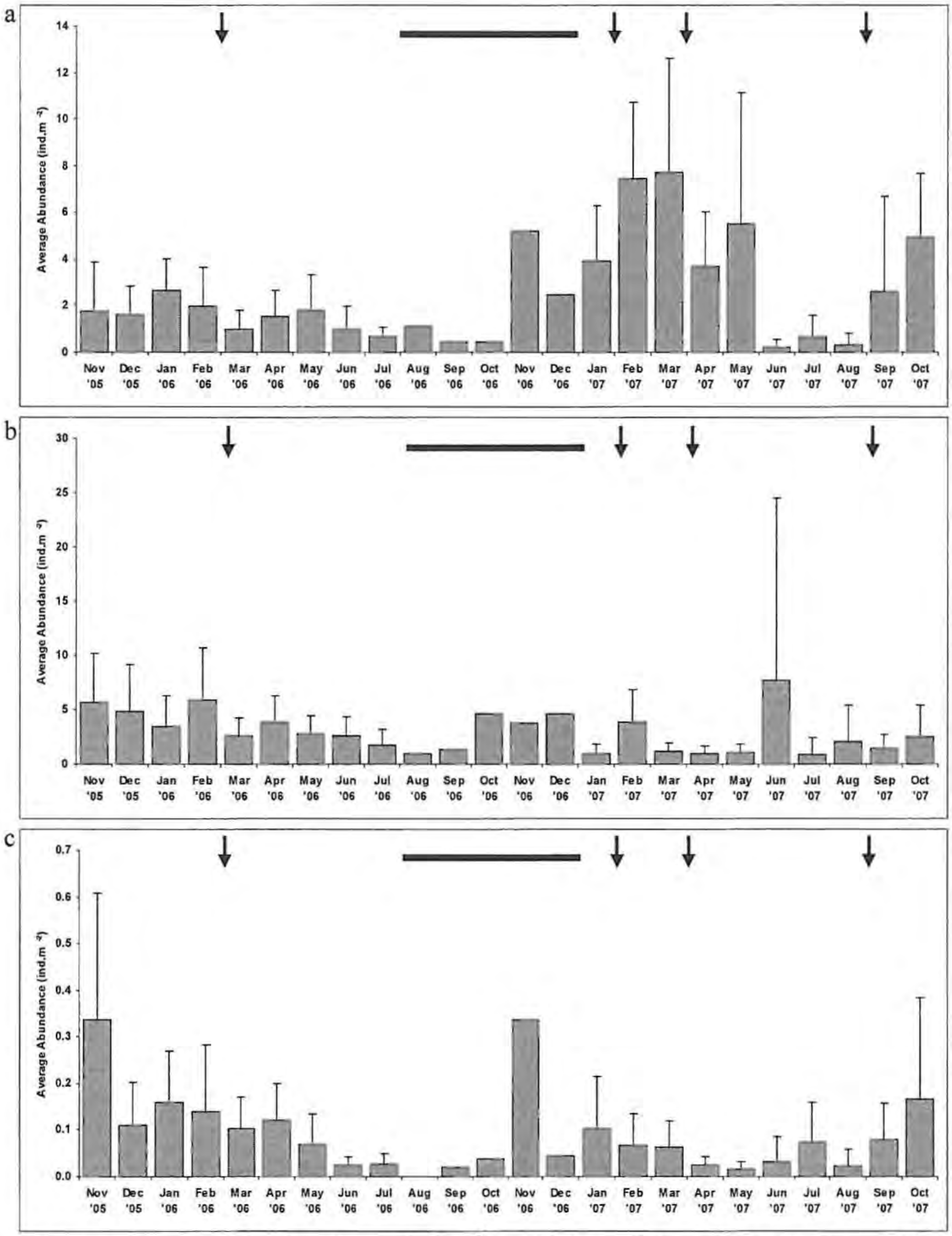

Figure 4.3: Average monthly abundance (ind.m^{-2}) of (a) juvenile/larval ichthyofauna, (b) estuarine and smaller marine spawning species and (c) larger marine and freshwater spawning species sampled in the littoral zone and channel of the Mpekweni Estuary. Error bars indicate standard deviation; there are no standard deviations during the open period as only a single station was sampled each month due to the shallow water depth. Vertical arrows indicate overwash events and the horizontal bar shows the period when the mouth was open.

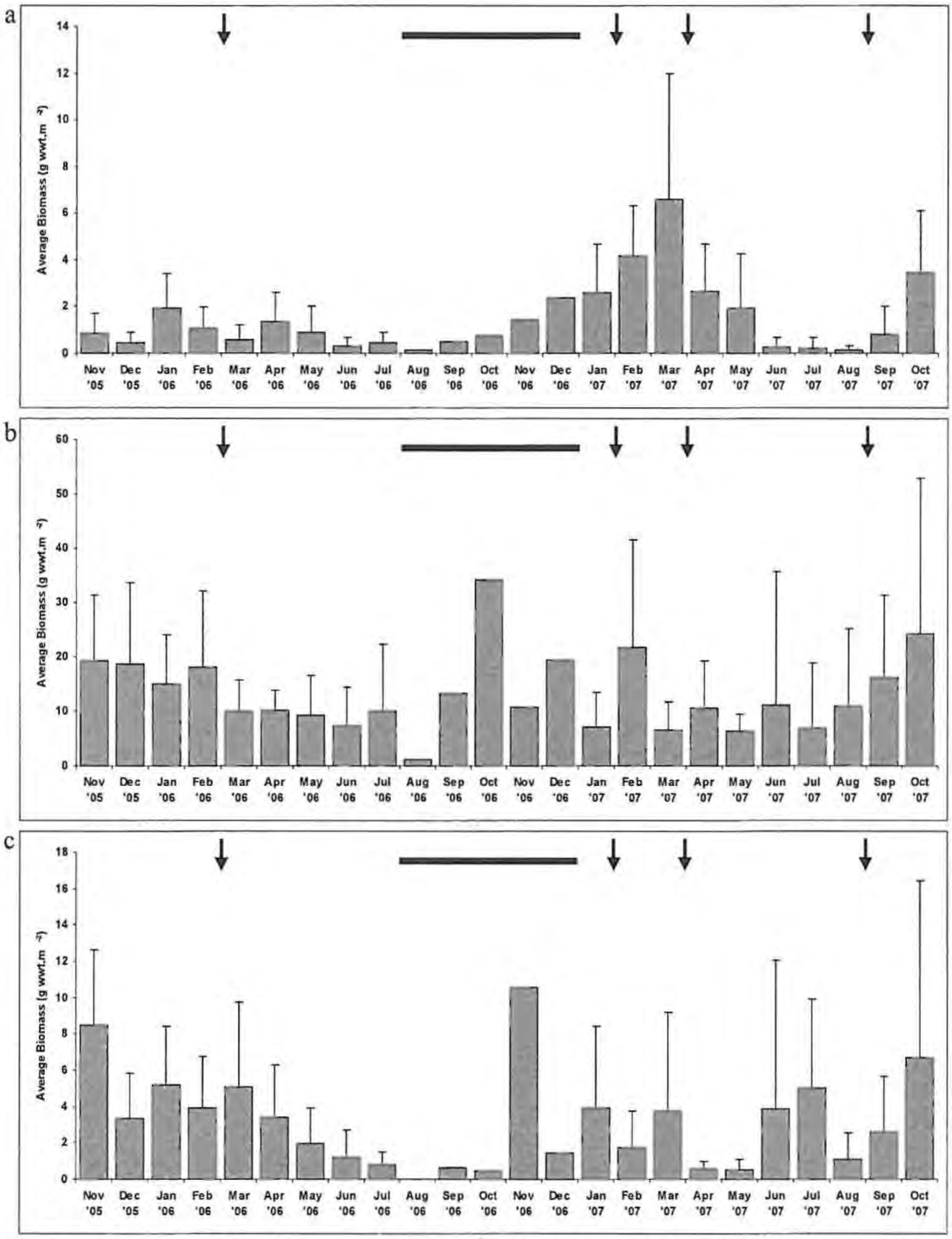

Figure 4.4: Average monthly biomass (g wwt.m^{-2}) of (a) juvenile/larval ichthyofauna, (b) estuarine and smaller marine spawning species and (c) larger marine and freshwater spawning species sampled in the littoral zone and channel of the Mpekweni Estuary. Error bars indicate standard deviation; there are no standard deviations during the open period as only a single station was sampled each month due to the shallow water depth. Vertical arrows indicate overwash events and the horizontal bar shows the period when the mouth was open.

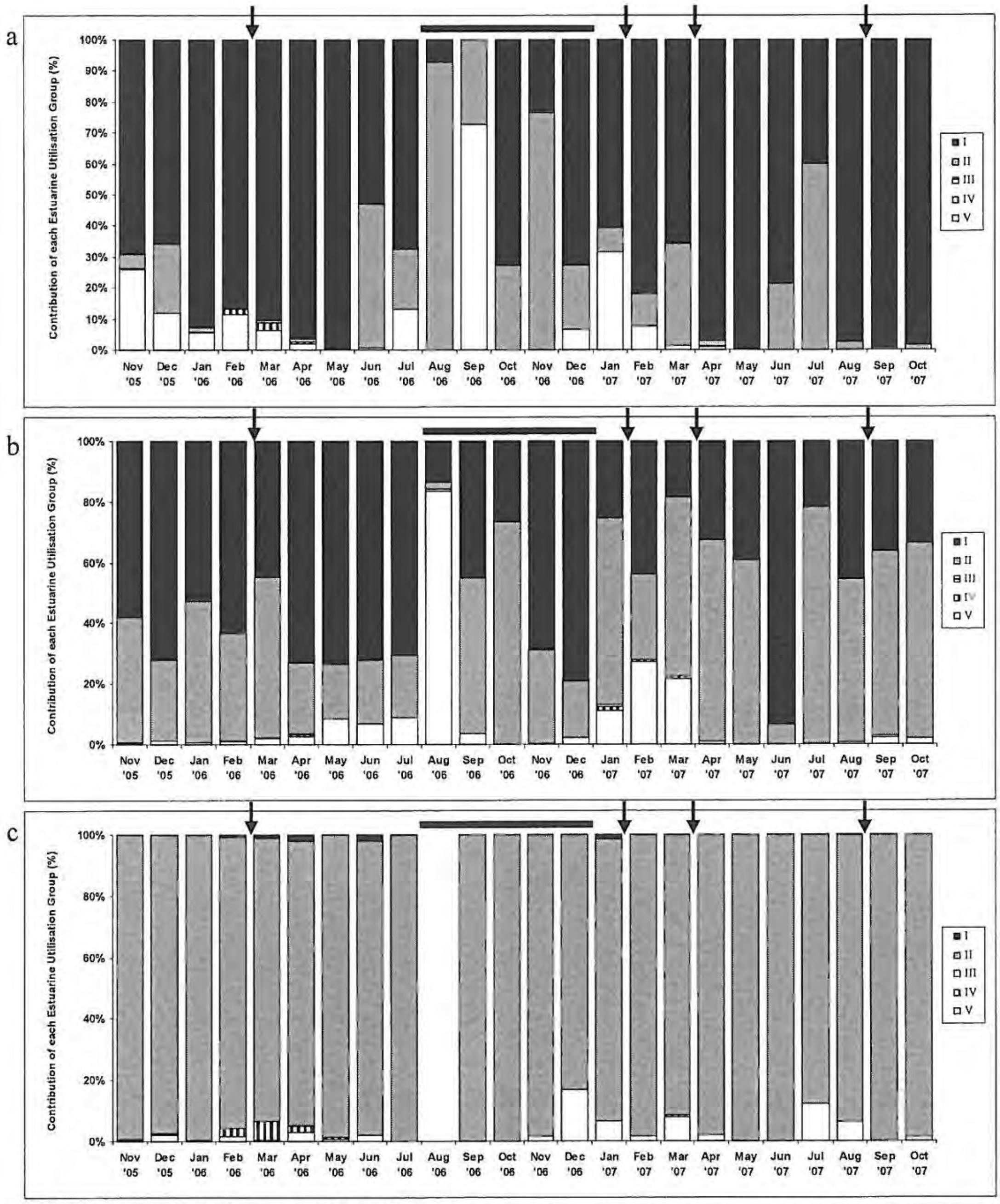

Figure 4.5: The contribution (%) of each estuarine group to the monthly abundance of (a) juvenile/larval ichthyofauna, (b) estuarine and smaller marine spawning species and (c) larger marine and freshwater spawning species sampled in the littoral zone and channel of the Mpekweni Estuary. Vertical arrows indicate overwash events and the horizontal bar shows the period when the mouth was open.

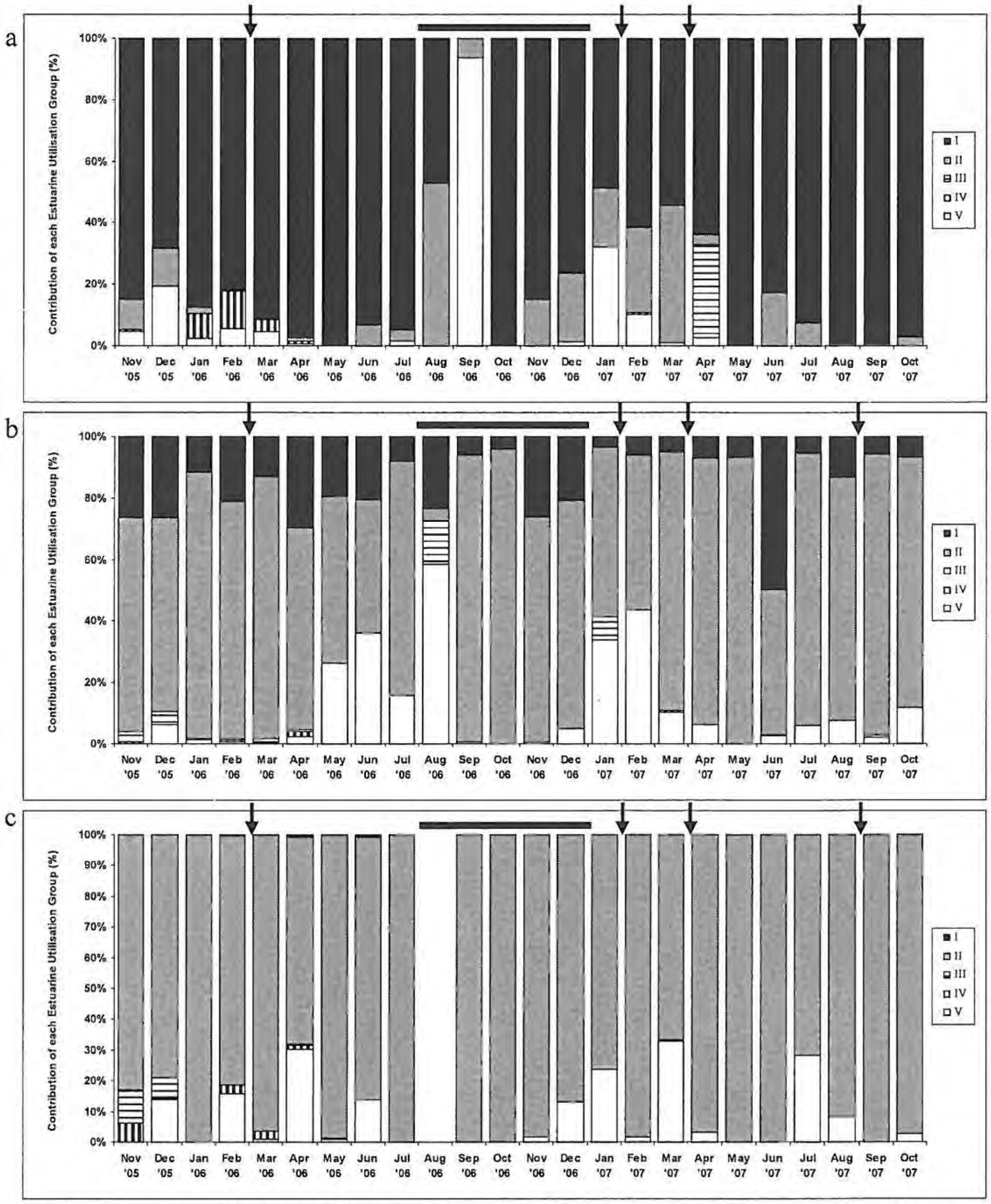

Figure 4.6: The contribution (%) of each estuarine group to the monthly biomass of (a) juvenile/larval ichthyofauna, (b) estuarine and smaller marine spawning species and (c) larger marine and freshwater spawning species sampled in the littoral zone and channel of the Mpekweni Estuary. Vertical arrows indicate overwash events and the horizontal bar shows the period when the mouth was open.

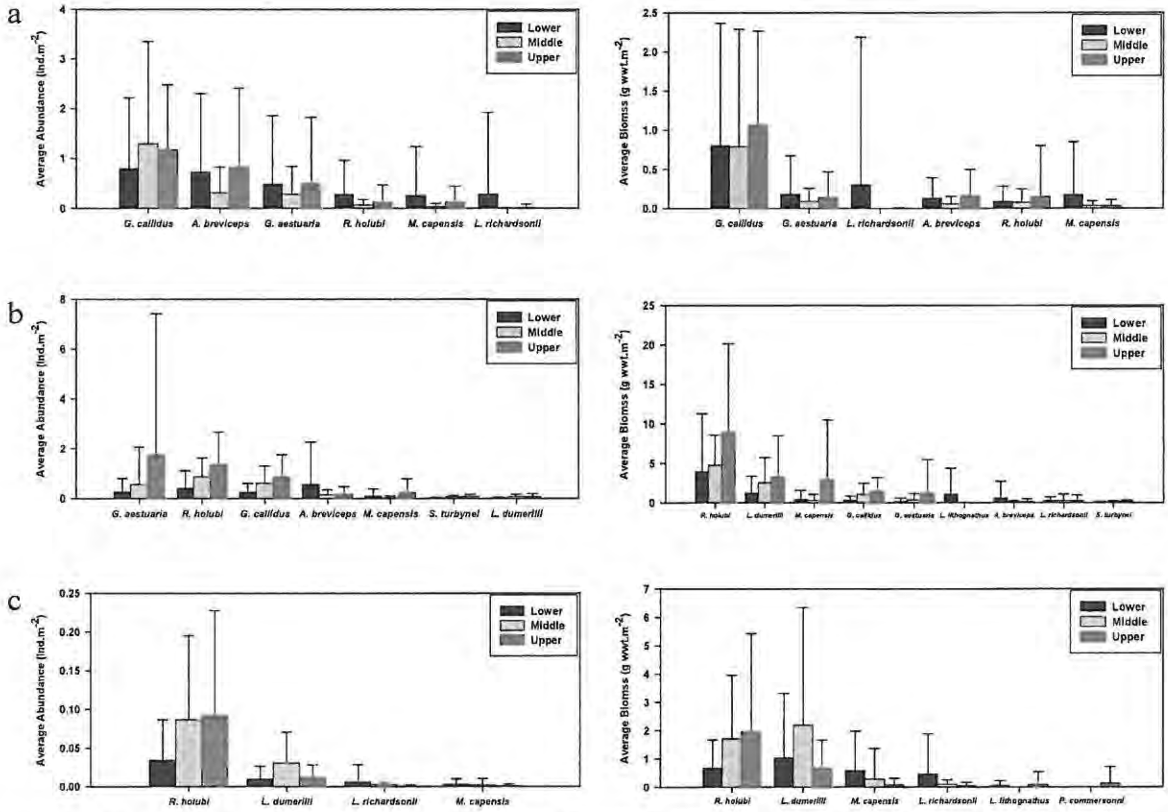

Figure 4.7: The mean abundance (ind.m^{-2}) (left column) and biomass (g wwt.m^{-2}) (right column) of (a) the seven numerically and six gravimetrically dominant juvenile/larval species, (b) seven numerically and nine gravimetrically dominant estuarine and smaller marine spawning species and (c) four numerically and six gravimetrically dominant larger marine and freshwater spawning species sampled in the upper, middle and lower reaches of the littoral zone of the Mpekweni Estuary from November 2005 to October 2007. Error bars indicate standard deviation.

4.3.2 Species diversity

4.3.2.1 Juvenile and larval ichthyofauna

The diversity and species richness of the smaller juvenile/larval fish sampled in the littoral zone displayed fairly low average values at both temporal and spatial scales (Figure 4.8). The values ranged between 0.3 and 0.9 over the initial closed period (November 2005 to July 2006). During the open period (August 2006 to December 2006) the values ranged from ~ 0.2 to 1.7. After the estuary re-closed (late December 2006), ichthyofaunal species diversity decreased gradually from 0.7 in January to 0.2 in July 2007, before slowly increasing back to 0.7 (Figure 4.8). There were significant seasonal variations for Margalef's ($F_{(3,\ 85)} = 4.462$ $p < 0.01$) and Shannon-Wiener ($F_{(3,\ 85)} = 4.46$ $p < 0.01$) indices values. Post-hoc tests revealed that species richness was significantly higher in summer and autumn and diversity values were significantly higher in summer (Tukey $p < 0.05$ in both cases). There were no significant spatial variations in species richness or diversity between stations or reaches (P > 0.05 in both cases, Figure 4.8).

4.3.2.2 Estuarine and smaller marine spawning species

There was a trend of an increase in diversity of the smaller estuarine and marine spawning ichthyofauna from the mouth to the upper reaches of the system. However, there were no significant variations for Shannon-Wiener's diversity indices ($F_{(4, 94)} = 0.49$ $p > 0.05$). Margalef's species richness indices (Figure 4.8) showed significance only on a spatial scale, with Station 1 exhibiting higher values than Station 2 ($F_{(4, 94)} = 3.64$ $p < 0.01$) (Tukey $p < 0.05$). Species richness was highest on average at the mouth station with a mean value of 1.4 while the other stations the species richness ranged from 1.0 (± 0.4 SD) to 1.2 (± 0.3 SD). Seasonally Margalef's richness indices showed that winter abundances were significantly lower than summer and autumn (Tukey $p < 0.0005$ in both cases) and spring abundances were also lower than autumn abundances ($p < 0.02$) ($F_{(3, 95)} = 13.63$ $p < 0.0000$).

Shannon-Wiener's diversity indices also revealed the same significant patterns as Margalef's richness indices, with winter values significantly lower than summer and autumn (Tukey $p < 0.01$ and Tukey $p < 0.0002$, respectively) and spring being lower than autumn (Tukey $p < 0.01$) ($F_{(3, 95)} = 9.53$ $p < 0.0002$). Diversity values fluctuated slightly (1.1 – 1.5) during the first part of the study with a drop initially during the open period, with subsequent fluctuations between 0.7 and 1.6, which subsequently levelled out at ~ 1.2 before decreasing to ~ 0.6 in June 2007, before slowly increasing again from July (0.7 ± 0.3 SD) to October 2007 (1.0 ± 0.1 SD). A comparison of the initial closed, open and re-closed periods displayed a significantly higher value for both Margalef's and Shannon-Wiener's indices in the initial closed period, compared to the re-closed period (Tukey $p < 0.05$ and Tukey $p < 0.001$ respectively) (Margalef's: [$F_{(2, 96)} = 4.94$ $p < 0.01$]; Shannon-Wiener's: [$F_{(2, 96)} = 7.31$ $p < 0.002$]). The similarity in patterns between the species richness and diversity indices highlights the importance of the breaching event on the diversity and richness of the fish species and abundance.

4.3.2.2 Larger marine and freshwater spawning species

Spatially there was a significant difference (station: $F_{(4, 82)} = 3.87$ $p < 0.01$) in the species richness (Margalef's index) of the larger marine and freshwater spawning ichthyofauna, with a post-hoc test showing higher values at Station 1 versus Station 2 (Tukey $p < 0.005$) (Figure 4.8). Although small, the average diversity values assessed show a general increase from November 2005 to February/March 2006, followed by a decrease to July 2006. The lowest diversity (Shannon-Wiener's Index) was experienced in the August 2006 immediately after the breaching estuary, with a sharp increase in December 2006. Fluctuations in diversity continued after the estuary re-closed in

December 2006 until a low value with a relatively limited standard deviation was recorded in June 2007, before increasing again (Figure 4.8). Seasonally there were higher diversity estimates ($F_{(3,95)} = 4.98$ $p < 0.005$) in summer (Tukey $p < 0.01$) and autumn (Tukey $p < 0.05$) than in winter. Species richness (Figure 4.8) was higher ($F_{(3,83)} = 3.87$ $p < 0.01$) in summer than in spring (Tukey $p < 0.005$).

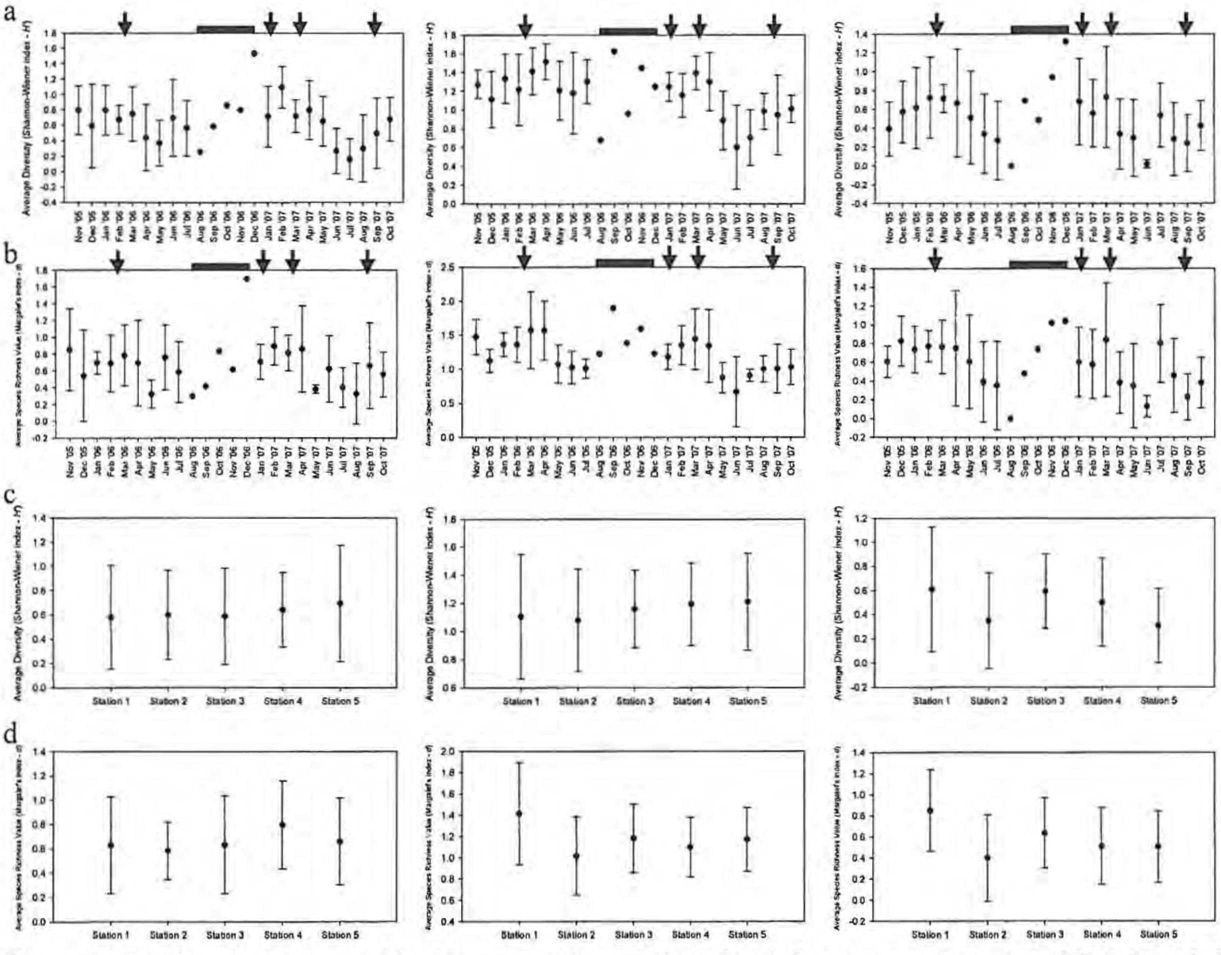

Figure 4.8: The average monthly Shannon-Wiener diversity index (a), average monthly Margalef's species richness index (b), average spatial Shannon-Wiener diversity index (c) and average spatial Margalef's species richness index (d) for the juvenile/larval ichthyofauna (left column), estuarine and smaller marine spawning species (middle column) and larger marine and freshwater spawning species (right column). Error bars indicate the standard deviation in all cases. There are no standard deviations during the open period as only a single station was sampled each month due to the shallow water depth. Vertical arrows indicate overwash events and the horizontal bar shows the period when the mouth was breached.

4.3.3 Numerical analysis

4.3.3.1 Juvenile and larval ichthyofauna

The Bray-Curtis measure of similarity was applied to the average abundance to examine spatial and temporal patterns in the littoral zone fish community structure of the Mpekweni Estuary. The MDS plot (Figure 4.9) did not display any clear evidence of seasonal patterns in the juvenile/larval ichthyofaunal community composition (Figure 4.9). A clearer separation of groupings was observed when comparing initial closed vs. open vs. re-closed periods of the estuary (Figure 4.10). The increased abundance of *R. holubi* and a decrease in the total number and contribution of EUC I species sampled during the open period was the main contributing factor to the variations in the ichthyofaunal composition between the initial closed, open and re-closed periods (Table 4.8). An ANOVA for both abundance and biomass indicated a significant variation (abundance: $F_{(2, 96)} = 5.83$ $p < 0.005$; biomass: $F_{(2, 96)} = 4.85$ $p < 0.01$) with higher abundances (Tukey $p < 0.005$) and biomass (Tukey $p < 0.01$) after the estuary had re-closed.

Spatially, the non-parametric multi-dimensional scale plot indicated the presence of two distinct groupings (Figure 4.10); Group 1 comprised the station at the mouth of the estuary (marine sand sediment) while Group 2 comprised the remaining stations (estuarine mud sediment) occupied in the middle and upper reaches of the estuary. Although the community composition varied on a spatial scale, the overall abundance and biomass values did not show any significant variation between the station at the mouth and the remaining stations (abundance $F_{(1, 97)} = 0.01$ $p > 0.05$; biomass: $F_{(1, 97)} = 0.19$ $p > 0.05$). The SIMPER analysis (PRIMER v5.4.2) indicated that the stations comprising the mud sediment group had an average similarity of ~ 85 %, with the major contributing species being *G. callidus*, *A. breviceps*, *G. aestuaria* and *R. holubi*. Differences between the marine sand sediment group and estuarine mud sediment group (Table 4.9) could largely be attributed to changes in the relative abundances of the numerically dominant species, rather than the presence or absence of individual species. The higher abundances of Mugilidae at the mouth region as well as the inverse distribution of *G. callidus* and *Psammogobius knysnaensis* were the main contributors to the dissimilarity between the two groupings. Higher abundances of *G. callidus* were recorded in the upper reaches while *P. knysnaensis* was recorded only at the mouth of the estuary on the sandy substrate.

4.3.3.2 Estuarine and smaller marine spawning species

There was no distinct seasonal pattern in the total smaller estuarine and marine spawning ichthyofaunal abundance (Figure 4.9). The MDS plots did show some grouping of the species composition for the initial closed vs. open vs. re-closed periods of the estuary (Figure 4.9) (see Table 4.10 for dissimilarity percentages between the different mouth phase groups). However, ANOVAs (STATISTICA v.8) did not show any significant differences. The outlier was August 2006: the first month that the estuary remained open. The ichthyofaunal abundance of the smaller estuarine and marine spawning species did exhibit significant correlations in terms of a decrease in abundance as the duration of the study increased, likewise in terms of the initial closed, open and re-closed periods (Appendix, Table IV).

The MDS and dendrogram plots (Figure 4.10) for the spatial distribution of the smaller estuarine and marine spawning ichthyofaunal abundance data showed limited separation at ~ 33.20 % dissimilarity level between the station at the mouth of the estuary and the remaining stations (Table 4.11). The dissimilarity between the two groups could be attributed primarily to the dominance of *G. callidus* and *S. turbynei* in the upper muddy stations, and the prevalence of *A. breviceps* at the station occupied at the mouth of the estuary (Table 4.11).

4.3.3.3 Larger marine and freshwater spawning species

There was a large amount of seasonal overlap in the MDS analysis (Figure 4.9). A greater degree of separation was evident for the initial closed vs. open vs. re-closed periods (Figure 4.9). The composition and contribution of species sampled during the open period displayed a wider spread in the MDS plot (Figure 4.9), indicating higher variability between samples. The three main larger marine and freshwater spawning species accounting for the dissimilarity between the closed and open phases were *L. richardsonii*, *L. dumerilii* and *M. capensis*, with *L. richardsonii* displaying a significantly higher abundance ($F_{(2,96)} = 10.83$ $p < 0.0001$) during the open period over the initial closed (Tukey $p < 0.0005$) and re-closed periods (Tukey $p < 0.0005$) (Table 4.12).

Spatially, there was no significant variation in the abundance ($F_{(1,97)} = 1.64$ $p > 0.05$) and biomass ($F_{(1,97)} = 0.20$ $p > 0.05$) of the larger marine and freshwater spawning ichthyofauna between the station at the mouth and the rest of the estuary, however the MDS and dendrogram plot for the fish sampled (Figure 4.10) did identify two groupings in terms of the species contribution and composition data between the sandy mouth region and the other stations (77.57 % similarity). The main contributors to the dissimilarity (37.48 %) between the two groups (Table 4.13) were *L. richardsonii*, *M. capensis* and *Lithognathus lithognathus* that showed percentage contributions of 18.87 %, 13.58 % and 13.52 %, respectively.

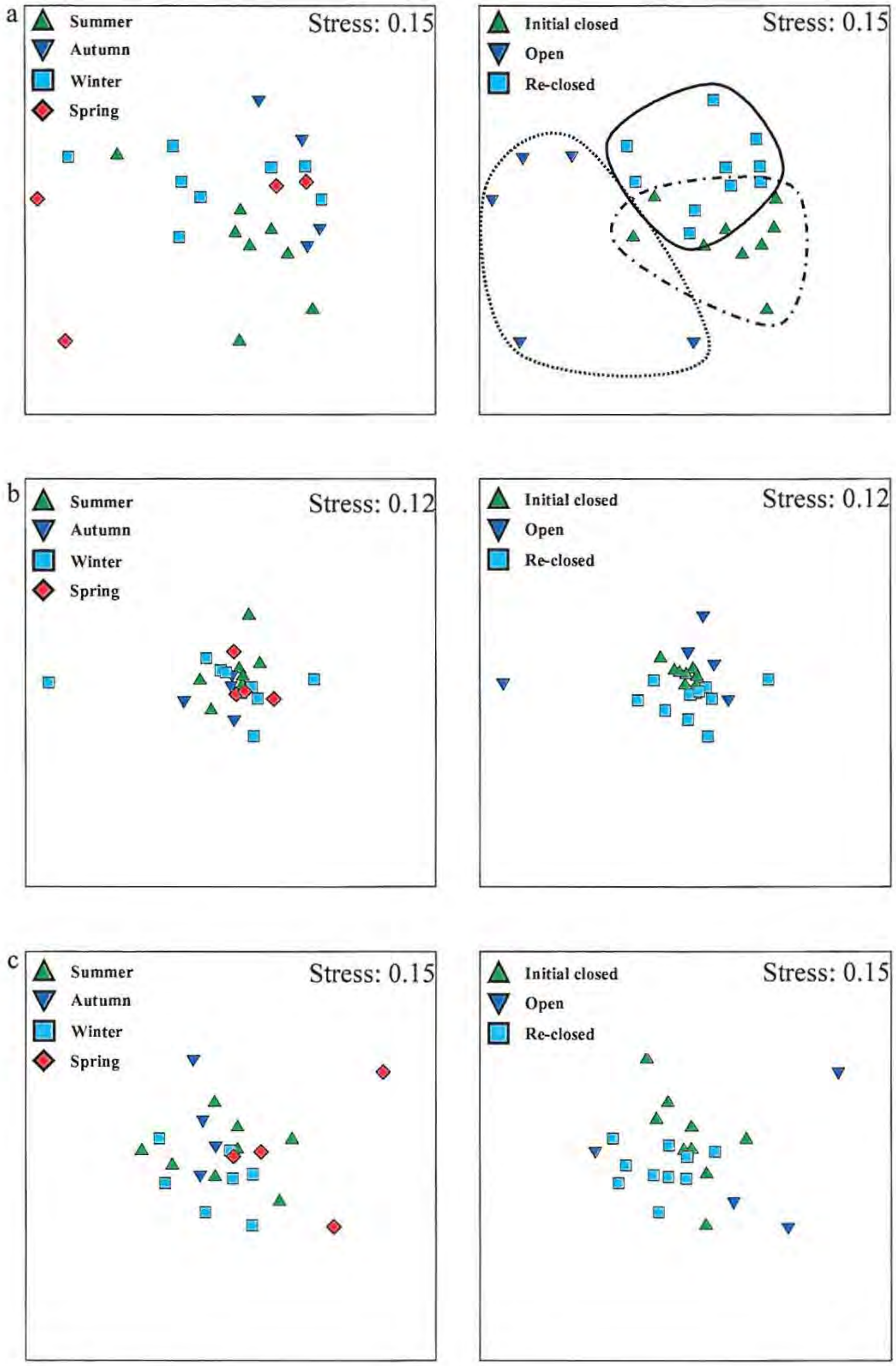

Figure 4.9: Multi-dimensional plots of the seasonal (left column) and mouth phase (right column) fish abundances (ind.m^{-2}) for the juvenile/larval ichthyofauna (a), estuarine and smaller marine spawning species (b) and larger marine and freshwater spawning species (c). The dot-dashed line indicates the initial closed period and the dotted and the dot/dashed lines indicate the open and re-closed periods.

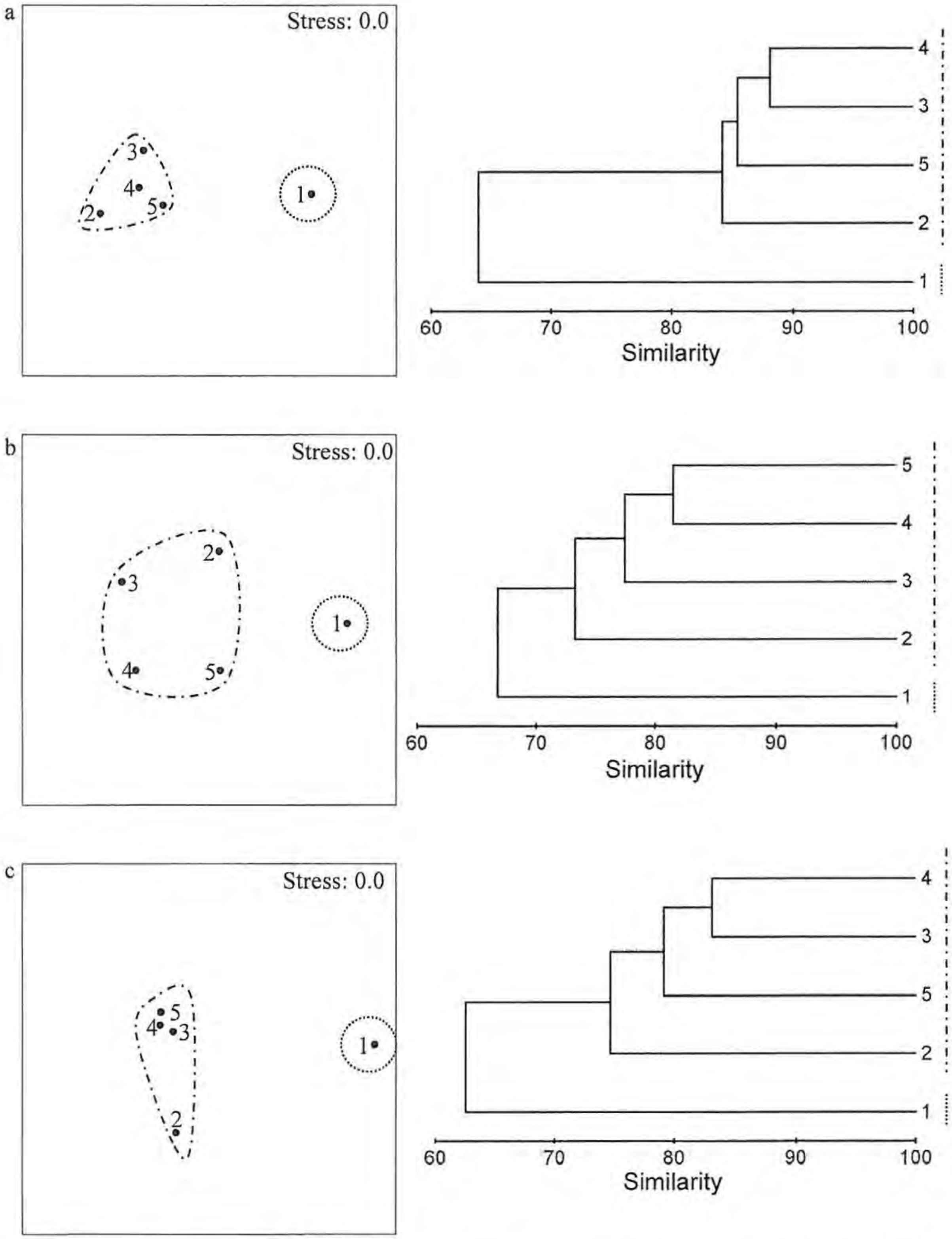

Figure 4.10: Multi-dimensional scaling plot (left column) and dendrogram (right column) of the spatial distribution (sites) for juvenile/larval fish (a), estuarine and smaller marine species (b) and larger marine and freshwater spawning species (c). The dotted line indicates the marine sand sediment group and the dotted-dashed line indicates the estuarine mud sediment group.

Table 4.8: The species contributing > 90 % of the dissimilarity between the different groupings (initial closed, open and re-closed) identified in the MDS plot (Figure 4.9) of juvenile/larval ichthyofauna sampled in the littoral zone.

Species	Initial closed period (69.09 % Similarity)	Open (44.01 % Similarity)	Dissimilarity (62.64 %)	
	Average abundance	Average abundance	Percentage contribution	Accumulative percentage
Atherina breviceps	11.25	6.40	20.38	20.38
Rhabdosargus holubi	2.00	25.40	19.54	39.92
Glossogobius callidus	20.21	6.40	16.28	56.20
Myxus capensis	3.36	2.40	13.52	69.71
Psammogobius knysnaensis	0.04	2.40	8.85	78.56
Gilchristella aestuaria	0.48	2.00	6.22	84.78
Heteromycteris capensis	0.00	3.00	5.54	90.32

Species	Initial closed period (69.09 % Similarity)	Re-closed (67.23 % Similarity)	Dissimilarity (37.59 %)	
	Average abundance	Average abundance	Percentage contribution	Accumulative percentage
Gilchristella aestuaria	0.48	21.28	21.93	21.93
Myxus capensis	3.36	4.48	18.09	40.01
Rhabdosargus holubi	2.00	4.44	16.79	56.81
Atherina breviceps	11.25	23.02	12.82	69.63
Glossogobius callidus	20.21	32.56	7.86	77.49
Liza richardsonii	0.98	5.26	6.88	84.37
Oreochromis mossambicus	0.23	0.08	4.16	88.53
Solea turbynei	0.00	0.22	2.95	91.49

Species	Open (44.01 % Similarity)	Re-closed (67.23 % Similarity)	Dissimilarity (60.57 %)	
	Average abundance	Average abundance	Percentage contribution	Accumulative percentage
Atherina breviceps	6.40	23.02	19.79	19.79
Rhabdosargus holubi	25.40	4.44	16.39	36.18
Gilchristella aestuaria	2.00	21.28	15.36	51.54
Glossogobius callidus	3.40	32.56	14.00	65.54
Myxus capensis	2.40	4.84	11.03	76.58
Psammogobius knysnaensis	2.40	0.10	8.91	85.49
Heteromycteris capensis	3.00	0.00	5.64	91.13

Table 4.9: The species contributing > 90 % of the dissimilarity between the sand sediment group and the mud sediment group of the littoral zone juvenile/larval fish (Figure 4.10).

Species	Sand sediment	Mud sediment	Dissimilarity (average = 36.08)	
	Average abundance	Average abundance	Percentage contribution	Accumulative percentage
Liza richardsonii	11.38	0.46	20.67	20.67
Gilchristella aestuaria	2.21	14.03	13.34	34.01
Rhabdosargus holubi	11.42	2.15	13.18	47.19
Myxus capensis	10.04	2.03	12.56	59.75
Glossogobius callidus	9.83	30.94	9.55	69.30
Psammogobius knysnaensis	0.79	0.00	6.56	75.85
Heteromycteris capensis	0.63	0.00	5.54	81.39
Liza dumerilii	0.71	0.05	5.32	86.70
Atherina breviceps	20.25	15.82	3.60	90.30

Table 4.10: The species contributing > 90 % of the dissimilarity between the different groupings of the estuarine and smaller marine spawning ichthyofauna (initial closed, open and re-closed periods) identified in the MDS plot (Figure 4.9).

Species	Initial closed period (79.05 % Similarity)	Open (51.13 % Similarity)	Dissimilarity (39.77 %)	
	Average abundance	Average abundance	Percentage contribution	Accumulative percentage
Atherina breviceps	82.96	103.00	12.31	12.31
Glossogobius callidus	135.98	24.20	11.70	24.01
Myxus capensis	14.04	27.20	11.37	35.38
Rhabdosargus holubi	146.06	150.80	10.92	46.30
Gilchristella aestuaria	119.87	104.20	8.92	55.22
Solea turbynei	11.48	0.80	8.47	63.69
Liza dumerilii	9.91	4.20	6.01	69.70
Liza richardsonii	5.19	6.00	5.31	75.01
Psammogobius knysnaensis	0.93	3.20	5.02	80.03
Lithognathus lithognathus	0.73	6.00	4.93	84.96
Heteromycteris capensis	0.87	3.40	4.32	89.28
Pomadasys olivaceum	0.41	2.20	1.83	91.11

Species	Initial closed period (79.05 % Similarity)	Re-closed (65.88 % Similarity)	Dissimilarity (31.10 %)	
	Average abundance	Average abundance	Percentage contribution	Accumulative percentage
Atherina breviceps	82.96	7.36	16.55	16.55
Myxus capensis	14.04	21.78	11.60	28.15
Gilchristella aestuaria	119.87	135.52	10.68	38.83
Rhabdosargus holubi	146.06	103.90	9.84	48.66
Liza dumerilii	9.91	5.44	8.28	56.95
Glossogobius callidus	135.98	35.66	7.29	61.24
Liza richardsonii	5.19	1.26	6.55	70.79
Solea turbynei	11.48	5.42	6.49	77.28
Monodactylus falciformis	0.69	0.76	2.48	79.76
Diplodus sargus capensis	0.09	0.54	2.30	82.06
Oreochromis mossambicus	0.95	0.72	2.29	84.36
Liza tricuspidens	0.16	1.16	2.14	86.50
Lithognathus lithognathus	0.73	0.32	1.64	88.14
Heteromycteris capensis	0.87	0.14	1.48	89.62
Psammogobius knysnaensis	0.93	0.12	1.36	90.99

Species	Open (51.13 % Similarity)	Re-closed (65.88 % Similarity)	Dissimilarity (45.71 %)	
	Average abundance	Average abundance	Percentage contribution	Accumulative percentage
Atherina breviceps	103.00	7.36	12.30	12.30
Myxus capensis	27.20	21.78	11.83	24.13
Rhabdosargus holubi	150.80	103.90	10.94	35.07
Gilchristella aestuaria	104.20	135.52	9.33	44.40
Glossogobius callidus	24.20	35.66	8.56	52.96
Solea turbynei	0.80	5.42	6.63	59.59
Liza dumerilii	4.20	5.44	5.73	65.32
Liza richardsonii	6.00	1.26	5.41	70.73
Psammogobius knysnaensis	3.20	0.12	5.23	75.96
Heteromycteris capensis	3.40	0.14	4.56	80.51
Lithognathus lithognathus	6.00	0.32	4.55	85.06
Diplodus sargus capensis	1.80	0.54	2.02	87.08
Pomadasys olivaceum	2.20	0.08	1.69	88.77
Monodactylus falciformis	0.00	0.76	1.61	90.38

Table 4.11: The estuarine and smaller marine spawning ichthyofaunal species contributing > 90 % of the dissimilarity between the sand sediment group and the mud sediment group (Figure 4.10).

Species	Sand sediment	Mud sediment	Dissimilarity (average = 33.20)	
	Average abundance	Average abundance	Percentage contribution	Accumulative percentage
Atherina breviceps	91.21	32.23	11.24	11.24
Glossogobius callidus	17.21	96.86	8.76	20.00
Solea turbynei	0.50	10.86	8.00	28.00
Myxus capensis	20.79	18.03	6.68	34.68
Lithognathus lithognathus	2.79	0.13	5.18	39.86
Heteromycteris capensis	2.58	0.01	5.11	44.97
Caffrogobius gilchristi	0.07	5.75	5.07	50.04
Liza tricuspidens	2.50	0.07	4.94	54.98
Psammogobius knysnaensis	2.54	0.04	4.92	59.90
Diplodus sargus capensis	1.67	0.00	3.67	63.57
Mugil cephalus	0.03	3.34	3.48	67.06
Gilchristella aestuaria	43.33	152.00	3.43	70.49
Hyporhamphus capensis	0.05	3.32	3.40	73.89
Rhabdosargus globiceps	1.38	0.00	3.14	77.03
Caffrogobius nudiceps	0.15	2.76	3.09	80.13
Liza richardsonii	3.46	3.01	2.51	82.64
Pomadasys commersonnii	0.00	3.09	2.50	85.14
Liza macrolepis	0.00	2.04	2.36	87.49
Pomadasys olivaceum	0.92	0.14	2.06	89.55
Amblyrhynchotes honckenii	0.12	0.75	1.95	91.50

Table 4.12: The species contributing > 90 % of the dissimilarity between the different groupings (initial closed, open and re-closed periods) of the larger marine and freshwater spawning species identified in the MDS plot (Figure 4.9).

Species	Initial closed period (69.02 % Similarity)	Open (49.02 % Similarity)	Dissimilarity (45.09 %)	
	Average abundance	Average abundance	Percentage contribution	Accumulative percentage
Liza richardsonii	0.96	15.00	20.29	20.29
Liza dumerilii	4.78	2.25	18.39	38.69
Myxus capensis	0.42	1.25	9.77	48.45
Lithognathus lithognathus	0.44	1.00	8.99	57.45
Solea turbynei	0.49	0.00	6.88	64.33
Oreochromis mossambicus	0.65	0.00	6.31	70.64
Rhabdosargus globiceps	0.00	0.25	5.68	76.32
Platycephalus indicus	0.00	0.25	5.68	82.00
Rhabdosargus holubi	39.57	23.75	4.05	86.05
Monodactylus falciformis	0.27	0.00	2.52	88.57
Diplodus sargus capensis	0.11	0.25	2.19	90.75

Species	Initial closed period (69.02 % Similarity)	Re-closed (74.23 % Similarity)	Dissimilarity (31.06 %)	
	Average abundance	Average abundance	Percentage contribution	Accumulative percentage
Liza dumerilii	4.78	6.68	15.91	15.91
Myxus capensis	0.42	1.04	13.68	29.60
Liza richardsonii	0.96	0.44	11.79	41.38
Solea turbynei	0.49	0.04	9.37	50.76
Oreochromis mossambicus	0.65	0.02	8.79	59.55
Lithognathus lithognathus	0.44	0.16	6.82	66.36
Rhabdosargus holubi	39.57	17.06	5.53	71.89
Mugil cephalus	0.17	0.12	4.73	76.62
Monodactylus falciformis	0.27	0.12	4.72	81.35
Glossogobius callidus	0.16	0.06	3.64	84.98
Diplodus sargus capensis	0.11	0.06	2.79	87.78
Liza tricuspidens	0.02	0.00	1.87	89.65
Caffrogobius nudiceps	0.02	0.00	1.62	91.27

Species	Open (49.02 % Similarity)	Re-closed (74.23 % Similarity)	Dissimilarity (43.22 %)	
	Average abundance	Average abundance	Percentage contribution	Accumulative percentage
Liza dumerilii	2.25	6.68	26.70	26.70
Liza richardsonii	15.00	0.44	22.18	48.88
Myxus capensis	1.25	1.04	13.12	62.00
Lithognathus lithognathus	1.00	0.16	9.36	71.36
Rhabdosargus globiceps	0.25	0.00	6.19	77.55
Platycephalus indicus	0.25	0.00	6.19	83.75
Rhabdosargus holubi	23.75	17.06	4.41	88.16
Mugil cephalus	0.00	0.12	2.88	91.03

Table 4.13: The larger marine and freshwater spawning species contributing > 90 % of the dissimilarity between the sand sediment group and the mud sediment group (Figure 4.10).

Species	Sand sediment	Mud sediment	Dissimilarity (average = 37.48)	
	Average abundance	Average abundance	Percentage contribution	Accumulative percentage
Liza richardsonii	3.71	0.45	18.87	18.87
Myxus capensis	1.83	0.42	13.58	32.45
Lithognathus lithognathus	1.00	0.11	13.52	45.97
Diplodus sargus capensis	0.38	0.00	8.61	54.58
Solea turbynei	0.00	0.33	6.39	60.97
Oreochromis mossambicus	0.00	0.39	5.69	66.66
Sarpa salpa	0.21	0.00	5.67	72.33
Liza dumerilii	4.04	6.07	4.35	76.68
Glossogobius callidus	0.00	0.13	2.98	79.66
Monodactylus falciformis	0.04	0.22	2.96	82.62
Rhabdosargus holubi	14.79	29.71	2.92	85.54
Mugil cephalus	0.13	0.21	2.45	87.99
Heteromycteris capensis	0.04	0.00	1.43	89.42
Liza tricuspidens	0.04	0.00	1.43	90.85

4.4 DISCUSSION

The Mpekweni Estuary has been the subject of a few surveys with limited temporal coverage (Vorwerk, 2001; Harrison, 2002; 2004; 2005; Vorwerk *et al.*, 2003; Harrison and Whitfield, 2006). Therefore, in comparison to other TOCEs in the same geographic region such as East Kleinemonde (Cowley, 1998; Bell *et al.*, 2001; Vorwerk, 2001; James, 2007; Whitfield *et al.*, 2008) our understanding of the temporal patterns in the dynamics of ichthyofaunal community structure within the Mpekweni Estuary is limited.

This study has increased the recorded number of species found in the estuary from an initial 25 by Vorwerk (2001) to 41 species overall with 37 species sampled during this study (36 in the seine nets and one other species in the trap [Chapter 6]). This study increased the number of families recorded in the Mpekweni Estuary from 15 (Vorwerk, 2001) to 21. The number of species recorded during this study is higher than that recorded in both TOCEs and POEs within the same geographic region (Vorwerk, 2001; Vorwerk *et al.*, 2003). In three other studies conducted in the nearby TOC East Kleinemonde Estuary, Cowley (1998) found 30 species representing 17 families. Subsequently Vorwerk (2001) and James (2007) recorded a further one and eight species, respectively, to account for a total of 39 species and 20 families within the estuary. The species found by these three authors (Cowley, 1998; Vorwerk, 2001; James, 2007) that were not recorded during the sampling of the Mpekweni Estuary were predominantly transient predatory marine species (EUC III) with a limited number sampled and the endangered estuarine pipefish (*Syngnathus watermeyeri*) which is limited to the East Kleinemonde and the Kariega estuaries (Vorwerk *et al.*, 2007). The inclusion of other gear type may have increased the number of fish species recorded in the estuary. However, a comparison of the seine net and gill net data of fish species sampled by Cowley (1998) and Vorwerk (2001) in closed TOCEs within the same geographic region failed to identify differences in the ichthyofaunal community structure sampled with the two gear types. Potter *et al.* (1990) also suggested that the inclusion of gill net data rarely changed the ranking of the abundant species and families recorded in estuaries. Thus the observed ability of the larger marine and freshwater fish species to actively avoid seine nets (Cowley, 1998; Vorwerk, 2001) is unlikely to have affected the overall species rankings of this study.

Published literature suggests that there is limited seasonal variation in the abundance and biomass of ichthyofauna within TOCEs in both the WTZ and CTZ, due to reduced recruitment opportunities (Whitfield and Kok, 1992; Cowley, 1998; Vorwerk, 2001; Vorwerk *et al.*, 2003; Lukey, 2006; James, 2007, Whitfield *et al.*, 2008; Perissinotto *et al.*, 2010a). In comparison, a weak but not significant seasonal pattern was observed in the ichthyofaunal abundances and biomass within the Mpekweni Estuary during this study. The apparent seasonal patterns in ichthyofaunal abundance/biomass observed in the Mpekweni Estuary is in contrast to Australian systems (Potter *et al.*, 1990; Pollard, 1994; Griffiths, 2001b). The high number of overwash events recorded during the summer months, which represent important recruitment opportunities for marine spawning fish species to enter the estuary (Bell *et al.*, 2001; Cowley, 1998; Cowley *et al.*, 2001; Kemp and Froneman, 2004), may have contributed to the seasonal patterns in abundance and biomass observed in this study during the closed phase of the estuary. Diversity values were also higher during the summer months, largely reflecting the increased contribution of marine spawning species to the total abundance (Figures: 4.2, 4.5, 4.7 for abundance, diversity and species composition and Table II in the Appendix for the correlations of abundance and season).

The decrease in abundance and biomass and an increase in ichthyofaunal diversity and species richness during the open phase further highlights the influence breaching events have in determining the ichthyofaunal community structure within southern African TOCEs (Cowley, 1998; Vorwerk, 2001; Tweddle, 2004; Lukey, 2006; James, 2007). Numerical analysis indicated that the breaching events coincided with a change in the ichthyofaunal community structure of the estuary, largely reflecting the decreases in abundance of the marine and estuarine spawning species within the system followed by the subsequent recruitment of marine species into the estuary (Figure 4.5 and Tables: 4.8, 4.9, 4.12). Breaching not only allows species to emigrate from the system, but also provides opportunities for others to enter the system and is not limited to the overwash specialists (Mugilidae and *R. holubi*) (James, 2007; Kemp and Froneman, 2004). The timing of the breaching event and the subsequent period when the mouth of the Mpekweni Estuary remained open coincided with the primary spawning and subsequent recruiting period of juvenile fish along the southern African coastline (Whitfield and Kok, 1992). Seasonal variation in ichthyofauna is exhibited in estuaries where breaching events are more frequent due to seasonal rainfall (Harrison and Whitfield, 1995; Bennett, 1989a). The uncharacteristic seasonal variations in the ichthyofauna identified in the Mpekweni Estuary further highlight the importance and timing of mouth opening events on the estuarine ichthyofauna.

Only fish sampled in the littoral zone of the estuary (small juvenile and larval fish) exhibited a significant increase in abundance and biomass after the estuary closed. Becker and Laurenson (2008) recorded high abundances of fish in inundated flood areas of a small Australian estuary, which was attributed to increased food availability, predator avoidance and seeking refuge from hypoxic conditions in the deeper water. The significant increase in the littoral zone ichthyofauna in the Mpekweni Estuary may be attributed to the increase in abundance of zooplanktivorous fish species subsequent to the increased inundation of the littoral zone. These species, in particular *G. aestuaria*, displayed a significant positive correlation to zooplankton abundance (Appendix, Table III). The increased abundance may have been in response to the inundation of the littoral zone, resulting in higher abundances of zooplankton and the increase in nutrients and re-suspended detritus observed in Chapter 3 (Whitfield, 1980; Winemiller and Jepsen, 1998).

The average abundance/density (1.89 ind.m^{-2}) and biomass data for the fish sampled in the Mpekweni Estuary (abundance; juvenile/larval fish: 2.65 ind.m^{-2}; smaller estuarine and marine spawning species: 2.92 ind.m^{-2}; marine and freshwater spawning species: 0.09 ind.m^{-2}) were similar to values reported for other TOCEs within the same geographic region (values ranging from ~ 2.18 ind.m^{-2} for the Bot Estuary (Bennett, 1989a) to ~ 4.27 ind.m^{-2} in the Kleinemonde Estuary (Cowley, 1998)). Interestingly, the biomass estimates (average: 5.85 g wwt.m^{-2}, juvenile/larval fish: 1.60 g wwt.m^{-2}; estuarine and marine spawning species: 12.70 g wwt.m^{-2}; marine and freshwater spawning species: 3.25 g wwt.m^{-2}) were predominantly higher than those reported in South Africa literature, which varied between 1.13 g.m^{-2} and 1.84 g.m^{-2} (Bennett and Branch, 1990; Whitfield, 1993). In the similarly located East Kleinemonde a total annual estimate of ichthyofaunal productivity provided a biomass value of 28.44 g m^{-2} (Cowley and Whitfield, 2002). Under closed conditions the actual numbers of marine species were likely to decline, although the biomass due to growth would likely increase as was evident particularly in the estuarine and smaller marine spawning species of this study (Figure 4.4.a) (Cowley and Whitfield, 2002; Whitfield *et al.*, 2008).

In South African and Australian TOCEs, breaching events generally coincide with an increase in the fish species diversity within the system due to recruitment of marine spawning and estuarine-dependant species into these estuaries (Potter *et al.*, 1990; Cowley and Whitfield, 2001; James, 2007; Whitfield *et al.*, 2008). The extended period during which the Mpekweni Estuary remained open may have resulted in a reduction in the recruitment of the larger marine spawning species due to a dilution in possible recruitment cues as a result of tidal mixing. The reduction in recruitment of the larger fish species, particularly the predatory species, may also have contributed to the higher abundances of the smaller estuarine-dependant fish species due to a possible reduction in predation. Blaber (1973) identified different population sizes of *R. holubi* in subsequent years and attributed the variation to differences in the number of piscivorous birds present.

Variations in the distribution of ichthyofauna are prominent in the larger permanently open northern hemisphere systems (Desmond *et al.*, 2002) as well as those studied in Australia (Potter & Hyndes, 1999) and South Africa (Bok, 1979; Whitfield, 1998). Here, recorded environmental and biological factors including temperature, salinity, turbidity, vegetation cover/type and seasonal movement patterns of fish species contribute to the spatial variation in ichthyofauna distribution within the larger permanently open estuaries (Whitfield, 1998; Attrill and Power, 2004). In the smaller TOCEs, the reduced/non-existent tidal effect and the shallow nature of these systems results in horizontally and vertically well mixed homogenous systems (Whitfield, 1992; 1998; Cowley, 1998; Vorwerk, 2001; Froneman, 2002a; 2002b; Tweddle, 2004; Lukey, 2006).

The virtual absence of any horizontal gradients in physico-chemical and biological variables recorded in the Mpekweni Estuary (Chapter 3) may account for the general lack of spatial stratification in abundance, biomass, species diversity and species richness patterns observed for ichthyofauna within the system during this investigation. A notable exception was recorded at the mouth of the estuary, where the numerical analysis identified a distinct ichthyofaunal community (Figure 4.10). Several previous studies (Cowley, 1998; Vorwerk, 2001; Tweddle, 2004) have shown that there is a distinct difference between the fish assemblages at the mouth of TOCEs and the rest of the estuary. Cowley (1998) attributed this difference to the sediment type at the mouth of the estuary, which are predominantly marine/sand sediments as compared to the muddy sediments throughout the rest of the estuary.

It should be noted, however, that the majority of the species accounting for the differences between the two groups in the Mpekweni Estuary are not primarily linked to sediment type (Tables: 4.9, 4.11

and 4.13) and this pattern may only apply to the closed period as the middle and upper reaches were not sampled during the open period. The species that accounted for the majority of the difference between the group at the mouth and the rest of the estuary during this study were the larger and juvenile/larval sized individuals of the marine spawning *L. richardsonii* and the small estuarine spawning *A. breviceps*. In Australian estuaries (Potter *et al.*, 1990), the Atherinidae display spatial segregation, with certain species displaying greater abundances in the lower reaches, while other species are sampled in higher abundance in the middle and upper reaches (Potter *et al.*, 1990). The same inverse distribution has been shown for several species of Gobiidae in Australian estuaries (Potter *et al.*, 1990). The fish species in the littoral zone of the Mpekweni Estuary that displayed similar inverse spatial variation/segregation were *G. callidus* and *P. knysnaensis*. Although *G. callidus* were found throughout the estuary, they exhibited a preference for the middle and upper reaches of the system (Figure 4.7). *Psammogobius knysnaensis* were restricted to the marine sediments at the mouth of the estuary. The same distribution pattern has also been shown in other estuaries in the same geographic area, viz., the East Kleinemonde (Cowley, 1998) and the Kasouga Estuary (Tweddle, 2004).

Euryhaline marine spawning species numerically dominated (51.4 %) the fish species recorded in the Mpekweni Estuary, while the estuarine and marine straggler groups contributed 24.3 % and 18.9 %, respectively to the number of species sampled. These values fall within the range reported by Vorwerk (2001) for POEs and TOCEs within the warm temperate region of South Africa (Figure 4.11). In south-western Australian TOCEs and POEs (Potter and Hyndes, 1999) the estuarine and euryhaline species generally contribute equally to the species contribution (~ 40 % - Figure 4.11). This is in stark contrast to southern African estuaries where the estuarine spawning species contribute over 50 % of the total number of species recorded in these systems (James, 2007; Vorwerk, 2001; Lukey, 2006; Tweddle, 2004; Whitfield, 1998). The elevated percentage contribution of euryhaline or marine-estuarine opportunists in the South African estuaries in comparison to Australian systems is probably attributable to the lack of sheltered inshore coastal waters that are prevalent along the Australian coastline, providing protection for juvenile teleost species (Potter *et al.*, 1990).

Since 1999, there has been an increase in the number of tropical species sampled in TOCEs within the warm temperate biogeographic zone of southern Africa (five new tropical species were recorded in the East Kleinemonde Estuary by James *et al.* [2008a]). Along the southern African coastline from the north east coast to the south west coast there is generally a distinct decrease in the number of ichthyofaunal species recorded in estuaries (Whitfield, 1994a; Maree *et al.*, 2000; Turpie *et al.*, 2000; Sink *et al.*, 2004). This pattern is attributed to colder summer maximum water temperatures in the coastal region and the upwelling events that occur along the south-east coast of southern Africa (Potter *et al.*, 1990; Whitfield and Marais, 1999; Maree *et al.*, 2000; Turpie *et al.*, 2000). The increased frequency of occurrence of tropical species within estuaries in the WTZ of South Africa has been attributed to climate change, which allows certain species to increase their distribution range (Schumann *et al.*, 1995; Mbande *et al.*, 2005; Clark, 2006; James *et al.*, 2008a).

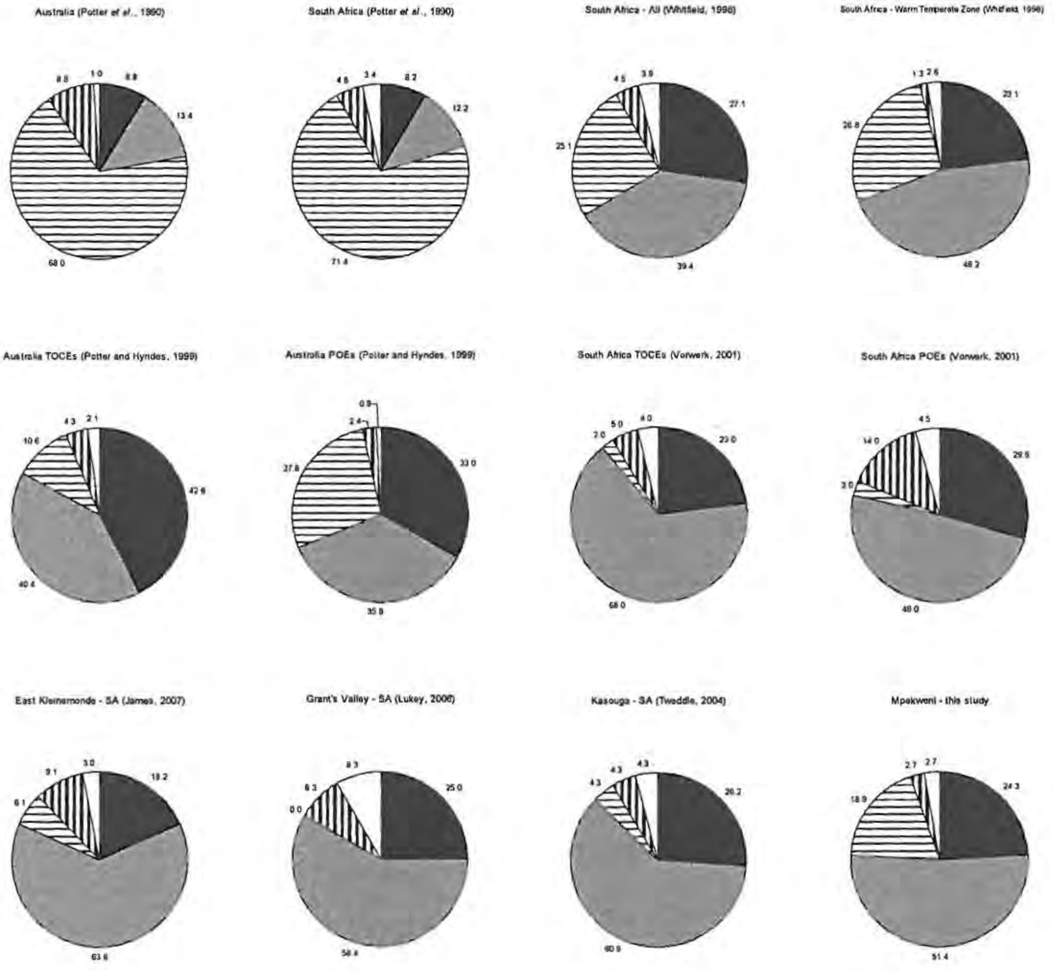

Figure 4.11: The percentage contribution of ichthyofaunal species numbers to the different estuarine utilisation groups for estuaries that are found in the Warm Temperate Zones of south-western Australia and southern Africa (see each figure for relevant reference). Black Shading – Estuarine-Dependant/Spawning species, Grey Shading – Euryhaline Marine Spawning species; Horizontal Shading – Marine Stragglers species; Vertical Shading – Freshwater species; White Shading– Catadromous species.

In the Mpekweni Estuary only two sub-tropical species were recorded, *Liza macrolepis* and *Monodactylus argenteus*. These two species have, however, been recorded as far south as the Breede River (see Lamberth *et al.*, 2008) and are likely stragglers and thus may possibly be indicators of climatic changes if observed in greater numbers. This study does, however, provide a baseline indication of what species are prevalent in this system and provide a comparison if the presence of sub-tropical and tropical species are observed in future sampling surveys.

4.4.1 Summary

The composition and abundance of ichthyofauna in Mpekweni Estuary, and in other TOCEs, has been linked to a variety of factors including temperature, salinity (Harrison, 2003) and spawning season (Whitfield, 1998; James, 2007). More recently however, breaching events have been identified as the dominant factor affecting the ichthyofauna composition in TOCEs (James *et al.*, 2008b; Whitfield *et al.*, 2008). Results of the current study highlight the importance of mouth phase in determining the ichthyofaunal species composition in the Mpekweni Estuary. The general lack of spatial variation for the fish abundance, biomass and species composition observed within the Mpekweni Estuary is consistent with previous studies conducted in TOCEs within the WTZ of southern Africa and can probably be related to the virtual absence of horizontal stratification in physico-chemical parameters.

CHAPTER 5

POPULATION STRUCTURE, RECRUITMENT PATTERNS, COHORT AND GROWTH ANALYSIS OF SELECTED ESTUARINE AND MARINE SPAWNING ICHTHYOFAUNAL SPECIES

5.1 INTRODUCTION

The analysis of length frequency data can provide important information on the population dynamics of both invertebrates and vertebrates within aquatic ecosystems (Ferguson *et al.*, 1982; Camargo and Isaac, 1998; Bernard and Froneman, 2005; Lukey, 2006; James, 2007). For example, studies of the age and growth of species are commonly employed to identify the status and strength of fish stocks within aquatic systems (El-Haweet *et al.*, 2005). In South Africa, length frequency data of specific fish species have been used to determine minimum size limits and bag limits (Vorwerk, 2001).

Permanently open estuaries experience continuous recruitment and emigration and as a result identification of specific cohorts is difficult, if not impossible (Lukey, 2006). In TOCEs, however, due to the infrequent events during which recruitment can occur, the identification of distinct cohorts is possible (Griffiths, 2001c). Several studies have utilised cohort analyses to demonstrate the importance of mouth opening/breaching as recruitment events for ichthyofauna in TOCEs. For example, Cowley *et al.* (2001) used length frequencies to retrospectively trace cohorts of fish species in a South African TOCE to specific recruitment events including overwash and breaching. In an intermittently open estuary in Australia, Griffiths (2001c) tracked and determined growth rates of juveniles of the marine spawning sparid *Acanthopagrus australis*. Similarly, James *et al.* (2007a) identified possible recruitment events of two estuarine fish species using length frequency analyses in a South African TOCE.

This chapter examines the role of both breaching and overwash events as a means of recruitment for fish species from different estuarine utilisation categories in the Mpekweni Estuary (see Chapter 1, Table 1.1) over a two year period using cohort analysis.

5.2 MATERIALS AND METHODS

Refer to Chapter 4 for the methods used to capture the fish data on which this chapter is based.

Length frequency analysis requires a large number of individuals to give an accurate representation of the population (Iversen, 1996 cited in El-Haweet *et al.*, 2005). As a consequence, only the eight numerically most abundant species sampled (as determined in Chapter 4) during this study were analysed. The eight fish species included four estuarine-resident species (*Atherina breviceps*, *Gilchristella aestuaria*, *Glossogobius callidus* and *Solea turbynei* (previously *Solea bleekeri* [Vachon *et al.*, {2005}]), three marine migrant species (*Liza dumerilii*, *L. richardsonii* and *Rhabdosargus holubi*) and one catadromous species (*Myxus capensis*). Collectively, these species accounted for 98.9 % of the total fish sampled from the littoral zone (5 m seine net), 98.4 % of the estuarine and smaller marine spawning species in the channel (30 m seine net) and 95.8 % of the larger marine and freshwater spawning channel species (50 m seine net) (see Chapter 4).

Length frequency proportions were drawn up from the data using Microsoft Excel and Sigma Plot (v.8.0). Only the data for the species accounting for > 90 % of the total abundance (individuals) in the 5 m, 30 m and 50 m seine nets were analysed. To assess the overall population length distribution of each of the selected species within the entire estuary, the data from each of the seine nets was pooled. In order to counteract the differences in selectivity of the three seine nets that include variations in mesh size, length, depth and surface area covered, the monthly length frequencies of each species from each net were standardised to an estimate of individuals per square metre (Ter Morshuizen and Whitfield, 1994) and then pooled. In order for the adjusted length frequency data to be recognised by FiSAT II (FAO-ICLARM Stock Assessment Tools II, Gayanilo *et al.* [2005]), any value in a length category had to have at least a value of one, so the adjusted CPUE data for each month's length frequency distribution was then raised to an estimate of 2000 m^2 as this was the area when the lowest adjusted abundance returned a value of at least one. Coefficient of variance estimation for CPUE (individuals per metre squared) of the individual sampling gear and the adjusted pooled data (CPUE per 2000 m^2) are shown in Table 5.1. Pooling of the data in most cases reduced monthly variations in abundance and cumulative length frequency distributions (Appendix, Figures: V and VI) of the individual and pooled data and displayed a limited overlap in the majority of length categories between the various gear types.

In order to assess the effect of the breaching event and the subsequent immigration/emigration on the population structure, the data were analysed as a whole and compared according to the three periods of mouth phase: initial closed period (November 2005 to July 2006), when the estuary breached and remained open (August 2006 to December 2006) and after the estuary had re-closed (January 2007 to October 2007),. The monthly average Standard Lengths (mm) and standard deviations for each species (those contributing > 90 % of each net) and each seine net were determined and represented graphically.

Table 5.1: The average, standard deviation and coefficient of variance (CV) of the monthly CPUE (ind.m^{-2}) estimates for each the fish species sampled by each net and the adjusted and pooled data (CPUE: ind.$2000m^{-2}$).

	Combined (ind.$2000m^{-2}$)		5 m CPUE (ind.m^{-2})		30 m CPUE (ind.m^{-2})		50 m CPUE (ind.m^{-2})	
Species	Average	CV	Average	CV	Average	CV	Average	CV
Atherina breviceps	1970.54 ± 2265.33 SD	114.96	0.61 ± 0.80 SD	132.57	0.38 ± 0.68 SD	178.65		
Gilchristella aestuaria	2440.45 ± 2854.64 SD	116.97	0.38 ± 0.70 SD	184.69	0.84 ± 1.37 SD	163.27		
Glossogobius callidus	2768.00 ± 2033.56 SD	73.47	0.90 ± 0.91 SD	101.10	0.48 ± 0.51 SD	104.75	0.0002 ± 0.001 SD	233.83
Rhabdosargus holubi	2531.55 ± 2068.43 SD	81.71	0.32 ±0.77 SD	243.31	0.89 ± 0.70 SD	79.59	0.06 ± 0.07 SD	110.59
Solea turbynei	100.38 ± 90.56 SD	90.21	0.004 ± 0.01 SD	321.6	0.05 ± 0.04 SD	90.33	0.001 ± 0.001 SD	186.50
Liza dumerilii	132.51 ± 118.27 SD	89.25	0.01 = 0.03 SD	420.00	0.05 ± 0.05 SD	104.36	0.01 ± 0.01 SD	87.71
Liza richardsonii	270.78 ± 885.10 SD	326.87	0.10 ± 0.43 SD	420.57	0.03 ± 0.03 SD	133.38	0.01 ± 0.03 SD	372.39
Myxus capensis	579.74 ± 815.21 SD	140.62	0.15 ± 0.28 SD	182.94	0.14 ± 0.25 SD	180.42	0.002 ± 0.003 SD	136.33

Length at age estimates were taken from the following sources: *A. breviceps* (Ratte, 1989), *G. aestuaria* (Ratte, 1989; Talbot, 1982), *G. callidus* (Boullé, 1989 cited in Vorwerk, 2001), *L. dumerilii* (van der Horst and Erasmus, 1981), *L. richardsonii* (de Villiers, 1987), and *R. holubi* (Beckley, 1984; Cowley, 1998; Vorwerk, 2001). *Solea turbynei* was estimated from van Schie and de Boer (2003) and *M. capensis* was determined from Bok (1984 cited in Whitfield, 1998).

5.2.1 Cohort and growth parameters

The analyses of the different species for growth parameters, longevity and growth performance and mortality parameters were conducted on the length data (Standard Length, SL, to the nearest millimetre) from all of the seine net data (Gayanilo *et al.*, 2005).

The growth of all the fish species was assumed to follow the von Bertalanffy Growth Function (VBGF) ($L_t = L_\infty[1\text{-}\exp(-K(t\text{-}t_0))]$). The estimates of asymptotic length (L_∞) and the growth coefficient (K) were determined using the ELEFAN routine in FiSAT II (FAO-ICLARM Stock Assessment Tools II, Gayanilo *et al.* [2005]). The estimates of theoretical age at length zero (t_0) were calculated in Excel employing Pauly's (1979) equation (Ofori-Danson *et al.*, 2001):

$$\log_{10}(-t_0) = -0.392 - 0.275 \log_{10}L_\infty - 1.038 \log_{10}K$$

The longevity was calculated from Pauly's (1984) equation: $t_{\max} = 3/K$ (Ofori-Danson *et al.*, 2001). The growth performance index or phi-prime index (ϕ') was determined in FiSAT II, which utilises Pauly and Munro's (1984) equation (Koranteng *et al.*, 2000; Garcia *et al.*, 2008):

$$\phi' = \log_{10}K + 2 \log_{10}L_\infty$$

The observed extreme length (OEL) and predicted extreme length (PEL) were estimated using FiSAT II. Total annual instantaneous mortality rates (*Z*), were estimated using two different methods; from the length frequency data using the length-converted catch curve application and the Jones and van Zalinge plot in FiSAT II. Two methods were used due to the known limitations of these regression analyses and other analyses. The Chapman and Robson (1960) equation gives an estimate of Z with a lower root mean squared error than regression analyses (Dunn *et al.*, 2002), However the data in this study does not include the necessary age-length conversion data and all the values determined by FiSAT II are estimates. Dunn *et al.* (2002) did identify that regression analyses returned lower root mean squared errors in data with high levels of error in ageing data and when levels of variation in recruitment were high. It must be noted that the fish analysed from this system are not targeted commercially and due to the limited development along the banks there is very limited recreational fishing. Thus, because $Z = F + M$ (Pauly, 1980) with no/limited fishing ($F = 0$), natural mortality (M) estimates are assumed to be the same as Z (Pauly, 1983). These data are presented purely to show the differences in the survivability estimates of the different estuarine utilisation categories.

Recruitment estimates were determined by inverting the relative percentage results from the Recruitment Pattern application in FiSAT II. As a stock assessment package, FiSAT II, estimates recruitment for maximum yield/fishing, a basic assumption was made that, by inverting the relative percentages an approximation of the recruitment by the smaller larval/juvenile fish was estimated. The resulting recruitment patterns exhibited were similar to those of larval and juvenile fish species observed and reported by Whitfield (1990) and Whitfield and Kok (1992). The results are treated as approximations as they are based on two assumptions that are rarely met in reality: (i) all fish in the sample grow as described by a single set of growth parameters and (ii) one month out of twelve always has zero recruitment (in regards to the fish entering the fisheries) (Gayanilo *et al.*, 2005). As a comparison, diagrammatic representations of the known immigration and spawning periods of the eight species in the Eastern Cape region (Whitfield, 1998) are provided below the recruitment graphs for each species. The gray kite diagrams represent the known immigration periods while the overlaid lines with diamond shaped ends indicate the spawning period.

The total monthly CPUE (ind.m^{-2}) of each species were plotted for each seine net and the total combined and adjusted numbers (ind.$2000m^{-2}$) to show the number of fish used each month for the cohort analysis (James *et al.*, 2007a).

To determine the monthly growth increments (mm.month^{-1}) of each species, the Bhattacharya Method (in FiSAT II) was used to estimate the computed mean of the various cohort peaks in the length frequency distributions (Bhattacharya, 1967). The Bhattacharya estimates of the means were then adjusted using the NORMSEP (Hasselblad, 1966; Pauly and Caddy, 1985) application in FiSAT II (Gayanilo *et al.*, 2005). The "computed means" of clearly identifiable cohorts were tracked through each month and the incremental differences between the monthly means were averaged for each species, providing a monthly growth estimate (mm.month^{-1}) (Bennett, 1989a).

The parameter estimates for each of the species in the different estuarine utilisation groups are presented separately.

5.3 RESULTS

5.3.1 *Atherina breviceps*

The number of *Atherina breviceps* sampled from the littoral zone (juvenile and larval ichthyofauna) (Figure 5.1.a) during the re-closed period (January 2007 to October 2007) was over twice that sampled during the initial closed period from November 2005 to July 2006. The modal size class for the re-closed period (Figure 5.1.a.iv) was two size classes smaller than the initial closed period data (Figure 5.1.a.ii), indicating an emigration or mortality of the larger *A. breviceps* followed by recruitment of younger age classes. The size classes during the re-closed period covered a wider range (< 5 mm – 55 mm SL) than for the initial closed period (10 mm – 50 mm SL). During the open period (Figure 5.1.a.iii) all of the fish (32) sampled were between 35 mm and 55 mm SL, with no larval or juvenile fish present.

In the estuarine and smaller marine spawning ichthyofauna from the channel (Figure 5.1.b), most of the *A. breviceps* sampled were over 1 year old with 61.5 % of the fish sampled in the initial closed period were > 40 mm SL (Figure 5.1.b.ii). During the re-closed period (Figure 5.1.b.iv) 86.1 % of the fish were > 40 mm SL (length at age 1yr). During the open period the +1 yr group accounted for 89.9 % of the fish sampled (Figure 5.1.b.iii). After breaching and during the re-closed period, the total abundance for the 30 m net comprised only 22 % of the *A. breviceps* sampled during the initial closed period.

Overall, two modal size classes for *A. breviceps* were identified: 15 – 20 mm and 40 –°50 mm. The 25 – 30 mm and 45 – 50 mm classes numerically dominated the initial closed period, the open period was dominated by the fish ranging from 40 – 50 mm and in the re-closed period the 15 – 20 mm class was most prominent.

The average lengths of *A. breviceps* sampled each month are shown in Figure 5.2. No *A. breviceps* were sampled during the first month of the estuary being open (August 2006). After the estuary re-closed, the juvenile and larval fish sampled in the littoral zone were smaller (18.54 mm SL ± 8.05) than the fish sampled during the initial closed period (27.26 mm SL ± 6.21). The individuals sampled from the channel were larger after the estuary had closed (45.20 mm SL ± 5.92) than during the initial closed period (40.90 mm SL ± 8.59).

The original (ind.m^{-2}) and adjusted CPUE (ind.2000m^{-2}) estimates of *A. breviceps* sampled during each month are shown in Figure 5.3. Monthly growth increments of the adjusted and pooled data were estimated at 1.84 mm.month^{-1} (Table 5.2).

The length frequency distributions for *A. breviceps* were used to estimate the von Bertalanffy growth parameters K (0.81), L_∞ (70.88 mm) and t_0 (Table 5.2), which were plotted ($L_t = 70.88[1-\exp(-0.81(t-t_0))]$) on to Figure 5.4.

Other growth parameters: t_{max}, ϕ', OEL and PEL are provided in Table 5.2. The growth performance index (ϕ') gave a value of 3.61 and a predicted maximum length of 71.79 mm. Instantaneous total (Z) mortality rates calculated using length-converted catch curves and the Jones and van Zalinge plots were 3.16 year^{-1} and 3.90 year^{-1}, respectively (Table 5.2).

The recruitment patterns for the juvenile *A. breviceps* estimated for each sampling year showed an extended period of recruitment of *A. breviceps* primarily from the mid winter months (July/August) till the end of summer (February) or autumn months (March/April) (Figure 5.5). The lowest estimates of recruitment were between April and May 2007, coinciding with the winter period. Maximum recruitment was recorded during the spring and summer months (November 2005 to February 2006; September 2006 to February 2007) and minimum in winter (May 2006 to August 2006 and April/May 2007).

Table 5.2: The von Bertalanffy Growth Function, longevity, growth performance and mortality parameters were estimated using FiSAT from the pooled length frequency data of the species *Atherina breviceps*, *Gilchristella aestuaria*, *Glossogobius callidus* and *Rhabdosargus holubi*. * Average of multiple estimates of Z determined from the catch-curve.

Description of parameter	**Parameter**	***Atherina breviceps***	***Gilchristella aestuaria***	***Glossogobius callidus***	***Rhabdosargus holubi***
Von Bertalanffy growth function	L_∞ (SL, mm)	70.88	70.88	118.13	225.75
	K (year^{-1})	0.81	0.65	0.45	0.21
	t_0 (years)	-0.16	-0.20	-0.25	-0.46
Longevity	T_{max} (years)	3.70	4.62	6.67	14.29
Growth Performance Index	ϕ'	3.61	3.51	3.80	4.03
Average Monthly Growth Increments (mm.month^{-1})		1.87	2.17	2.79	4.09
Observed Extreme Length (mm)		67.50	67.50	112.50	215.00
Predicted Extreme Length (mm)		71.79	71.62	119.02	-
Mortality Z (year^{-1}) (r^2) [as a percentage]	Catch Curve Regression	3.16 (0.94) [96 %]	3.14 (0.95) [96 %]	2.15 (0.93) [88 %]	1.53 (0.94) [78 %]
Mortality Z (year^{-1}) (as a percentage)*	Catch Curve Regression	3.68 (97 %)	2.66 (93 %)	1.56 (79 %)	1.11 (67 %)
Mortality Z (year^{-1}) (r^2) [as a percentage]	Jones and van Zalinge Plot	3.90 (0.93) [98 %]	4.59 (0.95) [99 %]	4.67 (0.95) [99 %]	5.21 (0.89) [99 %]
Mortality Z (year^{-1}) (as a percentage)*	Jones and van Zalinge Plot	4.91 (99 %)	4.53 (99 %)	3.51 (97 %)	3.39 (97 %)

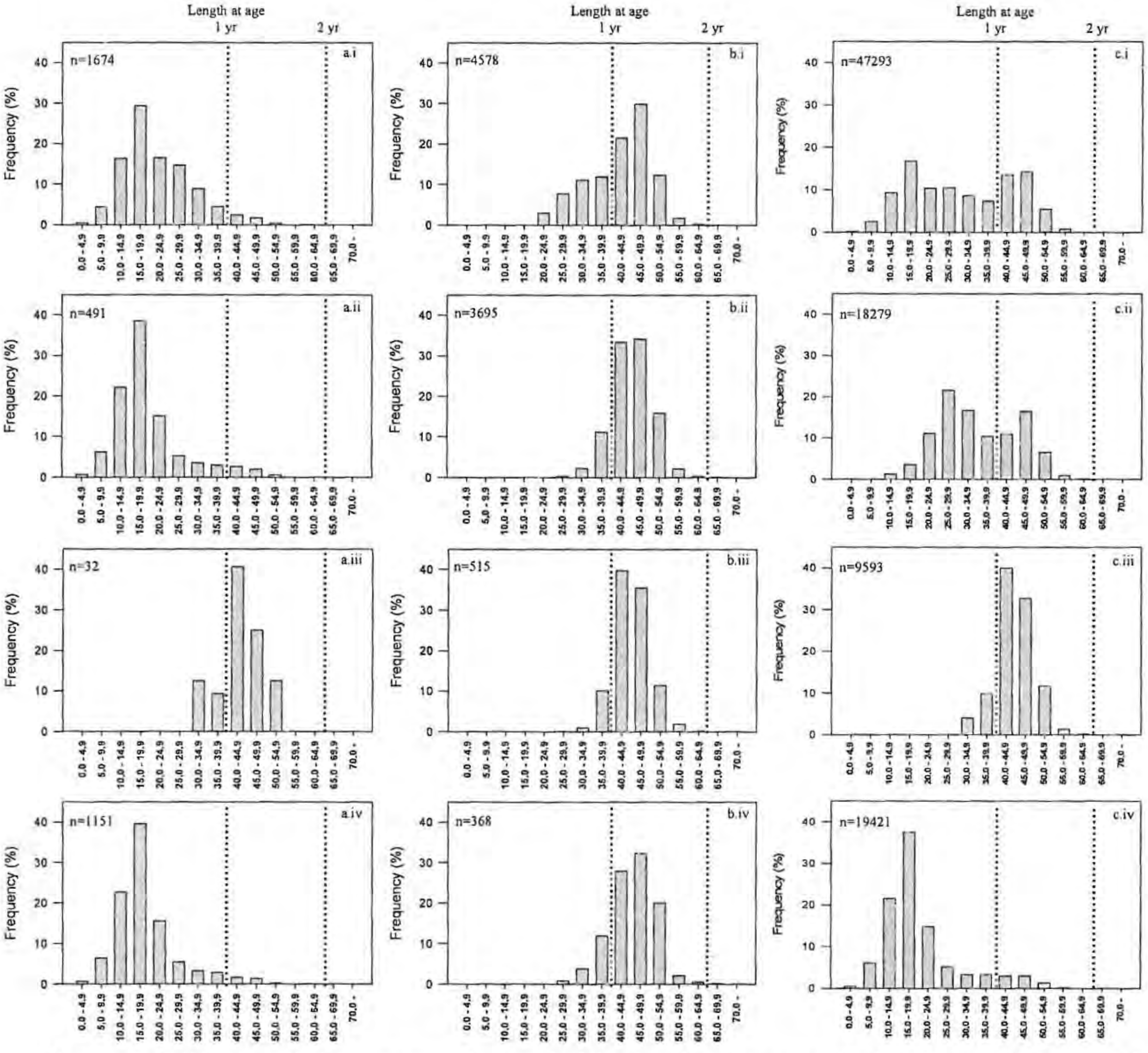

Figure 5.1: The length frequency cohorts of *Atherina breviceps* in the Mpekweni Estuary. (a) and (b) represent the data recorded from the 5 m and 30 m seine nets. The adjusted and pooled data are represented by (c). The combined cohorts are shown in each graph labelled .i for each seine net. The initial closed, open and re-closed periods are represented by .ii, .iii and .iv. Dotted lines indicate estimated length at age.

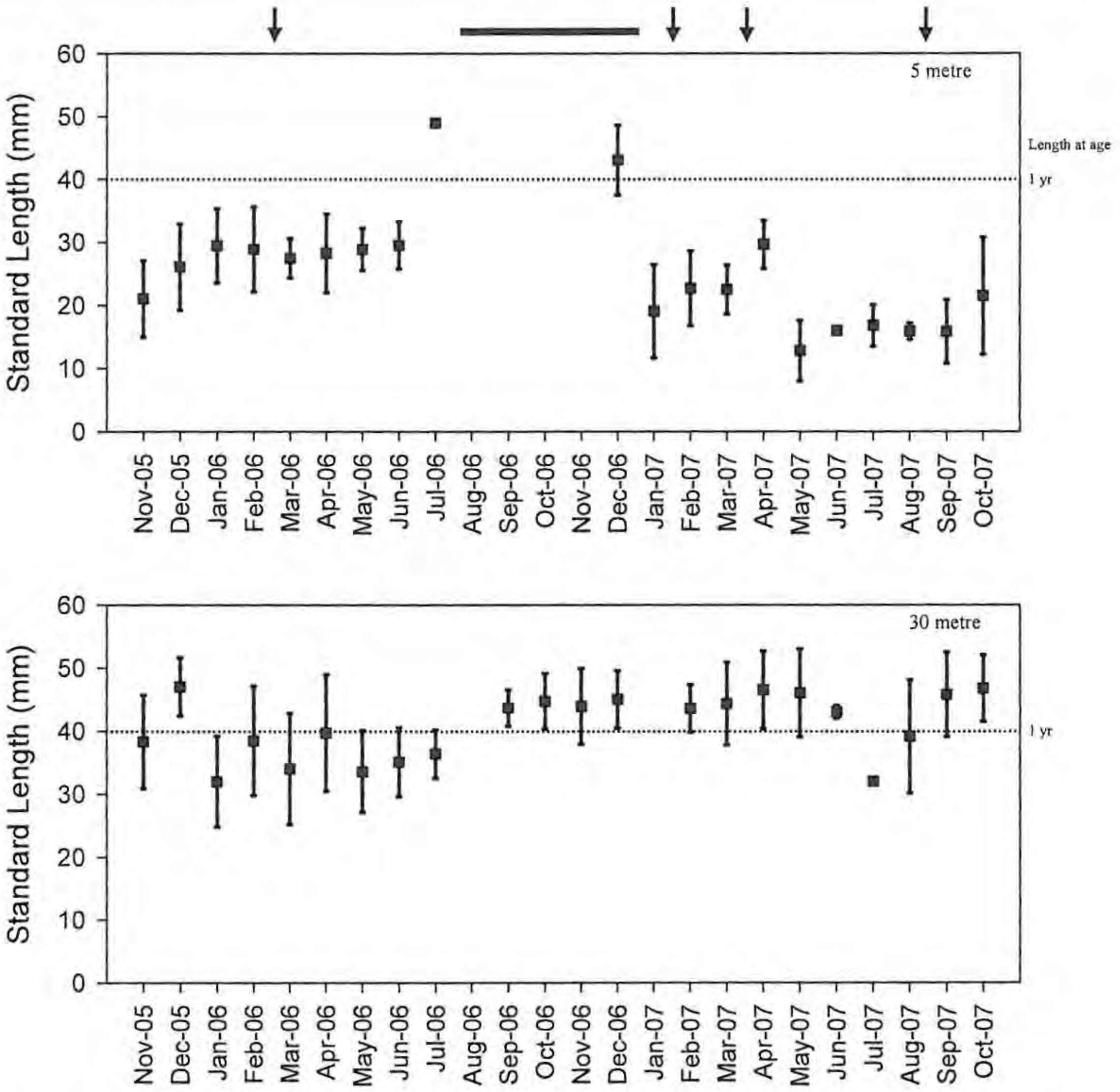

Figure 5.2: The average length (± SD) of *Atherina breviceps* recorded for each month in the Mpekweni Estuary. The top and bottom graphs show the fish sampled using the 5 m and 30 m seine nets, respectively. Dotted lines indicate estimated length at age. The bar indicates the period when the mouth was open and the arrows, overwash events. No data points indicate that no fish were sampled during that month.

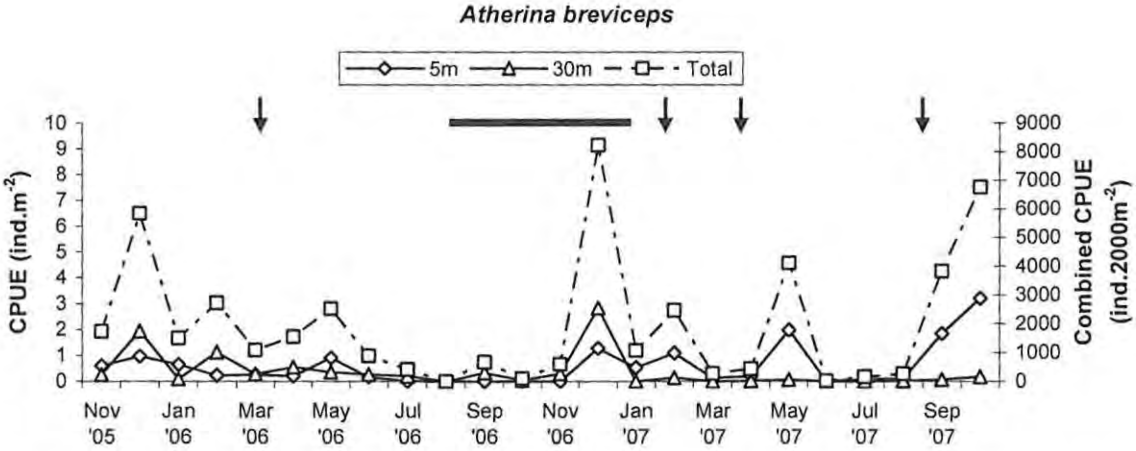

Figure 5.3: The CPUE (ind.m^{-2}) of *Atherina breviceps* sampled by each seine net for each month and the adjusted and pooled CPUE (ind.2000m^{-2}). The bar indicates the period when the mouth was open and the arrows, overwash events.

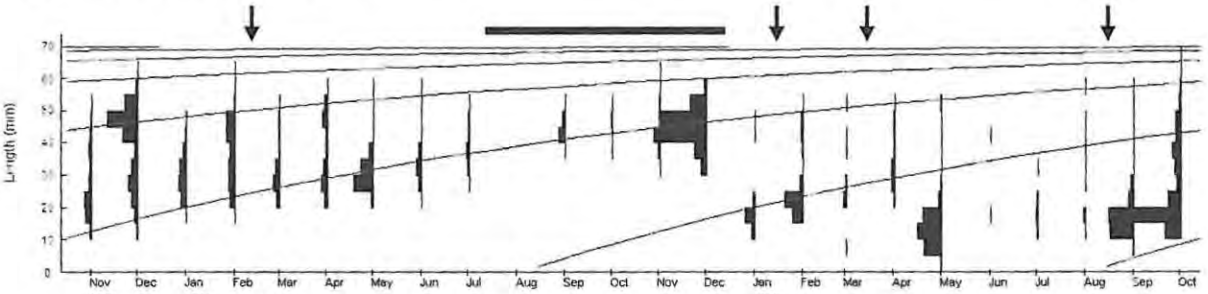

Figure 5.4: The monthly length frequencies and von Bertalanffy Growth Function curves for *Atherina breviceps* determined by ELEFAN I in FiSAT II. See Table 5.2 for calculated L_∞ and K values. The bar indicates the period when the mouth was open and the arrows, overwash events.

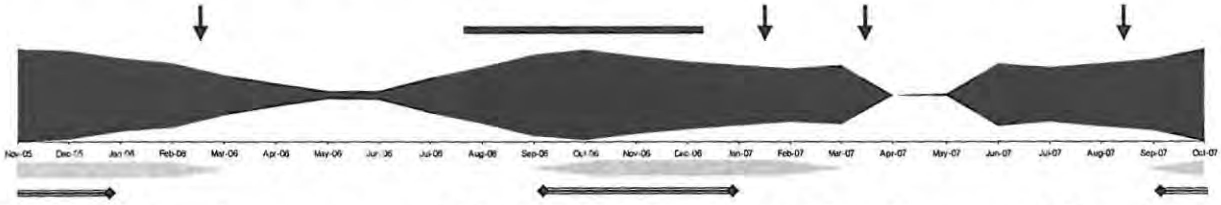

Figure 5.5: Recruitment patterns of *Atherina breviceps* calculated from November 2005 to October 2007 using FiSAT II. The bar indicates the period when the mouth was open and the arrows, overwash events.

5.3.2 *Gilchristella aestuaria*

The *G. aestuaria* sampled in the littoral zone recorded a modal size class of 25 - 30 mm SL (Figure 5.6.a.i). Only 21 individuals were sampled in the littoral zone during the initial closed period (November 2005 to July 2006) (Figure 5.6.a.ii). During the period when the mouth of the estuary was open, ten individuals were sampled of which half were over the year one age class (Figure 5.6.a.iii). After the estuary mouth re-closed (January 2007 to October 2007) (Figure 5.6.a.iv) 1064 individuals were sampled, the majority of which were in the < 5 mm – 35 mm age class, < 1 year old (97.7 %) (Figure 5.6.a.iv). During the initial closed period and overall the *G. aestuaria* sampled from the channel were in the modal size class just below the 1 year age length (Figures: 5.6.b.i and 5.6.b.ii). During the open and re-closed periods (Figures: 5.6.b.iii and 5.6.b.iv) the modal size of *G. aestuaria* was above the length at age (year 1). The pooled and adjusted length frequencies identified a modal class ranging from 25 – 35 mm overall and during the closed periods, however, during the open period the mode was one size class higher.

The average lengths of *G. aestuaria* sampled each month are shown in Figure 5.7, there was a wide variation in sizes and monthly variability of records for the larval/juvenile individuals, however, the larger individuals from the channel were recorded throughout the study period. The original ($ind.m^{-2}$) and adjusted CPUE ($ind.2000m^{-2}$) estimates of *G. aestuaria* sampled during each month are shown in Figure 5.8. A growth increment of 2.17 $mm.month^{-1}$ was estimated using the adjusted and pooled data (Table 5.2).

The length frequency distributions for *G. aestuaria* were used to estimate the von Bertalanffy growth parameters K (0.65), L_∞ (70.88 mm) and t_0 (Table 5.2), which were plotted ($L_t = 70.88[1-\exp(-0.65(t-t_0))]$) on to Figure 5.9.

Other growth parameters: t_{max}, ϕ', OEL and PEL are provided in Table 5.2. The growth performance index (ϕ') was calculated at 3.36 and a maximum length of 71.62 mm was predicted. Instantaneous total (Z) mortality rates calculated using length-converted catch curves and the Jones and van Zalinge plots were 3.14 $year^{-1}$ and 4.59 $year^{-1}$, respectively (Table 5.2).

Gilchristella aestuaria showed variable recruitment throughout the duration of the study, with the majority of the spawning and recruitment occurring between the months of July through to January. The lowest estimates of recruitment were observed in the colder months between February and June (Figure 5.10).

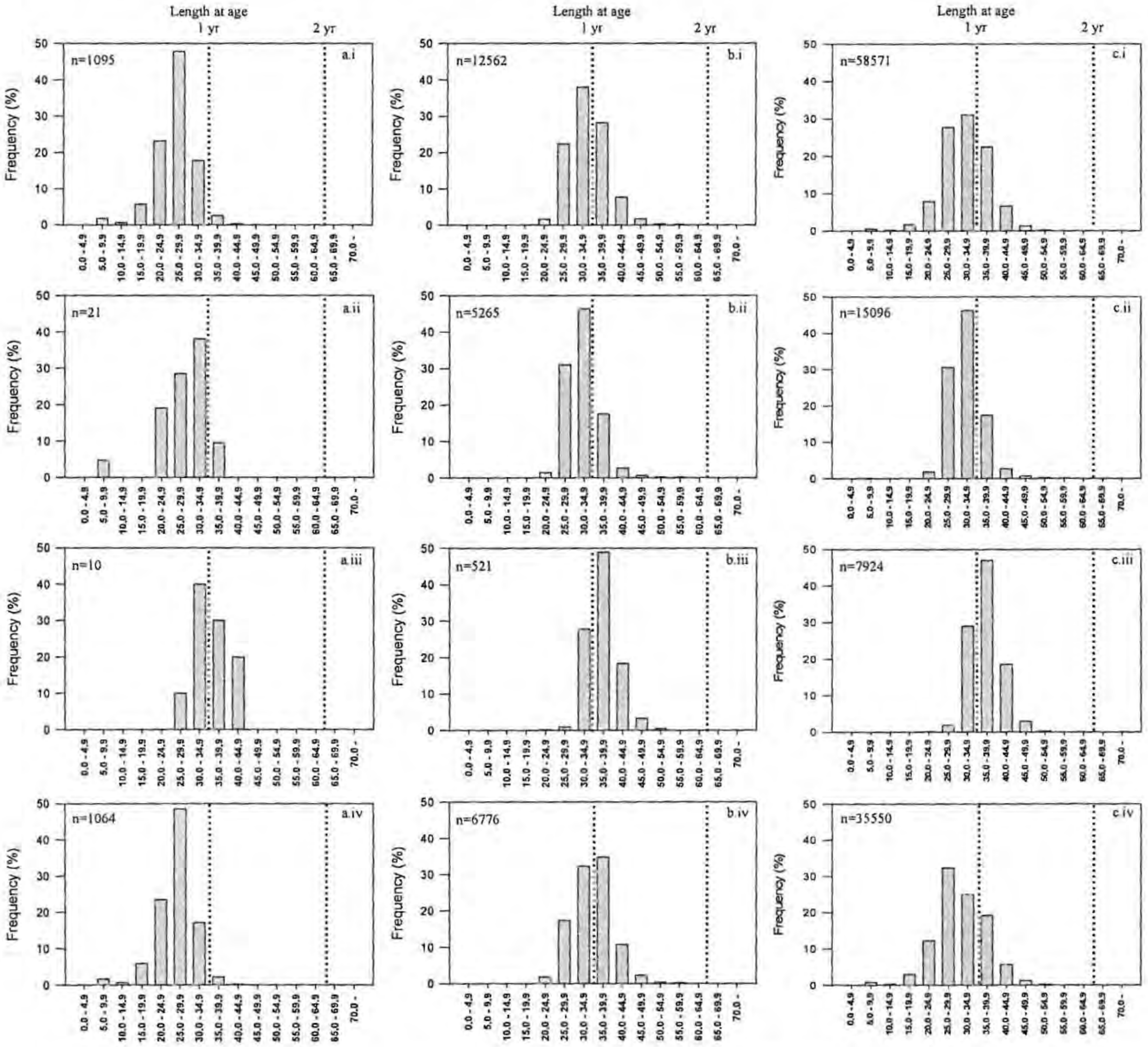

Figure 5.6: The length frequency cohorts of *Gilchristella aestuaria* in the Mpekweni Estuary. (a) and (b) represent the data recorded from the 5 m and 30 m seine nets. The adjusted and pooled data are represented by (c). The combined cohorts are shown in each graph labelled .i for each seine net. The initial closed, open and re-closed periods are represented by .ii, .iii and .iv. Dotted lines indicate estimated length at age.

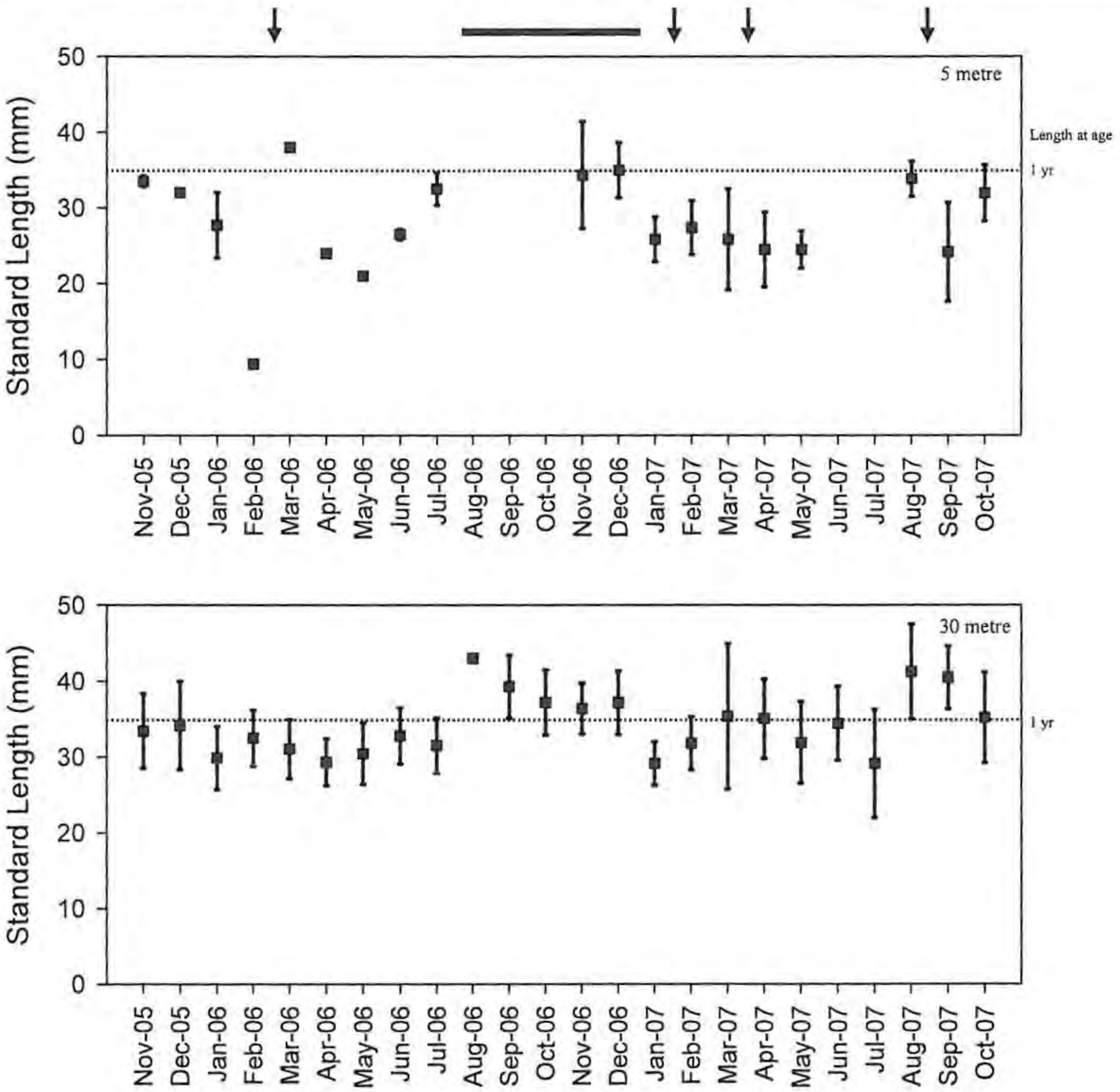

Figure 5.7: The average length (± SD) of *Gilchristella aestuaria* recorded for each month in the Mpekweni Estuary. The top and bottom graphs show the fish sampled using the 5 m and 30 m seine nets respectively. Dotted lines indicate estimated length at age. The bar indicates the period when the mouth was open and the arrows, overwash events. No data points indicate that no fish were sampled during that month.

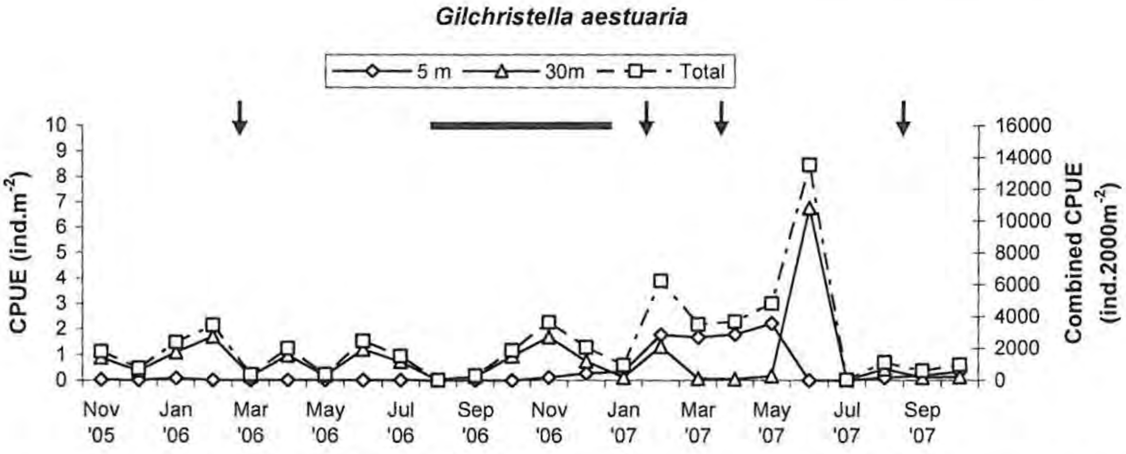

Figure 5.8: The CPUE (ind.m^{-2}) of *Gilchristella aestuaria* sampled by each seine net for each month and the adjusted and pooled CPUE (ind.2000m^{-2}). The bar indicates the period when the mouth was open and the arrows, overwash events.

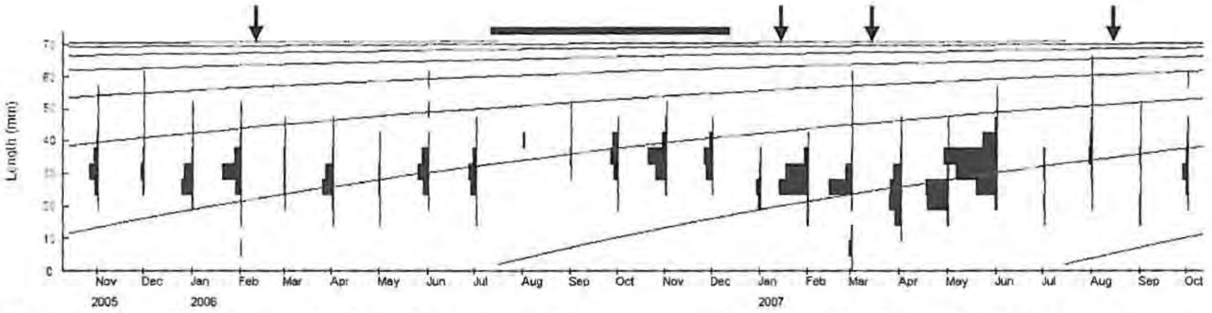

Figure 5.9: The monthly length frequencies and von Bertalanffy Growth Function curves for *Gilchristella aestuaria* determined by ELEFAN I in FiSAT II. See Table 5.2 for calculated L_∞ and K values. The bar indicates the period when the mouth was open and the arrows, overwash events.

Figure 5.10: Recruitment patterns of *Gilchristella aestuaria* calculated from November 2005 to October 2007 using FiSAT II. The bar indicates the period when the mouth was open and the arrows, overwash events.

5.3.3 *Glossogobius callidus*

Glossogobius callidus demonstrated a normally distributed length frequency pattern for the pooled data of the populations sampled from the littoral zone and channel (Figure 5.11.c.i). Sampling of the littoral zone of the estuary suggests that *G. callidus* utilising this part of the estuary were mostly (70 %) < 1 year old (Figure 5.11.a.i). In the re-closed period, almost double the numbers of fish were sampled from the littoral zone in comparison to the initial closed period (895 individuals or 99 ind.month^{-1} [Figure 5.11.a.ii] versus 1628 individuals or 163 ind.month^{-1} [Figure 5.11.a.iv]). The peak size classes of *G. callidus* sampled from the littoral zone during the initial closed period ranged across a number of size classes: 20 mm – 40 mm (SL), while the length data from the fish sampled during the re-closed period displayed a more normally distributed population structure. The larger *G. callidus* sampled from the channel were mostly (60 %) 1 – 2 years old and displayed a normally distribution (Figure 5.11.b.i). Over three times as many *G. callidus* were sampled in the channel during the initial closed period in comparison to the re-closed period (Figure 5.11.b.ii versus Figure 5.11.b.iv). The pooled data identified a single modal normal size distribution during the initial closed period, however, during the re-closed period two modal peaks were evident.

The average size of *Glossogobius callidus* sampled in the littoral (overall average 34.20 mm, Table 4.2, in Chapter 4) and channel (overall average 44.41 mm, Table 4.4, in Chapter 4) nets demonstrated a cyclic increase and decrease on a monthly basis throughout the study period (Figure 5.12: top). The larger *G. callidus* sampled from the channel displayed an increase in the average length of the fish during the open period in comparison to the months when the estuary was closed (Figure 5.12: bottom).

The original (ind.m^{-2}) and adjusted CPUE (ind.2000m^{-2}) estimates of *G. callidus* sampled each month are shown in Figure 5.13. The estimated monthly growth rate for the adjusted and pooled data was calculated at 2.79 mm.month^{-1} (Table 5.2).

The length frequency distributions for *G. callidus* were used to estimate the von Bertalanffy growth parameters K (0.45), L_∞ (118.13 mm) and t_0 (Table 5.2), which were plotted ($L_t = 118.13[1\text{-exp}(-0.45(t\text{-}t_0))]$) on to Figure 5.14.

Other growth parameters: $t_{\max}$, ϕ', OEL and PEL are provided in Table 5.2. The growth performance index (ϕ') was calculated at 3.80 and a maximum length of 119.02 mm was predicted.

Instantaneous total (*Z*) mortality rates calculated using length-converted catch curves and the Jones and van Zalinge plots were 2.15 year^{-1} and 4.67 year^{-1}, respectively (Table 5.2).

Recruitment patterns for *G. callidus* estimated for each year (Figure 5.15) demonstrated that the highest estimates of recruitment occurred in the summer months of October to December in both years. In 2006 the lowest estimate occurred in March while in 2007 the months of March to June showed the lowest recruitment (Figure 5.15).

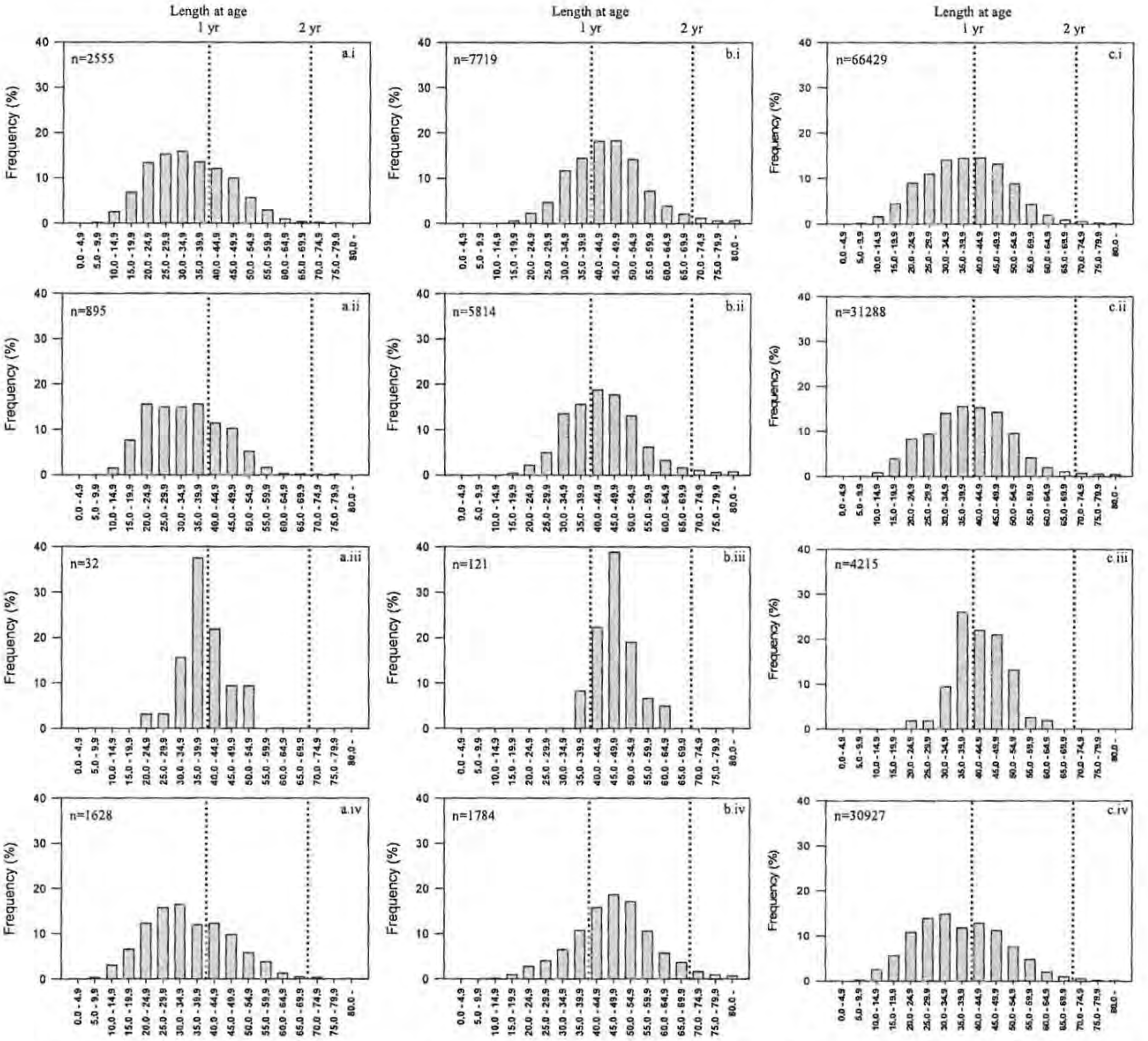

Figure 5.11: The length frequency cohorts of *Glossogobius callidus* in the Mpekweni Estuary. (a) and (b) represent the data recorded from the 5 m and 30 m seine nets. The adjusted and pooled data are represented by (c). The combined cohorts are shown in each graph labelled .i for each seine net. The initial closed, open and re-closed periods are represented by .ii, .iii and .iv. Dotted lines indicate estimated length at age.

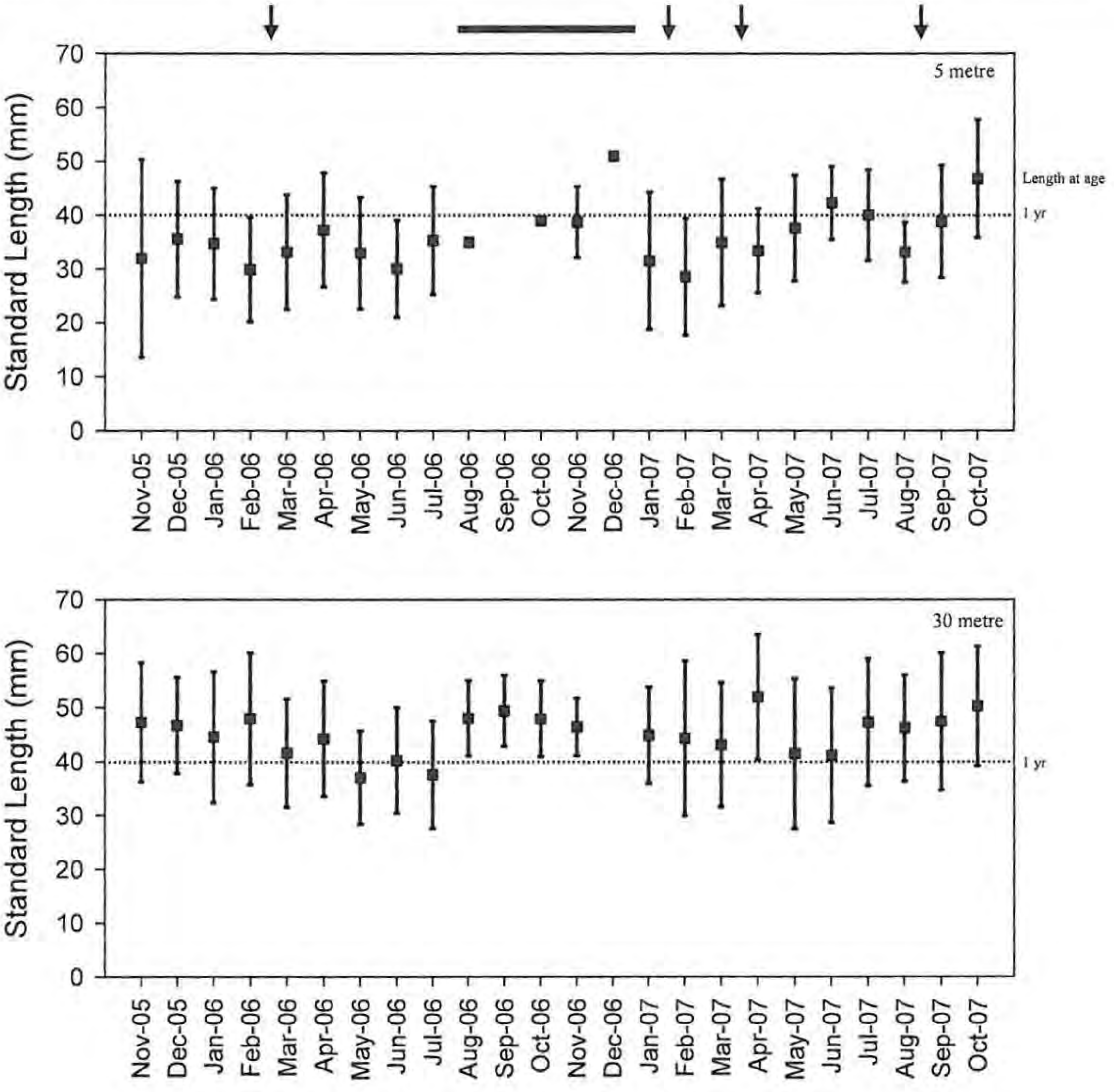

Figure 5.12: The average length (± SD) of *Glossogobius callidus* recorded for each month in the Mpekweni Estuary. The top and bottom graphs show the fish sampled using the 5 m and 30 m seine nets respectively. Dotted lines indicate estimated length at age. The bar indicates the period when the mouth was open and the arrows, overwash events. No data points indicate that no fish were sampled during that month.

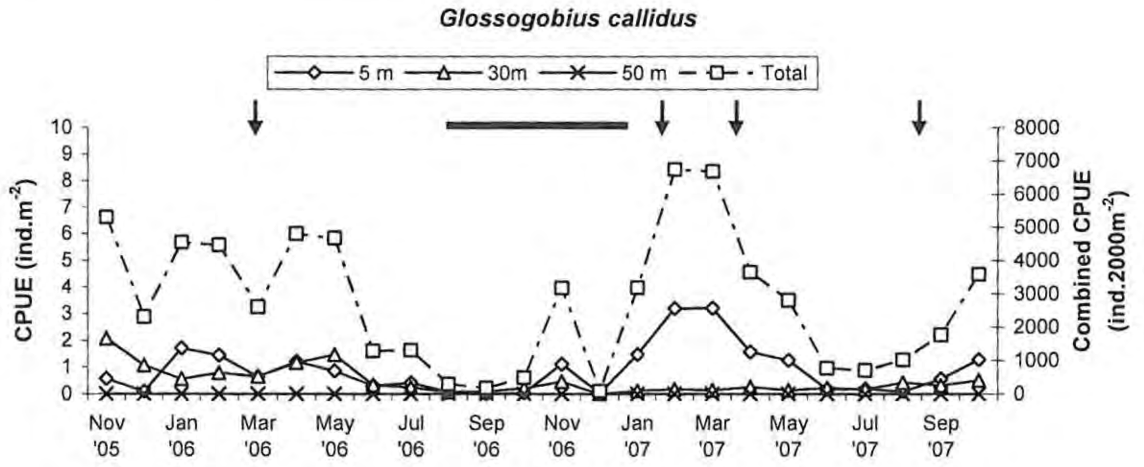

Figure 5.13: The CPUE (ind.m^{-2}) of *Glossogobius callidus* sampled seine net for each month and the adjusted and pooled CPUE (ind.2000m^{-2}). The bar indicates the period when the mouth was open and the arrows, overwash events.

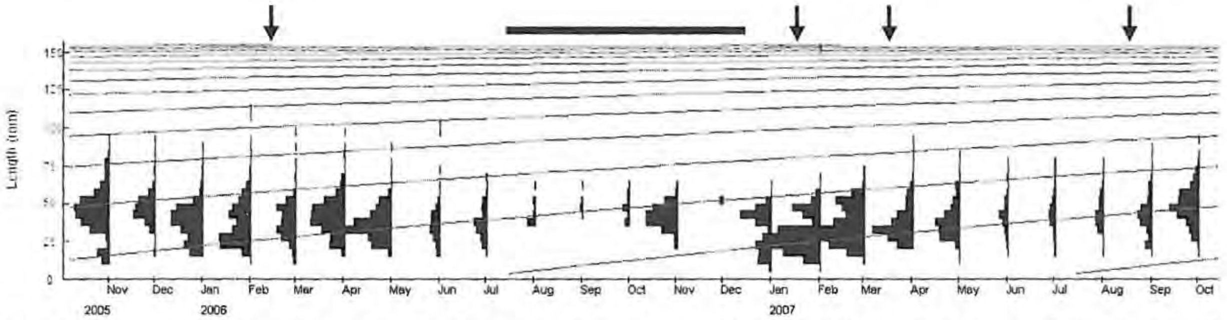

Figure 5.14: The monthly length frequencies and von Bertalanffy Growth Function curves for *Glossogobius callidus* determined by ELEFAN I in FiSAT II. See Table 5.2 for calculated L_∞ and K values. The bar indicates the period when the mouth was open and the arrows, overwash events.

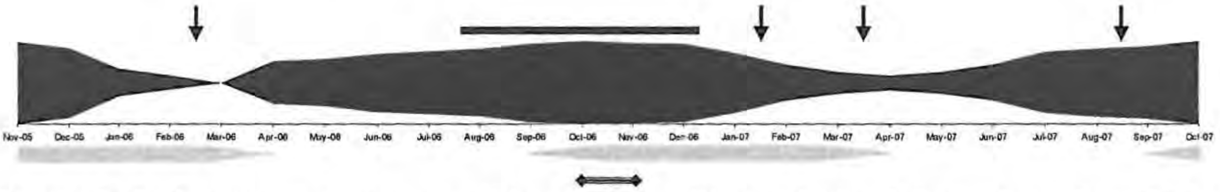

Figure 5.15: Recruitment patterns of *Glossogobius callidus* calculated from November 2005 to October 2007 using FiSAT II. The bar indicates the period when the mouth was open and the arrows, overwash events.

5.3.4 *Rhabdosargus holubi*

Rhabdosargus holubi was the numerically dominant fish species sampled in all regions throughout the duration of the study. Most (96 %) of the fish sampled by all gear were less than 100 mm SL (Figure 5.16.d.i). The majority (97 %) of the *R. holubi* sampled in the littoral area were < 50 mm SL (Figure 5.16.a.i), with the initial closed period being dominated by fish ranging from 10 mm to 20 mm SL. During the re-closed period, over double the number of fish were recorded (222 versus 88 individuals) and the size classes ranged between < 10 mm and 40 mm SL. When the estuary breached and was open (August 2006 to December 2006), 96.9 % of the fish (127 individuals) sampled in the 5 m net were < 20 mm SL. This accounted for 12.8 % of all the *R. holubi* sampled (976 individuals) during this period (Figure 5.16.a.iii). After the estuary re-closed a wider size range of juvenile *R. holubi* were sampled. Overall the pooled and adjusted data identified two modal peaks, 0 – 10 mm and 40 – 50 mm (Figure 5.16.a.iv). During the initial closed period, overall, the modal peak of the *R. holubi* population was in the 40 – 50 mm class (Figure 5.16.d.ii) and during the re-closed period there was a wider spread with the modal peak encompassing a broader range of size classes (20 – 70 mm) (Figure 5.16.d.iv). In the open period two distinct modal peaks were observed, 0 – 10 mm and 50 – 70 mm (Figure 5.16.d.iii).

The mean and standard deviations of the lengths of *R. holubi* for each net are shown in Figure 5.17. The average standard lengths recorded in the 5 m, 30 m and 50 m seine nets were 19.48 mm, 53.02 mm and 81.7 mm respectively (Tables: 4.2, 4.4 and 4.6 in Chapter 4). In the first month of sampling after the estuary had breached (August 2006) no *R. holubi* were sampled by the 30 m and 50 m nets (Figure 5.17, middle and bottom), however, 124 pre-flexion to post-larval (10 mm - 30 mm SL [Whitfield, 1998]) *R. holubi* were sampled in the littoral zone during this month (August 2006, Figure 5.19).

Most of the *R. holubi* (12234 individual) were sampled by the net used to target the estuarine and smaller marine spawning species (Figure 5.16.b.i). The initial closed period showed two modal groups, the 40 mm – 50 mm and the 90 mm – 100 mm age groups (Figure 5.16.b.ii). The majority of fish sampled were under a year old (98.4 %). The open and re-closed periods exhibited a wider spread of age classes (Figures: 5.16.b.iii and 5.16.b.iv), with 95.6 % of fish sampled < 1 year old. The number of fish sampled (5195 individuals, 519.5 ind.month^{-1}) for the period re-closed period was lower than the initial period (6285 individuals, 698 ind.month^{-1}) (Figures: 5.16.b.ii and 5.16.b.iv). During the open and re-closed period, the fish that either remained or recruited into the estuary were larger than those recorded prior to opening (Figures: 5.16.b.ii, 5.16.b.iii and 5.16.b.iv).

During the open period, 98.9 % of the fish sampled from the channel were < 1 year old. After re-closing there was a slightly lower contribution (95.4 %) of fish < 1 year old, indicating an increase in the contribution of larger individuals.

The larger fish sampled from the channel were predominantly between the size classes of 60 mm – 120 mm (~ 97 %) (Figure 5.16.c.i). During the initial closed period, 8.5 % of *R. holubi* sampled by the 50 m net were > 1 year old (Figure 5.16.c.ii). During the open period all fish sampled ranged between 60 mm and 100 mm (< 1 year) (Figure 5.16.c.iii). After the estuary had re-closed, 21.5 % (273 individuals) of the larger *R. holubi* sampled from the channel were > 1 year old (Figure 5.16.c.iv), of which only six individuals were greater than the length at sexual maturity (150 mm [Wallace, 1975b).

The original (ind.m^{-2}) and adjusted CPUE (ind.2000m^{-2}) estimates of *R. holubi* for each month are shown in Figure 5.18. Growth increments were estimated at 5.21 mm.$month^{-1}$ using the adjusted and pooled data (Table 5.2).

The length frequency distributions for *R. holubi* were used to estimate the von Bertalanffy growth parameters K (0.21), L_∞ (225.75 mm) and t_0 (Table 5.2), which were plotted ($L_t = 225.75[1\text{-}\exp(-0.21(t\text{-}t_0))]$) on to Figure 5.19.

Other growth parameters: t_{max}, ϕ', OEL and PEL are provided in Table 5.2. The growth performance index (ϕ') was calculated at 4.03 and the. Instantaneous total (Z) and natural (M) mortality rates were calculated at 1.53 $year^{-1}$ and 5.21 $year^{-1}$ respectively (Table 5.2).

Recruitment patterns for *R. holubi* were estimated for each year (Figure 5.20). In both years the highest recruitment occurred during the summer months (December to February 2006 [Figure 5.20]). Lowest recruitment was evident during mid and late winter (June to September [Figure 5.20]).

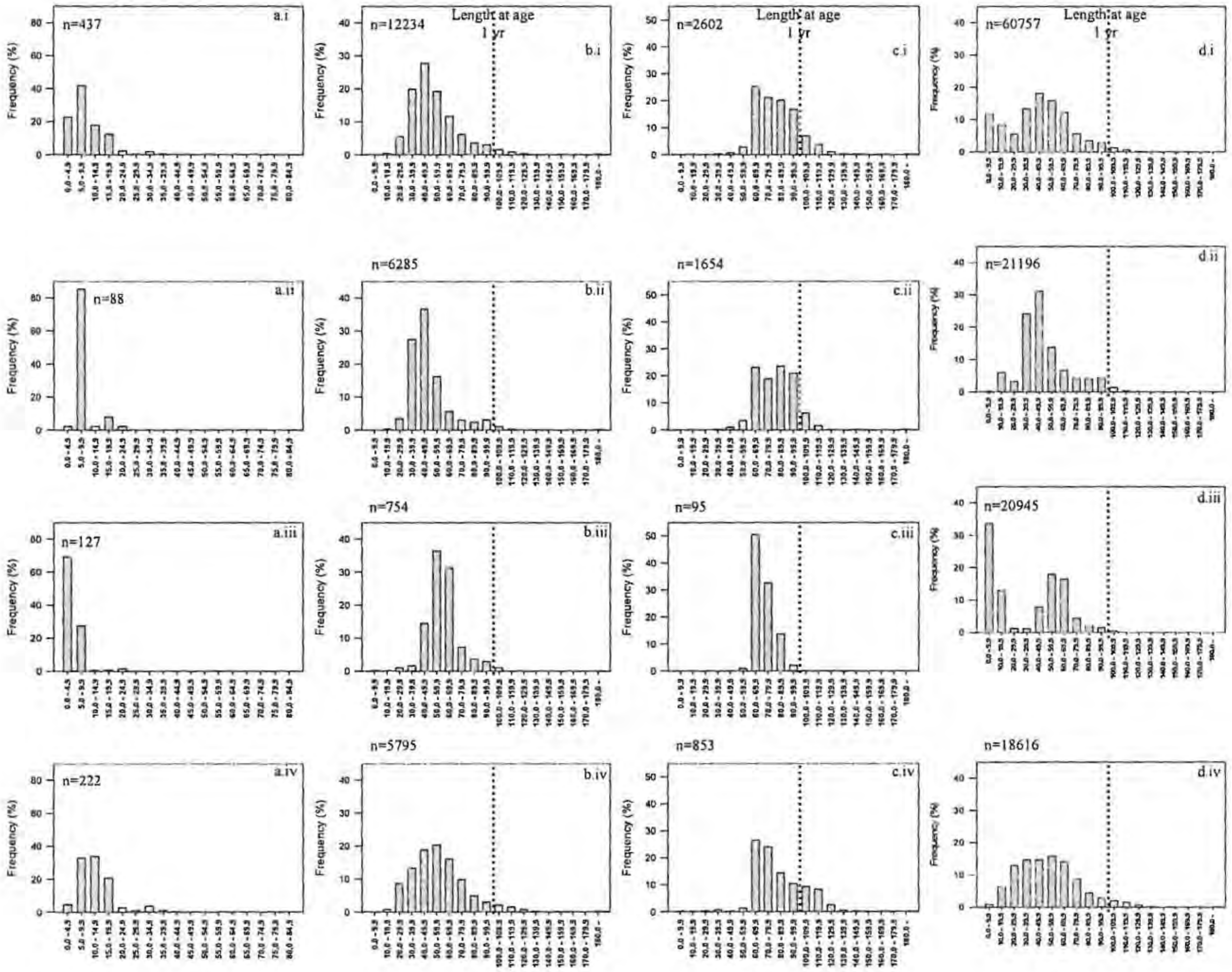

Figure 5.16: The length frequency cohorts of *Rhabdosargus holubi* in the Mpekweni Estuary. (a), (b) and (c) represent the data recorded from the 5 m, 30 m and 50 m seine nets. The adjusted and pooled data are represented by (d). The combined cohorts are shown in each graph labelled .i for each seine net. The initial closed, open and re-closed periods are represented by .ii, .iii and .iv. Dotted lines indicate estimated length at age.

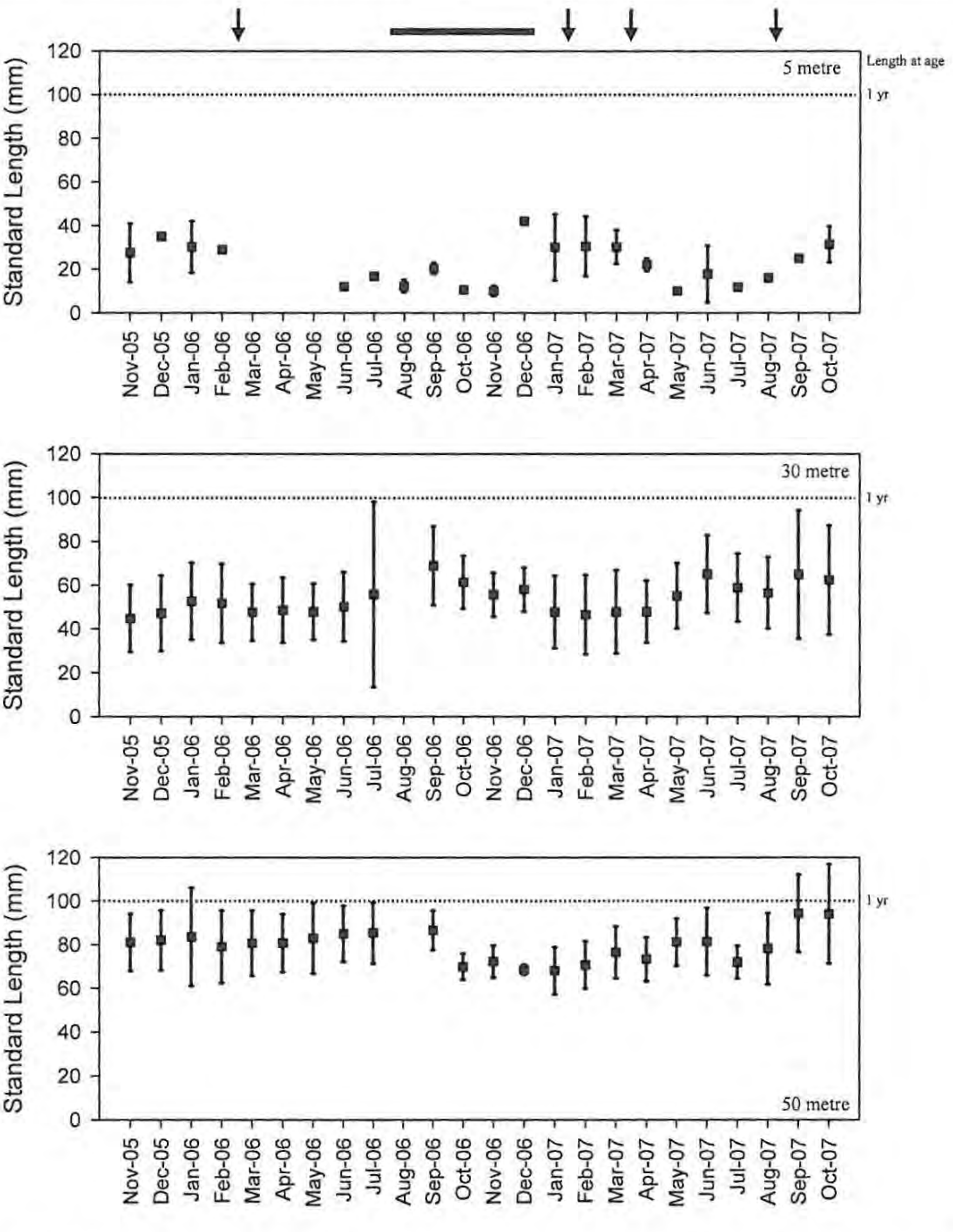

Figure 5.17: The average length (± SD) of *Rhabdosargus holubi* recorded for each month in the Mpekweni Estuary. The top, middle and bottom graphs show the fish sampled using the 5 m, 30 m and 50 m seine nets respectively. Dotted lines indicate estimated length at age. The bar indicates the period when the mouth was open and the arrows, overwash events. No data points indicate that no fish were sampled during that month.

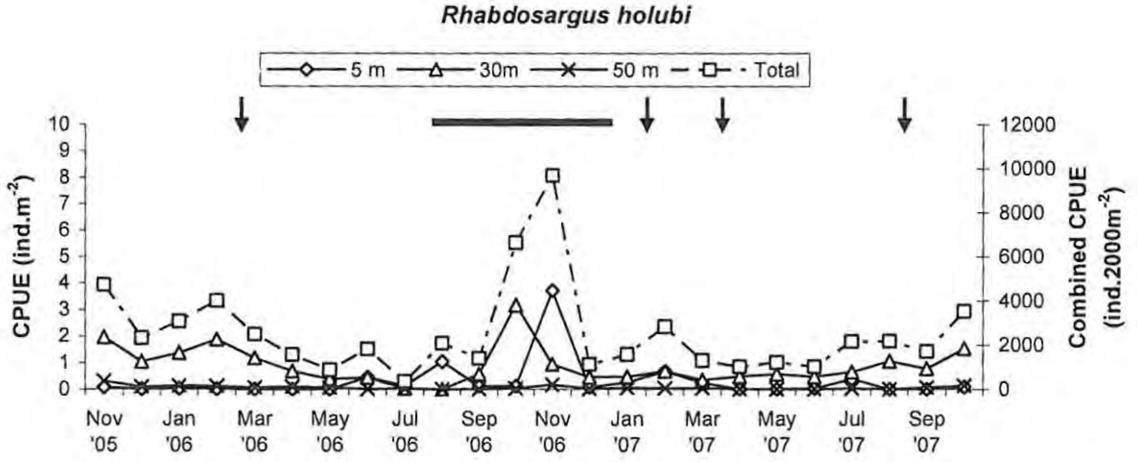

Figure 5.18: The CPUE (ind.m^{-2}) of *Rhabdosargus holubi* sampled by each seine net for each month and the adjusted and pooled CPUE (ind.2000m^{-2}). The bar indicates the period when the mouth was open and the arrows, overwash events.

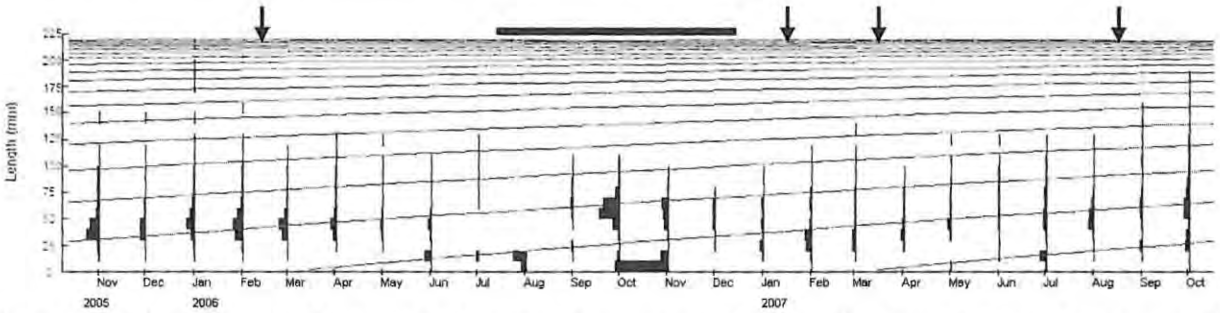

Figure 5.19: The monthly length frequencies and von Bertalanffy Growth Function curves for *Rhabdosargus holubi* determined by ELEFAN I in FiSAT II. See Table 5.2 for calculated L_∞ and K values. The bar indicates the period when the mouth was open and the arrows, overwash events.

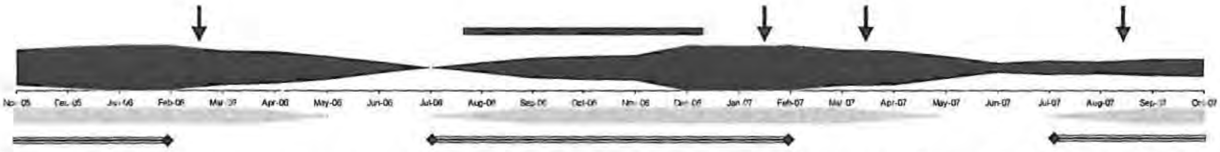

Figure 5.20: Recruitment patterns of *Rhabdosargus holubi* calculated from November 2005 to October 2007 using FiSAT II. The bar indicates the period when the mouth was open and the arrows, overwash events.

5.3.5 *Solea turbynei*

Solea turbynei was sampled from the littoral/benthic region of the estuary primarily using the 5 m and 30 m seine nets (Figure 5.21). The majority of the fish (88.4 %) were < 60 mm SL (length at age 1) and were sampled in the larger 30 m seine net targeting the channel region. In the two closed periods, the modal sizes were the same, at an estimated 45 - 50 mm SL (Figure 5.21.a.ii and Figure 5.21.a.iv). The length distribution for the initial closed period showed a higher frequency (15.74 %) of the larger fish between the ages of 1 and 2 years being present in the system. After the estuary re-closed the frequency of capture of the larger fish (> 1 year i.e. > 60 mm SL) dropped (10.21 %), indicating a loss of the larger individuals (Figure 5.21.a.iv). Overall the pooled and adjusted data was dominated by the samples from the 30 m seine net (Figure 5.21.b).

The average length (Figure 5.22) of *S. turbynei* for each month did not vary to any great extent from the overall 49.7 mm SL, and only four individuals were sampled during the open period of August 2006 to December 2006.

The original (ind.m^{-2}) and adjusted CPUE (ind.2000m^{-2}) estimates of *S. turbynei* sampled each month are shown in Figure 5.23. Growth increments were estimated at 1.67 mm.month^{-1} using the adjusted and pooled data (Table 5.3).

The length frequency distributions for *S. turbynei* were used to estimate the von Bertalanffy growth parameters K (0.50), L_∞ (107.63 mm) and t_0 (Table 5.3), which were plotted ($L_t = 107.63[1-\exp(-0.50(t-t_0))]$) on to Figure 5.24.

Other growth parameters: t_{max}, ϕ', OEL and PEL are provided in Table 5.3. The growth performance index (ϕ') (3.76) and a predicted maximum length of 103.57 mm were calculated in FiSAT. Instantaneous total (Z) mortality rates calculated using length-converted catch curves and the Jones and van Zalinge plots were 1.77 year^{-1} and 3.25 year^{-1} respectively (Table 5.3).

Recruitment patterns for *S. turbynei* were estimated for each sampling year (Figure 5.25), experiencing the lowest recruitment around the months of March to May. Maximum recruitment estimates were between the months of September and November.

Table 5.3: The von Bertalanffy Growth Function, longevity, growth performance and mortality parameters were estimated using FiSAT from the pooled length frequency data of the species *Solea turbynei*, *Liza dumerilii*, *Liza richardsonii* and *Myxus capensis*. * Average of multiple estimates of Z determined from the catch-curve.

		Solea turbynei	*Liza dumerilii*	*Liza richardsonii*	*Myxus capensis*
Description of parameter	Parameter	Overall	Overall	Overall	Overall
Von Bertalanffy growth function	L_∞ (SL, mm)	107.63	320.25	330.75	330.75
	K (year^{-1})	0.50	0.13	0.22	0.18
	t_0 (years)	-0.23	-0.69	-0.40	-0.49
Longevity	T_{max} (years)	6.00	23.08	13.64	16.67
Growth Performance Index	ϕ'	3.76	4.13	4.38	4.29
Average Monthly Growth Increments (mm.month^{-1})		1.67	9.67	3.47	4.10
Observed Extreme Length (mm)		102.50	305.00	315.00	315.00
Predicted Extreme Length (mm)		103.57	-	-	-
Mortality Z (year^{-1}) (r^2) [as a percentage]	Catch Curve	1.77 (0.90) [96 %]	0.46 (0.97) [37 %]	0.85 (0.80) [57 %]	0.71 (0.88) [51 %]
Mortality Z (year^{-1}) (as a percentage)*		1.74 (82 %)	0.39 (32 %)	0.63 (47 %)	0.52 (41 %)
Mortality Z (year^{-1}) (r^2) [as a percentage]	Jones and van Zalinge	3.25 (0.95) [97 %]	3.53 (0.97) [97 %]	3.67 (0.88) [97 %]	3.84 (0.91) [98 %]
Mortality Z (year^{-1}) (as a percentage)*		2.79 (94 %)	3.07 (95 %)	2.27 (90 %)	2.67 (93 %)

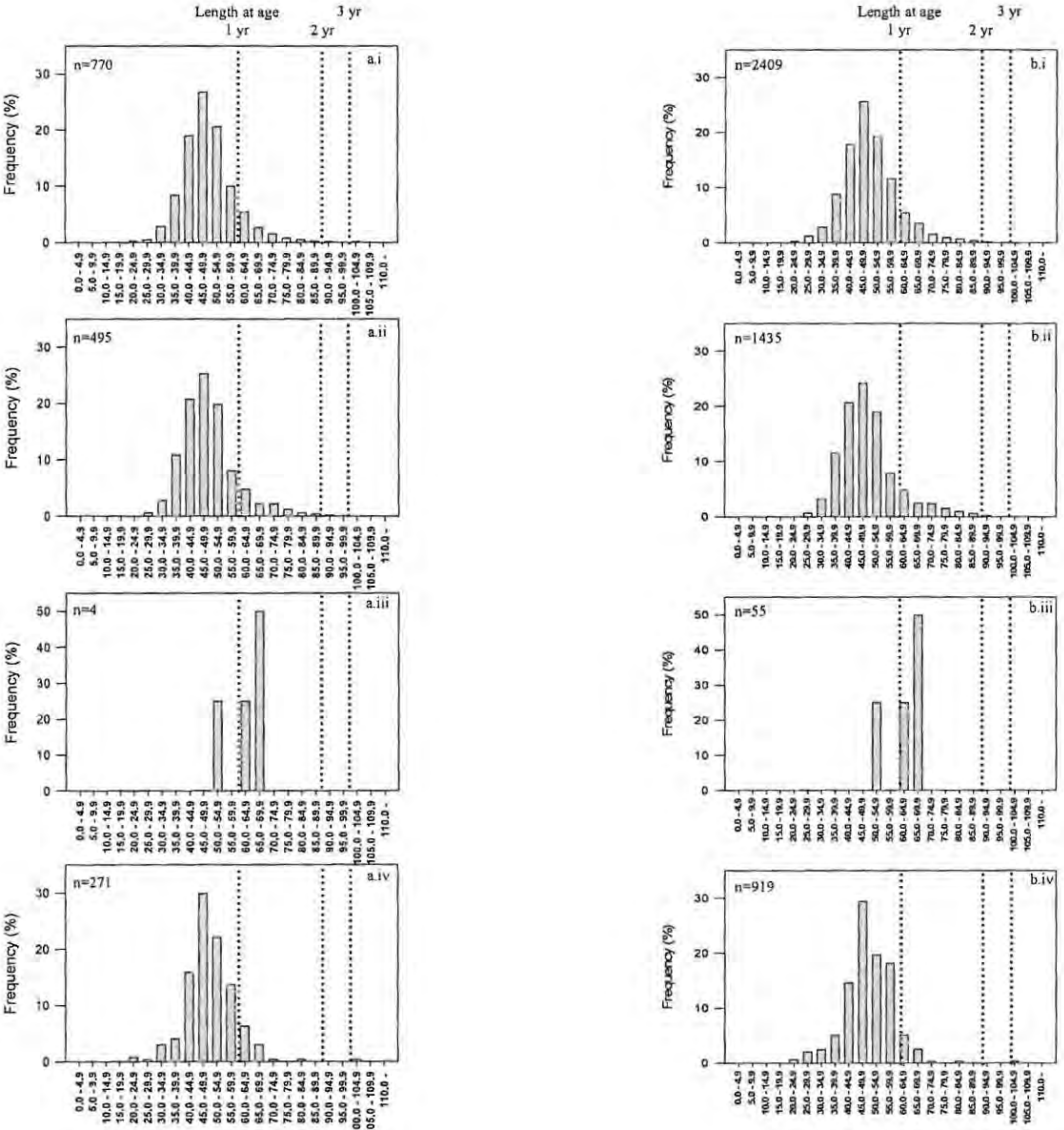

Figure 5.21: The length frequency cohorts of *Solea turbynei* in the Mpekweni Estuary. (a) represents the data recorded from the 30 m seine net. The adjusted and pooled data are represented by (b). The combined cohorts are shown in each graph labelled .i. The initial closed, open and re-closed periods are represented by .ii, .iii and .iv. Dotted lines indicate estimated length at age.

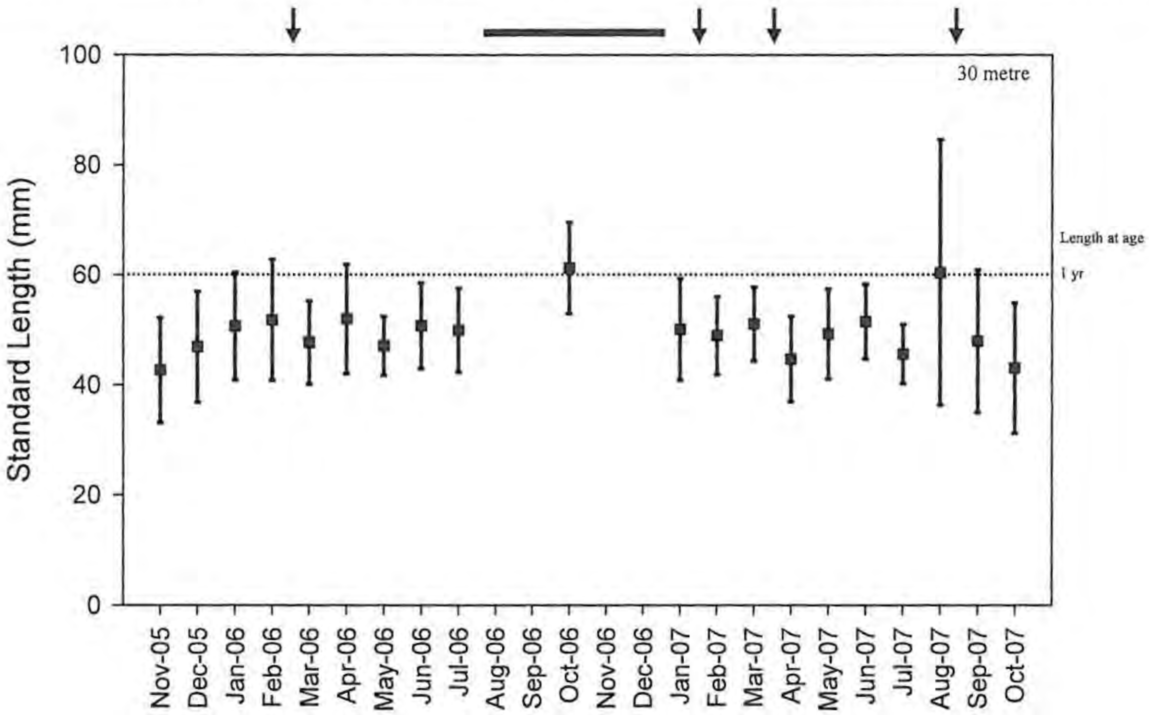

Figure 5.22: The average length (± SD) of *Solea turbynei* recorded for each month in the Mpekweni Estuary. Dotted lines indicate estimated length at age. The bar indicates the period when the mouth was open and the arrows, overwash events. No data points indicate that no fish were sampled during that month.

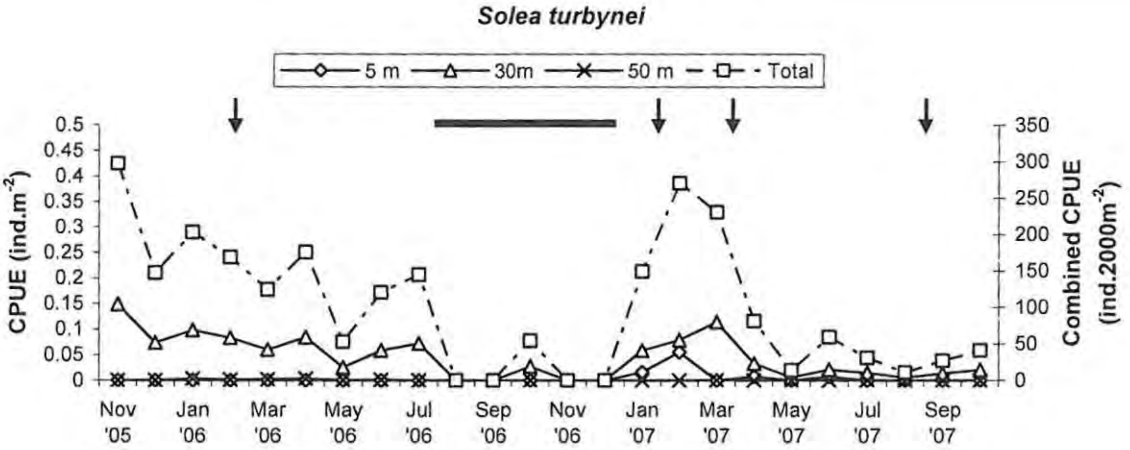

Figure 5.23: The CPUE (ind.m^{-2}) of *Solea turbynei* sampled by each seine net for each month and the adjusted and pooled CPUE (ind.2000m^{-2}). The bar indicates the period when the mouth was open and the arrows, overwash events.

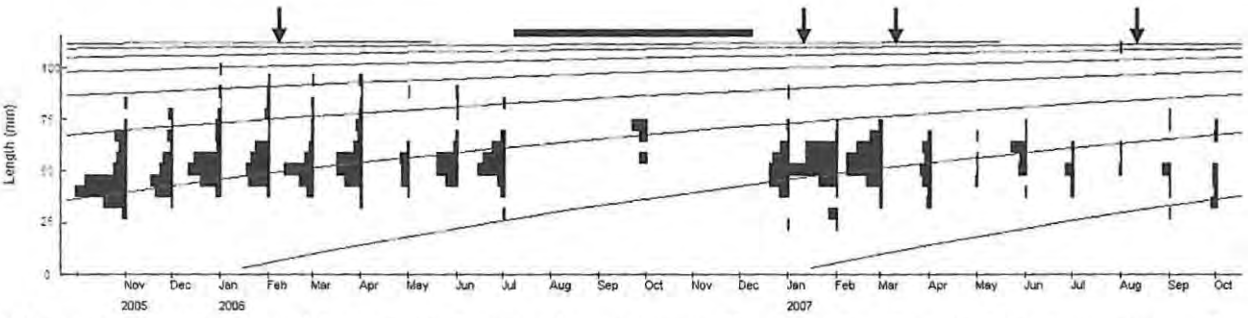

Figure 5.24: The monthly length frequencies and von Bertalanffy Growth Function curves for *Solea turbynei* determined by ELEFAN I in FiSAT II. See Table 5.3 for calculated L_{∞} and K values. The bar indicates the period when the mouth was open and the arrows, overwash events.

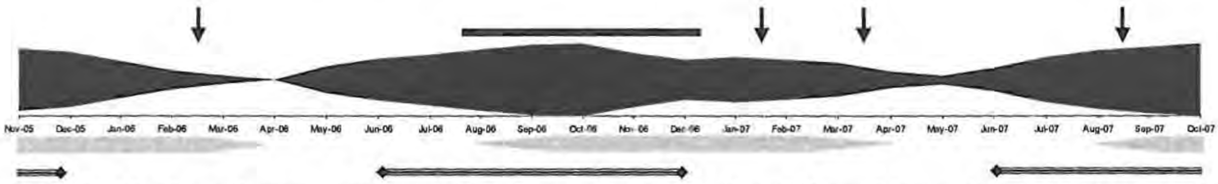

Figure 5.25: Recruitment patterns of *Solea turbynei* calculated from November 2005 to October 2007 using FiSAT II. The bar indicates the period when the mouth was open and the arrows, overwash events.

5.3.6 *Liza dumerilii*

Liza dumerilii sampled from the channel demonstrated modal length size classes of 100 – 120 mm (Figure 5.26.a.i) and 120 – 160 mm SL, respectively (Figure 5.26.b.i). Both gear types used to target the larger individuals sampled fish in the < 1 year, > 1 year and > 2 year length classes, with a higher frequency of the larger/older fish sampled by the largest gear. There was very little difference in the distributional ranges between the fish sampled during the initial and re-closed periods, however the smaller individuals targeted in the channel displayed an increase in the number of smaller fish sampled after the estuary re-closed, which could be indicative of recruitment having occurred (Figure 5.26.a.iv). The adjusted and pooled data exhibited a fairly normal population distribution (Figure 5.26.c.i) around a modal peak of 110 – 120 mm, with the exception of one peak over the 80 – 90 mm size class (this can be tracked back to 12 individuals sampled from the littoral zone of March 2007 which were over-compensated by the adjusting and pooling of the data set). During the initial closed period there was a sharp change around the 80 mm size class and the larger size classes dominated the population (Figure 5.26.c.ii). After the estuary re-closed there were a broader range of modal peaks (Figure 5.26.c.iv).

Prior to the breaching event, the average lengths of targeted smaller individuals in the channel for each month was relatively consistent (average 115.4 mm SL, range: 106.7 – 128.8 mm SL) (Figure 5.27). After the estuary re-closed there was an increase in average length from 103 mm to 180 mm SL of these individuals. The larger fish targeted in the channel exhibited an average length for each month that remained above the length at age 1 year. There were no fish sampled during the initial three months of the mouth remaining open (Figure 5.27).

The original (ind.m^{-2}) and adjusted CPUE (ind.2000m^{-2}) estimates of *L. dumerilii* sampled each month are shown in Figure 5.28. Growth increment was estimated at 9.67 mm.month^{-1} using the adjusted and pooled data (Table 5.3).

The length frequency distributions for *L. dumerilii* were used to estimate the von Bertalanffy growth parameters K (0.13), L_∞ (320.25 mm) and t_0 (Table 5.3), which were plotted ($L_t = 320.25[1\text{-exp}(-0.13(t-t_0))]$) on to Figure 5.29.

Other growth parameters: t_{max}, ϕ', OEL and PEL are provided in Table 5.3. The growth performance index (ϕ') was calculated at 4.13. Instantaneous total (Z) mortality rates calculated using length-converted catch curves and the Jones and van Zalinge plots were 0.46 year^{-1} and 3.53 year^{-1}, respectively (Table 5.3).

Recruitment patterns for *L. dumerilii* were estimated for each sampling year (Figure 5.30). In 2006 there were low recruitment estimates from April to September. In 2007 recruitment estimates were at their lowest between February and June (Figure 5.30). Maximum recruitment is likely to have occurred during the spring and summer months (September to February).

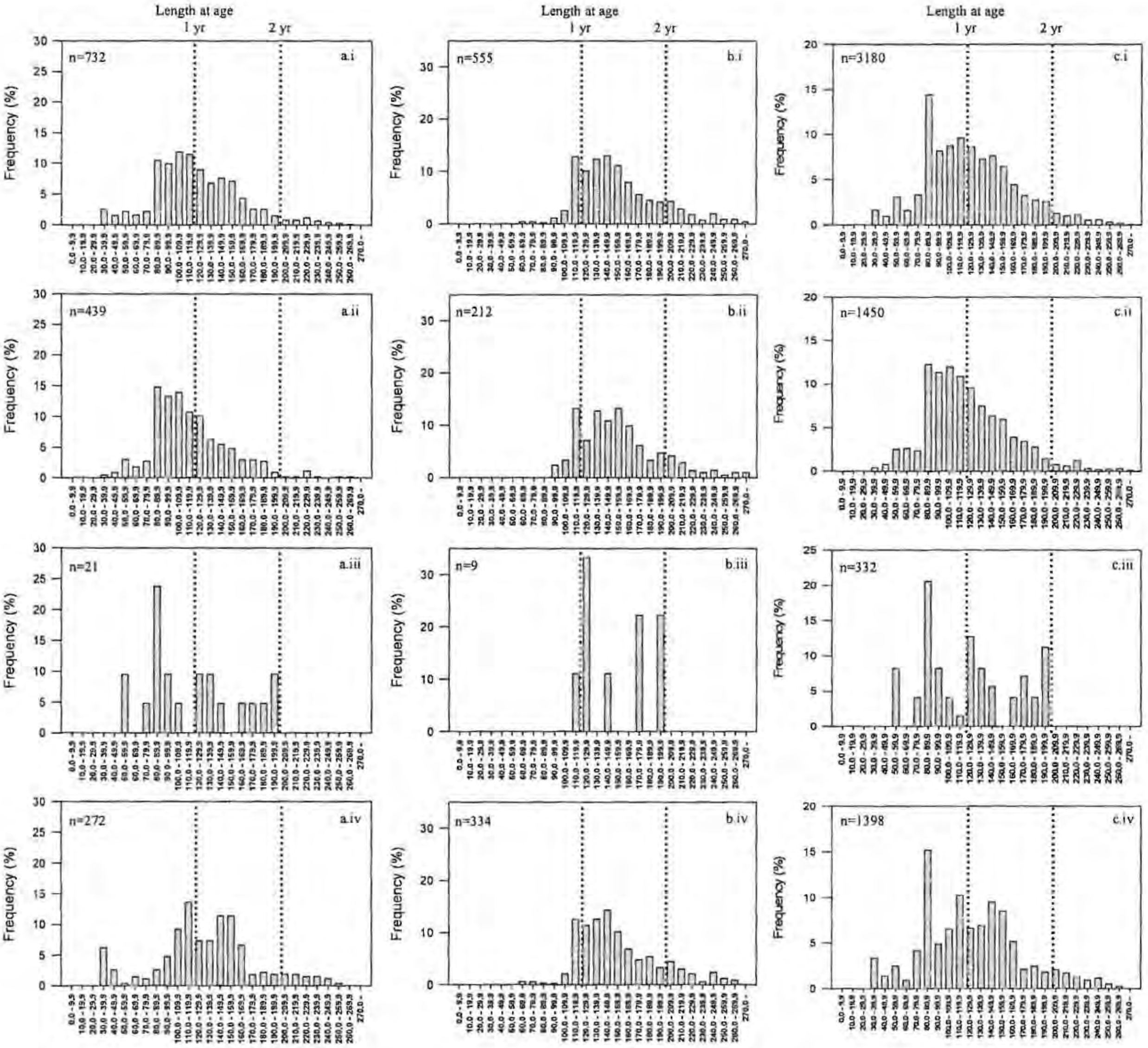

Figure 5.26: The length frequency cohorts of *Liza dumerilii* in the Mpekweni Estuary. (a) and (b) represent the data recorded from the 30 m and 50 m seine nets. The adjusted and pooled data are represented by (c). The combined cohorts are shown in each graph labelled .i for each seine net. The initial closed, open and re-closed periods are represented by .ii, .iii and .iv. Dotted lines indicate estimated length at age.

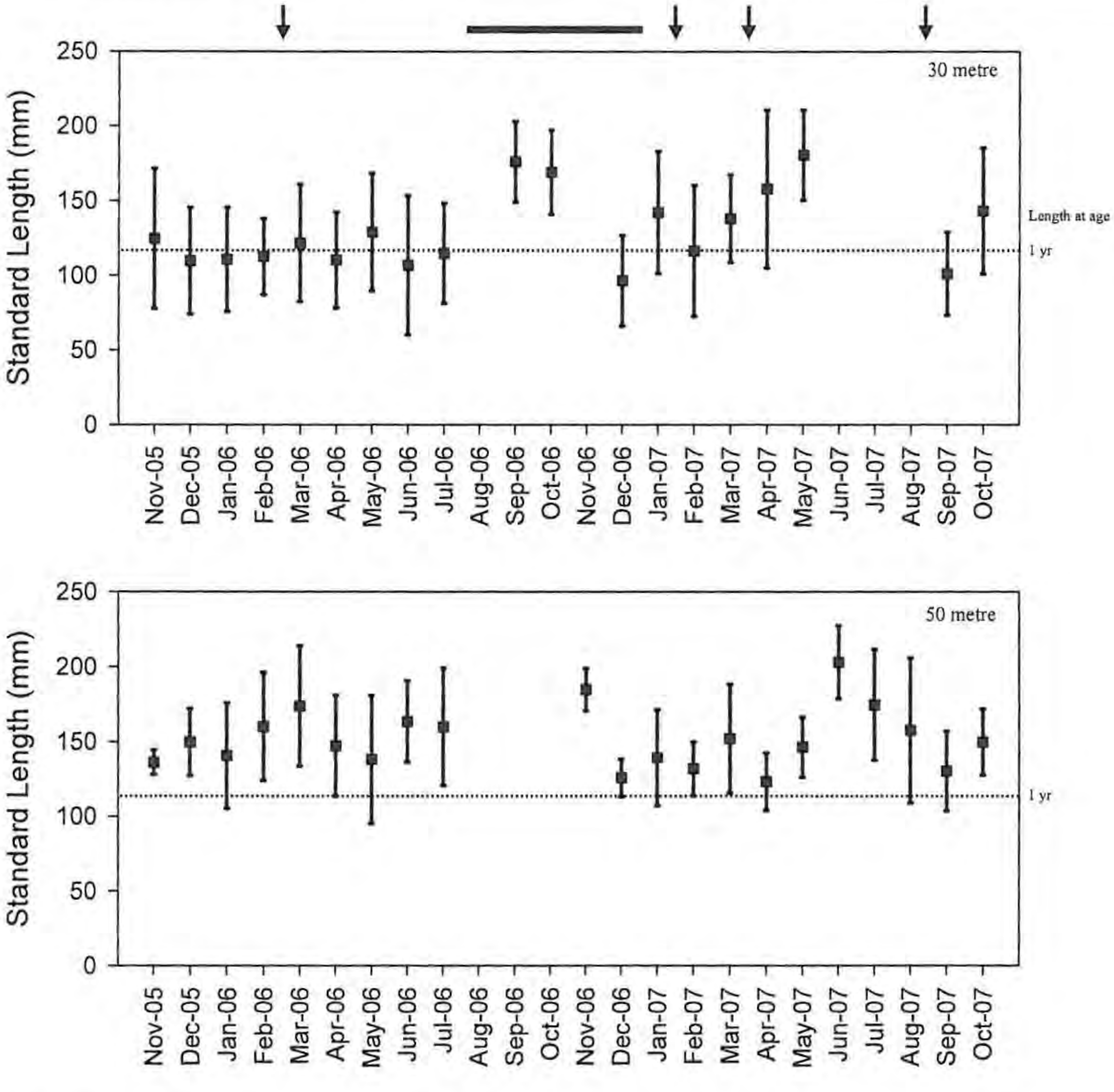

Figure 5.27: The average length (± SD, error bars) of *Liza dumerilii* recorded for each month in the Mpekweni Estuary. The top and bottom graphs show the fish sampled using the 30 m and 50 m seine nets respectively. Dotted lines indicate estimated length at age. The bar indicates the period when the mouth was open and the arrows, overwash events. No data points indicate that no fish were sampled during that month.

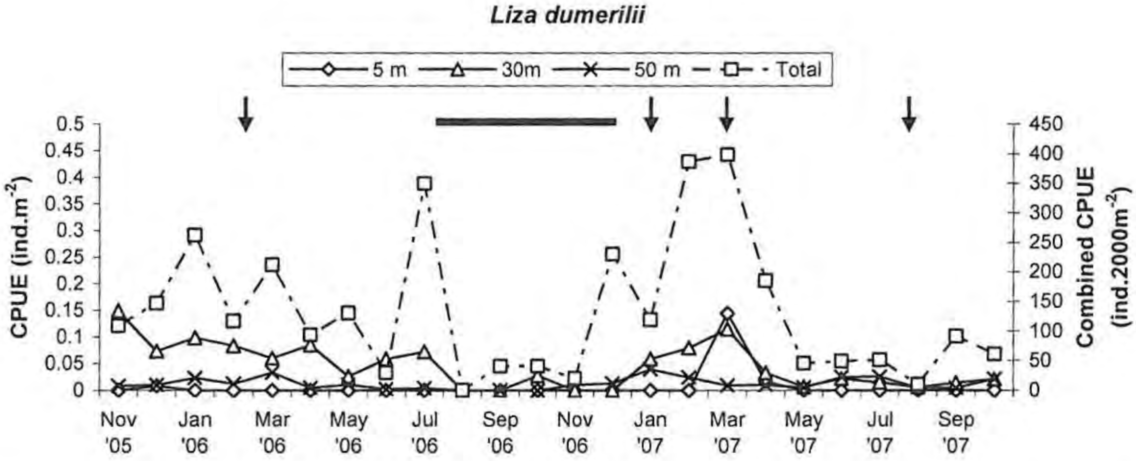

Figure 5.28: The CPUE (ind.m^{-2}) of *Liza dumerilii* sampled by each seine net for each month and the adjusted and pooled CPUE (ind.2000m^{-2}). The bar indicates the period when the mouth was open and the arrows, overwash events.

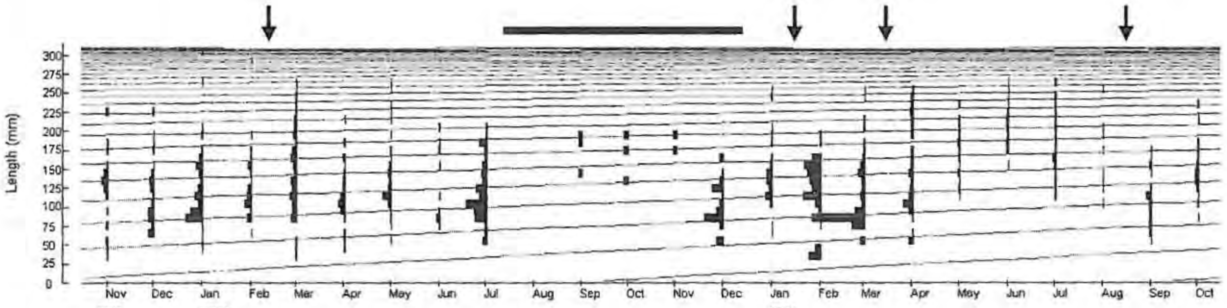

Figure 5.29: The monthly length frequencies and von Bertalanffy Growth Function curves for *Liza dumerilii* determined by ELEFAN I in FiSAT II. See Table 5.3 for calculated L_∞ and K values. The bar indicates the period when the mouth was open and the arrows, overwash events.

Figure 5.30: Recruitment patterns of *Liza dumerilii* calculated from November 2005 to October 2007 using FiSAT II. The bar indicates the period when the mouth was open and the arrows, overwash events.

5.3.7 *Liza richardsonii*

The length frequency distribution of larval/juvenile and larger *Liza richardsonii* sampled from the littoral and channel regions are shown in Figure 5.31. During the initial closed period, the larval and juvenile fish sampled from the littoral zone (Figure 5.31.a.ii) were primarily between 10 mm and 20 mm in length (SL). When the mouth was open no *L. richardsonii* were sampled (Figure 5.31.a.iii). After the estuary re-closed, the juvenile fish had a modal size class of 40 – 45 mm SL (Figure 5.31.a.iv). The larger individuals sampled from the channel (Figure 5.31.b) were primarily (96.7 %) older than 1 year (> 100 mm SL length at age).

Sixty of the larger channel individuals (12 ind.month^{-1}) were sampled during the open phase (Figure 5.31.b.iii) in comparison to 41 fish (4 ind.month^{-1}) during the initial closed period (Figure 5.31.b.ii) and 22 (2.2 ind.month^{-1}) after the estuary had re-closed (Figure 5.31.b.iv). These newly recruited fish dominated the larger individuals from the channel during the re-closed period (Figure 5.31.b.iv). When the mouth was open to the sea the length frequency of *L. richardsonii* sampled from the channel were dominated by fish of 1 year old. After re-closing the length frequency was bimodal with peaks corresponding to ages > 1 year and > 2 years (Figure 5.31.b.iv). Despite the low sample size the average lengths did not demonstrate any particular seasonal or temporal patterns although there were peaks in late summer (Figure 5.32). Overall the pooled data indicates that *L. richardsonii* in the Mpekweni Estuary is dominated by smaller individuals sampled in the littoral zone, although this is likely to be an over estimation as a result of the extrapolation of the CPUE estimates. The closed periods are also dominated by smaller individuals, however, the open period displays a wider range of the larger size classes.

The original (ind.m^{-2}) and adjusted CPUE (ind.2000m^{-2}) estimates of *L. richardsonii* sampled for each month are indicated in Figure 5.33. Growth increments were estimated as 3.47 mm.month^{-1} using the adjusted and pooled data (Table 5.3).

The length frequency distributions for *L. richardsonii* were used to estimate the von Bertalanffy growth parameters K (0.22), L_∞ (320.75 mm) and t_0 (Table 5.3), which were plotted ($L_t = 320.75[1\text{-exp}(-0.22(t-t_0))]$) on to Figure 5.34.

Other growth parameters: $t_{\max}$, ϕ', OEL and PEL are presented in Table 5.3. The growth performance index (ϕ') was calculated at 4.38. Instantaneous total (Z) mortality rates calculated using length-converted catch curves and the Jones and van Zalinge plots were 0.85 year^{-1} and 3.67 year^{-1} respectively (Table 5.3). Recruitment patterns estimated each year for *L. richardsonii* (Figure 5.35) identified the winter months (May to August) to have the lowest recruitment in the 2006 and 2007. Maximum recruitment was likely to occur during the spring and summer months (September to March) (Figure 5.35).

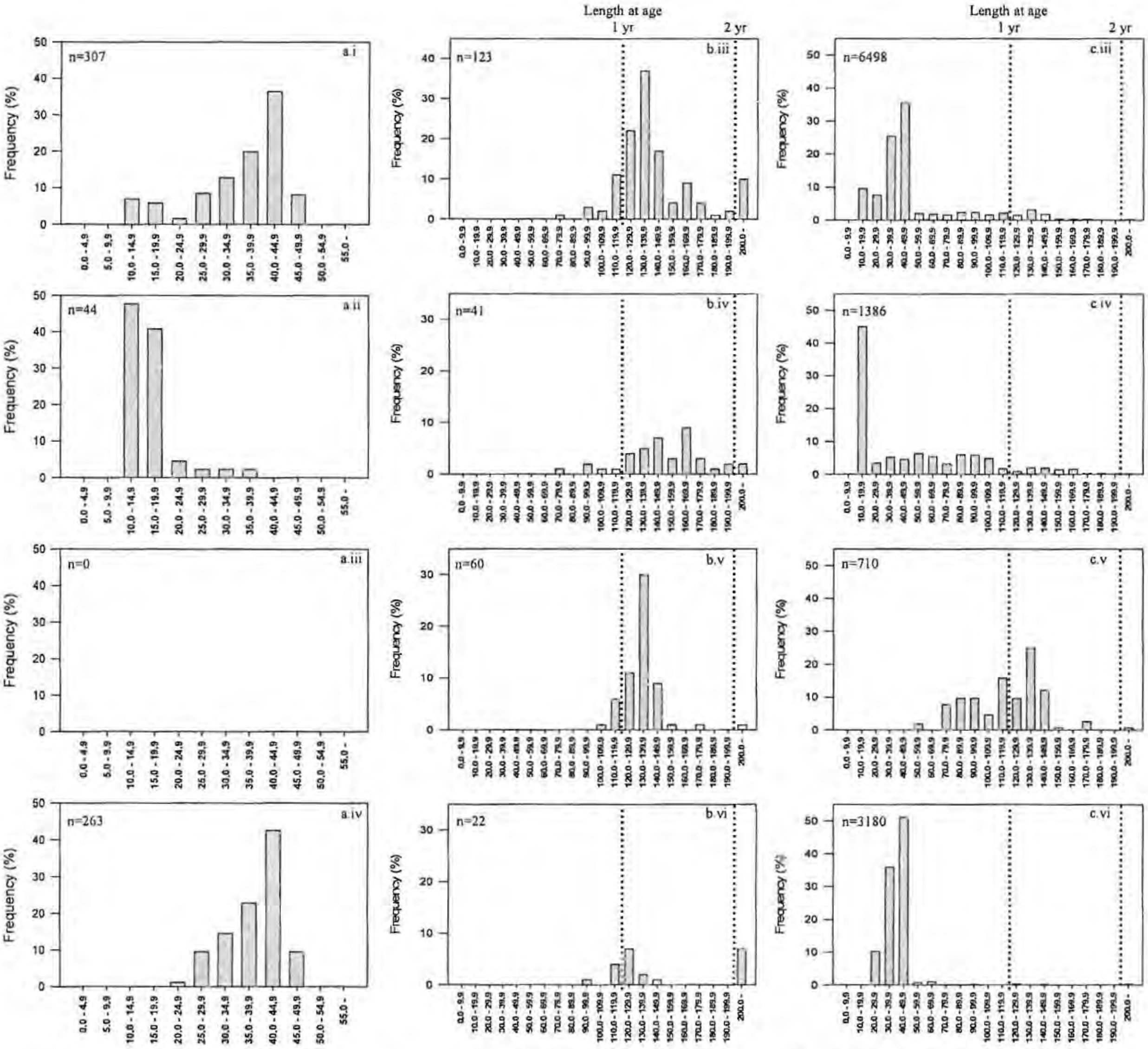

Figure 5.31: The length frequency cohorts of *Liza richardsonii* in the Mpekweni Estuary. (a) and (b) represent the data recorded from the 5 m and 50 m seine nets. The adjusted and pooled data are represented by (c). The combined cohorts are shown in each graph labelled .i for each seine net. The initial closed, open and re-closed periods are represented by .ii, .iii and .iv. Dotted lines indicate estimated length at age.

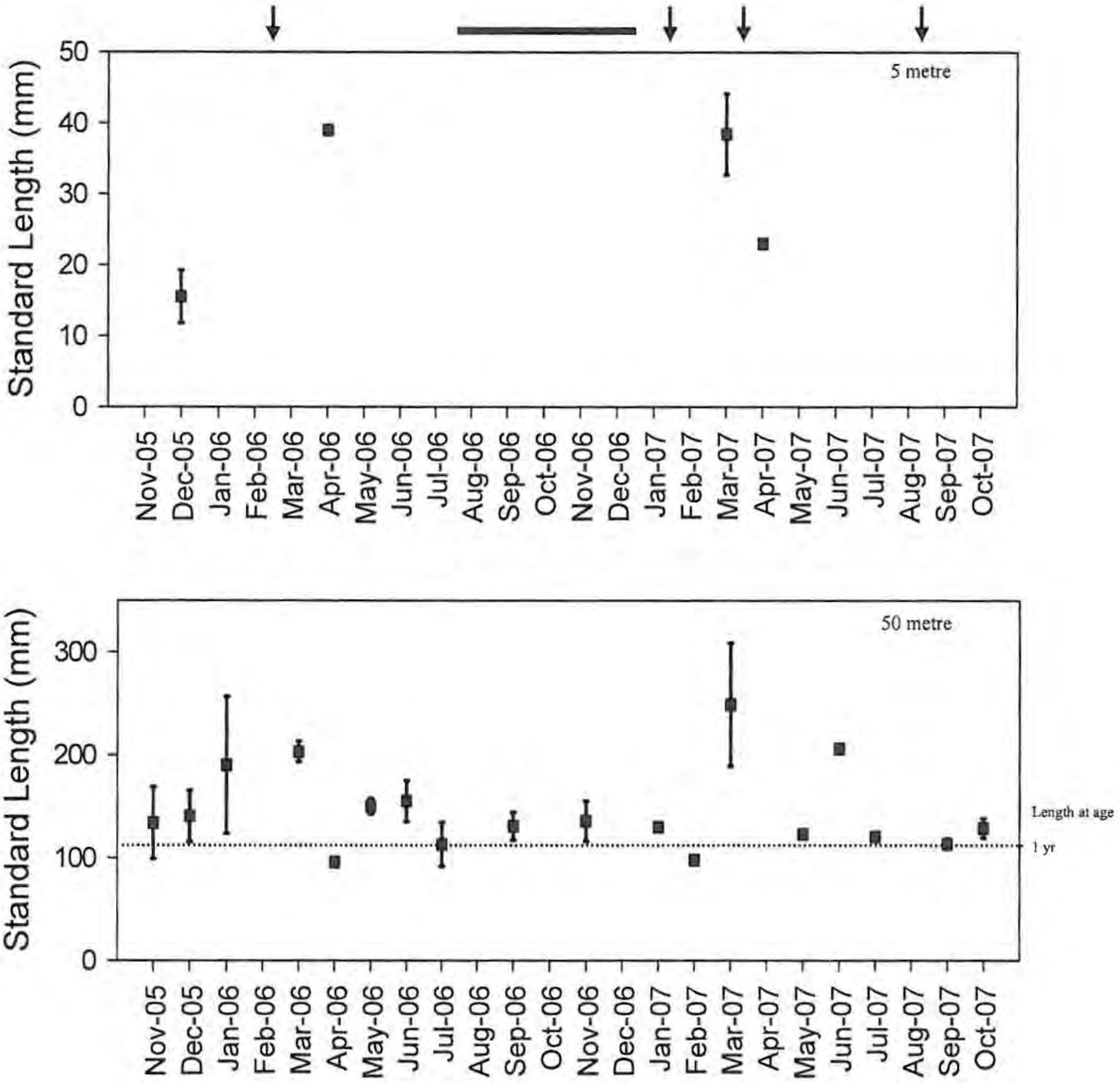

Figure 5.32: The average length (± SD, error bars) of *Liza richardsonii* recorded for each month in the Mpekweni Estuary. The top and bottom graphs show the fish sampled using the 5 m and 50 m seine nets respectively. Dotted lines indicate estimated length at age. The bar indicates the period when the mouth was open and the arrows, overwash events. No data points indicate that no fish were sampled during that month.

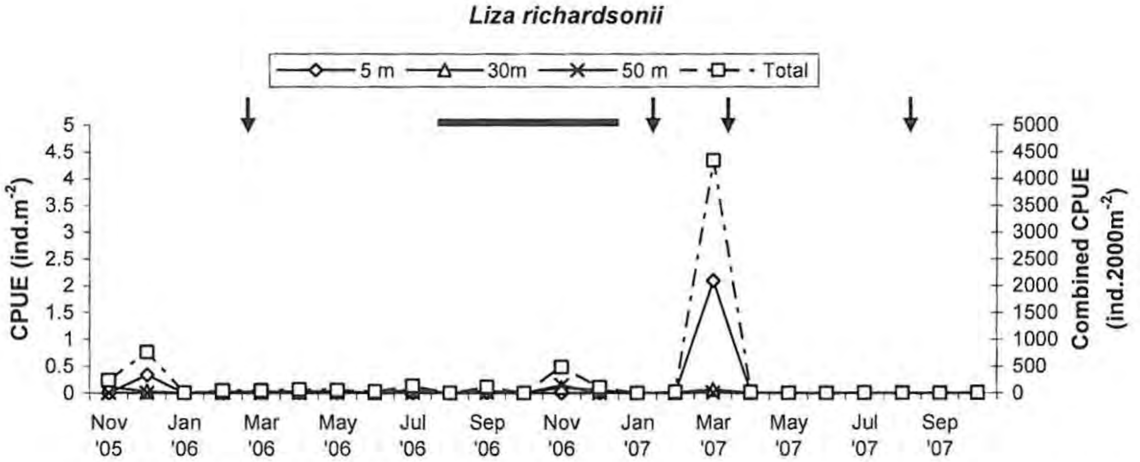

Figure 5.33: The CPUE (ind.m^{-2}) of *Liza richardsonii* sampled by each seine net for each month and the adjusted and pooled CPUE (ind.2000m^{-2}). The bar indicates the period when the mouth was open and the arrows, overwash events.

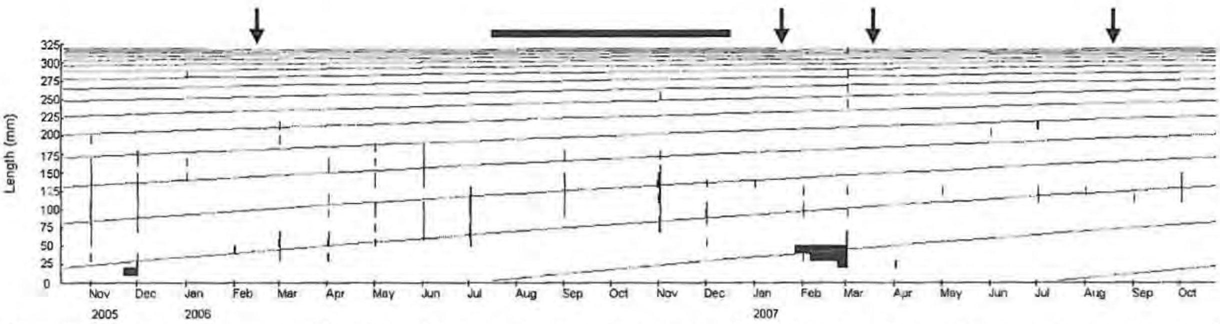

Figure 5.34: The monthly length frequencies and von Bertalanffy Growth Function curves for *Liza richardsonii* determined by ELEFAN I in FiSAT II. See Table 5.3 for calculated L_∞ and K values. The bar indicates the period when the mouth was open and the arrows, overwash events.

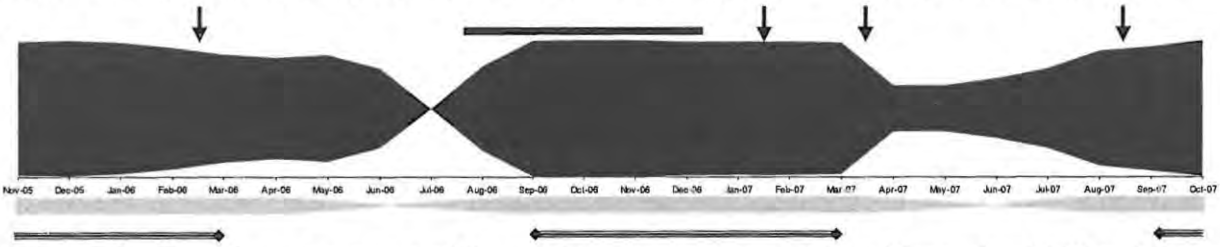

Figure 5.35: Recruitment patterns of *Liza richardsonii* calculated from November 2005 to October 2007 using FiSAT II. The bar indicates the period when the mouth was open and the arrows, overwash events.

5.3.8 *Myxus capensis*

The average length for each month for each gear varied from month to month with no specific patterns evident (Figure 5.37). During the first three months of the estuary being open, no *M. capensis* were sampled (Figure 5.37). The smaller individuals sampled from the channel (Figure 5.36.b.i) showed two main modal size classes for *M. capensis* of 30 - 40 mm and 80 - 90 mm, with very minor peaks at 160 – 170 mm and also 220 – 230 mm. During the initial closed period (Figure 5.36.b.ii) the modal length for the smaller channel individuals was 90 – 100 mm SL, just short of the length at age 1 year. After re-closing (Figure 5.36.b.iv) two modal classes of 30 – 40 mm and 70 – 80 mm were observed. The majority (98.6 %) of the larger fish sampled from the channel (Figure 5.36.c.i) were in the size classes above length at age 1 year (~ 100 mm). Overall the pooled data identified that there were two modal peaks present throughout the estuary during both closed and open periods. A modal peak varying between 20 – 40 mm indicates a cohort comprised of juvenile fish (Figure 5.36.a.iv), while another modal peak over the 70 – 100 mm size classes suggests another less abundant cohort of larger individuals.

The original (ind.m^{-2}) and adjusted CPUE (ind.2000m^{-2}) estimates of *M. capensis* of each month are shown in Figure 5.38. The growth increment was estimated as 4.10 mm.month^{-1} using the adjusted and pooled data (Table5.3).

The length frequency distributions for *M. capensis* were used to estimate the von Bertalanffy growth parameters K (0.18), L_∞ (330.75 mm) and t_0 (Table 5.3), which were plotted ($L_t = 330.75[1-\exp(-0.18(t-t_0))]$) on to Figure 5.39.

Other growth parameters: $t_{\max}$, ϕ', OEL and PEL are provided in Table 5.3. The growth performance index (ϕ') was calculated at 4.29. Instantaneous total (Z) mortality rates calculated using length-converted catch curves and the Jones and van Zalinge plots were 0.71 year^{-1} and 3.84 year^{-1} respectively (Table 5.3). Recruitment patterns for *M. capensis* were estimated for each sampling year (Figure 5.40). Although recruitment appeared to occur throughout the year higher values were observed in summer (Figure 5.40).

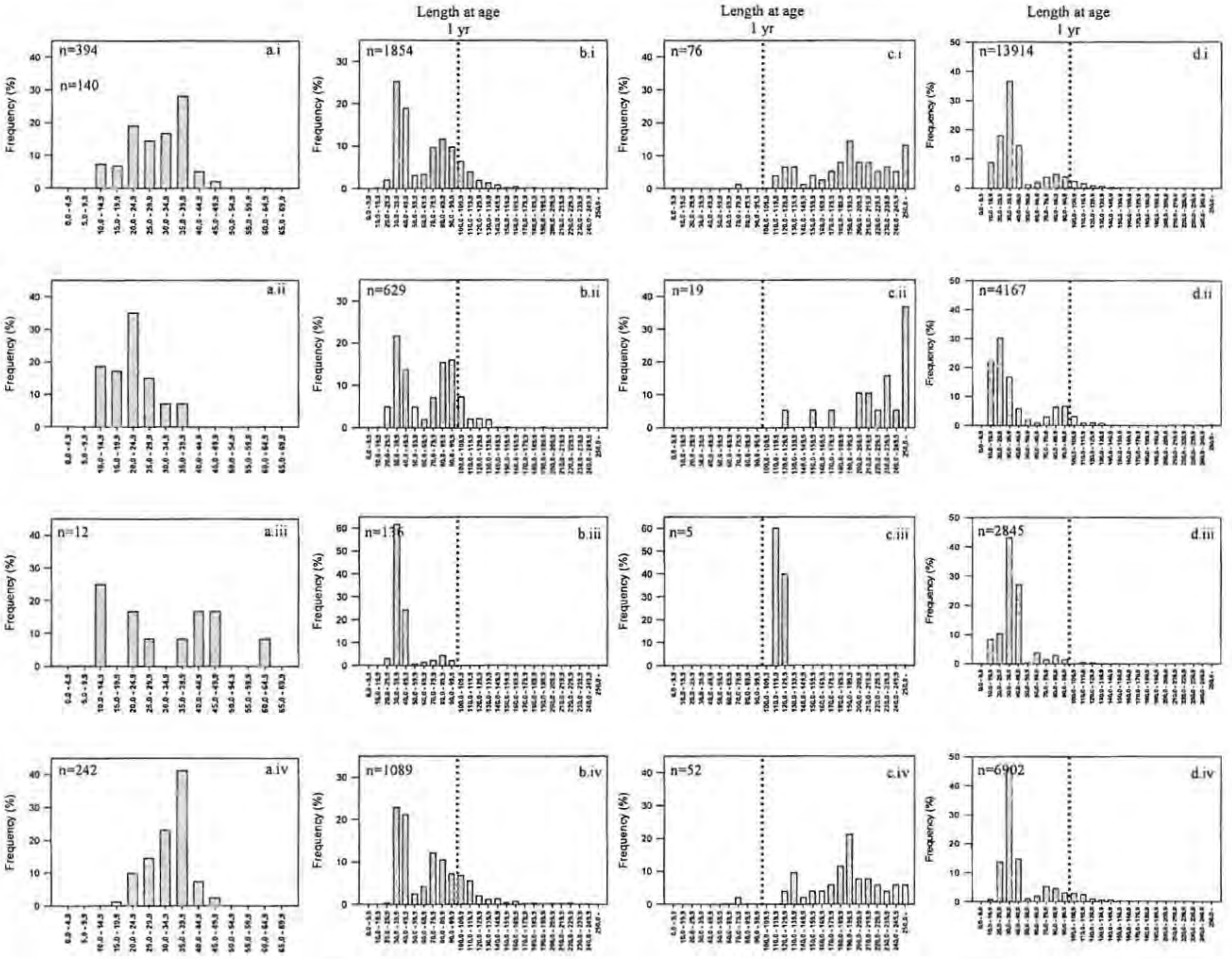

Figure 5.36: The length frequency cohorts of *Myxus capensis* in the Mpekweni Estuary. (a), (b) and (c) represent the data recorded from the 5 m, 30 m and 50 m seine nets. The adjusted and pooled data are represented by (d). The combined cohorts are shown in each graph labelled .i for each seine net. The initial closed, open and re-closed periods are represented by .ii, .iii and .iv. Dotted lines indicate estimated length at age.

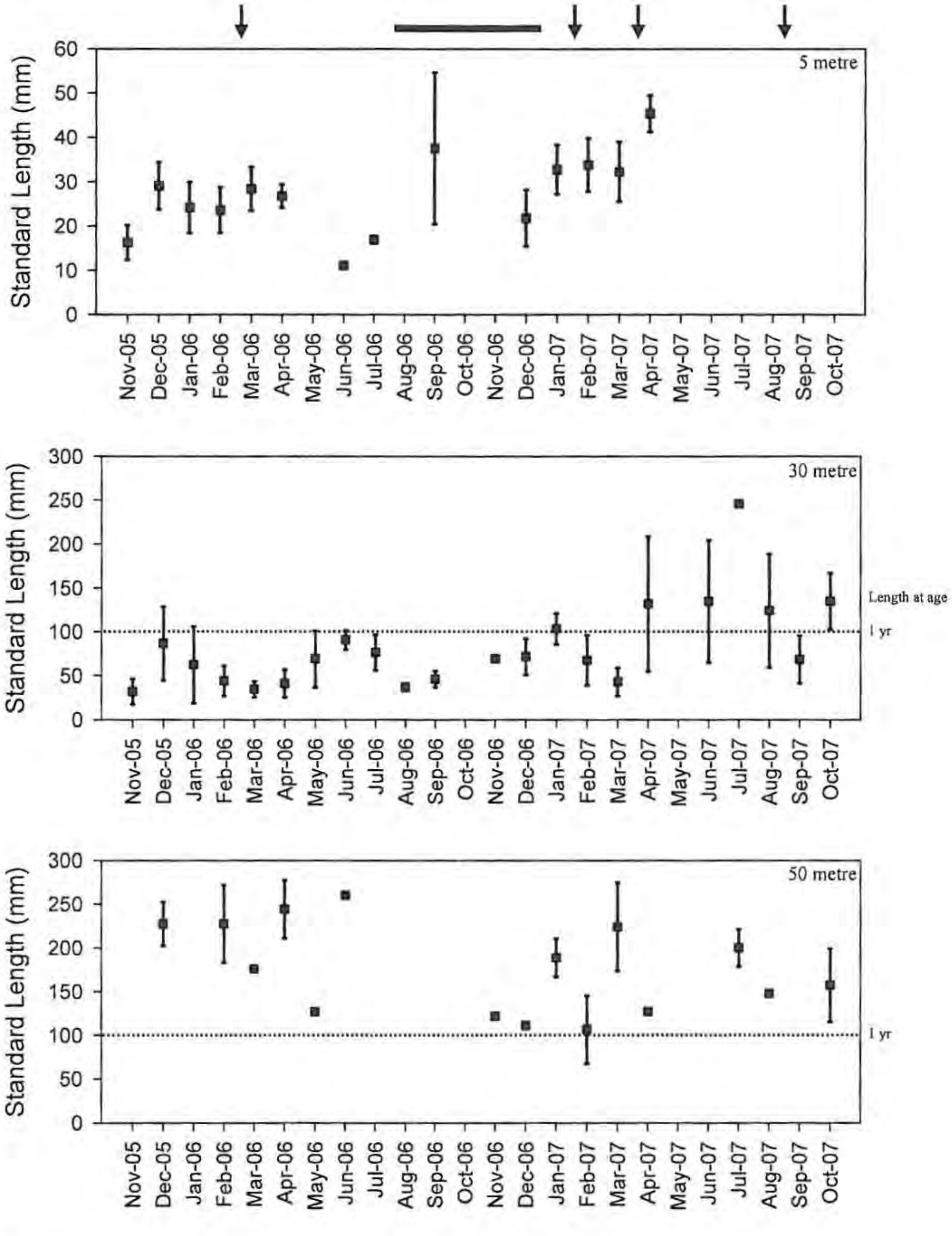

Figure 5.37: The average length (± SD, error bars) of *Myxus capensis* recorded for each month in the Mpekweni Estuary. The top, middle and bottom graphs show the fish sampled using the 5 m, 30 m and 50 m seine nets respectively. Dotted lines indicate estimated length at age. The bar indicates the period when the mouth was open and the arrows, overwash events. No data points indicate that no fish were sampled during that month.

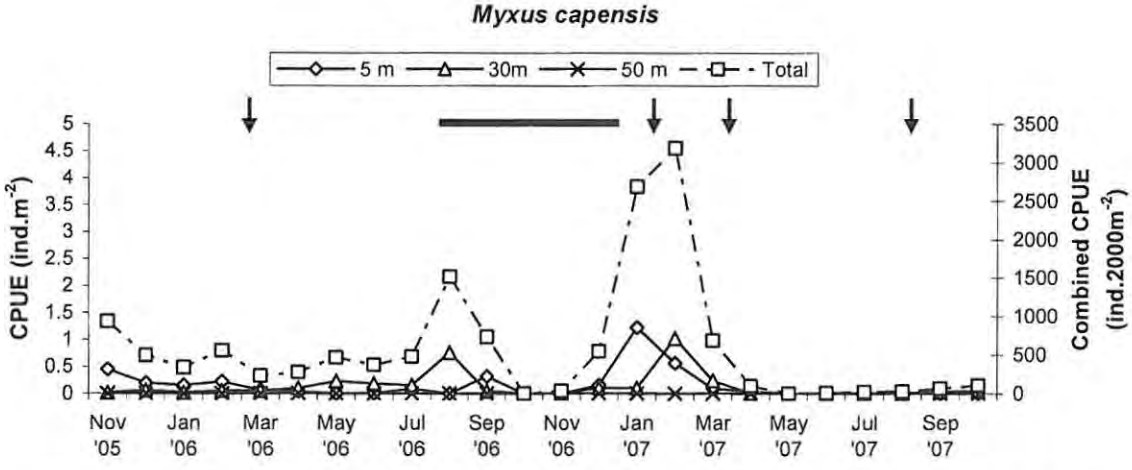

Figure 5.38: The CPUE (ind.m^{-2}) of *Myxus capensis* sampled by each seine net for each month and the adjusted and pooled CPUE (ind.2000m^{-2}). The bar indicates the period when the mouth was open and the arrows, overwash events.

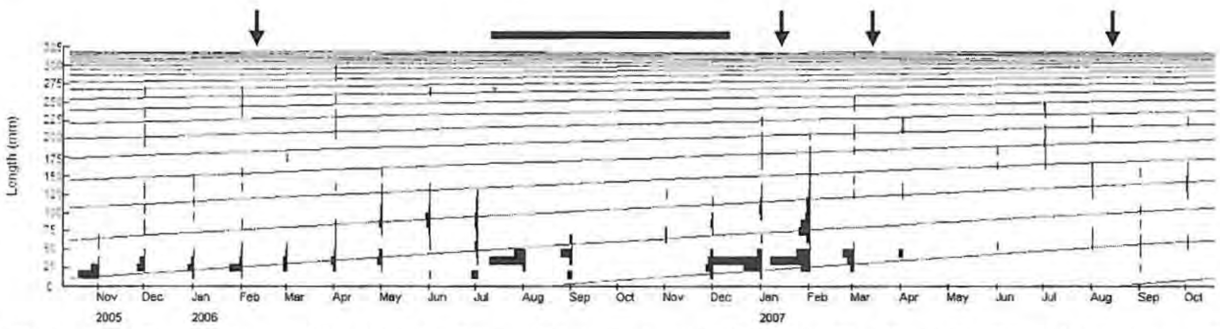

Figure 5.39: The monthly length frequencies and von Bertalanffy Growth Function curves for *Myxus capensis* determined by ELEFAN I in FiSAT II. See Table 5.3 for calculated L_∞ and K values. The bar indicates the period when the mouth was open and the arrows, overwash events.

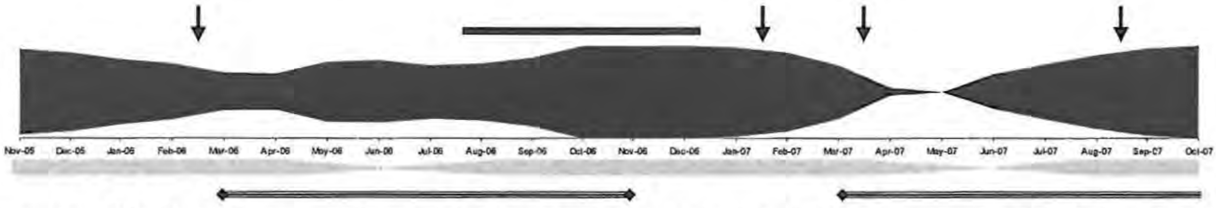

Figure 5.40: Recruitment patterns of *Myxus capensis* calculated from November 2005 to October 2007 using FiSAT II. The bar indicates the period when the mouth was open and the arrows, overwash events.

5.4 DISCUSSION

The eight numerically dominant species sampled from the estuary were analysed to determine recruitment patterns, temporal distribution of age classes and the tracking of identifiable cohorts to indicate growth parameters. The estuarine spawners *Gilchristella aestuaria* and *Glossogobius callidus,* had normally distributed populations throughout the period of study (Figures: 5.6 and 5.11). The sole, *Solea turbynei*, also showed a similar distribution (Figure 5.21), which is indicative of continuous recruitment throughout the duration of the sampling and evidence of estuarine spawning (Cyrus, 1991). For two of the species, *G. aestuaria* and *S. turbynei*, the VBGF plots did not provide any particular evidence of episodic recruitment (Figures: 5.9 and 5.24), suggesting that larval/juvenile recruitment was continuous through out the year although there was evidence of increased recruitment during the summer months. Despite the fine mesh size of the 5 m seine net there may not have been complete representation of the larval and juvenile fish in the samples. *Gilchristella aestuaria* is the only EUC I species that showed an increase in abundance after the estuary closed. This could be attributed to the initially reduced salinity levels (Chapter 3) cueing a spawning event (Newton, 1996; Strydom and Whitfield, 2000; Strydom *et al.*, 2002). An apparent increase in abundance of *G. aestuaria* was also observed in months sampled after overwash events (Appendix, Figure VII).

As an alternative explanation to a large spawning event, the higher abundances of the smaller *G. aestuaria* may reflect the reduced predation impact of the larger teleosts and an increase in the inundation of the littoral zone providing safer areas for the smaller fish, thus increasing survival rates (Becker and Laurenson, 2008). The reduction in abundance of *S. turbynei* and the lack of clear cohorts after the estuary breached could be evidence of emigration from the system during the open period (Figure 5.23). *Glossogobius callidus*, however, still showed clear cohorts despite a reduction in abundance (Figures: 5.13 and 5.14). These cohorts do not appear to be linked to either the breaching or overwash events but seem to be driven by seasonality. Summer maxima and winter minima recruitment estimates were evident in *G. callidus* despite the overall abundances and biomass estimates being affected by the breaching event. The reduction in abundance of *G. callidus* sampled in the estuary could be attributed either to the fish being washed out with the breaching of the estuary, or, possibly, to reduced sampling effort as only the mouth area was sampled (due to shallow depth and lack of access to the rest of the estuary) during the open period or increased predation. Importantly, this study showed that continuous recruitment of the estuarine spawning species takes place, although the peaks in the values were recorded in the warmer summer months, coinciding with the spawning season and increases in food availability (Talbot and Baird, 1985). The breaching event had little affect on the size distribution of the EUC I species, however a drop in overall abundance of the EUC I species was observed. This decrease was, however, not as marked as the marine spawning species.

Atherina breviceps is an estuarine resident that undergoes annual marine spawning migrations (Whitfield, 1998). Unlike *G. aestuaria* which is recorded only in the surf zone after mouth opening events (Whitfield, 1989a; 1989b), *A. breviceps* is frequently found in the near-shore marine environment (Lasiak, 1984; Bennett, 1989b). *Atherina breviceps* spawns during the spring and summer months, peaking between September and January (Whitfield, 1998). The recruitment patterns observed during this study reflect this spawning cycle (Figure 5.5). The overall length frequency analysis (Figure 5.1) showed three modal peaks occurring over the duration of the study. These peaks were dominated by mature fish (40 mm SL) (Ratte, 1989), indicating that the majority of this species in the estuary were mature. Previous evidence of *A. breviceps* emigrating from estuaries during flooding events may account for the observed decline in abundances of *A. breviceps* during the open period (Whitfield, 1989b). During the open phase, the majority of *A. breviceps* sampled in the estuary were sexually mature (according to literature [Ratte, 1989]). After the estuary closed smaller larval and juvenile fish dominated the populations (Figures: 5.1 and 5.4). The increase in the smaller size classes may be linked to recruitment during the various overwash events that occurred.

The maximum estimated recruitment patterns recorded for the marine spawners during the study coincided with their spawning seasons (Whitfield and Kok, 1992). Harrison and Whitfield (1995) used length frequencies and species abundance to support the utilisation of estuaries as nursery areas for juvenile marine migrant species. The size distribution and abundances of *R. holubi* (Figure 5.16) in this study showed a skewed distribution towards the smaller size classes. This is further indication of the increased number of smaller (juvenile) individuals within the system suggesting that the juvenile fish utilise the estuary.

There was a clear increase in the number of juvenile *R. holubi* recorded in the littoral zone during the open period and after the estuary had closed (Figure 5.16). The adjusted and pooled data showed that the recruitment is not limited to the juveniles but also sub adults. The larger *R. holubi* individuals sampled covered a broader size range, suggesting the possibility of periodic recruitment, or that the larger individuals remained in the estuary (Figure 5.16.c). This is true until breaching occurs and then, not only did the total numbers fall, but the fish sampled were smaller. This result is consistent with the work of Blaber (1974) which indicated that *R. holubi* remain in estuaries until approximately 140 mm (SL). The *R. holubi* sampled in the 100 mm – 140 mm size categories may have remained in the estuary during the breaching event or possibly recruited from the marine environment during the open phase. This is corroborated by the lack of the larger *R. holubi* being sampled during the first sampling after the breaching event in August 2006 (Figure 5.17), although due to the shallowness of the estuary during the open period only the mouth region could be sampled and as a result the population sampled is likely to be an under-representation of the total. Unusually, in the re-closed period the overall modal peak of the *R. holubi* sampled from the channel (30 m seine net) was one length class higher than the initial closed period. This suggests that there has either been the retention of some individuals or that during the extended period during which the estuary remained open there was recruitment or re-recruitment of a broader range of age/length classes into the estuary.

In the first month of sampling during which the estuary was open (after breaching) all the marine migrant species (*S. turbynei*, *L. dumerilii*, *L. richardsonii* with the exception of *R. holubi*) and the freshwater mullet (*M. capensis*) were absent from the samples. *Rhabdosargus holubi* were only sampled in the shallow littoral zone of the estuary during this month of sampling and had an average length of 12.2 mm SL (± 2.8 SD). The lack of any larger marine migrants sampled in the channel suggests that emigration to the marine environment had occurred. Cohort analysis of *R. holubi* in the East Kleinemonde Estuary by James (2007) allowed the author to determine possible recruitment time of juvenile and larval fish, and linked the period of recruitment to possible overwash events as a means of recruitment.

Retrospective analysis of the VBGF curve of *R. holubi* sampled during this study puts T_0 at -0.46 (or five and a half months) placing the actual spawning and gestation period within the known spawning period of July to February (Whitfield, 1998). Literature on similar sparid species such as *R. sarba* suggest an incubation of ~ 24 – 30 hours and 30 days to obtain ~ 10 mm SL (Leu, 1994; Mihelakakis and Yoshimatsu, 1998; Radebe *et al.*, 2002; Hughes *et al.*, 2008). The size classes of the fish present in the samples during the open and re-closed period indicate that the recruitment of the smaller size classes sampled from November 2006 to February/March 2007 were likely to have recruited during the open period where the open mouth coincided with the spawning period (Figure 5.19). There was also evidence of recruitment into the system after the estuary closed, possibly during overwash events. The last cohort to enter the system according to the VBGF plot would most likely have entered some time between February and April 2007 (Figure 5.19).

The other non-estuarine spawning species analysed in this chapter were the larger Mugilidae species which covered a larger range of sizes. Based on estimated ages, the population encompassed a number of age classes up to 3 years and older (van der Horst and Erasmus, 1981; de Villiers, 1987; Whitfield, 1998). The length classes showed numerous peaks for the mullet species, indicating a number of cohorts in the system from various recruitments events. Unlike the estuarine spawners, there are gaps in the length frequency distribution of the mullet which could be attributed to a lack of steady recruitment due to the closed phase of the mouth. Although the mullet, like *R. holubi*, are also known to utilise overwash events as a means of recruitment (James, 2007; Kemp and Froneman, 2004), these events are infrequent and thus minimise the chances of consistent recruitment. During the initial closed period of the study, the VBGF plots (Figures: 5.29, 5.34 and 5.39) identified the recruitment of a cohort for all three mullet species that could be attributed to an overwash event. This recruitment, however, is more likely to have occurred during the breaching event prior to the start of the study (September/October 2005). Later, cohorts show evidence of recruitment in conjunction with the open period (August 2006 to December 2006), and the loss of the larger cohorts suggests the emigration of the larger fish into the marine environment at the same time.

The annual mortality of the various species indicated that there was a greater annual survival (53 to 68 %) of the larger Mugilidae species, while the smaller *A. breviceps* and *G. aestuaria* had low annual survival rates of 3 % and 7 %, respectively. The estimated annual survival rates of *R. holubi*, *G. callidus* and *S. turbynei* were 33 %, 21 % and 18 %, respectively. Literature on survival and mortality rates for these and similar fish species is limited (Clark *et al*., 1994), however, there are some estimates for comparative species. Thompson (1959 cited in Blaber, 1973) estimated an annual mortality rate of 78 % for *R. sarba*, which was higher than recorded for the *R. holubi* (67 %). In 1971, Blaber (1973) estimated an 80 % mortality rate for *R. holubi* over seven months using mark and recapture techniques, but in the subsequent year negligible mortality rates were observed. Blaber (1973) linked the high variation in mortality to decreased fish and piscivorous bird densities in the second year.

In the southern Arabian Gulf, Grandcourt *et al*. (2011) estimated an annual survival rate of 35 % for *R. sarba*, which was very similar to the survival rate of *R. holubi* in the Mpekweni Estuary. The annual survival rate of the Mugilidae in the Mpekweni Estuary was higher than that recorded for *L. aurata* in the Caspian Sea, which exhibited an annual survival rate of 49 % (Fazli *et al.*, 2008). Hellmair (2011) estimated the annual instantaneous mortality of a highly endangered goby species to be ~ 97.6 %, which is much higher than estimated for *G. callidus* during this study. An Atherinidae species similar to *A. breviceps* was studied in estuarine systems in northern Greece where annual mortality rates were estimated to be ~ 72 % (Koutrakis *et al.*, 2004). This estimate is lower than estimates in the Mpekweni estuary. The breaching event and the reduced recruitment during the re-closed period may have reduced mortality estimates for the *A. breviceps* population in the Mpekweni Estuary. Estimates of annual mortality for Soleidae species in Kuwait waters (83 % Bawazeer [1987 cited in van Schie and de Boer, 2003]) and off Inhaca Island, Moçambique (81.5 % van Schie and de Boer [2003]) were similar to that of *S. turbynei* in the Mpekweni.

Clark *et al.* (1994) suggested that a monthly mortality estimate for juvenile fish in the surf zone of False Bay, South Africa, was ~ 30 % for most species. This was similar to the monthly mortality estimates recorded by Blaber (1973) for *R. holubi* (30 %). In the northern hemisphere, estimates for monthly flat fish mortality ranged between 31 % and 62 % (see Clark *et al.*, 1994; Meise *et al.*, 1999). Monthly mortality rates for the species sampled in the Mpekweni Estuary were lower with estimates ranging between 0 % and 5 % for the Mugilidae, 20 % to 26 % for *A. breviceps* and *G. aestuaria* and 9 %, 12 % and 13 % for *R. holubi*, *G. callidus* and *S. turbynei*, respectively. Comparing the smaller zooplanktivorous species, *A. breviceps* and *G. aestuaria* revealed that the survival rate of estuarine spawning *G. aestuaria* had a higher survival rate, which was also evident in the overall numbers, particularly after the breaching event and open period.

The lower monthly and annual mortality estimates of these fish species in the TOC Mpekweni Estuary indicate the benefits of these systems as stable protected areas and thus highlighting their functional importance as nursery areas along the South African coastline. Mortality estimates, however, as described by Blaber (1973) are subject to numerous factors including the densities of piscivorous birds. Through out this study although un-documented, there was a limited presence of piscivorous birds during the sampling periods (pers. obs.), which may account for the higher survival rates estimated.

Overall the growth estimates of the fish species during the study were in the range reported by the literature (Table 5.4) (Blaber, 1973; 1974; Beckley, 1984; Whitfield and Kok, 1992; Cowley, 1998; Lukey, 2006; James, 2007). Discrepancies in the growth rates between the different authors (Table

5.4) may be attributable to a variety of conditions and available resources within the different estuarine systems and the subsequent affect on growth rates (Sogard, 1992). The growth rates of the Mugilidae (Tables 5.3 and 5.4) were variable, and specifically in the case of *L. richardsonii* slower than the published lengths at age (year 1). The Mugilidae on average should be growing between 8.33 mm.month^{-1} and 10.00 mm.month^{-1} in their first year to achieve the reported length at age (year 1) (van der Horst and Erasmus, 1981; Bok, 1984 [cited in Whitfield, 1998]; de Villiers, 1987).

Table 5.4: Monthly growth increments (mm.month^{-1}) for the eight numerically dominant fish species sampled in the Mpekweni Estuary and previously published growth rates with size ranges where available.

	Atherina breviceps	*Gilchristella aestuaria*	*Glossogobius callidus*	*Rhabdosargus holubi*	*Solea turbynei*	*Liza dumerilii*	*Liza richardsonii*	*Myxus capensis*
This study	1.87	2.17	2.79	4.09	1.67	9.67	3.47	4.10
Lukey, 2006	1.90 11-51 mm SL	3.42 9-54 mm SL	0.30 9-98 mm SL	3.13 20-96 mm SL				1.75E-05 15-115 mm SL
Cowley, 1998				~ 8.00 20-150 mm SL		3.10 51-248 mm SL	8.40 49-300 mm SL	3.90 88-306 mm SL
Ratte pers comm. In Cowley and Whitfield, 2002 Ratte, 1989	3.33 19-62 mm SL ~ 5.00							
Talbot pers comm. In Cowley and Whitfield, 2002 Talbot, 1982		2.92 15-60 mm SL ~ 4.00						
Boullé, 1989 cited in Vorwerk, 2001			3.33					
Wallace and van der Elst, 1975; Beckley, 1984; James, 2007				~ 8.00 7-282 mm TL				
Whitfield and Kok, 1992				~ 8.00				10.00
Blaber, 1974				3.50-10.30[1]				
Van Schie and de Boer, 2003					3.30-13.20[1] 8-154 mm SL			
van der Horst and Erasmus, 1981						~ 10.00		
de Villiers, 1987							~ 16.00	
Bok, 1984 cited in Whitfield, 1998								8.30

[1] – winter minimum and summer maximum growth rates

The variation in the estimation of the growth rates of the different fish are more likely to be present, particularly amongst the larger fish species as the exclusion of the larger individuals results in an underestimation of growth rates (Worthington *et al.*, 1992; Griffiths, 2001c). The inability of the FiSAT II program to estimate maximum lengths for a number of fish species (Tables: 5.2 and 5.3) also highlights the problems associated with these techniques when assessing incomplete populations. These fish utilise the estuaries as nursery areas and therefore it can be assumed that the larger individuals will leave the estuary at the first opportunity once they have reached the age/size of emigration as was evident from the length frequency distributions. Thus, the populations in the TOCEs are not representative of the entire population structure. The marine spawning *R. holubi* has been reported to stay in the estuarine environment until 130 - 140 mm SL, after which they return to the marine environment (Blaber, 1974; Day *et al.*, 1981). The low abundance of the larger size classes of marine spawners can be partly linked to the emigration of fish prior to, or having reached sexually maturity or through net avoidance (pers. obs; Cowley, 1998; Vorwerk, 2001).

Rhabdosargus holubi reach sexual maturity at 150 mm SL (Wallace, 1975b; Whitfield, 1998), *Liza dumerilii* (van der Horst and Erasmus, 1981; Vorwerk, 2001) and *L. richardsonii* (de Villiers, 1987; Vorwerk, 2001) are sexually mature at 180 mm SL. Male *M. capensis* mature at 190 mm SL and the females at 230 mm SL (Bok, 1983).

5.4.1 Summary

The evenly distributed population structure of the estuarine spawning species through-out the study, indicated a stable population with continuous recruitment that was predominantly unaffected by the breaching event. The length frequency analyses identified a non-continuous population distribution for the marine spawning species as demonstrated by the multiple modal peaks. This suggests that recruitment into the estuary was sporadic, which is not surprising given that the estuary was separated from the marine environment by the presence of a sand bank at the mouth for ~ 79 % of the duration of the study. The length frequency and retrospective analyses of cohorts suggest that recruitment of the marine spawning species into the Mpekweni Estuary takes place mainly during the period when the estuary was open and to a lesser extent, during the overwash events.

CHAPTER 6

VARIABILITY IN THE RECRUITMENT OF ICHTHYOPLANKTON DURING THREE DIFFERENT HYDROLOGICAL PHASES

6.1 INTRODUCTION

Estuaries represent important nursery areas for both estuarine and marine spawning invertebrate and vertebrate species (Wallace *et al.*, 1984; Whitfield, 1998; Young *et al.*, 1997; Vivier *et al.*, 2010). Without direct access to the estuary, organisms with an obligate estuarine phase are affected by their inability to recruit into the system (Vivier and Cyrus, 2001). The steep gradient in geological structure along the Eastern Cape coastline contributes to reduced catchments sizes of estuaries within the region (Crossley, pers com). In conjunction, the generally low rainfall recorded in the Eastern Cape region results in low freshwater runoff into the rivers and estuaries (Kopke, 1988). As a consequence, the majority (~70%) of the estuaries within the Eastern Cape region do not experience a continuous inflow of fresh water (Whitfield, 1992). This reduced flow is exacerbated by freshwater abstraction for domestic and agricultural demands. The reduced or non-existent flow rate contributes to the closing of the estuarine mouths often for duration in excess of 95 % of the year (Cowley *et al.*, 2001).

Mouth closure limits the potential for recruitment of marine and estuarine organisms into TOCEs (Whitfield, 1996). Several authors have suggested that the reduced diversity values of zooplankton and ichthyofauna recorded in southern African TOCEs in comparison to permanently open systems within the same geographic region can be related to the reduced recruitment opportunities (Begg, 1984; Bennett, 1989a; 1989b; Whitfield *et al.*, 1989; Cowley *et al.*, 2001). Recruitment of marine spawning species into TOCEs can be achieved in one of two ways; either through direct recruitment when the estuary breaches or via overwash events that involve the marine waters washing over the sand bar during spring high tides or severe storms (Whitfield, 1992; Cowley *et al.*, 2001; Vivier and Cyrus, 2001; Kemp and Froneman, 2004).

Breaching events are recognised as the main mechanism of emigration and immigration of organisms in and out of the TOCEs in southern Africa (Whitfield, 1998; Cowley *et al.*, 2001). The importance of overwash as recruitment events for ichthyofauna into southern African TOCEs is not as well studied. The recruitment mechanism via overwash events has been demonstrated using indirect methods including the presence of stranded larvae in pools on the berm (Cowley, 1998;

Cowley *et al.*, 2001) or the back extrapolation of modal length frequencies of fish which were then correlated to specific overwash events (Whitfield, 1992; Cowley, 1998; Bell *et al.*, 2001; Vivier and Cyrus, 2001; Cowley and Whitfield, 2002). Froneman (2004) demonstrated that the increase in species diversity within the plankton community of a TOCE following an overwashing event was attributed to an increase in contribution of marine spawning species to the total zooplankton abundance and biomass. Bernard and Froneman (2005) and Froneman (2006a) demonstrated that the peak in recruitment of the swimming prawn, *Palaemon peringueyi*, into the TOC West Kleinemonde Estuary, occurred during breaching events, with only minor recruitment occurring during the overwash event.

The presence of estuarine dependant ichthyofauna within the surf zone has been documented along the South African coast particularly in the vicinity of estuarine mouths (Harris and Cyrus, 1996; Whitfield, 1989a; Harris *et al.*, 1999; Bell *et al.*, 2001; Cowley *et al.*, 2001; Watt-Pringle and Strydom, 2003; James *et al.*, 2008a), Bell *et al.* (2001) identified a strong seasonal component to the waiting time and recruitment potential of surf zone ichthyofauna that may utilise overwash events to enter South African TOCEs. The strong association of larval stages of estuarine-dependant ichthyofauna suggest the zone is used as intermediate nursery area prior to recruitment (Strydom and d'Hotman, 2005). The observed utilisation of trough habitats as a possible means of maintaining position in the surf zone, may thus allow energy conservation prior to possible overwash events (Watt-Pringle and Strydom, 2003).

Only a single study has attempted to quantify the recruitment of both invertebrates and vertebrates into TOCEs during overwash events (Kemp and Froneman, 2004). The results of this study indicated that overwash events provide a large contribution to the recruitment of fish species into TOCEs, with an estimated potential recruitment of between 8 000 and 33 500 larval *R. holubi* per hour during a high spring tide. These results suggest that overtopping events may potentially play an important role in structuring the ichthyofaunal assemblages within TOCEs. The aim of this study was to quantitatively estimate the recruitment of ichthyoplankton into the Mpekweni Estuary during distinct hydrological phases: the overwash phase when the estuary was closed and during the two phases experienced by TOCEs when breaching occurs and the mouth remains open for an extended period of time, the initial out-flow phase and the subsequent tidal phase (Whitfield *et al.*, 2008).

6.2 MATERIALS AND METHODS

6.2.1 Sampling procedure

Sampling of water washing over of the sand-bar/berm during the closed period and water flowing through a channel in the berm during the open period was conducted on two separate occasions during overwash events and twice during the open phase (out-flow and tidal phases). Sampling was conducted using a custom-made funnel-trap (1.5 m long with a mouth opening of 1 m by 0.5 m) according to Kemp and Froneman (2004). The trap was covered with a mesh size of ~ 500 µm which funnelled down to a removable cod-end with a mesh size of 100 µm. The funnel trap was anchored on the substratum on the backward slope of the sand bar in the deepest part of the channel. Due to tidal and general water flow pressure, anchors were buried in the sand and held in place by weights. A General Oceanics flow meter was attached to the net to determine current speed of overwash waves ($m.s^{-1}$) which was then used to calculate the volume of water filtered by the trap during each sampling period. After each sampling period, the cod-end was removed and all its contents were filtered through a 300 µm mesh to remove sand and other organic material. The samples were then preserved in 10 % buffered formaldehyde for later analysis in the laboratory.

Figure 6.1: The image on the left shows the anchoring of the trap on the sand berm and the image on the right shows the mouth of the trap and the attached flow meter.

As discussed in the introduction of this chapter, the question is not whether there are ichthyofauna in the surf zone but under what conditions is recruitment most successful. On two separate occasions, overwash events were sampled during the day and night. During the first spring high sampling period, eight tidal surges over an hour-long period were sampled during the daytime and five during the night. During the second sampling period, a total of 12 day and six night-time tidal surges were sampled in an hour. Overwash surges were sampled by deploying the trap for 60 seconds during each surge according to Kemp and Froneman (2004).

When the estuary breached, the channel water was sampled during the initial out-flow phase and later during the tidal phase. The out-flow phase was sampled just after the estuary had breached, with sampling encompassing a 24 hour period from early morning of the 7th to the early morning of the 8th of September 2006. Tidal regimes in open TOCEs are usually established quickly with rapid increases in salinity of the lower and middle reaches before extending into the upper reaches (Whitfield *et al*., 2008). However, rainfall and terrestrial run-off influence river flow which has a subsequent affect on how long it takes for the salinity in the estuary to becomes spatially uniform (Whitfield *et al*., 2008). A period of a week was deemed a suitable enough time for the estuary to enter the tidal phase before sampling commenced. The limited variation in the salinity during this sampling period (Figure 6.2) indicates that the estuary was in the tidal phase. The sampling of the tidal phase took place over a period of 24 hours from the 13th to the 14th of September 2006. Samples were collected every two hours during the out-flow phase and every four hours during the tidal phase. Day time and night time samples were pooled and analysed separately.

At every sampling interval the water temperature (°C), salinity and dissolved oxygen ($mg.L^{-1}$) were recorded using the equipment described in Chapter 3. Flow meter readings were taken and water depth at the mouth of the trap and the width of the channel (m) were also recorded at each sampling interval with a surveyor's tape measure to estimate the volume of water flowing through the open mouth and though the trap.

6.2.2 Sample analysis

Fish species were counted and identified using Smith and Heemstra (1991), and the abundance data expressed as $ind.m^{-3}$ for the overwash events and $ind.m^{-3}$ for the open phases.

6.2.3 Statistical analysis

Margalef's species richness and Shannon-Weiner diversity indices were calculated for each hydrological phase using PRIMER v.5.2.4 (Clarke and Warwick, 1994). Data were transformed: Log(x+1) and a Bray-Curtis similarity matrix was generated using PRIMER v.5.2.4 and a multi-dimensional scale (MDS) plot calculated. SIMPER (PRIMER v.5.2.4) was run to identify the species responsible for the different groups identified in the MDS plot and to determine whether the groupings identified were significantly different from one another.

6.3 RESULTS

6.3.1 Physico-chemical variables

The salinity of the water during the overwash events was 35. The estuarine water temperature during the sampling period was 23 °C, while that of the marine water overwash was 18 °C (data not shown). Physico-chemical variables fluctuated throughout the day during the out-flow phase with temperature ranging from 15.5°C to 20.9°C and salinity between eight and 39. Water temperature decreased as the tidal waters flowed into the estuary, at the same time there was an increase in dissolved oxygen concentrations ($mg.L^{-1}$) due to the inflow of well-aerated inshore waters into the estuary. During the tidally dominated phase the water temperatures ranged from 15.1°C to 19.3°C and salinity between 30 and 40 (Figure 6.2).

6.3.2 Overwash events

A total of five species were sampled during the first overwash event, and six during the second. The average ichthyofaunal recruitment during the day-time and night-time of the first overwash event was 4.19 $ind.m^{-3}$ (± 3.10 SD) and 6.68 $ind.m^{-3}$ (± 4.10 SD), respectively (event average: 5.44 $ind.m^{-3}$ ± 3.53 SD). During the second overwash event, the average recruitment abundance for the day-time samples was 1.49 $ind.m^{-3}$(± 2.60 SD) and 11.79 $ind.m^{-3}$ (± 18.20 SD) during the night (average: 6.64 $ind.m^{-3}$ ± 12.92 SD). The species sampled during the overwash events (Figure 6.4) consisted of estuarine spawning species (EUC I), marine spawning species (EUC II) and a catadromous species (EUC V) which contributed 24.7 %, 72.1 % and 3.2 % to the total abundance, respectively. There were no significant differences in the abundances of estuarine recruits recorded between the two overwash events ($F_{(1, 29)} = 0.05$ $p > 0.05$). Similarly there were no significant differences in the abundance between the day- and night-time samples (first event: $F_{(1, 11)} = 0.70$ $p > 0.05$; second event: ($F_{(1, 16)} = 0.94$ $p > 0.05$) although there was a trend of higher abundances at night (Figure 6.3).

During the first overwash event (Table 6.1), *Rhabdosargus holubi* made up the bulk of the samples (60 %), with an average abundance of 3.25 $ind.m^{-3}$ (± 2.05 SD). The Gobiidae (20.24 % of the total samples) with an average abundance of 1.10 $ind.m^{-3}$ (± 1.63 SD) was the second most abundant group sampled. During the second overwash event (Table 6.1), the Mugilidae were the most numerous, contributing 68.52 % of the total abundance (average recruitment: 4.55 $ind.m^{-3}$ ± 10.17 SD), followed by *Atherina breviceps* with 14.31 % (average recruitment: 0.95 $ind.m^{-3}$ ± 1.46 SD) and *R. holubi* (average recruitment: 0.70 $ind.m^{-3}$ ± 1.40 SD; contribution: 10.54 %). With the exception of *R. holubi*, Mugilidae and Gobiidae spp., which had average abundances > 1.1 ind.m^{-3}, the abundances of the remaining species recorded during the overwash events had average combined (day/night) daily values < 1.00 ind.m^{-3}.

Table 6.1: The abundance and species contribution of ichthyofauna collected in the funnel trap during the two overwash events. (1 and 2 = sampling trip day 1 and day 2, respectively; D and N = day-time and night-time samples, respectively).

Species	**Sampling trip**	**Day/ Night**	**Abundance (ind.m^{-3} ± SD)**	**Percentage Contribution**
Rhabdosargus holubi	1	D	2.20 ± 1.90	52.51
	1	N	4.30 ± 1.90	64.37
	2	D	0.30 ± 0.10	20.13
	2	N	1.10 ± 2.10	9.33
Monodactylus falciformis	1	D		
	1	N		
	2	D	0.20 ± 0.40	13.42
	2	N		
Atherina breviceps	1	D	0.20 ± 0.30	4.77
	1	N	0.09 ± 0.00	1.35
	2	D	0.60 ± 1.30	40.27
	2	N	1.30 ± 1.80	11.03
Myxus capensis	1	D	0.09 ± 0.00	2.15
	1	N	0.09 ± 0.00	1.35
	2	D	0.09 ± 0.00	6.04
	2	N	0.40 ± 0.10	3.39
Mugilidae	1	D	1.60 ± 0.70	38.19
	1	N	0.10 ± 0.30	1.50
	2	D	0.30 ± 0.50	13.42
	2	N	8.90 ± 14.20	75.49
Gobiidae	1	D	0.10 ± 0.20	2.39
	1	N	2.10 ± 1.90	31.44
	2	D	0.10 ± 0.30	6.71
	2	N	0.09 ± 0.00	0.76

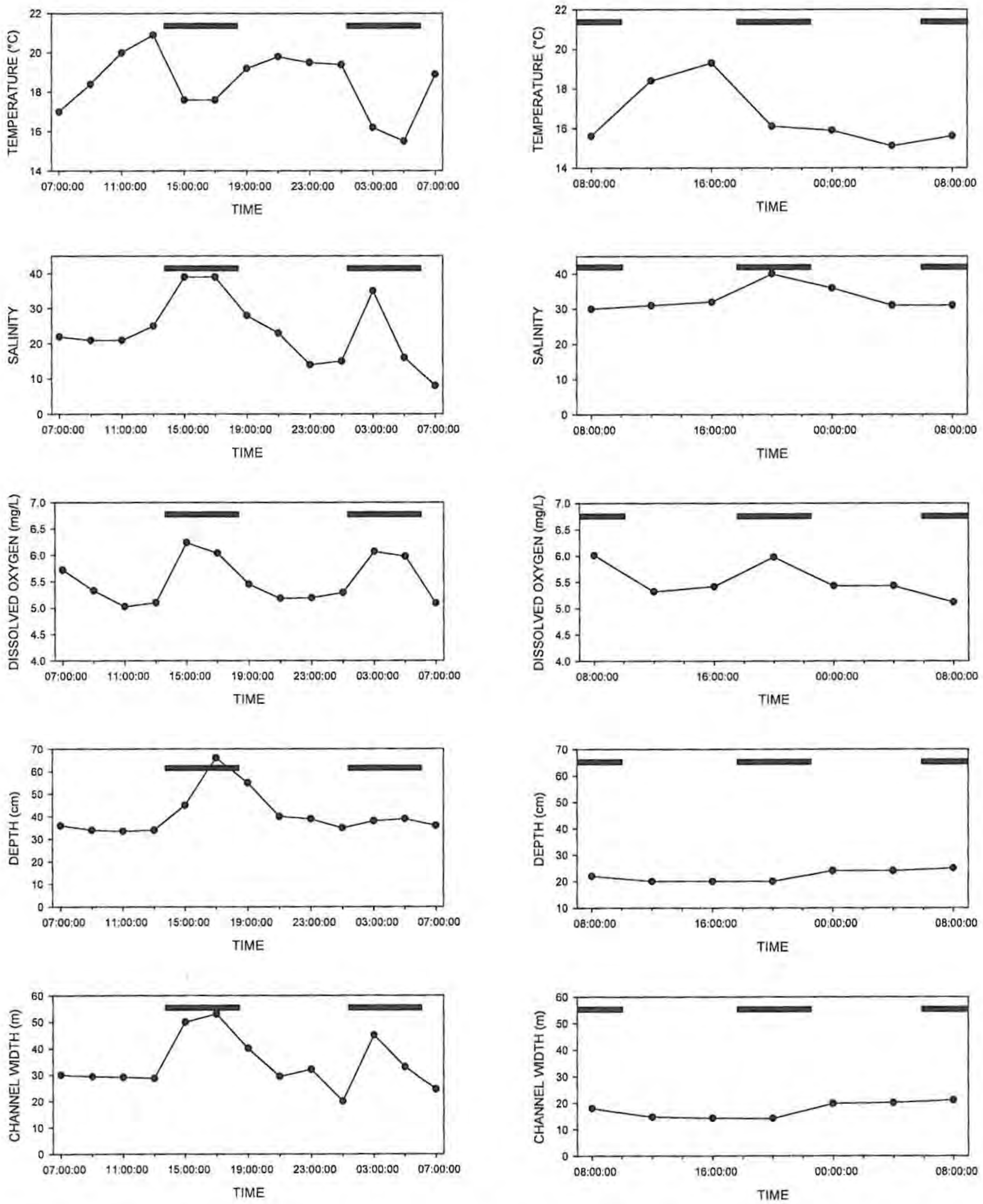

Figure 6.2: The physical and chemical parameters during the out-flow phase (all the graphs on the left-hand side) and the tidal phase (all the graphs on the right-hand side) of the Mpekweni Estuary. The horizontal bars indicate the periods of high tide. From the top the graphs indicate temperature (°C), salinity, dissolved oxygen (mg/L), channel depth (cm) and channel width (m).

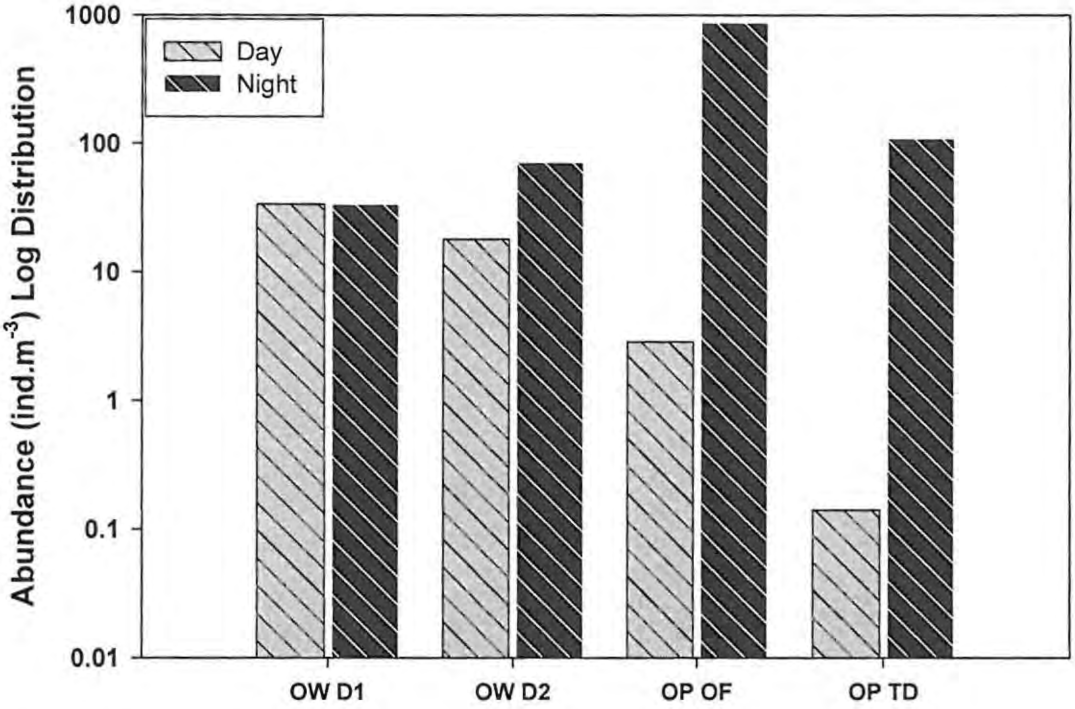

Figure 6.3: The total abundance (ind.m^{-3}) for the day and night sampling periods during the two overwash events (OW D1 = overwash day 1 and OW D2 = overwash day 2) and the two open mouth phases (OP OF = open out-flow phase and OP TD = open tidal phase).

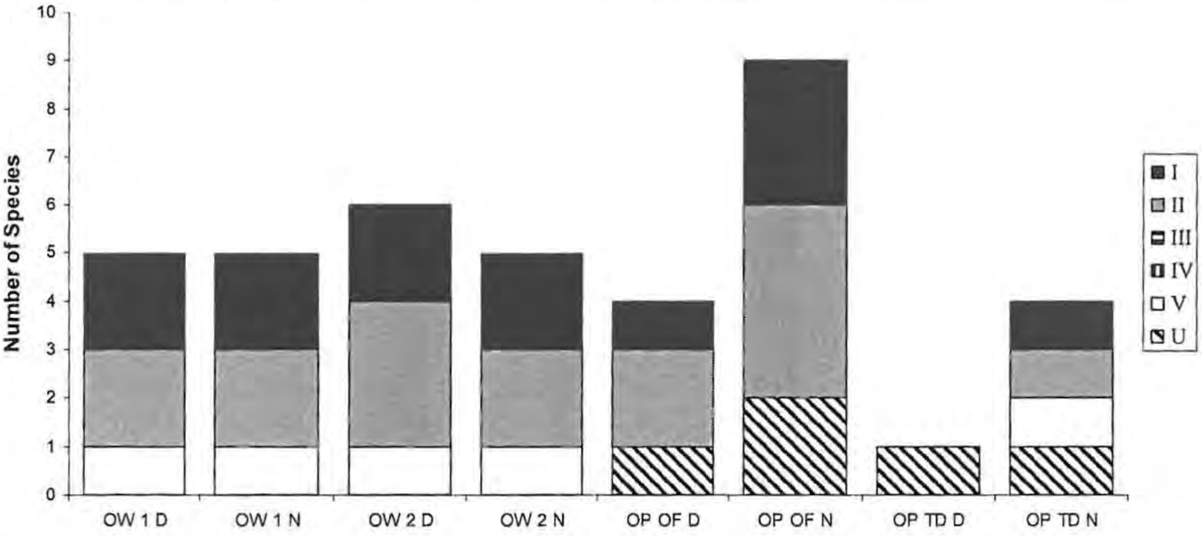

Figure 6.4: The number of ichthyofaunal species collected during each sampling event pooled into day and night categories. The numbers of fish species from each estuarine utilisation category are also presented. OW = overwash, 1 = first sampling period and 2 = second sampling period, OP OF = open out-flow phase, OP TD = open tidal phase, D = day-time sampling, N = night-time sampling, I – V indicate estuarine utilisation categories (Whitfield, 1994b) and U indicates unknown utilisation category.

6.3.3 Open phase

A total of ten fish species/groups were recorded during the period when the mouth breached and the estuary was open (Table 6.2). Nine species/groups were recorded during the out-flow phase of which five had a daily average abundance > 1.0 ind.m^{-3}. During the tidal phase only four species/groups were recorded recruiting into the estuary (Table 6.2), of which only two species/groups exhibited average abundance > 1.0 ind.m^{-3}. Recruitment abundance during the out-flow phase ranged between 0.00 ind.m^{-3} and 2.84 ind.m^{-3} during the day-time and between 0.00 ind.m^{-3} and 521.19 ind.m^{-3}, during the night-time (event average: 72.48 ind.m^{-3} ± 171.26 SD). During the tidal phase, the day-time samples ranged from 0.00 ind.m^{-3} to 0.14 ind.m^{-3} and between 0.00 ind.m^{-3} and 108.82 ind.m^{-3} during the night-time (event average: 24.36 ind.m^{-3} ± 58.99 SD). The species composition throughout the day-time sampling of the out-flow phase comprised one EUC I species, two EUC II species and one species of unknown EUC. During the night samples three EUC I species, four EUC II species and two unknown EUC species were recorded recruiting into the estuary (Figure 6.4). During the tidal phase of the open period only one species of unknown EUC was sampled during the day, while during the night samples one species of each of EUC I, II, V, and unknown EUC were recorded (Figure 6.4). During the out-flow phase, the estuarine species (EUC I) contributed 6 % to the total, and marine spawning species (EUC II) 94 %. Similarly, during the tidal phase, estuarine species (EUC I) contributed < 0.1 % to the total while the marine spawning species (EUC II) contributed > 99.9 % and the catadromous species (EUC V) < 0.1 %.

Individual species recruitment during the out-flow phase ranged between 0.05 ind.m^{-3} (± 0.18 SD) for *S. turbynei* and 43.59 ind.m^{-3} (± 150.41 SD) for the unidentified sparid species 2. During the tidal phase species abundance rates varied between 0.01 ind.m^{-3} (± 0.01 SD) for *M. capensis* and 12.09 ind.m^{-3} (± 29.54 SD) for the unidentified sparid species 2. The most abundant fish species under both conditions of the open period was the unidentified sparid species 2, which contributed 60.14 % during the out-flow phase and 66.56 % during the tidal phase. *Salpa salpa* was the second-highest contributing fish species (23.04 %, average abundance: 16.70 ind.m^{-3} ± 57.27 SD) during the out-flow phase, while *R. holubi* was the second-highest contributing species (33.35 %, average abundance: 6.06 ind.m^{-3} ± 14.76 SD) during the tidally dominated phase.

The total abundances of recruits recorded during the freshwater and tidal phases did not differ significantly ($F_{(1,16)} = 0.44$ $p > 0.05$), although higher abundances were recorded during the out-flow phase (Figure 6.3). Similarly there were no significant differences between the day and night samples during each of the open phases (out-flow: $F_{(1,10)} = 2.39$ $p > 0.05$; tidal:

($F_{(1, 4)} = 1.01$ $p > 0.05$), although there was a trend of higher numbers sampled during the night time samples (Figure 6.3).

Table 6.2: The abundance and species contribution of ichthyofauna collected in the funnel trap during the out-flow and tidal phases. (D and N = day-time and night-time samples respectively).

Species	Sampling Events	Day/ Night	Abundance (ind.m^{-3} ± SD)	Percentage Contribution
Rhabdosargus holubi	Out-flow	D		
	Out-flow	N	0.31 ± 0.77	0.22
	Tidal	D		
	Tidal	N	12.11 ± 20.86	33.39
Atherina breviceps	Out-flow	D		
	Out-flow	N	0.21 ± 0.51	0.14
	Tidal	D		
	Tidal	N		
Liza richardsonii	Out-flow	D	0.09 ± 0.21	18.37
	Out-flow	N	10.24 ± 24.18	7.09
	Tidal	D		
	Tidal	N		
Myxus capensis	Out-flow	D		
	Out-flow	N		
	Tidal	D		
	Tidal	N	0.01 ± 0.02	0.03
Gilchristella aestuaria	Out-flow	D	0.05 ± 0.12	10.20
	Out-flow	N	0.10 ± 0.26	0.07
	Tidal	D		
	Tidal	N	0.02 ± 0.00	0.06
Sarpa salpa	Out-flow	D	0.30 ± 0.73	63.27
	Out-flow	N	33.09 ± 81.06	22.90
	Tidal	D		
	Tidal	N		
Unidentified sparid 1	Out-flow	D	0.04 ± 0.10	8.16
	Out-flow	N	9.93 ± 24.32	6.87
	Tidal	D		
	Tidal	N		
Unidentified sparid 2	Out-flow	D		
	Out-flow	N	87.18 ± 212.63	60.34
	Tidal	D	0.05 ± 0.08	100.00
	Tidal	N	24.13 ± 41.79	66.52
Syngnathus acus Linnaeus, 1758	Out-flow	D		
	Out-flow	N	3.31 ± 8.11	2.29
	Tidal	D		
	Tidal	N		
Solea turbynei	Out-flow	D		
	Out-flow	N	0.10 ± 0.26	0.07
	Tidal	D		
	Tidal	N		

6.3.4 Comparing the overwash and open phases

The number of fish species and the contribution of each estuarine utilisation category were fairly consistent during the overwash phase, with five and six species recorded during both day and night samples, respectively. During the open period, however, the number of fish species recorded was more variable, ranging between one and nine (Figure 6.4 and Table 6.3). There were no significant differences in the estimates of recruitment during the three different hydrological phases of the estuary ($F_{(1, 45)} = 0.70$ $p > 0.05$). Although not significant, lower fish recruitment estimates were recorded during the overwash events and maximum recruitment estimates occurred during the out-flow phase (Figure 6.5).

6.3.5 Community analysis

The overwash events and open phase samples were analysed using PRIMER (v.5.2.4) to determine the species richness and the diversity (Table 6.3). Analysis of species richness did not identify any significant difference between the overwash events and open phase ($F_{(3, 31)} = 6.94$ $p < 0.01$) (Tukey $p > 0.05$). The second overwash event, however, had significantly higher richness values than the first overwash event (Tukey $p < 0.05$). Analysis of the species diversity indices showed significant differences ($F_{(3, 4555)} = 27.30$ $p < 0.01$), with a post-hoc test revealing that the diversity during the open phases were not different from each other but were significantly lower than the overwash events (Tukey $p < 0.05$), and the diversity of the second overwash event was significantly higher than the first overwash event (Tukey $p < 0.05$).

The MDS plot identified three distinct groupings: the overwash events group, the out-flow phase group and the tidally dominated phase group (Figure 6.6). A SIMPER analysis (using PRIMER), run on the average abundance data for the different groups, displayed a dissimilarity of 97.55 % between the overwash events and the out-flow phase group and 88.93 % between the overwash and tidal groups. Between the out-flow group and the tidal group there was a 91.20 % dissimilarity. Table 6.4 lists the species that accounted for > 90 % of the similarity within each of the groupings identified in the MDS plot. The overwash samples were dominated by *R. holubi*, juvenile Mugilidae, *A. breviceps* and a Gobiidae species. Four species accounted for > 90 % of the similarity for the out-flow phase grouping, with the dominant species being *S. salpa*. In the tidal grouping, the unidentified sparid sp. 2 was the dominant species, contributing > 90 % of the similarity within the grouping.

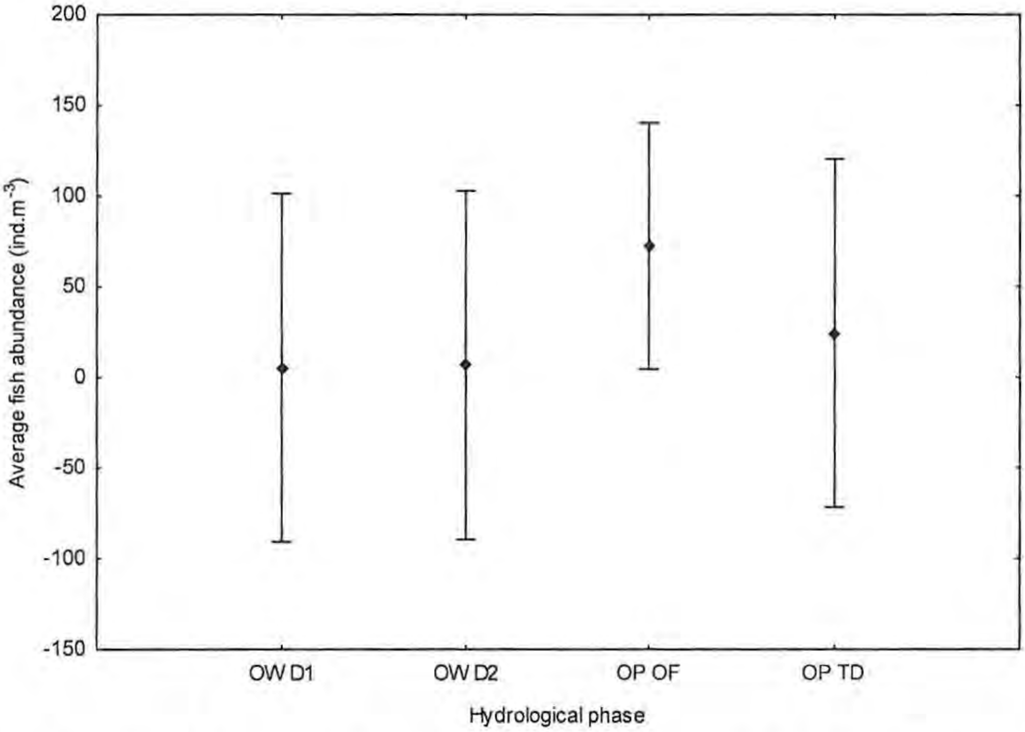

Figure 6.5: The average estimated ichthyofaunal abundance (ind.m^{-3}) of the different sampling events displaying the lack of any significant variation $F_{(1, 45)} = 0.70$ $p > 0.05$). OW = Overwash, OP = Open, D1 = the first sampling day and D2 = the second sampling day, OF is the out-flow phase and TD is the tidal phase. Vertical bars denote 0.95 confidence intervals.

Table 6.3: Abundance, diversity and species richness of the ichthyofauna sampled during the overwash and open phases.

Mouth Status	Day / Night	Number of Species	Abundance (ind.m^{-3} ± SD)	Combined Abundance (ind.m^{-3} ± SD)	Margalef's Species Richness	Shannon's Species Diversity
Overwash 1	D	5	4.19 ± 3.10	5.44 ± 3.53	2.79	1.02
	N	5	6.68 ± 4.10		2.11	0.83
Overwash 2	D	6	1.49 ± 2.60	6.64 ± 12.92	12.54	1.58
	N	5	11.79 ± 18.20		1.62	0.83
Out-flow (Open)	D	4	0.47 ± 1.16	72.48 ± 171.26	-	1.13
	N	9	144.48 ± 228.21		1.61	1.13
Tidal (Open)	D	1	0.05 ± 0.08	24.36 ± 58.99	-	0
	N	4	36.27 ± 62.62		0.84	0.64

Table 6.4: The species contributing > 90 % of the dissimilarity between the different hydrological phases (overwash, out-flow and tidal) highlighted in the MDS plot (Figure 6.6).

Species	Overwash (42.70 % Similarity)	Out-flow Phase (4.90 % Similarity)	Dissimilarity (97.55 %)	
	Average abundance	Average abundance	Percentage contribution	Accumulative percentage
Rhabdosargus holubi	1.98	0.16	17.46	17.46
Mugilidae	2.70	0.00	14.79	32.25
Sarpa salpa	0.00	16.66	14.12	46.37
Unidentified sparid sp. 2	0.00	43.59	13.01	59.37
Liza richardsonii	0.00	5.16	8.59	67.96
Atherina breviceps	0.5	0.10	7.80	75.76
Unidentified sparid sp. 1	0.00	4.98	7.66	83.41
Gobiidae	0.60	0.00	6.62	90.04
Species	Overwash (42.70 % Similarity)	Tidal Phase (1.53 % Similarity)	Dissimilarity (88.93 %)	
	Average abundance	Average abundance	Percentage contribution	Accumulative percentage
Rhabdosargus holubi	1.98	6.01	30.08	30.08
Unidentified sparid sp. 2	0.00	4.4812.09	22.49	52.58
Mugilidae	2.70	0.00	20.43	73.00
Atherina breviceps	0.55	0.00	11.63	84.63
Gobiidae	0.60	0.00	9.19	93.82
Species	Out-flow Phase (4.90 % Similarity)	Tidal Phase (1.53 % Similarity)	Dissimilarity (91.197 %)	
	Average abundance	Average abundance	Percentage contribution	Accumulative percentage
Unidentified sparid sp. 2	43.59	12.09	26.96	26.96
Sarpa salpa	16.66	0.00	25.53	52.49
Rhabdosargus holubi	0.16	6.01	14.88	67.36
Liza richardsonii	5.16	0.00	13.43	80.79
Unidentified sparid sp. 1	4.98	0.00	10.20	90.99

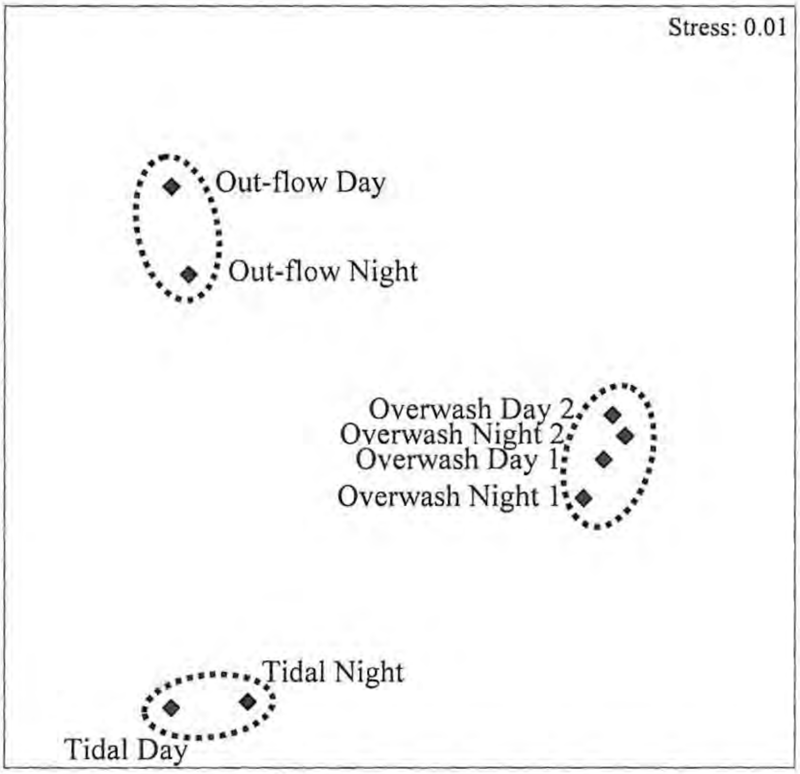

Figure 6.6: The multi-dimensional scale plot of the day- and night-time average abundances of ichthyofauna recruiting into the estuary during the different hydrological phases. The dotted circles indicate the overwash, out-flow and tidal groups at 23 % similarity (PRIMER).

6.4 DISCUSSION

The ability to recruit into an estuary is an important component in the lifecycle of many marine spawning invertebrate and vertebrate species in southern Africa (Vorwerk *et al.*, 2003; Froneman 2004; Kemp and Froneman, 2004; Perissinotto *et al.*, 2004; Froneman, 2006a). There are approximately 155 species of fish that routinely utilise southern African estuaries (Wallace, 1975a; Whitfield, 1998) of which ~ 78 species are strongly associated with the estuarine environment in the warm temperate zone (WTZ) of South Africa (Whitfield, 1998; Table 13 pg 171). In the WTZ, 36 marine spawning fish species are strongly associated with the estuarine environment (Whitfield, 1998; Table 13 pg 171). In permanently open estuaries, the recruitment of marine species is continuous due to the existence of a permanent link between the estuarine and the marine environment (Whitfield and Kok, 1992; Whitfield, 1998; Vorwerk, 2001). In TOCEs, however, the presence of a sand bar at the mouth, separating the estuary from the marine environment, represents a significant barrier to the recruitment of marine spawning species into the system. Breaching and overwash events are the only means by which recruitment of marine spawning species can occur into these systems (Whitfield, 1992; Cowley *et* al., 2001; Vivier and Cyrus, 2001; Kemp and Froneman, 2004).

The recruitment of ichthyofauna into the Mpekweni Estuary was assessed during both overwash events and while the mouth was open after a breaching event. The open period was separated into two phases: the out-flow phase and the tidal phase. Kemp and Froneman (2004) demonstrated that in the TOC West Kleinemonde Estuary within the same geographic region, there was an average ichthyofaunal recruitment abundance of 0.53 ind.m^{-3} (± 1.90 SD) during high spring tide overwashing events. The estimates of fish recruitment during the overwash events of this study (5.44 ind.m^{-3} ± 3.53 SD and 6.64 ind.m^{-3} ± 12.92 SD) were higher than the average abundance estimates of Kemp and Froneman (2004). Their study, however, recorded a maximum abundance of 9.64 ind.m^{-3} for *R. holubi*. These data show that overwash events can contribute to recruitment of marine spawning species to estuaries during the closed phase. However, fish recruitment in the Mpekweni Estuary was substantially higher during the freshwater-dominated out-flow phase, with an average estimate of 72.48 ind.m^{-3} (± 171.26 SD). Estimates of recruitment potential during the tidal phase were lower than the out-flow phase, with an average estimate of 24.36 ind.m^{-3} (± 58.99 SD), but higher than the overwash events (Figure 6.5 and Table 6.3).

The results of this investigation provide further support for the contention that breaching events are the primary means of fish recruitment into southern African TOCEs (Whitfield, 1998; Bell *et al.*, 2001; Kemp and Froneman, 2004; Cyrus and Vivier, 2006b; Whitfield *et al.*, 2012a). Initially the breaching of the estuary results in the mass emigration of species from the estuarine to the marine environment (Whitfield, 1998; Griffiths and West, 1999; Cowley *et al.*, 2001; Tweddle, 2004; James *et al.*, 2008a). This is followed by the recruitment of marine spawning species into the system (see Chapter 4 and Chapter 5). Seasonality may be an important variable in determining which species are able to recruit. For example, the availability of recruiting larval and juvenile fish is linked to spawning periods (Whitfield, 1998; Bell *et al.*, 2001; Cowley *et al.*, 2001; Kemp and Froneman, 2004). The elevated recruitment during the out-flow phase can probably be attributed to species responding to strong cues (e.g. *R. holubi* [James, 2007]). Nonetheless, recruitment does still occur during the tidal phase, which is consistent with Quinn *et al.* (1999), who showed that marine species still recruited into the Great Brak Estuary, South Africa, even after the salinity gradients between the out-flowing water and the marine water were < 20. The continued recruitment could be linked to the presence of olfactory cues that could be derived from the terrestrial run-off into the system (Quinn *et al.*, 1999). Whitfield (1989a) found that the species composition in the surf zone adjacent to the mouth of the Swartvlei Estuary (Western Cape) was higher than that recorded upstream and downstream of the mouth. This was linked to possible seepage of estuarine water through the sand berm, resulting in olfactory cues in the immediate vicinity of the estuarine mouth region. In the smaller systems, the reduced volume of water results in less seepage out of the system (Vorwerk, 2006). The biological response adjacent to these systems is, therefore, likely to be less conspicuous.

The trends in recruitment abundance between the different phases is further emphasised by the numerical analysis, which identified that each of the three phases; overwash, out-flow and tidal periods were distinct (Figure 6.6 and Table 6.4). Species composition in the marine near-shore and estuarine environment is determined by, amongst others, zoogeography, physiography (Harris *et al.*, 2001) and nearshore hydrodynamics (Porri *et al.*, 2007). During the overwash phase, the majority of the fish sampled comprise species which are known to passively utilise overwash events to recruit into TOCEs (e.g. *R. holubi*, Mugilidae and *A. breviceps* [James, 2007; Kemp and Froneman, 2004]). In comparison, the tidal phase was dominated by a single sparid species, while in the out-flow phase a larger number of species recruited into the system (Table 6.4), suggesting an increased species response to cues attributed to the opening event (James, 2007). The teleost species that were recorded recruiting into the estuary during the various hydrological phases of the Mpekweni Estuary are those species that make a substantial contribution in terms of both biomass and numerically to the ichthyofauna in the estuary during the closed period (Appendix, Figure

VIII). These include the sparid, *R. holubi* and the Mugilidae, which have been shown to have both extended spawning periods (Whitfield, 1998) that vary according to biogeographic region (Harrison, 2003). This provides increased recruitment opportunities in unpredictable environments.

Currently there are two main factors that need to be taken into consideration when assessing TOCEs; the effects of climate change and the increased freshwater abstraction. Mouth status has been identified as the predominant ecological factor affecting recruitment of zooplankton, hyperbenthos and ichthyofauna and into TOCEs (Wooldridge, 1991; Haines and Thom, 2007; James *et al.*, 2007b; Perissinotto *et al.*, 2010b; Vivier *et al.*, 2010; Whitfield *et al.*, 2012a). Recent work on Intermittently Closed and Open Lakes and Lagoons (ICOLLs) along the coast of New South Wales, Australia (Haines and Thom, 2007) suggests that a rise in sea level associated with climate change will affect the position and height of the sand berm that separates the estuary from the marine environment. The position and width of the sand berms will move landward and narrow, respectively, in areas that experience high erosion, while areas that are more susceptible to sand deposition berms are likely to increase in height and width (Haines and Thom, 2007). These possible changes in mouth characteristics and condition will subsequently affect recruitment of fish into these estuaries (Baldock *et al.*, 2005; Weir *et al.*, 2006). Estuaries with narrower and shallower berms may experience an increase in the frequency of overwash events while other estuaries where the berm has been heightened there could be a reduction in overwash events, as well as a reduction in the number of mouth opening events. The evidence from this study suggests that in cases of an increased frequency of overwash events, the net result could be an increase in the numbers of ichthyofaunal species known to utilise this method of recruitment, while in other systems a reduction in breaching events and recruitment potential will reduce stocks. Although recruitment through overwash could increase, the overall effect would be a net decrease of the stock sizes due to the reduction of the breaching events. Species richness and diversity would also likely decrease due to selectivity for the overwash recruiting species.

An increase in water abstraction from the catchment regions may also result in a reduction of breaching events and hypersalinity (James *et al.*, 2007b; Potter *et al.*, 2010). The resulting increase in duration that TOCEs may remain closed is of concern; Wooldridge (1991) suggested that if mouth opening events became less frequent and duration of closure increased, the biota would be negatively affected and some species may disappear entirely from certain systems. These changes were evident in the St. Lucia system where an extended mouth closure of 30 months resulted in a decline in CPUE and a 40 % loss of common estuarine associated species. Considering the environmental and economic value of estuaries as nursery areas (Turpie and Clark, 2007) and the equivalent importance of POEs and TOCEs (Lamberth and Turpie, 2003), any changes that may affect the functioning of these systems and the subsequent survival of dependant fish stocks should be a priority for management strategies.

6.4.1 Summary

In conclusion, this study provides quantitative data on the ability of estuarine and estuarine-obligate marine spawning fish species to recruit into TOCEs during both overwash events and the various phases that an open estuary undergoes after breaching. The main recruitment pulse takes place immediately following the breaching of the estuary during the out-flow phase. The tidal phase recruitment is lower, suggesting a reduction of recruitment cues. The estuarine or estuarine-obligate species are the dominant species during the overwash and open conditions, and these same species make a large contribution to the abundance and community structure of ichthyofauna during the close periods. The lower abundances and biomass of marine spawning ichthyofauna recorded in the estuary after it had re-closed, (see Chapter 4 and Chapter 5) could be attributed to a reduced re-recruitment after emigration during the initial breaching.

CHAPTER 7

GENERAL DISCUSSION

Over the past decade numerous studies have been conducted in temporarily open/closed estuaries in both the warm temperate and subtropical biogeographic zones along the southern African coastline (Cowley, 1998; Perissinotto *et al.*, 2000; Vorwerk, 2001; Harrison, 2003; Perissinotto *et al.*, 2004; James, 2007; Whitfield *et al.*, 2008; Riddin and Adams, 2010). These investigations have greatly increased our understanding of the interplay between the hydrology (freshwater inflow and mouth phase), physico-chemical and biological variables within these systems. To date, the majority of the investigations in TOCEs have focussed specifically on the ichthyofauna. This study contributes to our understanding of the link between the physical environment, plankton and the ichthyofaunal community composition within a medium sized TOCE in the warm temperate region of the southern African and the influence that breaching events have on the ecology of these systems. This chapter puts into context the ecosystem dynamics of this study and how these ecosystems may be influenced by global climate change.

7.1 ECOSYSTEM DYNAMICS

7.1.1 Closed phase

Temporarily open/closed estuaries such as the Mpekweni Estuary and other warm temperate estuaries within the same geographic region of South Africa (Cowley, 1998; Vorwerk, 2001; Perissinotto *et al.*, 2000; 2002; 2003; Froneman, 2002a; 2002b; 2004; Harrison, 2003; Tweddle, 2004; Thomas *et al.*, 2005; Lukey, 2006; Vorwerk, 2006; James, 2007) and warm temperate estuaries along the south eastern and south western coastlines of Australia (Griffiths, 2001a; 2001b; Potter *et al.*, 1990) are typically stable, homogenous environments under closed conditions. A comparison of this study with local (Cowley, 1998; Vorwerk, 2001; Harrison, 2003; Tweddle, 2004; Vorwerk, 2004; 2006; Lukey, 2006; James, 2007) and international studies on TOCEs (Potter *et al.*, 1990) identified seasonal variations in physico-chemical parameters and that these systems are also characterised by the virtual absence of horizontal and vertical stratification. The lack of spatial variability can be attributed to several factors including small catchment size, sporadic rainfall and strong coastal winds which facilitate vertical and horizontal mixing of the water column (Whitfield, 1998; Walker *et al.*, 2001; Froneman, 2002b; 2004).

The estimates of the total chlorophyll-*a* concentration and the zooplankton abundance and biomass recorded in the Mpekweni Estuary during this study were in the range reported for TOCEs in both the STZ and the WTZ along the southern African coastline (Perissinotto *et al.*, 2000; 2002; 2003; Froneman, 2004; Nozais *et al.*, 2005). The seasonal patterns of the plankton biomass and to a lesser extent, ichthyofauna, under closed periods reflect the influence of temperature on the metabolic processes of organisms within the system (Potter *et al.*, 1990; Wooldridge 1999; Perissinotto *et al.*, 2000; 2002; 2003; Griffiths, 2001a; 2001b; Froneman, 2002a; 2002b; 2004; 2008; Harrison, 2003; Kibirige and Perissinotto, 2003a; Thomas *et al.*, 2005; Everett *et al.*, 2007; Montoya-Maya and Strydom, 2009; van Niekerk *et al.*, 2008; Whitfield *et al.*, 2008). The absence of any distinct spatial variation in the physico-chemical parameters likely accounts for the lack of patterns in the phytoplankton and zooplankton data from the Mpekweni Estuary. Likewise, there were limited spatial patterns in the ichthyofaunal community structure evident during the investigation (Chapter 4), which is consistent with the published literature for southern African TOCEs (Cowley, 1998; Vorwerk, 2001; Tweddle, 2004). The limited spatial variation observed in ichthyofauna community composition within WTZ TOCEs has been associated with sediment type, although this is inconclusive (Cowley, 1998; Vorwerk, 2001; Tweddle, 2004). The importance of niche interactions (Blaber, 1974) and interspecies competition in determining spatial patterns of ichthyofauna appears to be counteracted by the physico-chemical homogeneity of the TOCEs (Potter *et al.*, 1990).

7.1.2 Open phase and recruitment

The breaching event of the Mpekweni Estuary over mid-winter in 2006 showed that the open mouth affected the physico-chemical parameters (significantly lower temperature values and to some extent changes in salinity, POM, DO and Turbidity values) (Chapter 3) in the system which is consistent with similar studies conducted in South African (Perissinotto *et al.*, 2000; Perissinotto *et al.*, 2004; Froneman, 2004; Thomas *et al.*, 2005; Whitfield *et al.*, 2008) and Australian TOCEs (Griffiths, 1999; Close *et al.*, 2010). The decrease in plankton biomass when the estuary breached is also in agreement with other studies conducted within nearby WTZ TOCEs and TOCEs in the STZ (e.g. Perissinotto *et al.*, 2000; 2002; 2004). The observed pattern appeared to reflect the out-flow of biomass-rich estuarine waters into the marine environment and the loss of habitat (submerged macrophytes). Similar plankton export following the establishment of a link to the marine environment has also been recorded within Australian intermittently closed and open lakes and lagoons (ICOLL) (Everett, 2007). This loss of phytoplankton and zooplankton has a knock on affect within the food web structure reducing the productivity of these systems. Frequent and extending mouth opening events as a result of climate change may compound this and reduce the productivity of these systems.

Species composition of the ichthyofauna within the Mpekweni Estuary was influenced by the breaching event, which coincided with an increased contribution of marine spawning fish species to the total abundance within the system. Similar changes in community structure have been observed in similarly located TOCEs within the same geographic region (Whitfield *et al.*, 1983; Whitfield, 1989b; Cowley, 1998; Vorwerk, 2001; Tweddle, 2004; Lukey, 2006; James, 2007; Whitfield *et al.*, 2008) and around the world (Yáñez-Arancibia, 1981; Potter *et al.*, 1990; Mendoza *et al.*, 2009). In a tropical lagoon on the western coast of Mexico, Mendoza *et al.* (2009) also identified distinct fish communities between open and closed phases of the estuary, with marine species numerically dominating during the closed phase of the system. On the western coast of Mexico (Mendoza *et al.*, 2009), the eastern and western coast of Australia (Potter *et al.*, 1990) and tropical South America (Yáñez-Arancibia, 1981) these changes in distribution and community composition of ichthyofauna within TOCEs are, evidently seasonal, as spawning patterns of marine spawners coincide with seasonal rainfall and subsequently seasonal breaching events (Yáñez-Arancibia, 1981; Potter *et al.*, 1990; Mendoza *et al.*, 2009).

Although the open mouth phase represented the main mechanism responsible for determining the ichthyofaunal community composition within the Mpekweni Estuary, the breaching event was also associated with a decrease in the ichthyofaunal abundance and biomass within the system (Figures: 4.3 and 4.4). The local and international published literature ascribed this loss to the out-flow of biomass-rich estuarine waters into the marine environment and the loss of fringing habitats (Cowley, 1998; Griffiths, 1999; Vorwerk, 2001; Tweddle, 2004; Lukey, 2006; James, 2007). The estimates of the ichthyofaunal abundance (2.18 – 4.27 ind.m^{-2}) and biomass (1.13 – 1.84 g wwt.m^{-2}) during this study fell within the range reported in the published literature (see Chapter 4) for southern African TOCEs within the warm temperate biogeographic region of southern Africa. In similar Australian estuaries, the abundance estimates cover a wider range (0.01 – 17.08 ind.m^{-2}) than has been recorded for South African TOCEs (Jones and West, 2005; Pollard, 1994).

7.1.3 Overwash phase and recruitment

In addition to the breaching events, the overwash of marine waters into the estuary during high spring tides also represents recruitment opportunities for the marine spawning fish species within the Mpekweni Estuary (Table 6.1 and Figures: 6.3 and 6.4, Chapter 6). The recruitment of marine spawning species into the estuary during these events, mainly during summer, may in part account for the seasonality of the ichthyofauna abundance and biomass observed within the Mpekweni

Estuary during this investigation and in other TOCEs within the same geographic region (Vorwerk *et al.*, 2007).

Kemp and Froneman (2004), Bernard and Froneman (2005) and James *et al.* (2008b) identified and quantified the importance of overwash as potential recruitment events for marine spawning ichthyofauna, with Kemp and Froneman (2004) suggesting that recruitment of up to 9.64 ind.m^{-3} of *R. holubi* was possible during high spring tide overwash surges. Similar estimates were recorded for overwash events in this study (Chapter 6). Recruitment of fish species during the out-flow period (72.48 ind.m^{-3} ± 171.26 SD) far exceeded those recorded during the overwash events. Despite the influence of tidal influx and reduced estuarine input, the recruitment during the tidal phase, although patchy, was higher than the recruitment recorded during the overwash events (Figures: 6.3 and 6.5, Table 6.3). The use of olfactory cues as shown by the work of James *et al.* (2008a) on *R. holubi* may account for the initially larger recruitment after the breaching event. With the extended mouth opening event, the cues associated with estuarine and freshwater out-flow (whether olfactory or otherwise) are likely to have dissipated and culminated in reduced retention of marine spawning species (emigration) despite the winter-through-summer period of mouth opening, which coincides with the majority of spawning periods for many of the fish species utilising estuaries (Whitfield, 1998). Recruitment during overwash events is limited to what is present in the adjacent surf zone while marine water is flowing over the sand bar into the estuarine environment (Bell *et al.*, 2001), although some species may make better use of these events (e.g. Mugilidae and *R. holubi*) to recruit during periods when breaching events are limited or do not occur. These aforementioned species also have prolonged spawning periods (Whitfield, 1998; Vorwerk, 2001) which could be a possible adaptation to further extend the possibility of recruitment either via overwash events or breaching events.

7.1.4 Cohort analysis

Assessing the monthly length frequencies distributions of selected fish within the Mpekweni Estuary provided estimates of growth rates that were similar to other estuaries within the same geographic region (Chapter 5, Table 5.4). Some discrepancies in the growth rates of the fish species, particularly the sparid *R. holubi* and the Mugilidae, were noted. The discrepancy in the growth rate comparison may result from an artefact of the sampling. It is more likely that an under representation of the larger individuals in the population would account for the limited ability to derive mortality and growth parameters, however, generally juvenile growth rates are faster than mature fish suggesting that an over-estimation would be the more likely result. In comparison to

South African species (e.g.: Cowley, 1998; Whitfield and Kok, 1992) the growth rates of mullet species in the Western Australian Swan-Avon system showed a wider and higher variation in monthly growth increments (Chubb *et al.*, 1981). A study on growth of juvenile fish in estuaries in the USA identified differences in growth rates of three species between different habitat types and estuaries (Sogard, 1992). Thus it is likely that the growth rates of the South African fish species also demonstrate a wide variability and may in fact be system or temperature dependant and need further examination.

Cohort analysis can be used to back-calculate fish recruitment periods (Cowley *et al.*, 2001; Griffiths, 2001a; 2001b; Lukey, 2006; James, 2007) within the Mpekweni Estuary, particularly for the marine spawners who's recruitment can be linked to the period when the mouth was open and overwash events. The length frequencies of the EUC II species within the estuary revealed multiple peaks in size classes, suggesting that there were several distinct age classes present in the system over the period of investigation. The presence of these peaks provides evidence of non-continuous recruitment for EUC II species into the Mpekweni Estuary, as would be expected in a TOCE where closed mouth conditions limit recruitment (Cowley, 1998; Whitfield, 1998; James, 2007). These peaks in clearly distinct age classes indicate the likelihood of overwash recruitment and in reasonably high abundances. Conversely, the EUC I species displayed single normally-distributed populations, which would suggest less sporadic and continuous recruitment within the estuary.

Length frequency analysis was a useful tool in assessing the population structure, growth rates and tracking of cohorts to identify possible recruitment events. Critically, however, discrepancies within the process could be exaggerated when examining transitory species within the estuarine environment.

When scaling up samples collected by the small 5 m seine net in the littoral zone of the estuary, peaks in the adjusted abundances were evident for the Mugilidae and *R. holubi* (Chapter 5), particularly, during the open period and in the few months after the estuary re-closed. These peaks were also magnified by the lower abundances being recorded in the large size classes. Upon reflection, adjusting the length frequencies of fish sampled in the littoral zone using the 5 m seine to the same surface area as the data from the 30 m and 50 m seine net was not a true representation of pooling the ichthyofauna data within the estuary. The littoral or marginal zone of estuaries provides a refuge for the larval and juvenile fish (Becker and Laurenson, 2008) and there is evidence of higher species richness values for the post larval and juvenile fish in comparison to what was recorded in the channel (Wasserman *et al.*, 2010). This variation is also reflected in the species composition and food web structure of the channel versus the littoral zones (Patterson and Whitfield, 1997). Size classes and abundance values of the larval and juvenile fish within the littoral zone are also typically different to those recorded in the channel of the estuarine environment, particularly for certain species such as juvenile *M. capensis* which was only recorded in the littoral zone of the Nxaxo-Ngqusi Estuarine Complex (warm temperate, subtropical transition zone, South Africa) (Wasserman *et al.*, 2010). For the purpose of this study, however, using either the original CPUE estimates and/or the adjusted numbers would not make too much difference as the focus of Chapter 5 was to examine the population structure and look at modal peaks to identify cohorts, growth rates and extrapolate recruitment events. Other aspects of the analyses appear to be highly subjective and user dependant, specifically when it comes to growth rates and mortality estimates, however, by using a variety of methods, tracking multiple cohorts and averaging a series of regression values for mortality estimates, the user can be confident enough to compare the results.

7.2 GLOBAL CLIMATE CHANGE

The world's climate undergoes a continuous natural cyclic change, for example the glacial-interglacial cycle which influences the sea-level, wind pattern and ocean currents (Beal *et al.*, 2011). Natural cycles are, however, being increasingly influenced by anthropogenic processes (Walther *et al.*, 2002). Changes in sea-level resulting from human induced global climate change, as discussed in Chapter 6, can affect berm height which influences the frequency and duration of breaching events (Baldock *et al.*, 2005; Weir *et al.*, 2006; Haines and Thom, 2007; James and Paterson, 2011). Global Climate Models (GCMs) indicate sea water temperatures are increasing and the Agulhas Current that flows along the east coast of southern Africa is extending the reach of warmer waters southwards (Beal *et al.*, 2011). The subsequent increase in the sea temperatures is likely to result in an increase in rainfall along the eastern margins of South Africa and drier conditions along the south and west coasts of the country (Hewitson *et al.*, 2004; James and Paterson, 2011). Overall, the literature suggests that the rainy season along the South African coastline will decrease in duration but the intensity of rainfall events, particularly along the east coast, will increase (Hewitson *et al.*, 2004; James and Paterson, 2011). Similarly the frequency and severity of storm events will increase (New *et al.*, 2006; Theron, 2011). These predicted changes in the climate along the South African coastline will subsequently increase the frequency and likelihood of flash floods, overwash events and a general increase in the frequency and duration of mouth opening events in TOCEs (James and Paterson, 2011). There are thus two "conflicting" effects of climate change on TOCEs. Firstly increased water abstraction (due to possible increasing arid conditions and an increase in freshwater use associated with subsequent anthropogenic impacts and requirements (James and Paterson, 2011; Whitfield and Matlala, 2011)) with fewer breaching events and secondly, increased breaching events due to increased storm and rain intensity events. One may in fact cancel out the other, however in all likelihood there will be a continuum from increased breaching and overwash events on the east coast to fewer breaching events and extended mouth closure periods along the south and west coast (James and Paterson, 2011; Whitfield *et al.*, 2012a).

The change in abundance, biomass and diversity of ichthyofauna observed in the Mpekweni Estuary following the mouth opening event suggests that the predicted changes in the frequency of breaching events resulting from global climate change is likely to have a significant impact on the ecology of these systems (Hewitson *et al.*, 2004; James and Paterson, 2011). Moreover, the timing of these mouth opening events is critical as it has been considered to be a large component in determining the diversity and abundance of fauna within the TOCEs (Cowley, 1998; James *et al.*, 2007b; Whitfield *et al.*, 2008). If breaching events in the relevant regions are no longer seasonal as a result of climate change, these systems may in fact experience a reduction in recruitment. On an ecological and economic scale, Turpie *et al.* (2002) provide evidence that the productivity of a TOCEs is between 33 % and 50 % to that of comparatively sized POEs, indicating that increasingly open TOCEs may become more productive in terms of fisheries targeted and economically important species (Turpie *et al.*, 2002). This study, however, recorded a decline in abundance of ichthyofauna due to the extended breaching event and the possible changes to the functioning of TOC and PO estuaries could have dire consequences for the ecology of these systems and subsequently impact the economic value associated with these systems.

Along the southern and western coastline, the implications of climate change may be more severe due to the proposed drier conditions in the region associated with lower rainfall and increased water abstraction due to anthropogenic pressure (Hewitson *et al.*, 2004; James and Paterson, 2011). The projected increase in berm height of TOCEs will contribute to a decline in the frequency of breaching events in conjunction with an increase in the duration of mouth closure (Haines and Thom, 2007). The projected reduction in freshwater inflow coupled with the increased frequency of overwash events attributed to the increase in storm surges and evaporation may increase the salinity in these systems.

The relative stability of these systems under closed conditions and increased food availability accounts for the importance of TOCEs as nursery areas for many of the South African ichthyofaunal species (Whitfield *et al.*, 2008). The shallow nature and limited freshwater inflow of these systems, however, makes them highly susceptible to climate change (James *et al.*, 2008c; 2011; James and Paterson, 2011). The changes in freshwater inflow into these systems is likely to impact on the ecological functioning of these estuaries through changes in nutrient cycling and reductions in primary and secondary production rates within these systems. Additionally, the loss of submerged macrophytes associated with breaching events and increased salinity values may contribute to a loss of habitats within TOCEs, subsequently limiting refuge areas for juvenile ichthyofauna (Anandraj *et al.*, 2008; Riddin and Adams, 2008; Whitfield *et al.*, 2008; Elliott and Whitfield, 2011).

Increased salinity and reduced opportunities of estuarine inhabitants to return to the marine environment during extended mouth closures are likely to result in a reduction of abundance and diversity within TOCEs (Cyrus and Vivier, 2006a; James and Paterson, 2011). Other aspects to consider are the range expansion of tropical and subtropical species southwards (James *et al.*, 2011), which will increase diversity within these systems. The cold and warm temperate species are, however, unlikely to be able to compensate biologically to these changes in condition and a reduction in range will occur. The decrease in range for the warm and cold temperate species of which a large portion are endemic and the possible decline in abundances and diversity associated with increased mouth closure could result in a rapid decline of the indigenous and other species along the south and west coastline of South Africa (Whitfield, 1998; James *et al.*, 2011).

Figure 7.1 presents a stylised depiction of how the projected climate change may influence estuarine processes and subsequently the impact on fish population abundance and community structure along the South African coastline.

Commoner (1971) noted that “the more complex the ecosystem, the more successfully it can resist stress”. This can be interpreted as the more diverse the system the more likely it will be dynamically stable. This is fitting considering that the homogeneity of the TOCEs is evidence of stability within the system (Dando, 1984; Wallace *et al.*, 1984). The elevated productivity of these systems in comparison to the immediate freshwater and marine systems (Woodwell *et al.*, 1973; Haedrich and Hall, 1976) contributes to their role as a nursery area for ichthyofauna (Dando, 1984; Wallace *et al.*, 1984). Despite the upheaval of a major event such as breaching due to the complex interactions between the environmental and biological factors, these systems appear to rapidly recover from these perturbations. Recovery, however, does not imply instantaneous return to the previous state, but as is in evidence from James (2007) work on the long-term data sets of certain fish species, there is a natural cycle, which at some point is likely to coincide with other biological or environmental variables resulting in return to a similar state.

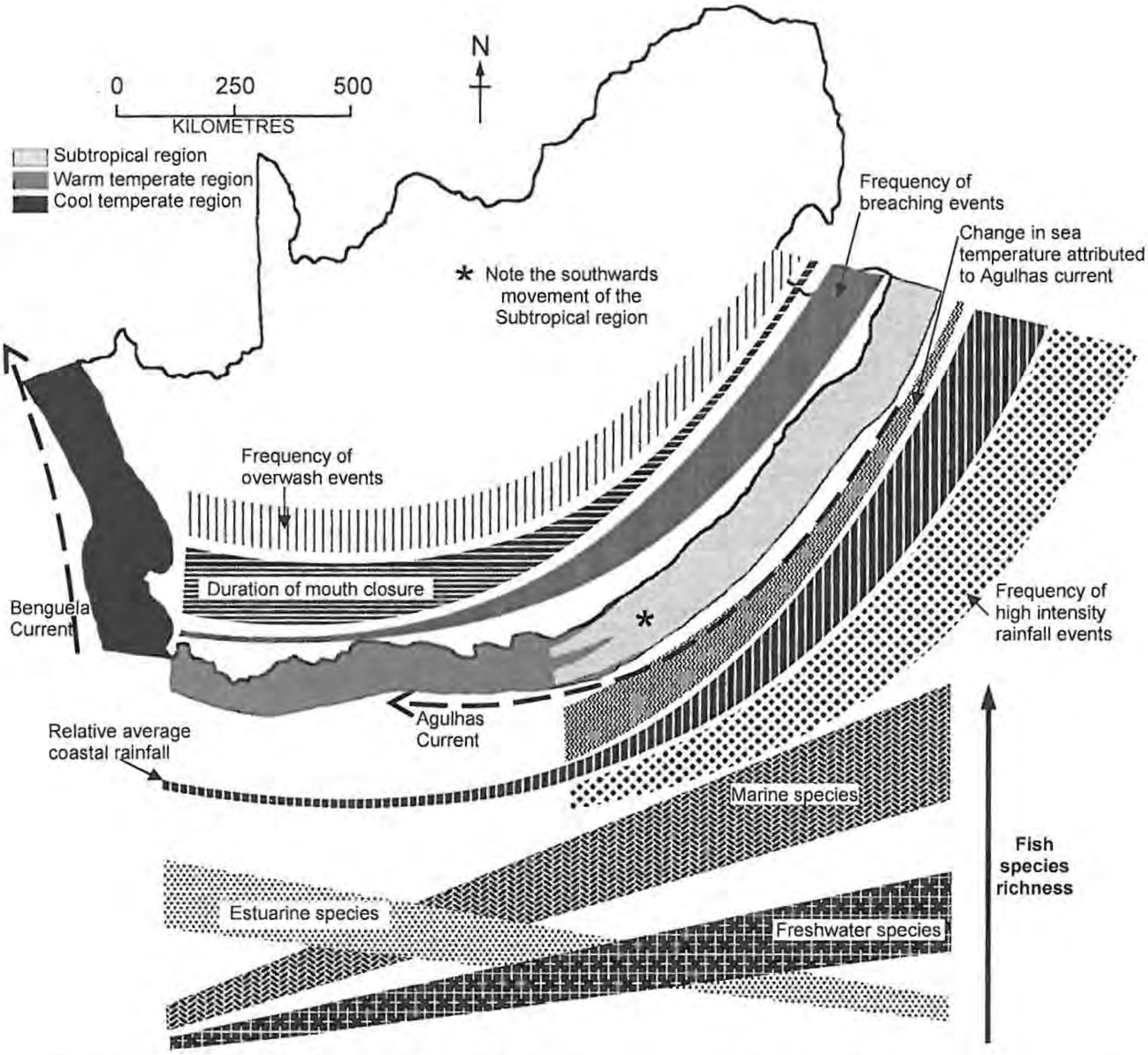

Figure 7.1: Diagrammatic representation of the effect of climate change on the South African estuarine processes, including a possible model (bottom) of the subsequent estuarine fish community composition and abundance (thickness of lines) adapted from Vorwerk (2001).

It is clear that due to overall global climate change and more locally there is likely to be a gradual shift in the function and status of TOCEs and this suggests that there needs to be more than a single management strategy for these valuable systems. Each system may need to be assessed on an individual basis and taking what has been learned from this study and the numerous other studies discussed in this thesis, dynamic micro-management may need to be implemented. For example in the future in order to maintain a level of endemicity and abundance, TOCEs along the south and west coast may need to be artificially breached and even re-closed at particular times of the year in order for recruitment and emigration of residing individuals to occur. The National Water Act (No. 36 of 1998) which requires that a certain minimum volume of water be left to enter the estuary will also need to be rigorously monitored for each system and even reassessed in order to limit the losses.

7.3 FUTURE STUDIES

This research has provided a clearer picture on the close interaction/interplay between the hydrodynamics, physico-chemical and biological variables within the TOC Mpekweni Estuary. There are a number of aspects of the biology of these systems that need further investigation and clarification including; the biological factors that may contribute to the limited spatial variability within TOCEs, further research on inter- and intra-species interactions, not only amongst the various fish species, but also between the different trophic levels of the estuarine food web, that contribute to the spatial and temporal variability within these systems. There is also a lack of comparable and quantifiable assessments of ichthyofaunal abundances and biomass within the present literature for South African TOCEs, possibly this could be dealt with by providing guidelines on sampling techniques and equipment to allow for comparison. Other systems need to be studied in order to provide baseline information that will allow for the structuring and implementation of management plans to limit or even counteract the effect of climate change.

Due to the high endemicity of ichthyofaunal species utilising South African estuaries for their entire lifecycle, or as nursery areas, the recruitment processes need further study. Identifying the possibility of further recruitment cues and whether they are diluted over time and whether there is a critical period after which the cues are non-existent. Emigration also needs to be investigated to identify possible cues that initiate a response in specific fish species to congregate near the mouth region before a possible breaching event. Genetic comparison of the marine spawning species that utilise estuaries may also be a possibility. This would involve the sampling of many estuaries to assess whether there are different genetic stocks utilising specific estuaries or whether there is a single large population spread out across a range of estuaries.

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APPENDIX

Table I: Pearson's correlation analysis indicating the relationship between selected physico-chemical and biological parameters in the Mpekweni Estuary (Chapter 3).

Shaded correlations are significant at p < .05000 N=114 (Casewise deletion of missing data)

	Average Temperature	**Average Salinity**	**Average POM**	**Average Dissolved Oxygen**	**Average Turbidity NTU**	**Average Total Chl-a Concentration**	**Average Total Chl-a Concentration 1 month lag**	**Zooplankton abundance log(x+1)**	**Zooplankton abundance log(x+1) 1 month lag**	**Zooplankton biomass log(x+1)**	**Zooplankton biomass log(x+1) 1 month lag**
Average Temperature		.1852 p=.049	.3770 p=.000	-.7161 p=0.00	.3862 p=.000	.1585 p=.092	.3010 p=.001	.4556 p=.000	.5029 p=.000	.4749 p=.000	.4672 p=.000
Average Salinity	.1852 p=.049		.1245 p=.187	-.3262 p=.000	.0102 p=.914	.2725 p=.003	.0869 p=.358	.4697 p=.000	.0729 p=.441	.1114 p=.238	-.0807 p=.393
Average POM	.3770 p=.000	.1245 p=.187		-.3938 p=.000	-.0667 p=.480	.2020 p=.031	.0656 p=.488	.4926 p=.000	.4492 p=.000	.1622 p=.085	.1034 p=.274
Average Dissolved Oxygen	-.7161 p=0.00	-.3262 p=.000	-.3938 p=.000		-.2088 p=.026	-.0709 p=.454	-.1088 p=.249	-.5563 p=.000	-.4609 p=.000	-.3072 p=.001	-.3161 p=.001
Average Turbidity NTU	.3862 p=.000	.0102 p=.914	-.0667 p=.480	-.2088 p=.026		.0107 p=.910	.1710 p=.069	.1884 p=.045	-.0070 p=.941	.4251 p=.000	.3297 p=.000
Average Total Chl-a Concentration	.1585 p=.092	.2725 p=.003	.2020 p=.031	-.0709 p=.454	.0107 p=.910		.1257 p=.183	-.0238 p=.801	.2280 p=.015	-.0239 p=.801	.0310 p=.743
Zooplankton Abundance log(x+1)	.4556 p=.000	.4697 p=.000	.4926 p=.000	-.5563 p=.000	.1884 p=.045	-.0238 p=.801	.0630 p=.506		.3472 p=.000	.4855 p=.000	.2686 p=.004
Zooplankton Biomass log(x+1)	.4749 p=.000	.1114 p=.238	.1622 p=.085	-.3072 p=.001	.4251 p=.000	-.0239 p=.801	.0888 p=.347	.4855 p=.000	.0557 p=.556		.2214 p=.018

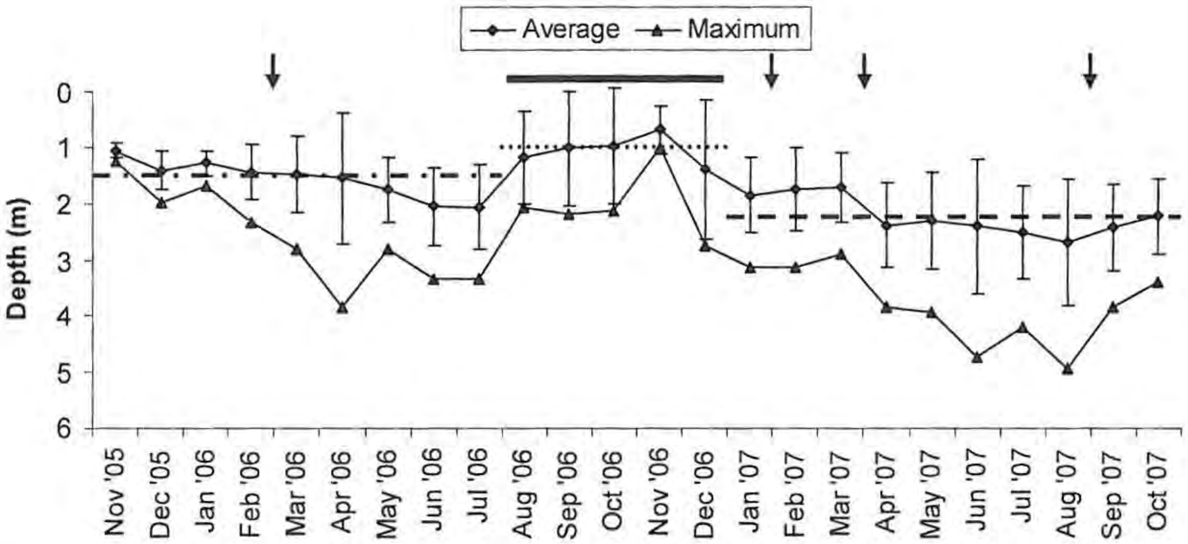

Figure I: Average and maximum depth measurements (m) for each month for the duration of the study. Error bars indicate standard deviation. The solid bar indicates the period when the mouth was open and the arrows, overwash events. The dashed and dotted line indicates the average depth (m) for the initial closed period, the dotted line indicates the average depth (m) during the open period and the dashed line indicates the average depth (m) for the re-closed period.

Table II: Pearson's correlation analysis of the species richness (Margalef's Index), species diversity (Shannon-Wiener's Index), abundance and biomass for the 5 m, 30 m and 50 m seine nets in comparison to temporal, spatial, physico-chemical and biological parameters.

Shaded correlations are significant at p < .05000 N=78 (Casewise deletion of missing data)

		5 m		30 m		50 m		5 m		30 m		50 m	
		Margalef's	Shannon-Wiener	Margalef's	Shannon-Wiener	Margalef's	Shannon-Wiener	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass
Study Duration		-.0633 p=.579	-.0615 p=.590	-.3495 p=.002	-.3327 p=.001	-.2817 p=.012	-.1236 p=.278	.3311 p=.003	.2707 p=.016	-.3667 p=.001	.0059 p=.959	-.2048 p=.070	-.0809 p=.478
Initial closed-Open-Re-closed		-.0073 p=.949	-.0175 p=.879	-.2660 p=.018	-.2911 p=.009	-.2016 p=.075	-.0424 p=.711	.4559 p=.000	.3743 p=.001	-.3481 p=.002	-.0020 p=.986	-.1497 p=.188	-.0522 p=.648
Open/Closed		.1364 p=.231	.1615 p=.155	.1875 p=.098	.0886 p=.437	.1298 p=.254	.1741 p=.125	-.0646 p=.572	-.0521 p=.648	.0564 p=.621	.0994 p=.383	.0114 p=.921	-.0186 p=.871
Season		-.2319 p=.040	-.1897 p=.094	-.3165 p=.004	-.2546 p=.024	-.3452 p=.002	-.3058 p=.006	-.0929 p=.415	-.0839 p=.462	-.2786 p=.013	.0081 p=.943	-.2522 p=.025	-.1441 p=.205
Distance from Mouth		.1277 p=.262	.1381 p=.225	-.1339 p=.239	.1974 p=.081	-.1483 p=.192	-.2019 p=.074	-.0414 p=.717	-.0317 p=.781	.3476 p=.002	.3372 p=.002	.2776 p=.014	.0222 p=.846
Reaches		.1589 p=.162	.1257 p=.270	-.0930 p=.415	.2043 p=.071	-.0975 p=.393	-.1275 p=.263	-.0305 p=.790	-.0540 p=.637	.3617 p=.001	.3775 p=.001	.2707 p=.016	.0585 p=.609
Depth		-.0107 p=.925	-.0422 p=.712	-.3652 p=.001	-.1467 p=.197	-.2845 p=.011	-.1485 p=.192	.1345 p=.237	-.0740 p=.517	-.1486 p=.191	-.0023 p=.984	-.2143 p=.058	.2211 p=.050
Average Temperature		.2578 p=.022	.1460 p=.199	.2460 p=.029	.1359 p=.232	.1707 p=.133	.1606 p=.157	.2154 p=.057	.2296 p=.042	.1964 p=.083	.1323 p=.245	.2947 p=.008	.1932 p=.088
Average Salinity		-.0176 p=.878	-.0366 p=.749	-.0179 p=.876	-.0602 p=.598	.0881 p=.440	.1167 p=.306	.1785 p=.115	.1411 p=.215	-.0492 p=.667	-.0602 p=.598	-.0426 p=.709	.0196 p=.864
Average Dissolved Oxygen		-.2657 p=.018	-.1684 p=.138	-.1283 p=.260	-.1992 p=.078	-.0122 p=.915	.0079 p=.945	-.1896 p=.094	-.1425 p=.210	-.2626 p=.019	-.1716 p=.130	-.2245 p=.047	.0047 p=.967
Turbidity NTU		.2017 p=.075	.1834 p=.106	.1923 p=.090	.2202 p=.051	.1414 p=.214	.0516 p=.651	-.1298 p=.254	-.0796 p=.485	.3828 p=.000	.1933 p=.088	.3035 p=.007	.1101 p=.334
Average POM		.1244 p=.275	.1657 p=.145	.1192 p=.296	.1154 p=.311	.0758 p=.507	.1989 p=.079	.4998 p=.000	.3979 p=.000	-.0793 p=.487	-.0661 p=.563	.0630 p=.581	.0112 p=.922
Average Total Chl-*a*		.0020 p=.986	.0043 p=.970	-.0022 p=.985	.1670 p=.141	.0303 p=.791	.1138 p=.318	.1029 p=.367	.1651 p=.146	.0040 p=.972	-.1705 p=.133	-.0382 p=.738	-.1054 p=.355
Zooplankton abundance log(x+1)		.0218 p=.849	-.0041 p=.972	.0196 p=.864	.1009 p=.376	.0374 p=.743	.0743 p=.515	.2037 p=.072	.1926 p=.089	-.0847 p=.458	-.0251 p=.826	.0666 p=.560	.0998 p=.381
Zooplankton biomass log(x+1)		.1179 p=.301	.1225 p=.282	.0135 p=.906	-.0309 p=.787	.0566 p=.621	.0966 p=.397	.4249 p=.000	.3691 p=.001	-.1270 p=.265	-.0614 p=.591	.0532 p=.642	.0836 p=.464
5 m	**Margalef's**		.7539 p=.000	.0967 p=.397	.1020 p=.371	.0593 p=.604	.1253 p=.271	.0873 p=.444	.1496 p=.188	.0531 p=.642	.0517 p=.651	-.0759 p=.506	-.0690 p=.546
	Shannon-Wiener	.7539 p=.000		.0412 p=.719	.1528 p=.179	.0491 p=.667	.1290 p=.257	.1968 p=.082	.2224 p=.049	.0216 p=.850	.0260 p=.820	-.0267 p=.816	-.0889 p=.436
30 m	**Margalef's**	.0967 p=.397	.0412 p=.719		.6375 p=.000	.4067 p=.000	.3775 p=.001	-.1070 p=.348	.0403 p=.724	-.0079 p=.945	.0255 p=.824	.0437 p=.702	.1862 p=.100
	Shannon-Wiener	.1020 p=.371	.1528 p=.179	.6375 p=.000		.0990 p=.385	.2078 p=.066	-.0850 p=.456	.0428 p=.708	-.0876 p=.443	-.1611 p=.156	-.0100 p=.931	.0230 p=.840
50 m	**Margalef's**	.0593 p=.604	.0491 p=.667	.4067 p=.000	.0990 p=.385		.8516 p=.000	-.1297 p=.255	.0559 p=.624	.1716 p=.131	.0776 p=.496	.2033 p=.072	.3682 p=.001
	Shannon-Wiener	.1253 p=.271	.1290 p=.257	.3775 p=.001	.2078 p=.066	.8516 p=.000		-.0338 p=.768	.0894 p=.433	-.0737 p=.519	-.0743 p=.515	.0200 p=.861	.2517 p=.025
5 m	**5m abundance**	.0873 p=.444	.1968 p=.082	-.1070 p=.348	-.0850 p=.456	-.1297 p=.255	-.0338 p=.768		.7469 p=.000	-.1725 p=.128	-.0637 p=.577	-.0600 p=.599	-.0043 p=.970
	5m biomass	.1496 p=.188	.2224 p=.049	.0403 p=.724	.0428 p=.708	.0559 p=.624	.0894 p=.433	.7469 p=.000		-.0481 p=.674	.0236 p=.837	.0369 p=.747	.2208 p=.050
30 m	**30m abundance**	.0531 p=.642	.0216 p=.850	-.0079 p=.945	-.0876 p=.443	.1716 p=.131	-.0737 p=.519	-.1725 p=.128	-.0481 p=.674		.6379 p=.000	.5282 p=.000	.3030 p=.007
	30m biomass	.0517 p=.651	.0260 p=.820	.0255 p=.824	-.1611 p=.156	.0776 p=.496	-.0743 p=.515	-.0637 p=.577	.0236 p=.837	.6379 p=.000		.4552 p=.000	.3839 p=.001
50 m	**50m abundance**	-.0759 p=.506	-.0267 p=.816	.0437 p=.702	-.0100 p=.931	.2033 p=.072	.0200 p=.861	-.0600 p=.599	.0369 p=.747	.5282 p=.000	.4552 p=.000		.7958 p=.000
	50m biomass	-.0690 p=.546	-.0889 p=.436	.1862 p=.100	.0230 p=.840	.3682 p=.001	.2517 p=.025	-.0043 p=.970	.2208 p=.050	.3030 p=.007	.3839 p=.001	.7958 p=.000	

Table III: Pearson's correlation analysis of the abundance and biomass of the six dominant juvenile/larval ichthyofaunal species sampled in the littoral zone using a 5 m seine net in comparison to temporal, spatial, physico-chemical and biological parameters.

Shaded correlations are significant at p < .05000 N=89 (Casewise deletion of missing data)

		G. callidus		*A. breviceps*		*G. aestuaria*		*R. holubi*		*M. capensis*		*L. richardsonii*	
		Abundance	**Biomass**	**Abundance**	**Biomass**	**Abundance**	**Biomass**	**Abundance**	**Biomass**	**Abundance**	**Biomass**	**Abundance**	**Biomass**
Study Duration		.0839 p=.434	.1690 p=.113	2515 p=017	.0823 p=.443	2665 p=012	2762 p=009	.0798 p=.457	.1017 p=.343	-.0491 p=.648	.0279 p=.795	.0407 p=.705	.0630 p=.558
Initial closed-Open-Re-closed		.1841 p=.084	2081 p=050	2097 p=049	.0354 p=.742	3593 p=001	3630 p=000	.1019 p=.342	.2078 p=.051	.0563 p=.600	.1308 p=.222	.0858 p=.424	.1032 p=.336
Open/Closed		-.1399 p=.191	-.1242 p=.246	-.0769 p=.474	.1189 p=.267	-.0785 p=.465	-.0596 p=.579	3847 p=000	-.0201 p=.852	-.0285 p=.791	-.0006 p=.995	-.0304 p=.777	-.0265 p=.806
Season		-2101 p=048	-.0249 p=.817	.2023 p=.057	.0082 p=.939	-.0345 p=.748	-.0439 p=.683	-.1106 p=.302	-2130 p=045	-2460 p=020	-.1943 p=.068	-.0426 p=.692	-.0240 p=.823
Distance from Mouth		.1883 p=.077	.1704 p=.110	.0248 p=.818	.0625 p=.561	.0430 p=.689	-.0257 p=.811	-.1872 p=.079	.0759 p=.480	-.1209 p=.259	-.1765 p=.098	-.1435 p=.180	-.1388 p=.195
Reaches		.1310 p=.221	.0946 p=.378	.0634 p=.555	.1079 p=.314	.0110 p=.918	-.0531 p=.621	-.1447 p=.176	.0703 p=.513	-.0918 p=.392	-.1448 p=.176	-.1203 p=.262	-.1136 p=.289
Depth		-.0217 p=.840	-.0569 p=.596	.2000 p=.060	.0690 p=.521	.1876 p=.078	.1633 p=.126	-.1318 p=.218	-.0723 p=.501	-.1127 p=.293	-.0944 p=.379	-.0920 p=.391	-.0839 p=.434
Average Temperature		2714 p=010	.1759 p=.099	.0509 p=.636	.1321 p=.217	.1170 p=.275	.1332 p=.213	-.0689 p=.521	2232 p=035	2319 p=029	.1966 p=.065	.0804 p=.454	.0629 p=.558
Average Salinity		.1997 p=.061	.1841 p=.084	.1410 p=.187	.1000 p=.351	.1141 p=.287	.1176 p=.272	-.0727 p=.498	.0125 p=.908	-.0565 p=.599	-.0441 p=.682	-.0016 p=.988	.0070 p=.948
Average Dissolved Oxygen		-2456 p=020	-.1698 p=.112	-.0482 p=.654	-.0709 p=.509	-.1880 p=.078	-.1903 p=.074	.0594 p=.580	-.1461 p=.172	-.0791 p=.461	-.0389 p=.717	-.0093 p=.931	.0042 p=.969
Turbidity NTU		.0841 p=.433	.0009 p=.993	-.1053 p=.326	.0546 p=.612	-.1724 p=.106	-.1621 p=.129	-.0544 p=.612	-.0616 p=.566	.0264 p=.806	-.0298 p=.781	-.0671 p=.532	-.0643 p=.550
Average POM		2972 p=005	2118 p=046	.0068 p=.950	-.0043 p=.968	3705 p=000	3769 p=000	4115 p=000	2604 p=014	.1658 p=.120	2176 p=040	.1041 p=.332	.1136 p=.289
Average Total Chl-*a*		.1865 p=.080	.0777 p=.469	-.1342 p=.210	-.0016 p=.988	.0892 p=.406	.0675 p=.529	-.1828 p=.086	.0870 p=.417	.0744 p=.488	.0846 p=.430	.1372 p=.200	.1222 p=.254
Zooplankton abundance log(x+1)		2277 p=032	2180 p=040	.1005 p=.349	.0236 p=.826	3133 p=003	2967 p=005	.0890 p=.407	.1958 p=.066	.1358 p=.205	.1287 p=.230	.1085 p=.312	.1130 p=.292
Zooplankton biomass log(x+1)		.1301 p=.224	.0210 p=.845	-.1291 p=.228	-.0381 p=.723	.0836 p=.436	.0501 p=.641	.1319 p=.218	3269 p=002	.0391 p=.716	-.0252 p=.815	.0048 p=.965	.0001 p=.999
5 m	**Margalef's**	.0499 p=.643	-.0184 p=.864	.0129 p=.904	2475 p=019	-.0256 p=.812	.0396 p=.712	.0932 p=.385	.1965 p=.065	.0135 p=.900	-.0171 p=.874	.1535 p=.151	.1580 p=.139
	Shannon-Wiener	.0911 p=.396	.0961 p=.370	.0948 p=.377	2599 p=014	.1512 p=.157	.1729 p=.105	.1333 p=.213	3003 p=004	.0416 p=.699	-.0176 p=.870	.1155 p=.281	.1114 p=.299
5 m	**Abundance**	5684 p=000	4787 p=000	5347 p=000	2886 p=006	6162 p=000	5480 p=000	.1764 p=.098	2568 p=015	.1674 p=.117	.1610 p=.132	3844 p=000	3894 p=000
	Biomass	5587 p=000	6449 p=000	.1218 p=.255	.1225 p=.253	3189 p=002	3128 p=003	.1501 p=.160	4159 p=000	.1989 p=.062	.2040 p=.055	6132 p=000	6236 p=000

Table IV: Pearson's correlation analysis of the abundance and biomass of the nine dominant estuarine and smaller marine spawning ichthyofaunal species sampled in the channel using a 30 m seine net in comparison to temporal, spatial, physico-chemical and biological parameters.

Marked correlations are significant at p < .05000 N=98 (Casewise deletion of missing data)

		G. aestuaria		*R. holubi*		*G. callidus*		*A. breviceps*		*M. capensis*		*S. turbynei*		*L. dumerilii*		*L. lithognathus*		*L. richardsonii*	
		Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass
Study Duration		.0106 p=.917	.0413 p=.686	-.1284 p=.208	.1134 p=.266	-.4115 p=.000	-.3565 p=.000	-.2499 p=.013	-.1967 p=.052	-.0024 p=.981	.0537 p=.599	-.3643 p=.000	-.3491 p=.000	-.1856 p=.067	-.1132 p=.267	-.0874 p=.392	-.0572 p=.576	-.2375 p=.019	-.2686 p=.007
Initial closed-Open-Re-closed		.0124 p=.903	.0404 p=.693	-.1120 p=.272	.0629 p=.538	-.4404 p=.000	-.3197 p=.001	-.2377 p=.018	-.1762 p=.083	.0586 p=.567	.0819 p=.423	-.2755 p=.006	-.2744 p=.006	-.1634 p=.108	-.0631 p=.537	-.0118 p=.908	-.0150 p=.883	-.1584 p=.119	-.2052 p=.043
Open/Closed		-.0107 p=.917	.0041 p=.968	.0449 p=.661	.0714 p=.485	-.1176 p=.249	-.1051 p=.303	.0810 p=.428	.0819 p=.423	.0327 p=.749	-.0471 p=.645	-.1668 p=.101	-.1506 p=.139	-.0548 p=.592	-.0603 p=.555	.1352 p=.184	.0668 p=.513	.3133 p=.002	.3702 p=.000
Season		-.0080 p=.938	.0157 p=.878	-.0992 p=.331	.1614 p=.112	-.1664 p=.101	-.2017 p=.046	-.2004 p=.048	-.1813 p=.074	-.1410 p=.166	-.0728 p=.476	-.3794 p=.000	-.3645 p=.000	-.2009 p=.047	-.1817 p=.073	-.1953 p=.054	-.1148 p=.260	-.1593 p=.117	-.1576 p=.121
Distance from Mouth		.1958 p=.053	.1802 p=.076	.3990 p=.000	.2373 p=.019	.4205 p=.000	.4260 p=.000	-.1608 p=.114	-.1573 p=.122	.1454 p=.153	.2570 p=.011	.4518 p=.000	.3343 p=.001	.2441 p=.015	.2138 p=.034	-.2131 p=.035	-.1756 p=.084	-.1734 p=.088	-.1938 p=.056
Reaches		.1828 p=.072	.1717 p=.091	.4062 p=.000	.2583 p=.010	.3956 p=.000	.3978 p=.000	-.1520 p=.135	-.1407 p=.167	.1450 p=.154	.2299 p=.023	.4406 p=.000	.3124 p=.002	.2432 p=.016	.2445 p=.015	-.2248 p=.026	-.2001 p=.048	-.1386 p=.174	-.1516 p=.136
Depth		-.0702 p=.492	-.0463 p=.651	-.1029 p=.313	-.0582 p=.569	-.1311 p=.198	-.1435 p=.159	-.1700 p=.094	-.1400 p=.169	-.0747 p=.465	-.0250 p=.807	-.0699 p=.494	-.0858 p=.401	-.0069 p=.946	.0676 p=.508	-.1265 p=.215	-.0659 p=.519	-.2328 p=.021	-.2509 p=.013
Average Temperature		-.0912 p=.372	-.1069 p=.295	.2277 p=.024	.0825 p=.419	.1117 p=.273	.2180 p=.031	.1411 p=.166	.1460 p=.151	.1128 p=.269	.0897 p=.380	.3558 p=.000	.3119 p=.002	.1725 p=.089	.1908 p=.060	.1928 p=.057	.1457 p=.152	.1301 p=.202	.0960 p=.347
Average Salinity		-.0237 p=.817	-.0348 p=.734	.0490 p=.632	.0500 p=.625	-.0172 p=.866	-.0279 p=.785	.0120 p=.906	.0055 p=.957	-.0163 p=.873	-.0289 p=.777	-.0515 p=.614	.0168 p=.870	-.0015 p=.988	-.0240 p=.815	-.0507 p=.620	-.0133 p=.897	-.1884 p=.063	-.3218 p=.001
Average Dissolved Oxygen		.1078 p=.291	.1277 p=.210	-.2561 p=.011	-.0823 p=.421	-.2226 p=.028	-.3094 p=.002	-.0719 p=.482	-.0609 p=.552	-.1510 p=.138	-.1094 p=.283	-.3765 p=.000	-.3306 p=.001	-.1896 p=.061	-.1884 p=.063	-.0881 p=.388	-.0810 p=.428	-.0963 p=.345	-.0884 p=.387
Turbidity NTU		.0240 p=.815	-.0048 p=.963	.3869 p=.000	.1938 p=.056	.3205 p=.001	.3446 p=.001	.0689 p=.500	.0309 p=.763	.0023 p=.982	-.0531 p=.603	.3686 p=.000	.3494 p=.000	.2450 p=.015	.1339 p=.189	.0230 p=.822	-.0086 p=.933	.0809 p=.428	.1178 p=.248
Average POM		.0743 p=.467	.0753 p=.461	-.1013 p=.321	-.1200 p=.239	-.2391 p=.019	-.1531 p=.132	-.0387 p=.705	-.0238 p=.816	.1423 p=.162	.0830 p=.417	.0008 p=.994	.0135 p=.895	.0299 p=.770	.1045 p=.306	.2009 p=.047	.0983 p=.336	-.0578 p=.572	-.1672 p=.100
Average Total Chl-*a*		.0923 p=.366	.0767 p=.453	-.1080 p=.290	-.2065 p=.041	.1010 p=.322	.0594 p=.561	.0561 p=.584	.0511 p=.617	.0771 p=.450	.0355 p=.729	.1317 p=.196	.1575 p=.121	.0809 p=.428	.0616 p=.547	.0244 p=.811	.0378 p=.712	-.0919 p=.368	-.1152 p=.259
Zooplankton abundance log(x+1)		-.0758 p=.458	-.0794 p=.437	-.0233 p=.820	-.0489 p=.633	-.2680 p=.008	-.1681 p=.098	-.0341 p=.739	-.0185 p=.857	.0571 p=.577	-.0054 p=.958	.0013 p=.990	.0033 p=.975	.0051 p=.960	.0648 p=.526	.0919 p=.368	.0586 p=.566	.0344 p=.736	-.0346 p=.735
Zooplankton biomass log(x+1)		-.0284 p=.781	-.0381 p=.709	.0288 p=.778	-.1395 p=.171	.1487 p=.144	.1519 p=.135	.2727 p=.007	.2315 p=.022	.3508 p=.000	.2754 p=.006	.2706 p=.007	.2807 p=.005	.2613 p=.009	.2463 p=.014	-.0042 p=.967	-.0454 p=.657	.3040 p=.002	.2727 p=.007
30 m	**Margalef's**	-.1311 p=.198	-.1347 p=.186	.0026 p=.980	-.0678 p=.507	-.0235 p=.818	-.0013 p=.990	.0888 p=.385	.0603 p=.555	.1601 p=.115	.0698 p=.495	.1858 p=.067	.1997 p=.049	.2368 p=.019	.3526 p=.000	-.0021 p=.983	.0013 p=.990	.0055 p=.957	.0085 p=.934
	Shannon-Wiener	-.1994 p=.049	-.2133 p=.035	-.0756 p=.460	-.2176 p=.031	.1581 p=.120	.1283 p=.208	-.0596 p=.560	-.0979 p=.337	.1358 p=.182	.0624 p=.542	.3776 p=.000	.3705 p=.000	.3405 p=.001	.4236 p=.000	.0071 p=.945	-.0142 p=.889	-.0968 p=.343	-.0879 p=.390
30 m	**Abundance**	.8897 p=.000	.8824 p=.000	.5151 p=.000	.4559 p=.000	.4448 p=.000	.4458 p=.000	.2556 p=.011	.2427 p=.016	.0886 p=.386	.1340 p=.188	.1567 p=.123	.1398 p=.170	.0703 p=.492	-.0199 p=.846	-.0319 p=.755	-.0751 p=.463	.0463 p=.651	.1193 p=.242
	Biomass	.3850 p=.000	.3913 p=.000	.7145 p=.000	.7928 p=.000	.3745 p=.000	.4472 p=.000	.1877 p=.064	.2094 p=.039	.3324 p=.001	.4905 p=.000	.1806 p=.075	.1036 p=.310	.2681 p=.008	.2412 p=.017	-.0589 p=.565	-.0932 p=.361	.0165 p=.872	.1162 p=.255

Table V: Pearson's correlation analysis of the abundance and biomass of the six dominant larger marine and freshwater spawning ichthyofaunal species sampled in the channel using a 50 m seine net in comparison to temporal, spatial, physico-chemical and biological parameters.

Shaded correlations are significant at p < .05000 N=86 (Casewise deletion of missing data)

		R. holubi		*L. dumerilii*		*L. richardsonii*		*M. capensis*		*L. lithognathus*		*P. commersonnii*	
		Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass
Study Duration		-.2023 p=.062	-.0950 p=.384	.0950 p=.384	.0927 p=.396	-.0041 p=.970	-.0033 p=.976	.1287 p=.238	.0503 p=.646	-.1019 p=.351	.0476 p=.664	-.2527 p=.019	-.2082 p=.054
Initial closed-Open-Re-closed		-.1668 p=.125	-.1078 p=.323	.1647 p=.130	.1200 p=.271	-.0235 p=.830	.0045 p=.967	.1699 p=.118	.0917 p=.401	-.1062 p=.330	.0445 p=.684	-.1790 p=.099	-.1446 p=.184
Open/Closed		-.0241 p=.826	-.0628 p=.566	-.0910 p=.405	-.0737 p=.500	.4846 p=.000	.3538 p=.001	.0332 p=.762	-.0557 p=.611	-.0121 p=.912	-.0262 p=.811	-.0395 p=.718	-.0319 p=.770
Season		-.1981 p=.068	-.0384 p=.726	-.1330 p=.222	-.0257 p=.815	-.0880 p=.421	-.0996 p=.362	-.0869 p=.426	-.0871 p=.425	-.0909 p=.405	-.0107 p=.922	-.2137 p=.048	-.1726 p=.112
Distance from Mouth		.3031 p=.005	.2781 p=.010	.0483 p=.659	-.0820 p=.453	-.2182 p=.044	-.2670 p=.013	-.2081 p=.055	-.2858 p=.008	-.2105 p=.052	-.2982 p=.005	.1166 p=.285	.1746 p=.108
Reaches		.2894 p=.007	.2590 p=.016	.0427 p=.696	-.0746 p=.495	-.1818 p=.094	-.2221 p=.040	-.1676 p=.123	-.2355 p=.029	-.2395 p=.026	-.3003 p=.005	.1053 p=.335	.1519 p=.163
Depth		-.1956 p=.071	-.1817 p=.094	.0183 p=.867	.0019 p=.986	-.1753 p=.106	-.1942 p=.073	-.0572 p=.601	-.1035 p=.343	-.1178 p=.280	-.0721 p=.510	-.1570 p=.149	-.1418 p=.193
Average Temperature		.2703 p=.012	.2041 p=.059	.1147 p=.293	-.0487 p=.656	-.0680 p=.534	-.0155 p=.887	.0148 p=.893	.0129 p=.906	-.0117 p=.915	.0261 p=.812	.2065 p=.056	.1673 p=.124
Average Salinity		.0223 p=.839	.0516 p=.637	.1719 p=.114	.1374 p=.207	-.0347 p=.751	-.0169 p=.877	.0084 p=.939	.0110 p=.920	.0865 p=.428	.0541 p=.621	-.2100 p=.052	-.2150 p=.047
Average Dissolved Oxygen		-.2354 p=.029	-.1369 p=.209	.0091 p=.933	.1900 p=.080	.0745 p=.496	.0611 p=.576	.0189 p=.863	.0462 p=.672	.0007 p=.995	.0357 p=.744	-.2222 p=.040	-.2243 p=.038
Turbidity NTU		.3133 p=.003	.2339 p=.030	.0521 p=.634	-.0628 p=.565	-.0021 p=.985	-.0040 p=.971	-.1832 p=.091	-.1931 p=.075	.0079 p=.943	-.0809 p=.459	.1123 p=.303	.1586 p=.145
Average POM		-.0206 p=.851	-.0892 p=.414	.0831 p=.447	.0244 p=.824	.5039 p=.000	.4338 p=.000	.0911 p=.404	.0223 p=.839	.0324 p=.767	.0104 p=.924	-.1234 p=.258	-.1044 p=.339
Total Chl-*a*		-.0410 p=.708	-.0761 p=.486	.0350 p=.749	-.1512 p=.165	-.1372 p=.208	-.0598 p=.584	-.0135 p=.902	-.0026 p=.981	.0265 p=.808	-.0721 p=.509	-.0195 p=.858	-.0555 p=.612
Zooplankton abundance log(x+1)		.0356 p=.745	-.0063 p=.954	.2115 p=.051	.1472 p=.176	.0181 p=.869	.0799 p=.465	.1515 p=.164	.1346 p=.217	.0360 p=.742	.0794 p=.468	-.0253 p=.817	-.0144 p=.895
Zooplankton biomass log(x+1)		.1240 p=.256	.0325 p=.766	.0329 p=.764	-.0199 p=.856	.0023 p=.983	.0182 p=.868	-.0297 p=.786	.0165 p=.880	.1044 p=.339	-.0666 p=.542	.1883 p=.082	.1528 p=.160
50 m	**Margalef's**	.1442 p=.185	.1049 p=.336	.1577 p=.147	.1355 p=.214	.1718 p=.114	.2350 p=.029	.3566 p=.001	.3969 p=.000	.0813 p=.457	.1090 p=.318	.0599 p=.584	.0434 p=.692
	Shannon-Wiener	-.0790 p=.470	-.0884 p=.418	.2712 p=.012	.1484 p=.173	.1516 p=.164	.2515 p=.019	.4101 p=.000	.4431 p=.000	.0402 p=.713	.1261 p=.247	-.1318 p=.226	-.1225 p=.261
50 m	**Abundance**	.9585 p=.000	.8612 p=.000	.3353 p=.002	.2073 p=.056	.2369 p=.028	.1708 p=.116	.1075 p=.324	.0713 p=.514	.0873 p=.424	.0180 p=.869	.5114 p=.000	.5582 p=.000
	Biomass	.6111 p=.000	.6562 p=.000	.5650 p=.000	.6379 p=.000	.2259 p=.037	.3288 p=.002	.3943 p=.000	.3947 p=.000	.0443 p=.686	.0601 p=.583	.2485 p=.021	.2715 p=.011

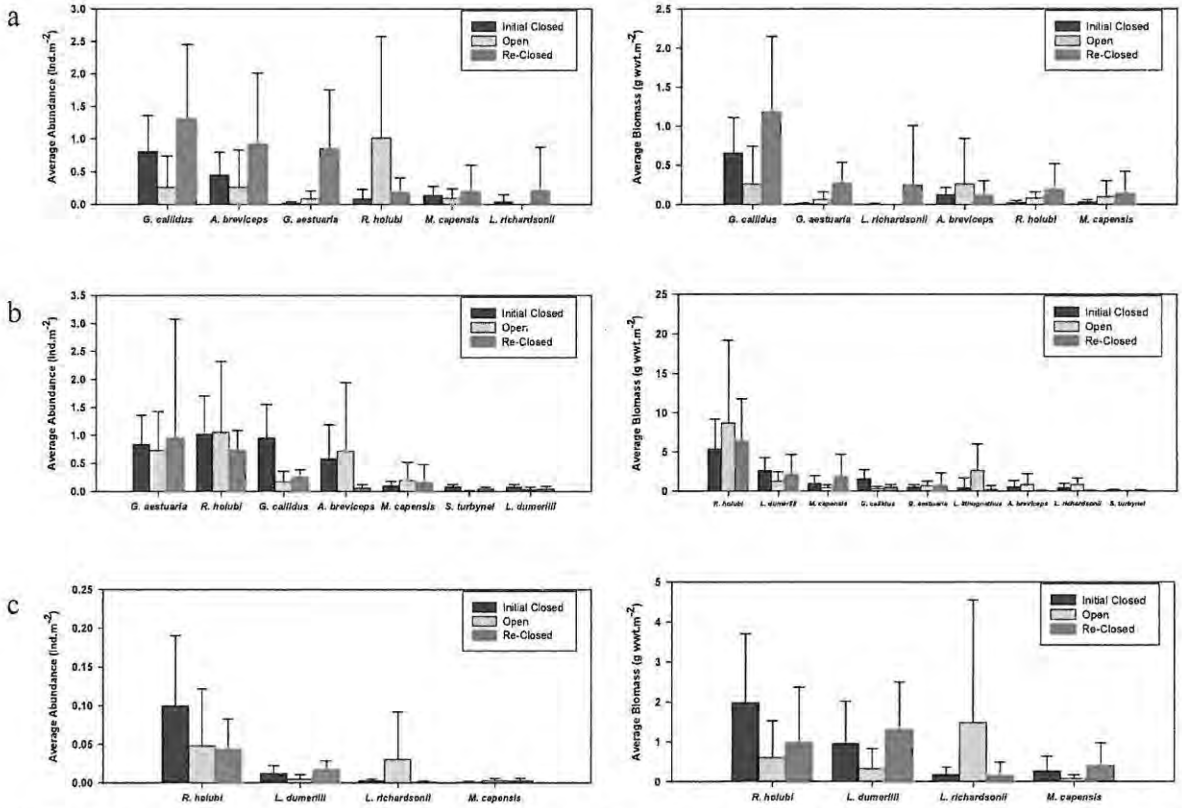

Figure II: The mean abundance (ind.m^{-2}) (left) and biomass (g wwt.m^{-2}) (right) of the (a) six numerically and gravimetrically dominant species sampled in the littoral zone of the Mpekweni Estuary using the 5 m seine net, (b) seven numerically and nine gravimetrically dominant smaller estuarine and marine spawning species sampled using the 30 m seine net and (c) four numerically and five gravimetrically dominant larger marine and freshwater spawning species sampled using the 50 m seine net during the initial closed, open and re-closed phases of the Mpekweni Estuary from November 2005 to October 2007. Error bars indicate standard deviation.

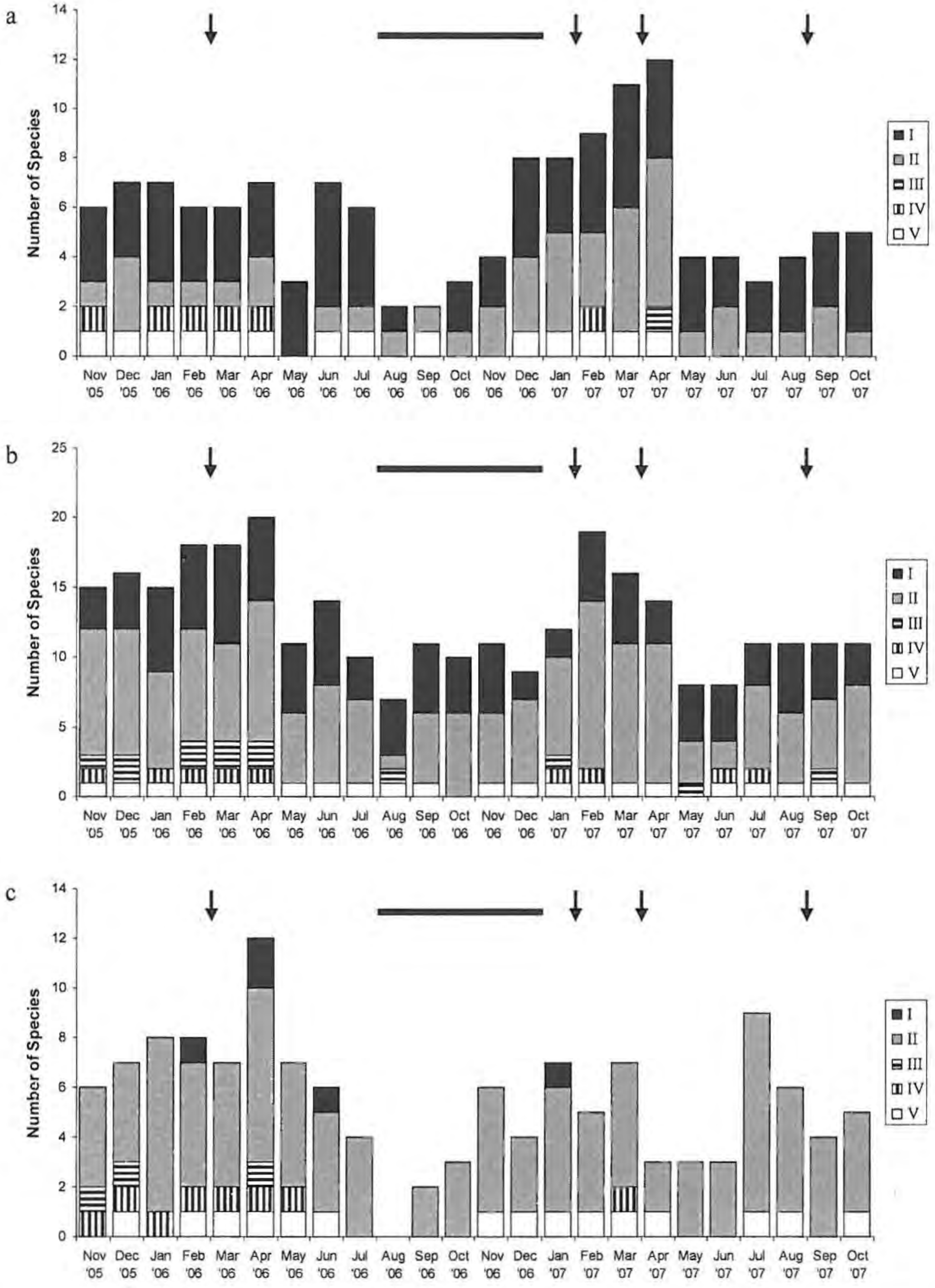

Figure III: The number of fish species and representation of estuarine utilisation categories sampled by the (a) 5 m, (b) 30 m and (c) 50 m seine nets for each month. The horizontal bar indicates the open period and the arrows, overwash events.

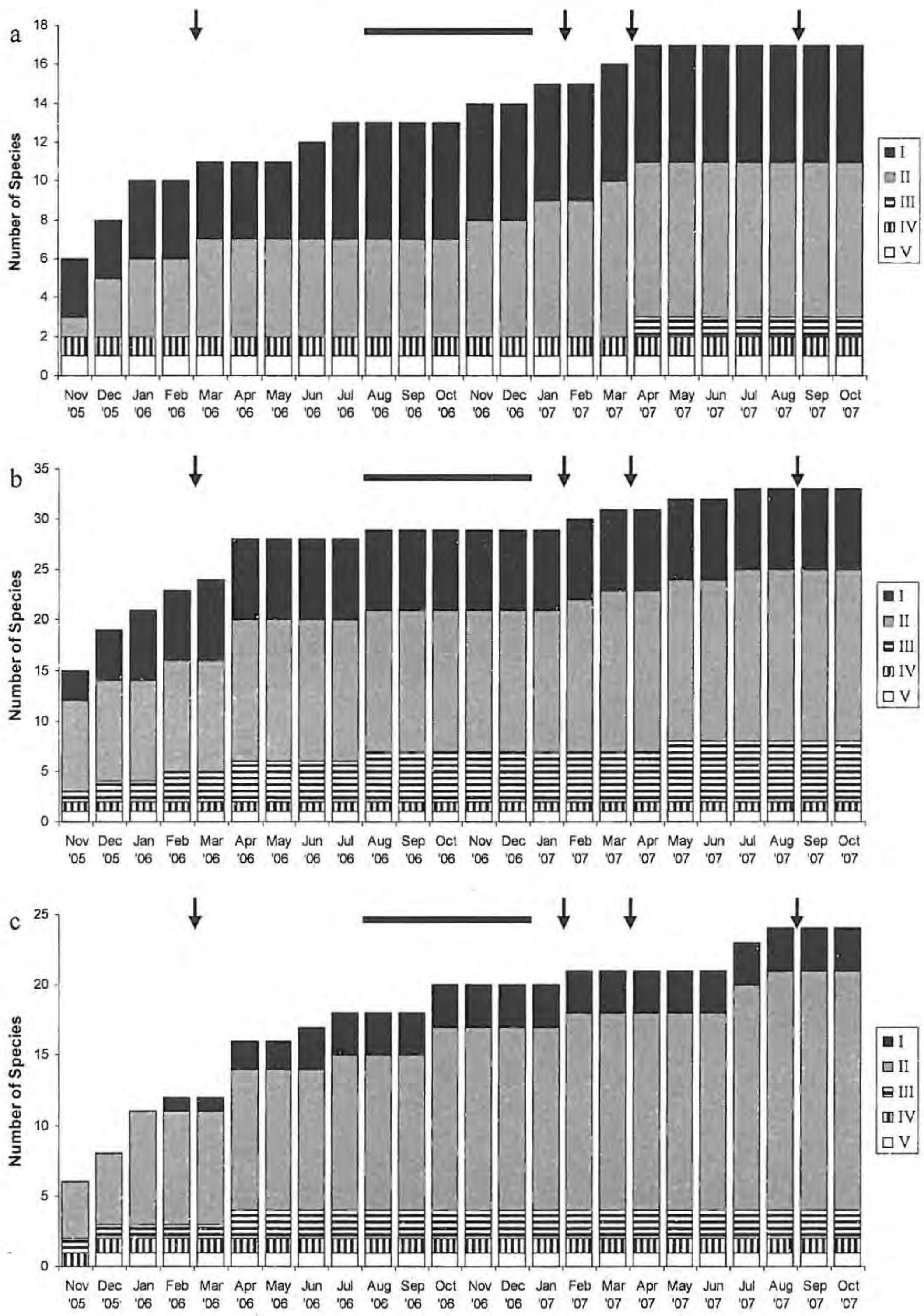

Figure IV: The accumulated number of species sampled each month in the (a) 5 m, (b) 30 m and (c) 50 m seine nets and the contribution to each estuarine utilisation category. The horizontal bar indicates the open period and the arrows, overwash events.

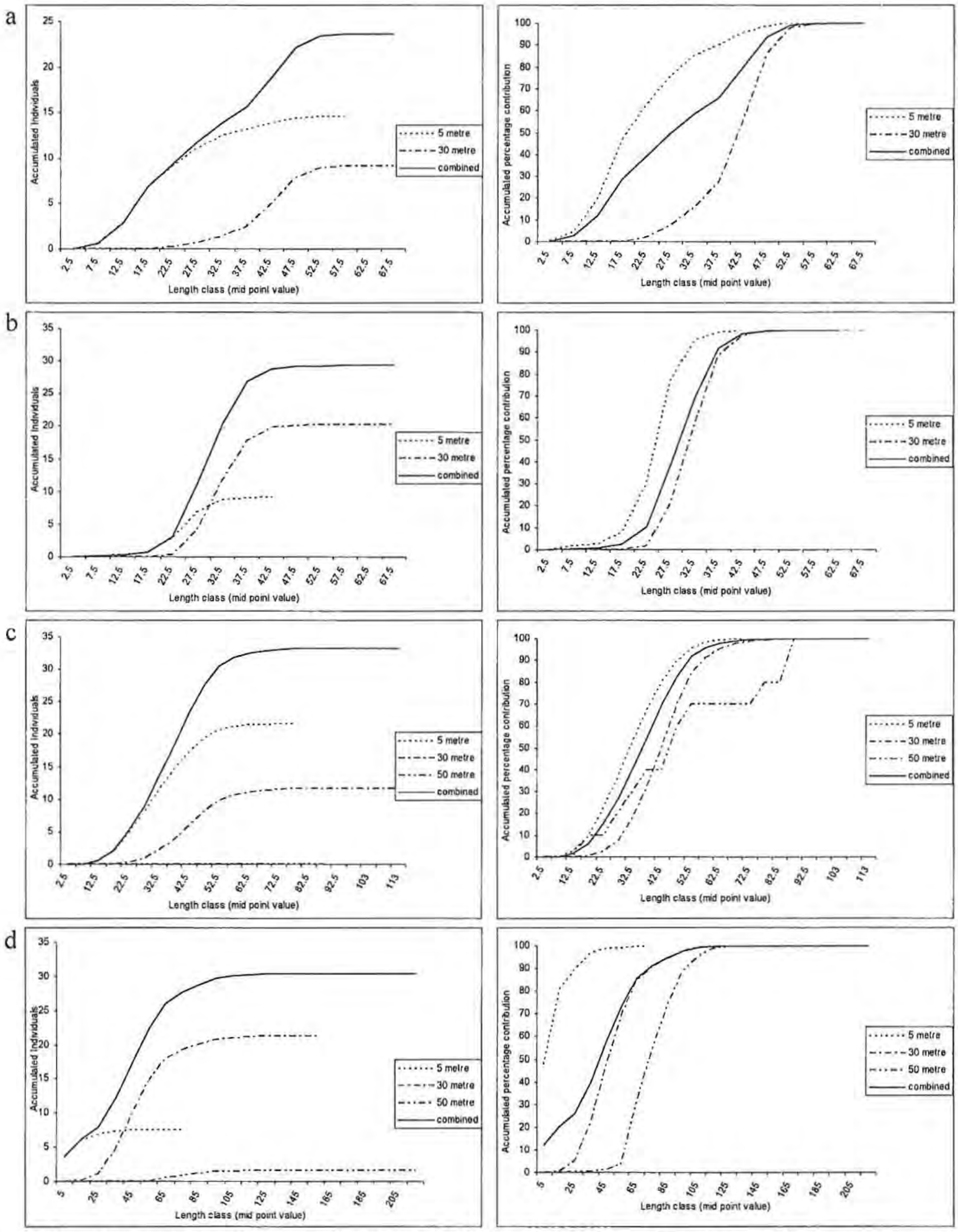

Figure V: The combined accumulated individuals per length class (left column) and percentage contribution of individuals per length class (right column) for (a) *Atherina breviceps*, (b) *Gilchristella aestuaria*, (c) *Glossogobius callidus* and (d) *Rhabdosargus holubi*.

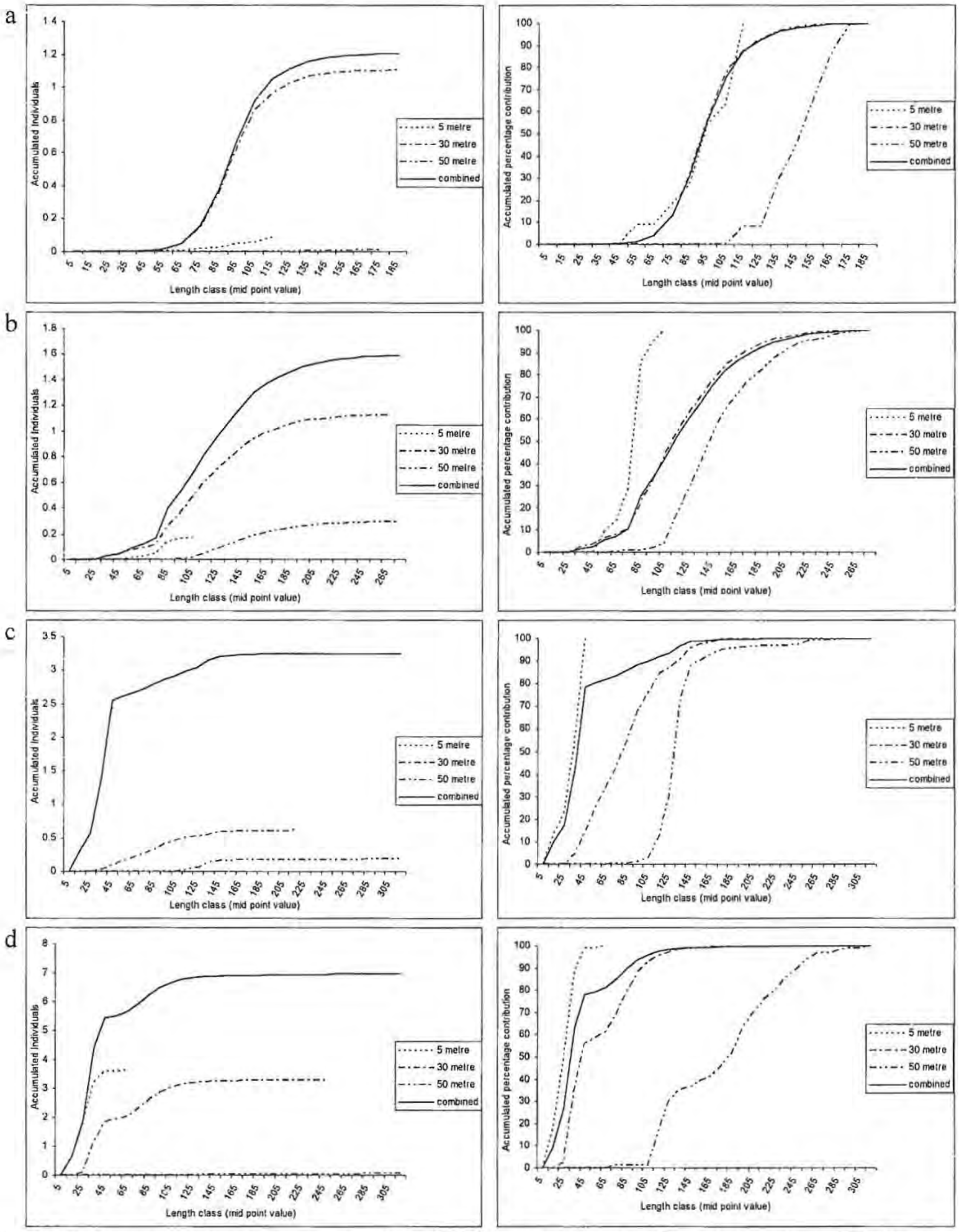

Figure VI: The combined accumulated individuals per length class (left column) and percentage contribution of individuals per length class (right column) for (a) *Solea turbynei*, (b) *Liza dumerilii*, (c) *Liza richardsonii* and (d) *Myxus capensis*.

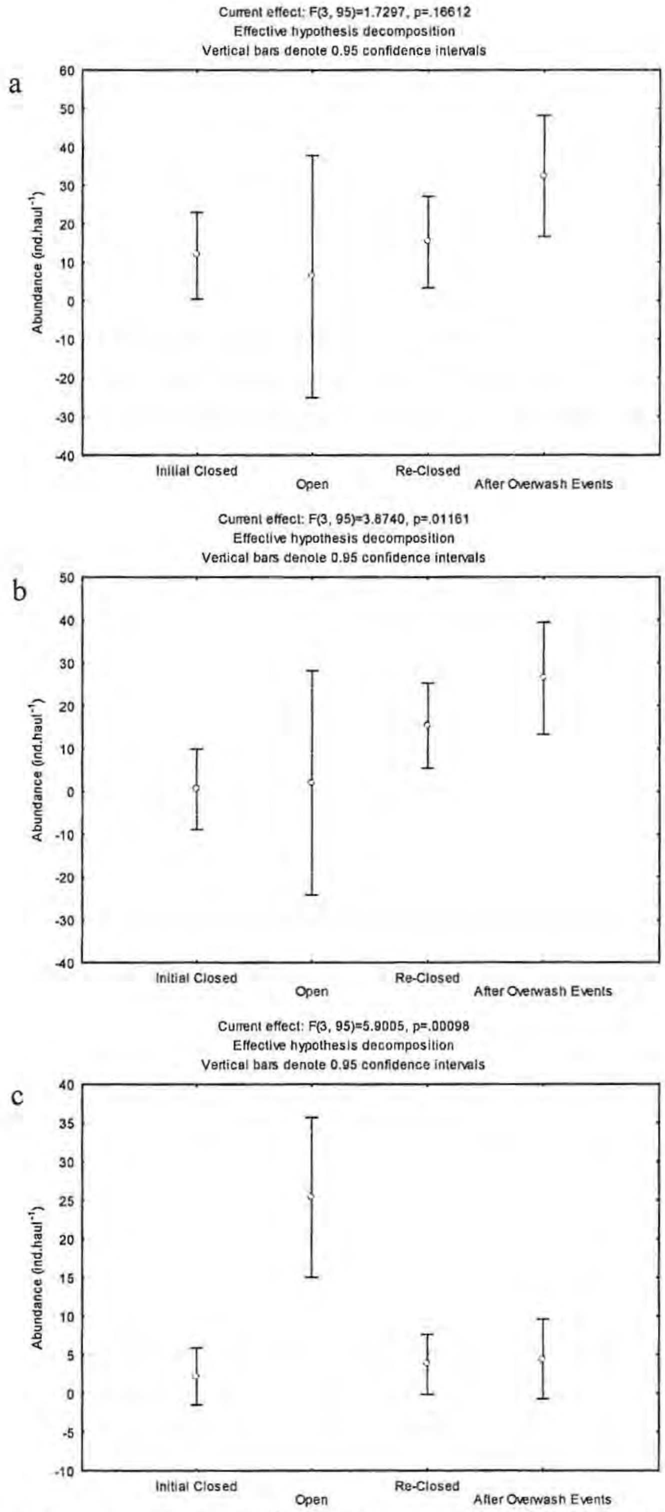

Figure VII: The average number (ind.haul^{-1}) of (a) *Atherina breviceps*, (b) *Gilchristella aestuaria* and (c) *Rhabdosargus holubi* sampled by the 5 m seine net during the initial closed period, open period, re-closed period and post overwash events.

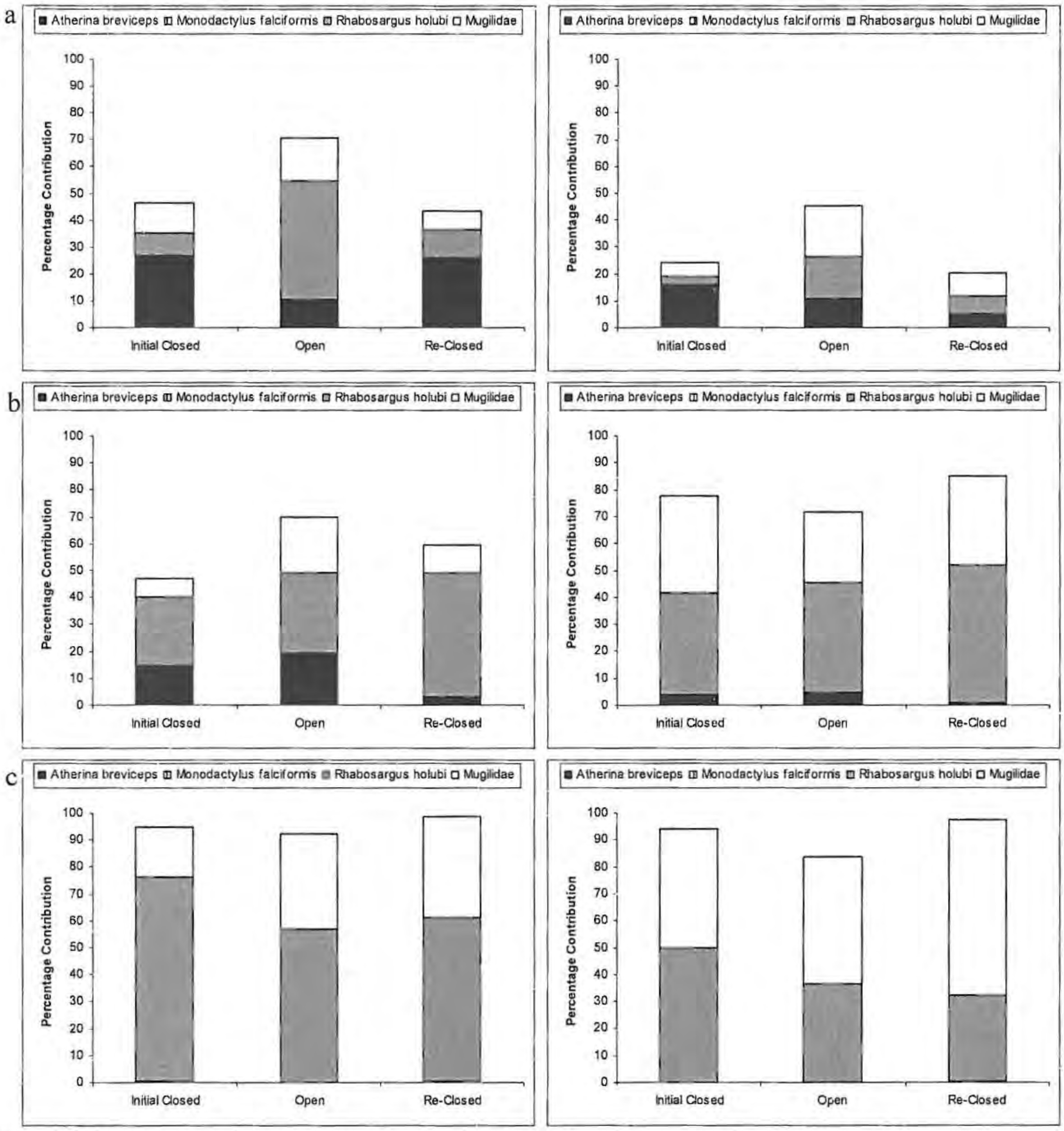

Figure VIII: The percentage contribution of the fish species recorded during the recruitment study (Chapter 6) to the total abundance (ind.m^{-2}) (left) and biomass (g wwt.m^{-2}) (right) of the fish sampled throughout the different phases of study using the (a) 5 m, (b) 30 m and (c) 50 m seine nets.