TRENDS IN FISH COMMUNITY STRUCTURE AND RECRUITMENT IN A TEMPORARILY OPEN/CLOSED SOUTH AFRICAN ESTUARY

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ABSTRACT

Long-term interannual changes in richness, abundance, diversity and structure of the fish community in the temporarily open/closed East Kleinemonde Estuary, Eastern Cape, are described and the recruitment success of two estuary-dependent marine species assessed. In addition, laboratory experiments were conducted to assess the possible role of olfaction in the recruitment process of an estuary-dependent marine fish species.

Multivariate analyses of the annual marine fish communites identified two distinct groups with more species recorded during years that succeeded spring (September to November) mouth opening events than in years following no mouth opening events in spring. Interannual community stability (IMD) and seriation (IMS) also increased from the ‘other’ to the ‘spring’ years. These results highlight the importance of the timing of mouth opening to the marine fish community in a temporarily open/closed estuary.

This study also made use of long-term records of daily mouth state and linked them to the recruitment of distinct year-class cohorts in two spardis with contrasting life-history characteristics. *Lithognathus lithognathus* only recruited into the estuary in years when the mouth opened between late August and January. This was linked to the limited spawning season of this species and its inability to enter closed estuaries via wave overwash events. In contrast, recruitment by *Rhabdosargus holubi* juveniles appeared to be uninterrupted and was not determined by the seasonality of mouth opening. This species dominates the marine-spawning component of the East Kleinemonde Estuary and its success is attributed to an extended spawning season and its ability to recruit into estuaries during both overwash and open mouth conditions.

Attraction of postflexion *Rhabdosargus holubi* larvae to estuary, surf zone and river water was also measured using a rectangular choice chamber. In two sets of experiments, conducted during peak recruitment periods, larvae from both the surf zone and estuary mouth region selected estuary water with a significantly higher frequency than sea water. Larvae collected in the mouth region showed a stronger preference for river water than those collected in the surf zone, thus suggesting that

these fish are more attracted to freshwater influenced nursery areas once they have entered the estuary than those in the surf zone. Larvae collected in the marine environment also selected surf zone water with significantly higher frequencies than estuary water or offshore sea water, thus confirming the importance of the surf zone as an interim nursery area for postflexion *R. holubi*.

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CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

Estuaries are the meeting place of freshwater from rivers and saltwater from the sea and, as such, are dynamic environments characterised by large fluctuations in environmental conditions. Whitfield (1992a) identified five estuary types in southern Africa: permanently open estuaries, temporarily open/closed estuaries, river mouths, estuarine lakes and estuarine bays. In contrast to estuaries within the temperate regions of the northern hemisphere, which are predominantly permanently open, the majority of estuaries along the coast of southern Africa are relatively small and are closed off from the sea for varying periods by a sand bar which forms at the mouth (Potter *et al.* 1990, Whitfield 1998). Similarly, of the 80 estuaries and coastal lagoon systems found along the 1200 km coastline of temperate Western Australia, only nine are permanently open to the sea, while 64 only open to the sea seasonally or less frequently and seven are permanently closed (Hodgkin and Lenanton 1981).

According to Whitfield (1992a) most temporarily open/closed estuaries in South Africa have small river catchments (<500 km^2) and, in many systems, river flow may be minimal or absent for extended periods. The tidal prism is generally small ($<1 \times 10^6$ m^3) when the mouth is open and absent when the mouth is closed. Although the salinity regime in these estuaries may range from fresh (during episodic floods) to hypersaline (during prolonged droughts) mesohaline conditions (5.1 to 18 ‰) usually prevail (Whitfield 1992a) and horizontal gradients in temperature and salinity are generally absent (Lukey *et al.* 2006). Water circulation during open mouth conditions is driven by both tidal and river flow and by wind when the mouth is closed (Whitfield 1992a).

Temporarily open/closed estuaries (TOCEs) were recently divided into two sub-categories based on the duration of the open mouth phase (Whitfield and Bate 2006). Intermittently open estuaries (IOEs) are defined as systems that are, on average, closed for most (>50%) of the year and only open intermittently; intermittently closed estuaries (ICEs) have, on average, a link with the sea for more that 50% of the time (Whitfield and Bate 2006). Along the Eastern Cape coast of South Africa between

Port Elizabeth and East London, TOCEs tend to open sporadically and mouth opening depends mainly on rainfall in the catchment areas and the extent of sand bar development at the mouth (Cowley 1998).

The aquatic fauna of TOCEs is dominated by marine and estuarine species, many of which occur in large numbers (Whitfield 1998). Research on estuarine fish communities in South Africa has focused mainly on large permanently open systems, despite the predominance of TOCEs (Vorwerk *et al*. 2001). Whitfield (2000) identified 258 functional estuaries along the South African coastline, extending from the Namibian border at the Orange (Gariep) Estuary on the Atlantic Ocean coast in the west, to the Kosi Estuary on the Indian Ocean coast in the east. Along this stretch of coast, 183 (approximately 71%) estuaries are classified as TOCEs

From a scientific and administrative perspective it is vital to gain a proper understanding of the processes occurring within TOCEs prior to making recommendations on their management, water allocations, exploitation or conservation (Whitfield 1998). This is particularly important, as the South African National Water Act No. 36 of 1998 requires that the amount and quality of water needed by all aquatic ecosystems, including estuaries, be determined. This study was designed to contribute towards a better understanding of the fundamental processes driving marine fish recruitment and community structuring within a typical Eastern Cape TOCE.

Differences between fish assemblages in permanently and temporarily open/closed estuaries

Studies have shown that permanently open estuaries generally have a higher diversity of species than TOCEs (Bennett 1989, Whitfield and Kok 1992, Potter and Hyndes 1994, Young and Potter 2002). The higher species richness in permanently open estuaries is often attributed to an increase in the number of estuary-dependent marine species in permanently open estuaries (Bennett 1989). In the permanently open Palmiet Estuary, marine species made up 53% of the catch by numbers compared with only 19% of the catch in the nearby temporarily open/closed Kleinmond Estuary (Bennett 1989). Marine stragglers, which are not dependent on estuaries, are virtually absent from TOCEs (Harrison 2003), and this may also contribute to the differences observed in species richness.

Cluster analysis of seine net data from several Eastern Cape estuaries demonstrated that the greatest differences in fish assemblages occurred between permanently open and temporarily open/closed estuaries, which separated at the 50% similarity level. Smaller and larger TOCEs, on the other hand, separated at a 65% similarity level (Vorwerk *et al.* 2003). Differences in fish assemblages were found to be significant and were attributed to higher species richness in permanently open estuaries and a greater abundance of fish in TOCEs. Both estuary-dependent marine and estuarine resident species accounted for these differences. Overall, *Gilchristella aestuaria* and *Atherina breviceps*, two shoaling estuarine resident species, comprised a larger percentage of the catch, by numbers, in TOCEs than in permanently open estuaries (Vorwerk *et al.* 2003). Estuary-dependent marine species generally represented a larger proportion of the catch, by numbers, in permanently open estuaries. This was attributed to their year-round access, while recruitment opportunities into TOCEs are more limited (Vorwerk *et al.* 2003).

Strydom *et al.* (2003) also found that permanently open and temporarily open/closed estuaries in the Eastern Cape showed a distinct separation in fish assemblage structure, based on early life stages (larvae and early juveniles). Again, estuary-dependent marine species were mainly responsible for this separation. Although the ichthyofauna of TOCEs may be less diverse than in permanently open estuaries, these estuaries still provide important nursery areas for the juveniles of many estuary-dependent marine species (Whitfield 1998).

Fish communities in temporarily open/closed estuaries

TOCEs in the subtropical region (KwaZulu-Natal) of South Africa have been the focus of recent research (Perissinotto *et al.* 2004), but less is known about these systems in the warm- and cool-temperate regions (Eastern, Western and Northern Cape provinces). Harrison (2002) conducted an extensive survey of the biogeography and community structure of the ichthyofauna in 109 estuaries along the South African coastline, of which 67 were TOCEs. Results from the above survey identified a biogeographical break between the warm-temperate and subtropical zones for permanently open estuaries at the Mdumbi Estuary, south of Port St Johns. The break was slightly different for TOCEs, occurring in the vicinity of the Mbashe Estuary (south of the Mdumbi Estuary) and this difference was attributed to the lack of TOCEs sampled in this transitional region (Harrison 2003). The ichthyofaunal break identified by Harrison (2002) between the warm-temperate and cool-temperate regions for both estuarine types occurred at Cape Agulhas (Figure 1.1).

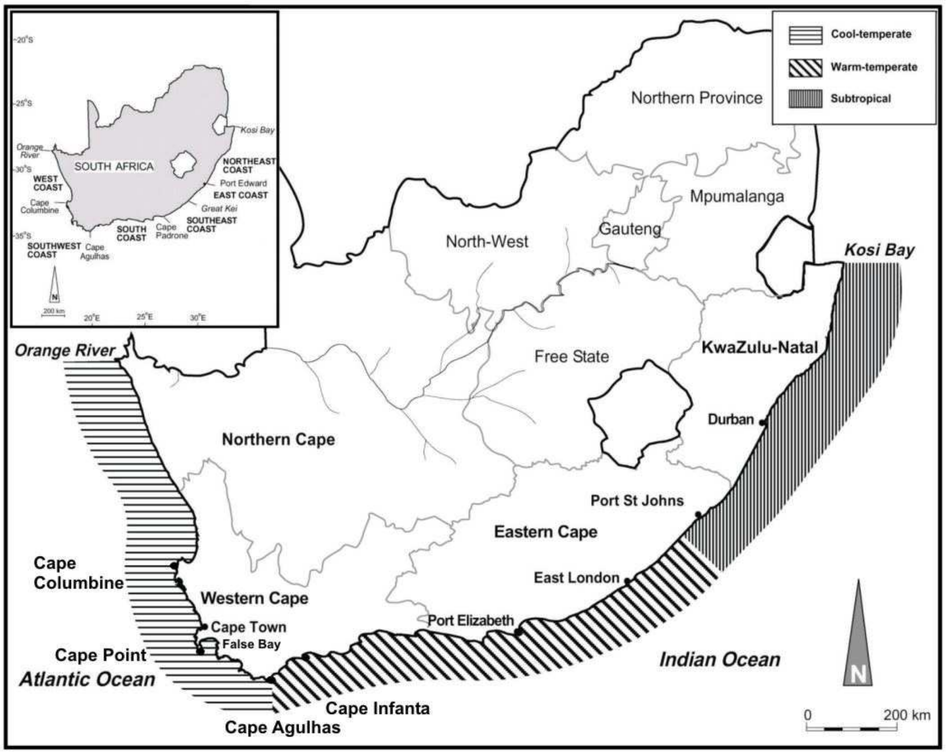


Figure 1.1. Map of South Africa indicating the three biogeographic provinces, based on estuarine fish communities (after Harrison 2002).

Differences in estuarine fish assemblages around the South African coastline were recorded (Harrison 2005). The gradual decrease in taxonomic richness from east to west was attributed to a decreasing number of tropical marine species, primarily associated with a decrease in the influence of the warm Agulhas Current in the same direction. Maree *et al.* (2000) also recorded a decrease in the number of fish species in a south-westerly direction, with a substantial decline occurring west of the permanently open Swartkops Estuary. This was attributed to the Agulhas Current moving further offshore in the Algoa Bay region and consequently tropical coastal species reaching the southern limit of their distribution. Despite a gradual loss of tropical species, the number of endemic species increases south of KwaZulu-Natal before declining again along the cool-temperate southwest (Cape Columbine to Cape Agulhas) and west coasts (Orange River to Cape Columbine). However, the diversity of widespread and temperate taxa is low around the entire coast (Harrison 2005).

Tropical species are more abundant further southwards in estuaries of Australia than in temperate South African estuaries. For example, *Rhabdosargus sarba* is abundant in temperate Western Australian estuaries, but is only recorded in small numbers in temperate South African estuaries (Potter *et al*. 1990). These differences may be attributed to the influence of the warm southward flowing Leeuwin current (Potter *et al.* 1990)

Estuary-dependent marine species dominate the biomass of TOCEs in all biogeographic zones (Harrison 2005). In small subtropical estuaries the sharptooth catfish *Clarius gariepinus* usually dominates catches by mass (Harrison 2005), while in warm-temperate estuaries the sparid *Rhabdosargus holubi* tends to dominate catches by mass (Harrison 2005). The importance of estuary-dependent sparids, particularly *R. holubi*, decreases on the south-western coast and the mugilid, *Liza richardsonii*, becomes dominant in catches both by number and mass (Harrison 1998).

In contrast to South Africa, where there is a relative shortage of protected inshore marine waters, the coast of Australia has numerous large marine embayments and fringing reefs that provide alternative nursery habitat for juvenile marine fishes (Loneragan *et al.* 1989, Potter and Hyndes 1994). Consequently, in temperate Western Australia the juveniles of many marine fish species found in estuaries are also found in marine embayments further north and are termed estuarine-opportunists (Lenanton and Potter 1987).

Although only a few species are able to complete their entire life cycle in estuaries (Day *et al*. 1981) short-lived estuarine resident species can dominate the fish communities of estuaries numerically (Potter *et al.* 1990). Estuarine resident species comprised well over 50% of the catch (by numbers) in warm-temperate TOCEs

(Dundas 1994, Vorwerk *et al.* 2001, Cowley and Whitfield 2002, Harrison 2003). In terms of abundance, the contribution of estuarine resident species is more variable in cool-temperate and subtropical estuaries. Harrison (2003) found that estuarine resident species contributed from 0.7% in the Mhlangeni Estuary to 93.1% in the Little Manzimtoti Estuary. In cool-temperate estuaries estuary-dependent marine species tend to dominate catches by number and mass, with estuarine resident taxa sometimes poorly represented (Harrison 2003). However, Clark *et al.* (1994) found that the estuarine resident *Gilchristella aestuaria* was numerically dominant in the temperate Sand Estuary. In temperate Western Australia the number of estuarine resident taxa increases, for example the Atherinidae are represented by five species in temperate Australian estuaries but by only one species in South African estuaries (Potter *et al*. 1990). *Oreochromis mossambicus* is the only freshwater species recorded in most TOCEs in South Africa, particularly on the southeast coast (Whitfield 1998).

Distribution of fish in estuaries

Although Vorwerk *et al.* (2001) found no clear evidence of an overall longitudinal fish distribution pattern in different warm-temperate estuaries on the south-eastern Cape coast, on an individual species basis there were discernible trends. *Atherina breviceps* were generally more abundant in the lower reaches of estuaries and *Gilchristella aestuaria* tended to be more abundant further upstream. The freshwater species, *Oreochromis mossambicus*, exhibited a preference for the upper reaches of estuaries, with 43% of individuals being caught in this zone. Similarly, the mugilid *Myxus capensis* was also more abundant in the upper reaches. Van der Elst (1978) found that primary consumers (i.e. species that feed on organisms low down in the food chain, such as plankton, epiphytic algae and detritus) were common in the lower reaches of the Kobole Estuary, while tertiary feeders (i.e. predators such as *Caranx ignobilis*) predominated in the upper reaches.

Classification and ordination of large and small seine catches in the East Kleinemonde Estuary showed that the fish composition in the lower reaches of the estuary differed significantly from that in the middle and upper reaches of the Estuary (Cowley and Whitfield 2001a). This difference was attributed mainly to *Atherina breviceps*, *Psammagobius knysnaenis*, *Rhabdosargus holubi*, *Lithognathus lithognathus*, *Liza* *dumerili* and *Liza richardsonii* showing a preference for the lower reaches of the estuary, with an increase in catches of *Gilchristella aestuaria, Glossogobius callidus, Myxus capensis, Monodactylus falciformis* and *Oreochromis mossambicus* in an upstream direction.

Classification and ordination revealed that the composition of the fish fauna in the mouth and lower reaches of the Moore River Estuary (Australia) differed significantly to the middle and upper reaches (Young *et al.* 1997). This was attributed mainly to a sequential decline in marine species in an upstream direction and a concurrent increase in estuarine species. Similarly, in the Wellstead Estuary (Australia), samples from the lower reaches separated from those in the middle and upper reaches (Young and Potter 2002). In estuaries such as the Los Peñasquitos Lagoon (southern California), where the salinity fluctuates widely, euryhaline species dominate throughout the estuary (Desmond *et al.* 2002).

Influence of mouth state on fish communities in temporarily open/closed estuaries

Mouth state is regarded as the major determinant of species richness in TOCEs, with higher numbers of marine species being captured in estuaries that open more frequently (Hodgkin and Lenanton 1981, Potter *et al.* 1993, Young *et al.* 1997, Whitfield 1998). During extended closed phases, fish populations may also decrease considerably due to predation. Blaber (1973a) determined the size of the *Rhabdosargus holubi* population in the West Kleinemonde Estuary when it closed on two separate occasions in 1971 and 1972. In 1971 a population of *R. holubi* consisting of 55 360 individuals decreased to 11 485 individuals after six months, while in 1972 a new stock of 14 674 individuals decreased to 12 000 over a seven month period. The difference was attributed mainly to predation by piscivorous birds, particularly cormorants, darter and heron. Despite heavy predation, Day *et al.* (1981) using data from Blaber (1973a, 1974a) estimated that the biomass of *R. holubi* in the West Kleinemonde increased in 1971 from 1.7 g m^{-2} to 2.7 g m^{-2} and from 0.46 g m^{-2} to 2.8 g m^{-2} in 1972 when the mouth opened. The predation impact by piscivorous birds on a closed fish population has also been quantified in the East Kleinemonde Estuary. Cowley (1998) recorded a 70% reduction in the marine-spawning fish population during the winter of 1994 following an unusual invasion of Cape cormorants *Phalacrocorax capensis*, which are predominantly offshore marine piscivores.

Kok and Whitfield (1986) sampled the fish community of the warm-temperate Swartvlei Estuary during open and closed phases using seine and gill nets. Generally, marine migrant species caught in large mesh seine nets were, on average, larger in size during the closed phase as no new recruits entered the population, while estuarine resident species showed no major size differences according to mouth phase. Catch per unit effort of most marine species, particularly those belonging to the Mugilidae, decreased during the closed phase, again because no new recruits entered the population. Cowley and Whitfield (2001a) also recorded significantly higher numbers of estuary-dependent marine species following an extended mouth opening event in the East Kleinemonde Estuary.

The species composition, abundance and size distribution of marine fishes within southern African estuaries generally undergo seasonal variations that are directly related to migration patterns (Whitfield and Kok 1992). In TOCEs the seasonality of mouth opening can also influence the seasonal pattern of fish abundance. Bennett (1989) sampled the fish community of the seasonally open Kleinmond Estuary, and found that there were marked seasonal changes in the fish assemblages. The mouth of the estuary opened during July (1980) and remained open during spring and early summer. Estuary-dependent marine species along the south coast breed primarily in spring and recruit into estuaries during spring and early summer. Larvae and small juveniles were therefore able to enter the Kleinmond Estuary during spring and summer and remain there during the subsequent closed phase. The timing of mouth opening (coinciding with peak recruitment periods) in the Kleinmond Estuary meant that the closed phase had little impact on the typical seasonal patterns that occur in temperate estuaries.

Fishes and river flows in estuaries

Considerable research has been conducted on the effects of altered river flows on fish community structure, functioning and abundance in permanently open estuaries (Whitfield and Paterson 1995, Ter Morshuizen *et al.* 1996, Grange *et al.* 2000, Bate *et al.* 2002, Whitfield and Paterson 2003) but little work has been conducted on TOCEs (Whitfield 2005).

A change in river flow rate is accompanied by altered water flow volumes, velocity, nutrient level, organic matter, conductivity and turbidity (Ter Morshuizen *et al.* 1996). River flow was found to have a major impact on the structure and functioning of fish communities within the permanently open Kariega and Great Fish estuaries, particularly in the upper reaches or river-estuary interface (REI) zone (Whitfield *et al.* 2003, Bate *et al.* 2002). High conductivity in the REI of the Great Fish Estuary, a freshwater ‘enriched’ system, in which natural run-off is augmented by an inter-basin transfer of water from the Orange River (Grange *et al.* 2000), resulted in an abundance of marine and estuarine species in both the REI and river above the ebb and flow. In contrast, the REI zone of the freshwater deprived Kariega Estuary was much smaller, resulting in fewer individuals and species being recorded in this part of the system (Bate *et al.* 2002). Similarly, Whitfield *et al.* (1994) documented a higher biomass of fish in the Great Fish Estuary compared with the freshwater deprived Kowie Estuary, and this was attributed to greater nutrient and organic matter input to the Great Fish Estuary, which led to elevated levels of primary and secondary production.

Marais (1988) surveyed Eastern Cape and Transkei estuaries using gill nets and found that catch rates, by number and mass, were positively correlated with catchment size. Estuaries with large catchments generally received consistently more run-off, and consequently experienced higher turbidity and lower salinity, along with pronounced salinity gradients. The highest fish catches were recorded in the Great Fish Estuary (Marais 1988).

In TOCEs, mouth opening and closing is directly linked to freshwater input. Reduced river inflow leads to prolonged mouth closure and shorter open phases, which inhibits immigration and emigration of marine fish species between estuaries and the sea (Whitfield and Wooldridge 1994), thus resulting in a reduction in species richness and abundance. One of the major effects of impoundments in catchment areas is to reduce the amplitude of floods in rivers and estuaries (Whitfield and Bruton 1989). Freshwater may also play an essential role in attracting larval and juvenile estuary-dependent marine species into estuaries. Indirect evidence suggests that fish trace land-based cues back to an estuary by following the olfactory concentration gradient (Whitfield 1994a).

Whitfield (1994a) also hypothesised that larvae and juveniles of estuary-dependent species orientate towards TOCEs when closed, by using dissolved organic and/or inorganic olfactory cues present in the estuarine water that seeps through the sand bar at the mouth of these systems. Without the proposed cues associated with estuarine and freshwater discharge, migratory fishes may have difficulty locating estuaries which, if true, would have serious consequences for these species. Grange *et al.* (2000) speculated that the higher ichthyoplankton densities in the Great Fish Estuary, when compared to the freshwater deprived Kariega Estuary, was due to a combination of stronger olfactory cues and elevated food stocks in the former system.

Rationale for this study

Although published research findings provide some understanding of the overall structure, distribution and abundance of fish communities in TOCEs, few studies have been conducted over a medium to long term (>10 years) (Flint 1985, Wolfe *et al.* 1987, Jackson and Jones 1999). Long-term studies allow for an understanding of changes in estuarine processes and physical variables and their effects on fish community structure (Flint 1985, Jackson and Jones 1999, Desmond *et al.* 2002, Power *et al.* 2002). In addition, numerous studies have focused on the nursery function of estuaries and the recruitment of larvae and juveniles into estuaries (e.g. Wallace 1975, Wallace and van der Elst 1975, Melville-Smith and Baird 1980, Day *et al.* 1981, Whitfield 1994a, Strydom 2003) but little is known about the factors governing the recruitment of estuary-dependent marine fish into estuaries (Whitfield 1989a, Strydom 2003). Several researchers have suggested that olfaction is the primary sense responsible for the successful location of estuarine environments (Boehlert and Mundy 1988, Stabell 1992, Whitfield 1994a) but no experiments have been conducted to test this theory.

The East Kleinemonde Estuary in the Eastern Cape Province (Figure 1.2) was selected as the study site, as it is fairly typical of small temporarily open/closed estuaries in this region, and is relatively undisturbed (Cowley 1998). Despite a history of intensive research on this estuary (Cowley 1998, Cowley and Whitfield 2001a, Cowley and Whitfield 2001b, Cowley *et al*. 2001, Vorwerk *et al*. 2001, Cowley and Whitfield 2002) concerning various aspects of estuarine fish population dynamics, relatively little is known about the long-term relationships between environmental variables and consequential changes in fish populations and assemblages within this system.

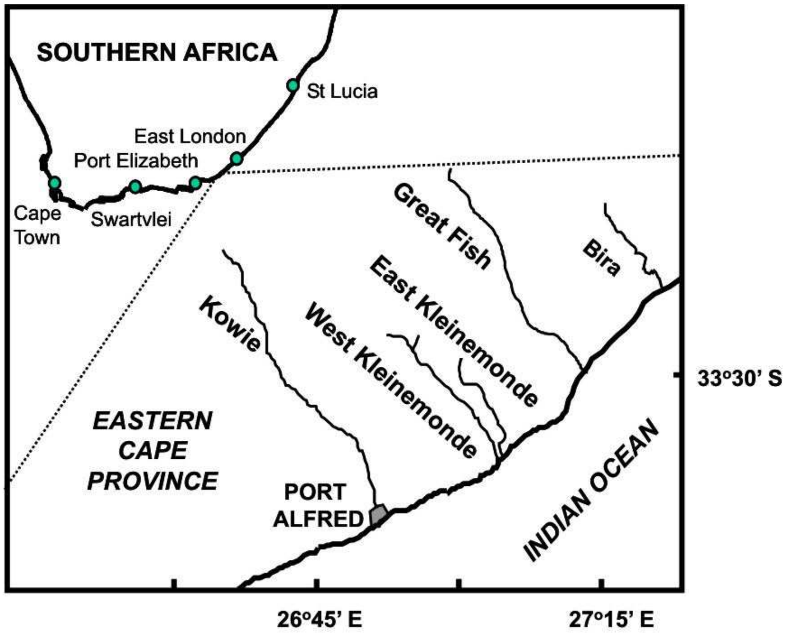


Figure 1.2. The location of the East Kleinemonde Estuary and other estuaries on the south-eastern coastline of South Africa (after Cowley 1998).

As part of an ongoing monitoring programme, initiated in December 1994, the fishes of the East Kleinemonde Estuary have been sampled bi-annually together with selected environmental parameters. This study included the analysis and continuation of the long-term monitoring programme with fieldwork undertaken in 2004 and 2005. This extensive data set was analysed to determine whether the fish assemblages found in a temporarily open/closed estuary are a function of long-term changes in physical conditions such as the frequency, timing and duration of mouth opening events, rainfall and water temperature. In addition, laboratory experiments were conducted to test the importance of olfactory cues to the larvae of estuary-dependent marine fish species, using postflexion *Rhabdosargus holubi* larvae, the dominant marine species in most Cape TOCEs.

Specific hypotheses tested included:

1. Fish compositions in TOCEs are a result of historical mouth states and are driven primarily by mouth opening events (Chapter 3).
2. Extended mouth closure reduces the potential for marine larval recruitment, which in turn reduces fish diversity and abundance (Chapter 3 and Chapter 4).
3. Optimum mouth opening for fish recruitment is during spring (September-November) in Cape TOCEs (Chapter 3 and Chapter 4).
4. Larval fish use olfactory cueing, along with other physical cues, to find their way into estuaries (Chapter 5).

CHAPTER 2

STUDY AREA

INTRODUCTION

The East Kleinemonde Estuary is a medium-sized, mostly shallow estuary situated approximately 15 km north of Port Alfred on the southeast coast of South Africa (Cowley 1998). The surface area of the estuary ranges from 11.627 ha during spring low tide to 26.627 ha during spring high tide (Bornman, unpublished data – Figure 2.1). The mouth meets the sea at 33º32´42″S and 27º03′05″E and the coastal road from Port Alfred (R72) crosses the estuary about 500 m from the mouth (Vorwerk 2001). The small township of Seafield surrounds most of the lower parts of the estuary and the neighbouring West Kleinemonde Estuary (Cowley 1998). A large majority (65%) of the estuaries situated between Port Elizabeth and East London are closed off from the sea for varying periods and the East Kleinemonde Estuary falls into this category (Whitfield 2000).

The estuary is navigable for about 3 km and narrows upstream of the lower reaches. The widest portion is 120 m in the lower reaches. The water level varies depending on the mouth state. When the mouth is closed the water level rises and during extended periods of mouth closure the water level in the estuary may exceed mean sea level by as much as 2.5 m. After a mouth opening event the estuary becomes very shallow, with a maximum channel depth of only 1 m (Cowley 1998). The cross-sectional area of the system decreases steadily from the mouth region (154 m^2) to the head (24.5 m^2) with an average of 82.1 m^2 (Vorwerk 2001).

The catchment area is approximately 46.3 km^2 and is relatively undisturbed (Badenhorst 1988). It consists of a gently sloping high lying region, which is predominantly degraded agricultural land used for cattle farming, and steep sloped stream and river valleys which are relatively undisturbed and covered by Valley Bushveld vegetation (Cowley 1998). The simulated mean annual run-off from the East Kleinemonde catchment is approximately 2×10^6 m^3 and is very erratic (Badenhorst 1988). Harrison *et al.* (1996), using the water quality rating index, gave the system a water quality rating of 7.3 out of 10, because slightly elevated levels of *Escherichia coli* were recorded in the system.

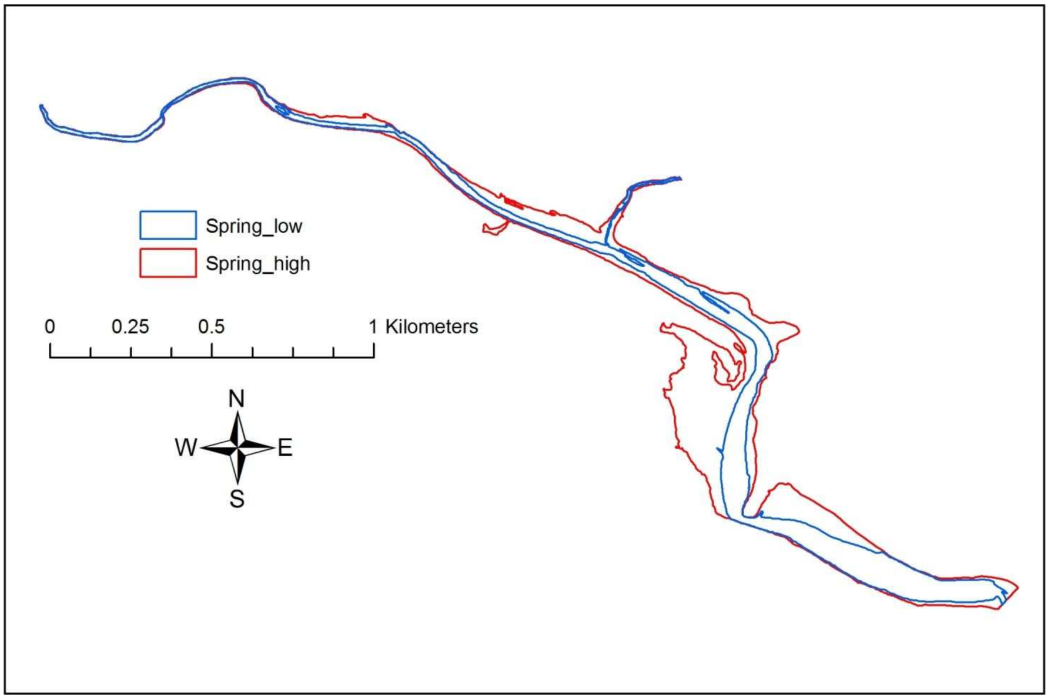


Figure 2.1. Map of the East Kleinemonde Estuary showing the surface water area during spring low and spring high tides (after Bornman, unpublished data).

CLIMATIC CONDITIONS

Temperature and wind

The coastal region between Port Alfred and East London experiences relatively mild summers and winters (Kopke 1988) and is influenced by the cooling and warming effects of the sea (Stone *et al*. 1998). Prevailing north-westerly winds are a feature of the region in both summer and winter (Stone *et al*. 1998) and windiness reduces both heat and humidity in summer (Kopke 1988). The maximum and minimum temperatures recorded at Port Alfred from 1994 to 2005 were 39.7 °C (November 2005) and 0.9 °C (June 2005) respectively (South African Weather Bureau, *in litt.*). There has been a significant positive trend in mean annual maximum air temperatures recorded at Port Alfred ($r^2 = 0.72$, $P = 0.001$) for the period 1994-2005 (Figure 2.2). Mean annual minimum temperatures did not show any obvious trends. Similarly, average annual minimum, maximum and annual mean temperatures recorded at East London between 1960 and 2003 have increased significantly (Kruger and Shongwe 2004).

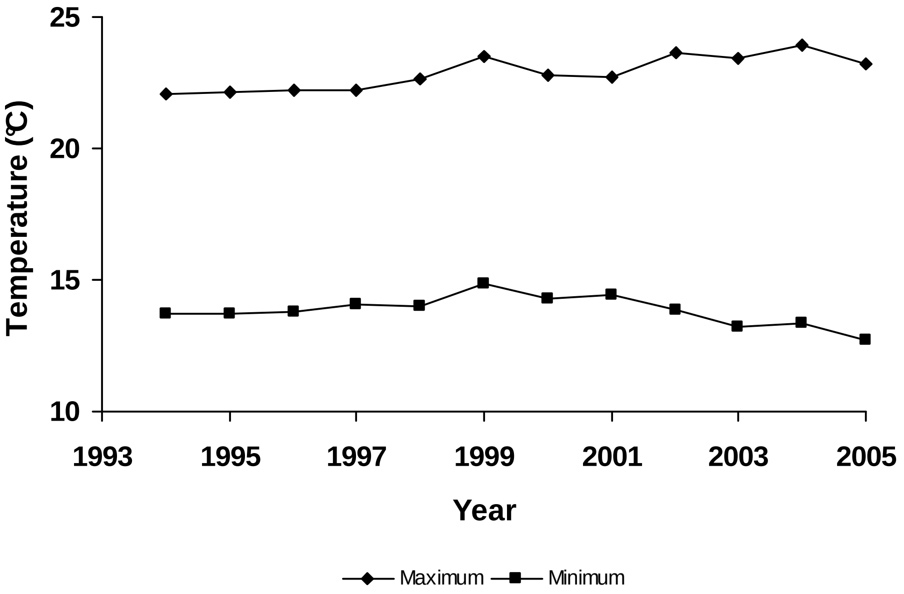


Figure 2.2. The mean annual air temperatures (°C) measured at Port Alfred for the years 1994-2005 (South African Weather Bureau, *in litt.*).

Rainfall

The Eastern Cape is largely in a climatic transition zone and as a result seasonality of rainfall is less pronounced and more unpredictable than in other parts of the country (Stone *et al.* 1998). Although rainfall may occur at any time of the year, long-term records demonstrate an autumn-spring bimodal pattern with a spring peak (Kopke 1988). The bimodal rainfall pattern for Port Alfred is depicted in Figure 2.3. The mean annual rainfall recorded at Port Alfred between 1994 and 2005 was 662 mm (± 234 mm). The lowest annual rainfall was recorded in 1999 (Figure 2.4), with only 308 mm in total and the highest in 2005 with 1288 mm of rainfall recorded (South African Weather Bureau, *in litt.*).

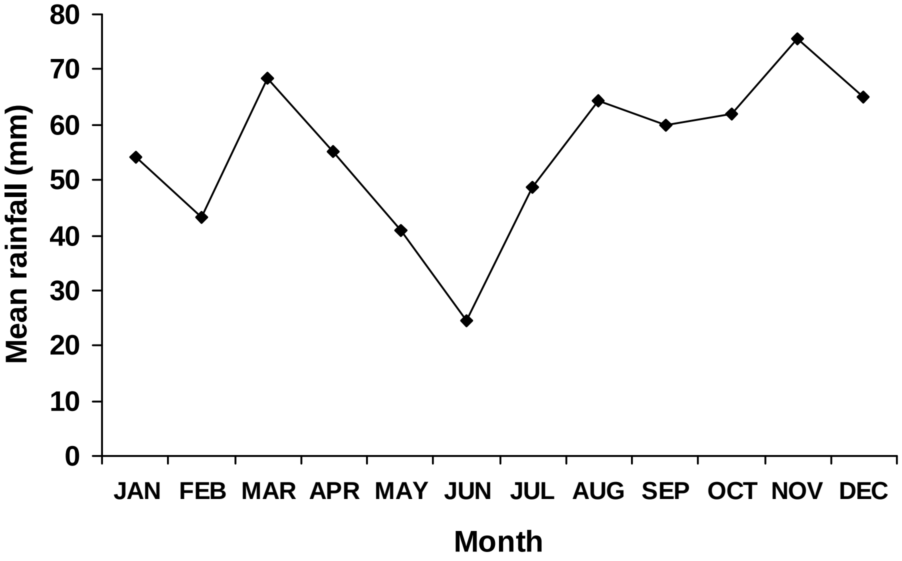


Figure 2.3. Mean monthly rainfall recorded at Port Alfred between 1994 and 2005 (South African Weather Bureau, *in litt.*).

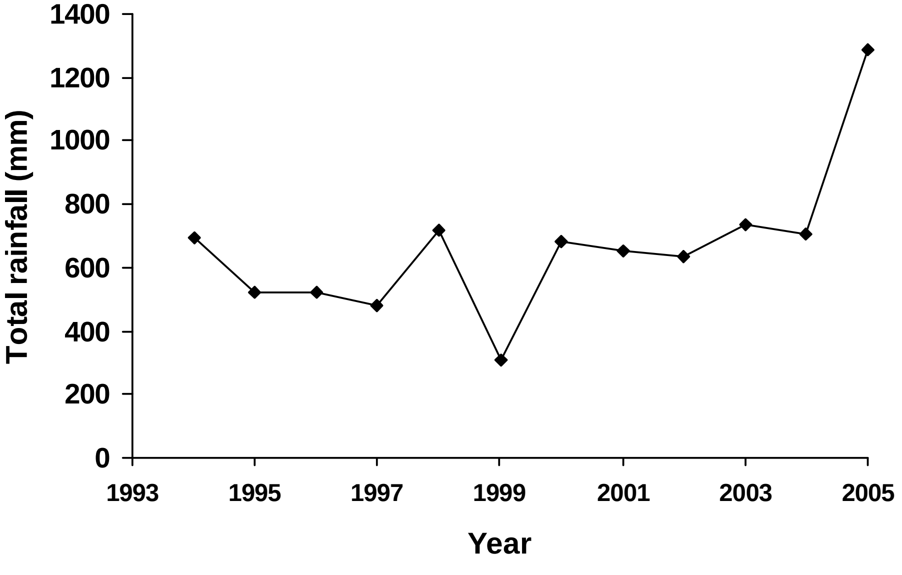


Figure 2.4. Total annual rainfall recorded at Port Alfred between 1994 and 2005 (South African Weather Bureau, *in litt.*).

THE COASTAL ENVIRONMENT

Coastal hydrography

Northeast of Cape Padrone (which is situated approximately 60 km south of the East Kleinemonde Estuary) there is a narrow, well-defined continental shelf (± 30 km wide) with a steep shelf slope (Lutjeharms 1998). The southeast coast has one of the steepest inshore shelf areas in the subcontinent (Heydorn and Tinley 1980). In this area the Agulhas Current flows close inshore, following the shelf edge very closely (Lutjeharms 1998). West of Cape Padrone the shelf starts to broaden considerably to form the Agulhas Bank and the current progresses slowly southwards (Lutjeharms *op. cit.*). In this region, where the shelf moves from a narrow to a wider shelf, upwelling is induced inshore of the current forming the Port Alfred upwelling cell (Lutjeharms 2006). Sea surface temperatures are extremely variable in this area and the cold upwelled water moves over the bottom of the Agulhas Bank in the form of a cold ridge (Lutjeharms 2006).

Coastal water movement tends to be wind driven northeast of Cape Padrone and water temperature and salinity are fairly uniform due to wind-driven mixing (Lutjeharms 1998). Despite this, there has been a positive increase in mean annual sea surface temperatures (SST) recorded at Port Alfred ($r^2 = 0.19$, $P = 0.21$) between 1996 and 2005 (Figure 2.5). Sea surface temperatures have shown an even stronger increase further north at East London. Mean annual sea surface temperatures recorded at Nahoon Beach (Figure 2.6) showed a significant increase between 1983 and 1993 ($r^2 = 0.36$, $P = 0.05$), while mean annual sea surface temperatures recorded at Orient Beach also increased between 1982 and 1993 (Figure 2.7), although not significantly ($r^2 = 0.28$, $P = 0.08$).

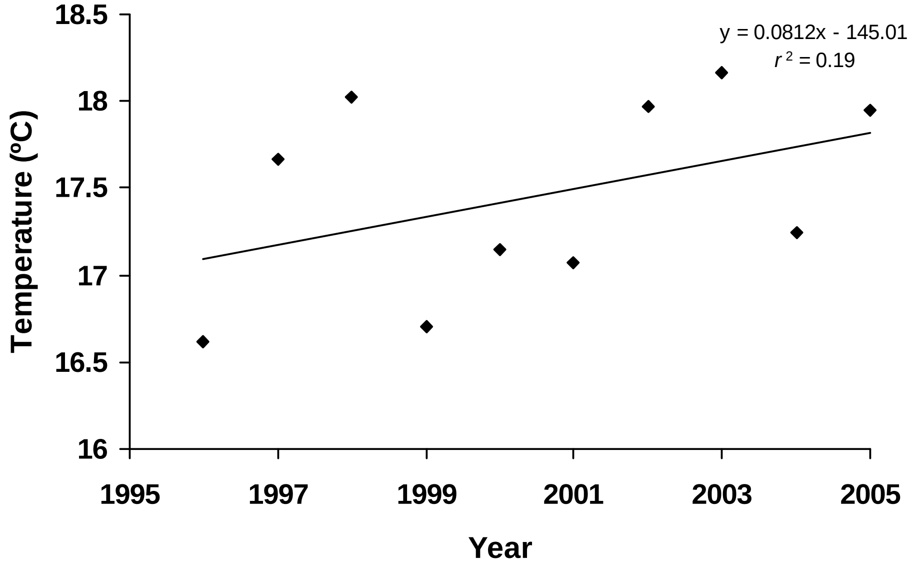


Figure 2.5. Mean annual sea surface temperatures (ºC) recorded at Port Alfred between 1996 and 2005 (Data courtesy Ocean Africa).

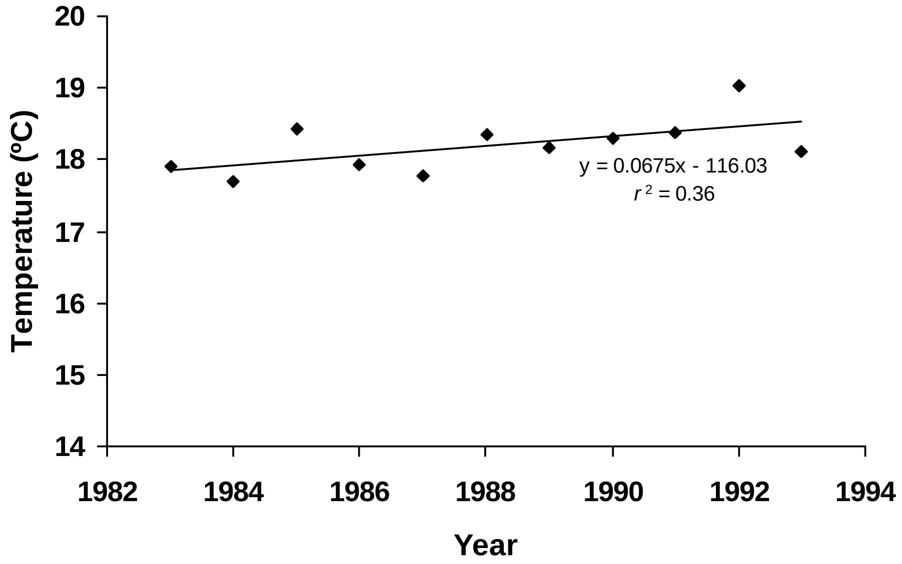


Figure 2.6. Mean annual sea surfaces temperatures (ºC) recorded at Nahoon Beach, East London, between 1983 and 1993 (Data courtesy Ocean Africa).

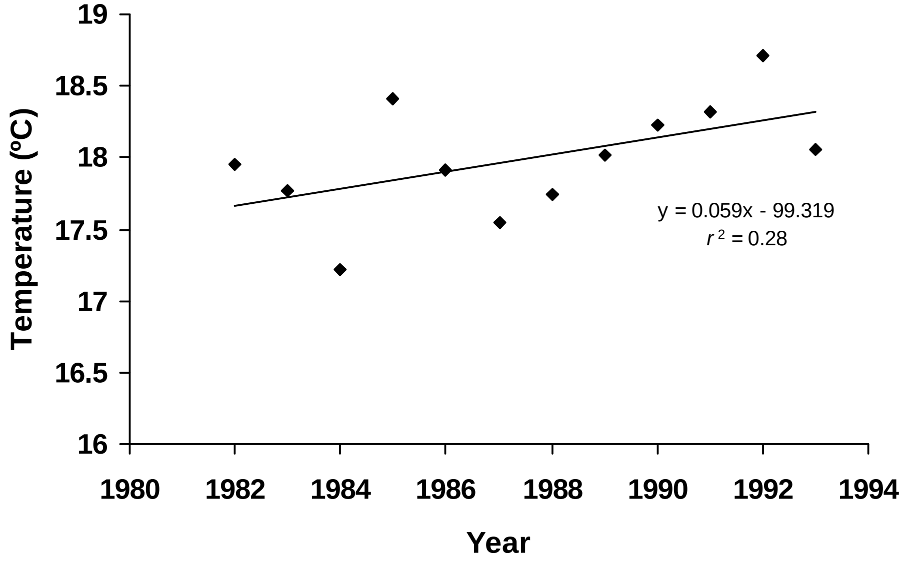


Figure 2.7. Mean annual sea surface temperatures (ºC) recorded at Orient Beach, East London, between 1982 and 1993 (Data courtesy Ocean Africa).

Coastal hydraulics, wind and aeolian sand transport

Wind frequencies and directions that were recorded on voluntary observing ships and observed data for the Fish River Lighthouse were used by Badenhorst (1988) to determine aeolian sand transport and to describe coastal hydraulics in the Kleinemonde region. Waves approaching the coastline from an oblique angle generate a predominantly eastbound longshore current and net sediment movement is towards the northeast. Transported sand generally accumulates in the mouths of the East and West Kleinemonde estuaries from the southwest.

THE ESTUARINE ENVIRONMENT

As part of a long-term study (details of the methods used in this study can be found in Chapter 3) physico-chemical measurements were recorded in summer and winter from 1995 to 2003. Up to five sites (in the mouth, lower, middle and upper reaches and the head) were monitored along the length of the estuary during each sampling session. Bottom and surface measurements were made of temperature (°C), salinity (‰) and turbidity (NTU), although not all measurements were recorded on every sampling session. Sampling was normally conducted during early mornings (approximately 06h00 in summer and 07h00 in winter) and mid-afternoons (approximately 14h00-15h00).

Water temperature was recorded in the field using an alcohol thermometer, while salinity (measured using a Reichert optical salinometer) and turbidity (measured using a Hach 2100A turbimeter) were measured from water samples. From 2004 onwards, as part of a more detailed study (Cowley *et al.,* unpublished data), bottom and surface measurements of temperature, salinity and turbidity were made at six sites (refer to Figure 2.8) along the length of the estuary on at least three days per month.

As part of the long-term monitoring program, daily estuarine mouth state has been recorded since 1993 (Cowley *et al.* unpublished data; Appendix I).

Temperature

Physico-chemical parameters were not always recorded consistently each season and year (for example water temperature was not measured in the summer or winter of 1995) and were generally averaged (across sites and bottom and surface measurements) to give an estimate for the estuary. There was also very little horizontal stratification in physico-chemical parameters throughout the estuary as is evident in the temperature data (Figure 2.9). According to Cowley (1998) mean monthly temperatures in the East Kleinemonde Estuary vary on a seasonal basis, with vertical stratification slightly more pronounced in summer.

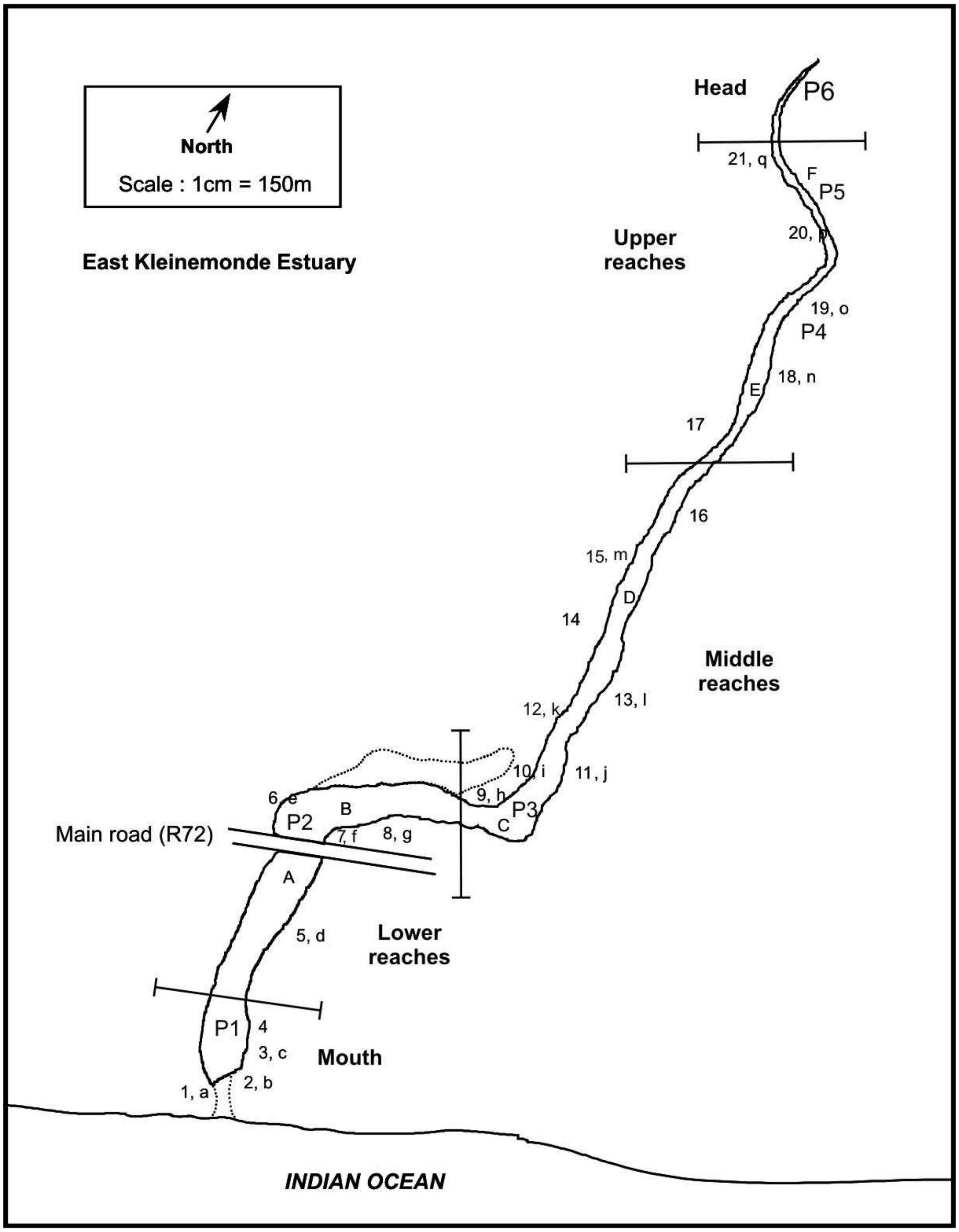


Figure 2.8. Map of the East Kleinemonde Estuary showing the sampling stations (a-q = small mesh seine sites, 1-21 = large mesh seine sites, A-F = gill net sites, P1-P6 = physico-chemical sites sampled after 2004).

The mean winter and summer temperatures measured throughout the study period were 16.7 ºC and 27.1 ºC, respectively. Mean summer temperatures ranged from 25.2ºC in 1998 to 29.6 ºC in 1997, while winter temperatures ranged from 15.2 ºC in 1996 to 17.6 ºC in 2003 (Table 2.1).

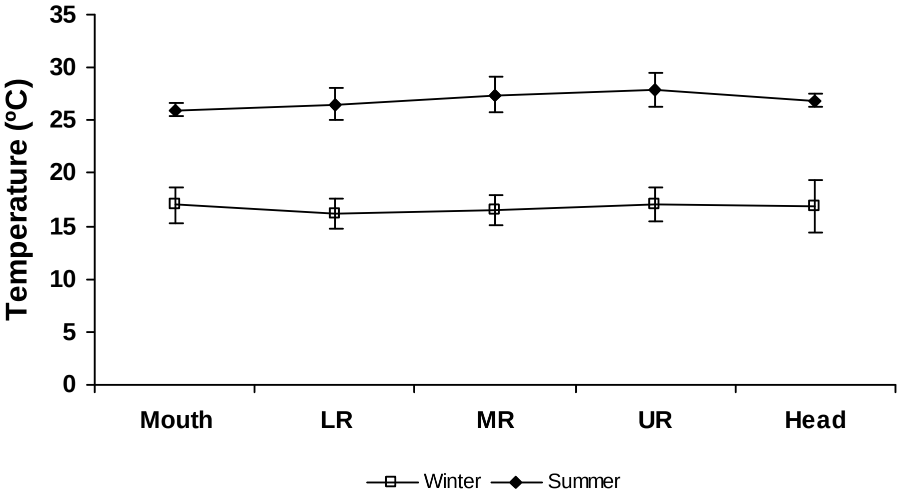


Figure 2.9. Mean (±SD) summer and winter temperature measurements for different localities in the East Kleinemonde Estuary. LR = lower reaches, MR = middle reaches, UR = upper reaches. The mean was determined from morning and afternoon samples collected in surface and bottom waters between 1995 and 2005.

Salinity

The salinity regime in the East Kleinemonde Estuary varies from oligohaline conditions (<5 ‰) to mostly mesohaline conditions (5-18 ‰), and salinity is a factor of the amount of rainfall and the condition of the estuary mouth (Cowley 1998). Generally, salinity levels decline rapidly prior to mouth opening events owing to riverine input, and rise during and after mouth closure. The final salinity levels after mouth closure depend on the extent of bar overwash events. During periods of extended mouth closure, salinities throughout the estuary tend to be fairly uniform (Cowley 1998). Mean salinities recorded in the estuary from 1995 to 2005 are depicted in Table 2.2 and were highly variable. Mean salinities ranged from 8.5 ‰ in February 2001 to 33.5 ‰ in July 2004 (Table 2.2).

Table 2.2. Mean salinities (‰) recorded in the East Kleinemonde Estuary between 1995 and 2005. The mean was determined from morning and afternoon samples collected in surface and bottom waters.

Year	**Summer**	**Winter**
1995	12.0	10.6
1996	16.3	18.0
1997	18.5	-
1998	26.7	22.3
1999	10.7	12.7
2000	14.9	15.0
2001	8.5	10.2
2002	12.7	28.0
2003	28.4	24.5
2004	28.8	33.5
2005	18.4	29.6

Horizontal salinity stratification was not apparent (Figure 2.10). However, there was a slight difference observed between mean salinities in the mouth region in summer and winter. Salinities were generally lower in the mouth region during winter (Figure 2.10).

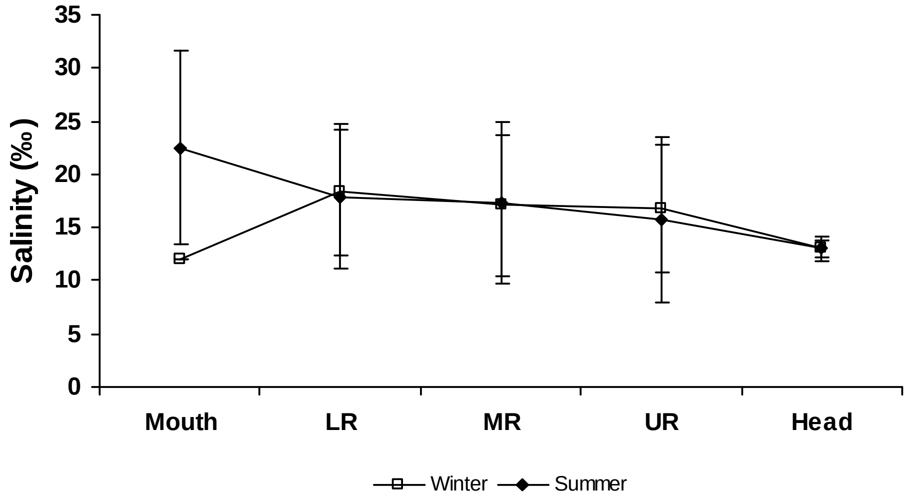


Figure 2.10. Mean (±SD) summer and winter salinity measurements for different localities in the East Kleinemonde Estuary. LR = lower reaches, MR = middle reaches, UR = upper reaches. The mean was determined from morning and afternoon samples collected in surface and bottom waters between 1995 and 2005.

Turbidity

Turbidity variations in the East Kleinemonde Estuary have been noted as being extremely low (Vorwerk 2001). Mean summer turbidities ranged from 5.9 NTU in 2000 to 11.6 NTU in 2005, while winter turbidities ranged from 1.8 NTU in 2004 to 8 NTU in 2000 (Table 2.3). These were within the range of turbidities recorded by Vorwerk (2001) in 1999 and 2000.

Table 2.3. Mean turbidities (NTU) recorded in the East Kleinemonde Estuary between 1995 and 2005. The mean was determined from morning and afternoon samples collected in surface and bottom waters.

Year	Summer	Winter
1995	-	-
1996	-	12.5
1997	-	-
1998	6.3	4.2
1999	6.2	3.5
2000	5.9	12.8
2001	-	-
2002	-	-
2003	-	-
2004	-	1.8
2005	11.6	2.9

Particle size composition

During February 2000, Vorwerk (2001) collected a sediment sample from each region (mouth, lower, middle, upper and head) of the East Kleinemonde Estuary using a coring apparatus. These samples were analysed for organic content and sediment particle size distribution. Vorwerk (*op. cit.*) found that all sites in the East Kleinemonde Estuary contain mostly fine sands (0.5-0.063 mm). Generally, larger particles such as gravel (>2 mm), coarse sand (2-0.5 mm) and silt (<0.063 mm) decrease from the head to the mouth of the estuary. The sediment organic content also decreased from the head to the mouth, with all sites having a relatively low organic content of between 0.8% and 6.5% (Figure 2.11).

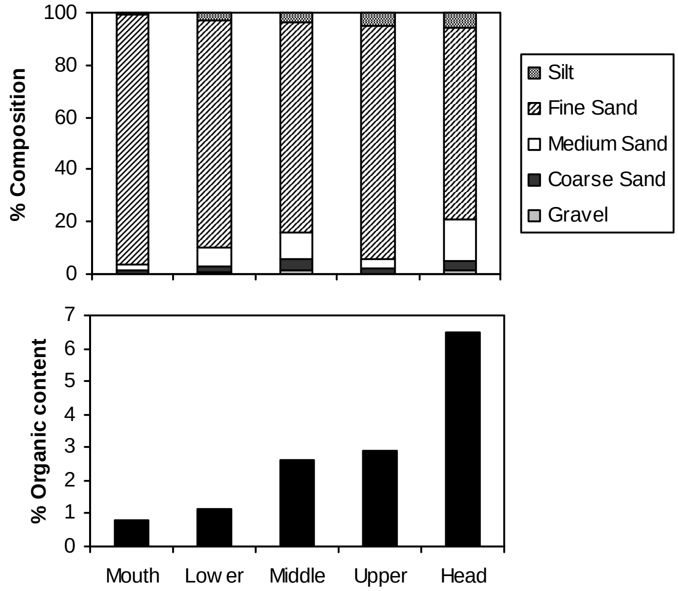


Figure 2.11. Particle size composition and organic content of the sediments in the East Kleinemonde Estuary (after Vorwerk 2001).

Mouth dynamics

The East Kleinemonde Estuary is separated from the sea by a broad sand barrier that forms across the mouth and usually only opens only after heavy rainfall, which is highly variable along the south-eastern Cape coast (Kopke 1988, Stone *et al.* 1998). The majority of mouth opening events occurred after rain events of more than 100 mm (Figure 2.12). When the mouth is closed seawater can enter the system via overwash events, which usually occur during rough sea conditions when pulses of surging waves enter the estuary (Adams 1997, Cowley *et al.* 2001). Larval fish can only enter the estuary when the estuary is open or when waves sweep over the bar (overwash). These events are classified by Bell *et al.* (2001) as estuarine access opportunities (EAO).

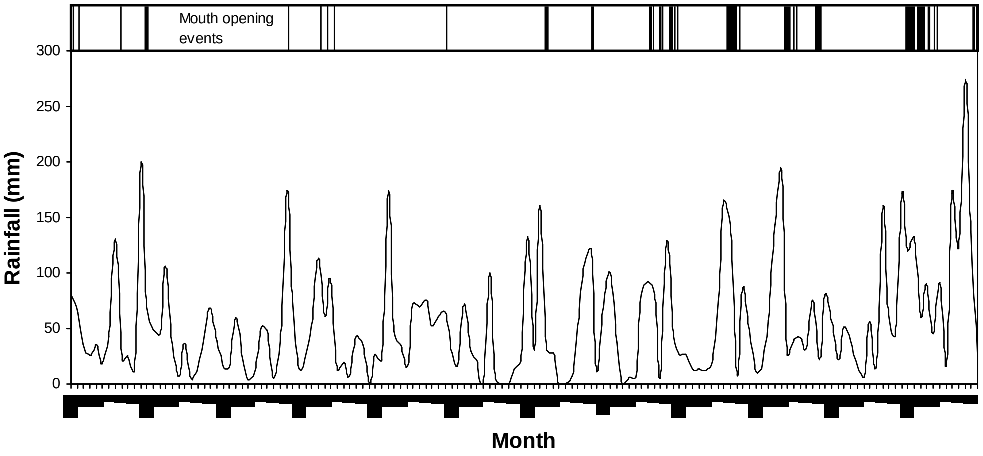


Figure 2.12. Total monthly rainfall recorded at Port Alfred between 1994 and 2005 (South African Weather Bureau, *in litt.*). Mouth opening events are indicated by black bars.

Frequency of estuarine access opportunities (EAO)

As part of the long-term monitoring program, the estuary mouth state was recorded on a daily basis from March 1993 (Cowley *et al.* unpublished data; Appendix I). EAO status was recorded for each day in five categories (1) no overwash and estuary closed, (2) wave overwash of duration <3 h (small overwash), (3) wave overwash of duration 3 to 6 h (large overwash), (4) estuary open and (5) water trickling out of the mouth (after Bell *et al*. 2001). Analysis of these records revealed that open mouth conditions were recorded on average for 6% of the year throughout the study period, and overwash events were recorded for 16% of the year. The mouth dynamics of the system change on an annual basis. Between 1994 and 1998, the mouth was open for a maximum of 12 days in 1994 to only one day in 1998 (Table 2.4). However, overwash events, which usually occur during rough sea conditions (Cowley *et al.* 2001), occurred fairly frequently throughout this period. Overwash events occurred particularly frequently in 1994, 1995 and 1997 when overwash events were recorded 23%, 56% and 16% of the time respectively (Table 2.5).

Table 2.4. State of the East Kleinemonde Estuary mouth (in days) recorded between 1994 and 2005.

Year	Closed	Small OT	Large OT	Open	Link	EAO
1994	270	78	5	12	0	95
1995	154	188	15	8	0	211
1996	319	38	6	3	0	47
1997	296	53	5	11	0	69
1998	354	7	3	1	0	11
1999	365	0	0	0	0	0
2000	308	25	4	29	0	58
2001	259	44	1	55	6	106
2002	279	22	11	48	5	86
2003	229	53	19	64	0	136
2004	325	27	5	9	0	41
2005	179	62	34	90	0	186

Table 2.5. State of the East Kleinemonde Estuary mouth (percentage) recorded between 1994 and 2005.

Year	Closed	Small OT	Large OT	Open	Link	EAO
1994	74	21	1	3	0	26
1995	42	52	4	2	0	58
1996	87	10	2	1	0	13
1997	81	15	1	3	0	19
1998	97	2	1	0	0	3
1999	100	0	0	0	0	0
2000	84	7	1	8	0	16
2001	71	12	0	15	2	29
2002	76	6	3	13	1	24
2003	63	15	5	18	0	37
2004	89	7	1	2	0	14
2005	49	17	9	25	0	51

No overwash or open mouth events were recorded in 1999 (Table 2.4). From 2000, however, the frequency of these events increased significantly. Open mouth events occurred 8% of the time in 2000 to a maximum of 25% of the time in 2005 (Table 2.5). Similarly, overwash events were recorded 8% of the time in 2000 and 26% of the time in 2005 (Table 2.5).

Table 2.6. Average waiting time (days) between EAOs in the East Kleinemonde Estuary between 1994 and 2005.

Year	Average waiting time
1994	16
1995	33
1996	34
1997	26
1998	62
1999	270
2000	31
2001	32
2002	24
2003	13
2004	16
2005	8

For each day the waiting time (waiting time in number of days) to the next EAO was calculated and plotted as per the methods of Bell *et al*. (2001). The waiting time between EAOs was highly variable and ranged from zero to a maximum of 479 days in December 1998 (Figure 2.13). As a result, the average waiting time per year (Table 2.6) ranged from a low of only 8 days in 2005 to a maximum of 270 days in 1999.

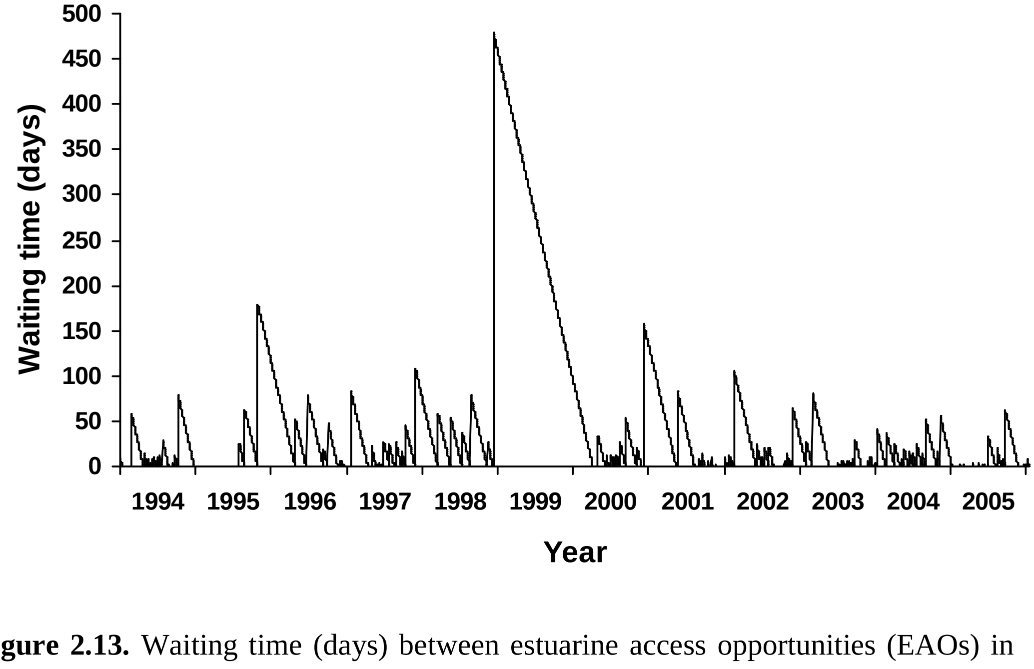


Figure 2.13. Waiting time (days) between estuarine access opportunities (EAOs) in the East Kleinemonde Estuary between 1994 and 2005.

Timing of estuarine access opportunities (EAOs)

The timing of mouth opening and overwash events is important for the recruitment of marine-spawning species into estuaries. Peak recruitment of most estuary-associated marine species into Eastern Cape estuaries occurs in spring between September and November (Whitfield 1998). Timing of these events was, however, highly variable each year (Figure 2.14; Appendix I). In 1993, open mouth conditions were recorded in spring and summer and overwash events occurred throughout the year. Similarly, overwash events occurred throughout the year in 1994, but the mouth opened in summer and late winter (August). In 1995, the mouth also opened in summer and an extended period of overwashing occured from summer to winter. In 1996 the mouth opened in spring and overwash events occurred in each season. In 1997 and 1998 overwash events again occurred throughout the year, with the mouth opening in autumn and winter in 1997 and for only one day in December 1998. No overwash or mouth opening events were recorded between January 1999 and March 2000.

Overwash events occurred throughout the year from 2000 to 2005. The mouth opened for long periods in autumn and spring in 2000, in winter, spring and summer in 2001, in late winter and spring in 2002 and in autumn, winter and spring in 2003. Open mouth events in 2004 were only recorded in December, but in 2005 the greatest number of mouth opening events were recorded in summer, autumn and spring.

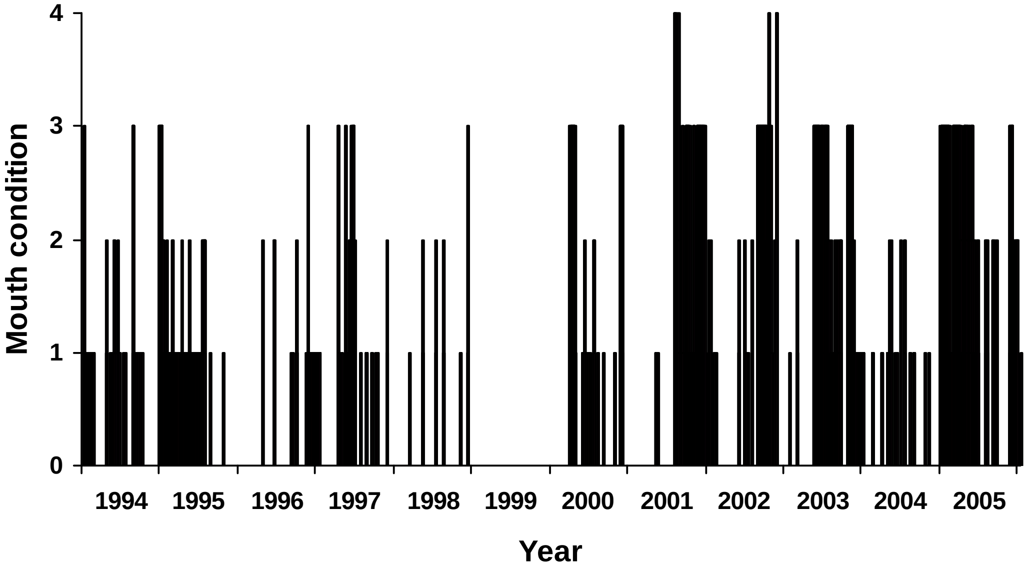


Figure 2.14. Timing and duration of estuarine access opportunities (EAO) in the East Kleinemonde Estuary. 0 = closed, 1 = small overwash, 2 = large overwash, 3 = open, 4 = trickling out.

Duration of estuarine access opportunities

Table 2.7. Maximum duration (days) of estuarine access opportunities (EAO) in the East Kleinemonde Estuary between 1994 and 2005.

Year	Open	Overwash	Trickling out	EAO (open +/ overwash)
1994	5	41	-	43
1995	8	201	-	209
1996	3	13	-	14
1997	6	14	-	15
1998	1	2	-	2
1999	0	0	-	0
2000	20	6	-	26
2001	21	9	5	25
2002	26	9	5	52
2003	24	10	-	45
2004	9	6	-	9
2005	31	13	-	41

The maximum duration of an open mouth event ranged from one day in 1998 to a high of 31 consecutive days in 2005 (Table 2.7) and was highest between 2000 and 2005. The maximum duration of overwash events ranged from 201 consecutive days in 1995 to only two consecutive days in 1998. Open mouth conditions were normally preceded and/or followed by overwash conditions and as a result the average duration of EAOs (mouth opening and/or overwash events) ranged from 209 days in 1995 to only two days in 1998.

Vegetation

Although no published information is available on the vegetation of the East Kleinemonde Estuary, Adams (1997) conducted a brief botanical survey of the estuary on the 21st and 22nd of January 1997. The findings of that report are detailed below.

Phytoplankton

Average water column chlorophyll-a in the estuary was 4.2 ± 0.9 (n = 10) and was highest in the upper reaches (5.2 ± 0.6), decreasing towards the mouth (2.7 ± 0.5). The dominant microalgal group identified in the estuary was small flagellates, which occurred in fairly consistant numbers throughout the estuary. The number of green algae increased towards the mouth (Adams 1997).

Submerged macrophytes

The dominant submerged macrophyte recorded in 1997 was *Ruppia cirrhosa*, which occurred in a continuous band along both banks above the road bridge (Figure 2.15). The seagrass *Halophilia ovalis* was also present (Adams 1997). A major flash flood in May 2003, and subsequent prolonged exposure of the *Ruppia cirrhosa* and *Potamogeton pectinatus* plants, resulted in an almost complete loss of most of these macrophyte beds (P. Cowley. pers. comm.). Recovery of the aquatic macrophytes from seed banks has been slow and in 2006 they were found in scattered patches along both banks.

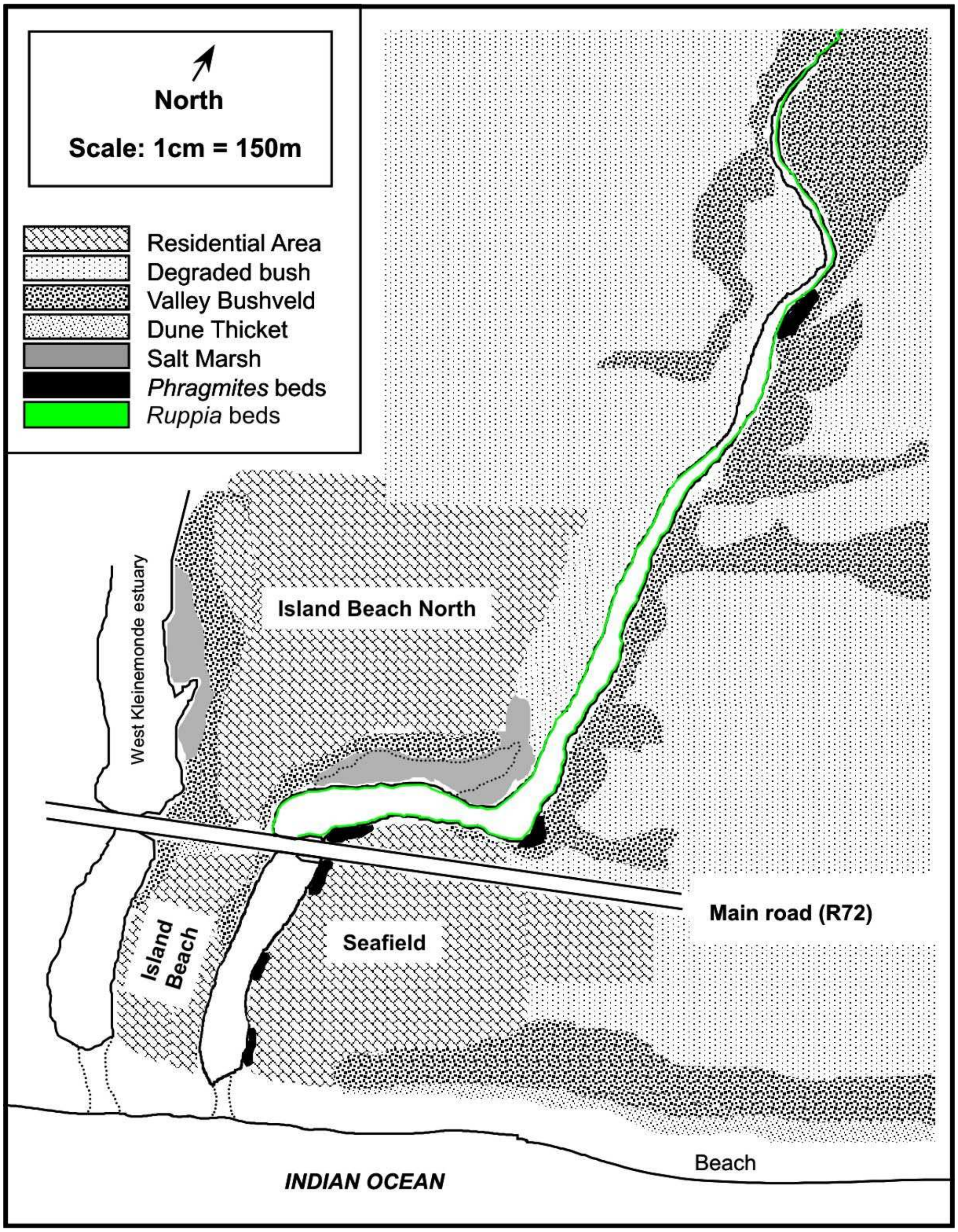


Figure 2.15. Map of the East Kleinemonde Estuary showing the main vegetation types (adapted from Adams 1997) and location of residential areas (after Cowley 1998).

Table 2.8. List of the dominant plants recorded in the East Kleinemonde Estuary in 1997 (after Adams 1997).

Family	**Species**	**Common name**
Ruppiaceae	*Ruppia cirrhosa*	-
Hydrocharitaceae	*Halophila ovalis*	-
Chenopodaiceae	*Salicornia meyeriana*	Marsh samphire
	Chenopodium album	Seepbossie (weed)
	Sarcocornia decumbens	-
Cyperaceae	*Fuirena hirsuta*	-
Juncaceae	*Juncus kraussii*	Sharp rush
Juncaqinaceae	*Triglochin striata*	-
Poaceae	*Phragmites australis*	Common reed
	Sporobolus virginicus	Brakgras
	Stenotaphrum secundatum	Buffelsgrass/Strandkweek

Salt marsh, reeds and sedges

There are numerous houses with lawns almost to the water's edge in the lower reaches of the estuary and consequently there is little supratidal vegetation in the mouth region. On the east bank, below the road bridge, a stand of the reed *Phragmites australis* was recorded in 1997. Scattered *Juncus kraussii* and *Sporobolus virginicus* plants occur on the west bank, which is mostly rocky (Adams 1997).

A small salt marsh is located on the west bank just above the road bridge. Salt marsh zonation was evident, with *Sarcocornia perennis* forming a 1 m band close to the waters edge, followed by a 2 m zone of *Sporobolus virginicus* and *Sarcocornia decumbens* and then a 5 m zone of *Juncus kraussii*. Two stands of *Phragmites australis* occur on the east bank, approximately 0.5 and 1 km from the mouth. Apart from these stands, little intertidal vegetation is recorded because the banks are steep and Valley Bushveld extends to the water's edge. The east banks were found to be grassy, with scattered *Acacia cyclops* trees. Dominant fringing marsh species were *Sporobolus virginicus, Salicornia meyeriana, Juncus kraussii, Sarcocornia decumbens* and the sedge, *Fuirena hirsuta* (Adams 1997).

CHAPTER 3

FISH ASSEMBLAGE TRENDS

INTRODUCTION

The importance of estuaries as nursery areas has meant that these systems have been the subject of considerable ichthyological research focussing on the key environmental factors affecting estuarine fish community structure (Power *et al.* 2002). Estuaries are, however, highly dynamic and their physical and chemical characteristics can change over a scale of hours to years (Flint 1985). Consequently estuarine fish assemblages often exhibit large year-to-year variations in abundance and composition (Methven *et al.* 2001).

Although long-term studies are important in order to understand the functioning of estuaries, most fish studies in these systems have tended to be short in duration (1-3 years). These short-term studies have shown that most estuarine fish assemblages undergo significant changes in community structure, often related to changes in estuarine mouth phase, flood events, season etc. (e.g. Marais 1983, Kok and Whitfield 1986, Potter *et al.* 1993). Long-term studies have shown that although cyclic patterns of interannual variation may be observed, and these are often related to random climatic events, such as severe storms, droughts, cold winters, etc., longer term climatic trends, such as El Niño events and global warming result in a restructuring of fish assemblages (Nichols 1985, Jackson and Jones 1991, Vance *et al.* 1996, Warwick *et al*. 2002, Garcia *et al.* 2003, Hawkings *et al*. 2003).

The most important environmental variables structuring estuarine fish communities in temporarily open/closed estuaries (TOCEs) are the timing, duration and frequency of mouth opening events (e.g. Wallace and van der Elst 1975, Beckley 1984, Kok and Whitfield 1986, Young *et al.* 1997, Griffiths 1998). Mouth opening events allow juvenile fish to recruit into estuaries and adult fish to migrate seawards. It is argued that an extended open phase will increase the likelihood of more fish entering the estuary. This may be even more apparent if the mouth is open during a period of peak recruitment. Similarly, the frequency of estuary openings may affect the abundance and diversity of fish entering estuaries (Griffiths and West 1999, Griffiths 2001).

In this chapter, long-term interannual changes in richness, abundance, diversity and structure of the fish community in the temporarily open/closed East Kleinemonde Estuary is described. Emphasis is placed on investigating linkages between environmental variables and changes in fish abundance. It is hypothesised that annual patterns of marine fish abundances are driven by the timing, frequency and duration of mouth opening events. Specifically, that an extended mouth closure reduces the potential for marine larval recruitment, which in turn reduces fish diversity and abundance, and optimum mouth opening for fish recruitment is during spring (September-November) in Cape TOCEs. Based on previous work (Vorwerk *et al.* 2001) seasonal trends in fish composition should be absent and this is tested.

MATERIALS AND METHODS

Ichthyofaunal sampling

As part of an ongoing monitoring programme, the fishes of the East Kleinemonde Estuary were sampled bi-annually, during winter (June, July or August) and summer (December, January or February), on two consecutive days, between December 1994 and July 2005.

Different gear types have been used to sample estuarine fish assemblages, ranging from seine (e.g. Bennett 1989, West and King 1996, Methven *et al.* 2001) or gill nets (e.g. Marais and Baird 1980, Marais 1981) to a suite of different net types (e.g. Kok and Whitfield 1986, Robertson and Duke 1990, Potter and Hyndes 1994, Whitfield *et al.* 1994). Fish communities are often inadequately described when only a single net type is used. For example, gillnets tend to be selective for more mobile fish that actively avoid seine nets and are found in the deeper regions of the estuary, while beach seines often catch many slower moving pelagic species (Methven *et al.* 2001). Hence sampling using a variety of collection methods is preferable to survey as many species as possible. In this study, two different types of beach seines and a fleet of gill nets were used to sample as many and as great a size range of fish as possible over a range of different habitat types.

A large mesh seine net (50 m x 2 m) with a 15 mm bar mesh was used to sample marine-spawning and freshwater species. The number of large mesh seine net hauls per sampling trip usually varied between 8 and 18, with the final number dependant on access to sampling sites, as well as a flattening of the species: sampling effort curve. On some occasions when the mouth was closed several sites were completely submerged and during the open mouth phase some sites were completely exposed. On all sampling occasions all possible littoral habitats in the lower, middle and upper reaches of the estuary were sampled. The net was laid in a semi-circle from the bank using a small motorized boat and then hauled ashore by three to four people. All fish caught were identified and measured to the nearest millimetre standard length (SL) before being released. Where large catches of a species were made, only a sub-sample was measured, although all individuals were counted. Cowley (1998) conducted a more intensive survey of the estuary, sampling monthly between April 1993 and March 1996, using the above seine net and these data were also analysed to determine if any seasonal trends were apparent in the data.

A small mesh seine net (30 m x 2 m) with a 5 mm bar-mesh was used to sample estuarine-spawning species. The number of small mesh seine hauls per sampling trip usually varied from six to 10. The sampling protocol was identical to that used with the large mesh seine net, except the fish captured were kept and returned to the laboratory where they were identified and measured (mm SL). Again, where large catches of a species were made only a sub-sample was measured and the rest enumerated.

Monofilament gillnets were used to sample larger individuals of marine-spawning and freshwater species, especially those species that actively avoid seine nets. The nets were 10 m in length and 2 m in depth and consisted of three equal sections of 45 mm, 75 mm and 100 mm stretch meshes. Generally two nets were set in each of the lower, middle and upper reaches of the estuary. Gillnets were set in the evening and retrieved the following morning. All fish caught were identified to species level and measured (mm SL).

Data analysis

Richness and diversity indices

Data collected from all gear sets were combined to investigate interannual trends in community composition and diversity. Thereafter, gear sets were analysed separately.

Seasonal trends

Monthly fish abundance data (catch per unit effort - CPUE) from the April 1993 to March 1996 large mesh seine subset collected by Cowley (1998) were analysed using classification and ordination in the PRIMER package (Version 5.2.9, Plymouth Marine Laboratory, Plymouth, UK) (Clarke and Gorley 2001) to determine if monthly samples exhibited a seasonal pattern. In the context of South Africa the four seasons were: summer (December to February), autumn (March to May), winter (June to August) and spring (September to November). Prior to classification and ordination CPUE data were root-root transformed and the Bray Curtis similarity measure was used to produce an association matrix. Possible seasonal patterns were examined using dendrograms, non-metric multidimensional scaling (nMDS) and analysis of similarities (ANOSIM).

Annual trends

Kendall’s coefficient of concordance (*W*) was used to examine annual variation in rank abundance of the eight species that occur in all sampling years. Spearman rank correlation coefficients were also calculated to examine differences between all pairs of years. Analysis of variation in species composition was based on annual abundance indices of all species caught during the 11-year study period (December 1994 to July 2005). The index of abundance calculated for each species was the annual mean CPUE of all seine hauls. Individual species CPUEs were also divided by total species CPUE to determine the percent contribution of each species to the annual fish community. Several diversity indices were calculated for each sampling year: the total number of species (S), the Shannon-Wiener diversity index (H´), the Margalef species richness index (D) and Pielou’s eveness (J´); the last three indices used $\log_e$ in their formulation

Fish assemblage structure and environmental variables

Annual large mesh seine CPUE data (summer, winter and pooled summer and winter samples) from all the sampling stations between December 1994 and July 2005 were fourth root transformed and ordinated using the non-metric multidimensional scaling (nMDS) techniques in the PRIMER package (Version 5.2.9, Plymouth Marine Laboratory, Plymouth, UK) (Clarke and Gorley 2001) to determine differences in fish assemblages between years based on the timing, duration and frequency of mouth opening events. Fish assemblages were related to mouth opening events from the year preceding sampling because fish caught in the large mesh seine net were large enough to have recruited into the estuary in the year preceding sampling. According to Clarke and Warwick (1994) fourth root transformation ensures that the ordination reflects trends in abundance of all fish species instead of one or two species that dominate the catches. Prior to ordination the Bray-Curtis similarity measure was used to produce the association matrix. Analysis of similarities (ANOSIM) was used to test whether the fish assemblages separated in the nMDS ordination were significantly different from each other. Similarity percentages (SIMPER) were used to determine which species were most responsible for the Bray-Curtis dissimilarity between groups (Clarke and Warwick 1994).

Two multivariate measures of community stress were also calculated, the index of multivariate dispersion (IMD, Clarke and Warwick 1994) using the MVDISP routine in the PRIMER package and the index of multivariate seriation (IMS, Clarke and Warwick 1994) using the RELATE significance test. These indices were used as multivariate indices of stability as per the methods of Warwick *et al.* (2002). The IMD is used here as a measure of interannual variability. The index contrasts the average rank of similarities among one set of samples (1995-1996, 1998-2000) with the average rank among another set (1997, 2001-2005). These groupings were identified in the nMDS plot. The IMD has a maximum value of +1 when all similarities among the first group of samples are higher than any similarities among the second group, the reverse gives a minimum value of –1, and values near zero indicate no difference between the two groups (Clarke and Warwick 1994).

The IMS is a measure of the degree to which community change conforms to a perfectly linear sequence. If the community changes with time exactly match this linear sequence (e.g. sample 1 is close in composition to sample 2, samples 1 and 3 are less similar etc.) then the IMS has a value of 1. If there is no discernible biotic pattern then the IMS will be close to zero (Clarke and Warwick 1994). Spatial breakdown of the seriation pattern has been suggested as a measure of community stress and is used by Warwick *et al.* (2002) to examine interannual changes in community composition. Community composition in one year is assumed to be determined by biological mechanisms such as reproduction and species interactions during the preceding year, resulting in a serial pattern of interannual community change. Disturbance will result in a breakdown of this seriation (Warwick *et al.* 2002).

As a final measure of fish assemblage structure, changes in functional diversity were assessed. Functional diversity is the value and range of functional traits of the organisms present in an ecosystem (Bremner *et al.* 2003, Dumay *et al.* 2004). Bremner *et al.* (2003) investigated differences in feeding mechanisms between assemblages, which are thought to be one of the central processes structuring marine ecosystems. These analyses have been used to investigate pollution effects, habitat modification, fishing impacts and variability in environmental parameters (Schlosser 1982, Livingston 1997, Mistri *et al.* 2000, Chicharo *et al.* 2002). Each species caught in the large mesh seine net was classified as either feeding predominantly on fish (piscivores - group 1); seaweed, seagrass, weeds, algae, diatoms or dinoflagellates (herbivores - group 2); crustaceans, sponges, tunicates, cnidarians, molluscs, benthic crustaceans, echinoderms, insects and worms (zoobenthivores - group 3); hydroids, planktonic crustaceans and other planktonic invertebrates, fish eggs and larvae (zooplanktivores – group 4) or decaying organic matter and microphytobenthos (detritivores - group 4), based on the hierarachical food items table in FishBase (Froesa and Pauly 2006). Mean annual CPUE values were then summed for each trophic group and ordinated using nMDS (in the same manner as the species data).

RESULTS

Species composition

A total of 33 species from 18 families were recorded in the East Kleinemonde Estuary between 1996 and 2005 (Table 3.1). Between 16 and 26 species were caught annually depending on the year (mean = 19.5, SD = 3.3). Twenty-one species were caught in large mesh seine nets, 10 in small mesh seine nets and 17 in gill nets. The small mesh seine net was found to be selective for small estuarine fish between 10 mm SL and 149 mm SL (Mean = 35.3 mm SL, SD = 10.5), while the large mesh seine net was selective for juvenile marine fish between 21 mm SL and 570 mm SL (Mean = 105 mm SL, SD = 44.6). Gill nets were selective for larger, more mobile fish between 64 mm SL and 930 mm SL (Mean = 223 mm SL, SD = 120).

The sampling regime used throughout this long-term study was sufficient to sample the variability in assemblages between sites and over time. On average, eight large mesh seine and six small mesh seine net hauls were conducted per sampling trip, while an average of six gill nets were set each sampling trip. The number of large mesh seine hauls required each sampling trip to obtain 75% of the species recorded ranged from 1 to 9 (mean = 4.4, SD = 2). The number of small mesh net hauls required to obtain 75% of the species recorded ranged from 1 to 4 (mean = 2.1, SD = 0.9), while the number of gill nets required to achieve 75% ranged from 1 to 5 (mean = 2.9, SD = 1).

In terms of the number of species recorded Mugilidae and Sparidae were the most important families, with eight and four species recorded respectively, followed by Gobiidae represented by three species. The remaining families were represented by one or two species each. The dependence of fish species on estuaries ranges from complete to opportunistic. Whitfield (1994b) divided South Africa’s estuary-associated species into five categories depending on their degree of dependence on estuaries (Table 3.2). Marine species whose juveniles are dependent on estuaries to varying degrees (Categories IIa, IIb and IIc) were the most numerous species recorded and collectively comprised 64% of the species. Estuarine resident species that are able to breed and complete their life cycle within an estuary (Categories Ia and Ib) together comprised 18% of the species recorded. Three freshwater species were recorded, namely *Oreochromis mossambicus*, *Glossogobius giuris* and the introduced spotted bass (*Micropterus punctulatus*). *Myxus capensis* was recorded as a catadromous species because it spends the majority of its life in low salinity regions (estuaries and rivers) but returns to the sea to breed (Potter *et al.* 1990). Two marine 'stragglers', *Pseudorhombus arsius* and *Pomadasys olivaceum*, were also recorded.

The majority of species recorded (42%) were those with a subtropical to warm-temperate distribution. Widespread species, which occur all around southern Africa, were also abundant (39%). Fourteen of the 33 species recorded are endemic to southern Africa, with one species, *Syngnathus watermeyeri*, only occurring in a few estuaries along the Eastern Cape coast. Five new species of tropical fishes that typically occur from the Transkei in the south to the equator in the north were recorded in the catches from 1999 onwards. Of those five, *Valamugil cunnesius* and *Liza macrolepis* were recorded in catches almost every year after 2002 and were found in both summer and winter samples.

The ten most abundant species caught were *Gilchristella aestuaria, Atherina breviceps, Rhabdosargus holubi, Glossogobius callidus, Myxus capensis, Monodactylus falciformis, Oreochromis mossambicus, Liza richardsonii, Liza dumerili* and *Lithognathus lithognathus*. These species were consistently recorded throughout the study period.

Table 3.1. Fish species recorded in the East Kleinemonde Estuary between 1996 and 2005 using a range of gear types. Range and category taken from Whitfield (1998). *Indicates southern African endemic species. S = Subtropical, W = Warm-temperate, C = Cool-temperate. For a description of estuarine-dependence categories see Table 3.2. Tropical species are highlighted in grey.

Family	**Scientific name**	**Range**	**Category**	**96**	**97**	**98**	**99**	**00**	**01**	**02**	**03**	**04**	**05**
Clupeidae	*Gilchristella aestuaria**	S/W/C	Ia	■	■	■	■	■	■	■	■	■	■
Atherinidae	*Atherina breviceps**	S/W/C	Ib	■	■	■	■	■	■	■	■	■	■
Sparidae	*Rhabdosargus holubi**	S/W/C	IIa	■	■	■	■	■	■	■	■	■	■
Gobiidae	*Glossogobius callidus**	S/W	Ib	■	■	■	■	■	■	■	■	■	■
Mugilidae	*Myxus capensis**	S/W	Vb	■	■	■	■	■	■	■	■	■	■
Monodactylidae	*Monodactylus falciformis*	S/W	IIa	■	■	■	■	■	■	■	■	■	■
Cichlidae	*Oreochromis mossambicus*	S/W/C	IV	■	■	■	■	■	■	■	■	■	■
Mugilidae	*Liza richardsonii**	S/W/C	IIc	■	■	■	■		■	■	■	■	■
Mugilidae	*Liza dumerili*	S/W	IIa	■	■	■	■	■	■	■	■	■	■
Sparidae	*Lithognathus lithognathus**	S/W/C	IIa	■	■	■	■	■	■	■	■	■	■
Mugilidae	*Mugil cephalus*	S/W/C	IIa	■	■	■	■	■	■	■	■	■	■
Soleidae	*Heteromycteris capensis**	S/W/C	IIb	■		■	■	■	■	■		■	■
Soleidae	*Solea turbynei*[+]*	S/W/C	IIb	■	■	■	■	■	■	■	■	■	■
Haemulidae	*Pomadasys commersonnii*	S/W	IIa	■	■	■	■	■	■	■	■	■	■
Syngnathidae	*Syngnathus watermeyeri**	W	Ia	■	■	■	■	■	■		■		
Carangidae	*Lichia amia*	S/W/C	IIa		■		■	■		■			■
Gobiidae	*Psammogobius knysnaensis**	S/W/C	Ib	■	■		■			■	■	■	■
Hemiramphidae	*Hyporhamphus capensis**	S/W	Ia					■			■	■	
Mugilidae	*Liza tricuspidens**	S/W	IIb		■		■	■	■	■	■	■	■
Sciaenidae	*Argyrosomus japonicus*	S/W	IIa			■				■	■	■	■
Sparidae	*Rhabdosargus sarba**	S/W	IIa								■		■
Carangidae	*Caranx sexfasciatus**	S/W	IIb										■
Elopidae	*Elops machnata*	S/W	IIa				■						
Haemulidae	*Pomadasys olivaceum**	S/W	III										■
Paralichthyidae	*Pseudorhombus arsius*	S/W	III								■		
Pomatomidae	*Pomatomus saltatrix*	S/W/C	IIc									■	
Sparidae	*Diplodus sargus capensis**	S/W/C	IIc									■	
Centrarchidae	*Micropterus punctulatus*	S/W/C	IV										■
Mugilidae	*Valamugil cunnesius*	S	IIa				▨	▨	▨	▨		▨	▨
Mugilidae	*Valamugil robustus**	S	IIa							▨		▨	
Mugilidae	*Liza macrolepis*	S	IIa							▨	▨	▨	▨
Gobiidae	*Glossogobius giuris*	S	IV										▨
Teraponidae	*Terapon jarbua**	S	IIa										▨

[+] Previously known as *Solea bleekeri*

Table 3.2 Estuary-association categories of southern African fish fauna (after Whitfield 1994b).

Category	**Description**
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.

Species diversity

Largely as a result of the increase in tropical species recorded in the estuary, there has been a significant increase in the number of species recorded since 1996 ($r^2 = 0.78$, $P = 0.0006$) (Figure 3.1).

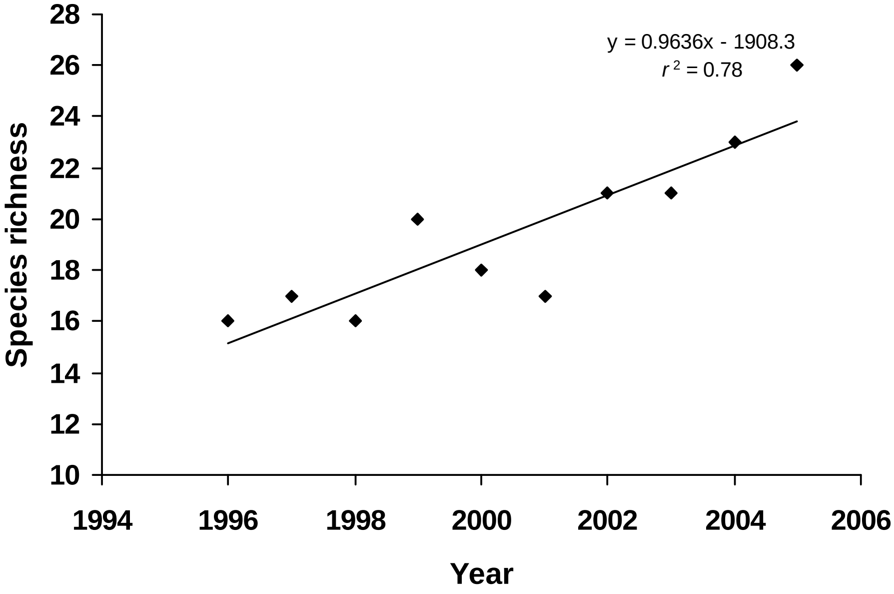


Figure 3.1. Total number of species recorded from all net types in the East Kleinemonde Estuary between 1996 and 2005.

Large mesh seine net

Seasonal trends

The number of species caught (Figure 3.2a) in monthly large mesh seine samples between April 1993 and March 1996 was slightly higher in winter, with an average of 24 (SD = 2.6) species recorded. An average of only 15 species (SD = 9.2) were recorded in summer, although these trends were not significant (ANOVA, $F = 0.84$, $P > 0.05$). In contrast, the large mesh seine net CPUE increased in summer and autumn, and decreased in winter and spring (Figure 3.2b). Again, this trend was not significant (ANOVA, $F = 1.18$, $P > 0.05$).

Classification based on monthly CPUE revealed that samples taken between May 1993 and September 1993 separated from samples taken in other months at ~ 72% similarity (Figure 3.3). Samples taken in July 1993 and 1995 did not fall into either of the two groups. Ordination did not separate summer, autumn, winter and spring samples (Figure 3.4). ANOSIM revealed that fish assemblages in different seasons were not significantly different (Global $R = 0.02$, $P = 0.40$).

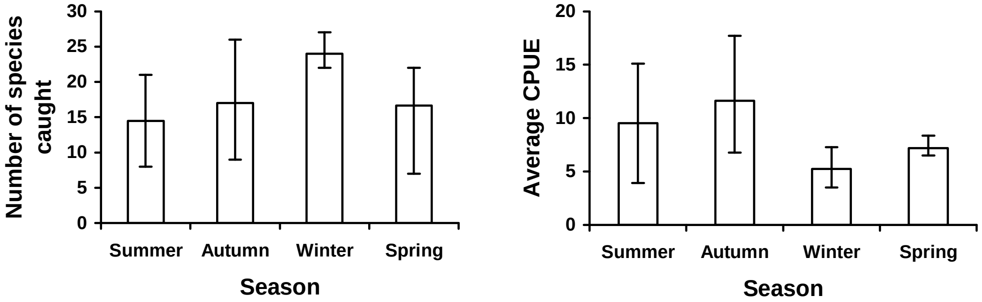


Figure 3.2. Histograms depicting (a) the number of species caught and (b) average CPUE from the large mesh seine net in the East Kleinemonde Estuary between 1993 and 1996. Errors bars indicate the range in values.

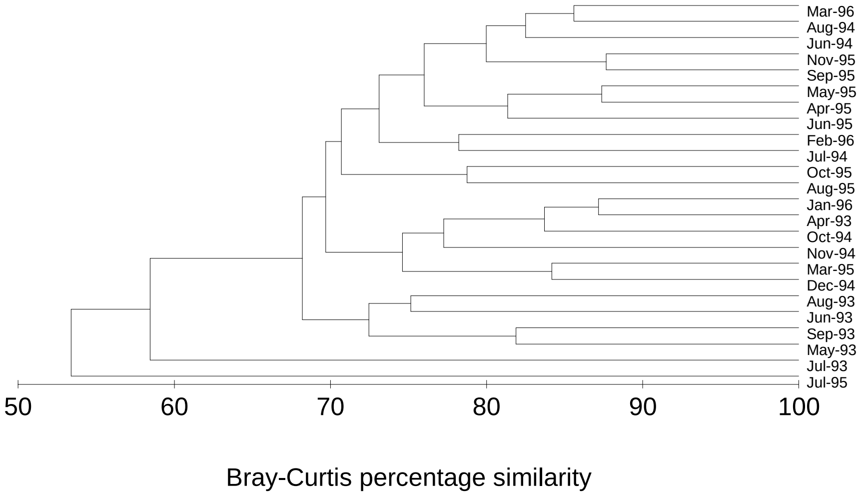


Figure 3.3. Classification of monthly large mesh seine net CPUE data from the East Kleinemonde Estuary between April 1993 and March 1996.

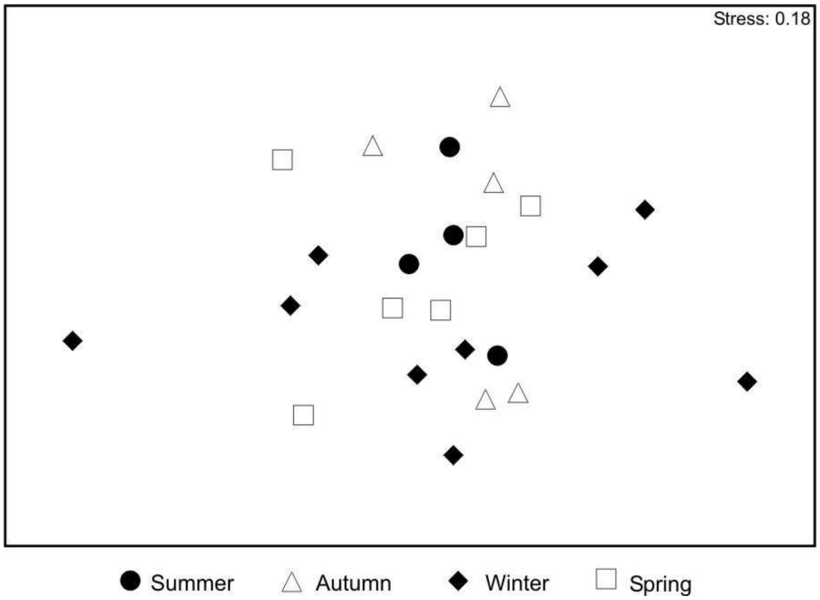


Figure 3.4. Ordination of large mesh seine net seasonal CPUE data from the East Kleinemonde Estuary between April 1993 and March 1996.

Diversity and stability trends

A total of 19 673 fish, represented by nine families and 21 species were caught in the large mesh seine net between 1995 and 2005 (Table 3.3). Mean species richness over the sampling period was 11 (± 3.2) with a significant increase in species richness (S) between 2000 and 2005 (r^2 = 0.85, P = 0.01) (Figure 3.5). Similarly, there was a positive, although not significant, increase in the Margalef index between 2000 and 2005 (r^2 = 0.52, P = 0.10). The Shannon-Wiener index and Pileou's eveness index varied each year but did not show significant trends with time (Figure 3.5).

The overall mean CPUE varied on an annual basis (Figure 3.5) and this reflected the considerable variation in the CPUE for individual species (Table 3.3). CPUE for *R. holubi* peaked in 1998 (135.6 fish/haul) and 2003 (264.4 fish/haul), while CPUE for the mugilids *L. richardsonii* and *L. dumerili* peaked in 1998 and 2004. Peak CPUEs of 7.7 fish/haul and 24.3 fish/haul were recorded for *L. lithognathus* and *M. falciformis* respectively in 1997. Peak CPUE for *M. capensis* was recorded in 2004 and in 2002 for *Mugil cephalus*.

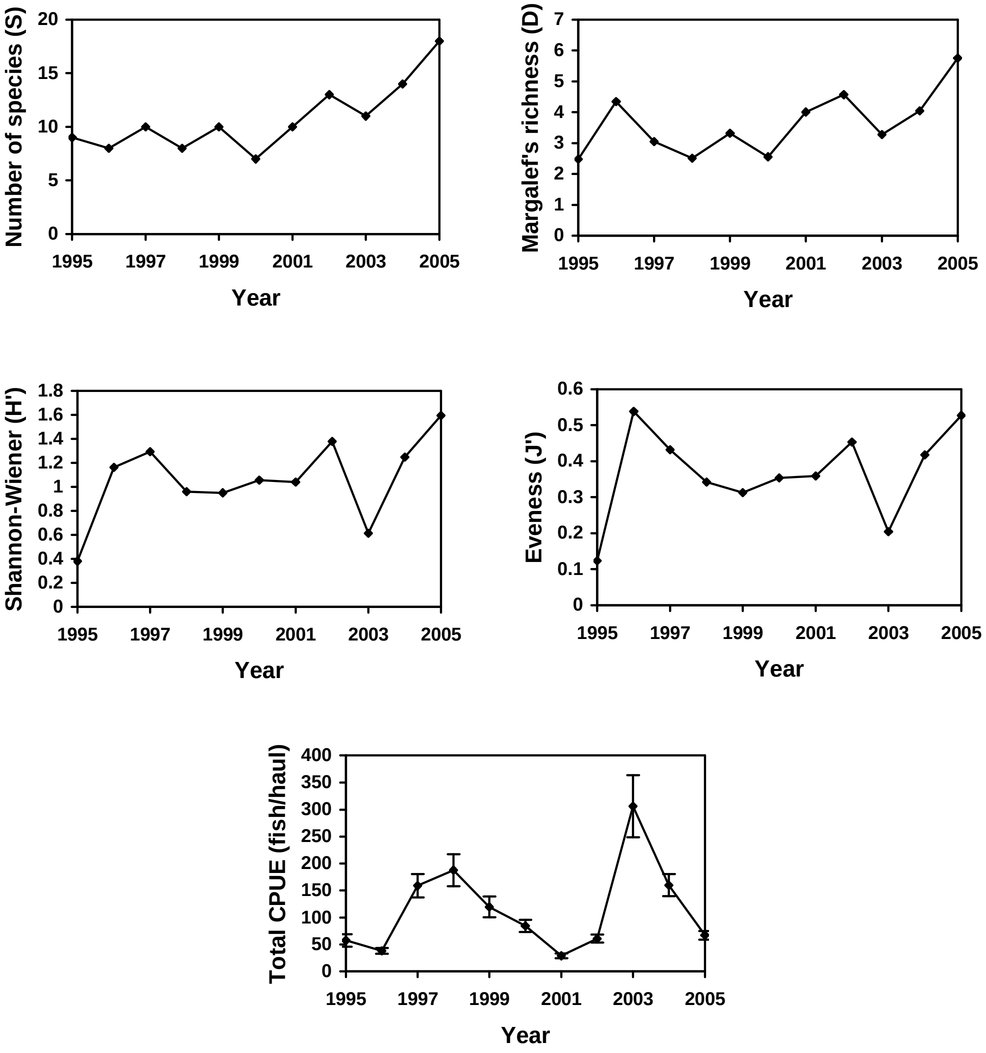


Figure 3.5. Annual trends in the number of species (S), the Margalef richness index (D), the Shannon-Wiener index (H'), Pielou's Eveness index (J') and mean total CPUE (±SD) from large mesh seine net samples taken in the East Kleinemonde Estuary between 1995 and 2005.

Table 3.3. Mean annual CPUE for all species caught in the large mesh seine net in the East Kleinemone Estuary between 1995 and 2005 (values shown are fish/haul).

Species	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**
Argyrosomus japonicus	0	0	0	0	0	0	0	0	0	0.1	0.1
Caranx sexfasciatus	0	0	0	0	0	0	0	0	0	0	0.1
Diplodus sargus capensis	0	0	0	0	0	0	0	0	0	0.1	0
Lichia amia	0.5	0	0	0	0	0	0	0	0	0	0.3
Lithognathus lithognathus	1.5	0.9	7.7	2.8	2.0	1.0	0.4	0.3	1.8	2.1	3.1
Liza dumerili	0.2	0.8	4.6	13.3	0.5	0.9	1.8	1.7	1.6	6.6	3.9
Liza macrolepis	0	0	0	0	0	0	0	0.1	0.1	0	0.1
Liza richardsonii	0.6	4.1	5.1	24.4	3.2	0.0	1.1	1.8	5.8	7.0	3.3
Liza tricuspidens	0	0	0.3	0	0	0	0.4	0.7	0.8	0.8	1.0
Monodactylus falciformis	1.2	0.4	24.3	9.6	13.2	7.3	0.8	0.6	2.2	4.1	2.7
Mugil cephalus	0.1	0.2	0.8	0	0.1	0.2	0.1	6.9	1.1	0.9	0.2
Myxus capensis	0.2	2.6	16.3	0.3	8.9	34.8	2.7	25.2	19.5	82.6	18.8
Oreochromis mossambicus	0	3.7	2.8	1.4	2.8	0.1	0.2	0.5	8.4	0.0	3.4
Pomadasys commersonnii	0	0	0.1	0.4	0.1	0	0.3	0.2	0.3	0.3	0.1
Pomadasys olivaceum	0	0	0	0	0	0	0	0	0	0	0.1
Pomatomus saltatrix	0	0	0	0	0	0	0	0	0	0.1	0
Rhabdosargus holubi	53.3	25.4	97.0	135.6	88.6	40.2	21.3	22.8	264.4	54.1	30.2
Rhabdosargus sarba	0	0	0	0	0	0	0	0	0	0	0.1
Terapon jarbua	0	0	0	0	0	0	0	0	0	0	0.1
Valamugil cunnesius	0	0	0	0	0.1	0	0	0	0	0.2	0.1
Valamugil robustus	0	0	0	0	0	0	0	0.1	0	1.2	0

The coefficient of concordance, an index of community stability, among the rankings of the top 8 species from all eleven years of sampling indicated a 57% (0.57) concordance in the East Kleinemonde Estuary over time. A concordance of 100% would have indicated no change in species rank over the study period (Kendall 1962). Kendall's *W* was higher for the period 2001-2005 (0.72) than 1995-2000 (0.61). Spearman rank correlations for all possible pairs of years showed significant differences in 22 out of 121, also indicating similar rank order of abundance for the different species each year.

The dominant species was *Rhabdosargus holubi* and comprised more than 50% of the catch in all years except 2000, 2002, 2004 and 2005. In years when *R. holubi* comprised less than 50% of the catch, *Myxus capensis* comprised a large proportion of the catch (Figure 3.6). Other dominant species were *Monodactylus falciformis*, comprising between 0.7% (2003) and 15% (1997) of the catch and *Lithognathus lithognathus* comprising between 0.4% (2002) and 4.8% (1997) of the catch.

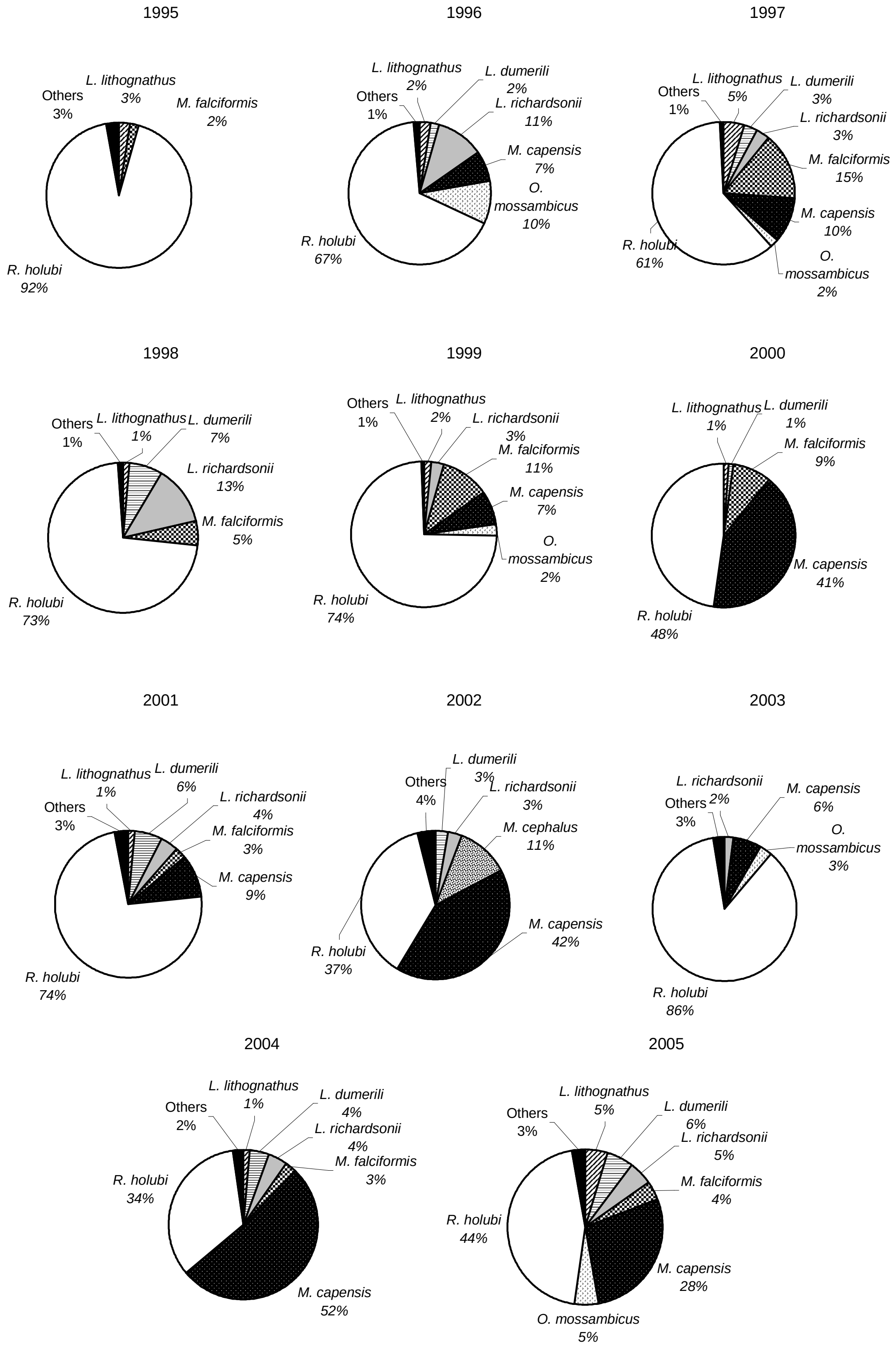


Figure 3.6. Annual catch composition (%) of species caught in the large mesh seine net in the East Kleinemnonde Estuary between 1995 and 2005.

Length composition

Average lengths of *Rhabdosargus holubi*, *Monodactylus falciformis* and *Lithognathus lithognathus* were highest in 2001 (Table 3.4), following a period when the mouth of the estuary had only opened for a single day between 1 December 1998 and 28 March 2000. Minimum average lengths for these species were recorded in 2005, 2003 and 1995 respectively. In these years extended open mouth conditions (8-31 days, see Table 2.7, Chapter 2) were recorded. Mugilid species, *Myxus capensis*, *Liza richardsonii*, *Liza dumerili* and *Mugil cephalus*, showed no obvious trends in mean size.

Table 3.4. Average length (mm SL) of the seven most abundant species caught in the large mesh seine net in the East Kleinemonde Estuary between 1995 and 2005.

Year	*R. holubi*	*M. capensis*	*M. falciformis*	*L. richardsonii*	*L. dumerili*	*L. lithognathus*	*M. cephalus*
1995	77.3 (±11.9)	220.6 (±53.5)	61.2 (±13.5)	164.6 (±85.8)	256.0 (±12.7)	64.9 (±25.7)	124.5 (±14.9)
1996	81.3 (±16.4)	134.4 (±15.7)	68.4 (±19.7)	75.2 (±26.7)	123.5 (±21.6)	72.6 (±45.9)	154.7 (±12.7)
1997	79.0 (±16)	147.4 (±47.8)	86.1 (±25.8)	135.1 (±35.4)	123.0 (±21.1)	157.3 (±29.2)	169.6 (±57)
1998	93.0 (±18.7)	163.5 (±82.7)	68.7 (±24.5)	142.6 (±26.9)	160.2 (±25.2)	179.4 (±49.4)	-
1999	83.9 (±14.6)	150.1 (±51)	74.6 (±12.1)	148.1 (±28.9)	177.9 (±48.5)	184.3 (±30.8)	357.5 (±20.5)
2000	102.2 (±15.1)	161.2 (±38.7)	99.3 (±15.3)	-	184.2 (±22.1)	234.1 (±68.2)	238.7 (±52.2)
2001	112.9 (±15.1)	165.1 (±28.7)	108.7 (±22)	156.8 (±44.3)	159.7 (±26.2)	273.3 (±61)	280.0
2002	78.1 (±12)	174.6 (±33.4)	67.5 (±20.8)	147.3 (±40)	123.1 (±25)	241.6 (±90.7)	153.7 (±60.8)
2003	87.6 (±15.6)	127.4 (±27.4)	54.9 (±15.6)	166.4 (±53.9)	149.0 (±18.5)	101.1 (±12.2)	142.6 (±43.7)
2004	81.0 (±12.4)	152.6 (±26.2)	67.1 (±11.7)	130.2 (±29.5)	143.3 (±31)	136.1 (±50)	155.6 (±23.4)
2005	68.6 (±7.1)	138.8 (±30.5)	71.4 (±14.5)	153.1 (±30.8)	134.8 (±28.6)	150.9 (±38.4)	159.0 (±13.1)

Fish assemblage structure

The nMDS ordinations showed similar patterns of interannual community change in both summer and winter (Figure 3.7) and as a result summer and winter samples were pooled to examine mean annual patterns (Figure 3.8). nMDS ordination separated the fish community into two main groups based on whether the mouth was open in spring of the previous year (1997, 2001-2005) or only open in other seasons (1995-1996, 1998-2000) (Figure 3.8). These groupings were obvious regardless of the frequency and duration of mouth opening. For example, the 1997 fish assemblage grouped with the 2003 fish assemblage despite the fact that the mouth had only opened for three days between September 1996 and November 1996, while between September and November of 2002 the mouth was open for 32 days. Although no opening events were recorded in the spring of 2004, the 2005 sample grouped with 'spring' years. This was probably because marine overwash events were recorded in the spring of 2004 and the mouth was open for extended periods in 2005 (see Figure 2.14, Chapter 2 and Appendix 1).

ANOSIM revealed that the fish assemblages grouped by nMDS (spring and other years) were significantly different (Global $R = 0.54$, $P < 0.002$). Data analysis using the SIMPER routine showed that nine species, *Myxus capensis*, *Liza tricuspidens*, *Rhabdosargus holubi*, *Liza richardsonii*, *Monodactylus falciformis*, *Liza dumerili*, *Mugil cephalus*, *Pomadasys commersonnii* and *Lithognathus lithognathus*, accounted for 83% of the dissimilarity between these two groupings. Species richness was also highest in the "spring" years (Figure 3.5).

Of the nine 'discriminating' species, mean annual CPUE for *Liza tricuspidens, Myxus capensis, Mugil cephalus, Pomadasys commersonnii* and *Lithognathus lithognathus* were generally higher in the 'spring' years, although trends were only significant for *L. tricuspidens* ($P < 0.001$) which was completely absent from catches in the 'other' years (Figure 3.9). Mean annual CPUE for *Rhabdosargus holubi, Monodactylus falciformis* and *Liza dumerili* were fairly even during both periods, while mean annual CPUE for *Liza richardsonii* was greater in the 'other' years (although not statistically significant).

Interannual variability was higher in the 'other' years than the 'spring' years, giving a positive value for the IMD (0.573), thus rejecting the null hypothesis of no variability differences between groupings. The index of multivariate seriation (IMS expressed as the Spearman rank correlation coefficient, ρ_s) was only 0.3 ($p = 0.12$) between 1995 and 2000, indicating no correlation with a linear sequence during this period. In contrast ρ_s was 0.51 (although not significant, p = 0.08) between 2001 and 2005 indicating a more linear sequence during this period.

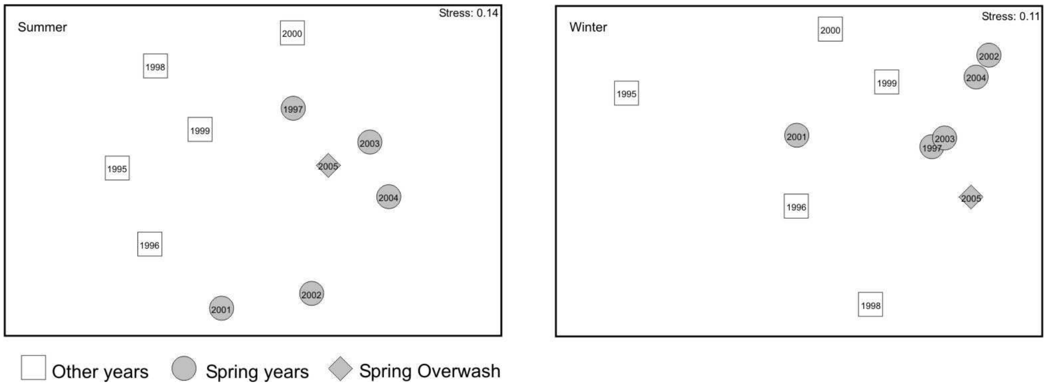


Figure 3.7. Ordination of the mean large mesh seine net annual CPUE data, for summer and winter sampling, from the East Kleinemonde Estuary (between 1995 and 2005).

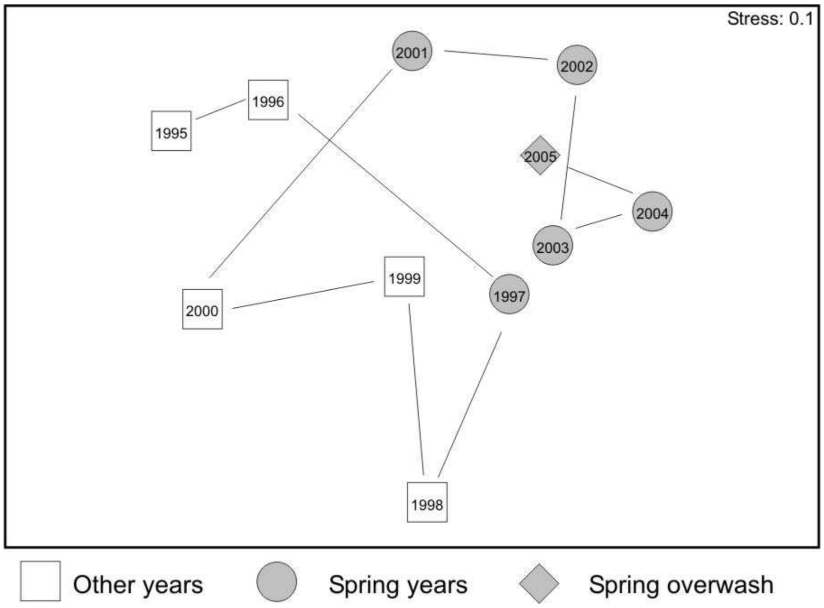


Figure 3.8. Ordination of the mean large mesh seine net annual CPUE data (pooled summer and winter samples) from the East Kleinemonde Estuary (between 1995 and 2005).

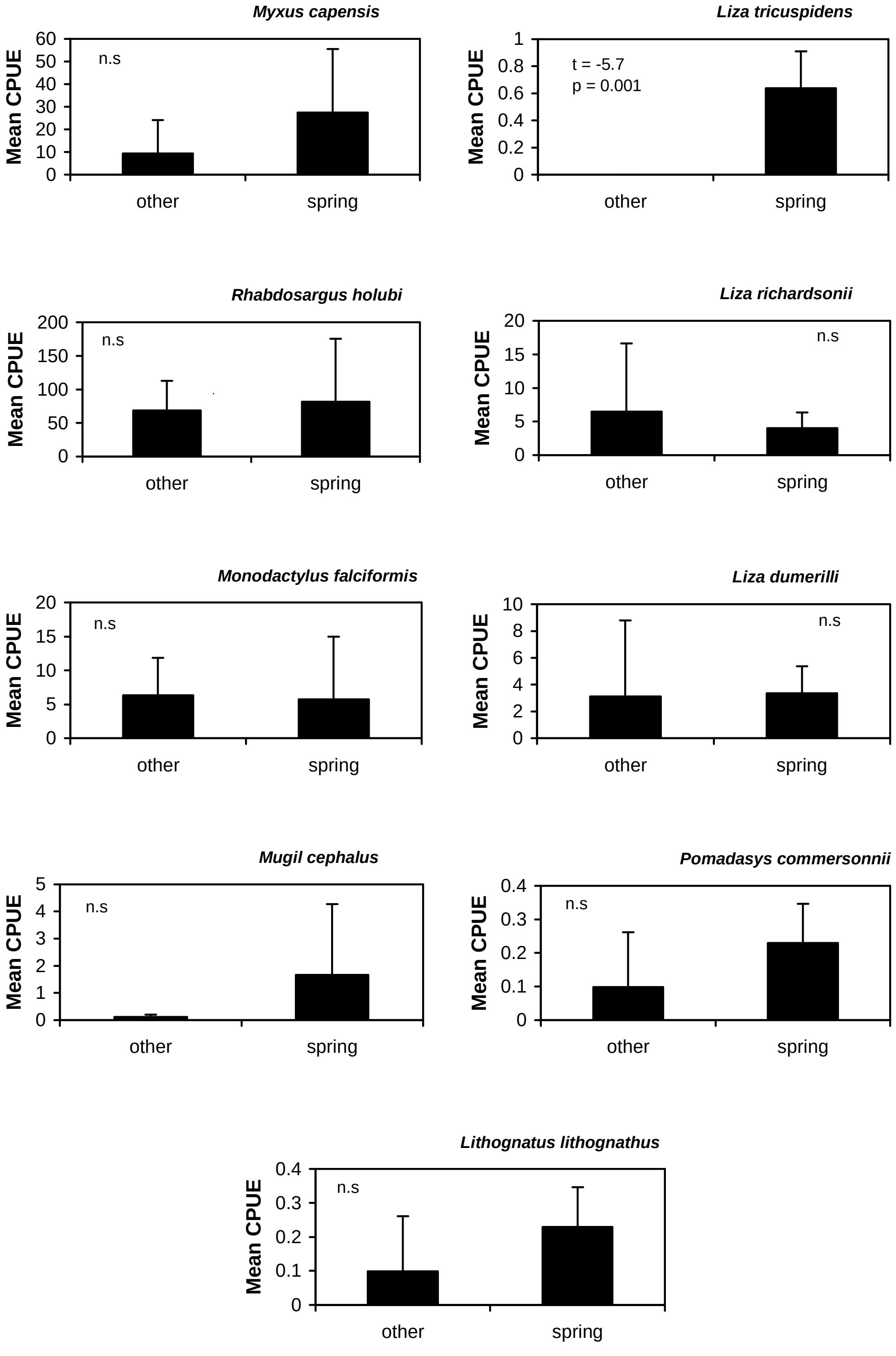


Figure 3.9. Mean CPUE (+SD) for the nine discriminating species in ‘spring’ and ‘other’ years. The results of *t*-tests between the periods are given (n.s = not significant).

Table 3.5. Feeding groups of East Kleinemonde marine fish taxa, taken from the hierarchical food items table in FishBase (Froese and Pauly 2006).

Piscivores Group 1	**Herbivores** Group 2	**Zoobenthivores** Group 3	**Zooplanktivore** Group 4	**Detritivores** Group 5
Argyrosomous japonicus	*Diplodus sargus capensis*	*Lithognathus lithognathus*	*Monodactylus falciformis*	*Liza dumerili*
Caranx sexfasciatus	*Rhabdosargus holubi*	*Pomadasys commersonnii*		*Liza macrolepis*
Lichia amia	*Rhabdosargus sarba*	*Pomadasys olivaceum*		*Liza richardsonii*
Pomatomus saltatrix		*Terapon jarbua*		*Liza tricuspidens*
				Mugil cephalus
				Valamugil cunnesius
				Valamugil robustus
				Myxus capensis

The nMDS ordination of the trophic group data (Figure 3.10) showed no obvious groupings, as were apparent in the species composition ordination (Figure 3.8). This was probably because there are only five trophic groups, each with relatively few species (Table 3.5), and the system was fairly stable with time. Superimposing annual CPUE for the vegetation-associated taxa (Group 2 and Group 4) indicates that abundance of these groups was highest in 1997-1999 and 2003 (Figure 3.10a). Abundance of these groups was also much higher in the summer of 2003 (238 fish/haul) than in the winter of 2003 (29 fish/haul). A flood in May 2003 destroyed many of the submerged macrophytes in the estuary and may account for the low CPUE recorded for these groups in winter 2003 and in 2004 and 2005. In contrast, the highest CPUE value for detritivores was recorded in 2004 (Figure 3.10b), a year after the episodic flood event when submerged macrophyte coverage was at a minimum.

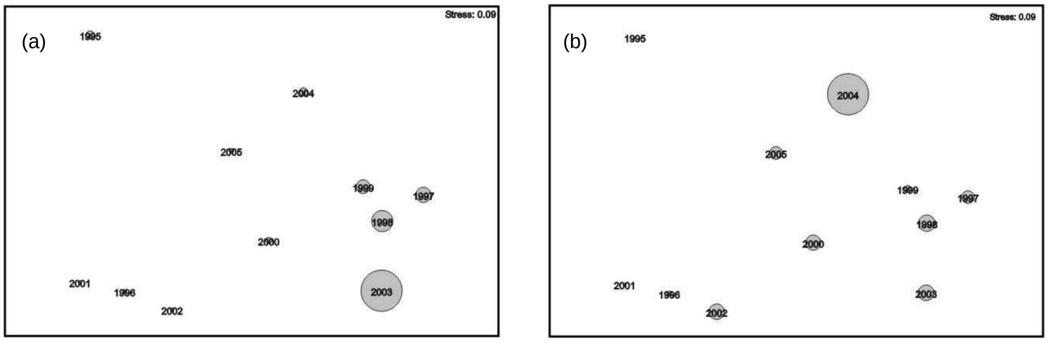


Figure 3.10. Ordination of the large mesh seine net annual samples, based on the trophic composition of fish communities as per Table 3.5, with superimposed circles of increasing size with increasing CPUE of (a) vegetation-associated taxa (groups 2 and 4) and (b) detritivores.

Small mesh seine net

Annual trends

A total of 92 689 fish, represented by 10 species from eight families were recorded in small mesh seine net samples between 1996 and 2005 (Table 3.6). The number of species caught annually varied from five to seven (mean = 6, SD = 1). The annual composition of catches from 1996 to 2005 are depicted in Figure 3.11. *Gilchristella aestuaria* was the most abundant species recorded and comprised between 33% (1996) and 94% (2005) of the catch. *Atherina breviceps*, which is also a small shoaling species, ranged between 33% (1996) to only 5% (2005) of the catch. The gobiid, *Glossogobius callidus* was the third most abundant species and comprised up to 15% of the small mesh seine net catch.

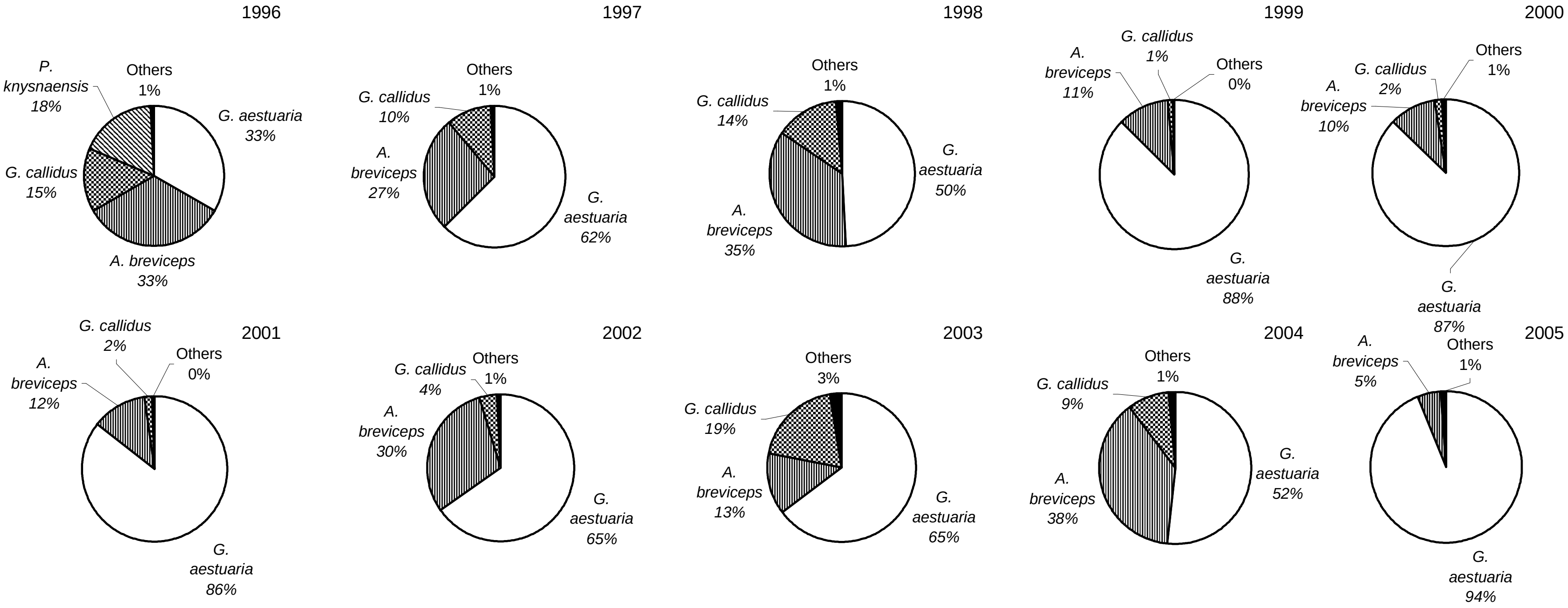


Figure 3.11. Annual catch composition (%) of species caught in the small mesh seine net in the East Kleinemonde Estuary between 1996 and 2005.

Table 3.6. Mean annual CPUE for all species caught in the small mesh seine net in the East Kleinemonde Estuary between 1996 and 2005 (values shown are number of fish per haul).

Species	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**
Atherina breviceps	97.2	309.8	75.8	74.9	94.8	41.2	295.8	149.1	217.2	89.2
Micropterus punctulatus	0	0	0	0	0	0	0	0	0	0.1
Gilchristella aestuaria	97.5	728.9	105.0	587.6	790.3	293.9	642.3	720.3	293.3	1662.1
Glossogobius callidus	42.8	120.6	30.1	7.5	13.7	6.4	36.8	214.6	51.1	0.0
Heteromycteris capensis	0.7	0	0.9	0	0	0.7	0	0	0.6	0.6
Hyporhamphus capensis	0	0	0	0	0	0	0	0.3	0.6	0.0
Oreochromis mossambicus	1.5	7.1	0.3	0	8.1	0.8	9.0	24.9	2.5	0.1
Psammogobius knysnaensis	51.5	0.1	0	0.3	0	0	0.1	0.9	1.0	0.2
Solea bleekeri	0.2	0.3	0.9	0	0.1	0	0	1.8	2.5	0.4
Syngnathus watermeyeri	0.2	0.8	1.0	0.9	0.4	0.1	0	0.1	0	0

Although mean annual CPUE for all species varied, values were consistently higher for *Gilchristella aestuaria* and *Atherina breviceps* (Table 3.6). In 2005 an exceptionally high catch of *G. aestuaria* (mean fish per haul = 1662) was recorded, while CPUE for other species was much lower. The high catch of *G. aestuaria* in 2005 led to a peak in total CPUE in this year (Figure 3.12).

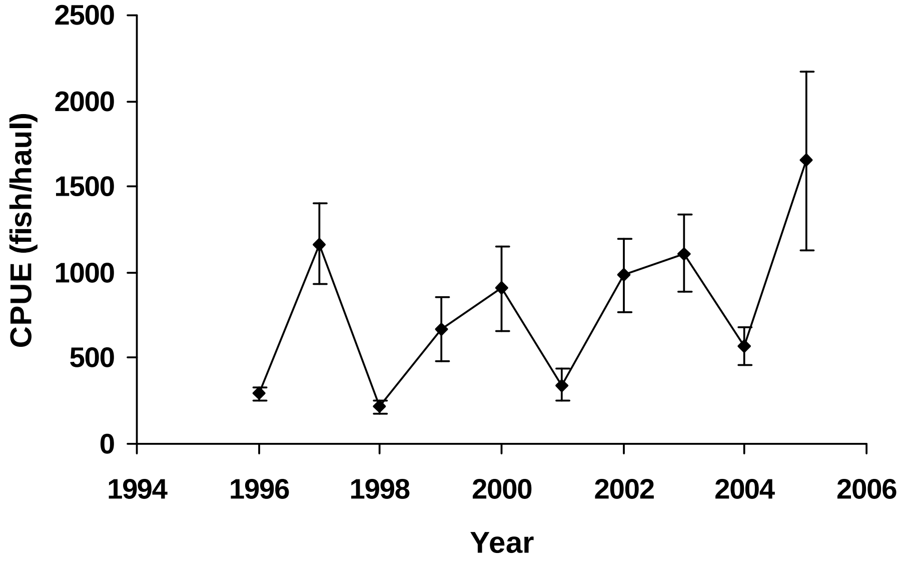


Figure 3.12. The mean annual CPUE (±SD) for all fish caught in the small mesh seine net in the East Kleinemonde Estuary between 1996 and 2005.

The estuarine pipefish, *Syngnathus watermeyeri*, was recorded in small numbers in the small mesh seine net. Maximum catches were recorded in 1998, when 1 fish/haul were caught (Table 3.6). This species disappeared from catches after a flash flood in May 2003 destroyed many of the submerged macrophytes, which are the principal habitat for *S. watermeyeri* (Whitfield 1995).

Length composition

The mean annual size of *Gilchristella aestuaria* varied from 28.4mm SL in 1999 to 37.6 mm SL in 2005, while the mean annual size of *Atherina breviceps* caught varied from 30.6 mm SL in 1996 to 42.6 mm SL in 2005 (Table 3.7). The majority of *G. aestuaria* individuals captured in most years were mature and over one year old. The exception was 1999, when 50% of the individuals captured were immature and less than one year old. In contrast, all of the individuals caught in 2005 were mature. *A. breviceps* catches were dominated by immature individuals in most years except 2005, when the majority of individuals sampled were mature. The mean annual size of *Glossogobius callidus* and *Psammogobius knysnaensis* was more variable.

Table 3.7. Average lengths (mm SL) of the four most abundant species caught in the small mesh seine net in the East Kleinemonde Estuary between 1996 and 2005.

Year	***Gilchristella aestuaria***	***Atherina breviceps***	***Glossogobius callidus***	***Psammogobius knysnaensis***
1996	33.1 (±9.2)	30.6 (±6.2)	41.5 (±13.4)	34.6 (±8.2)
1997	33.2 (±4.7)	35.8 (±9.2)	46.0 (±9.6)	58.0
1998	35.6 (±4.1)	35.7 (±8.0)	42.7 (±11.2)	-
1999	28.4 (±13.3)	35.9 (±7.1)	35.1 (±15.1)	22.8 (±3.8)
2000	33.4 (±6.6)	33.7 (±8.1)	32.9 (±15.2)	-
2001	31.1 (±8.3)	31.7 (±6.3)	28.7 (±7.3)	-
2002	32.3 (±7.4)	39.3 (±8.8)	38.2 (±14)	28.0
2003	30.7 (±7.8)	39.2 (±10.7)	44.2 (±10.1)	44.0 (±3.1)
2004	36.9 (±5.1)	34.0 (±6.6)	40.2 (±10.8)	37.5 (±7.2)
2005	37.6 (±5.3)	42.6 (±6)	33.4 (±4.4)	40.7 (±5.5)

Gill nets

A total of 1065 fish, representing eight families and 17 species were caught in gill nets between 1995 and 2005 (Table 3.8). The number of species caught per year ranged from 8 to 13, with a mean of 10 (SD = 1.7). Marine-spawning species that are dependent on estuaries (category IIa) dominated catches. A single freshwater species, *Oreochromis mossambicus* was documented and no estuarine resident species were caught due to their small size. The most dominant species recorded was *Monodactylus falciformis* (5-46%), followed by *Mugil cephalus* (0-31%) and *Rhabdosargus holubi* (3-30%). Mugilidae were the most dominant family and collectively comprised between 40% (2003) and 81% (1998) of the total catch. Also of significance were catches of *Pomadasys commersonnii* and *Lithognathus lithognathus* (Figure 3.13).

Catches for *Monodactylus falciformis* declined from a high of 64 individuals in 1998 to only four in 2005 (Table 3.8). In contrast, catches for *A. japonicus* increased from an average of one individual per year between 1996 and 2002 to 21 individuals between 2003 and 2005. The above CPUE change coincided with the alteration in estuarine habitat following the episodic flood of 2003.

Table 3.8. Numbers and length (mm SL) of species caught using gill nets in the East Kleinemonde Estuary from 1996 to 2005.

	Year												
Species	**96**	**97**	**98**	**99**	**00**	**01**	**02**	**03**	**04**	**05**	***Tot. N***	**Mean length (mm)**	**Length range (mm)**
Argyrosomus japonicus	0	0	9	0	0	0	1	18	23	22	73	371	155-598
Caranx sexfasciatus	0	0	0	0	0	0	0	0	0	1	1	120	120
Elops machnata	0	0	0	1	0	0	0	0	0	0	1	455	455
Lichia amia	0	3	0	1	4	0	3	0	0	2	13	572	117-930
Lithognathus lithognathus	5	7	3	3	11	9	1	1	0	0	40	262	195-372
Liza dumerili	4	3	0	2	3	3	10	0	1	5	31	200	161-313
Liza macrolepis	0	0	0	0	0	0	1	0	1	1	3	184	153-235
Liza richardsonii	8	6	1	1	0	0	0	4	0	0	20	226	163-302
Liza tricuspidens	0	2	0	1	0	2	0	5	14	3	27	296	209-456
Monodactylus falciformis	57	18	64	41	35	11	7	6	7	4	250	107	64-147
Mugil cephalus	22	40	37	15	34	0	33	14	0	2	197	333	181-500
Myxus capensis	7	13	5	12	18	9	35	14	0	2	115	231	163-365
Oreochromis mossambicus	3	13	4	1	1	0	2	3	1	11	39	235	106-315
Pomadasys commersonnii	1	9	2	10	12	4	22	15	5	0	80	310	143-645
Rhabdosargus holubi	32	11	12	22	32	1	9	34	3	0	156	109	92-171
Rhabdosargus sarba	0	0	0	0	0	0	0	1	0	0	1	258	258-258
Valamugil cunnesius	0	0	0	12	1	1	1	0	0	0	15	163	148-192

Only one species (*Elops machnata*) was caught in gill nets that was not recorded in the large mesh seine net. However, the gill nets caught a larger size class of species such as *Monodactylus falciformis* that were not well represented in seine net catches. Cowley and Whitfield (2002) estimated that *M. falciformis* was the third most abundant marine species (in terms of numbers) in the East Kleinemonde Estuary when submerged aquatic macrophytes were present and this is reflected in the gill net catches.

The mean standard length of all species caught in gill nets was above 100 mm SL, which is typical of estuarine gill net catches and is largely dependent on the mesh size of the nets (Loneragan *et al.* 1989, Whitfield *et al*. 1994, Young and Potter 2002) (Table 3.8). The smallest fish caught was a *Monodactylus falciformis* of 64 mm SL in 1996 and the largest was a *Lichia amia* of 930 mm SL in 2002. The gill net assemblage was not analysed further, due to the paucity of data.

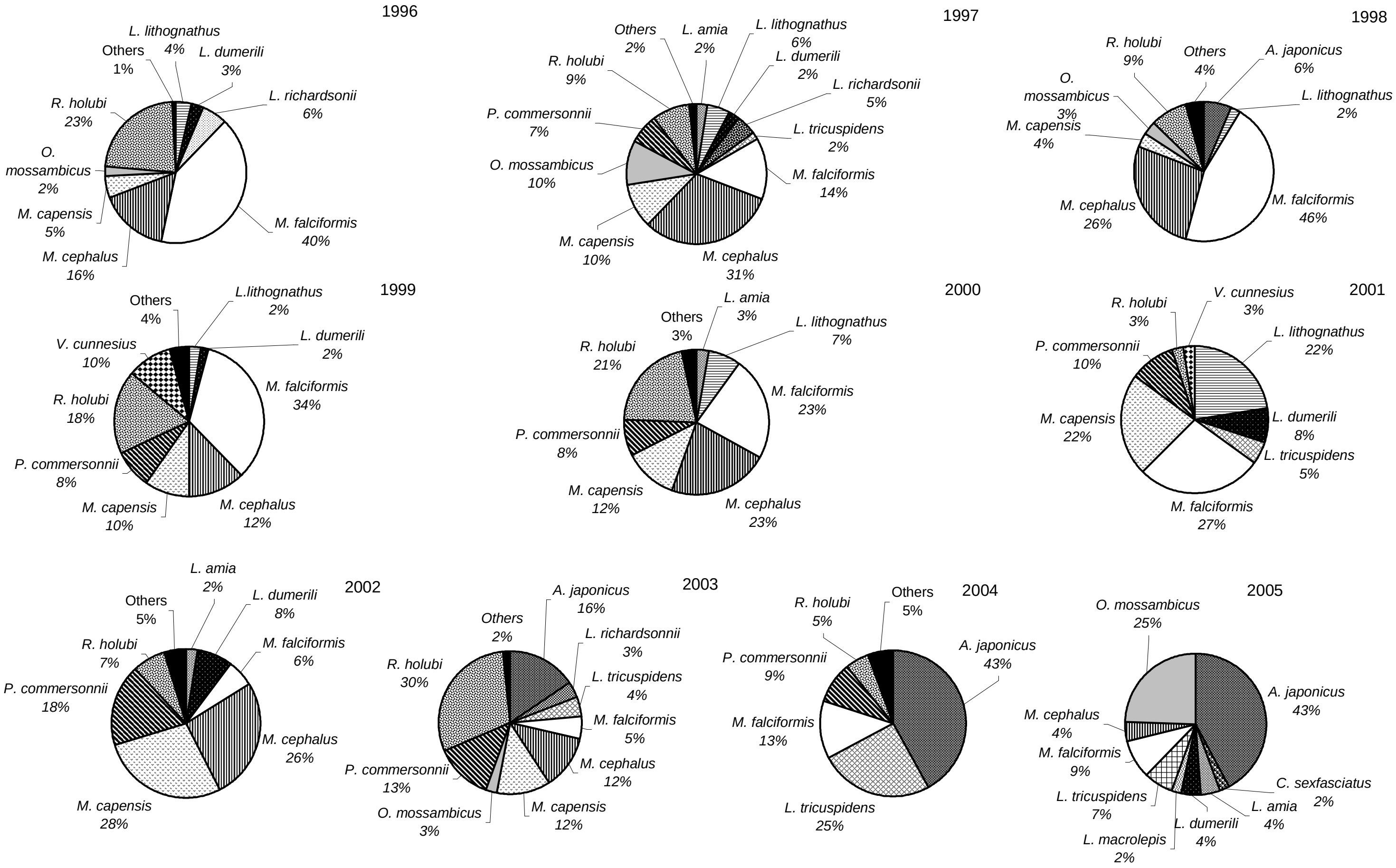


Figure 3.13. Annual catch composition (%) of species caught in gill nets in the East Kleinemonde Estuary between 1996 and 2005.

DISCUSSION

The small, temporarily open/closed East Kleinemonde Estuary has been the subject of considerable ichthyological research in recent years. Cowley and Whitfield (2001a) examined fish community structure as part of a larger study, while Cowley and Whitfield (2001b, 2002) used mark-recapture techniques and seine nets (density extrapolation) to estimate fish population sizes in the estuary. Vorwerk *et al.* (2001) compared fish assemblages in different Eastern Cape estuaries, including the East Kleinemonde Estuary, using non-parametric multivariate analyses. Despite a history of intensive research in this estuary, concerning various aspects of estuarine population dynamics, relatively little is known about the long-term relationships between environmental variables and changes in fish populations and assemblages.

When designing long-term monitoring programs, several questions arise, including the variability of assemblages between sites and the variability of assemblages over time (Desmond *et al.* 2002). The fish assemblage was adequately characterised by sampling using three different types of nets, which caught a large size range of fish. In addition, sufficient nets were set per session to collect more than 75% of species taken in this study.

This study has shown that the East Kleinemonde Estuary is an important habitat for a number of estuarine and marine fish species. A total of 33 fish species from 18 families were recorded during the 10 years of sampling (1996-2005) when all three net types were used. Mugilidae and Sparidae were represented by the greatest number of species. Mugilidae are abundant in temporarily open/closed and permanently open estuaries in South Africa (e.g. Marais and Baird 1980, Marais 1981, 1983, Kok and Whitfield 1986, Vorwerk *et al.* 2001) with a total of 10 species recorded from the cool- and warm-temperate regions (Harrsion 2005). In contrast only two mugilid species are recorded in temperate estuaries of south-western Australia (Potter *et al.* 1990). Sparidae are also represented by a large number of species in temperate estuaries of South Africa, with a total of 14 species of sparid recorded in these estuaries (Smith and Heemstra 1990).

Marine-spawning teleosts usually dominate the ichthyofauna (in terms of the number of species) of temperate estuaries of the northern and southern hemispheres (Loneragan *et al*. 1989, Whitfield *et al.* 1994, Potter *et al.* 1997, Griffiths 2001, Castillo-Rivera *et al*. 2002, Harrison 2005). In the East Kleinemonde Estuary, estuary-dependent marine species comprised 64% of the species recorded, while estuarine resident species comprised 18% of the species recorded. The contribution by estuarine resident species in temperate Australian estuaries is usually higher and has been attributed to an adaptation to extended periods of land-locking (Loneragan *et al.* 1989, Potter *et al.* 1993). Only two marine stragglers, *Pseudorhombus arsius* and *Pomadasys olivaceum,* were sampled in the East Kleinemonde Estuary between 1996 and 2005, but other marine stragglers have been recorded entering the system at certain times (*Trachinotus* sp. and *Epinephalus marginatus*) (P. Cowley. pers. comm.). Marine stragglers (category III) that are not dependent on estuaries are usually more abundant in the lower reaches of permanently open estuaries where marine conditions prevail (Whitfield 1998).

The top 10 species, in terms of numbers, were recorded consistently each year. This pattern is typical of estuaries worldwide, which are normally dominated by relatively few species (Jackson and Jones 1999, Garcia *et al.* 2003, Paperno and Brodie 2004). The majority of species recorded in the East Kleinemonde Estuary were species with a subtropical to warm-temperate distribution, which is also typical of temporarily open/closed estuaries in the South African warm-temperate region (Harrison 2005). However, five new species of tropical fishes (*Valamugil cunnesius, Valamugil robustus, Liza macrolepis*, *Glossogobius giuris* and *Terapon jarbua*) were recorded in the estuary from 1999 onwards.

The three tropical mugilid species and *Terapon jarbua* typically occur in the tropical and subtropical estuaries of southern Africa, although stragglers are occasionally recorded in the warm-temperate estuaries of the northern Eastern Cape (Smith and Heemstra 1990). *Glossogobius giuris* is a tropical and subtropical Indo-West Pacific species that has only been recorded as far south as the Mngazana Estuary on the Transkei coast (Mbande *et al.* 2005). *Valamugil cunnesius* and *Liza macrolepis* were recorded fairly consistently in both summer and winter samples from 2002, thus indicating that water temperatures were within the tolerance range of these species.

The increase in tropical taxa in the East Kleinemonde Estuary during the past decade has resulted in an increase in species richness over time and could be an indicator of climate change.

Mean sea surface temperatures (SST) recorded off Port Alfred and East London have been increasing over the past decade, which could affect the seasonal migrations of tropical and temperate fish species (Kennish 1986). According to Clark (2006) the notion that the earth's climate is changing is widely accepted. Sea surface temperatures off Port Elizabeth have been increasing by ±0.25ºC per decade for the past four decades (Schumann *et al.* 1995). Although 1-2ºC changes in temperature may seem insignificant to animals that thermoregulate, many aquatic organisms are thermoconformers, and therefore respond rapidly to changes in ambient temperature (Clark 2006). Clark (*op. cit.*) predicts the most obvious changes associated with increasing sea surface temperatures around South Africa will be shifts in the distributional patterns of individual species or species assemblages.

There has also been a general positive trend in South African air temperatures, although not always significantly, for the period 1960 to 2003 (Kruger and Shongwe 2004). For this period, East London has shown a significantly positive trend in annual average and annual average maximum and minimum temperatures (Kruger and Shongwe *op. cit.*). Increasing air temperatures may have a greater impact on temporarily open/closed estuaries than permanently open estuaries, as these systems are cut off for long periods from the effect of sea temperatures and therefore respond to a greater degree to prevailing land, air and river water temperatures.

The effects of climate change on coastal fish and invertebrate distributions have been recorded both locally and globally. Mbande *et al.* (2005) found that the variety of tropical species in the Mngazana Estuary increased during both summer and winter compared with a similar study conducted by Branch and Grindley (1979) 25 years earlier. Schleyer and Celliers (2003) recorded a steady increase in sea temperature of >2ºC on the Sodwana reefs, in northern KwaZulu-Natal, during the last decade. This has lead to small changes in coral community structure, with hard coral cover increasing and soft coral cover decreasing.

In the northern hemisphere, Cabral et al. (2001) recorded significant increases in water temperature in the Tagus Estuary, Portugal, between surveys conducted during 1980-1983 and 1995-1996. Fish species richness also increased between the two periods (Cabral et al. op. cit.). Climatic variability was found to have a principal controlling influence on the structure of the Thames Estuary fish assemblage, the growth of resident juveniles and the abundance of many species (Attrill and Power, 2002). Groundfish species with a wide distribution range (mainly subtropical species) have exhibited an increasing abundunce trend with time in the Bay of Biscay, while seven species with a narrow distribution range have declined in abundance (Poulard and Blanchard 2005). Parker and Dixon (1998) surveyed a North Carolina reef fish community over 15 years and found that the total species composition has become more tropical, with 29 new species of tropical reef fishes recorded. Similarly, Stebbing et al. (2002) correlated warming of the North Atlantic with the northward extension of warm water fish into coastal waters off the Cornish coast of the United Kingdom.

Distinct seasonal trends in species composition were not apparent in the East Kleinemonde Estuary when the marine fish assemblage was sampled monthly between April 1993 and March 1996. Similarly, Vorwerk *et al.* (2001) found no significant seasonal differences in the total number of individuals caught in other temporarily open/closed estuaries sampled along the southeast coast of South Africa. A total of 39 species were recorded during both summer and winter and only 15 species were restricted to either season (Vorwerk *op. cit.*). On average, the region between Port Elizabeth and East London experiences similar amounts of rainfall throughout the year, and there is no clear pattern to mouth opening which may explain the lack of seasonal patterns observed in species composition. These estuaries are usually closed for much of the year and consequently the fish populations are ‘captive’ which may also explain the lack of seasonal differences in composition and abundance.

Similarly, no clear seasonal pattern in species composition was observed in the temporarily open/closed Swan Lake and Lake Wollumboola in south-eastern Australia (Pollard 1994). These estuaries also experience unpredictable rainfall and consequently unpredictable mouth opening events. In contrast, Yánẽz-Arancibia

(1981) attributed seasonal fluctuations in species composition in the intermittently open Chautengo Lagoon in Mexico to the predictable fluctuations in salinity caused by seasonal rainfall and opening of the estuary mouth.

Resilience determines the persistence of relationships within a system and this can be measured by Kendall's coefficient of concordance (*W*) among the rankings of species per year (Dugan and Livingston 1982). The coefficient of concordance for the East Kleinemonde Estuary (0.57) indicates a 57% concordance among the rankings of the top 8 marine species, which were caught consistently each year, across the eleven years of sampling. This indicates that despite interannual changes in species richness, abundance, species composition and size composition the dominant assemblages maintain a degree of stability. Dugan and Livingston (1982) recorded a concordance of 0.61 among the rankings of invertebrate species in Apalachee Bay, Florida. Similarly, although individual fish species in Apalachicola Bay, Florida (Livingston *et al.* 1976) and the Port River-Barker Inlet, Australia (Jackson and Jones 1999) undergo considerable annual fluctuations, percentage representation of the dominant species remained relatively stable.

Total CPUE of marine species varied considerably per year, with peak CPUE recorded in 1998 and 2003. The variability in total CPUE was attributed to extreme changes in the annual CPUE of individual species. In large permanently open estuaries in the northern hemisphere, the strength of recruitment pulses for different marine species varies markedly from year to year. Furthermore, annual recruitment strength often differs among species (Philippart *et al.* 1996, Potter *et al.* 1997, 2001). This has been related to fluctuating environmental conditions in the estuarine and marine environments that influence reproductive success, larval survival and efficiency of larval transport mechanisms (Potter *et al.* 1997). Poizat *et al.* (2004) found that in the temporarily open/closed Vaccarés Lagoon (southern France) the annual abundance of marine species depended on recruitment success, which is in turn affected by limited and temporally variable mouth opening events.

Although numerous authors have suggested that the timing, frequency and duration of mouth opening events affect species composition, particularly of marine species (Wallace and van der Elst 1975, Beckley 1984, Kok and Whitfield 1986, Young *et al.*

1997, Griffiths 1998), there have been few attempts to quantify this. This study has shown that in the East Kleinemonde Estuary the timing of mouth opening had a significant affect on species composition. This is evident in the grouping of years by nMDS into two distinct groups. In years following mouth opening events in spring more species were recorded than in years following no mouth opening events in spring. As a result, the dominance of species such as *Rhabdosargus holubi* was slightly reduced in the 'spring' years.

There was also an increase in interannual community stability (IMD) and seriation (IMS) from the 'other' years to the 'spring' years. A higher value for Kendall's coefficient of stability (*W*) was also recorded between 2001 and 2005. Periods of both stability and instability were reported for the Tees Bay and Estuary in the North Sea, although this was attributed to environmental deterioration (Warwick *et al*. 2002).

In the East Kleinemonde Estuary, the predominance of spring opening events between 2001 and 2005 probably allowed for the regular recruitment of marine species into the estuary, many of which start entering Cape estuaries in late winter (August), with peak recruitment occurring during spring (September to November) (Whitfield 1998). Mean annual CPUE for species that recruit predominantly in spring (such as *Liza tricuspidens, Myxus capensis, Mugil cephalus, Pomadasys commersonnii* and *Lithognathus lithognathus*) were higher in 'spring' years. Species such as *Rhabdosargus holubi*, *Monodactylus falciformis* and *Mugil cephalus*, which are known to recruit during both overwash and open mouth conditions (Cowley *et al.* 2001), were recorded fairly evenly in both 'spring' and 'other' years, while *Liza richardsonii* that has been recorded entering Western Cape estuaries throughout the year (Bennett 1989, Whitfield and Kok 1992) was recorded in greater numbers in 'other' years.

Timing of mouth opening had little impact on the numbers of species and individuals recorded in three small temporarily open/closed estuaries in south-eastern Australia (Griffiths and West 1999). However, in south-eastern Australia there is considerable variability in the timing of spawning, recruitment and settlement of many estuary-associated marine species. Estuary openings during this wide recruitment period may result in increased abundances of juvenile marine fish (Griffiths and West 1999).

Many authors have suggested that the number of marine species and individuals likely to enter an estuary will increase with the duration of mouth opening and the frequency of estuary openings (e.g. Potter *et al.* 1993, Young *et al.* 1997, Griffiths and West 1999). However, duration and frequency of mouth opening within a particular season appeared to have little impact on species composition in the East Kleinemonde Estuary. The 1997 sampling period followed a three-day mouth opening event in the spring of 1996 and this year grouped together with the 2003 sampling period, prior to which the estuary had opened for two extended periods (up to 26 days) in spring separated by only twelve days of estuary closure. Potter *et al.* (1993) also found that the number of marine species in the temporarily open/closed Wilson Inlet was actually lower when the mouth was open for extended periods. This was attributed to the emigration of some species and a lack of compensating immigration.

Mouth state had a direct impact on the length frequencies of certain species (e.g. *Rhabdosargus holubi*, *Monodactylus falciformis* and *Lithognathus lithognathus*) in the East Kleinemonde Estuary. Average lengths of these species were highest in 2001, following an extended closed period, which prevented the return migration of adolescent or sexually mature fish to sea. Mouth opening had little effect on the size composition of mugilid species, which occur in estuaries as both juveniles and adults.

According to Livingston (1997) trophic organization is key to an understanding of fish distribution in space and time. Livingston (*op. cit.*) found that although the food web of the Apalachicola Estuary in Florida is relatively stable, periodic peak flows and droughts were important in altering patterns of individual fish abundance and biomass. Herbivore/omnivore abundance increased during the first year of a drought because of increased light penetration and subsequent increased primary production caused by low river flow. In the East Kleinemonde Estuary the overall trophic structure was relatively stable with time, with no obvious groupings. However, abundance of vegetation-associated taxa was low in 2004 and 2005, while abundance of detritivores was high in 2004 and 2005.

Whitfield (1984) found that *Rhabdosargus holubi* and *Monodactylus falciformis* were the principal species associated with submerged macrophytes in the Swartvlei

Estuary, as both species are dependent on littoral plants and associated invertebrates for food. In the spring of 1979 the submerged macrophyte community (primarily *Potamogeton pectinatus*) in Swartvlei underwent senescence that lasted more than a decade and led to a 60% decline in primary production. The final collapse of the *Potamogeton* beds and the disappearance of filamentous algal mats led to a dramatic decline in biomass and condition of both *R. holubi* and *M. falciformis* (Whitfield 1984), while there was an increase in abundance and biomass of mugilid species associated with the bare littoral zone (Whitfield 1986).

This may explain the decrease in abundance of vegetation-associated taxa and the increase in abundance of detritovores in the East Kleinemonde Estuary in 2004 and 2005. A flash flood in May 2003 destroyed many of the macrophyte beds in the system, and they have yet to fully recover (Chapter 2). The numbers of *Monodactylus falciformis* caught in gill nets in 2004 and 2005 has also declined dramatically and there has been an increase in the numbers of *Argyrosomus japonicus* caught, which may be linked to this and other environmental factors. Livingston (1997) found that long-term changes in carnivore populations were complex with carnivores responding to biological rather than environmental factors.

Also of concern is the disappearance of *Syngnathus watermeyeri* from catches after the flash flood in 2003. This small estuarine species was first described in 1963 by JLB Smith and was found in the permanently open Bushmans and Kariega estuaries and the temporarily open/closed Kasuka Estuary in association with submerged aquatic macrophytes (Whitfield 1995). However, freshwater deprivation in the former two systems has led to the disappearance of the estuarine pipefish, which was declared provisionally extinct in 1993 (Whitfield and Bruton 1996). Three years later a healthy population was discovered in the East Kleinemonde Estuary, which has a relatively undisturbed catchment and at the time extensive aquatic macrophyte beds (Cowley 1998).

Two estuarine-spawning species, *Gilchristella aestuaria* and *Atherina breviceps* consistently dominated small mesh seine net catches each year. Cowley and Whitfield (2001b, 2002) used seine nets (density extrapolation) and mark-recapture techniques to estimate fish population sizes in the East Kleinemonde Estuary and found that the total fish population was numerically dominated by *G. aestuaria* (47.4%) and *A. breviceps* (22.3%). This is fairly typical of warm-temperate temporarily open/closed estuaries in South Africa, where these two species dominate catches numerically (Dundas 1994, Vorwerk *et al.* 2001).

Gilchristella aestuaria comprised by far the greatest proportion of the catch (94%) taken in the small mesh seine net in 2005. Similarly, the highest total CPUE was recorded in 2005 and this was largely a result of the peak in CPUE of 1662 fish per haul recorded for *G. aestuaria.* The highest rainfall recorded during the 11-year study fell between December 2004 and December 2005, with 1436 mm of rain recorded in this period and may account for the high numbers of *G. aestuaria*. Freshwater input into estuaries significantly boosts nutrient input and subsequently promotes primary and secondary production, especially the planktonic food chain, which in turn would have a beneficial effect on planktivorous *G. aestuaria* stocks (Martin *et al*. 1992, Strydom *et al*. 2002).

The average length of *Gilchristella aestuaria* (38 mm SL) and *Atherina breviceps* caught (43 mm SL) was also highest in 2005. These lengths correspond to fish one year or older (Talbot 1982, Ratte 1989). Larvae and early juvenile fish may have been lost due to flushing of fish out of the estuary, thus accounting for the dominance of adults in the overall catch for these species. Strydom *et al.* (2002) attributed the absence of young *G. aestuaria* in the water column of the Great Fish River during periods of high flow to flushing of larval fish out of the estuary.

This study has highlighted the importance of long-term studies to understanding community changes in estuaries that are caused by local or global environmental variations. Although individual species showed large interannual variations in abundance, driven primarily by changing environmental conditions, the basic community structure remained relatively stable. Changes in marine fish community structure were driven primarily by mouth state, while individual estuarine species responded to changes in riverine input arising from catchment rainfall events. There has also been a significant increase in species richness, driven primarily by the increase in tropical species since 2002. This highlights how longer-term climatic trends, such as global warming may eventually result in a restructuring of estuarine fish assemblages.

CHAPTER 4

LONG-TERM TRENDS IN RECRUITMENT, ABUNDANCE AND RESIDENCY OF JUVENILE *RHABDOSARGUS HOLUBI* AND *LITHOGNATHUS LITHOGNATHUS* IN THE EAST KLEINEMONDE ESTUARY

INTRODUCTION

Amongst the estuary-associated species, the most common life-history pattern is spawning in the nearshore marine environment, followed by immigration of larvae, postflexion larvae or small juveniles into estuaries. Juveniles remain in estuaries for some time (1-3 years) before returning to sea prior to the onset of maturity (e.g. Day *et al.* 1989, Wallace *et al.* 1984, Robertson and Duke 1990, Whitfield 1990, 1999). Of the 142 estuary-associated fish taxa, 37 (26%) are entirely dependent on estuaries during the juvenile phase of their life cycle for survival (Whitfield 1994b).

The interaction of life-history parameters and behavioural characteristics of individual species may have a strong influence on the response of that species to changing environmental parameters. In order to manage and protect estuarine fish stocks adequately, it is important to understand the factors responsible for controlling long-term fluctuations in targeted taxa (Kupschus and Tremain 2001, Power and Attrill 2002, 2003). However, changes in the long-term status and biology of many estuary-associated species are not known because there are complex factors influencing their status and many are not of commercial importance (Power and Attrill 2003). Where studies have been conducted they are relatively short in duration and many have focussed on factors affecting species in permanently open estuaries, resulting in a lack of useful management information for estuaries that have a closed phase (Day and Grindley 1981, Kok and Whitfield 1986, Griffiths and West 1999, Cowley and Whitfield 2001a).

Two estuary-associated marine species, for which there is little published long-term data, are the Cape stumpnose *Rhabdosargus holubi* and the white steenbras *Lithognathus lithognathus*. These two members of the sparid family are endemic to southern Africa and are considered to be entirely dependent on estuarine habitats for at least the first year of life (Whitfield 1994b). However, a number of aspects of the biology and life-history of these two species are very different which in turn affects their response to fluctuations in environmental variables within estuaries.

This chapter focuses on the variation in the use of a temporarily open/closed estuary by juvenile *Rhabdosargus holubi* and *Lithognathus lithognathus*. Data are presented on long-term changes in the timing of recruitment, the period of residence, growth and habitat use while in the estuarine environment. It is hypothesised that these two species will have different strategies in terms of recruitment, which will affect their abundance in TOCEs.

METHODS

Between December 1994 and July 2006 the ichthyofauna of the East Kleinemonde Estuary was sampled using a variety of gear types (a small mesh seine net, a large mesh seine net and a fleet of gill nets). Data from 2006 have been included because it contributes to the size cohort analysis. Details of the methods used to record environmental variables and capture fish are given in Chapters two and three.

Size-frequency data presented are based on captures made with the large mesh seine net and gill nets. Information on age-at-length was obtained from Beckley (1984) for *Rhabdosargus holubi* and from Bennett (1993a) for *Lithognathus lithognathus*. Abundance estimates refer to the catch per seine net haul. Length-frequency histograms, based on pooled data from both net types, were plotted for each sampling date. Size classes within the population were determined using modal size class progression analysis (NORMSEP method) in the FiSAT stock assessment package. Using this method, different cohorts within the bi-annual size-frequency distribution data could be identified and a mean and standard deviation derived. Estimates of growth, recruitment and residency period were obtained by plotting the mean cohort length in the biannual samples for all 0+ fish and where possible also the 1+, 2+, 3+ and 4+ year classes.

Because sampling was undertaken twice a year instead of monthly, it was difficult to follow cohorts, and calculated growth curves were therefore fitted to the data. For *Rhabdosargus holubi*, a monthly growth increment of 8 mm has been estimated in KwaZulu-Natal estuaries (Wallace and van der Elst 1975) and the Knysna (Whitfield and Kok 1992) and Sundays estuaries (Beckley 1984), with juveniles growing between 90 mm and 100 mm SL during the first year (Wallace and van der Elst 1975, Beckley 1984, Whitfield and Kok 1992). Similarly, Cowley (1998) estimated a monthly growth increment of between 9.2 mm SL and 6.2 mm SL for *R. holubi* in the East Kleinemonde Estuary (average growth = 8 mm per month). Consequently growth of 8 mm/month was used to fit a growth curve to the bi-annual length frequency data. For *Lithognathus lithognathus* modal progressions in monthly samples of 0+ juveniles from the Knysna (Whitfield and Kok 1992), Sundays (Beckley 1984), Kleinmond and Palmiet (Bennett 1989) estuaries indicate growth rates of approximately 12–13 mm TL/month in the first year. This corresponds to a growth of approximately 10 mm SL/month. The length-age relationship of *Lithognathus lithognathus* based on otolith ring counts was determined by Bennett (1993a) and predicts a growth rate of approximately 6 mm SL per month from ages 1 to 4. Consequently, a growth curve with growth of 10 mm/month for the first year followed by 6 mm/month thereafter was fitted to the data.

As part of a long-term monitoring program, daily estuarine mouth state has been recorded since 1993 (Cowley *et al.* unpublished data; Appendix I). Recruitment opportunities for marine fish existed under three possible estuary mouth states; open, large overwash (>3 hours) and small overwash (3-6 hours) (after Bell *et al.* 2001), and were noted for each of the identifiable recruitment cohorts recorded during this study.

RESULTS

Rhabdosargus holubi

Abundance and length-frequency data

Rhabdosargus holubi was caught in both the large mesh seine net and the gill nets and comprised between 34% and 92% of the annual large mesh seine catch (Figure 3.6, Chapter 3) and between 3% and 30% of the annual gill net catch (Figure 3.13, Chapter

3). Mean annual catch per haul (CPUE) for *R. holubi* in the large mesh seine net varied considerably on an annual basis and was highest in 2003 with 264 fish per haul and lowest (fish per haul) in 1996 (Figure 4.1).

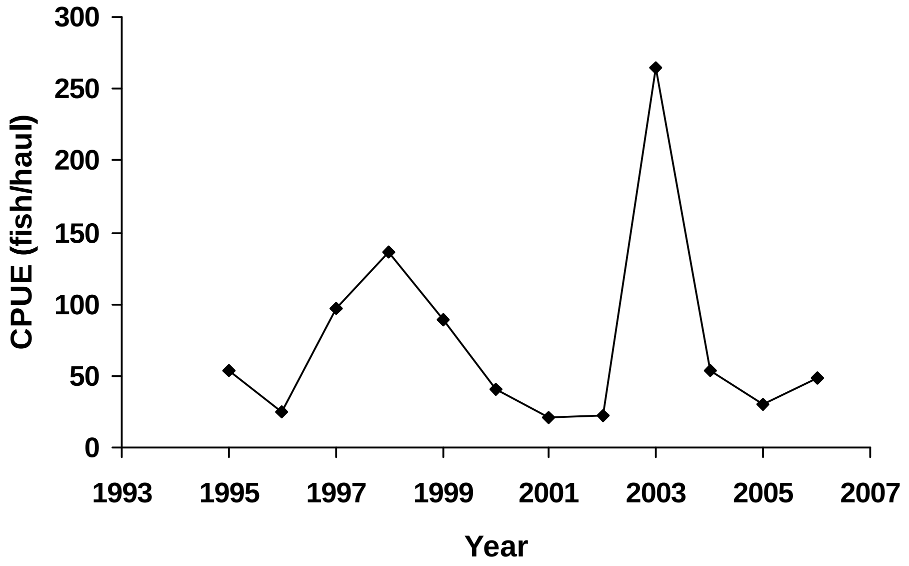


Figure 4.1. Mean annual CPUE for *Rhabdosargus holubi* caught in the East Kleinemonde Estuary between December 1994 and July 2006.

The pooled length-frequency data for *Rhabdosargus holubi* caught in gill nets and large mesh seine nets in the East Kleinemonde Estuary indicate that the population, in both summer and winter, consists predominantly of individuals belonging to the 0+ year class, ranging in size from 20 mm to 100 mm SL (Figure 4.2). The majority (80%) of individuals caught in the large mesh seine net were under one year old and probably recruited into the estuary in the year preceding sampling. The modal size class for *R. holubi* caught in the large mesh seine net was 70–80 mm SL. In contrast, the gill nets selected for larger individuals and the majority (84%) were over one year old with a modal size class of 100-110 mm SL (Figure 4.2).

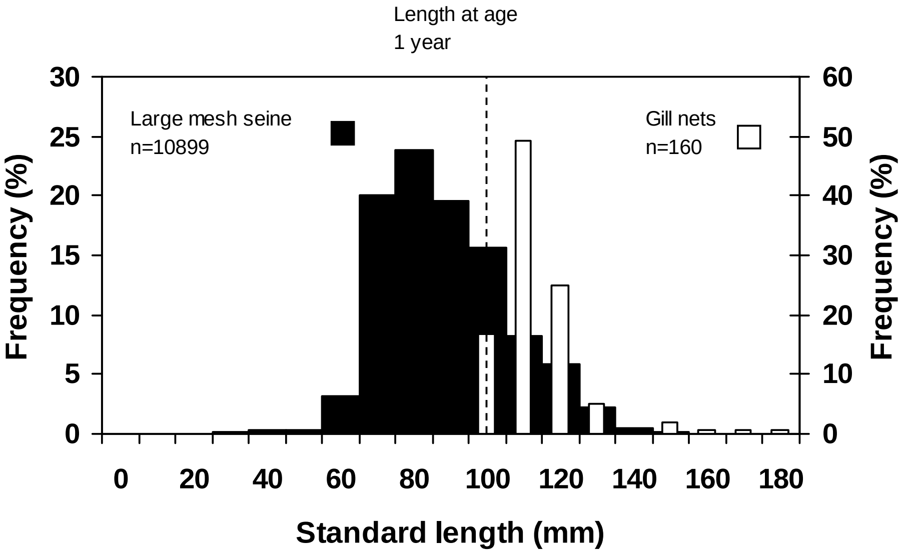


Figure 4.2. Length-frequency distributions of *Rhabdosargus holubi* caught in the large mesh seine net and gill nets in the East Kleinemonde Estuary between December 1994 and July 2006. The vertical dashed line represents the approximate size of one year old *R. holubi*.

Distribution

Table 4.1. Differences (*t*-test) between the abundance and lengths of *Rhabdosargus holubi* captured in each of the three reaches of the East Kleinemonde Estuary.

	Significance		
	Lower v. Middle	Lower v. Upper	Middle v. Upper
Abundance	*	**	*NS*
Lengths	***	***	***

NS = Not significant ($P > 0.05$)
* = Slightly significant ($P < 0.05$)
** = Significant ($P < 0.01$)
*** = Highly significant ($P < 0.001$)

Table 4.1 gives the results of a series of *t*-tests that were performed to assess possible differences between the abundance and lengths of *Rhabdosargus holubi* in each of the reaches. Juvenile *R. holubi* were captured in all regions of the estuary but in significantly higher numbers ($P < 0.05$) in the lower reaches (104 fish/haul) than in the middle (54 fish/haul) and upper reaches (46 fish/haul) (Figure 4.3). There was also significant variation in the lengths of *R. holubi* caught in the different reaches (*P* < 0.01, Figure 4.4), with the largest fish (160-170 mm SL) recorded in the lower reaches, declining to 150-160 mm SL maximum size in the middle reaches and 140-150 mm SL maximum size in the upper reaches (Figure 4.4).

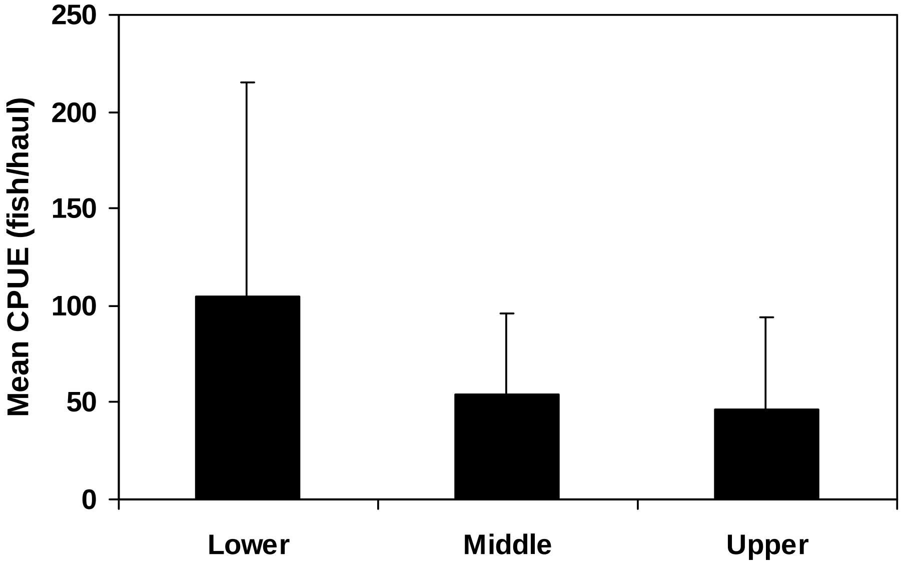


Figure 4.3. The mean CPUE (±SD) of *Rhabdosargus holubi* sampled with the large mesh seine net in the lower, middle and upper reaches of the East Kleinemonde Estuary.

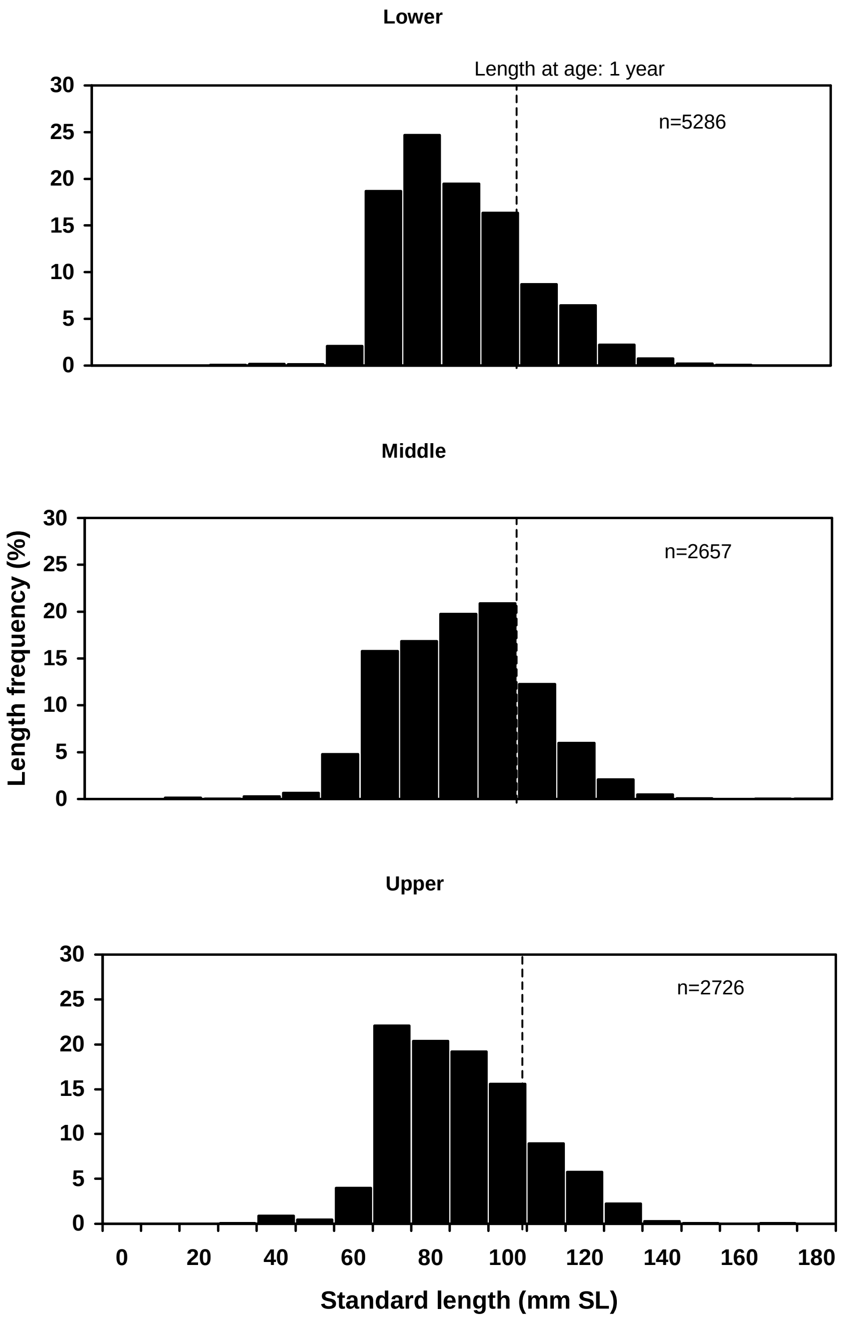


Figure 4.4. Size-frequency plots of *Rhabdosargus holubi* sampled with the large mesh seine net in the lower, middle and upper reaches of the East Kleinemonde Estuary. The vertical dashed line represents the approximate size of one-year old *R. holubi*.

Annual recruitment, growth and residency

The relatively constant presence of small individuals (<60 mm SL) in summer and winter indicated that recently spawned fish made use of many, if not all, mouth opening and/or marine overwash events to recruit into the estuary. Consequently, it was difficult to identify distinct cohorts and track the residency period of each recruitment cohort. At least seven 0+ cohorts could be identified from the biannual length-frequency histograms (Figure 4.5, Figure 4.6). These cohorts exist between July 1995 to November 1995 (Figure 4.7), November 1995 to June 1996 (Figure 4.8), July 1997 to February 1998 (Figure 4.9), January 1999 to June 1999 (Figure 4.10), August 2000 to July 2001 (Figure 4.11), February 2003 to June 2003 (Figure 4.12) and February 2006 to July 2006 (Figure 4.13). Details of the recruitment size and date, residency period, emigration (departure) size and date and estuary mouth state for each of the identified cohorts are summarised in Table 4.2.

Table 4.2. Recruitment, residency period and growth of *Rhabdosargus holubi* size cohorts in the East Kleinemonde Estuary between December 1994 and July 2006. The size at recruitment and departure is a calculated estimate based on extrapolation.

Cohort	**Date of recruitment**	**Size at recruitment (mm SL)**	**Date of departure**	**Size at departure (mm SL)**	**Residency period (months)**	**Estuary mouth state**	
						At recruitment	**At departure**
I	9/01/1995 – 28/07/1995	9	18/11/1996 – 20/11/1996	200	22	Small and large overwash	Open
II	23/08/1995	6	18/11/1996 – 20/11/1996	140	15	Small overwash	Open
III	01/01/1997 – 15/01/1997	10	03/12/1998	240	23	Small overwash	Open
IV	06/06/1998 – 07/06/1998	8	28/03/2000 – 16/04/2000	199	22	Small and large overwash	Open
V	28/03/2000 – 31/03/2000	28	1/08/2001 – 16/08/2001	180	16	Open	Open
			19/09/2001 – 30/09/2001	188	17		Open
			29/10/2001 – 30/10/2001	196	18		Open
			10/11/2001 – 30/11/2001	204	19		Open
			6/12/2001 – 10/12/2001	212	20		Open
VI	1/09/2002 – 30/09/2002	8	13/10/2003 – 04/11/2003	136	14	Open	Open
VII	20/07/2005 – 23/07/2005	6	4/08/2006 – 7/09/2006	120	12	Small and large overwash	Open

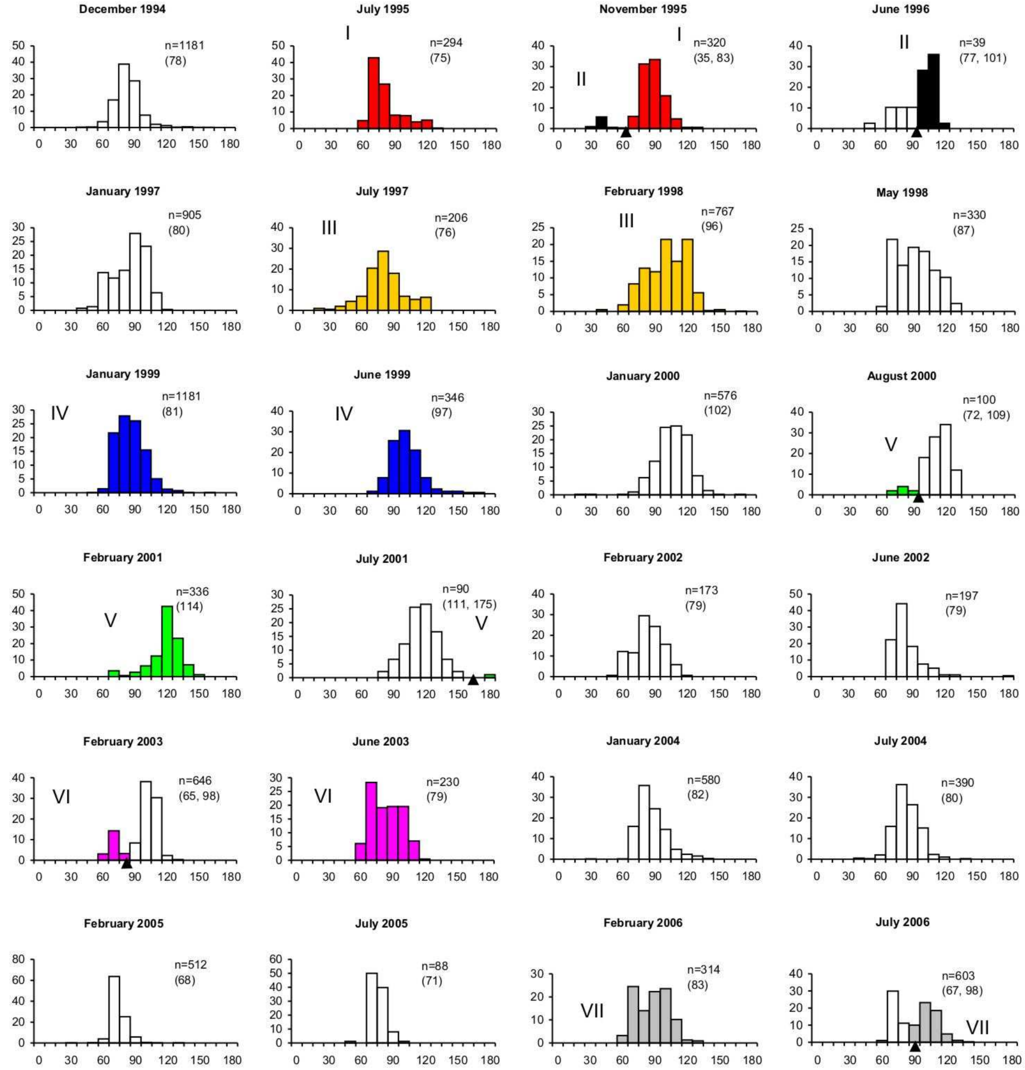


Figure 4.5. Bi-annual length-frequency distributions for *Rhabdosargus holubi* in the East Kleinemonde Estuary from December 1994 to July 2006. Cohort means are shown in brackets and a triangle (▲) marks the point of separation of two cohorts (determined using the NORMSEP method).

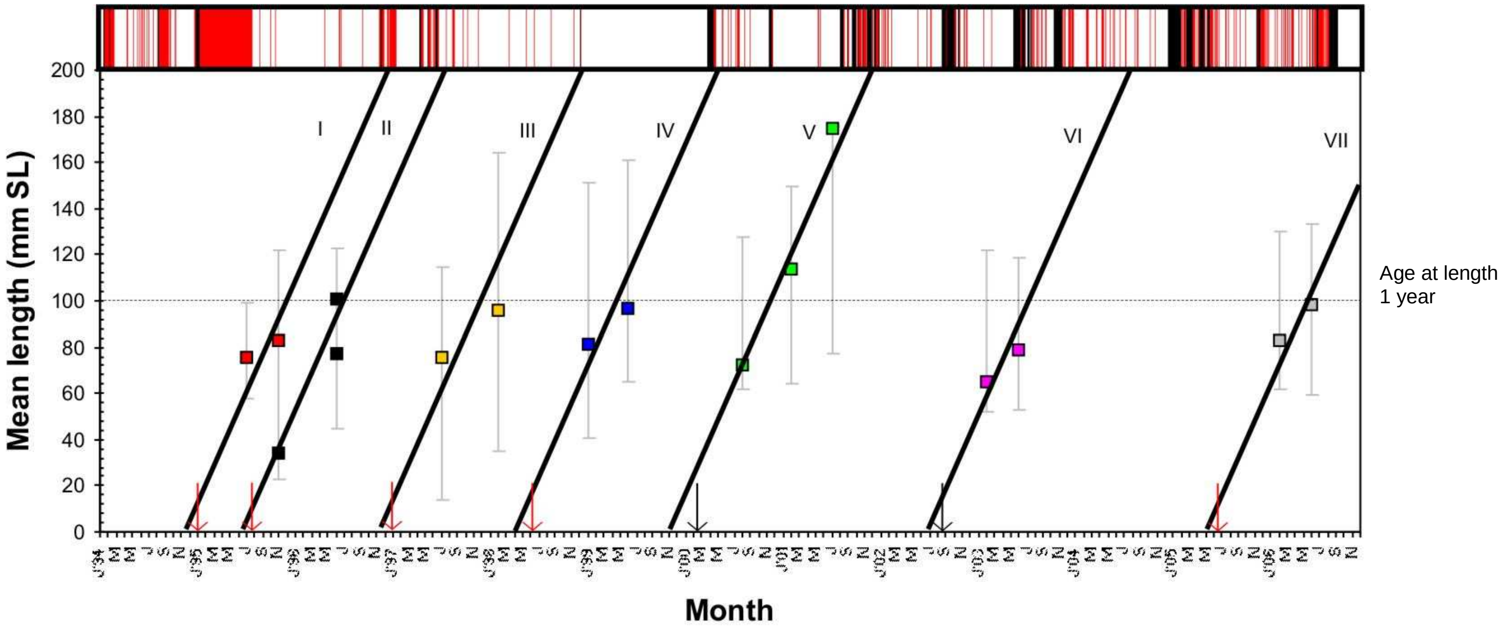


Figure 4.6. Mean lengths and size range of *Rhabdosargus holubi* cohorts captured in the East Kleinemonde Estuary from December 1994 to July 2006. Black bars and arrows indicate mouth opening events and red bars and arrows overwash events.

Cohort I

Cohort I probably entered the estuary at *ca*. 9 mm SL during a small overwash event (< 3 hours) in January 1995. Small and large overwash events were recorded from January to July 1995 providing an opportunity for recruitment. The cohort remained in the estuary for 22 months and left at a size of *ca*. 200 mm SL (growth = 191 mm SL) during a mouth opening event that was recorded in November 1996. This was the only mouth opening event recorded for 22 months, explaining the large size at departure (Figure 4.7).

Cohort II

This cohort entered the estuary at *ca.* 6 mm SL during a small overwash event in August 1995. The cohort remained in the estuary for just over a year (15 months) and left at a size of *ca.* 140 mm SL during a mouth opening event in November 1996. During this period growth of approximately 134 mm SL was estimated (Figure 4.8).

Cohort III

This cohort entered the estuary at a size of *ca*. 10 mm SL during a small overwash event in January 1997. The cohort remained in the estuary for approximately 23 months and left at a size of *ca*. 240 mm SL during a mouth opening event in December 1998. Again, this was the only mouth opening event recorded for 17 months explaining the large size at departure. A growth of *ca*. 230 mm SL was estimated (Figure 4.9).

Cohort IV

Cohort IV entered the estuary at a size of *ca*. 8 mm SL during small and large overwash events in June 1998. The cohort remained in the estuary for 22 months and left when the mouth opened between March and April 2000 at a size of *ca*. 199 mm SL. During this period a growth of *ca*. 191 mm SL was estimated (Figure 4.10).

Cohort V

This cohort entered the estuary during a mouth opening event in March 2000 at a size of *ca*. 28 mm SL. This was the first estuarine access opportunity recorded for 14 months (waiting time to EAO = 479 days, Figure 2.13; Chapter 2) accounting for the large size at recruitment. The cohort remained in the estuary for between 16 and 20 months and was estimated to leave at sizes ranging from 180 mm SL to 212 mm SL during mouth opening which took place from August to December 2001. Growth of between 152 mm SL and 184 mm SL was estimated (Figure 4.11).

Cohort VI

This cohort entered the estuary at a size of *ca*. 8 mm SL during a mouth opening event in September 2002 and remained in the estuary for 14 months. The cohort left the estuary during a mouth opening event in October and November 2003 at a size of *ca*. 136 mm SL. During this period a growth of *ca*. 128 mm SL was estimated (Figure 4.12).

Cohort VII

This cohort entered the estuary in July 2005 during small and large overwash events at a size of *ca*. 6 mm SL. The cohort remained in the estuary until the mouth opened in August and September 2006 and left at a size of *ca*. 120 mm SL. During the 12 months the cohort remained in the estuary a growth of *ca*. 114 mm SL was estimated (Figure 4.12).

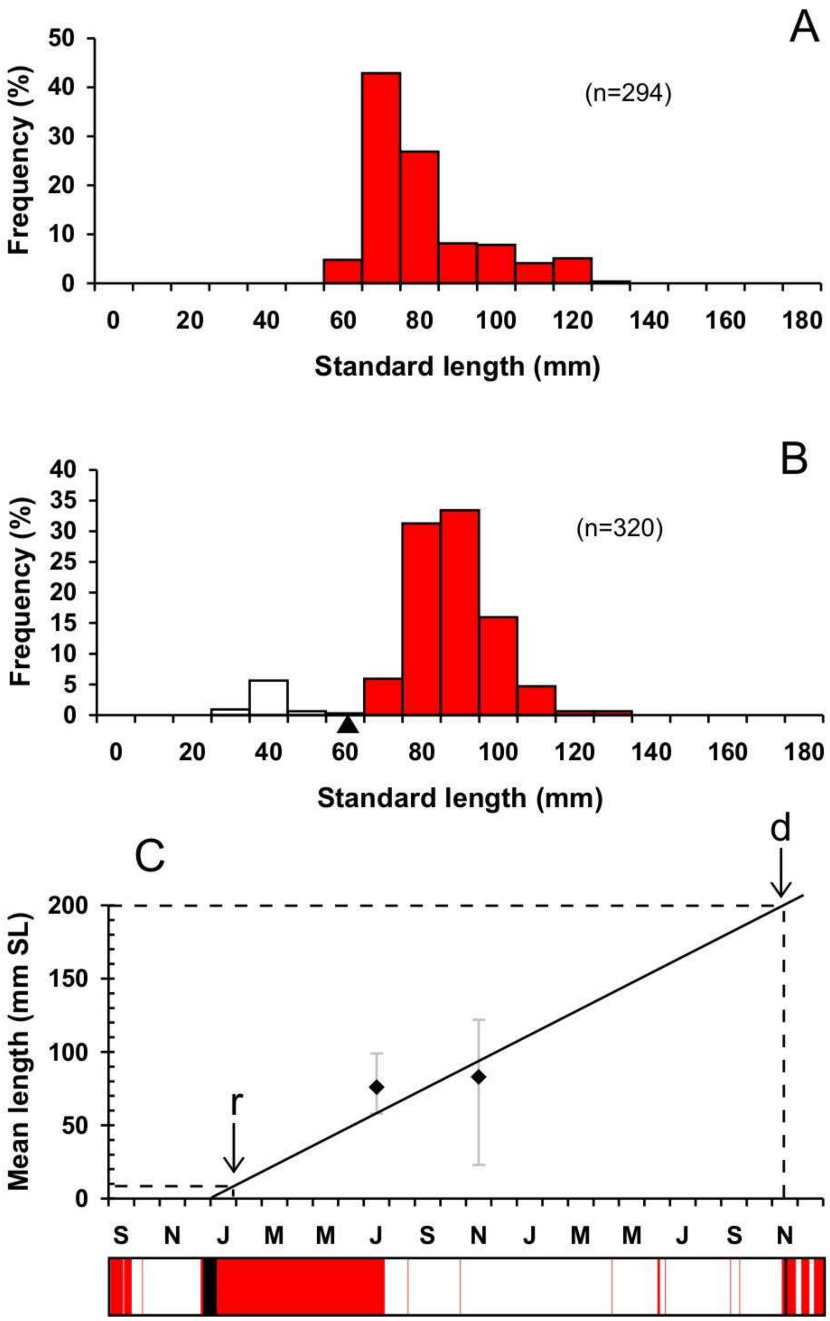


Figure 4.7. Length-frequency plots for *Rhabdosargus holubi* (cohort I) caught in July 1995 (A) and November 1995 (B) and mean length against time (C). A triangle (▲) marks the point of separation of the cohort (determined using the NORMSEP method). Dotted lines indicate the date and size at recruitment (**r**) and departure (**d**) and were linked to either mouth opening events (black bars) or overwash events (red bars).

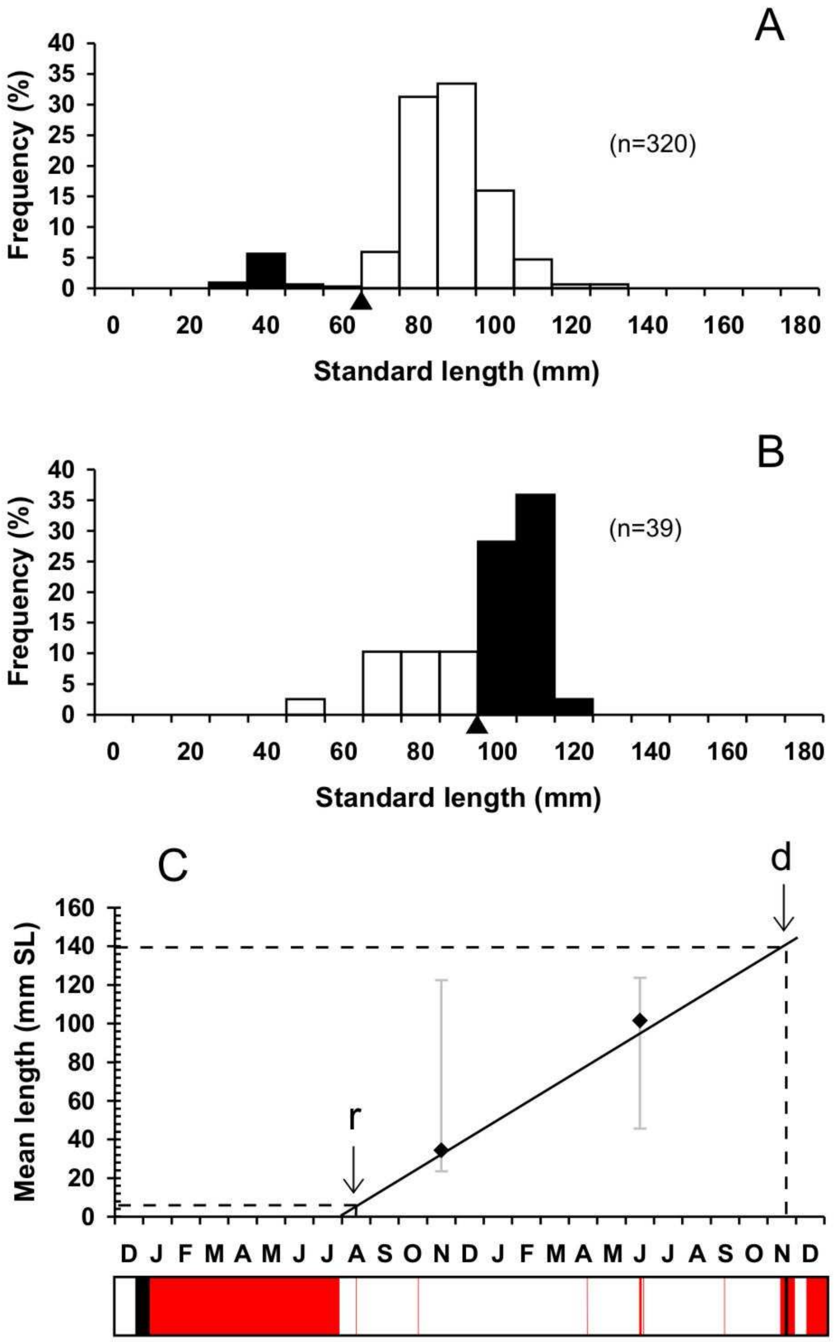


Figure 4.8. Length-frequency plots for *Rhabdosargus holubi* (cohort II) caught in November 1995 (A) and June 1996 (B) and mean length against time (C). A triangle (▲) marks the point of separation of the cohort (determined using the NORMSEP method). Dotted lines indicate the date and size at recruitment (**r**) and departure (**d**) and were linked to either mouth opening events (black bars) or overwash events (red bars).

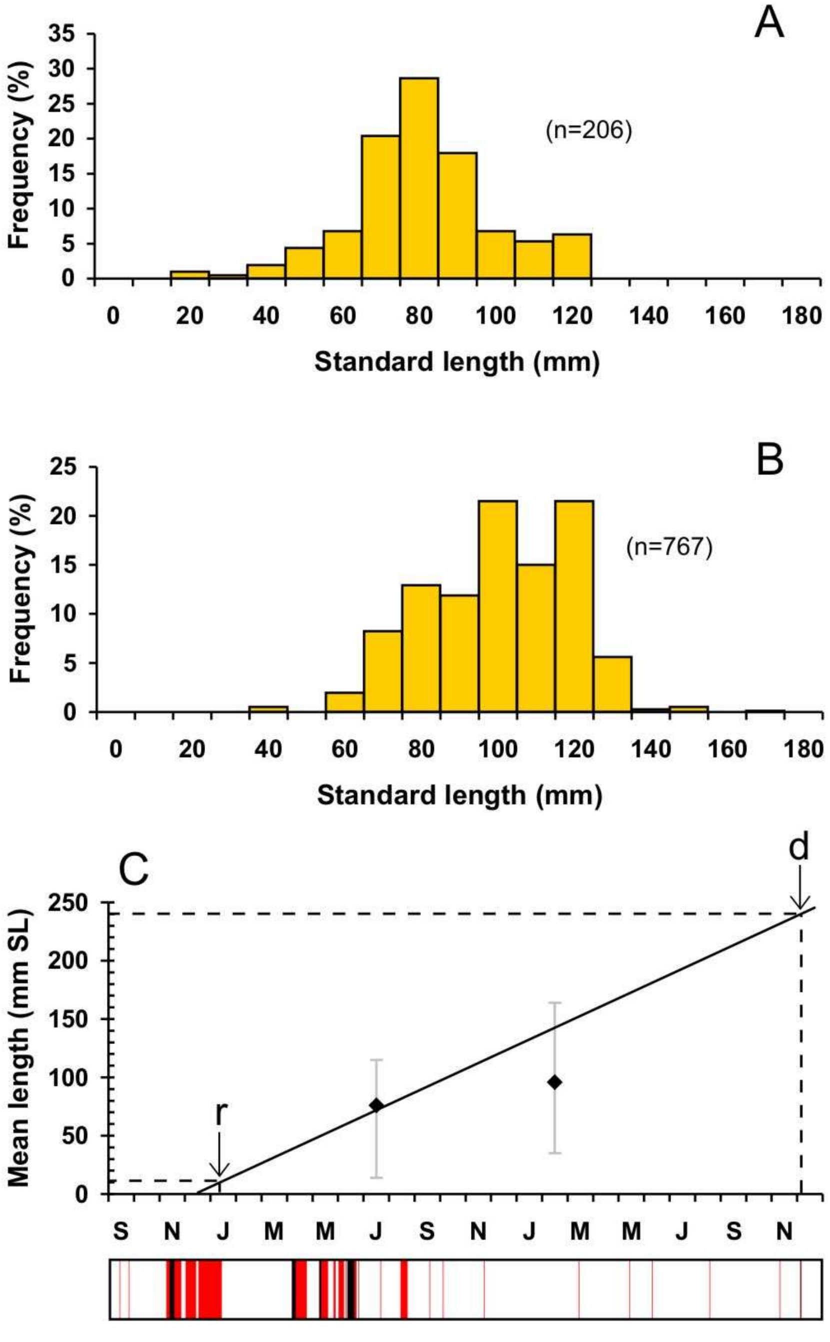


Figure 4.9. Length-frequency plots for *Rhabdosargus holubi* (cohort III) caught in July 1997 (A) and February 1998 (B) and mean length against time (C). Dotted lines indicate the date and size at recruitment (**r**) and departure (**d**) and were linked to either mouth opening events (black bars) or overwash events (red bars).

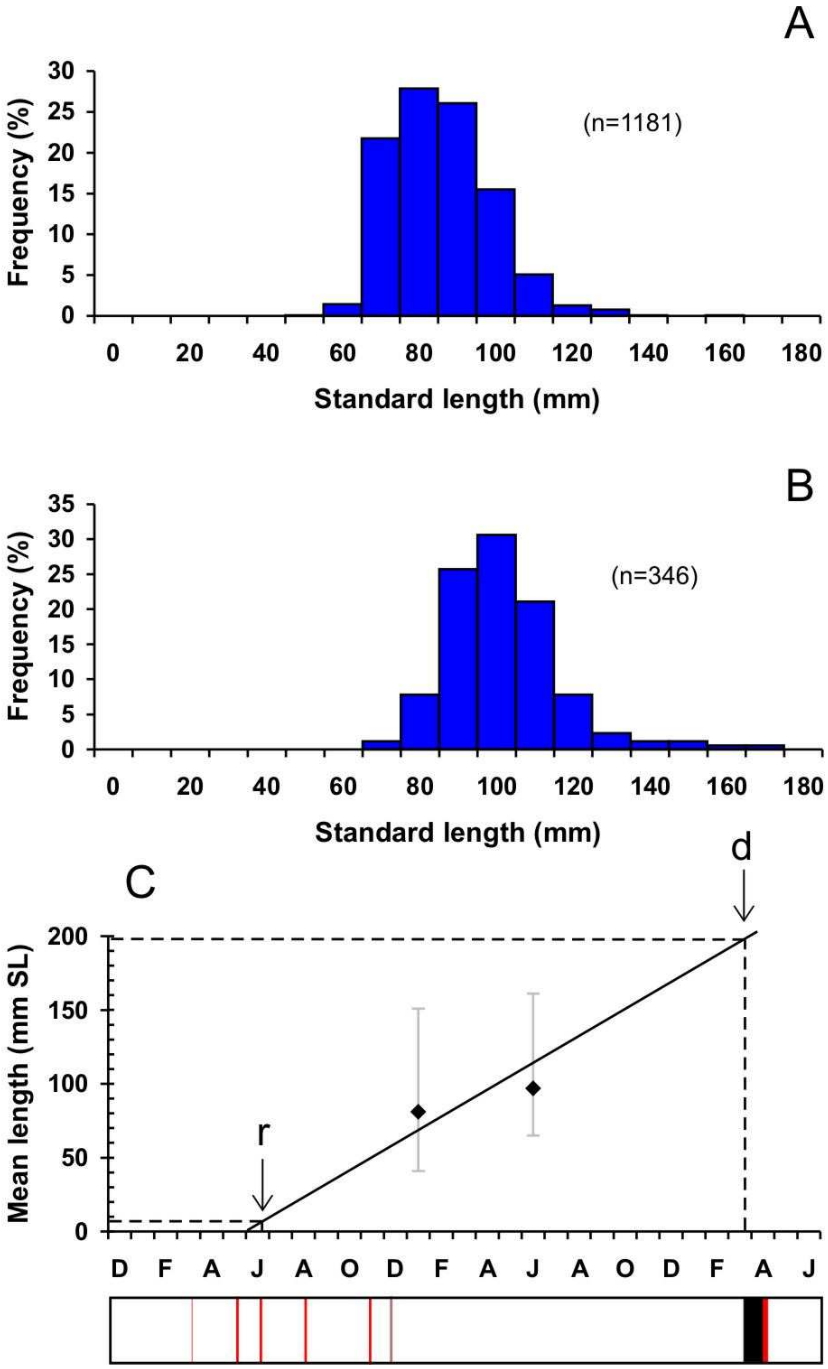


Figure 4.10. Length-frequency plots for *Rhabdosargus holubi* (cohort IV) caught in January 1999 (A) and June 1999 (B) and mean length against time (C). Dotted lines indicate the date and size at recruitment (**r**) and departure (**d**) and were linked to either mouth opening events (black bars) or overwash events (red bars).

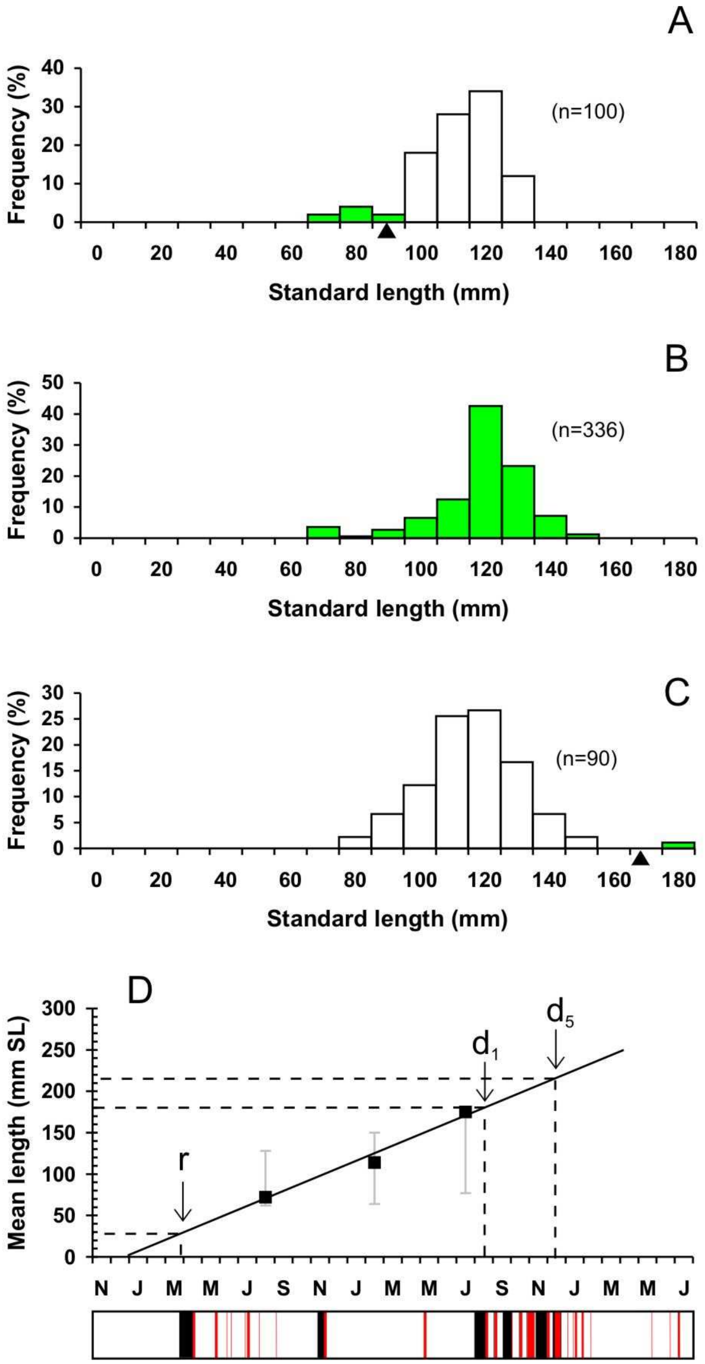


Figure 4.11. Length-frequency plots for *Rhabdosargus holubi* (cohort V) caught in August 2000 (A), February 2001 (B) and July 2001 (C) and mean length against time (D). A triangle (▲) marks the point of separation of the cohort (determined using the NORMSEP method). Dotted lines indicate the date and size at recruitment (**r**) and departure (**d**) and were linked to either mouth opening events (black bars) or overwash events (red bars).

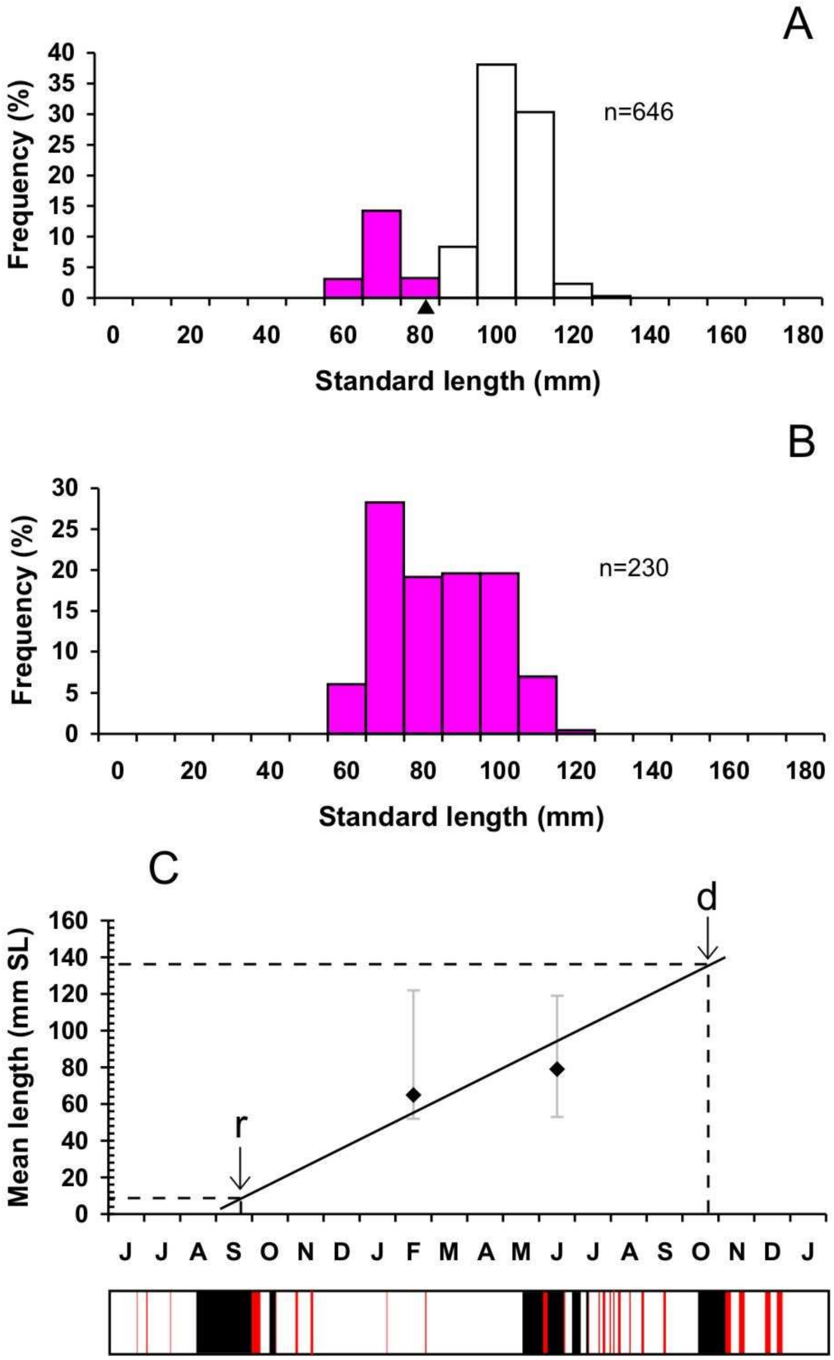


Figure 4.12. Length-frequency plots for *Rhabdosargus holubi* (cohort VI) caught in February 2003 (A) and June 2003 (B) and mean length against time (C). A triangle (▲) marks the point of separation of the cohort (determined using the NORMSEP method). Dotted lines indicate the date and size at recruitment (**r**) and departure (**d**) and were linked to either mouth opening events (black bars) or overwash events (red bars).

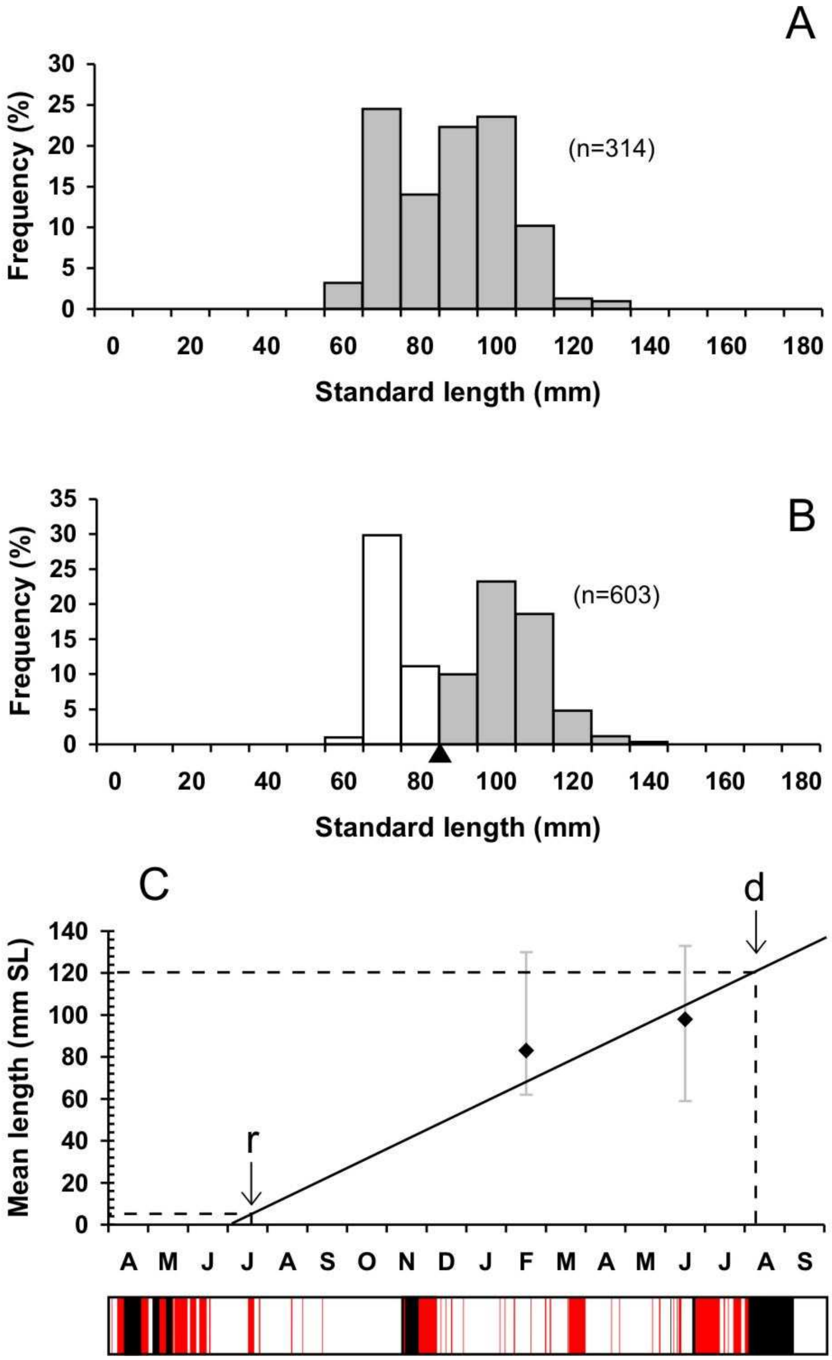


Figure 4.13. Length-frequency plots for *Rhabdosargus holubi* (cohort VII) caught in February 2006 (A) and July 2006 (B). A triangle (▲) marks the point of separation of the cohort (determined using the NORMSEP method). Dotted lines indicate the date and size at recruitment (**r**) and departure (**d**) and were linked to either mouth opening events (black bars) or overwash events (red bars).

Lithognathus lithognathus

Abundance and length-frequency data

Lithognathus lithognathus was caught in both the large mesh seine net and gill nets and comprised between 1% and 5% of annual large mesh seine net catches (Figure 3.6, chapter 3) and between 0% and 22% of annual gill net catches (Figure 3.13, chapter 3). CPUE for *L. lithognathus* caught in the large mesh seine net varied on an annual basis and was highest in 1997 (7.7 fish/haul) and lowest in 2002 (0.2 fish/haul) (Figure 4.14).

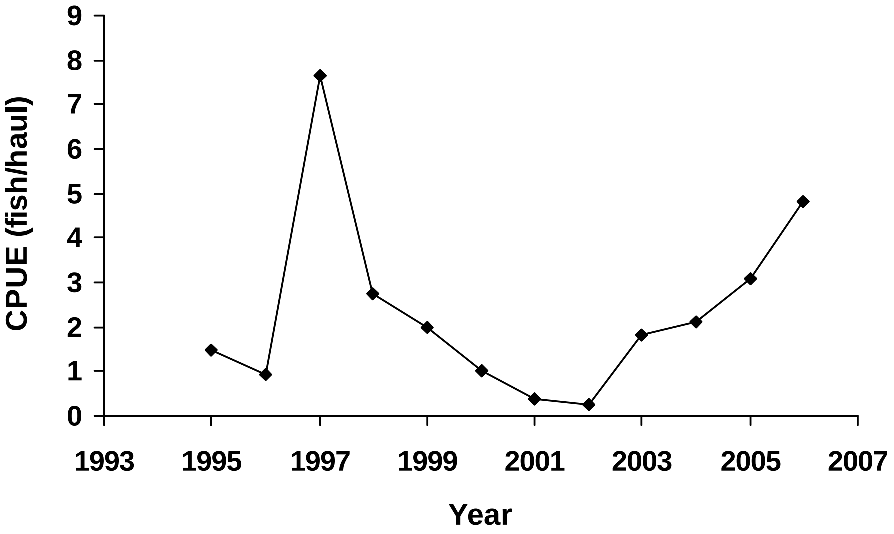


Figure 4.14. Mean annual CPUE for *Lithognathus lithognathus* caught in the East Kleinemonde Estuary between 1995 and 2006.

The majority of individuals caught in large mesh seine nets were in the 0+ and 1+ year classes, and exhibited a bimodal size class distribution. The gill nets targeted larger juveniles, the majority (95%) being older than 2 years, with a modal size class of 260-300 mm SL (Figure 4.15). The pooled length-frequency data from the seine and gill nets for *Lithognathus lithognathus* indicate that the population consists of individuals from 30 mm to 350 mm SL (Figure 4.15).

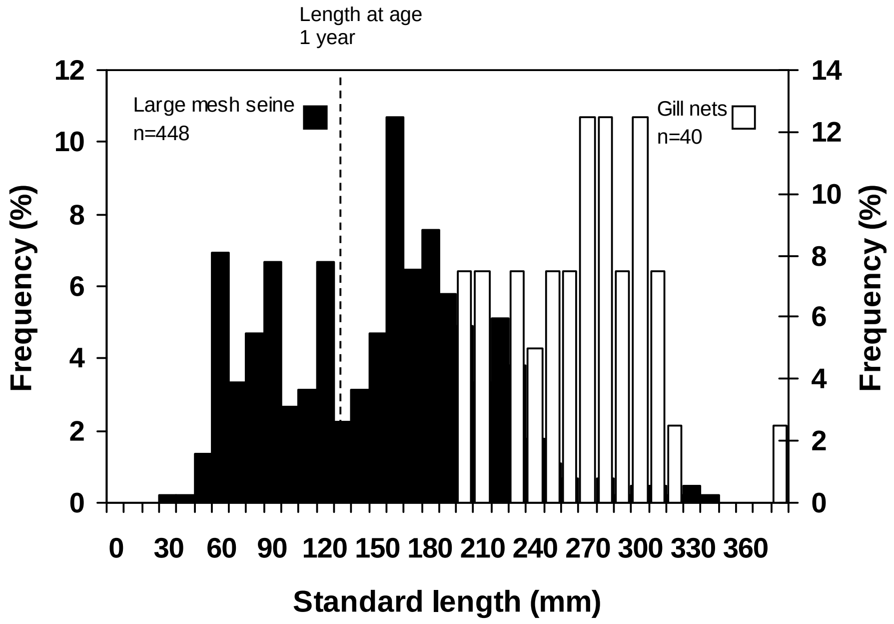


Figure 4.15. Length-frequency distributions of *Lithognathus lithognathus* caught in the large mesh seine net and gill nets in the East Kleinemonde Estuary between December 1994 and July 2006. The vertical dashed line represents the approximate size of one-year old *L. lithognathus.*

Distribution

Table 4.3. Differences (*t*-test) between the abundance and lengths of *Lithognathus lithognathus* captured in each of the three reaches of the East Kleinemonde Estuary.

	Significance		
	Lower v. Middle	Lower v. Upper	Middle v. Upper
Abundance	*NS*	*NS*	*NS*
Lengths	***	**	**

NS = Not significant ($P > 0.05$)
* = Slightly significant ($P < 0.05$)
** = Significant ($P < 0.01$)
*** = Highly significant ($P < 0.001$)

Table 4.3 gives the results of a series of *t*-tests that were performed to assess possible differences between the abundance and lengths of *Lithognathus lithognathus* in each of the reaches. Mean CPUE for *L. lithognathus* was higher in the lower reaches (5 fish/haul) than in the middle (1 fish/haul) and upper (1 fish/haul) reaches (Figure

4.16) although not significantly different (*P* > 0.05, Table 4.3). There was a significant difference in the modal lengths of individuals caught in the different reaches (*P* < 0.01, Figure 4.17). Individuals in the lower reaches showed a bimodal size distribution and were smaller in size (modal size = 50-60 mm SL and 150-160 mm SL) than individuals caught in the middle (modal size = 180-190 mm SL) and upper reaches (modal size = 160-170 mm SL).

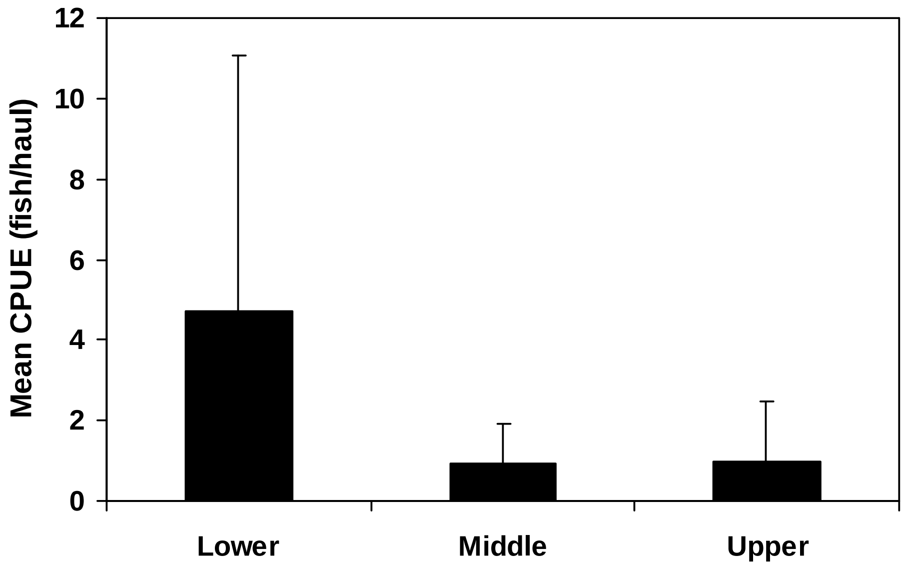


Figure 4.16. The mean CPUE (±SD) of *Lithognathus lithognathus* sampled with the large mesh seine net in the lower, middle and upper reaches of the East Kleinemonde Estuary.

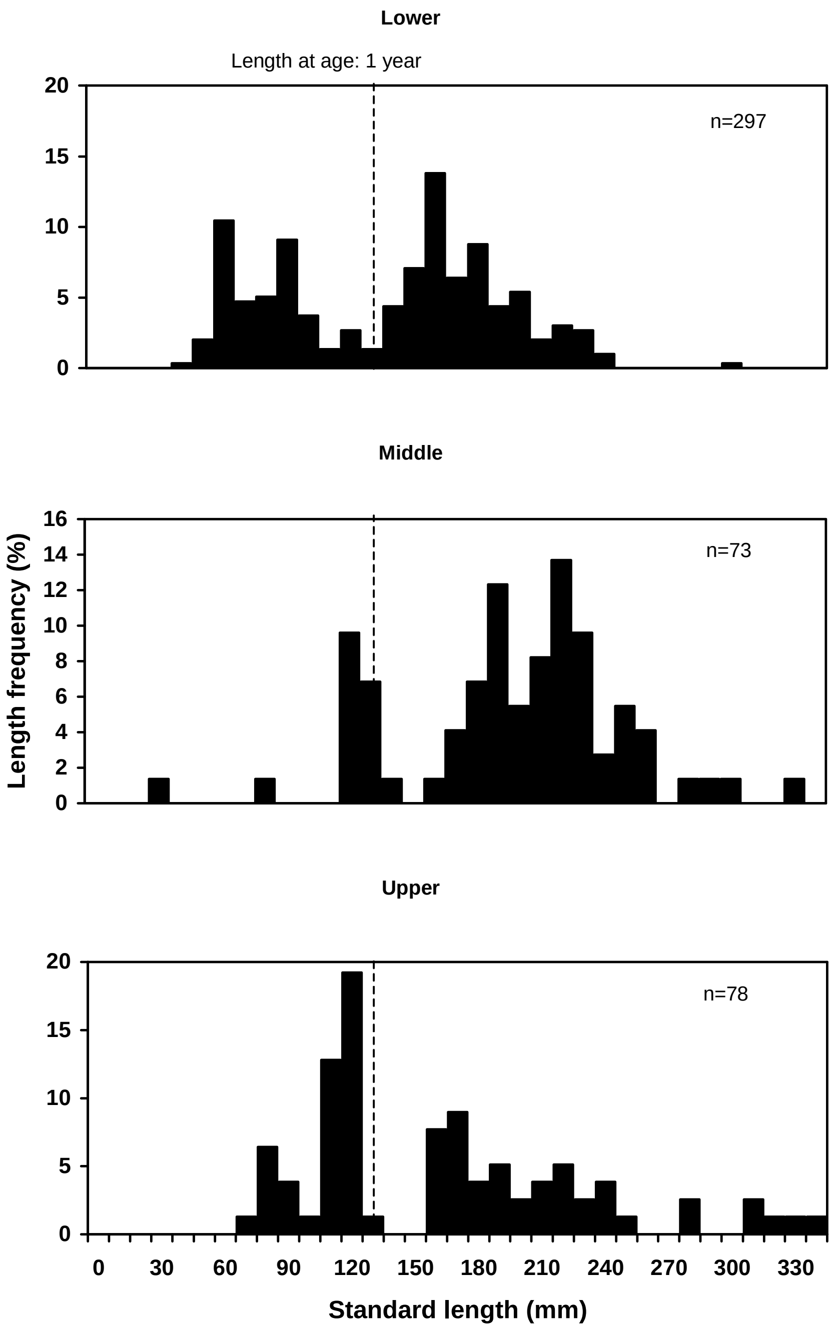


Figure 4.17. Size-frequency plots of *Lithognathus lihognathus* sampled with the large mesh seine net in the lower, middle and upper reaches of the East Kleinemonde Estuary. The vertical dashed line represents the approximate size of one-year old *L. lithognathus.*

Annual recruitment, growth and residency

A total of nine distinct cohorts were identified from the biannual length frequency histograms between 1994 and 2006 (Figure 4.18, Figure 4.19). Successful recruitment did not take place every year, for example no recruitment was recorded in 1997 and between 1999 and 2000. Recruitment into the estuary increased from 2002, when the yearly occurrence of spring openings allowed early juveniles to enter the estuary on an annual basis. Details of the recruitment size and date, residency period, departure size and date and estuary mouth state for each identified cohort are given in Table 4.4

Table 4.4. Recruitment, residency period and growth of *Lithognathus lithognathus* cohorts in the East Kleinemonde Estuary between December 1994 and July 2006. The size at recruitment and departure is a calculated estimate based on extrapolation.

Cohort	**Date of recruitment**	**Size at recruitment**	**Date of departure**	**Size at departure**	**Residency period (months)**	**Estuary mouth state**	
						At recruitment	**At departure**
I	25/09/1993 – 01/10/1993	35	18/11/1996 – 20/11/1996	305	38	Open	Open
II	23/08/1994 – 27/08/1994	15	18/11/1996 – 20/11/1996	210	27	Open	Open
III	27/12/1994 – 08/01/1995	15	03/12/1998	290	47	Open	Open
IV	18/11/1996 – 20/11/1996	20	17/11/2000 – 25/11/2000	330	48	Open	Open
V	3/12/1998	38	16/08/2002 – 30/09/2002	340	45	Open	Open
VI	16/08/2002 – 30/09/2002	35	23/12/2004 – 6/05/2005	210-225	28-32	Open	Open
VII	13/10/2003 – 4/11/2003	25	4/08/2006 – 7/09/2006	270	33	Open	Open
VIII	23/12/2004 – 28/01/2005	45	Still in system	-	-	Open	-
IX	8/11/2005 – 21/11/2005	40	Still in system	-	-	Open	-

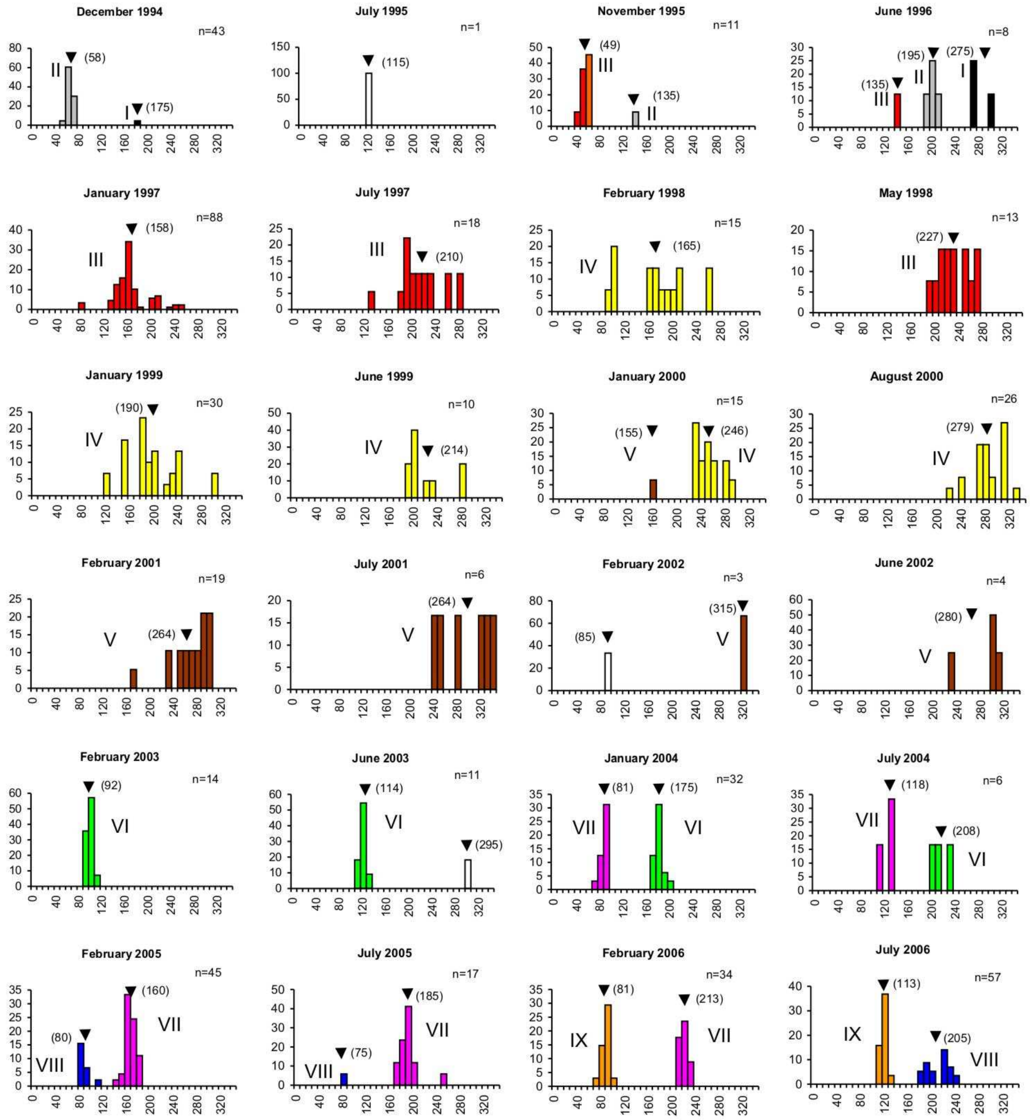


Figure 4.18. Bi-annual length-frequency distributions for *Lithognathus lithognathus* in the East Kleinemonde Estuary from December 1994 to July 2006. Cohort means are shown in brackets and a triangle (▲) marks the mean (determined using the NORMSEP method).

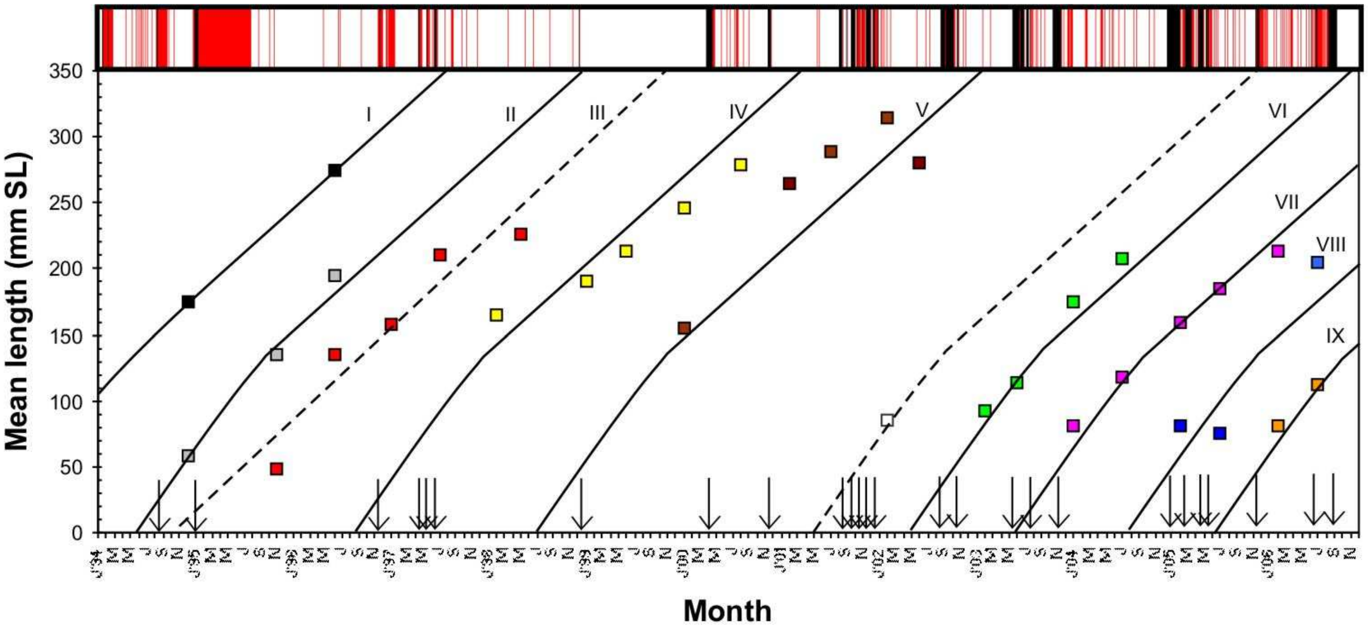


Figure 4.19. Mean lengths of *Lithognathus lithognathus* cohorts captured in the East Kleinemonde Estuary in the East Kleinemonde Estuary from December 1994 to July 2005. Black bars and arrows indicate mouth opening events and red bars overwash events.

Cohort I

Cohort I entered the estuary during open mouth conditions between September and October 1993 at a size of *ca*. 35 mm SL. The cohort remained in the estuary for 38 months leaving when the mouth opened in November 1996 at a size of *ca*. 305 mm SL. During this period a growth of 270 mm SL was estimated (Figure 4.20).

Cohort II

This cohort entered the estuary at a size of *ca*. 15 mm SL during a mouth opening event that took place in August 1994. The cohort remained in the estuary until the mouth opened in November 1996 (27 months) and left at a size of *ca*. 210 mm SL. During the 27 months of residency a growth of *ca*. 195 mm SL was estimated (Figure 4.21).

Cohort III

This cohort entered the estuary during a mouth opening event in December 1994 and January 1995 at a size of *ca*. 15 mm SL. During the 47 months the cohort remained in the estuary a growth of *ca*. 275 mm SL was estimated with individuals leaving at a size of *ca*. 290 mm SL. The cohort left the estuary when the mouth opened in December 1998 for a single day (Figure 4.22).

Cohort IV

Cohort IV entered the estuary at a size of *ca*. 20 mm SL during a mouth opening in November 1996 (Figure 4.23). Individuals remained in the estuary for 48 months and probably left during a mouth opening event in November 2000 at a size of *ca*. 330 mm SL (growth of 310 mm SL was estimated).

Cohort V

This cohort entered the estuary during a mouth opening event recorded on a single day in December 1998 at a size of *ca*. 38 mm SL. The cohort remained in the estuary for a period of 45 months leaving during an extended period of mouth opening between August and September 2002 at a size of *ca*. 340 mm SL. During this period a growth of 302 mm SL was estimated (Figure 4.24).

Cohort VI

One of the most easily traceable cohorts (cohort VI) entered the estuary during an extended period of mouth opening between August and September 2002 at a size of *ca*. 35 mm SL. Individuals remained in the estuary for between 28 months (2.4 years) and 32 months (3.2 years) and probably left the estuary during mouth opening events in December 2004 at a size of *ca*. 210 mm SL or in May 2005 at a size of *ca*. 225 mm SL. During their period in the estuary it is estimated that fish grew between 175 and 190 mm SL (Figure 4.25).

Cohort VII

This cohort entered the estuary when the mouth opened between October and November 2003 at a size of *ca*. 25 mm SL. Individuals left the estuary when the mouth opened between August and September 2006 (33 months) at a size of *ca*. 270 mm SL. During this period a growth of *ca*. 245 mm SL was estimated (Figure 4.26).

Cohort VIII

Cohort VIII entered the estuary at a size of *ca*. 45 mm SL during a mouth opening event in December 2004 and January 2005. The cohort does not appear to have left the estuary (Figure 4.27).

Cohort IX

This cohort entered the estuary at a size of *ca*. 40 mm SL in November 2005 when the estuary mouth opened and is still in the estuary (Figure 4.28).

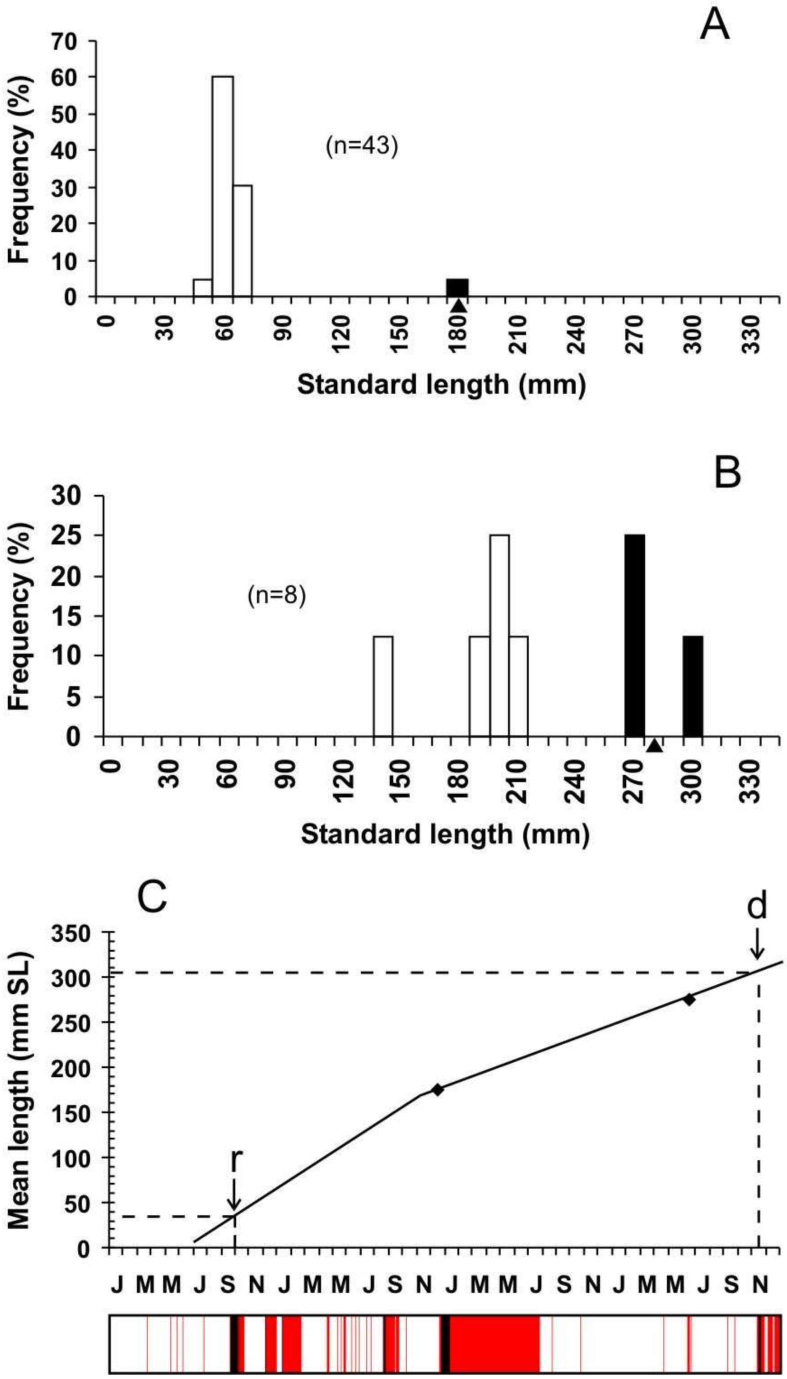


Figure 4.20. Length-frequency plots for *Lithognathus lithognathus* (cohort I) caught in December 1994 (A) and June 1996 (B) and mean length against time (C). A triangle (▲) marks the mean (determined using the NORMSEP method). Dotted lines indicate the date and size at recruitment (**r**) and departure (**d**) and were linked to either mouth opening events (black bars) or overwash events (red bars).

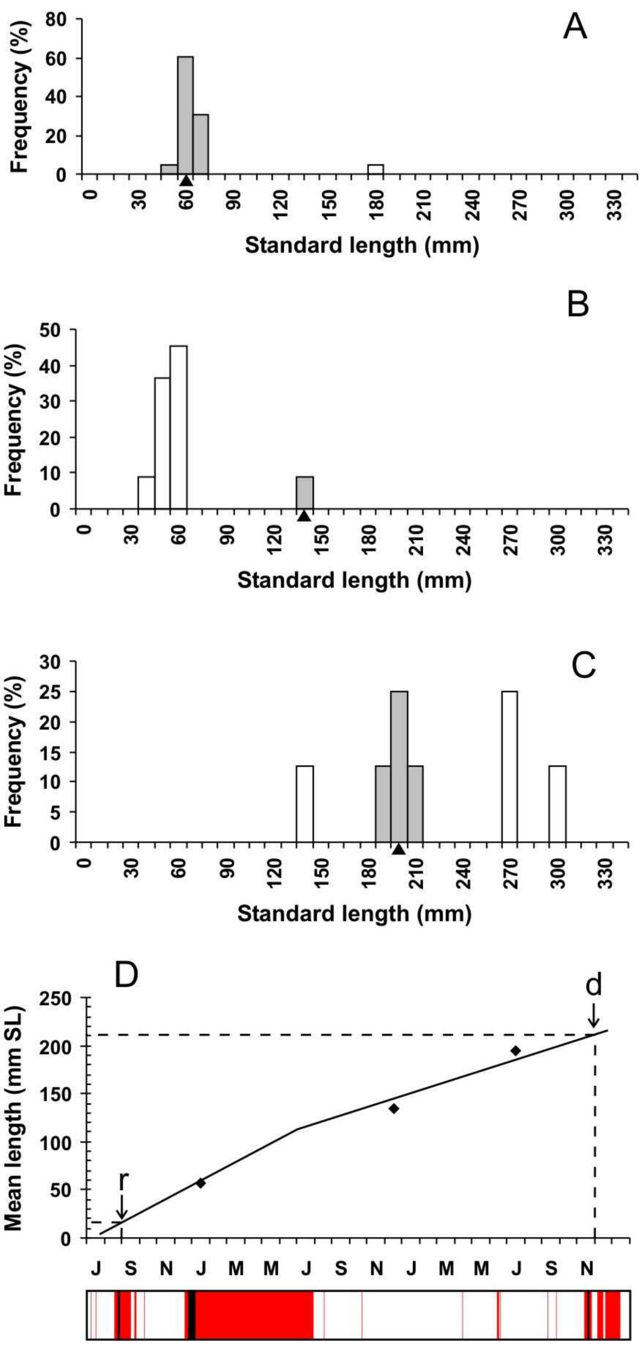


Figure 4.21. Length-frequency plots for *Lithognathus lithognathus* (cohort II) caught in December 1994 (A), November 1995 (B) and June 1996 (C) and mean length against time (D). A triangle (▲) marks the mean (determined using the NORMSEP method). Dotted lines indicate the date and size at recruitment (**r**) and departure (**d**) and were linked to either mouth opening events (black bars) or overwash events (red bars).

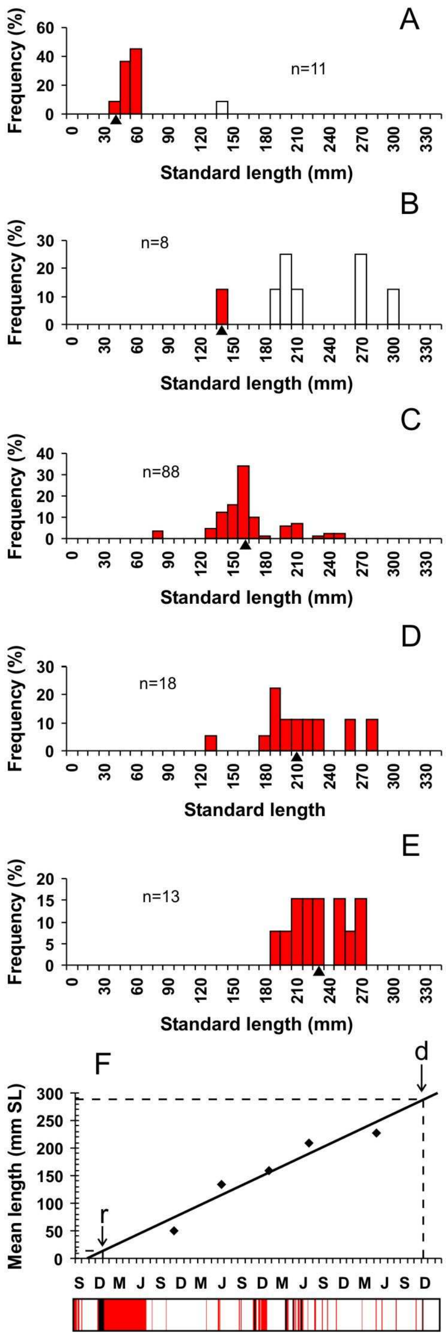


Figure 4.22. Length-frequency plots for *Lithognathus lithognathus* (cohort III) caught in November 1995 (A), June 1996 (B), January 1997 (C), July 1997 (D) and May 1998 (E) and mean length against time (F). A triangle (▲) marks the mean (determined using the NORMSEP method). Dotted lines indicate the date and size at recruitment (**r**) and departure (**d**) and were linked to either mouth opening events (black bars) or overwash events (red bars).

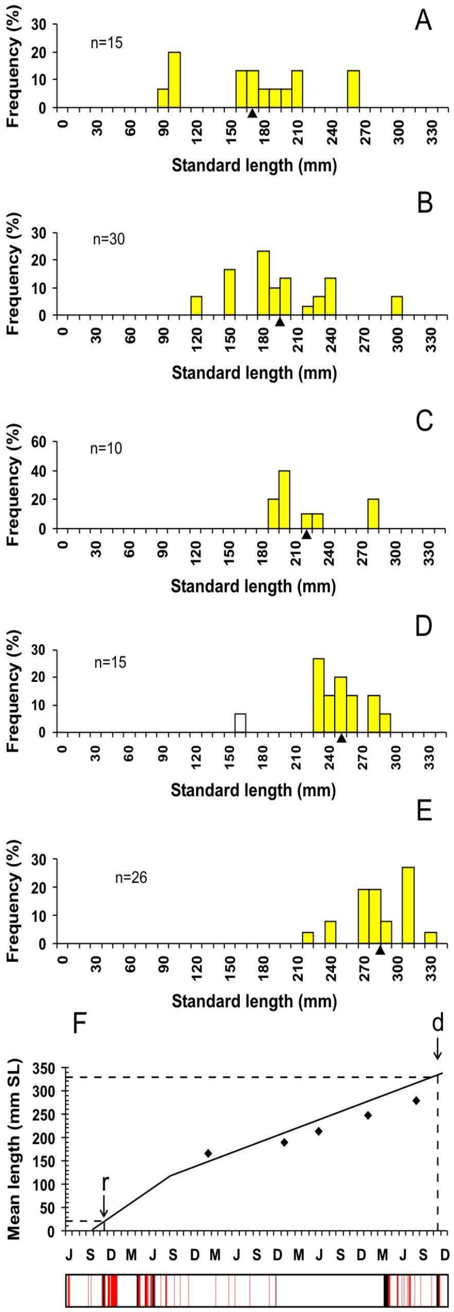


Figure 4.23. Length-frequency plots for *Lithognathus lithognathus* (cohort IV) caught in February 1998 (A), January 1999 (B), June 1999 (C), January 2000 (D) and August 2000 (E) and mean length against time (F). A triangle (▲) marks the mean (determined using the NORMSEP method). Dotted lines indicate the date and size at recruitment (**r**) and departure (**d**) and were linked to either mouth opening events (black bars) or overwash events (red bars).

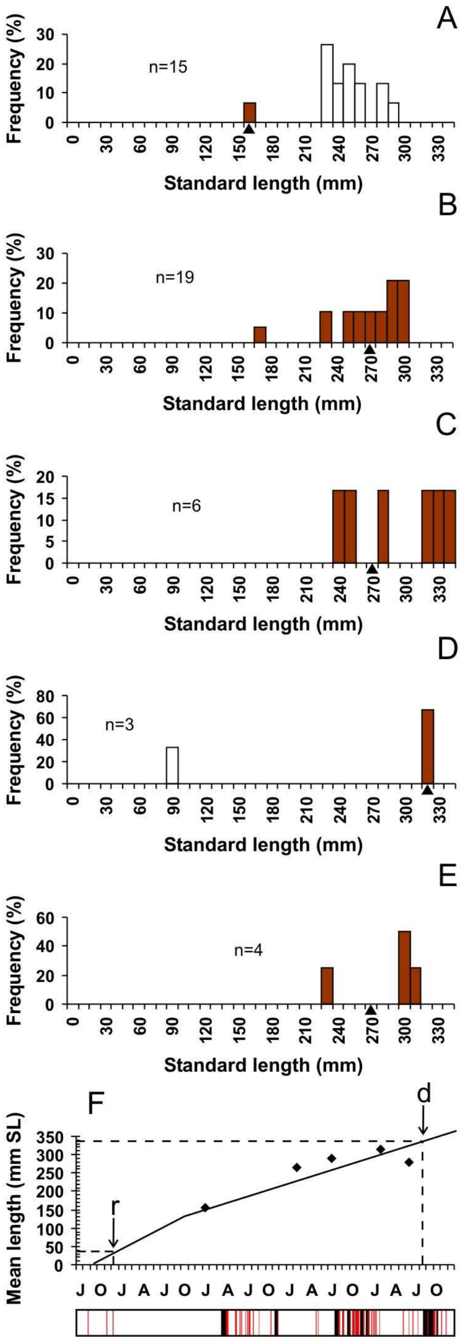


Figure 4.24. Length-frequency plots for *Lithognathus lithognathus* (cohort V) caught in January 2000 (A), February 2001 (B), July 2001 (C), February 2002 (D) and June 2002 (E) and mean length against time (F). A triangle (▲) marks the mean (determined using the NORMSEP method). Dotted lines indicate the date and size at recruitment (**r**) and departure (**d**) and were linked to either mouth opening events (black bars) or overwash events (red bars).

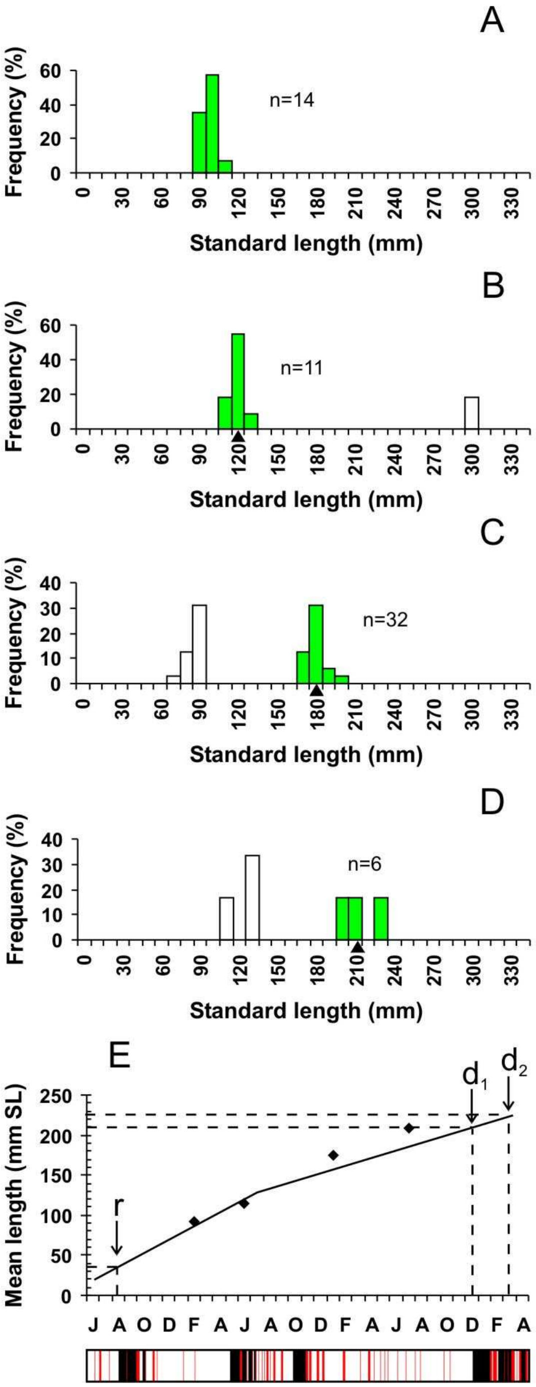


Figure 4.25. Length-frequency plots for *Lithognathus lithognathus* (cohort VI) caught in February 2003 (A), June 2003 (B), January 2004 (C) and July 2004 (D) and mean length against time (E). A triangle (▲) marks the mean (determined using the NORMSEP method). Dotted lines indicate the date and size at recruitment (**r**) and departure (**d**) and were linked to either mouth opening events (black bars) or overwash events (red bars).

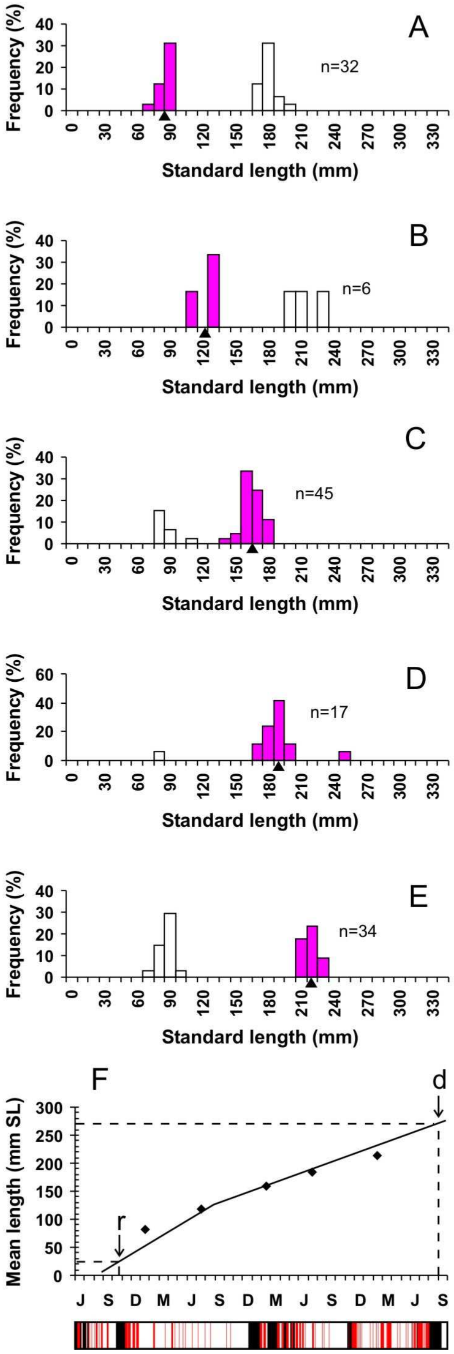


Figure 4.26. Length-frequency plots for *Lithognathus lithognathus* (cohort VII) caught in January 2004 (A), July 2004 (B), February 2005 (C), July 2005 (D) and February 2006 (E) and mean length against time (F). A triangle (▲) marks the mean (determined using the NORMSEP method). Dotted lines indicate the date and size at recruitment (**r**) and departure (**d**) and were linked to either mouth opening events (black bars) or overwash events (red bars).

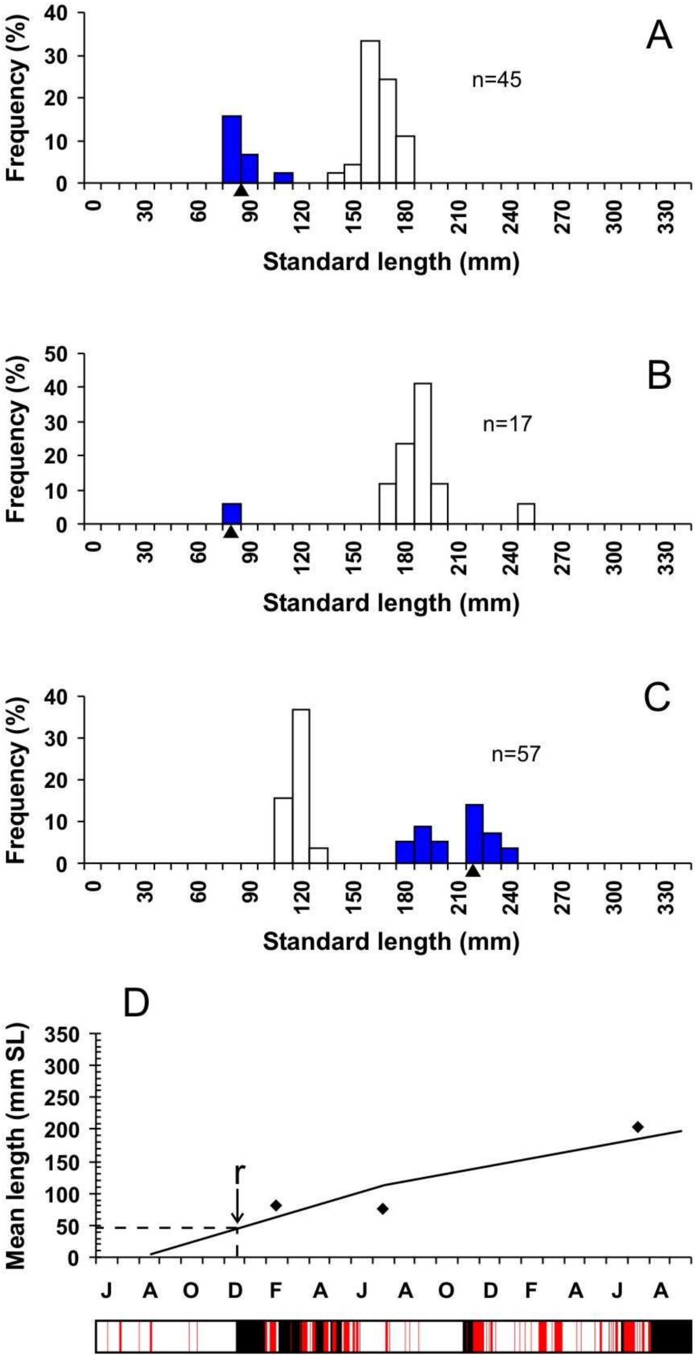


Figure 4.27. Length-frequency plots for *Lithognathus lithognathus* (cohort VIII) caught in February 2005 (A), July 2005 (B) and July 2006 (C) and mean length against time (D). A triangle (▲) marks the mean (determined using the NORMSEP method). Dotted lines indicate the date and size at recruitment (**r**) and departure (**d**) and were linked to either mouth opening events (black bars) or overwash events (red bars).

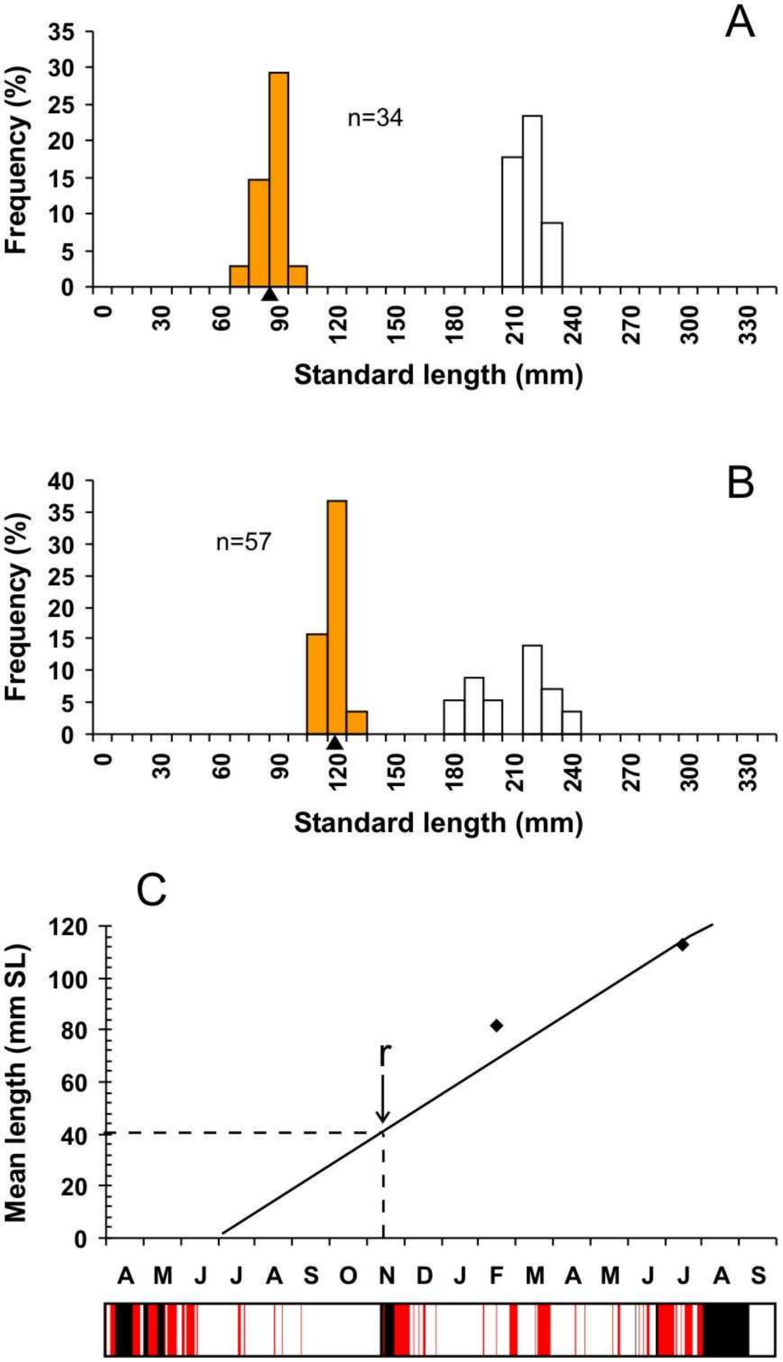


Figure 4.28. Length-frequency plots for *Lithognathus lithognathus* (cohort IX) caught in February 2006 (A), and July 2006 (B) and mean length against time (C). (▲) marks the mean (determined using the NORMSEP method). Dotted lines indicate the date and size at recruitment (**r**) and departure (**d**) and were linked to either mouth opening events (black bars) or overwash events (red bars).

DISCUSSION

Both *Rhabdosargus holubi* and *Lithognathus lithognathus* (Family Sparidae) are endemic to southern Africa, with *R. holubi* occurring from the Berg Estuary in the southwest to Inhaca Island in the northeast (Whitfield 1998). *L. lithognathus* occurs between the mouth of the Orange River in the southwest to KwaZulu-Natal in the northeast (Smith and Heemstra 1990). Both species are considered to be entirely dependent on estuarine habitats for the first year of life (Whitfield 1994b).

Large numbers of *Rhabdosargus holubi* juveniles are found in the estuaries of southeast Africa, with temperature restricting *R. holubi* mainly to the area between the Cape Point and northern KwaZulu-Natal. *R. holubi* is replaced by *Rhabdosargus sarba* in the northeast (subtropical region) and by *Rhabdosargus globiceps* in the southwest (cool-temperate region) (Blaber 1973b). *R. holubi* was the most abundant marine species recorded in both temporarily open/closed and permanently open estuaries in the warm-temperate region of South Africa (Vorwerk *et al.* 2001, Harrison 2005). It was also the main species caught in the large mesh seine net in this study and, although CPUE varied on an annual basis, *R. holubi* comprised between 34% and 92% of the annual catch. Cowley and Whitfield (2002) found that *R. holubi* was the third most abundant species in the East Kleinemonde Estuary and the dominant marine species, accounting for 57% of the biomass and the bulk of the estuarine fish production (74%) in the East Kleinemonde Estuary.

Although *Lithognathus lithognathus* juveniles are abundant in some permanently open warm-temperate estuaries (Whitfield 1998), Harrison (2005) sampling with seine nets found that *L. lithognathus* comprised 3% of the catch composition in warm-temperate temporarily open/closed estuaries and was the seventh most important marine species recorded. Similarly, Marais and Baird (1980) sampling with gill nets in the Swartkops Estuary found that *L. lithognathus* was the eighth most abundant species. *L. lithognathus* was only the seventh most important marine species, in terms of abundance, recorded in the East Kleinemonde Estuary (Cowley and Whitfield 2002). In this study, *L. lithognathus* comprised between 1% and 5% of annual large mesh seine catches and between zero and 22% of annual gill net catches, with CPUE varying considerably on an annual basis. The differences observed in abundance of these two species, particularly in temporarily open/closed estuaries, have been attributed to aspects of their reproductive biology and recruitment behaviour (Cowley 1998, Cowley and Whitfield 2001a, Cowley *et al.* 2001, Vorwerk *et al.* 2001). *Rhabdosargus holubi* has an extended breeding season, with spawning occurring in the nearshore marine environment between July and February in the Eastern and Western Cape (Blaber 1973c, Whitfield and Kok 1992, Whitfield 1998). Postflexion larvae and early juveniles enter estuaries at a small size of between 9 and 15 mm SL (Cowley *et al.* 2001) and *R. holubi* of less than 40 mm SL have been recorded throughout the year in the Knysna, Swartvlei (Whitfield and Kok 1992) and Swartkops (Beckley 1983) estuaries.

Rhabdosargus holubi was the dominant ichthyoplankton species (77%) recorded within the surf zone at Kleinemonde and, although postflexion larvae were recorded throughout the year, a statistically significant peak in abundance was recorded in late winter (August) (Cowley *et al* 2001). This corresponds with the main recruitment period into south-eastern Cape estuaries which is from August to April (Blaber 1974a, Beckley 1983, Whitfield and Kok 1992). During this study recruitment of postflexion larvae and early juveniles (6–28 mm SL) was recorded in January, March, June, July, August and September and small juveniles (<60 mm SL) were recorded in the estuary on all summer and winter sampling trips, thus indicating continual recruitment into the estuary. Individuals generally recruited at a small size (6-10 mm SL), which is slightly smaller than the range reported by Cowley *et al.* (2001) and may be because these are calculated estimates based on extrapolation. Individuals larger than 20 mm SL were only recorded recruiting into the estuary following a period of extended mouth closure. The continual recruitment of juveniles into estuaries along the south-eastern Cape coast will have a buffering effect against recruitment failure as this region has unseasonal and low annual rainfall (mean = 661 mm per year – Chapter 2) with river flooding and thus mouth opening events (Figure 2.12, Chapter 2) likely to occur at almost any time of the year (Bok 1979).

In contrast, *Lithognathus lithognathus* exhibits distinct spawning seasonality. Spawning takes place in the nearshore environment off the Eastern Cape and Transkei coasts primarily between June and August (Mehl 1973). Eggs and larvae drift southwards and enter estuaries along the south-eastern, southern and south-western

Cape coasts at sizes below 50 mm TL (Bennett 1993a). Recruitment takes place primarily between September and January (Bennett *op. cit.*), with peak recruitment recorded in the Sundays Estuary, in the south-eastern Cape, between September and November (Beckley 1984); and in both the Knysna and Swartvlei estuaries, in the southern Cape, during November (Whitfield and Kok 1992). In the East Kleinemonde Estuary, back extrapolated growth of identified cohorts revealed that recruitment of individuals between 15 to 45 mm SL took place from late August to January, which coincides with the recruitment period and size recorded by Bennett (1993a) for this region. The size at recruitment was also much larger than for *Rhabdosargus holubi* which generally recruited at sizes below 15 mm SL. Recruitment into the estuary increased from 2002, when the yearly occurrence of spring and/or summer openings allowed recently spawned fish to enter the estuary on an annual basis. Similarly, the CPUE of small and larger juvenile *L. lithognathus* in the East Kleinemonde Estuary has been increasing since 2002.

In addition to an extended recruitment period, *Rhabdosargus holubi* have been shown to enter estuaries using two access routes. During open mouth conditions they enter estuaries directly via the mouth and during closed mouth conditions they remain in the surf zone and enter via wave overwash events (Cowley *et al.* 2001, Vivier and Cyrus 2001, Kemp and Froneman 2004). In the East Kleinemonde Estuary, back extrapolated growth for seven distinct *R. holubi* cohorts, caught between 1994 and 2006, revealed that five recruitmed during overwash conditions and two recruited under open mouth conditions. Cowley *et al.* (2001) suggested that the timing of peak larval abundance in late winter in the Kleinemonde surf zone may be an adaptation to take advantage of overwash events generated by strong south-westerly winds at this time of the year, rather than openings.

In contrast, *Lithognathus lithognathus* have not been recorded in overwash samples from the East and West Kleinemonde estuaries (Cowley *et al.* 2001, Kemp and Froneman 2004). Back extrapolation of growth curves of *L. lithognathus* cohorts, caught between 1994 and 2006, confirmed that this species only recruits into estuaries during open mouth conditions. This, together with a restricted breeding season can result in recruitment failure on a given year. This was recorded in 1997 and between 1999 and 2000 in the East Kleinemonde. Considering the dominance of temporarily open/closed estuaries along the southeast coast of South Africa recruitment failure into these estuaries may impact on the stock of this important fishery species. Furthermore, for species such as *L. lithognathus* that do not make use of overwash conditions for either recruitment or emigration, prolonged estuary mouth closure may impact on coastal fisheries. The inability to recruit during overwash conditions may also explain the lower numbers of *L. lithognathus* recorded in temporarily open/closed estuaries. Furthermore, *L. lithognathus* has a more specialised diet and would therefore be expected to be less abundant in estuaries. It also has to compete with other specialist zoobenthic feeding estuarine species. In contrast the high abundance of *Rhabdosargus holubi* can be attributed to its omnivorous feeding habits, as it can supplement its diet with plant material (A. Whitfield. pers. comm.).

Estuaries are highly variable environments, with factors such as salinity, temperature and turbidity fluctuating widely. Juvenile *Rhabdosargus holubi* are well adapted to the estuarine environment and can maintain a relatively constant internal osmotic pressure over salinities ranging from 1 to 65 ‰ (Blaber 1974b). This species is also associated with a wide range of water turbidities, although most (65%) individuals occur in water less than 10 NTU (Cyrus and Blaber 1987a). Growth of juveniles in estuaries is rapid, with Cowley (1998) estimating a monthly growth of approximately 8 mm for *R. holubi* juveniles in the East Kleinemonde system. Similarly, Beckley (1984) estimated a growth of between 90 and 100 mm SL in the Sundays Estuary during the first year. Blaber (1973a) found that all seine netted individuals in the West Kleinemonde Estuary were less than 150 mm SL. Following their return migration to sea, adults seldom return to estuaries due to ontogenetic changes in dentition and food requirements (Blaber 1974c). Individuals larger than 150 mm SL occur in intertidal and subtidal areas over reefs and sandy substrata (Lasiak 1982, Beckley 1984).

During this study most *Rhabdosargus holubi* captured in the large mesh seine net were less than 100 mm SL (mean size = 85 mm SL), while the modal size class of individuals caught in gill nets was between 100 and 110 mm SL. Vorwerk *et al.* (2001) surveyed permanently and temporarily open/closed estuaries along the southeast coast using a large mesh seine net and found that the mean length of individuals caught in open systems (75 mm SL) was smaller than the mean length caught in closed systems (78 mm SL). This was attributed to individuals being trapped in closed estuaries for longer periods. During this study the largest individual (an adult of 176 mm SL) was caught in the large mesh seine net in July 2001, following an extended period of mouth closure (8 months). Size cohorts remained in the estuary for between 1 year to 1 year and 11 months, with growth of between 114 mm SL and 230 mm SL occurring during estuarine residence. The greatest calculated growth (230 mm SL) was estimated following an extended period of mouth closure, which prevented fish from leaving the estuary (although fish larger than 176mm SL were not sampled).

Lithognathus lithognathus juveniles are also well adapted to the estuarine environment and have been recorded in salinities ranging from 1 – 90 ‰ (Mehl 1973). Growth is fairly rapid in the estuarine environment, with monthly growth increments ranging between 5 and 13 mm (Blaber 1973a, Mehl 1973, Beckley 1984, Bennett 1989, Whitfield and Kok 1992). Although the overwhelming majority of *L. lithognathus* recorded in the East Kleinemonde and other estuaries are less than 250 mm SL (i.e. less than two years old) (Blaber 1973a, Mehl 1973, Beckley 1984, Bennett 1989, Whitfield and Kok 1992), larger fish have been recorded in estuaries (Bennett 1989, Bennett 1993a) and re-enter under suitable mouth conditions (Bennett 1993a). Results from this study suggest that juvenile *L. lithognathus* make extensive use of the East Kleinemonde Estuary and remain in the estuary for between 2 to 4 years, even though they have the opportunity to leave in most years. During estuarine residency growth of between 175 mm SL and 310 mm SL was recorded.

Cowley (1998) recorded small shoals of fish leaving the East Kleinemonde Estuary during large overwash events. However, neither *Rhabdosargus holubi* or *Lithognathus lithognathus* appeared to make use of overwash conditions to leave the estuary and are capable of remaining in the estuary until conditions are favourable for emigration. This may also account for the differences observed in the mean size of *R. holubi* caught in temporarily open/closed and permanently open estuaries (Vorwerk *et al.* 2001)

South African estuaries are usually characterised by a longitudinal grading of fish species (Ter Morshuizen and Whitfield 1994). *Rhabdosargus holubi* individuals were captured in all regions of the estuary, but higher numbers were recorded in the lower reaches than in the middle and upper reaches. Similar results were recorded by Cowley and Whitfield (2001a) during an earlier study of the East Kleinemonde Estuary and by Vorwerk *et al.* (2001) in other Eastern Cape estuaries. This is interesting as *R. holubi* is one of the species that has been found to be closely associated with macrophyte beds in the Knysna and Swartvlei estuaries (Whitfield and Kok 1992), the Kromme Estuary (Hanekom and Baird 1984), the Kariega Estuary (Ter Morshuizen and Whitfield 1994, Paterson and Whitfield 2000) and the Swartkops Estuary (Beckley 1983). Prior to 2003, macrophyte beds were found in the middle and upper reaches of the East Kleinemonde Estuary. Cowley and Whitfield (2001a) suggested that the predominance of *R. holubi* in the lower reaches of the East Kleinemonde Estuary might be associated with episammic filamentous algal mats that develop in late winter and early summer. Whitfield (1984) found that *R. holubi* abundance in Swartvlei, an estuarine lake, was highest when an extensive mat of episammic filamentous algae developed in the littoral zone, covering an area previously occupied by *Potamogeton* plants that had undergone senescence.

Lithognathus lithognathus was also recorded in higher numbers in the lower reaches of the East Kleinemonde Estuary and this has been attributed to the abundance of sand prawns (*Callianassa kraussi*) in this region (Cowley and Whitfield 2001a). Also of interest was the smaller size of *L. lithognathus* recorded in the lower reaches of the estuary and may indicate that young fish use the shallow areas of the lower reaches more extensively as nursery areas than the middle and upper reaches. Whitfield (1980) also found that juvenile *Pomadasys commersonnii*, which are benthic invertebrate feeders, were common in the lower reaches of the Mhlanga Estuary and were associated with sand prawn beds.

In summary, the life cycle characteristics, which are considered to affect the annual success of these two species in temporarily open/closed estuaries are listed below:

1. *Rhabdosargus holubi* has an extended juvenile recruitment period, while *Lithognathus lithognathus* has a short, well-defined juvenile recruitment period.

2. *Rhabdosargus holubi* use overwash events as an alternative means to recruit into estuaries when closed, while *Lithognathus lithognathus* only access estuaries during the open mouth phase.
3. *Rhabdosargus holubi* remain in estuaries for less than two years, and do not return to these systems, while *Lithognthus lithognathus* may remain in estuaries for up to four years and may return as larger juveniles or adults.

Although both species are well adapted to the estuarine environment, the above differences indicate that *Rhabdosargus holubi* is better adapted to making use of temporarily open/closed estuaries as nursery areas. The dominance of this species in the East Kleinemonde and other temporarily open/closed estuaries can be attributed to the extended breeding season of this species and its ability to use both overwash events and mouth openings to recruit into estuaries. Other taxa which adopt a similar strategy include many species of mullet (particularly *Myxus capensis, Mugil cephalus, Liza dumerili* and *Liza macrolepis*) and the Cape moony (*Monodactylus falciformis*) (Cowley *et al.* 2001, Kemp and Froneman 1994, Vivier and Cyrus 2001). This recruitment strategy may account for the dominance of these species in the East Kleinemonde (Cowley and Whitfield 2002) and other estuaries (e.g. Marais and Baird 1980, Marais 1981, 1983, Kok and Whitfield 1986, Vorwerk *et al*. 2001).

In contrast, a number of aspects of the biology of *Lithognathus lithognathus* make it vulnerable to decline as a result of human activities. Species with similar restricted spawning periods include *Pomadasys commersonnii* and *Liza tricuspidens*, both of which were found in low numbers in the East Kleinemonde Estuary (Chapter 3). *L. lithognathus* is an important component in the catches of coastal and estuarine anglers in the Cape (Day *et al.* 1981, Coetzee *et al.* 1989, Bennett 1993b) However, long-term catch data indicate major declines in this species, with the catch rate of recreational shore anglers declining by 90% since the mid 1970’s (Bennett 1993b). Bennett (1993a) found that the high degree of estuarine dependence, confinement of juveniles and subadults to the surf zone, large size at maturation, and predictable aggregation of mature individuals, make this species particularly vulnerable to estuarine degradation and over fishing. This study has shown that the short recruitment period and inability to access temporarily open/closed estuaries during overwash events may be added to this list of constraints to their overall population size.

CHAPTER 5

CHOICE CHAMBER EXPERIMENTS

INTRODUCTION

Although the recruitment of larvae and juveniles into estuaries has been well documented, little is known about the factors governing the immigration of marine fishes into estuaries (Whitfield 1989a, Strydom 2003). Several physical factors have been proposed as stimuli which could elicit a recruitment response in estuary-associated fish species, including current speed, salinity, temperature, turbidity, food gradients and olfactory cues (e.g. Norcross and Shaw 1984, Boehlert and Mundy 1988, Blaber and Blaber 1980, Kingsford and Suthers 1994, Whitfield 1994a). However, field studies have cast doubt over many of these factors playing a role in the recruitment process. For example, although the abundance of larvae and juveniles in estuaries along the southeast coast of South Africa is strongly associated with the magnitude of axial salinity gradients within these systems (Whitfield 1994a), it is unlikely that larvae are responding primarily to salinity gradients when recruiting into estuaries. Whitfield (1994a) found that pronounced salinity gradients were absent in the surf zone adjacent to estuaries where successful recruitment was recorded and hypothesised that axial salinity gradients within the estuaries were a surrogate indicator of olfactory cues being carried into the marine environment influencing marine fish recruitment into the study estuaries.

Turbidity does not appear to be a driving force behind the recruitment of most marine fish into estuaries (Whitfield 1994a), but certain species may be able to follow turbidity gradients into estuaries (Cyrus and Blaber 1987a). Whitfield (1994a) recorded equally successful recruitment into both the Great Fish and Sundays estuaries, even though a marked turbidity gradient was absent in the marine environment adjacent to the Sundays Estuary but present opposite the Great Fish Estuary. Marked turbidity gradients will also be absent in the marine environment adjacent to closed estuaries. Water temperature gradients may also play a role in influencing larval fish recruitment into estuaries (Boehlert and Mundy 1988). However, according to Whitfield (1994a) temperature is unlikely to be a major cue in attracting larval marine fish to estuaries along the southeast coast of South Africa, as thermal gradients within these systems are often irregular and prone to wide fluctuations depending on river flow, tidal regime, oceanic upwelling, cloud cover, etc.

Many researchers have suggested that olfaction is the primary sense responsible for the successful location of estuarine environments (Boehlert and Mundy 1988, Stabell 1992, Whitfield 1994a) as fish exhibit high chemo-sensitivity (Hara 1992). Chemical signals are important in the spawning of a diverse range of fish species (Bjerselius *et al.* 1995). Odour plays an important role in mate recognition for the swordtail *Xiphophorus cortezi* (McLennan and Ryan 1997). *Anguilla rostrata* elvers are attracted to odours emanating from organic components in coastal rivers when migrating to freshwater (Miles 1968, Sorenson 1986) and olfaction plays an essential role in the homing migration of salmonids to their natal streams (Scholz *et al.* 1976, Halser *et al.* 1978, Johnsen and Hasler 1980, Dittman *et al.* 1996, Montgomery *et al.* 2001).

Whitfield (1994a) hypothesised that larvae and juveniles of estuary-associated marine fish species may trace land-based cues back to an estuary by following the olfactory concentration gradient and could orientate towards temporarily open/closed estuaries when closed, by using dissolved olfactory cues present in the estuarine water that seeps through the sand bar at the mouth of these systems. Once an estuary mouth is breached, riverine and estuarine waters are flushed out, forming extensive plumes in the marine environment that seem to be attractive to recruiting fish larvae (Strydom 2003). However, no published studies have tested if estuary-associated marine fish species respond to olfactory cues.

The importance of olfactory cues to estuary-associated marine fish species was tested using *Rhabdosargus holubi*, as this species was numerically the most abundant marine species caught in the East Kleinemonde and other temporarily open/closed estuaries along the south-eastern Cape Coast (Chapter 3). In addition this species is able to recruit into estuaries during both open mouth events and wave overwash events and was found to be the dominant species in the ichtyoplankton adjacent to the East Kleinemonde Estuary throughout the year (Cowley *et al.* 2001).

In order to ascertain whether recruiting larvae are able to distinguish water from different sources, experiments were designed to test whether *Rhabdosargus holubi* can differentiate between marine, estuarine, coastal and river water, and to determine which type of water was most attractive to the postflexion larvae of this species.

MATERIALS AND METHODS

Experimental design

Experiments were conducted at the Rhodes University Marine Laboratory in Port Alfred, South Africa in the spring (October/November) of 2004 and 2005. The laboratory is situated on the banks of the permanently open Kowie Estuary (33°36.25′S, 27°54.20′E). Recently captured postflexion *Rhabdosargus holubi* larvae (10-15 mm SL) were tested in a choice chamber (Figure 5.1) based on a design by Atema *et al.* (2002). The sharp boundary maintained in rectangular choice chambers, which were first used by Höglund (1951), provides aquatic organisms with a choice of two water sources (Kroon and Housefield 2003).

The choice chamber was constructed from plywood and sealed with black waterproof paint. The chamber size was 121 cm x 25 cm, with a water depth of approximately 6 cm (Figure 5.1). Depending on the experiment, two different sources of water (e.g. sea water and estuary water) were pumped, using submersible powerhead pumps, from 1000-litre storage tanks into two 20-litre buckets fitted with taps that delivered the water at a flow of 2 cm s^{-1} into the adjacent sides of the upstream end of the choice chamber. The two water streams were separated into parallel streams by a central partition and each stream flowed through stacked drinking straws to reduce turbulence. The two streams then flowed through a fine mesh (~ 1 mm bar) into the 31 x 25 cm test area, where the flow maintained a sharp boundary between the two streams, despite the absence of a physical partition. Water then flowed through a downstream containment net (~ 1 mm bar mesh) and out over a bevelled outfall weir. To test the stability and sharpness of the demarcation of the two water types as they flowed through the test area, dye tracers were used. Flow speed was then adjusted to achieve optimum demarcation. Dye tests were repeated before each test to ensure proper separation of the water sources.

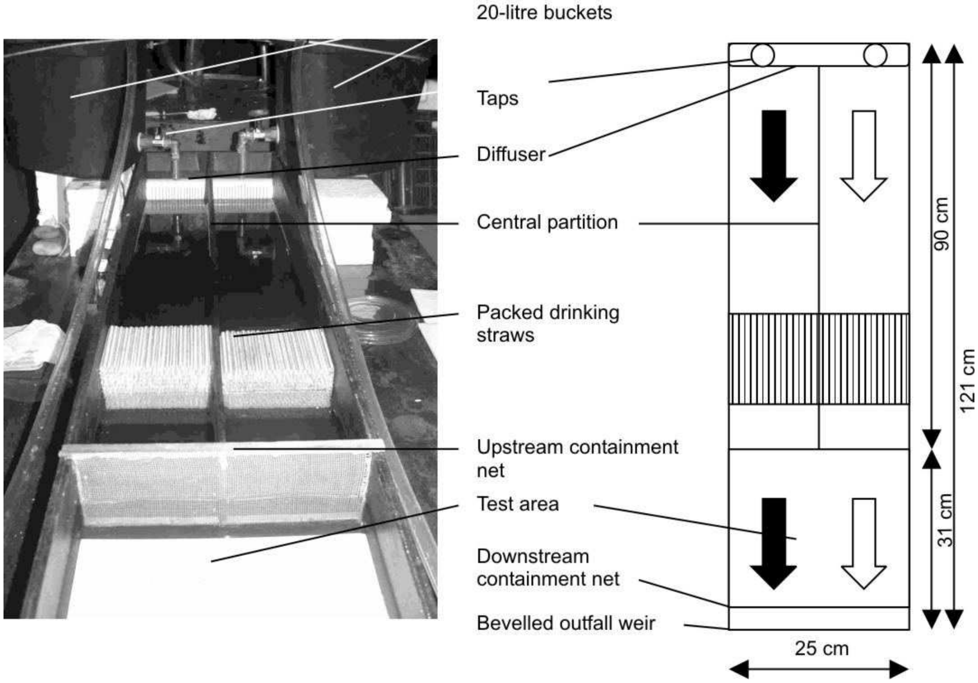


Figure 5.1. Choice chamber used in the larval fish experiments (based on the design of Atema *et al.* 2002).

Table 5.1. Initial physico-chemical properties of water used in Experiment 2.

	Surf zone water	**River water**	**Estuary water**	**Sea water**
Turbidity (NTU)	4	1	15	1
Dissolved oxygen (mg l^{-1})	4.8	5.0	4.5	6.0
Temperature (ºC)	20.3	17.2	19.2	18.8
pH	9.8	8.9	9.9	9.2
Salinity (‰)	35	35	35	35

Water used in the experiments was collected and stored in 1000-litre storage tanks. River water was collected just below the confluence of the Kowie and Lushington Rivers (33º30.17´S, 26º44.40´E), approximately 31 km above the head of the Kowie Estuary (Figure 5.2). Estuary water was collected from the lower reaches of the Kowie Estuary 5.2 km upstream of the mouth (33º35.09´S, 26º51.41´E) during the latter part of the ebb tide (Figure 5.2). Sea water was collected approximately 6 km out to sea from the Kowie Estuary (33º38.11´S, 26º57.21´E) where there is little or no estuarine influence. Surf zone water was collected from a rocky beach (33º36.31´S, 26º53.33´E) 1.1 km from the Kowie Estuary mouth (Figure 5.2). Water was stored for between 1 to 4 days prior to use which reduced temperature differences between the water sources. Prior to each experiment the estuarine and river water was adjusted to a salinity of 35 ‰ using artificial sea salt (Red Sea Salt® and Dopan Marine Salt®) to eliminate salinity as an influencing factor and also to prevent mixing of different water types in the experimental choice chamber. The physico-chemical parameters of the water used in the second experiment were measured prior to use in the experiment and are given in Table 5.1. There was little difference in temperature, dissolved oxygen, pH and turbidity between the different water types.

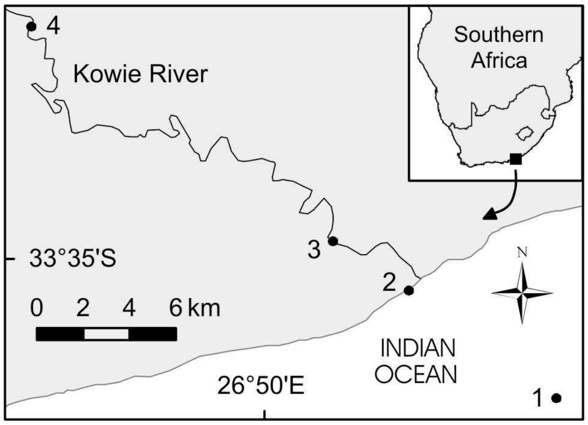


Figure 5.2. Map of the Kowie River, Port Alfred, showing the location of water collection points for (1) sea water, (2) surf zone water, (3) estuary water and (4) river water.

Two separate experiments were conducted and each experiment consisted of a series of tests in which larvae were given a choice between different water types. At the start of each test, the experimental chambers were filled with water from the larval acclimation holding tank. Five to nine postflexion larvae were introduced into the test area of the choice chamber and given 5 min to acclimate at no-flow. Each test consisted of two trials. In Trial 1, test water treatments (e.g. estuary and sea water) were simultaneously released from the 20-litre buckets and allowed to flow through the adjacent sides of the test chamber for 3 minutes. Movement of the larvae in the choice chamber was quantified by counting the number of individuals in each side of the test area in the last minute of each trial, with a recording made of any changes in numbers on either side of the test area during this minute. In Trial 2, the two water treatments were alternated to flow down opposite sides of the choice chamber. This was done to check for the possible influence of external stimuli, such as phototactic responses, on side selection. Test water treatments flowed for another 3 minutes and the movement of the larvae was again quantified in the last minute of the test condition.

Experiment 1: Determining whether estuary recruited **Rhabdosargus holubi** *larvae are attracted to the odour of estuary and river water*

In the first experiment, conducted in November 2004, postflexion larvae that had recently recruited into the lower reaches of the Kowie Estuary were exposed to estuary water, river water, sea water and a mixture of river water and estuary water to test the hypothesis that recruiting larvae are attracted to olfactory cues. Five different tests were conducted: (1) estuary water versus sea water, (2) river water versus sea water, (3) river water versus estuary water, (4) river water versus a 50:50 mixture of river water and estuary water and (5) estuary water versus a 50:50 mixture of river water and estuary water. The mixture tests were conducted to determine whether larvae are attracted to olfactory cues in both river water and estuary water or more strongly attracted to either estuary or river water.

Thirty-seven postflexion *Rhabdosargus holubi* larvae, between 13 mm and 15 mm SL, were collected using a fine-meshed hand net from the lower reaches of the Kowie Estuary. All fish were collected during November, a time when recruitment of *R. holubi* into Eastern Cape estuaries is at a peak (Beckley 1984). The larvae were randomly assigned to three groups (Group A – 12 larvae, Group B – 13 larvae and Group C – 12 larvae) to give three replicate groups, and they were acclimated for three days in water from the mouth region of the Kowie Estuary (salinity = 35 ‰) prior to the experimentation. Larvae were fed twice daily on *Artemia* spp. nauplii. Each test was repeated three times using each group of larvae (Group A, B and C).

Experiment 2: Determining whether surf zone recruited **Rhabdosargus holubi** *larvae are attracted to the odour of estuary, river and surf zone water*

In October 2005, postflexion larvae caught in the surf zone were exposed to seawater, estuary water, river water and surf zone water to substantiate the findings of the first experiment and to test whether larvae of this species are initially attracted to estuary, surf zone and possibly river water when accumulating in surf zones and migrating into estuaries. Five tests were conducted: (1) estuary water versus sea water, (2) river water versus sea water, (3) river water versus estuary water, (4) surf zone water versus sea water and (5) surf zone water versus estuary water. No mixture tests were conducted in experiment 2, as these tests were inconclusive in 2004 and surf zone tests were included.

Six postflexion *Rhabdosargus holubi* larvae, measuring 10-11 mm SL, were collected in October 2005 in the surf zone adjacent to the Kowie Estuary mouth using a floating plankton sled. Only six larvae were used in the experiment due to the difficulty encountered in capturing and identifying the target species. The sled was fitted with a 500-µm nylon mesh net, which sampled the upper 30 cm of the water column. The net had a mouth area of 0.17 m^2 and was attached to a 3-m rope and towed through the surf zone, parallel to the shoreline, in water that ranged in depth from approximately 0.5 to 1.5 m. The larvae were acclimated in sea water for four days in a holding tank prior to experimentation.

Data analysis

The null hypothesis of equal preference for each half of the test area was evaluated using the binomial distribution. According to Kroon and Housefield (2003) most statistical tests are based on the assumption that individual data points are statistically independent of each other. This assumption is often violated in two-choice choice chamber experiments where multiple records of an individual animal are treated as independent data points. Kroon and Housefield (2003) argue that the best way to overcome this problem is to average multiple records on the same subject. In these experiments repeated measurements (i.e. over 60 seconds) on the same subjects within each trial were averaged to obtain the mean percent occurrence of larvae in each half of the test area.

RESULTS

After approximately 3 minutes *Rhabdosargus holubi* larvae swam, often in a shoal, around the test area of the choice chamber. When the test water was introduced into the chamber individual fish initially darted in and out of the two odour plumes and usually orientated themselves in an upstream direction. Fish generally behaved as a shoal, but there were also individuals who did not participate in shoaling behaviour.

Experiment 1: Determining whether estuary recruited **Rhabdosargus holubi** *larvae are attracted to the odour of estuary and river water*

Larvae in groups A, B and C (Figure 5.3a) showed a significant preference ($P \leq 0.05$) for estuary water over sea water during both trials (i.e. when flows were assigned to different sides of the choice chamber). When the results from both estuary water versus sea water trials for all groups were averaged larvae showed a 75% mean occurrence in estuary water. Similarly, larvae in groups A and C showed a significant ($P \leq 0.01$) preference for river water over sea water during both trials (73% mean occurrence in river water) (Figure 5.3b), while larvae in group B selected river water significantly more often during Trial 1 ($P \leq 0.01$), but not during Trial 2 ($P > 0.05$).

The larvae were then given a choice between river water and estuary water to determine which water elicited a stronger response. Larvae in groups A and B showed a significant ($P \leq 0.05$) preference for river water during one trial and estuary water during the other trial (Figure 5.4a). Only larvae in Group C selected river water significantly ($P \leq 0.01$) more often over estuary water during both trials (70% mean occurrence in river water).

A 50:50 mixture of river water and estuary water was then tested separately against river water and estuary water to test if larvae were more strongly attracted to a mixture of cues from river and estuary water than to cues in estuary and river water alone. Larvae in all groups selected the mixed water significantly ($P \leq 0.01$) more often during one trial and the estuary water during the other trial (Figure 5.4b). When river water was tested against a mixture of river water and estuary water, larvae in groups A and B selected both water types significantly ($P \leq 0.01$) during different trials. Group C selected the mixture significantly ($P \leq 0.01$) more often during one trial only (Figure 5.4c).

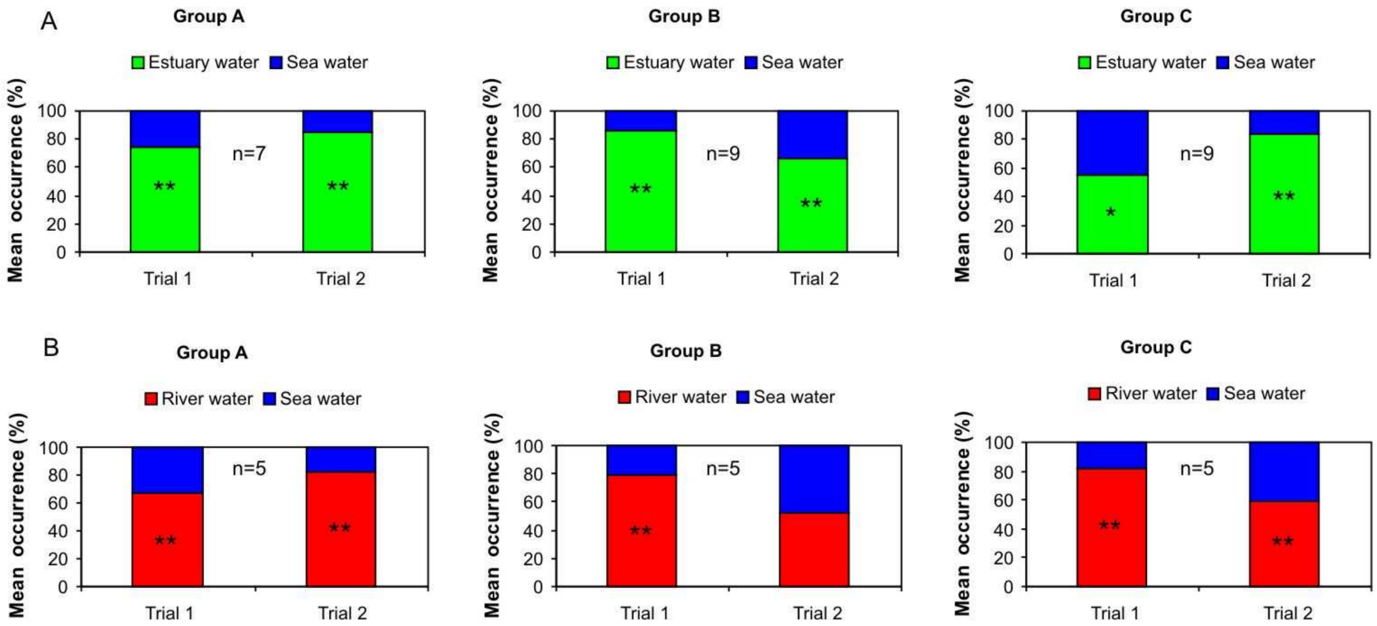


Figure 5.3. Mean percent occurrence in each side of the choice chamber for each trial within (A) the estuary water versus sea water and (B) river water versus sea water tests (Experiment 1). Preference was tested by a binomial test, * $P \leq 0.05$, ** $P \leq 0.01$.

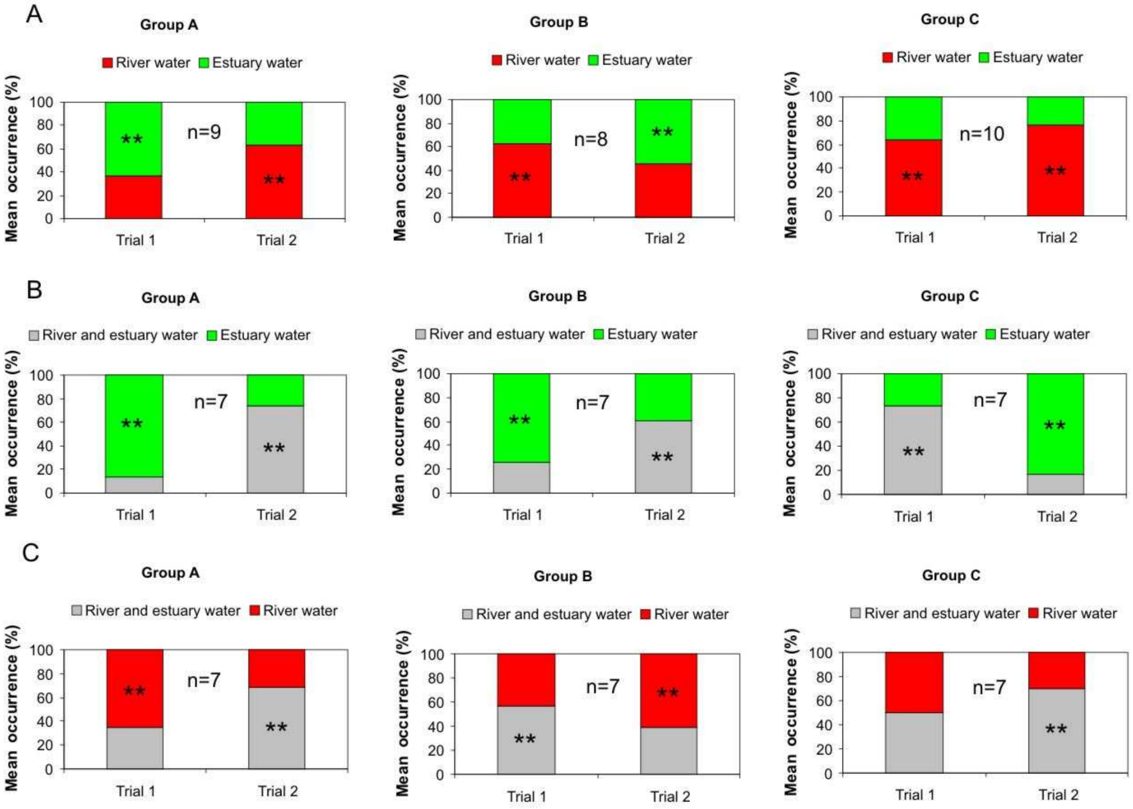


Figure 5.4. Mean percent occurrence in each side of the choice chamber for each trial within the (A) estuary water versus river water, (B) estuary water versus river and estuary water mixture and (C) river water versus river and estuary water mixture tests (Experiment 1). Preference was tested by a binomial test, * $P \leq 0.05$, ** $P \leq 0.01$.

Experiment 2: Determining whether surf zone recruited Rhabdosargus holubi *larvae are attracted to the odour of estuary, river and surf zone water*

Larvae showed a significant ($P \leq 0.01$) preference for estuary water over sea water during both trials (81% mean occurrence in estuary water) (Figure 5.5). When given a choice between river water and sea water the larvae selected river water significantly ($P \leq 0.01$) during one trial and sea water during the other trial. When the results from both river water versus seawater trials were averaged larvae showed a 56% mean occurrence in river water. Also, larvae showed a significant ($P \leq 0.01$) preference for estuary water over river water during both trials (64% mean occurrence in estuary water).

When given a choice between surf zone water and sea water larvae preferred ($P \leq 0.01$) surf zone water during both trials (81% mean occurrence in surf zone water). When given a choice between surf zone water and estuary water larvae selected surf zone water significantly ($P \leq 0.01$) more often than estuary water during both trials (74% mean occurrence in surf zone water) (Figure 5.5).

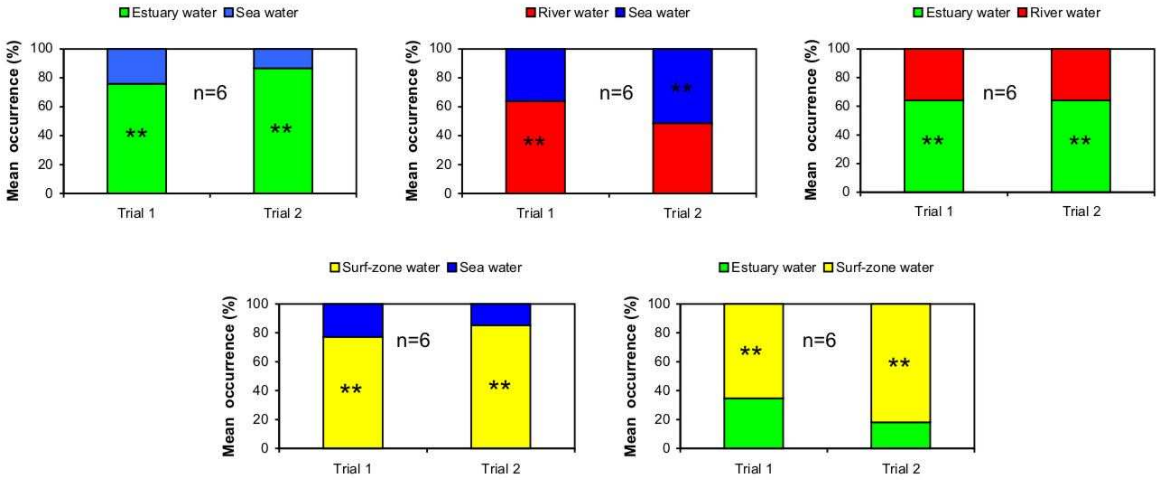


Figure 5.5. Mean percent occurrence in each side of the choice chamber for each trial within the estuary water versus sea water, river water versus sea water, river water versus estuary water, surf-zone water versus sea water and surf-zone water versus estuary water tests (Experiment 2). Preference was tested by a binomial test, * $P \leq 0.05$, ** $P \leq 0.01$.

DISCUSSION

Organisms using different habitats during different stages of their life cycle have to be able to respond to different stimuli to locate new habitats (Boehlert and Mundy 1988, Rothlisberg *et al.* 1995). Recruitment of estuary-associated marine fish to estuaries is believed to be an active behaviourally mediated process (Norcross and Shaw 1984, Boehlert and Mundy 1988, Norcross 1991, Strydom 2003). At first, larvae must move from an offshore planktonic habitat to nearshore areas. Although this process may be passive initially, active migration to surf zones is thought to occur during the later stages of larval development, as larvae develop the ability to respond to physico-chemical cues (Norcross and Shaw 1984, Boehlert and Mundy 1988, Norcross 1991, Strydom 2003). For fish species utilizing estuaries the surf zone is a transitory habitat, although accumulation of postflexion larvae in this zone may be prolonged in what has been suggested as an interim nursery area for certain estuary-associated taxa (Whitfield 1989b). Once larvae have recruited to the nearshore environment (surf zone) a new set of physical variables may influence their accumulation at estuary mouths and finally their movement upstream within the estuary (Boehlert and Mundy 1988).

Although empirical evidence (Whitfield 1994a, Strydom 2003) suggests that olfactory cues may be important in the recruitment of marine larvae and juveniles into estuaries, no experimental work has been conducted to test this hypothesis. The results from this experiment provide the first experimental indications of the importance of olfactory cues to migrating estuary-associated marine fish larvae. The experiment was conducted using a rectangular choice chamber. Rectangular choice chambers have been used successfully in a number of experiments to investigate the chemoresponses of aquatic animals. The responses of fishes to different pH gradients (Atland and Barlaup 1996), water quality (Kroon and Housefield 2003), olfaction (Atema *et al.* 2002, Benfield and Aldrich 1992), pheromones (Bjerselius *et al.* 1995) and the attraction of juveniles to conspecifics (Olsén and Höglund 1985, Olsén 1986, Baker 2003) have been monitored using rectangular choice chambers.

In the first experiment, postflexion *Rhabdosargus holubi* larvae, which had recently recruited into the lower reaches of the Kowie Estuary, showed a preference for estuary and river water over sea water. Similar results were recorded by Benfield and Aldrich (1992) who used a rectangular choice chamber to assess the attraction of post-larval brown shrimp *Penaeus aztecus* and white shrimp *Penaeus setiferus* to estuary water from Galveston Bay, Texas. Both species, which are dependent on estuaries as nursery areas, selected estuary water significantly more often than sea water. Salinity was eliminated as a factor by adjusting the test and control water to the same salinity. Benfield and Aldrich (1992) concluded that odour is one of several cues that post-larval penaeids use during their recruitment into estuaries.

Turbidities recorded during the experiments ranged from 1-15 NTU. The range in turbidity was, however, not large as values were all within the lower end of the clear to semi-turbid range (<10 – 50 NTU) identified by Cyrus and Blaber (1987a). In the St Lucia Estuary, Cyrus and Blaber (1987a) recorded a range of turbidities from 0.5 to 1472 NTU and although *Rhabdosargus holubi* juveniles showed a preference for clear water (<10 NTU) they were also caught in intermediate water (10-80 NTU). In each test, water treatments were changed so as to flow down opposite sides of the choice chamber. As the larvae showed no side preference and selected river and estuary water regardless of the side of the choice chamber this ruled out the possible influence of external stimuli, such as phototactic responses, on side selection. Larvae also showed a strong response to water types regardless of the presence and position of the observer.

When *Rhabdosargus holubi* larvae were given a choice between estuary and river water, or estuary and river water and a mixture of the two, the results were inconclusive. In future studies it could be tested whether certain key cues are present in both water types. Whitfield (1994a) recorded the immigration of larvae and juveniles of estuary-associated marine fish species into the Kariega Estuary in the absence of fresh water input, although at a considerably reduced rate. The findings from this experiment therefore validate the notion that estuary water on its own is sufficient to attract the larvae of estuary-associated fish species to these systems. The experiments also support the hypothesis that elevated fish recruitment into estuaries occurs when both estuarine and river water enters the sea since it has now been shown that larvae are attracted to cues from both the estuary and the river catchments.

In the second experiment, which was conducted to confirm the findings of the first experiment, postflexion larvae, which were smaller in size (10-11 mm SL) and had not recruited into an estuary were found to be significantly attracted to estuary water and weakly attracted to river water. When given a choice between estuary water and river water the larvae responded strongly to estuary water. These results suggest that migrating larvae in the sea respond primarily to cues in estuary water, and to a lesser extent river water, when recruiting into estuaries and probably develop a stronger attraction to river water once in the estuary, as observed in the first experiment. It is also important to note that estuarine water may contain cues of riverine or catchment origin.

Postflexion *Rhabdosargus holubi* larvae have been observed using various events such as flooding tides (Beckley 1984, Whitfield 1989a, Harrison and Whitfield 1990) and overtopping events in temporarily open/closed estuaries (Cowley *et al.* 2001) to move into the mouth areas of estuaries. Once in the estuary, larvae migrate to shallow nursery grounds higher up the estuary where water currents are reduced or absent (Beckley 1984, Whitfield 1989a, Harrison and Whitfield 1990).

Larvae may be responding to freshwater-based olfactory cues to migrate to these shallow upstream areas within estuaries. Transport within open estuaries may occur by selected tide transport, with larvae riding the upper water masses on the flood tide (Rijnsdorp and Straten 1985). Barbin (1998) examined the role of olfaction in homing migrations of American eel (*Anguilla rostrata*) and found that olfaction was used for the discrimination of the appropriate tide for transport to home sites within estuaries, although olfaction was not the only orientation cue used in estuaries.

When given a choice between sea water and surf zone water, *Rhabdosargus holubi* larvae selected surf zone water over sea water. This attraction to surf zone water confirms previous studies that have shown that this habitat is an important transit and accumulation zone for the larvae of estuary-associated species recruiting from nearshore spawning areas into estuarine nursery areas (Boehlert and Mundy 1988, Harris and Cyrus 1996, Harris *et al.* 2001, Cowley *et al.* 2001, Strydom 2003). Accumulation in surf zones may be prolonged for some species as immigration to estuaries may occur at ages of 60-90 days (Boehlert and Mundy 1988), and it has been suggested that many species spend some of their postlarval stage of their development in surf zones (Whitfield 1989b, Harris and Cyrus 1996, Strydom 2003). Larval *R. holubi* comprised more than 77% of the overall catch in the surf zone adjacent to the temporarily open/closed East and West Kleinemonde Estuaries in the Eastern Cape (Cowley *et al*. 2001).

Larvae of estuary-associated species, including *Rhabdosargus holubi,* have been observed actively accumulating in areas of low current velocity in the surf zone (Whitfield 1989b, Watt-Pringle and Strydom 2003), and the attraction of larvae to cues in surf zone water suggests that these larvae are responding to olfactory and other physical cues to accumulate and maintain position within the surf zone. According to Watt-Pringle and Strydom (2003) maintaining a shoreward position allows larvae to access shallow-water long-shore currents moving along the coast, and thus to gain access to estuaries.

When given a choice between estuary water and surf zone water larvae preferred surf zone to estuary water. These results suggest that these larvae (10-11 mm SL) were still using the surf zone as an accumulation area. The larvae caught in this study were of a size consistent with larvae caught in other surf zones. Watt-Pringle and Strydom (2003) recorded *Rhabdosargus holubi* with a mean size of 10.2 mm SL in the Kwaaihoek surf zone and Cowley *et al.* (2001) recorded *R. holubi* with a mean size of 11.3 mm SL in the Kleinemonde surf zone. Attraction to estuary water may get stronger with fish size, although there is no supporting evidence. In addition, the swimming abilities of larval fish have been shown to increase with their size, thus enabling larvae to orientate their movement towards favourable habitats (e.g. Fuiman and Webb 1988, Chick and Van Den Avyle 2000, Montgomery *et al.* 2001, Hunt von Herbing 2002).

The results of this study have indicated for the first time the importance of olfactory cues to migrating larvae of an estuary-associated marine fish species. Olfactory cues have been classified as long-distance signals in moving water (Dusenbery 1992). Fish have a well-developed sense of smell, with an olfactory bulb similar in organisation to that of higher vertebrates (Hara 1992). Some fish are able to detect and respond to olfactory signals as weak as 10^{-9} M (Hara 1992) and are able to discriminate between different odours in mixtures (Kleerekloper 1967). In many fish species, olfactory signals have been shown to be important in the synchronization of spawning, predation, alarm signalling, feeding and migration (McLennan and Ryan 1997).

Some late-stage reef larvae have similar sensory capabilities to adult fish and actively control their dispersal, at least during the latter stages of development (Dudley *et al.* 2000, Montgomery *et al*. 2001). Atema *et al.* (2002) using a rectangular choice chamber showed that larval apogonids were able to recognise different water masses by their odour and prefer ‘reef water’ to ocean water. In addition, apogonids and other settlement-stage reef larvae had well-developed nostrils to process olfactory information. Wright *et al.* (2005) showed that both pre- and post-settlement coral reef damselfish (*Pomacentrus nagasakiensis*) were able to detect amino acids in water, which could be a useful cue for larvae attempting to locate a reef. Lindsay and Vogt (2004) working with newly hatched zebrafish (*Danio rerio*) found that chemosensory systems of olfaction and taste are developed during the first week after fertilisation. Day 4 after fertilisation larvae responded significantly to water containing amino acid stimulants compared to water with no stimulants. Similarly, Sweatman (1988) provided evidence that larval damselfishes (*Dascyllus aruanus* (L.)) find corals with resident conspecifics using dissolved chemical cues.

The results of this study suggest that late-stage estuary-associated marine larvae are also able to recognise different water masses, probably based on odour. The migration of larvae from offshore spawning grounds to estuarine nursery areas has long been recognised as a poorly understood mechanism of transport associated with estuaries (Boehlert and Mundy 1988) and this study provides experimental evidence of the importance of olfactory cues to migrating larvae. Postflexion *Rhabdosargus holubi* larvae may use, along with other physical factors, olfactory cues to migrate to and maintain position within surf zones, and later to accumulate and move into estuary mouths and then into shallow estuarine nursery areas. However, with movement into each new habitat, *R. holubi* larvae appear to be responding to different combinations of olfactory and physical cues. Further research on this and other estuary-associated marine species is required to study the details of recruitment mechanisms and cues employed by these species to locate estuarine nursery areas.

CHAPTER 6

GENERAL DISCUSSION

Although estuaries are amongst the most fluctuating aquatic environments on earth (Day *et al.* 1989) they are important nursery areas for numerous fish species (Dando 1984, Wallace *et al.* 1984) and are known to be more productive than adjacent freshwater and marine environments (Woodwell *et al.* 1973, Haedrich and Hall 1976). Changes in environmental conditions within an estuary may be fairly predictable, or they may be caused by short and/or long-term unpredictable climatic fluctuations, all of which have large effects on the abundance and distribution of estuarine fish stocks (Flint 1985, Kupschus and Tremain 2001, Desmond *et al.* 2002). Variation in estuarine fish communities has been well studied on a spatial and seasonal scale, with most investigations ranging in duration from 1-3 years. These studies provide a short-term insight into the overall structure, abundance and distribution of fish communities in various estuary types. However, far less is known about estuarine fish community structure, particularly in temporarily open/closed estuaries (TOCEs) over the medium to long-term (Table 6.1). Only two published studies have been conducted on estuarine fish communities in TOCEs over a period of 10 years or more (Desmond *et al.* 2002, Poizat *et al.* 2004). The information gained from the 11-year East Kleinemonde Estuary study is therefore very significant, being the first long-term investigation on estuarine fish communities in a South African TOCE.

Long-term studies (10-40 years) are unusual in the coastal and estuarine environment (Flint 1985, Wolfe *et al.* 1987, Jackson and Jones 1999) but they are pivotal to understanding how fishes use the estuarine environment and are influenced by various factors (Flint 1985, Jackson and Jones 1999, Desmond *et al.* 2002, Power *et al.* 2002). Long-term studies also allow for an understanding of slow and complex processes such as stability and succession (Methven 2001), and allow for a partitioning of the effects of season, episodic events and long-term climatic trends on variability in the fish fauna (Wolfe *et al.* 1987). Long-term trends may be subtle and can easily be masked by large year-to-year variability. As a consequence, short-term sampling may lead to normal year-to-year changes being erroneously attributed to environmental change (Hurst *et al.* 2004). Breen *et al.* (2004) proposed a monitoring protocol for

South African estuaries and stressed the need to monitor key indicators over an extended time period (>5 years) to highlight long-term trends and identify possible cause and effect relationships. The compilation of continuous long-term records can then be used to support decision-making and management.

Short-term studies have also focussed extensively on the recruitment of fish larvae and juveniles into estuaries (e.g. Beckley 1985, Warlen and Burke 1990, Neira and Potter 1992, Harris and Cyrus 1995). However, the cueing of early stage estuary-dependent marine fishes is amongst the most important and least understood mechanism in the life cycles of these species (Whitfield 1989a, Whitfield 1994a, Boehlert and Mundy 1998). According to Strydom (2002), when assessing future research needs, information is needed on the factors driving the recruitment of larvae and juveniles into estuaries.

Table 6.1. A review of published information on fish communities in temporarily open/closed estuaries (TOCEs).

Reference	**Estuary**	**Duration**
Blaber (1974a)	West Kleinemonde Estuary, South Africa	2 years
van der Elst (1978)	Kobole Estuary, South Africa	single survey
Bennett (1989)	Kleinmond Estuary, South Africa	12 months
Humphries *et al*. (1992)	Wilson Inlet, Australia	12 months
Whitfield and Kok (1992)	Swartvlei Estuary, South Africa	18 months
Potter *et al.* (1993)	Wilson Inlet, Australia	18 months
Pollard (1994)	Lake Wollumboola, Australia	3 years
Potter and Hyndes (1994)	Wilson Inlet, Australia	11 months
Young *et al.* (1997)	Moore River Estuary, Australia	12 months
Griffiths and West (1999)	Bellombi Laggon, Fairy Creek and Werri Lagoon, Australia	12 months
Cowley and Whitfield (2001b)	East Kleinemonde, South Africa	2 years
Griffiths (2001)	Shellharbour Lagoon, Australia	14 months
Pampoulie *et al*. (2001)	Vaccarès Lagoon, France	5 years
Vivier and Cyrus (2001)	Nhlabane Estuary, South Africa	5 years
Cowley and Whitfield (2002)	East Kleinemonde, South Africa	4 years
Desmond *et al.* (2002)	**Los Peñasquitos Lagoon, San Diego**	**11 years**
Raz-Guzman and Huidobro (2002)	Laguna Salinas del Padre, Mexico	12 months
Young and Potter (2002)	Wellstead Estuary, Australia	21 months
Vorwerk *et al.* (2003)	Eastern Cape estuaries, South Africa	single survey
Poizat *et al*. (2004)	**Vaccarès Lagoon, France**	**10 years**
Harrison (2005)	South African estuaries	single survey
Lukey *et al.* (2006)	Grant’s Valley Estuary, South Africa	4 months

The overall aim of this study was to improve our understanding of fish recruitment processes into small TOCEs and to describe long-term interannual changes in richness, abundance, diversity and structure of the ichthyofaunal community in the East Kleinemonde Estuary. In the latter objective, emphasis was placed on investigating linkages between environmental variables and changes in fish composition and abundance within the estuary. This study also included an assessment of the year-to-year recruitment success of two estuary-dependent marine species that adopt different recruitment strategies. In addition, laboratory experiments were designed to assess some of the factors governing the immigration of marine fish larvae into estuaries, with particular focus on determining whether recruiting larvae are able to distinguish water from different sources (habitats).

Most fishes have complex life cycles and occupy different niches at different stages of their lives. The movements and migrations associated with this process have been debated in detail by numerous authors (e.g. Norcross and Shaw 1984, Beckley 1985, Boehlert and Mundy 1998). The term recruitment is often used in different contexts. Beverton and Holt (1957) defined recruitment as “the entrance of new individuals in the area where fishing occurs.” However, the definition most applicable to estuary-associated fishes is that given by Gulland (1983) who defined recruitment as the migration to/from nursery areas or a change in habitat use. The size and structure of estuarine fish populations are determined by the recruitment of marine, estuarine and freshwater spawning species, although in the East Kleinemonde Estuary the juveniles of marine-spawning species dominate the ichthyofauna with estuary-dependent marine species comprising 64% of the species recorded and estuarine-spawning species only 18% (Chapter 3). Similar findings in terms of marine migrant fish dominance have been reported from TOCEs and permanently open estuaries worldwide (Loneragan *et al*. 1989, Whitfield *et al.* 1994, Potter *et al.* 1997, Griffiths 2001, Castillo-Rivera *et al*. 2002, Harrison 2005).

The main feature of the life cycle of most marine-spawning species entering southern African estuaries is an obligate juvenile phase (Wallace 1975). Spawning occurs in the nearshore marine environment and once the preflexion larval stage is complete, fish movement becomes very active and individuals enter the surf zone (Whitfield

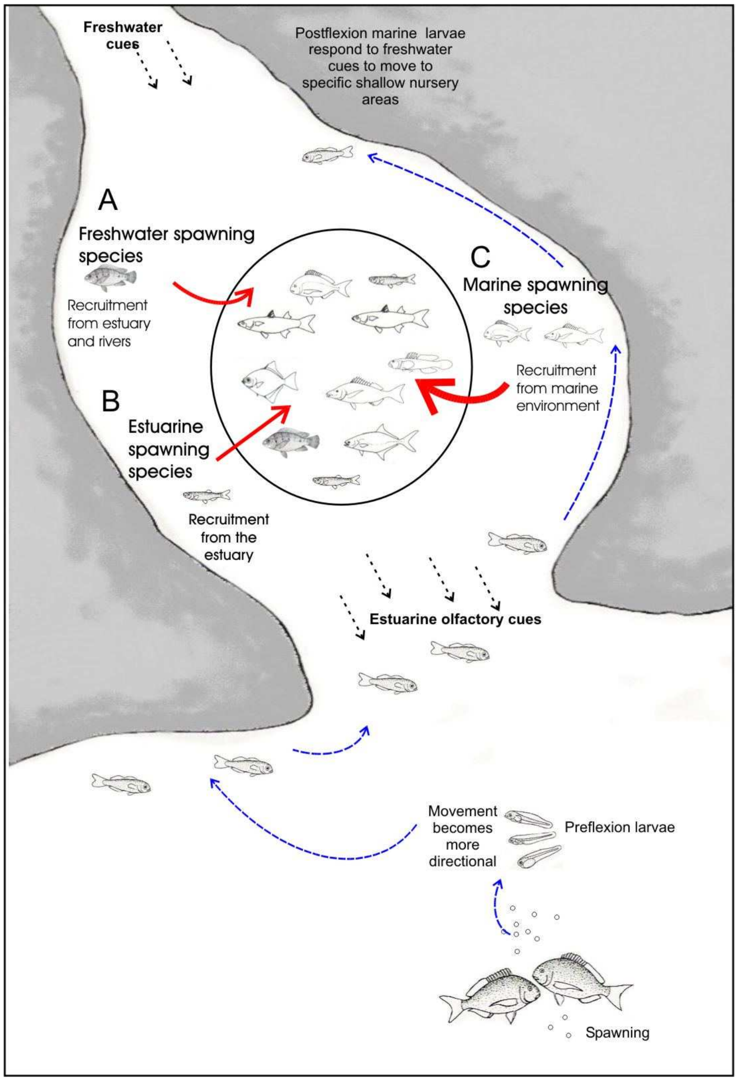
1998). For many estuary-associated taxa the surf zone is an important transit and accumulation zone (Boehlert and Mundy 1988, Harris and Cyrus 1996, Cowley *et al.* 2001, Harris *et al.* 2001, Strydom 2003) and may even be regarded as an interim nursery area (Whitfield 1989b). Larvae then move along the coast within the surf zone (Strydom and d'Hotman 2005) and accumulate at estuary mouths before moving upstream into estuarine nursery areas (Boehlert and Mundy 1988). After a residence time of between 1 to 3 years fish return to the sea where they join adult stocks (Whitfield 1998).

Numerous researchers have suggested that olfaction is the primary sense responsible for the successful location of estuarine environments (e.g. Whitfield 1994a, Cowley *et al.* 2001, Strydom 2003). However, a review of the literature (Table 6.2) indicates that no empirical evidence has been provided for estuary-associated marine fish species using olfaction as a mechanism to locate estuarine waters. Studies on catadromous and anadromous species (eels and salmon) and penaeids on the other hand, have confirmed the importance of olfaction in the migrations of these fishes between marine and riverine environments (Table 6.2).

This study provides the first empirical evidence on the use of olfaction in guiding an estuary-dependent marine spawning fish to its primary nursery area. Laboratory studies conducted on postflexion *Rhabdosargus holubi* larvae (Chapter 5) revealed that they are able to recognise different water masses. Several authors have proposed a likely recruitment pattern displayed by estuary-associated marine-spawning fish species. The findings of this study are in agreement with the pattern proposed by Whitfield (1994a), with additional refinements. Based on the evidence presented in Chapter 5, the proposed recruitment pattern adopted by marine-spawning estuary-dependent species is as follows; initially, larvae are attracted to surf zone water and maintain position within this zone but may move laterally along the coast. Only later, when accumulating and migrating into estuaries, are larvae attracted to estuarine water as opposed to other water types. Once in the estuary, larvae usually continue to move up the system towards littoral nursery areas and are now mainly attracted to river water cues. Larvae and early juveniles probably use olfaction, along with other cues such as salinity, temperature and turbidity gradients to 'fine tune' their movements to specific nursery areas within estuaries. Olfactory cues may be particularly important in orientating towards upstream nursery areas in TOCEs where strong horizontal gradients are often absent. The results from this study are illustrated in Figure 6.1.

Table 6.2. A review of published information on the importance of olfaction to the recruitment of estuary-associated taxa.

Reference	Country	Estuarine dependence guild	Spawning	Reference to olfaction	Empirical evidence
Boehlert and Mundy (1988)	America	Estuary-dependent	Marine spawning	Olfactory cues were identified as one of several point source stimuli that could elicit behavioural responses by larvae.	No
Whitfield (1994a)	South Africa	Estuary-dependent	Marine spawning	Suggested that olfaction assists the immigration of postflexion larvae into estuaries	No
Cowley *et al.* (2001)	South Africa	Estuary-dependent	Marine spawning	Larvae accumulate in the surf zone and may be responding to olfactory cues	No
Strydom (2003)	South Africa	Estuary-dependent	Marine spawning	Suggested that olfaction assists the immigration of euryhaline marine fish larvae into estuaries	No
Benfield and Aldrich (1992)	America	Estuary-dependent	Marine spawning	Attraction of postlarval prawn larvae to estuary water was tested in a choice chamber.	Yes
Miles (1968)	America	Catadromous	Marine spawning	American eels showed positive rheotaxis to fresh water	Yes
Johnsen and Hasler (1980)	America	Anadromous	Freshwater spawning	Chemical cues are used by salmon in their upstream migration	Yes
Sola and Tosi (1993)	Italy	Catadromous	Marine spawning	Migrating glass eels were shown to be attracted to bile salts and taurine	Yes
Dittman *et al.* (1996)	America	Anadromous	Freshwater spawning	Juvenile Coho Salmon learn odours associated with their home stream	Yes
Barbin (1998)	America	Catadromous	Marine spawning	Anosmic yellow-phase American eels were followed through an estuary	Yes
Barbin *et al.* (1998)	America	Catadromous	Marine spawning	Anosmic silver-phase American eels were followed through an estuary	Yes
Vrieze and Sorensen (2001)	America	Anadromous	Freshwater spawning	Migrating lamprey showed a strong attraction to stream water vs lake water	Yes



Community structure determined by the recruitment of (A) freshwater, (B) estuarine and (C) marine spawning species

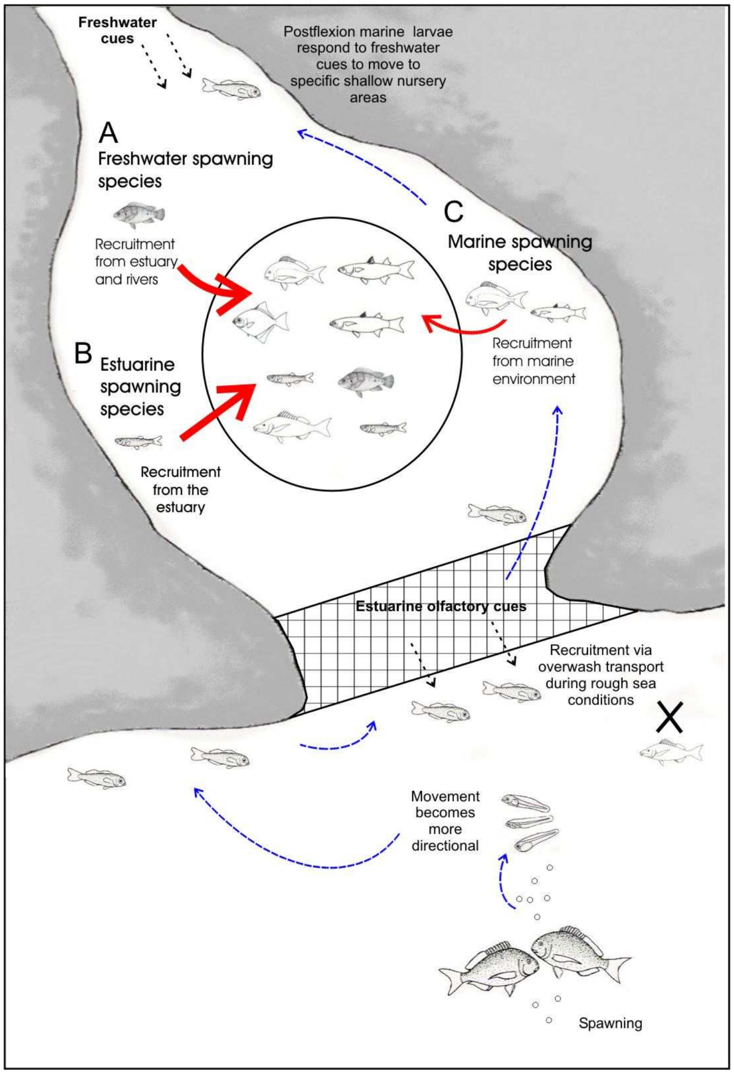
A) Spawning and nest building by *Oreochromis mossambicus* is disrupted when the mouth opens during peak breeding season resulting in a decrease in recruitment.

B) During periods of high river flow eggs and larvae of estuarine spawning species may be swept out to sea resulting in a decrease in recruitment.

C) The recruitment of marine spawning species is enhanced when the mouth is open (particularly during spring), thus leading to higher species richness of marine spawning species and a more stable marine community.

Figure 6.1. Determinants of fish community structure in the East Kleinemonde Estuary during open mouth conditions (red arrows) and movement of estuary-associated marine fish larvae into estuaries (blue arrows).

Under closed mouth states in TOCEs (refer to Figure 6.2), the larvae and juveniles of estuary-dependent species could orientate towards these estuaries by using olfactory cues present in the estuarine water that seeps through the sand bar at the mouth (Whitfield 1994a). Evidence from this study (Chapter 5) and other studies (Whitfield 1992b, Cowley *et al.* 2001, Vivier and Cyrus 2001, Kemp and Froneman 2004) have shown that *Rhabdosargus holubi* and certain other species are able to recruit into closed estuaries during bar overwash events. In fact, *R. holubi* appears to make more extensive use of overwash events to recruit into TOCEs than open mouth events. Back extrapolated growth for seven distinct *R. holubi* cohorts, caught between 1994 and 2006 in the East Kleinemonde Estuary, showed that five recruited during overwash conditions and only two recruited under open mouth conditions (Chapter 4). Cowley *et al.* (2001) also suggested that the timing of peak larval abundance in late winter in the Kleinemonde surf zone may be an adaptation to take advantage of overwash events generated by strong south-westerly winds at this time of the year, rather than openings.



Community structure determined by the recruitment of (A) freshwater, (B) estuarine and (C) marine spawning species

A) Closed conditions result in inundation of marginal vegetation, stable water levels and an absence of water currents providing favourable conditions for breeding of *Oreochromis mossambicus* and recruitment is therefore enhanced.

B) Recruitment of estuarine spawning species is greater during the closed phase as eggs and larvae are retained in the estuary, conditions are physically more stable, and marginal vegetation is inundated. Freshwater input leading to mouth opening may also enhance populations through nutrient input.

C) The recruitment of marine spawning species is lower when the mouth is closed (particularly during spring). Species such as *Rhabdosargus holubi* and various mullet are able to recruit via overwash transport but other species such as *Lithognathus lithognathus* and *Pomadasys commersonnii* are unable to recruit, resulting in lower marine species richness and a less stable marine community.

Figure 6.2. Determinants of fish community structure in the East Kleinemonde Estuary during closed conditions (red arrows) and movement of estuary-associated marine fish larvae into estuaries (blue arrows).

Doherty (1981) proposed that local reef fish populations might be sufficiently limited by the supply of recruits that competitive interactions rarely determine subsequent population size. This recruitment limitation hypothesis may be even more relevant to migrant marine fish populations in TOCEs. If no overwash or open mouth events occur during peak recruitment periods then recruitment into closed estuaries is prevented (refer to Chapter 4). In a survey of 62 small estuaries in KwaZulu-Natal, Begg (1984) found that prevailing mouth state had a significant influence on the abundance of marine-spawning species. Significantly fewer marine-spawning species were found in temporarily open/closed estuaries than in permanently open estuaries.

Numerous authors have suggested that the timing, duration and frequency of mouth opening events play an important role in determining fish species composition, diversity and seasonality within TOCEs (Wallace and van der Elst 1975, Beckley 1984, Kok and Whitfield 1986, Young *et al.* 1997, Griffiths 1998). According to Potter *et al.* (1993) researchers have not yet determined whether long-term changes in fish communities of TOCEs reflect the period that these estuaries were landlocked (isolated from the sea). This study has provided the first real opportunity to test this important hypothesis because it has combined a long-term dataset of fishes in a TOCE with a matching long-term dataset on estuary mouth state.

The timing of mouth opening did have a significant affect on species composition in the East Kleinemonde Estuary with MDS grouping years into two distinct groups (Chapter 3). More species were recorded during years that succeeded spring (September to November) mouth opening events than in years following no mouth opening events in spring. Mean annual CPUE for species that recruit predominantly in spring were higher in 'spring opening' years. Species that are known to recruit during both overwash and open mouth conditions were consistently recorded each year, irrespective of a 'spring opening'. *Liza richardsonii* has been recorded entering Western Cape estuaries throughout the year (Bennett 1989, Whitfield and Kok 1992) and this species was recorded in greater numbers in the East Kleinemonde during non 'spring opening' years.

Two different periods of stability were identified in the East Kleinemonde Estuary. (1995-2000; 2001-2005). During the 2001–2005 period a higher value for Kendall's coefficient of stability (*W*) was recorded and there was also an increase in interannual community stability (IMD) and seriation (IMS) from the 'other' years to the 'spring' years (Chapter 3). These results suggest that optimum mouth opening for fish recruitment is during spring (September-November) in Cape TOCEs and the predominance of spring opening events between 2001 and 2005 may have allowed for the regular recruitment of a wide variety of marine species into the estuary.

Other long-term studies have also noted serial patterns of community change (e.g. Potter *et al.* 1997, 2001, Warwick *et al.* 2002). Potter *et al.* (2001) collected fish from the intake screens of the Oldbury Power Station in the Severn Estuary, UK, between 1972 and 1977 and between 1996 and 1999. Ordination of abundance data revealed that the relative contribution and abundance of various species changed between the two decades and this was related to reductions in the discharges of industrial effluents. Similarly, Warwick *et al.* (2002) revealed a serial pattern of community change in the macrobenthic community in the Tees Estuary, UK, with a major shift in composition in 2004 coinciding with the construction of a barrage in the estuary.

The dynamic nature of individual populations in the East Kleinemonde Estuary was also highlighted as the abundance of all species varied markedly between years. For example, maximum abundance for *Rhabdosargus holubi* (264 fish/haul in 2003), *Myxus capensis* (83 fish/haul in 2004) and *Gilchristella aestuaria* (1662 fish/haul in 2005) was several times greater than in the years of least abundance (21 fish/haul for *R. holubi* in 2001, 0.2 fish/haul for *M. capensis* in 1995 and 97 fish/haul for *G. aestuaria* in 1996). This was because the recruitment strengths of juveniles varied among years and the years when recruitment was greatest varied among the different species. Similarly, Cowley and Whitfield (2001b) found that populations of marine-spawning species in the East Kleinemonde Estuary are characterised by a high degree of interannual variability. For example, the total population size of all marine fishes in the estuary increased by almost eight fold from a mark-recapture experiment conducted between October 1994 and December 1994 (~18 000 individuals) to a mark-recapture experiment conducted between October 1995 and February 1996 (~133 000 individuals). The large interannual variability was attributed to both abiotic (estuary mouth state) and biotic conditions.

Recruitment variability of estuarine fishes appears to be a common feature worldwide (Philippart *et al.* 1996, Potter *et al.* 1997, 2001, Poizat *et al.* 2004). Potter *et al.* (1997) found that the abundance of the main species caught in the Severn Estuary, UK, was at least one order of magnitude greater in years of maximum abundance than in years of least abundance. Potter *et al.* (1997) attributed this to recruitment variability. Year-class strengths of different species are largely determined at the early life-history stages through mechanisms that are poorly understood (Jobling 1995, Costa *et al.* 2002). As a result, egg and larval survival is particularly important in determining fluctuations in recruitment (Jobling 1995). The environmental factors that are most likely to effect egg and larval survival include feeding conditions, disease outbreak and predation rates (Jobling 1995).

In TOCEs, particularly the East Kleinemonde Estuary, mouth state is also extremely important in determining the abundance (and variability) of fishes (Cowley 1998). This study made use of long-term records of daily mouth conditions and linked them to the recruitment of distinct year class cohorts in two species with contrasting life-history characteristics. Significant recruitment of *Lithognathus lithognathus* into the East Kleinemonde Estuary only occurred in years when the mouth was open between late August and January. This species has a relatively constant and limited breeding season, with spawning by adults taking place in the nearshore environment off the Eastern Cape coast primarily between June and August (Mehl 1973). Recruitment and CPUE of small and larger juvenile *L. lithognathus* increased from 2002 onwards when the mouth opened consistently during spring, thus allowing recently spawned fish to enter the estuary on an annual basis (Chapter 4). There were also years of little or no recruitment when the mouth failed to open during spring (1997 and 1999) or where there was recruitment failure from the marine environment (2000). Recruitment failure into TOCEs may have major implications for this species that is an important and overexploited component of the recreational fishery. Year-class strengths of adults available to the fishery may decrease in the years following closed mouth conditions in spring, thus adding to the pressure exerted on the existing stock.

In contrast, 0+ *Rhabdosargus holubi* juveniles (<60 mm SL) were recorded consistently in summer and winter samples over the period studied. Recruitment by this species appeared to be uninterrupted and was not determined by seasonality of mouth opening events. This sparid overwhelmingly dominated the marine-spawning component of the East Kleinemonde Estuary and comprised 63% (range = 34-92%) of the catch composition sampled with the large mesh seine net (Chapter 3). The dominance of this species in the East Kleinemonde and other TOCEs can be attributed to the extended breeding season as well as its ability to recruit during both overwash and open mouth conditions (Chapter 4).

In the East Kleinemonde Estuary the timing of mouth opening events (abiotic factors) and life-history pattern (biotic factors) together influenced species composition and abundance. Species with medium to extended breeding seasons that recruit during overwash and open mouth conditions or breed in the estuary dominated catches numerically (Table 6.3). In contrast, species with restricted spawning seasons, most of which only recruit into estuaries during open mouth conditions, were found in low numbers within the estuary (Table 6.3). Life-history pattern has also been identified as an important factor determining species composition and abundance in other estuaries (Loneragan *et al*. 1989, Potter *et al.* 1990, 1993, 1997, Jones *et al*. 1996). In the permanently open Port River-Barker Inlet, species that enter estuaries as juveniles but are not entirely dependent on estuaries as nursery areas, dominated the littoral fish assemblage of this estuary (Jackson and Jones 1999).

Table 6.3. Reproductive seasonality and recruitment behaviour of the 10 most abundant species caught in the East Kleinemonde Estuary.

Species	Spawning period*		Recruit during overwash events	Life history	Rank
Gilchristella aestuaria	Breeds all year round	Extended	NA	Ia	1
Atherina breviceps	September - February	Medium	NA	Ia	2
Rhabdosargus holubi	July - February	Extended	Yes	IIa	3
Glossogobius callidus	October - November	Short	NA	Ib	4
Myxus capensis	March - November	Medium	Yes	Vb	5
Monodactylus falciformis	October - February	Medium	Yes	IIa	6
Oreochromis mossambicus	September - February	Medium	NA	IV	7
Liza richardsonnii	September - March	Extended	No	IIc	8
Liza dumerili	December - February	Short	Yes	IIa	9
Lithognathus lithognathus	June - August	Short	No	IIa	10

* Short 1 – 3 months
Medium 4 – 6 months
Extended > 7 months

In the East Kleinemonde Estuary, interannual changes in the abundance of certain estuarine-spawning species appeared to be related to rainfall and thus river pulses. A peak in CPUE of 1662 fish per haul was recorded for *Gilchristella aestuaria* in 2005. This coincided with the highest annual rainfall recorded during the 11-year study (which fell between December 2004 and December 2005). According to Whitfield (2005), river pulses are particularly important in influencing the abundance of estuarine resident species. The filter-feeding *G. aestuaria* is the most abundant species in the East Kleinemonde Estuary and forms an important link in the food chain in South African estuaries as it is preyed upon by various predatory fish (Whitfield and Blaber 1978). Martin *et al.* (1992) recorded an order of magnitude increase in the abundance of *G. aestuaria* in the St Lucia Estuary following minor flooding that led to the mouth of the estuary opening. This was attributed to the phytoplankton bloom and increased zooplankton stocks associated with the flooding. However, major flooding in estuaries can result in a decrease in estuarine resident species. Strydom *et al*. (2002) recorded an absence of young *G. aestuaria* in the water column of the Great Fish River during periods of high flow and attributed this to large numbers of eggs and larvae being swept out of the estuary.

Cowley (1998) found that mouth opening is important for the reproductive success of estuarine spawning species in the East Kleinemonde Estuary. Reproductive activity is halted during low level water conditions following a mouth opening event while closed mouth conditions result in more stable physical conditions, elevated water levels and habitat inundation resulting in an increase in breeding success.

Temporal changes in the abundance of *Oreochromis mossambicus*, the main freshwater species in the East Kleinemonde Estuary, were not a major topic of this thesis. However, a new study was instigated in 2005 to investigate spatial and temporal trends in the abundance of juveniles of this species (Ellender 2006). Mouth phase has been found to affect the abundance of *O. mossambicus* in TOCEs (Whitfield and Blaber 1979). Closure of estuaries often results in inundation of marginal vegetation, stable water levels and an absence of water currents, which together result in more favourable breeding conditions (Whitfield and Blaber 1979). In the East Kleinemonde Estuary a mouth opening event recorded during peak breeding season (spring and summer) resulted in a decrease in the abundance of juvenile *O. mossambicus* in late 2005. This was linked to a cessation of nest building and spawning behaviour (Ellender 2006).

On a broader scale, climate change may have a range of implications for estuarine fish population dynamics. Climate change has the potential to affect estuarine use by fishes through habitat alteration (for example an increase in the frequency of storms may lead to a loss of habitat) and major aspects of fish physiology, for example salinity and temperature tolerances of fishes, which will result in changes in the distribution of species (Elliot 2002). Clark (2006) predicts that the most obvious changes associated with increased sea surface temperatures around South Africa will be shifts in the distribution of individual species or species assemblages. Tropical fish species will occur in greater numbers and the distributional ranges of temperate species may be reduced. The combined result will be changed fish population dynamics within the estuaries affected by climate change, particularly those systems in the vicinity of biogeographical boundaries.

Harrison and Whitfield (2006) found that the occurrence and abundance of fish fauna in South African estuaries are linked to two primary variables: temperature and salinity. Although warm-water endemic species dominated the ichthyofauna of the East Kleinemonde Estuary both in terms of the number of species recorded and abundance there were also five tropical species recorded in catches from 1999 onwards (Chapter 3). The distribution of these species is strongly linked to temperature and they are normally only recorded in subtropical estuaries (Harrison and Whitfield 2006).

The appearance of tropical species in catches resulted in an increase in species richness over the study period (Chapter 3). There has also been an increase in sea surface temperatures recorded off East London and Port Alfred (Chapter 2). Although tropical species are still recorded in low numbers in the East Kleinemonde Estuary, in time there may be changes in the population dynamics in the estuary. Clark (2006) anticipates changes in the interactions between a species and its competitors, predators, prey and/or pathogens as a result of climate change.

One of the eight recognised threats to biodiversity in Eastern Cape estuaries is change to biochemical and estuary mouth characteristics caused by increasing riverine offtake. Abstraction and other water use changes the quality, quantity and timing of water reaching estuaries (Breen *et al.* 2004). This study has highlighted the importance of the timing of mouth opening to the fish community in a typical TOCE and also goes a long way towards understanding the natural variability within an Eastern Cape TOCE, which is a goal set out for the monitoring of South African estuaries (Breen *et al.* 2004). If upstream water abstraction continuously prevents the opening of Eastern Cape estuaries during spring then species richness in these estuaries will decline to the detriment of important fishery species such as *Lithognathus lithognathus* and *Pomadasys commersonnii*. These species are already overexploited and their restricted spawning seasons and inability to recruit into estuaries during overwash events make them especially vulnerable to reduced open mouth conditions and degradation.

It is recommended that the findings of this study be incorporated into a management protocol for the East Kleinemonde Estuary with further indicators being identified and monitored. Key indicators identified for monitoring in South African estuaries include land use, co-operative governance and co-management (Breen *et al.* 2004) and these need to be incorporated into the East Kleinemonde monitoring protocol. Further studies should also be conducted on the cueing of estuary-dependent and estuary-associated marine fish into estuaries. These could include an assessment of the importance of conspecifics already in the estuary to migrating larvae and the attraction of larvae to water from different estuaries, e.g. water from estuaries with excessive freshwater abstraction from the catchment versus water from undisturbed estuaries. Although Cyrus and Blaber (1987a, 1987b, 1987c) have conducted pioneering studies on the turbidity preferences of selected southern African estuary-associated fishes, further work also needs to be conducted on other possible recruitment cues such as salinity and temperature on a wide variety of species.

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APPENDIX 1

State of the East Kleinemonde Estuary mouth from March 1993 to September 2006 (Cowley *et al*., unpublished data).

Month	Day of month																													
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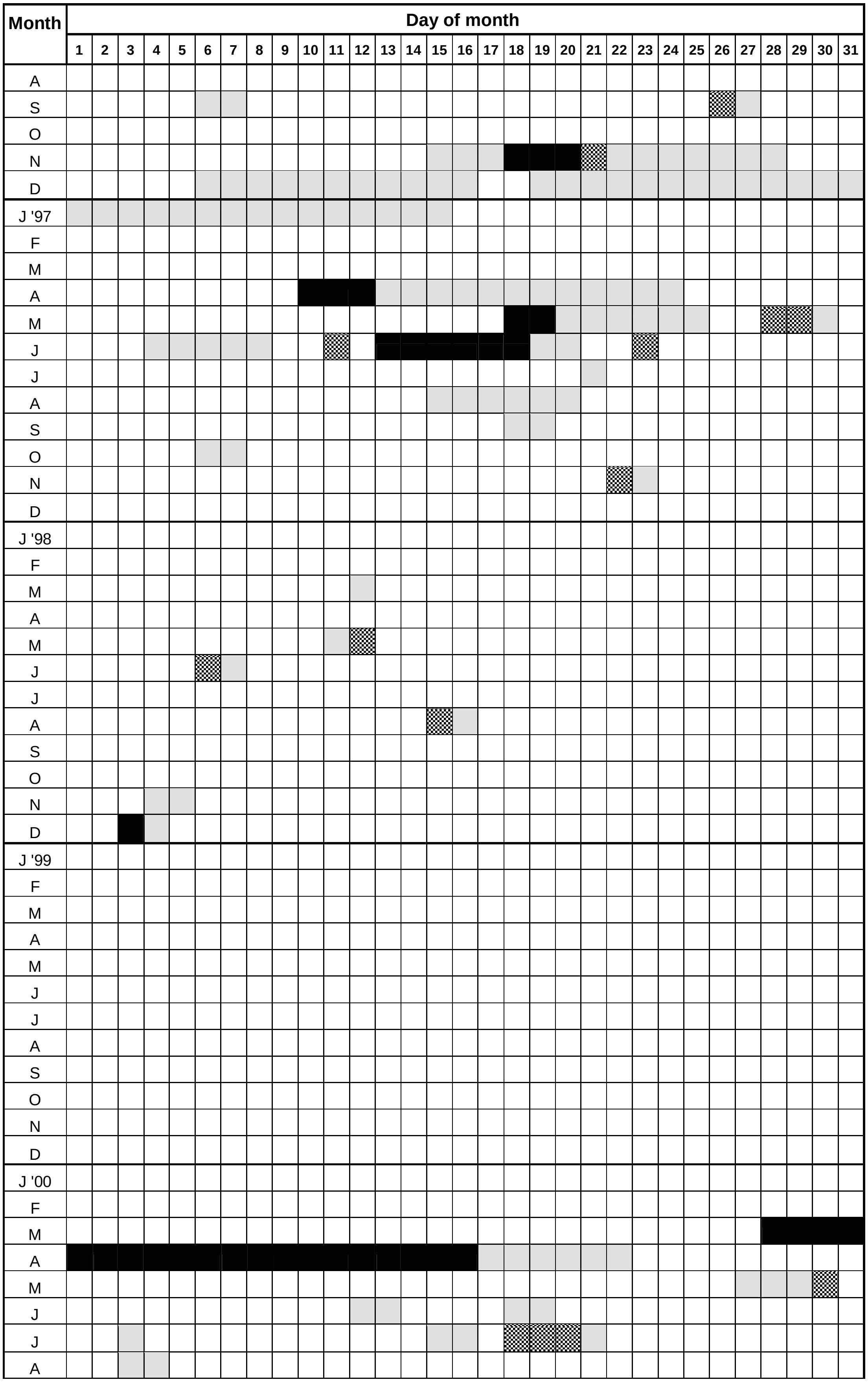

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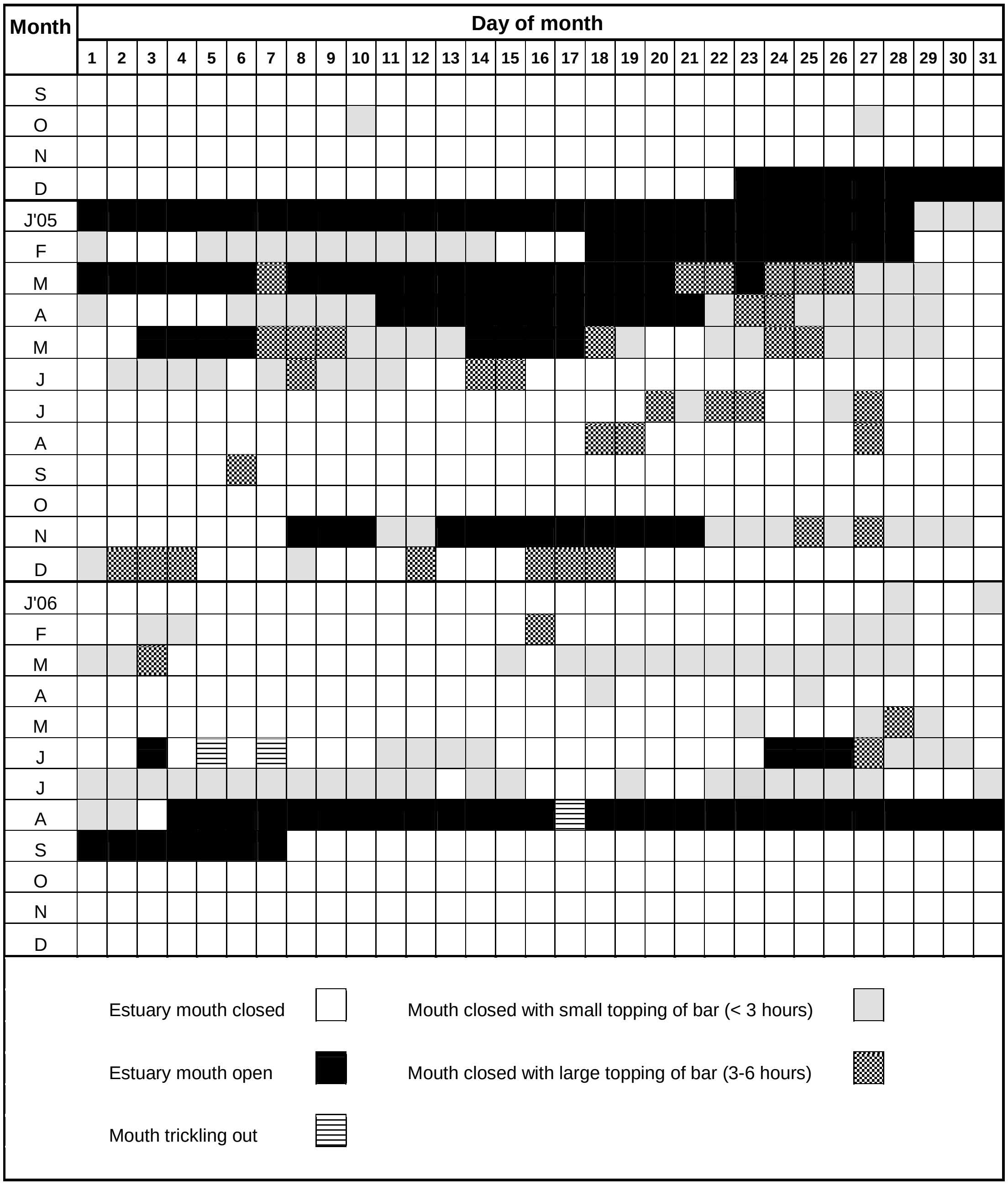

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Estuary mouth closed □

Mouth closed with small topping of bar (< 3 hours) ░

Estuary mouth open ■

Mouth closed with large topping of bar (3-6 hours) ▓

Mouth trickling out ☰