FISH POPULATION DYNAMICS IN A TEMPORARILY OPEN/CLOSED SOUTH AFRICAN ESTUARY

A thesis submitted in fulfilment of the
requirements for the degree of
Doctor of Philosophy
of Rhodes University

by

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Ecological communities do not exist in a benign harmony, but, instead, are shaped by many forces, some of them chaotic, some random. Above all, there is constant, dynamic change.

The neighbouring West Kleinemonde and East Kleinemonde estuaries on the south-eastern Cape coast of South Africa (Photo: 1973).

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ABSTRACT

The primary aim of this study was to investigate the population dynamics of the fishes associated with a small (17.5 hectares) temporarily open/closed estuary on the south east coast of South Africa. The results are based on the findings of an intensive sampling programme conducted over a period of four years in the East Kleinemonde estuary (33° 32' S : 27° 03' E). By adopting a quantitative approach, this study addresses the need for information on estuarine-associated fish population sizes, standing stock (biomass) estimates and productivity.

The ichthyoplankton assemblage in the surf zone adjacent to the mouth of the estuary was dominated by postflexion larvae representing at least 21 taxa in 14 families. *Rhabdosargus holubi* of sizes ranging between 9 mm and 21 mm BL was the most abundant species with a mean density of 7.3 individuals per 100 m^3. This species, which accounted for 77.6% of the catch composition, was recorded throughout the year but revealed a distinct peak in abundance in spring (August - September).

The ichthyofaunal community within the East Kleinemonde estuary was dominated by juvenile marine-spawning species and typical of a warm temperate southern African estuary. A total of 30 species in 17 families was recorded, including the endangered estuarine pipefish *Syngnathus watermeyeri*. Multivariate analyses (classification and ordination) of the catch assemblages revealed a high degree of similarity (> 70%) throughout the estuary, with two distinct groups being identified on the basis of substratum type. The sampling stations near the mouth with a sandy substratum were distinguished from all other sampling sites in the estuary.

The dominant estuarine-spawning species were represented by all life-history stages, suggesting that they bred successfully in the estuary. This group was numerically and gravimetrically dominated by the two zooplanktivorous shoaling species *Gilchristella aestuaria* and *Atherina breviceps* with density extrapolated population size estimates of 420 973 and 198 275 individuals, and biomass estimates of 1.6 and 0.6 g m^{-2} respectively. The total population size of all estuarine-spawning species with a mean biomass of 3.4 g m^{-2} was estimated at 754 217 individuals.

Population size estimates of the marine-spawning species were calculated using data obtained from three independent mark-recapture experiments. The assumptions for the

mark-recapture analyses were adequately met and it was concluded that the techniques provided reliable estimates of population size. However, estimates obtained from density extrapolation revealed enormous variability and were considered to be unreliable. The total population size was estimated at 63 342, 18 592 and 135 192 during the three mark-recapture experiments respectively. The numerically dominant species during all three experiments was *Rhabdosargus holubi*.

Biomass production of the marine-spawning species was evaluated over a 123 day census period when population sizes and estimates of growth rates were known. Productivity for all fishes with a standing stock of 26.2 g m^{-2} was calculated at 4.5 g m^{-2} $month^{-1}$. *Rhabdosargus holubi* accounted for more than 75% of the total marine fish productivity.

This study draws attention to the success of *Rhabdosargus holubi* in the East Kleinemonde estuary, which is ascribed to aspects of its biology. These include an extended breeding season, the ability to recruit into the estuary under adverse open mouth conditions and its omnivorous food habits. The dominance of this migratory species suggests that it plays an important role in the transfer of energy to the coastal marine environment when the mouth of the East Kleinemonde estuary opens.

Predation by birds and a dominant piscivorous fish (*Lichia amia*) was quantitatively assessed over a period of two years. Monthly food consumption by all piscivorous birds revealed large temporal variability, ranging from 32 to 466 kg $month^{-1}$. An unusual invasion of Cape cormorants during the winter of 1994 accounted for large scale mortality (2246 kg of fish) over a relatively short period. The predatory impact of this episodic event was reflected in the findings of the fish mark-recapture experiments, which revealed a 70% reduction in the total population of marine-spawning fishes (above a certain minimum size) in the estuary subsequent to this invasion. Monthly food consumption by the *Lichia amia* population in the estuary was calculated at 68 and 58 kg $month^{-1}$ for two distinct time periods when the population size was known. These findings suggest that this species is the top piscivorous predator in the East Kleinemonde estuary.

Finally, the findings of this study highlight the temporal variability of fish populations within a single estuary. It is suggested that predation and estuary mouth conditions are the main factors influencing the abundance (and its variability) of individual species in the East Kleinemonde estuary.

CHAPTER 1

INTRODUCTION

There are 250 functional estuaries along the South African coastline. Most of these systems are modest in size and represent drowned river valleys which were formed during earlier periods of lowered sea levels. Depending on the local geology, topography and physiography, each of these systems has evolved a suite of unique characteristics. These include depth, salinity and temperature regimes, access to the sea, vulnerability to flooding, mechanism of water mixing, and many more. Despite the high degree of variability between individual systems, Whitfield (1992a) developed a classification system to group southern African estuaries based on a variety of physiographical, hydrographical and salinity characteristics. The following five estuary types were identified: permanently open estuaries, temporarily open/closed estuaries, river mouths, estuarine lakes and estuarine bays.

Temporarily open/closed systems such as the East Kleinemonde estuary are by far the most numerous, comprising more than 70% of all South African estuaries. Throughout the scientific literature, these estuaries have been variously named or defined. For example, Begg (1978) referred to temporarily open/closed estuaries as 'lagoons', while Blaber (1981) and Day (1981) labeled them as 'blind' estuaries and Bennett (1989a) used the terms 'seasonally open' and 'normally closed' to describe two different temporarily open/closed estuaries. Other synonyms include 'seasonally closed' (Neira & Potter 1992), 'intermittently open' and 'bar-built' estuaries (Young *et al.* 1997). The use of various synonyms for this estuary type suggests that their suites of physiographical characteristics are specific to local conditions and possibly warrant further categorization. Despite this, the typical characteristics of temporarily open/closed estuaries include the following (after Whitfield 1992a):

- The link with the marine environment is blocked for varying lengths of time by a sand bar which forms at the mouth. Mouth opening events are usually sporadic and depend largely on rainfall in the catchment areas and the extent of the sand bar at the mouth.
- The tidal prism is normally small (less than 1×10^6 m^3 per spring tidal cycle) when the mouth is open and absent when the sand bar is fully formed.

- The salinity regimes of these systems range from typical riverine conditions during episodic flooding events to hypersaline conditions during prolonged droughts. However, mesohaline conditions (5.1 to 18 ‰) usually prevail under 'normal' conditions.
- The mixing process of these systems are influenced by both tidal and riverine inputs when the mouth is open and wind driven when the mouth is closed.

A large amount of scientific information is available on southern Africa estuaries, including a considerable amount published on their associated ichthyofauna (for a review see Whitfield 1998). The trends in estuarine ichthyological research over the past five decades were also recently documented by Whitfield (1996a). The latter review paper highlights the progress made from typical survey-type studies towards biological and ecological studies, and ultimately the assimilation and use of such information to address issues relating to the conservation, management and wise utilization of estuaries.

Most of the ichthyological research in Eastern Cape Province estuaries has been conducted in the larger permanently open systems such as the Kromme, Swartkops, Sundays, Kariega and Great Fish (Melville-Smith & Baird 1980; Beckley 1984; Hanekom & Baird 1984; Marais 1985; Harrison & Whitfield 1990; Ter Morshuizen *et al.* 1996; Paterson & Whitfield 1996), with little attention being directed at the smaller temporarily open/closed estuaries. Although Dundas (1994) provided a preliminary analysis of fish abundance and diversity in three temporarily open/closed systems in the St Francis Bay region (Kabeljous, Seekoei and Van Stadens) none of this information has been published. Elsewhere in South Africa several detailed studies have been conducted on temporarily open/closed estuarine systems. For example, Harrison & Whitfield (1995) documented the ichthyofaunal diversity and ecology of three small temporarily open/closed estuaries in KwaZulu-Natal. In the Western Cape Province detailed ichthyological studies have been conducted on the large temporarily open/closed estuarine lakes of Swartvlei (Whitfield 1988, 1993) and Bot/Kleinmond (Bennett 1985; Bennett *et al.* 1985; Bennett & Branch 1990).

Despite an early appeal by Day (1977) to conduct quantitative studies of estuarine biota, little information exists on the population sizes and productivity of estuarine faunal and floral communities. The difficulties associated with conducting quantitative studies on estuarine-associated fishes can be ascribed to a number of reasons. Firstly, fishes are highly mobile and require specialized sampling techniques to capture them. Secondly, estuaries are relatively unpredictable environments and numerous variables influence the abundance of fishes that utilize these ecosystems (for a review see Whitfield 1996b). Thirdly, it is well established that most South African estuarine-associated fishes spawn in the marine environment and immigrate into estuaries as larvae, postlarvae or small juveniles. The migration into estuaries is seasonal, but many species exhibit extended spawning periods often resulting in pulses of recruitment over a period of several months (Whitfield & Kok 1992). Juveniles then remain in estuaries for a short period of time (usually < 1 year) before emigrating back to sea. It is clear, therefore, that estuarine fish population sizes are seldom constant due to variable recruitment patterns and continuous migrations.

The ecological significance of the above life-history strategy is that migratory fishes are capable of exporting accumulated estuarine productivity (energy) to the marine environment (Deegan 1993). However, such assessments are only possible with knowledge of fish population sizes, growth rates and mortality (i.e. biomass production) during their estuarine residence phase. The importance of conducting quantitative studies is further highlighted by the fact that many estuarine-associated fishes (e.g. *Argyrosomus japonicus*, *Lichia amia*, *Lithognathus lithognathus* and *Pomadasys commersonnii*) have high recreational and commercial value. Quantitative information of early life-history population parameters such as recruitment success, population size and mortality will assist with the effective management of these fishery species.

The present study aims to provide a quantitative analysis of the ichthyofaunal population dynamics and productivity of the dominant fish species in a single estuarine system. The key objectives of the study were:

- To determine the seasonality and relative abundance of estuarine dependent ichthyoplankton in the surf zone adjacent to the mouth of the East Kleinemonde estuary.
- To investigate the fish community structure in the estuary.
- To determine the relative abundance, biomass and population dynamics of the resident estuarine-spawning fishes in the estuary.
- To estimate population size, growth rates and productivity of the dominant marine-spawning fishes in the estuary.
- To estimate fish predation (mortality) by piscivorous birds and fishes in the estuary.

In the following chapter the location, historical background, physico-chemical characteristics, mouth dynamics and floral characteristics of the East Kleinemonde estuary are described. In Chapter 3 the diversity, size composition, seasonality and abundance of the ichthyoplankton in the surf zone adjacent to the estuary mouth are studied. The ichthyofaunal community structure in the estuary is examined in Chapter 4, while the dynamics of resident estuarine-spawning fishes are investigated in Chapter 5. In Chapter 6 population size estimates (using mark-recapture techniques) of the marine-spawning fishes are documented, while estimates of fish predation losses by piscivorous birds and fishes are given in Chapter 7. Estimates of growth, biomass and production for the dominant marine-spawning species are provided in Chapter 8. Chapter 9 concludes with a general discussion on the important findings of this study and provides recommendations on the future management of the East Kleinemonde estuary.

CHAPTER 2

STUDY SITE

2.1 INTRODUCTION

The East Kleinemonde estuary is situated approximately 15 km north-east of Port Alfred in the Eastern Cape Province of South Africa and reaches the sea on the coordinates 33° 32′ S and 27° 03′ E (Figure 2.1). The mouth region of this estuary is accessible via either Diaz Road (eastern bank) or Island road (western bank) off the main coastal road (R72) between Port Elizabeth and East London, which crosses the estuary approximately 750 m from the mouth. The estuary and its entire catchment area falls within the jurisdiction of the Western Region District Council (WRDC), formally known as the Algoa Regional Services Council. Residential development in the area consists of three townships, namely Seafield on the eastern bank, and Island Beach and Island Beach North on the western bank (Figure 2.2). The controlling authority of these settlements is the Seafield Local Council District of Bathurst under the auspices of the WRDC. Recently, the Council made application to change the name of Seafield in an attempt to resurrect the historic and commonly used name of Kleinemonde. The name change was accepted, but as two words (*viz.* Kleine Monde) to avoid confusion with the Western Cape town of Kleinmond.

2.1.1 Historical background

Limited historical anecdotes exist for the Seafield/Kleine Monde area prior to the arrival of the British settlers in 1820. According to Jones (1969) the term Kleinemonde (Kleine Monden) was not the name given to the area but merely the word(s) used by early Dutch sailors to describe a shoreline feature where the mouths of the neighbouring East and West Kleinemonde estuaries approached the beach close together. The area, known then as the south-eastern part of the district of Albany, was first surveyed between 1820 and 1822 to show the situation and exact boundaries of the land allotted to the British settlers. During this survey the names Wellington River and Lyne Doch River were assigned to the East and West Kleinemonde estuaries respectively and were adopted by the settlers. However, the names East Kleinemonde (Kleinemonde Oos) and West Kleinemonde (Kleinemonde Wes) were later resurrected and are currently the official names for these two estuaries.

The land allotted to the 1820 settlers along the coastal strip was primarily used for agriculture (cattle grazing) and accessible only by road from the township of Bathurst. However, in 1847 a 'harbour' known as Port Jessie was established in the semi-sheltered bay (Cawood's Bay) on the leeward side of Kleinemonde Point. Port Jessie consisted of an anchorage in Cawood's Bay with beach-landings of cargoes by surf-boats over warps, immediately west of the Lyne Doch River mouth. Thorpe (1977) noted that regular sailing between Port Jessie and Cape Town took place, but in 1848 the cargo ship *Waterloo* was wrecked in the bay and the 'harbour' project was abandoned. This report dispels rumours that the mouths of these estuaries were once permanently open and deep enough for ships to enter. Most of the documented history during this era is recorded in *The Chronicle of Jeremiah Goldswain* (published by the Van Riebeeck Society).

Holiday cottages at the mouths of the Kleinemonde estuaries were first erected by local farmers subsequent to the establishment of the Seafield township in 1836 (Messrs T. Webb, Tharfield Farm and C. Fletcher, Clifton Farm pers. comm.). Today the township of Kleine Monde (Seafield, Island Beach and Island Beach North) comprises 500 plots zoned for residential development. The small residential area (Kleinemonde West Shareblock) on the western bank of the West Kleinemonde estuary consists of approximately 40 plots.

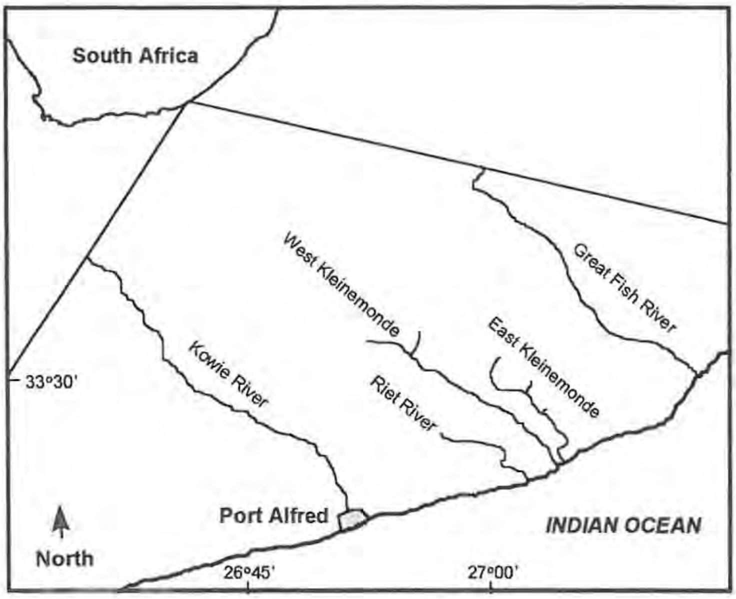

Figure 2.1 The location of the East Kleinemonde and other estuaries on the south-eastern coastline of South Africa.

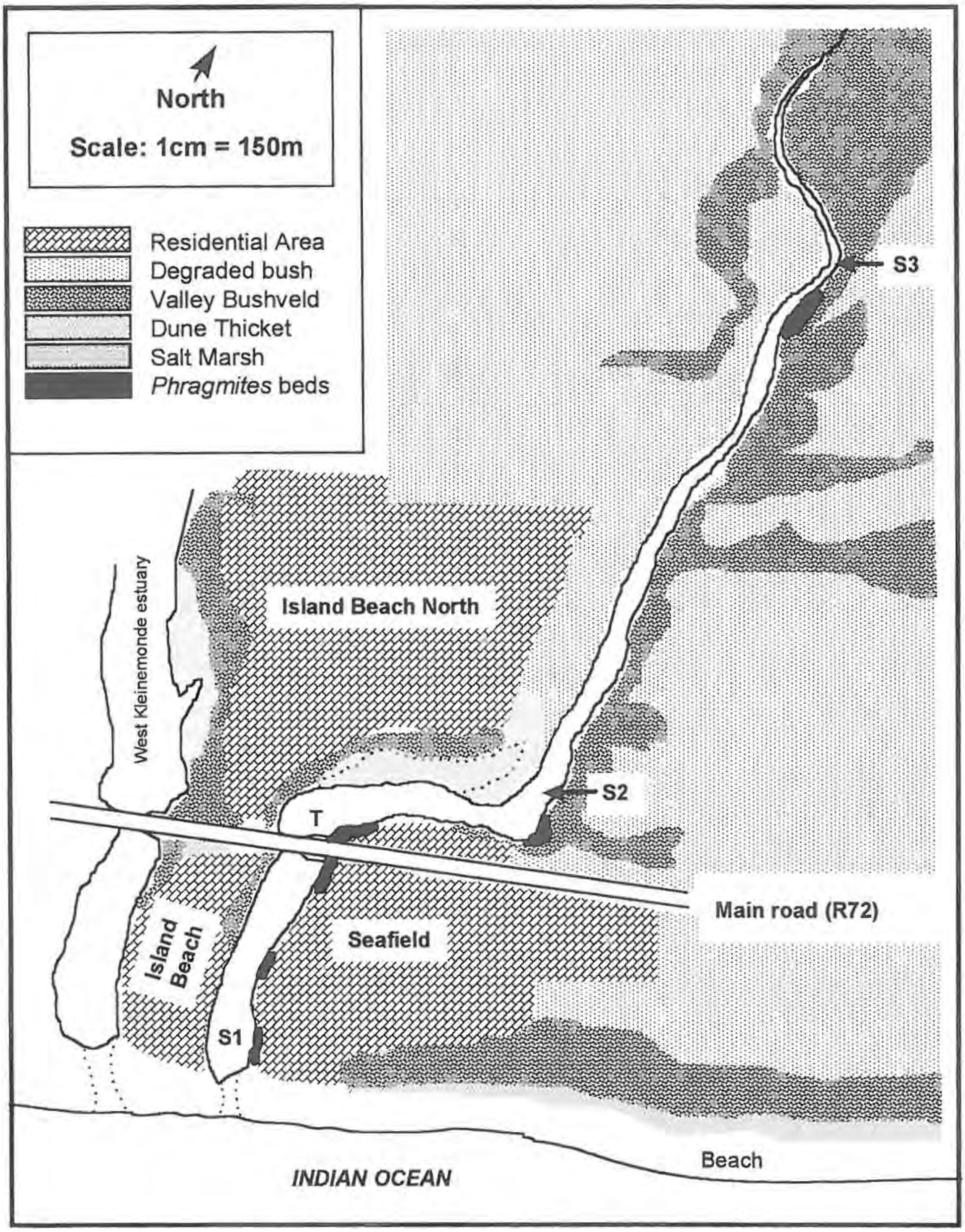

Figure 2.2 Map of the East Kleinemonde estuary showing the main vegetation types (adapted from Adams 1997), location of the residential areas and the stations where temperature (T) and salinity (S1, S2, S3) data were recorded.

2.1.2 Climatic conditions

The climate of the south-eastern part of the Eastern Cape Province has been described by several authors (*inter alia* Heydorn & Tinley 1980; Stone 1988; Stone *et al.* 1998). Along the coastal belt relatively mild summers and winters prevail. Although temperatures as high as 40 °C and as low as 0 °C have been recorded, the coastal region is generally influenced by both the cooling and warming effects (in summer and winter respectively) of the sea (Stone *et al.* 1998). Temperature data obtained from the Fish River Lighthouse (approximately 7 km from the mouth of the East Kleinemonde estuary) are shown in Figure 2.3. Mean monthly minimum air temperatures range from 10.2 °C (July) to 17.8 °C (January), and mean monthly maximum temperatures range of 19.7 °C (August) to 24.5 °C (January).

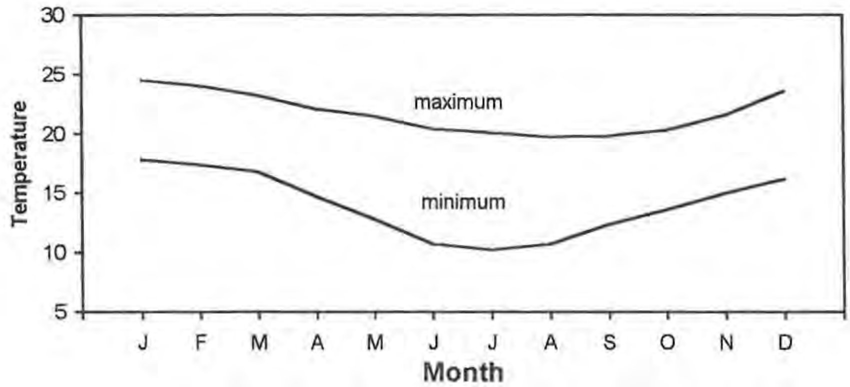

Figure 2.3 Mean monthly minimum and maximum air temperatures (°C) recorded at the Fish River Lighthouse between 1960 and 1997 (Source: Weather Bureau records, *in litt.*)

Rainfall along the south-eastern coastal belt of the Eastern Cape is highly variable. According to Kopke (1988) the area around Knysna in the south-west experiences all-year-round rainfall, with an average annual precipitation of 738 mm. Port Elizabeth, however, receives an overall winter maximum rainfall (mean annual rainfall = 616 mm). The area further east, on the other hand, exhibits a bimodal (spring and autumn) distribution of rainfall which is largely spring dominant. Kopke (*op cit.*) notes that an important feature of the climate along the south-eastern Cape coastal belt is the regular occurrence of three-day-rain events during March and/or late August. These rains are caused by either an intense influx of polar air or by a high pressure system to the south of Port Elizabeth feeding cool, moist air into the region. If the system coincides with a cutoff low pressure area over the interior, large floods can occur in the coastal region (Stone *et al.* 1998).

2.2 THE COASTAL ENVIRONMENT

2.2.1 Hydrography

The coastline adjacent to the East Kleinemonde estuary runs in a roughly north-east/south-west direction (Figures 2.1 and 2.2). The continental shelf in the area is fairly narrow with a steep shelf slope approximately 30 km offshore. However, approximately 60 km further south (near Cape Padrone) the continental shelf starts widening to form the broad Agulhas Bank. This transitional region, known as the Port Alfred upwelling cell, has a strong influence on the local hydrography. According to Lutjeharms (1998) sea surface temperatures of this sector are extremely variable and can change dramatically within days when the wind changes, sometimes resulting in mass mortalities of marine animals. Furthermore, during upwelling events the substantial body of cooler water resident on the shelf in this region may serve as an impenetrable barrier to coastal tropical organisms that would otherwise move much farther south.

Badenhorst (1988) made use of data obtained by Voluntary Observing Ships (after Swart & Serdyn 1981) to describe the coastal hydraulics in the Kleinemonde region. He noted that due to the orientation of the coastline and the screening off of swells by Cape Padrone to the south-west and Great Fish Point to the north-east only deep sea swells between 60° and 250° can reach the Kleinemonde beach unaffected. Waves approaching the coast at an oblique angle are predominantly from the south-eastern sector (200° to 250°). Therefore, the longshore current and longshore sediment movement is mostly in an easterly direction.

2.2.2 Wind and aeolian sand transport

Wind frequency and direction data collected from Voluntary Observing Ships and the Fish River Lighthouse weather station were used by Badenhorst (1988) to calculate aeolian sand transport at the Kleinemonde beach. He concluded that south-westerly and westerly winds occurred most frequently, while north-easterly winds were recorded only occasionally. The calculated aeolian drift revealed a net sediment movement towards the north-east (Table 2.1). Despite some variability, transported sand generally accumulates in the mouths of the East and West Kleinemonde estuaries from the south-west (Plate 2.1).

Table 2.1 The potential aeolian drift rate at the Kleinemonde beach (after Badenhorst 1988).

Directional component	Aeolian drift rate (m^3 yr^{-1} km^{-1})
Eastbound	24000
Westbound	6000
Northbound	2000
Southbound	600

Plate 2.1 The mouth regions of the East and West Kleinemonde estuaries showing the accumulation of sand (indicated by arrows) which moves mostly in an north-easterly direction (Photograph: A. K. Whitfield, May 1993).

2.3 THE ESTUARINE ENVIRONMENT

2.3.1 Physical and chemical characteristics

The East Kleinemonde estuary has the following physical and chemical characteristics:

Estuary type

According to the classification of estuarine types proposed by Whitfield (1992a), the East Kleinemonde system is a temporarily open/closed estuary.

Catchment

Badenhorst (1988) estimated the catchment size of the East Kleinemonde estuary at 46.3 km^2. Most of the gentle sloped high-lying region of the catchment area is characterized by degraded agricultural land which is used primarily for extensive cattle ranching. However, the stream and river valleys are relatively undisturbed and covered by Valley Bushveld vegetation.

Mean Annual Run-off

The simulated mean annual run-off is 2×10^6 m^3 (Badenhorst 1988).

Estuary size

This small estuary has a surface area of approximately 175 000 m^2, excluding the shallow salt marsh area which is only inundated during periods of high water levels. It is navigable for approximately 3 km and the widest portion (in the lower reaches) is 120 m (see Figure 2.2).

Bathymetry

The estuary is mostly shallow, with the main channel depth ranging between 1 and 2 m in the navigable portion of the system. After a mouth opening event the estuary is very shallow with a maximum channel depth of approximately 1 m. During periods of extended mouth closure the estuary water level often exceeds that of mean sea level (approximately MSL+2 m) due to extensive sandbar development on the seaward side of the mouth.

Temperature

Mean monthly surface temperatures range from 14.9°C (June) to 27°C (January) with some vertical temperature stratification which is slightly more pronounced during the summer (Figure 2.4).

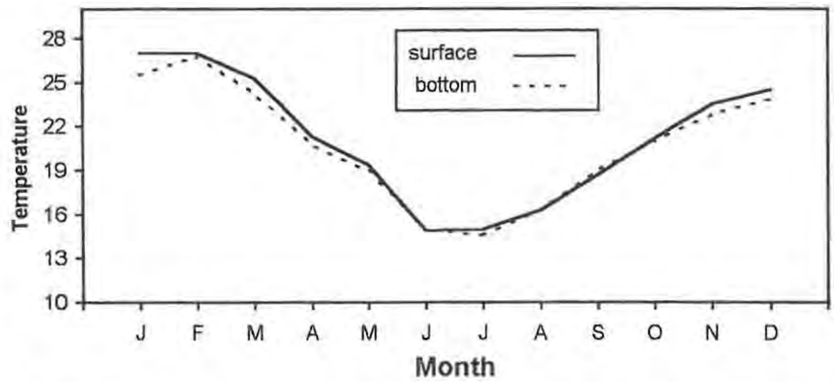

Figure 2.4 Mean monthly surface and bottom temperatures (°C) taken in the middle reaches of the East Kleinemonde estuary.

Salinity

Figure 2.5 illustrates the mean monthly salinities in the East Kleinemonde estuary from March 1994 to March 1996. During this period the salinity regime varied between oligohaline conditions (< 5‰) to mostly mesohaline conditions (5 - 18‰), depending on the amount of rainfall and condition of the estuary mouth. It was noted that mouth opening events occurred during or shortly after periods of high rainfall (usually in months with rainfall exceeding 100 mm) (see Figure 2.6). Salinity levels decline rapidly prior to mouth opening events (e.g. July - September 1994 and December 1994 - January 1995) due to riverine input. During the open mouth phase, seawater rarely extends beyond the lower reaches, thereby creating a steep salinity gradient between the mouth and head of the estuary (e.g. January - May 1995). After mouth closure, salinity levels rise and the rate at which they increase is dependent on the extent of bar topping (overwash) events. For example, during the period March to July 1994 salinity levels rose rapidly due to a number of large bar topping events. However, during the closed mouth phase subsequent to July 1996, salinity levels rose slowly due to evaporation not overwash events (see Figure 2.6). During periods of extended mouth closure salinities throughout the estuary are relatively uniform, with the exception of occasional declines in salinity in the upper reaches following river pulses.

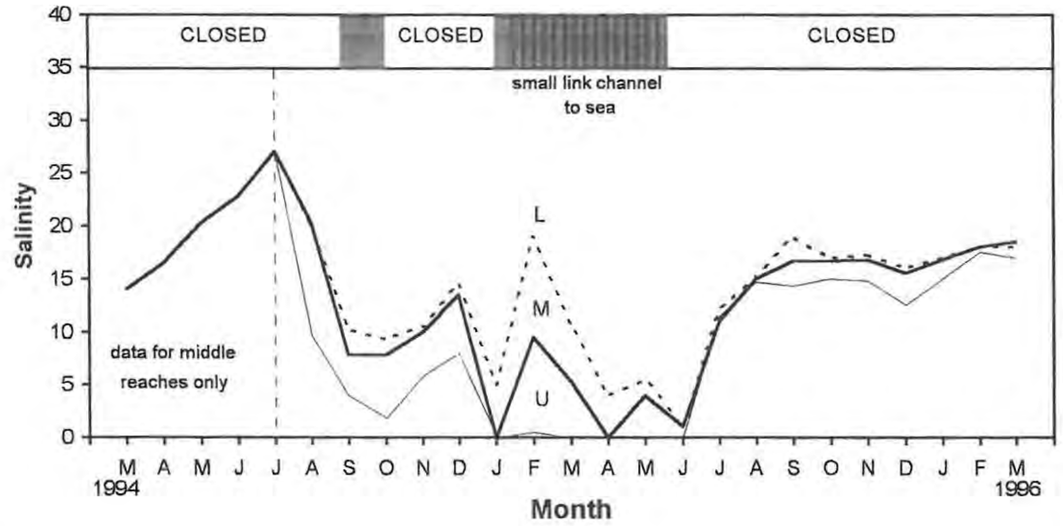

Figure 2.5 Mean monthly surface salinity in the lower (L), middle (M) and upper (U) reaches of the East Kleinemonde estuary between March 1994 and March 1996. Shaded areas indicate mouth opening events.

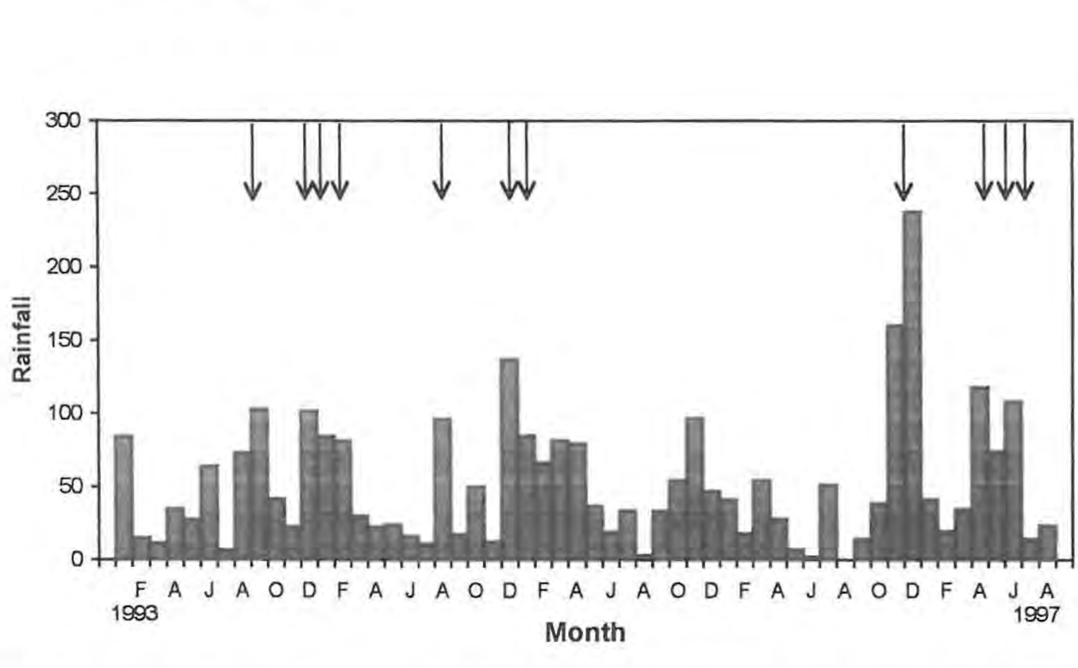

Figure 2.6 Monthly rainfall (mm) recorded at the Fish River Lighthouse from January 1993 to August 1997. Mouth opening events at the East Kleinemonde estuary are indicated by arrows.

Water quality

No comprehensive surveys of water quality in the East Kleinemonde estuary have been undertaken. However, Harrison *et al.* (1996) using the water quality rating index (after

Cooper *et al.* 1994) described the water quality of the East Kleinemonde estuary as being good and awarded it a score of 7.3 out of a possible 10. The water quality impairment was attributed to slightly elevated *E. coli* levels. Although there is currently no evidence of pollution, attention has been drawn to the potential threat of microbial contamination of the estuary from septic tank overflows (Kleine Monde Ratepayers *in litt.*).

2.3.2 Mouth dynamics

The condition of the East Kleinemonde estuary mouth was recorded on a daily basis from March 1993 to August 1997 (Figure 2.7). An analysis of these records revealed that the mouth was closed for 71.8% of the time, and open mouth conditions were recorded on only 43 days (2.6%). Overwash conditions consisting of small bar topping events (i.e. < 3 hours) occurred fairly frequently (23.7%), but large overwash events (i.e. 3 - 6 hours), associated with storm conditions and high seas, occurred on only 31 days (1.9%). During the study period, the mean duration of the open mouth phase was four days (range = 1 to 13).

Badenhorst (1988) states that the East and West Kleinemonde estuaries usually share a common mouth during the open phase. The brief periods of open mouth conditions are attributed to the predominantly north-east bound aeolian and longshore sediment movement, resulting in the formation of sandbanks and ultimately mouth closure. However, the mass removal of sand in the mouth region during the flood (mouth opening) lowers the sandbar and allows seawater to enter the estuary during bar topping events for varying lengths of time after mouth closure. Such conditions persisted for several months following the mouth opening event in December 1994/January 1995 (Figure 2.7). Owing to the very short periods of truly open mouth conditions, overwash events are important not only in elevating estuarine salinities but also to allow for recruitment and emigration of marine-spawning fishes. The importance of these events are discussed in Chapter 9.

Mouth opening was associated with periods of high rainfall (Figures 2.6 and 2.7). During the study period, mouth opening events were recorded during every month of the year except March and July, highlighting the unpredictable nature of these phases. Based on these observations the temporarily open/closed East Kleinemonde estuary can be classified as a system which is predominantly closed with sporadic unseasonal mouth opening events.

In an attempt to document the historical (later than 1938) changes in the lower region of the East and West Kleinemonde estuaries, Badenhorst (1988) examined six sets of aerial photographs taken between 1938 and 1987. He concluded that a natural process of sedimentation was taking place in both estuaries. Although the sedimentation was probably accelerated by the construction of the road bridges in 1974, sand banks and increasing salt marsh areas were first observed in 1955.

Although Badenhorst (1988) commented on the condition of the estuary mouths, a closer examination of his figures and additional aerial photographs (see Table 2.2) revealed that the two estuaries used to open via separate mouths. However, in more recent times (approximately 1980 onwards) the two estuaries tend to share a common outlet after a flood event. The reason for this phenomenon is ascribed to increased residential and infrastructure development (notably the construction of the Island Beach peninsula car park) which resulted in destabilization and eradication of the fore dune vegetation and ultimately the removal of a dune ridge which once separated the two mouths. This observation is supported by several residents who claim that the dune separating the two mouths was once a popular venue for sand-boarding by children (Messrs B. Purdon, Island Beach and C. Fletcher, Clifton Farm pers. comm.).

Table 2.2 Description of the aerial photographs examined to document changes in the mouth regions of the East and West Kleinemonde estuaries. Photographs obtained from the Department of Land Affairs Chief Directorate : Surveys and Mapping.

Year	Job No.	Photo No.	Scale	Badenhorst (1988)
1934	101 A	2587	1:20000	-
1938	134/38	14015	1:25000	Figure 12
1955	360	9199	1:36000	Figure 13
1956	385	857	1:30000	-
1973	721	3586	1:50000	-
1979	326	198	1:8000	Figure 14
1980	374	82	1:20000	-
1981	391	172/4	1:20000	Figure 15
1987	-	-	-	Figure 16
1990	938	6070	1:30000	-

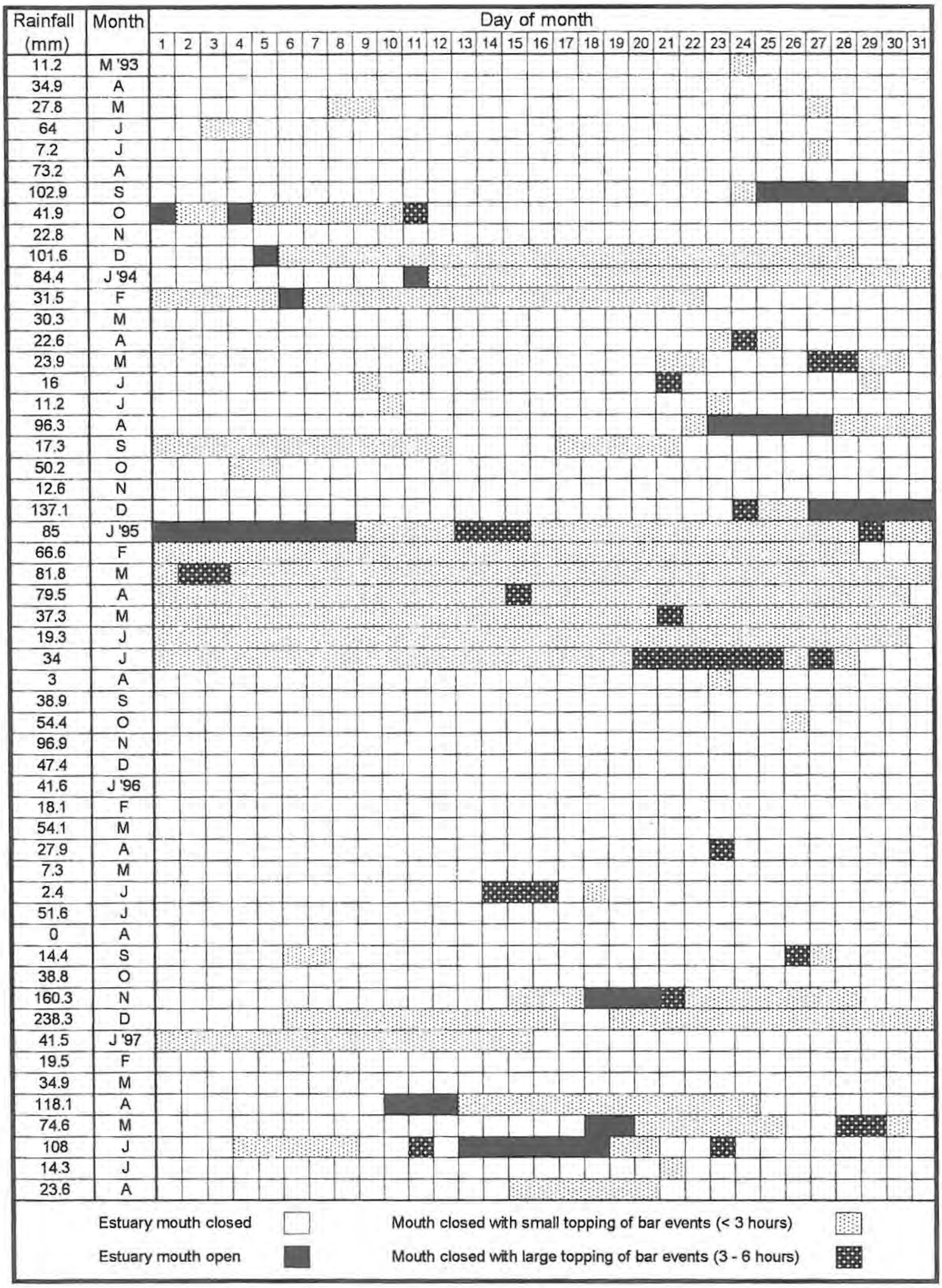

Figure 2.7 Monthly rainfall and condition of the East Kleinemonde estuary mouth from March 1993 to August 1997. Rainfall data obtained from the Weather Bureau records for the Fish River Lighthouse.

2.3.3 Floral characteristics

No published information is available on the terrestrial or aquatic vegetation associated with the East Kleinemonde estuary. However, a brief botanical survey was conducted on 21-22 January 1997 (Adams 1997). The findings of this survey are summarized below and a list of the dominant macrophyte species associated with the East Kleinemonde estuary are given in Table 2.3.

Table 2.3 The dominant macrophytes associated with the East Kleinemonde estuary (after Adams 1997).

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

Phytoplankton

Water column samples were collected at five sites in January 1997 and analyzed for chlorophyll-a content by Adams (1997). The mean chlorophyll-a content was generally low (4.2 ± 0.9 mg l^{-1}) and increased from the mouth region (2.7 ± 0.5 mg l^{-1}) towards the upper reaches (5.2 ± 0.6 mg l^{-1}). The dominant microalgal group was estuarine flagellates which occurred in similar densities throughout the estuary. Blue-green algae (*Euglena* spp.) and diatoms were also recorded.

Submerged macrophytes

The dominant submerged macrophyte was *Ruppia cirrhosa* which occurred mostly above the road bridge forming a continuous band along both banks of the estuary. The seagrass *Halophila ovalis* was also recorded.

Salt marsh vegetation, reeds and sedges

The lower reaches of the east bank is dominated by houses with lawns up to the water's edge, and several small stands of *Phragmites australis* (Figure 2.2). Scattered *Juncus kraussii* and *Sporobolus virginicus* plants occur close to the mouth on the west bank which is mostly steep and rocky.

A small salt marsh area occurs on the west bank just above the road bridge (Figure 2.2). *Sarcocornia perennis* forms a 1 m band close to the water's edge. Above this is a 2 m zone of *Sporobolus virginicus* and *Sarcocornia decumbens* followed by a 5 m zone of *Juncus kraussii*.

Three stands of *Phragmites australis* occur on the east bank above the road bridge, indicative of areas of freshwater seepage. Little other intertidal vegetation occurs along the fairly steep sloping east bank, and Valley Bushveld extends to the water's edge in most areas (Figure 2.2). The more gentle sloping west bank is grassy with scattered *Acacia cyclops* and *A. karroo* trees. The dominant fringe marsh species are *Sporobolus virginicus, Salicornia meyeriana, Juncus kraussii, Sarcocornia decumbens* and the sedge *Fuirena hirsuta*.

CHAPTER 3

SURF ZONE ICHTHYOPLANKTON

3.1 INTRODUCTION

The ichthyoplankton associated with estuaries originate from three possible sources. They are either recruited from the riverine areas above the head of the estuary, spawned in the estuary or recruited from the marine environment. Most of the fish species occurring in South African estuaries spawn in the marine environment and recruit at various stages of development (Wallace 1975; Melville-Smith & Baird 1980; Whitfield & Kok 1992). The species which recruit at an early larval stage are dependent on factors such as planktonic food availability (Whitfield 1985), estuary mouth conditions (Whitfield 1996b) and a number of other abiotic factors such as turbidity, temperature, salinity (Martin *et al.* 1992; Harris 1996).

Most studies on larval fishes in southern Africa have been conducted in either the offshore and nearshore marine environments (*inter alia* Olivar & Fortuno 1991; Beckley 1993; Olivar & Shelton 1993; Olivar & Beckley 1994; Tilney & Buxton 1994; Beckley & Connell 1996) or within estuaries (Melville-Smith & Baird 1980; Beckley 1985; Whitfield 1989a,b). Despite considerable research highlighting the importance of estuaries to the early life-history stages of marine-spawning fishes, very few studies have investigated the movement, abundance and seasonality of larvae in the surf zone adjacent to estuary mouths. Clearly, the surf zone represents an important transit region for larvae recruiting from the nearshore marine environment (spawning area) to an estuary (nursery area). However, only two studies in South Africa have investigated ichthyoplankton communities in the surf zone near estuary mouths. Whitfield (1989c) examined the larval fish assemblage in the Swartvlei Bay (southern Cape) and Harris & Cyrus (1996) studied the larval and juvenile fishes at St Lucia (northern KwaZulu-Natal).

The aim of this study was to investigate the ichthyoplankton species composition, seasonality and abundance in the surf zone adjacent to the mouth of the East Kleinemonde estuary. In addition, the role of the surf zone as a possible interim nursery area is examined. The findings of this study are also compared with those of Whitfield (1989c) and Harris & Cyrus (1996).

3.2 MATERIALS AND METHODS

3.2.1 Sampling procedure

Ichthyoplankton samples were collected monthly between August 1994 and September 1996 in the surf zone adjacent to the mouth of the East Kleinemonde estuary. Collections were made using a floating plankton sled fitted with a 500 µm nylon mesh net which sampled the upper 300 mm of the water column. The net, with a mouth area of 0.17 m^2 was attached to a 3 m rope and towed through the surf zone, parallel to the shoreline in water ranging from 0.5 to 1.5 m in depth. The net was towed at a rate of approximately 1 m s^{-1} for a duration of exactly two minutes. The mean volume of water passing through the net for each tow was estimated at approximately 20 m^3. Ichthyoplankton catches were recorded as the number of fish caught per two minute tow. For comparative purposes the catch per tow was multiplied by a factor of five to obtain a density value (i.e. number per 100 m^3). Initial sampling trials indicated that sampling over the low tide period was difficult due to a lack of water depth. According to the classification of beach types by Short & Wright (1983), the general beach morphology in the region was classified as an intermediate type with a ridge-runnel or low tide terrace. In an attempt to standardize the sampling procedure as far as possible, samples were only taken at or near high tide on days when sea conditions were fairly calm, with very little or no longshore current (side wash) and light winds. The number of plankton hauls and the environmental conditions recorded on all sampling days are given in Appendix 1. Two 24 hour sampling sessions were conducted on 11-12 February 1995 and 15-16 May 1995 respectively. On each occasion a triplicate series of two minute tows were taken every three hours over a full diel period.

3.2.2 Ichthyoplankton samples

Samples were preserved in the field with 10% formalin in seawater. After a period of one to two weeks fish samples were separated from the other plankton and debris, and stored in 60% propyl alcohol for subsequent analysis. All fish were measured to the nearest 0.1 mm body length (BL) using a dissecting microscope fitted with an eyepiece micrometer and identified to the lowest possible taxon using van der Elst & Wallace (1976), Melville-Smith (1978), Brownell (1979), Smith & Heemstra (1986), and Olivar & Fortuno (1991). Each taxa was assigned to an estuary-dependence category according to Whitfield (1998), where Ia = resident estuarine species which have not been recorded spawning in the marine or freshwater environment, Ib = resident estuarine species which also have marine or freshwater breeding populations, IIa = euryhaline marine species which breed at sea but juveniles are dependent on estuaries as nursery areas, IIb = euryhaline marine species which breed at sea while juveniles occur mainly in estuaries, but are also found at sea, IIc = euryhaline marine species which breed at sea while 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.

3.3 RESULTS

3.3.1 Taxonomic Composition

The catch composition and comparative abundance of ichthyoplankton captured in the surf zone adjacent to the mouth of the East Kleinemonde estuary are listed in Table 3.1. A total of 451 fishes, representing at least 21 taxa from 14 families were collected from 241 tows. All specimens captured, with the exception of five *Atherina breviceps*, were classified as larva according to Kendall *et al.* (1984). The majority of samples collected were in the postflexion stage of larval development.

The family Sparidae dominated the total catch composition with almost 85%, while Mugilidae, Soleidea, Monodactylidae and Atherinidae contributed 4.4%, 4.2%, 2% and 1.1% respectively. Each of the remaining eight families represented in the catch comprised less than 1%. The numerically dominant species was *Rhabdosargus holubi* which accounted for more than 77% of the overall catch. The other dominant taxa included unidentified Mugilidae (4.4%), *Diplodus sargus capensis* (4.2%), *Heteromycteris capensis* (3.6%), *Monodactylus falciformis* (2%) and a single unidentified sparid species (1.8%). The remaining taxa collectively only comprised 6.4% of the total catch.

Making use of Whitfield's (1998) estuary-dependence categorization of fishes, the overall ichthyoplankton catch composition revealed a high degree of estuarine dependence. Euryhaline marine species (category II) comprised almost 95% of the total catch. *Rhabdosargus holubi* was the most abundant species in category IIa. Other taxa in this category included *Monodactylus falciformis* (2%), *Elops machnata* (0.7%) and the unknown contribution of *Mugil cephalus* in the catch of Mugilidae.

Table 3.1 Ichthyoplankton catch composition (ranked according to family abundance) from the surf zone adjacent to the mouth of the East Kleinemonde estuary between August 1994 and September 1996. The estuary-dependence category for each species are according to Whitfield (1998).

Family	Species	Number caught	Percentage catch composition	Estuary-dependence category
Sparidae	*Rhabdosargus holubi*	350	77.6	IIa
	Diplodus sargus capensis	19	4.2	IIc
	Sarpa salpa	2	0.4	IIc
	Unidentified (1 species)	8	1.8	(?)
	Total	**379**	**84.0**	
Mugilidae	Unidentified, but including *Liza richarsonii* & *Mugil cephalus*	20	4.4	IIc, IIa
	Total	**20**	**4.4**	
Soleidea	*Heteromycteris capensis*	16	3.5	IIb
	Solea bleekeri	3	0.7	IIb
	Total	**19**	**4.2**	
Monodactylidae	*Monodactylus falciformis*	9	2.0	IIa
	Total	**9**	**2.0**	
Atherinidae	*Atherina breviceps*	1	0.2	Ib
	post larval specimens	5	1.1	
	Total	**6**	**1.3**	
Blenniidae	Unidentified (1 species)	3	0.7	(?)
	Total	**3**	**0.7**	
Clupeidae	*Gilchristella aestuaria*	1	0.2	Ia
	Unidentified (1 species)	2	0.4	(?)
	Total	**3**	**0.7**	
Elopidae	*Elops machnata*	3	0.7	IIa
	Total	**3**	**0.7**	
Gobiidea	*Psammogobius knysnaensis*	3	0.7	Ia
	Total	**3**	**0.7**	
Clinidae	*Clinus superciliosus*	1	0.2	Ib
	Unidentified (1 species)	1	0.2	(?)
	Total	**2**	**0.4**	
Tetradontidae	Unidentified (1 species)	2	0.4	III (?)
	Total	**2**	**0.4**	
Bothidae	Unidentified (1 species)	1	0.2	(?)
	Total	**1**	**0.2**	
Syngnathidae	*Syngnathus acus*	1	0.2	Ib
	Total	**1**	**0.2**	
Total		**451**	**100**	

The species in category IIb included *Heteromycteris capensis* (3.6%) and *Solea bleekeri* (0.7%). Species which are not dependent on estuaries (category III) contributed only 0.4% to the total catch, excluding the possible contribution of the 14 unidentified specimens. The capture of one *Gilchristella aestuaria* and three *Psammogobius knysnaensis* specimens occurred during and just after an open mouth phase of the estuary (26 August 1994 and February 1995, see Figure 2.6). This suggests that these individuals, which are resident estuarine species (category I) were washed out of the estuary at the time of opening.

3.3.2 Size Composition

The length frequencies for the three numerically dominant taxa (*viz. Rhabdosargus holubi, Diplodus sargus capensis* and Mugilidae) are given in Figure 3.1.

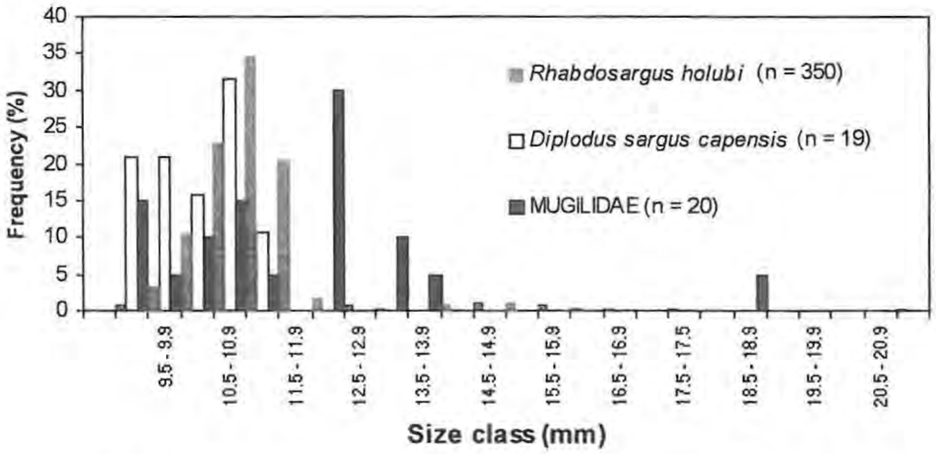

Figure 3.1 Length frequency distribution of the three most abundant taxa sampled in the surf zone adjacent to the mouth of the East Kleinemonde estuary (n = total number of fish sampled).

The mean individual size for *Rhabdosargus holubi* (11.3 mm), *Diplodus sargus capensis* (10.2 mm), Mugilidae (11.6 mm), *Heteromycteris capensis* (7.4 mm) and *Monodactylus falciformis* (5.3 mm) captured in the surf zone are similar to the size ranges reported in South African estuarine nursery habitats (Table 3.2). This possibly indicates that the taxa which are estuarine dependent as juveniles (category II) are in search of a suitable estuarine habitat for recruitment. Owing to the fact that the mouths of both the East and West Kleinemonde estuaries were closed for most of the sampling period (Appendix 1) it appears that the surf zone adjacent to these estuaries serves as an interim nursery area for estuarine dependent species.

Table 3.2 A comparison of size ranges (mm BL) of five abundant taxa recorded from the Kleinemonde surf zone and other estuarine localities in South Africa (TL = total length).

Reference	Locality	Species				
		Rhabdosargus holubi	*Diplodus sargus capensis*	Mugilidae	*Heteromycteris capensis*	*Monodactylus falciformis*
This study	Kleinemonde surf zone	9.3 to 21 mean = 11.3	9 to 11.4 mean = 10.2	9.2 to 18.5 mean = 11.6	6.3 to 8 mean = 7.4	4.6 to 6.1 mean = 5.3
Beckley (1985)	Swartkops estuary	9 to 13	9 to 10	12 to 14	7 to 10	
Harris (1996)	Richards Bay Habour Durban Harbour	6.5 to 11 7.5 to 11		9.5 to 11 2 to 10		
Harris & Cyrus (1995)	St Lucia estuary	6 to 12.2		5 to 23.5		
Harrison & Whitfield (1990)	Sundays estuary	mostly < 15		mostly < 15		
Melville-Smith (1978)	Swartkops estuary	7 to 20 (TL)			7 to 10 (TL)	6 to 11 (TL)
Whitfield (1989a)	Swartvlei estuary	9 to 10		8 to 11	6 to 8	4 to 7
Whitfield (1994a)	Great Fish estuary Sundays estuary Kariega estuary	5 to 10 (> 50%) 10 to 15 (> 40%) 15 to 20 (< 10%) mostly 10 to 15 mostly 10 to 15		mostly 15 to 30 mostly 15 to 30 mostly 15 to 30		

3.3.3 Seasonality

The mean monthly catches of ichthyoplankton in the surf zone adjacent to the East Kleinemonde estuary between August 1994 and September 1996 are given in Figure 3.2. Catches, expressed as the number caught per two minute tow, were lowest between November and April. The catch rate was highest between May and October with a distinct peak in abundance in August.

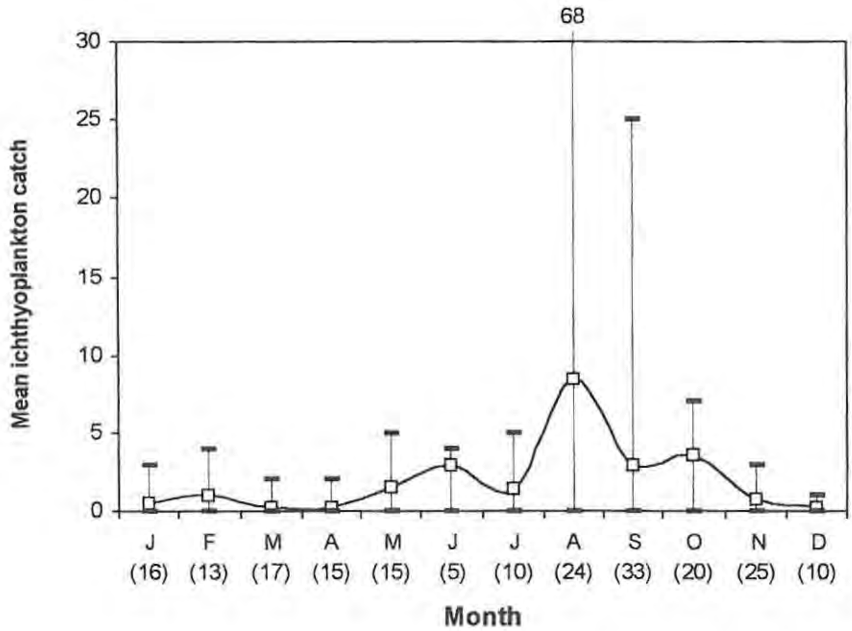

Figure 3.2 Mean monthly ichthyoplankton catches between August 1994 and September 1996 in the surf zone adjacent to the mouth of the East Kleinemonde estuary (vertical bars indicate minimum and maximum catch per two minute tow; numbers in parentheses indicate the total number of tows per month).

3.3.4 Larval Density

The density of the dominant species in the surf zone adjacent to the East Kleinemonde estuary were estimated by multiplying the catch (n per 2 min. tow) by five to obtain a value per 100 m^3 and compared with values obtained for the Swartvlei Bay (Whitfield 1989c) and St Lucia (Harris & Cyrus 1996) surf zones (Table 3.3). The densities of all the dominant taxa in the surf zone at Kleinmonde were lower than reported from both Swartvlei and St Lucia, with the exception of *Rhabdosargus holubi*, which was more abundant at Kleinemonde than St Lucia. The mean overall ichthyoplankton densities were also lowest at Kleinemonde with a mean density of 9 per 100 m^3, compared with 55 and 35 per 100 m^3 at Swartvlei and St Lucia respectively. These lower densities could be attributed to a number of reasons, such as different sampling techniques and different environmental and physical factors, including geographical location. Hence, a truly quantitative comparison of the three studies in the different regions would be speculative and inconclusive.

Table 3.3 Mean ichthyoplankton densities of certain taxa reported from the surf zones adjacent to the East Kleinemonde, Swartvlei and St Lucia estuaries.

Reference	This study	adapted from Whitfield (1989c)	Harris & Cyrus (1996)
Surf zone locality	Kleinemonde (diurnal sampling)	Swartvlei bay (diurnal sampling)	St Lucia (diel sampling)
Species	Mean Ichthyoplankton density (n per 100 m^3)		
Rhabdosargus holubi	7.3	13.4	3.5
Diplodus sargus capensis	0.4	3.3	2.1
Mugilidae	0.4	15.5	1.0
Heteromycteris capensis	0.3	7.2	*
Monodactylus falciformis	0.2	2.7	*

3.3.5 24-h experiments

The two 24-h sampling periods revealed no significant trends (Figure 3.3). A total of only 12 and 10 fish were caught during each 24-h sampling period, respectively. The corresponding mean densities over the 24-h period were calculated at 2.5 and 2.08 fish per 100 m^3. No significant differences ($F = 0.243$: $p = 0.629$) between day and night densities were observed, although Harris & Cyrus (1996) showed significantly higher nocturnal densities and Whitfield (1989c) showed significant diel differences in density only for *Rhabdosargus holubi*. Furthermore, statistical analyses of the East Kleinemonde data revealed no significant differences ($F = 0.636$: $p = 0.438$) for catches related to tidal phase.

3.4 DISCUSSION

The diversity of ichthyoplankton in the surf zone adjacent to the mouth of the East Kleinemonde estuary (21 taxa, 14 families) was similar to that found in the surf zone of the Swartvlei estuary (26 taxa, 16 families; Whitfield 1989c), but considerably less diverse than that reported from the subtropical region of St Lucia (88 taxa, 47 families; Harris & Cyrus 1996). The notable difference between the two temperate regions and St

Lucia is ascribed to the contribution of tropical offshore spawning species that are not dependent on estuaries as nursery areas (category III) at St Lucia.

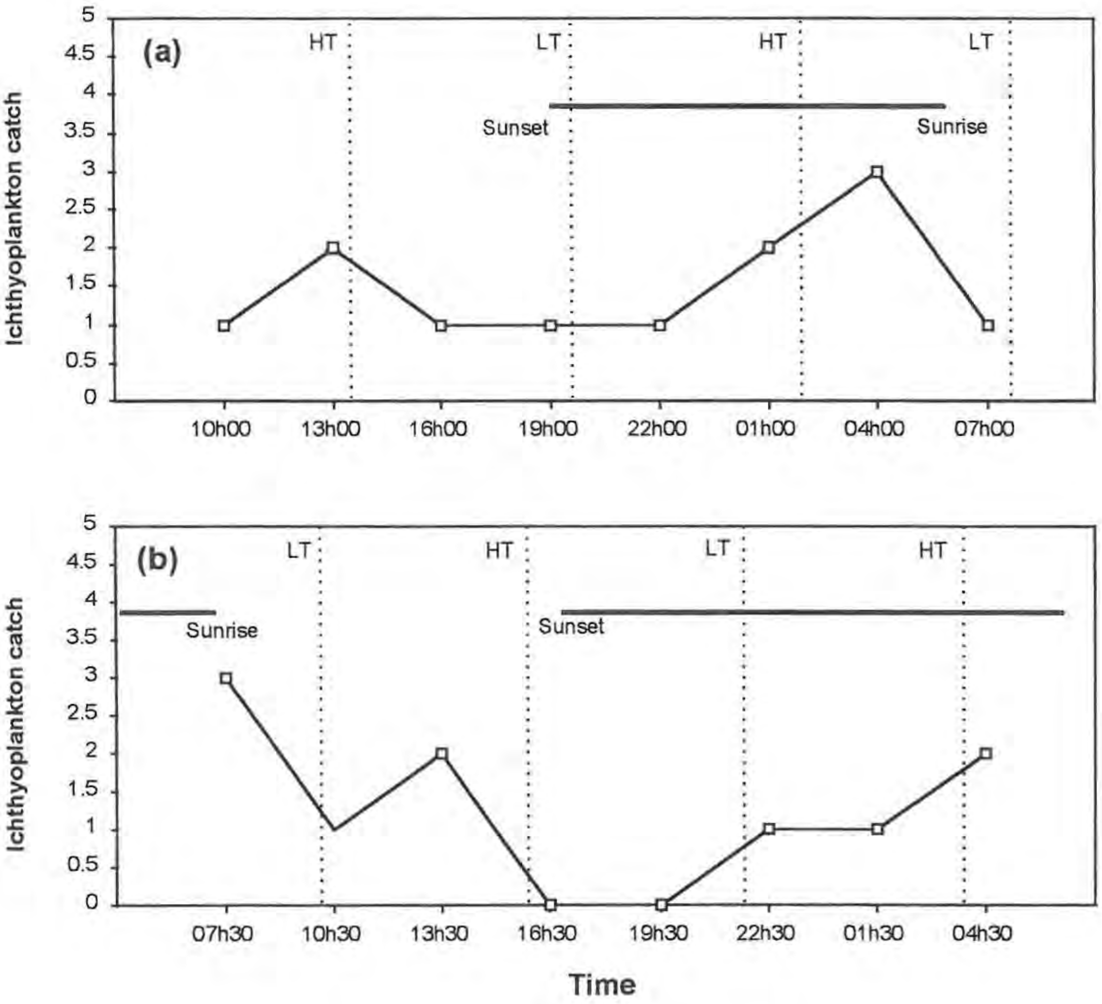

Figure 3.3 The combined ichthyoplankton catch from three tows for each sampling time, collected during two 24-h sampling periods conducted on **(a)** 11-12 February 1995 and **(b)** 15-16 May 1995. (LT = low tide; HT = high tide).

The high incidence of estuarine dependent ichthyoplankton in the surf zone at Kleinemonde coincides with the findings of Whitfield (1989c). His study revealed that more than 80% of the catch composition in the surf zone at Swartvlei consisted of category I and II species. Similarly, Harris & Cyrus (1996) found that taxa with some degree of estuarine association were most dominant and represented 60% in terms of density of larva in the surf zone at St Lucia. The predominance of estuary-associated marine species in all three studies could be interpreted to imply that the surf zone also serves as a nursery area. However, this study has provided increasing evidence to support the suggestion of Harris & Cyrus (1996) that the surf zone is used as a transit route or interim nursery area prior to estuarine recruitment and not as a true nursery area. The mean size of the estuarine associated larvae caught in the surf zone (mostly postflexion) corresponds with the documented size of larvae occurring in estuaries (Table 3.2). Therefore, the size of these species in the surf zone represents an optimal recruitment size. Furthermore, the stenotypic size frequency distributions and absence of larger individuals (post "recruitment size") suggests that the larvae do not remain in the area for long periods of time. The absence of larger specimens in the surf zone could however be attributed to net avoidance (i.e. inappropriate sampling gear) or that the larvae are subject to high mortality rates in this physically harsh environment. Lasiak (1981) did however record the presence of post-larval individuals at King's beach in Algoa Bay but the major species in her study were different from those associated with estuaries. Ruple (1984) also suggested that the degree to which ichthyoplankton use the surf zone in the northern Gulf of Mexico is species specific.

It is well known that many species which inhabit and utilize estuaries as nursery areas spawn offshore, but surprisingly little is known about the mechanisms surrounding the transportation of larvae from the marine environment to estuaries (Norcross & Shaw 1984; Boehlert & Mundy 1988). Ichthyoplankton aggregations in the inshore region have been allied to a number of physical and environmental factors. For example, many studies have reported higher densities in spring and summer in both the surf zone (Whitfield 1989c) and estuaries (Melville-Smith & Baird 1980; Whitfield 1989a; Neira *et al.* 1992; Neira & Potter 1994; Harris & Cyrus 1995). These peaks in abundance coincide with blooms of planktonic food sources which predominate during periods of warmer temperatures. Indeed, it has been suggested that the fish have adapted their spawning strategies to local hydrographic conditions to maximize the spatial and temporal coincidence of larvae and food items (Dickey-Collas *et al.* 1996). However, the occurrence of fish larvae throughout the year, particularly species associated with estuaries, is also well documented (Melville-Smith & Baird 1980; Yoklavich *et al.* 1992). Ichthyoplankton densities within the surf zone at Kleinemonde peaked during early spring (August and September) largely due to the contribution of a single species (*Rhabdosargus holubi*) which accounted for more than 77% of the overall catch. Harris & Cyrus (1996) also noted peaks of abundance for *R. holubi* in June and August and Melville-Smith & Baird (1980) recorded larvae of this estuarine dependent species (category IIa) throughout the year. Therefore, it appears that this and possibly other estuary-associated taxa exhibit a spawning strategy to ensure an almost continuous supply of larvae throughout the year to optimally utilize temporarily open/closed estuaries because of unpredictable and sporadic mouth opening events.

Grimes & Kingsford (1996) suggested that river discharge (plumes) carrying high nutrient loads play a significant role in the recruitment of fishes associated with estuaries. In addition, decreased salinity and increased turbidity, which characterize estuarine discharge water, may be important in eliciting a recruitment response for different fish species. Martin *et al.* (1992) found that the recruitment densities for most ichthyoplankton species in the St Lucia estuary increased with elevated turbidities. Harris & Cyrus (1996) recorded a decrease in fish densities and turbidity with increasing distance from the mouth of the St Lucia estuary. Whitfield (1989c) also found that mean overall densities were higher at sampling stations closer to the mouth of the Swartvlei estuary. These findings all support the suggestion that a suite of physical factors may act as cues for estuary-associated ichthyoplankton in search of estuary mouths (Boehlert & Mundy 1988; Whitfield 1989c).

Finally, estuaries are known to be valuable contributors to both recreational and commercial fisheries production (Houde & Rutherford 1993). However, the early life history (larval stage) of many exploited estuarine dependent species such as *Argyrosomus japonicus, Lichia amia, Lithognathus lithognathus* and *Pomadasys commersonnii* is poorly understood. The absence (or minor contribution) of their larvae or post-larvae in the catches in the surf zone at Kleinemonde (this study), Swartvlei (Whitfield 1989c) and St Lucia (Harris & Cyrus 1996) suggest that these species do not use the surf zone as an interim nursery area. It is possible that they utilize neritic offshore waters or coastal embayments as larval nursery areas and only enter estuaries as metamorphosed early juveniles. The reported minimum cohort size range for these species occurring in estuaries provides evidence for this hypothesis (Table 3.4). The general lack of information on the early larval stages of these and many other exploited linefish species warrants further detailed investigation.

Table 3.4 The reported minimum cohort size range of some important linefish species which are dependent on estuaries as juveniles.

Species	Size class	Reference
Argyrosomus japonicus	20 - 30 mm TL	Griffiths (1996)
Lichia amia	30 - 40 mm TL	Whitfield & Kok (1992)
Lithognathus lithognathus	18 - 50 mm TL	Bennett (1989a)
	15 - 20 mm TL	Whitfield & Kok (1992)
	34 mm SL (min)	this study
Pomadasys commersonnii	20 - 30 mm TL	Wallace & van der Elst (1975)

CHAPTER 4

ESTUARINE FISH COMMUNITY STRUCTURE

4.1 INTRODUCTION

Ichthyofaunal studies on individual South African estuarine systems at the community level are largely in the form of general surveys (e.g. Whitfield *et al.* 1994; Harrison & Whitfield 1995; Ter Morshuizen *et al.* 1996). The assimilation of baseline information such as species composition, size composition and distribution is however important to obtain a better understanding of the dynamics of these communities. Furthermore, the collection of such data assists with investigating human induced disturbances on estuarine fish communities and other management related issues such as resource utilization.

This study forms part of a wider investigation to elucidate aspects of the ecology, particularly population dynamics, of the fish community within the temporarily open/closed East Kleinemonde estuary. The aims of the present study were to examine the species composition, size composition and distribution of the ichthyofauna associated with this estuary.

4.2 MATERIALS AND METHODS

The ichthyofauna of the East Kleinemonde estuary was sampled using a variety of gear, which included a small mesh seine net, a large mesh seine net and a fleet of gill nets. Different gear types were used to target specific species groups and/or size ranges of the fishes (Table 4.1). Based on collection efficiency, quantitative catch data was gathered from either the small mesh or the large mesh seine net for individual species. For example, the catches of the smaller estuarine-spawning species were more representative using the small mesh seine net, therefore quantitative data for these species were not recorded from the large mesh seine net.

The large mesh seine net (50 m x 2 m with a 15 mm bar mesh), fitted with a bag, was used to target most of the marine-spawning species of all sizes excluding the small size classes (< 40 mm SL) which were able to escape through the net. Netting was carried out during daylight hours (mostly between 09h00 and 14h00) on 111 separate days between April 1993 and March 1996. Due to fluctuations in water depth during the study period, as a result of mouth opening and closing events, sampling stations where selected randomly in areas where the net could be laid unobstructed (Figure 4.1). Sampling was conducted in a variety of littoral habitats (i.e. sandy, muddy and vegetated areas) in each of the three reaches (lower, middle and upper) of the estuary. The net was laid in a semi-circle from a motorized boat and hauled ashore by three or four people, ensuring that the foot rope (lead line) was dragged along the bottom. The area covered by the net was dependent on the width of the estuary. In the lower reaches (widest portion of the estuary) the area sampled was calculated at approximately 550 m^2. In the middle and upper reaches the net covered areas of approximately 525 m^2 and 500 m^2 respectively. All fish captured with this seine net were measured with a measuring board to the nearest mm standard length (SL) in the field and returned alive to the water.

Table 4.1 The targeted species groups and size ranges for each sampling gear type used in the East Kleinemonde estuary.

Sampling gear	Targeted species group	Targeted size range as a result of net selectivity
Small mesh seine net	Estuarine-spawning species and small marine-spawning species	Entire size range excluding very small size classes (< 10 mm SL)
Large mesh seine net	Marine-spawning species and freshwater species	Entire size range excluding small size classes (< 40 mm SL)
Gill nets	Marine-spawning species and freshwater species	Larger size classes (> 100 mm SL)

The small mesh seine net (30 m x 2 m with a 5 mm bar mesh), fitted with a bag, was used to target the estuarine-spawning species and the smaller marine-spawning species (e.g. *Solea bleekeri* and *Heteromycteris capensis*). The general sampling procedure was the same as with the large mesh seine net. Netting was conducted during daylight hours at selected sites in the estuary on seven separate occasions between April 1995 and January 1997. A total of eight sampling stations, covering a range of habitats, were selected in unobstructed areas with gently sloping banks (Figure 4.1). The net was deployed from a motorized boat and the procedure was performed in the same manner at each sampling station. The area covered by the net was calculated at approximately 100 m^2. The fish captured using this net were brought back to the laboratory, with the exception of some larger individuals and *Syngnathus watermeyeri* which were measured in the field and released. Standard length measurements were taken for all species.

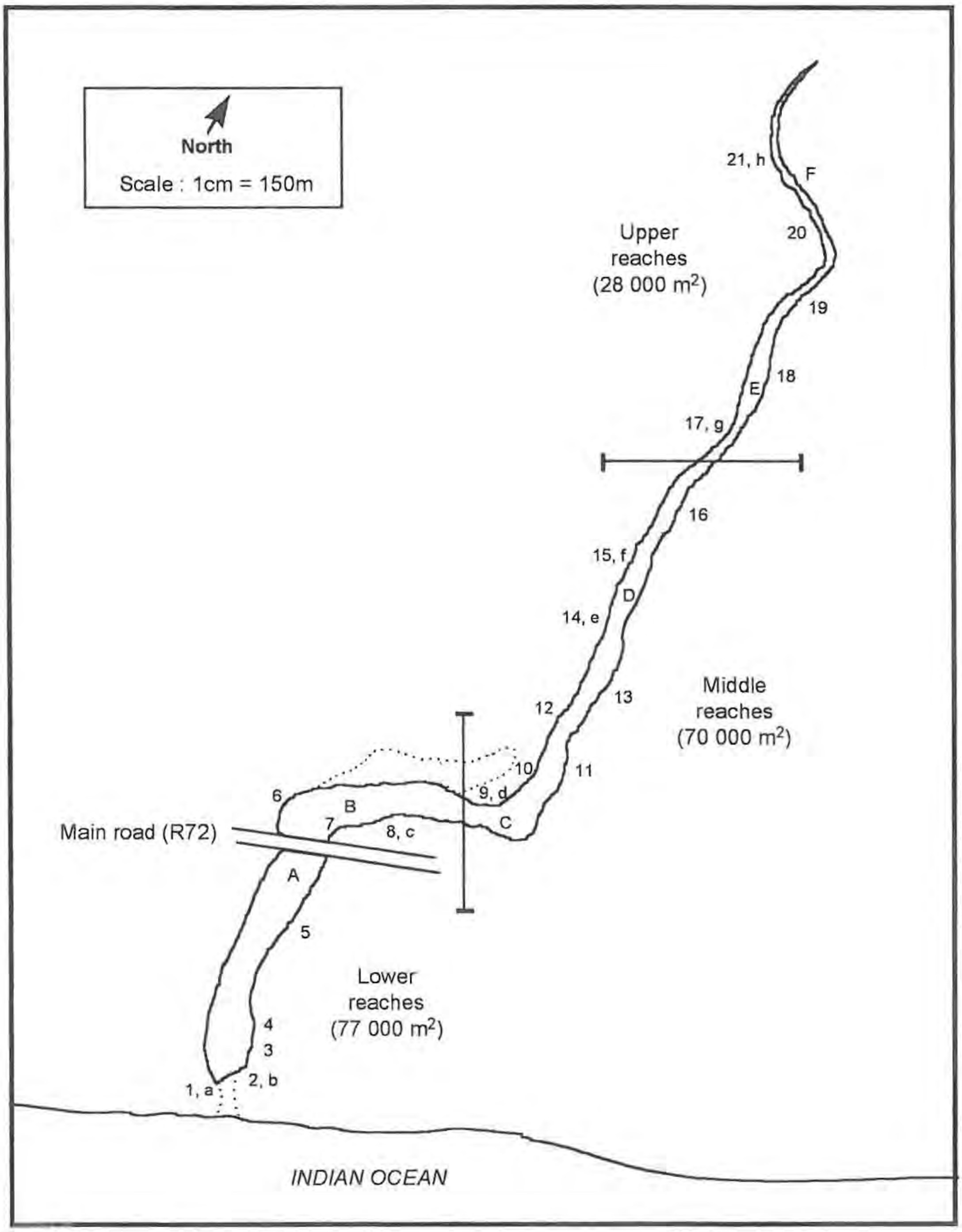

Figure 4.1 Map of the East Kleinemonde estuary showing the sampling stations (a-h = small seine net sites; 1-21 = large seine net sites; A-F = gill net sites) and the extent of the three reaches (lower, middle and upper).

Gill nets were used to sample both marine-spawning and freshwater species, particularly the larger individuals, which are known to actively avoid seine nets (Rozas & Minello 1997). Gill net sampling was kept to a minimum to avoid killing excessive numbers of fish in the estuary which would negatively influence the sampling program aimed at estimating population sizes, using mark-recapture techniques. Sampling was conducted at night on four separate occasions (2 November 1995, 2-3 June 1996 and 30 January 1997). Each net (10m) consisted of three equal lengths of 45 mm, 75 mm and 100 mm stretch mesh and were deployed in the evening (at approximately 18h00) and lifted the following morning (at approximately 06h00). On each sampling occasion two nets were set in each of three regions (lower, middle and upper) of the estuary (Figure 4.1).

All fish taxa sampled during this study were identified using Smith & Heemstra (1986) and assigned an estuary-association category using the descriptions given in Table 4.2. To avoid subjective evaluation of spatial trends in the fish community, multivariate analyses of the two seine netting data sets were performed using the software program PRIMER v3.1b (Clarke & Warwick 1994). The data for all samples obtained from each station throughout the study were pooled and the relationship between species groups and sampling stations were examined using classification (Bray-Curtis similarity) and ordination (multidimensional scaling) techniques.

Table 4.2 The estuarine association categories of fishes which utilize southern African estuaries (after Whitfield 1998).

Category	Description of categories
I	Estuarine species which breed in southern African estuaries. Further subdivided into: I a. Resident species which have not been recorded spawning in marine or freshwater environments. I b. Resident species which also have marine or freshwater breeding populations.
II	Euryhaline marine species which usually breed at sea with juveniles showing varying degrees of dependence on southern African estuaries. Further divided into: II a. Juveniles dependent on estuaries as nursery areas. II b. Juveniles occur mainly in estuaries, but are also found at sea. II c. 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 divided into: V a. Obligate catadromous species which require a freshwater phase in their development. V b. Facultative catadromous species which do not require a freshwater phase in their development.

4.3 RESULTS

4.3.1 Ichthyofaunal assemblage

Altogether, 30 fish species representing 17 families were recorded in the East Kleinemonde estuary (Table 4.3). Most families were represented by a single species, with the exception of the Carangidae (three species), Gobiidae (three species), Haemulidae (two species), Mugilidae (five species), Soleidae (two species) and Sparidae (four species). In terms of estuarine association categories, the euryhaline marine species (category II) dominated the catch composition (Figure 4.2). Marine-spawning species which are dependent on estuaries as nursery areas (category IIa) constituted 30% of all taxa recorded, followed by category IIb (17%) and category IIc (13%). The categories comprising the estuarine-spawning species (categories Ia and Ib) were represented by six species (20%), while the marine species which are not dependent on estuaries (category III) were represented by three species (10%). The euryhaline freshwater species (category IV), the obligate catadromous species (category Va) and the facultative catadromous species (category Vb) were each represented by a single species.

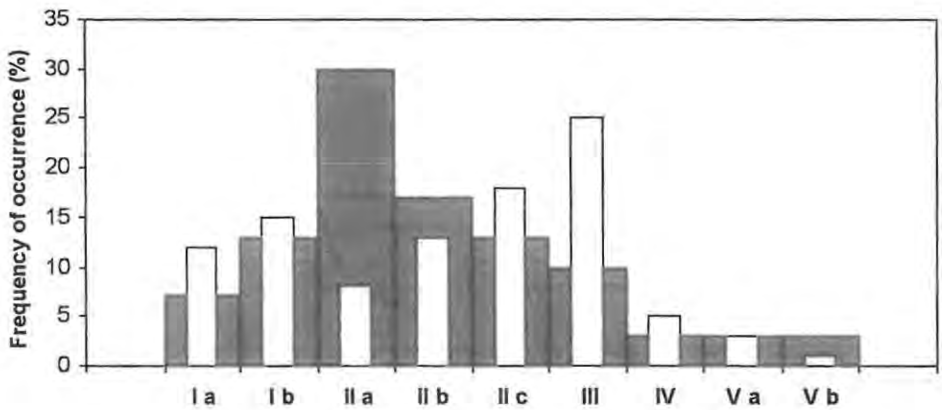

Figure 4.2 The percentage frequency of occurrence (% FO) of species in each estuary-dependence category sampled in the East Kleinemonde estuary between April 1993 and January 1997 (closed bars), and of all fishes which utilize southern African estuaries (open bars; after Whitfield 1998).

The occurrence (% FO) of species in the estuary-dependence categories Ia, Ib, IV, Va and Vb (i.e. estuarine, freshwater and catadromous species) in the East Kleinemonde estuary were similar to that of all species which utilize southern African estuaries (Figure 4.2). However, the frequency of marine species (categories IIa, IIb, IIc and III) in the

East Kleinemonde estuary decreased with a decreasing dependence on estuaries (i.e. from IIa to III), while Whitfield (1998) showed that the number of these species usually increases with decreasing estuarine dependence in southern African estuaries (Figure 4.2). This is probably a result of the predominantly closed condition of the mouth of the East Kleinemonde estuary during this study.

Table 4.3 Ichthyofaunal species recorded in the East Kleinemonde estuary using gill nets (GN), small (SS) and large mesh (LS) seine nets (* denotes a record from recreational angling). The estuary-dependence categories are after Whitfield (1998).

Family	Species	Common name	Estuary-dependence category	Sampling gear
Anguillidae	*Anguilla marmorata*	Madagascar mottled eel	Va	LS
Atherinidae	*Atherina breviceps*	Cape silverside	Ia	SS, LS
Carangidae	*Caranx* sp.	Kingfish	IIb?	LS
	Lichia amia	Leervis	IIa	LS,GN
	Trachinotus africanus	Southern pompano	III	LS
Cichlidae	*Oreochromis mossambicus*	Mozambique tilapia	IV	SS, LS, GN
Clupeidae	*Gilchristella aestuaria*	Estuarine roundherring	Ia	SS, LS
Elopidae	*Elops machnata*	Ladyfish	IIa	*
Gobiidae	*Caffrogobius gilchristi*	Prison goby	Ib	SS
	Glossogobius callidus	Estuarine goby	Ib	SS, LS
	Psammogobius knysnaensis	Knysna sandgoby	Ib?	SS, LS
Haemulidae	*Pomadasys olivaceum*	Piggy	III	LS
	Pomadasys commersonnii	Spotted grunter	IIa	LS,GN
Monodactylidae	*Monodactylus falciformis*	Cape moony	IIa	SS, LS, GN
Mugilidae	*Liza dumerilii*	Groovy mullet	IIb	SS, LS, GN
	Liza richardsonii	Southern mullet	IIc	SS, LS, GN
	Liza tricuspidens	Striped mullet	IIb	SS, LS
	Mugil cephalus	Flathead mullet	IIa	SS, LS, GN
	Myxus capensis	Freshwater mullet	Vb	SS, LS, GN
Pomatomidae	*Pomatomus saltatrix*	Elf	IIc	*
Sciaenidae	*Argyrosomus japonicus*	Dusky kob	IIa	LS
Soleidae	*Heteromycteris capensis*	Cape sole	IIb	SS, LS
	Solea bleekeri	Blackhand sole	IIb	SS, LS
Sparidae	*Diplodus sargus capensis*	Blacktail	IIc	LS
	Lithognathus lithognathus	White steenbras	IIa	LS,GN
	Rhabdosargus holubi	Cape stumpnose	IIa	SS, LS, GN
	Sarpa salpa	Strepie	IIc	LS
Syngnathidae	*Syngnathus watermeyeri*	Estuarine pipefish	Ia	SS, LS
Teraponidae	*Terapon jarbua*	Thornfish	IIa	*
Tetraodontidae	*Amblyrhyncotes honkenii*	Evileye blaasop	III	*

4.3.2 Small mesh seine net

Catch composition

Although 16 species were captured in the small mesh seine net (Table 4.3), quantitative records were only kept for the six estuarine-spawning species and the two small marine-spawning species (*viz. Heteromycteris capensis* and *Solea bleekeri*). The overall catch composition of these taxa was numerically dominated by *Gilchristella aestuaria* (59.6%), *Atherina breviceps* (23%) and *Glossogobius callidus* (14.4%), while *Psammogobius knysnaensis*, *Caffrogobius gilchristi*, *Syngnathus watermeyeri*, *Heteromycteris capensis* and *Solea bleekeri* collectively contributed only 3% (Table 4.4).

Table 4.4 The catch composition in order of family abundance and size composition (mean, standard deviation and range) of the fish taxa sampled with the small mesh seine net in the East Kleinemonde estuary between April 1995 and January 1997.

Species	Number caught	% catch composition	Rank	Mean SL (mm)	Standard deviation	Length range
Clupeidae			**1**			
Gilchristella aestuaria	7481	59.6	1	35.1	7.7	15 - 60
Antherinidae			**2**			
Atherina breviceps	2884	22.9	2	35.3	8.2	19 - 62
Gobiidae			**3**			
Glossogobius callidus	1808	14.4	3	41.6	12.8	10 - 92
Psammogobius knysnaensis	318	2.5	4	35.0	8.5	21 - 55
Caffrogobius gilchristi	5	0.04	7	37.4	3.5	33 - 42
Syngnathidae			**4**			
Syngnathus watermeyeri	43	0.3	5	104.3	9.5	84 - 128
Soleidae			**5**			
Heteromycteris capensis	7	0.05	6	69.1	8.1	56 - 79
Solea bleekeri	2	0.02	8	53.5	2.1	52 - 55

Analysis of the size range distributions revealed the presence of all post-larval life history stages for the dominant species. The sizes of *Gilchristella aestuaria* ranged between 15 mm and 60 mm SL, with a bimodal size class distribution (Figure 4.3a). The sizes of *Atherina breviceps*, *Glossogobius callidus* and *Psammogobius knysnaensis* ranged from 19 - 62 mm, 10 - 92 mm and 21 - 55 mm SL respectively (Table 4.4). The modal size class for *A. breviceps* and *G. callidus* were 30 - 34 mm SL (Figure 4.3b) and 40 - 44 mm

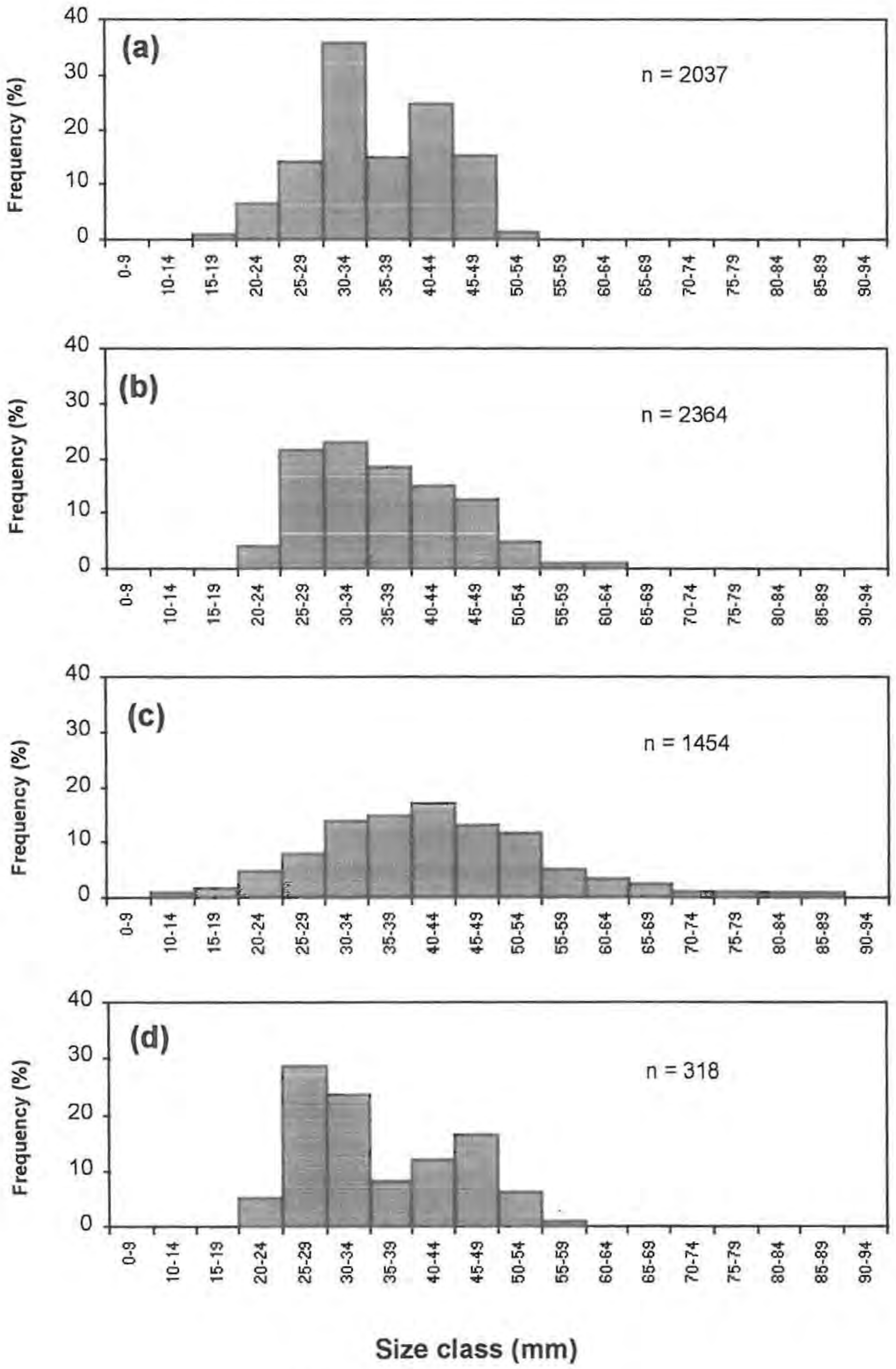

Figure 4.3 Length frequency distributions for **(a)** *Gilchristella aestuaria*, **(b)** *Atherina breviceps*, **(c)** *Glossogobius callidus* and **(d)** *Psammogobius knysnaensis* sampled with the small mesh seine net in the East Kleinemonde estuary between April 1995 and January 1997.

SL (Figure 4.3c) respectively. *Psammogobius knysnaensis* had a bimodal size distribution with peaks at 25 - 29 mm SL and 45 - 49 mm SL (Figure 4.3d). The catches of *Caffrogobius gilchristi*, *Heteromycteris capensis* and *Solea bleekeri* were represented by only a few juvenile individuals, and *Syngnathus watermeyeri* by a few adolescent and adult specimens. The absence of all life history stages for these estuarine-spawning species is attributed to the low sample sizes.

Distribution

The spatial trends in fish abundance were analysed from catch data. The mean catch per seine haul (CPUE) of the four dominant species sampled with the small mesh seine net in each of the three reaches of the estuary are given in Figure 4.4.

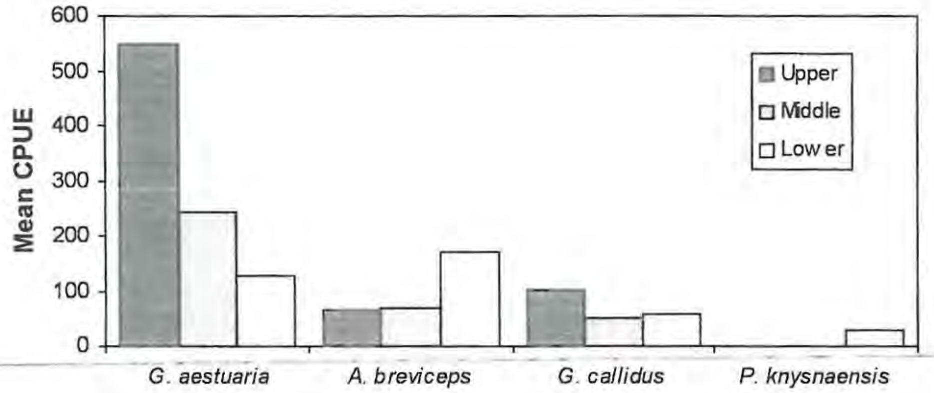

Figure 4.4 The mean CPUE of *Gilchristella aestuaria*, *Atherina breviceps*, *Glossogobius callidus* and *Psammogobius knysnaensis* sampled with the small mesh seine net in the upper, middle and lower reaches of the East Kleinemonde estuary.

The two dominant pelagic species showed inverse distributional patterns. *Gilchristella aestuaria* was more abundant in the upper reaches, while *Atherina breviceps* was more abundant in the lower reaches. A similar trend was observed for the two dominant benthic species. *Glossogobius callidus* occurred throughout the estuary but was more abundant in the upper reaches, while *Psammogobius knysnaensis* occurred only in the sandy areas of the lower reaches (Figure 4.4). The distribution of *Syngnathus watermeyeri*, on the other hand, was site specific because of their association with submerged macrophyte (*Ruppia cirrhosa*) beds, which occur mostly above the road bridge. The distribution of the other species caught with the small mesh seine net revealed no distinct trends. This is possibly due to the small sample sizes.

The distributional affinities of the eight species collected at each sampling site were analysed using the Bray-Curtis measure of similarity (Figure 4.5a). Despite the overall high level of similarity in the community, two distinct cluster groups were identified. The samples collected at sites with a sandy substratum in the lower reaches of the estuary (sites *a* and *b*) were distinguished from those collected at the other sites at the 70% similarity level. The other sampling sites (*c* to *h*) are characterized by a muddy substratum. This grouping was also portrayed in the ordination plot (Figure 4.5b) using multidimensional scaling on the same similarity matrix as above.

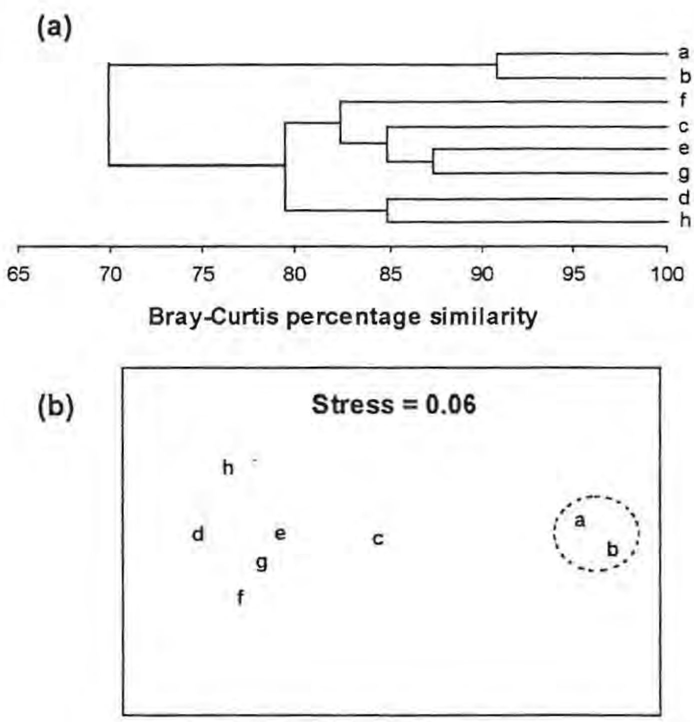

Figure 4.5 (a) Dendrogram showing the classification and (b) ordination by means of multi-dimensional scaling of the small mesh seine net fish assemblage. The sites with a sandy substratum in the lower reaches are encircled with a dashed line.

4.3.3 Large mesh seine net

Catch composition

A total of 25 species representing 18 families were recorded in the large mesh seine net catches (Table 4.3). The overall catch composition was dominated by the marine-spawning species. *Rhabdosargus holubi* was by far the most abundant species (75.3%), followed by three mugilids [*Liza richardsonii* (5.7%); *Myxus capensis* (5.5%); *Liza dumerilii* (4%)], *Monodactylus falciformis* (3.2%) and *Lithognathus lithognathus* (2.6%). The other species collectively contributed only 3.7% (Table 4.5).

Table 4.5 The catch composition in order of family abundance and size composition (mean, standard deviation and range) of fishes captured with the large mesh seine net in the East Kleinemonde estuary between April 1993 and March 1996.

Species	Number caught	% catch composition	Rank	Mean SL (mm)	Standard deviation	Length range
Sparidae			**1**			
Diplodus sargus capensis	12	0.04	12	52	21.8	26 - 80
Lithognathus lithognathus	842	2.6	6	144.1	71.6	34 - 382
Rhabdosargus holubi	24409	75.3	1	81.7	18.5	23 - 222
Sarpa salpa	224	0.7	8	84.4	8.1	37 - 107
Mugilidae			**2**			
Liza dumerilii	1303	4	4	138.2	44.8	51 - 285
Liza richardsonii	1861	5.7	2	157.1	46.5	49 - 309
Liza tricuspidens	37	0.1	11	127.4	35.4	93 - 244
Mugil cephalus	224	0.7	8	136	48.7	46 - 398
Myxus capensis	1785	5.5	3	166.6	48.4	63 - 375
Monodactylidae			**3**			
Monodactylus falciformis	1042	3.2	5	67.8	22.7	16 - 141
Cichlidae			**4**			
Oreochromis mossambicus	559	1.7	7	123.6	98.9	20 - 300
Carangidae			**5**			
Caranx sp.	12	0.04	12	130.8	19.5	104 - 164
Lichia amia	71	0.2	9	354.2	65.4	264 - 580
Trachinotus africanus	1	< 0.01	13	130	-	-
Haemulidae			**6**			
Pomadasys olivaceum	1	< 0.01	13	75	-	-
Pomadasys commersonnii	44	0.1	10	318.5	161.7	79 - 586
Sciaenidae			**7**			
Argyrosomus japonicus	1	< 0.01	13	446	-	-
Anguillidae			**7**			
Anguilla marmorata	1	< 0.01	13	not taken	-	-

The vast majority of fishes caught with the large mesh seine net were juveniles (Table 4.5). The species that were only represented by juvenile sizes classes included *Caranx* sp., *Lichia amia*, *Trachinotus africanus*, *Pomadasys olivaceum*, *Argyrosomus japonicus*, *Diplodus sargus capensis*, *Lithognathus lithognathus* and *Sarpa salpa*. Species that were also represented by adult specimens included *Pomadasys commersonnii*, *Monodactylus falciformis*, *Rhabdosargus holubi*, *Liza dumerilii*, *Liza richardsonii*, *Liza tricuspidens*, *Myxus capensis*, *Mugil cephalus*, and the freshwater cichlid *Oreochromis mossambicus*.

The length frequency distributions for the dominant species captured in the large mesh seine net are given in Figures 4.6 and 4.7.

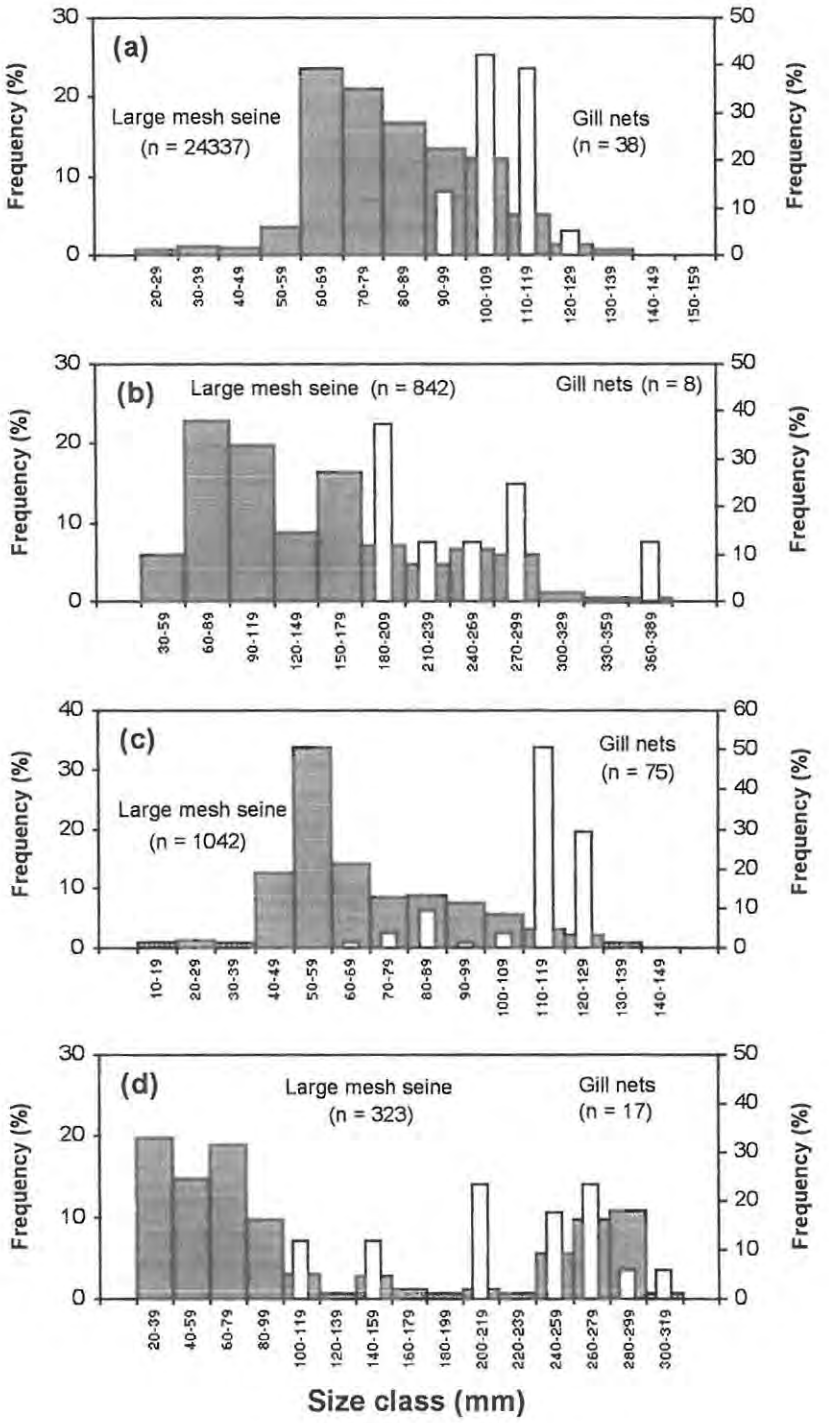

Figure 4.6 Length frequency distributions for **(a)** *Rhabdosargus holubi*, **(b)** *Lithognathus lithognathus*, **(c)** *Monodactylus falciformis* and **(d)** *Oreochromis mossambicus* sampled with the large mesh seine net (closed bars) and gill nets (open bars) in the East Kleinemonde estuary.

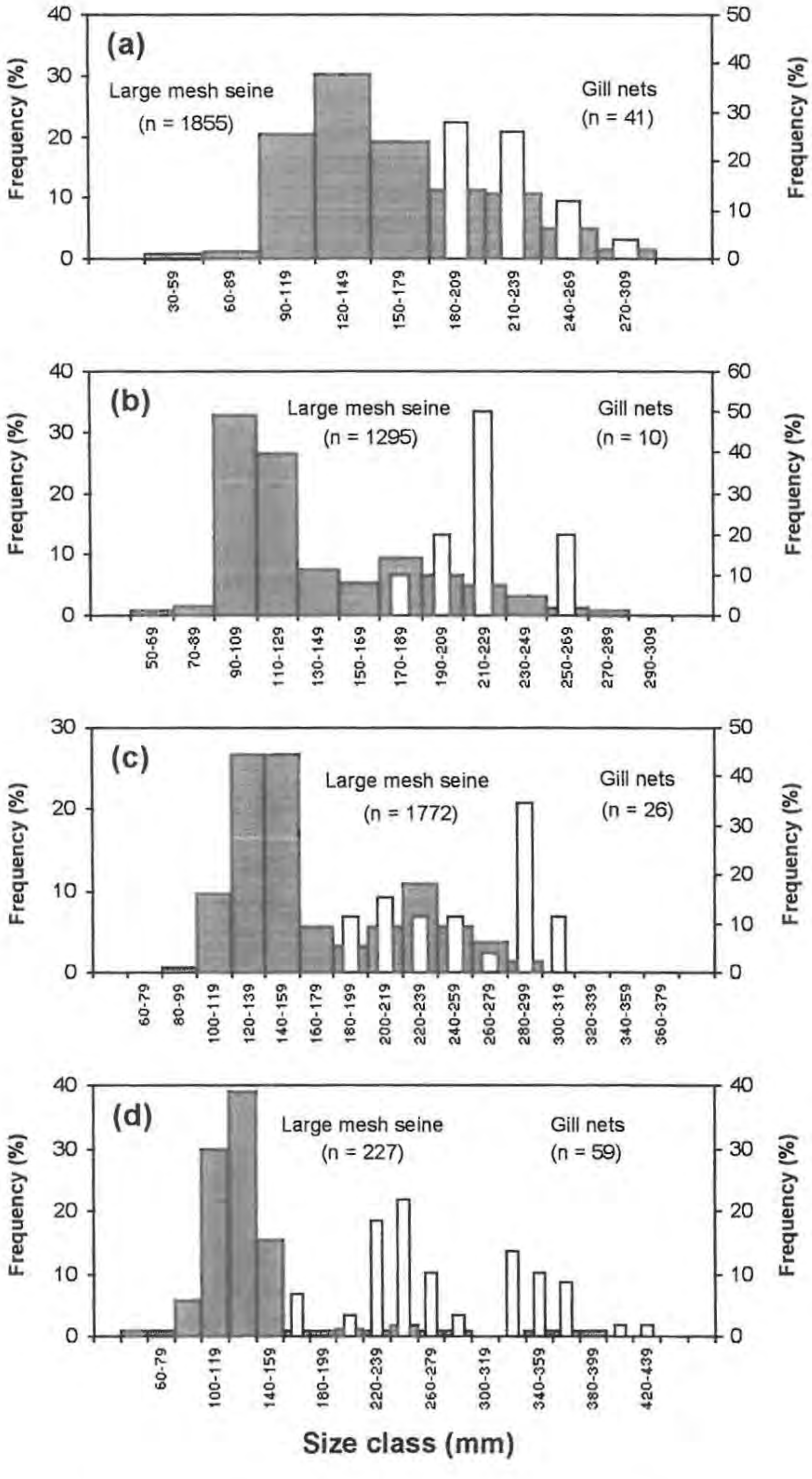

Figure 4.7 Length frequency distributions for **(a)** *Liza richardsonii*, **(b)** *Liza dumerilii*, **(c)** *Myxus capensis* and **(d)** *Mugil cephalus* sampled with the large mesh seine net (shaded bars) and gill nets (open bars) in the East Kleinemonde estuary.

Distribution

The principal marine-spawning species in the East Kleinemonde estuary, *Rhabdosargus holubi*, showed a clear preference for the lower reaches. The mean catch per seine haul (CPUE) in the lower reaches (47.7) was higher than in the middle (27.2) and upper (25.1) reaches. The distributional trends, based on CPUE, for the other dominant marine-spawning species captured in the large mesh seine net are given in Figure 4.8. *Liza richardsonii* showed no distinct distributional trends, but *Liza dumerilii* was more abundant in the lower reaches. Conversely, the other mugilids (*Mugil cephalus* and *Myxus capensis*) were more abundant in the upper reaches of the estuary. Most *Lithognathus lithognathus* were recorded in the lower reaches while the majority of *Monodactylus falciformis* were caught in the upper reaches (Figure 4.8).

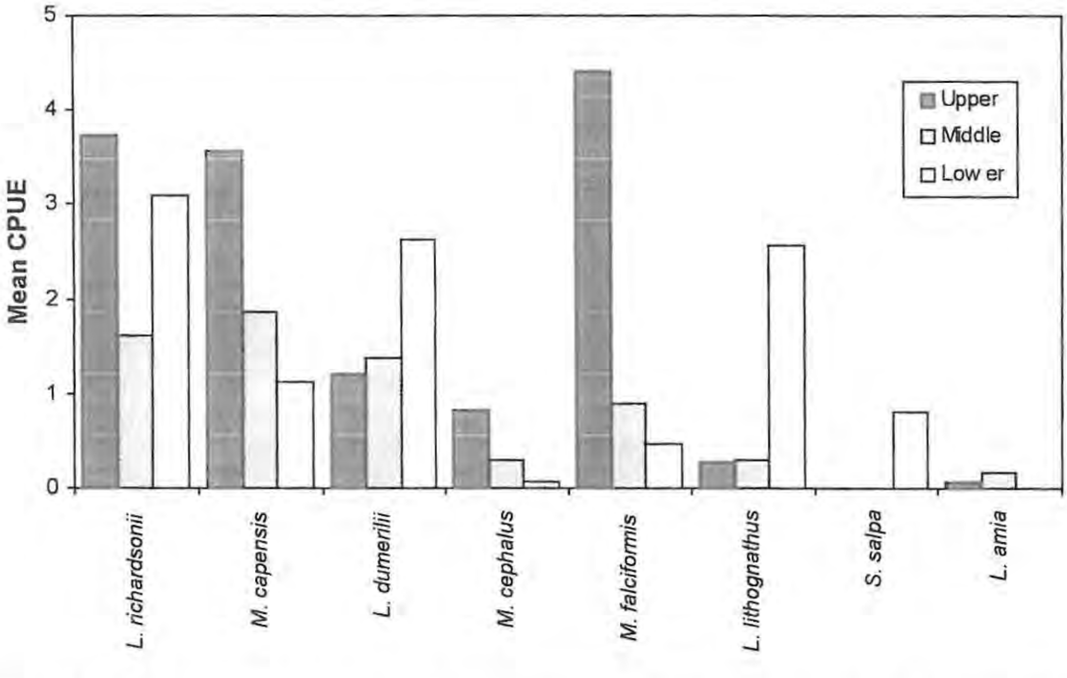

Figure 4.8 The mean CPUE for several marine-spawning species captured with the large mesh seine net in the three reaches of the East Kleinemonde estuary.

Classification and ordination of the fish fauna sampled with the large mesh seine net at sites 1-21 (excluding sites 4 and 18) are given in Figure 4.9. Sampling sites 4 and 18 were excluded because initial analyses revealed that they were unrepresentative due to the very low number of seine hauls conducted at these sites. The Bray-Curtis classification grouped the entire fish community at a similarity level in excess of 70%.

Similar to the small mesh seine net assemblage, the samples collected at sites in the sandy areas of the lower reaches (sites 1,2 and 3) were identified as a distinct cluster group (Figure 4.9).

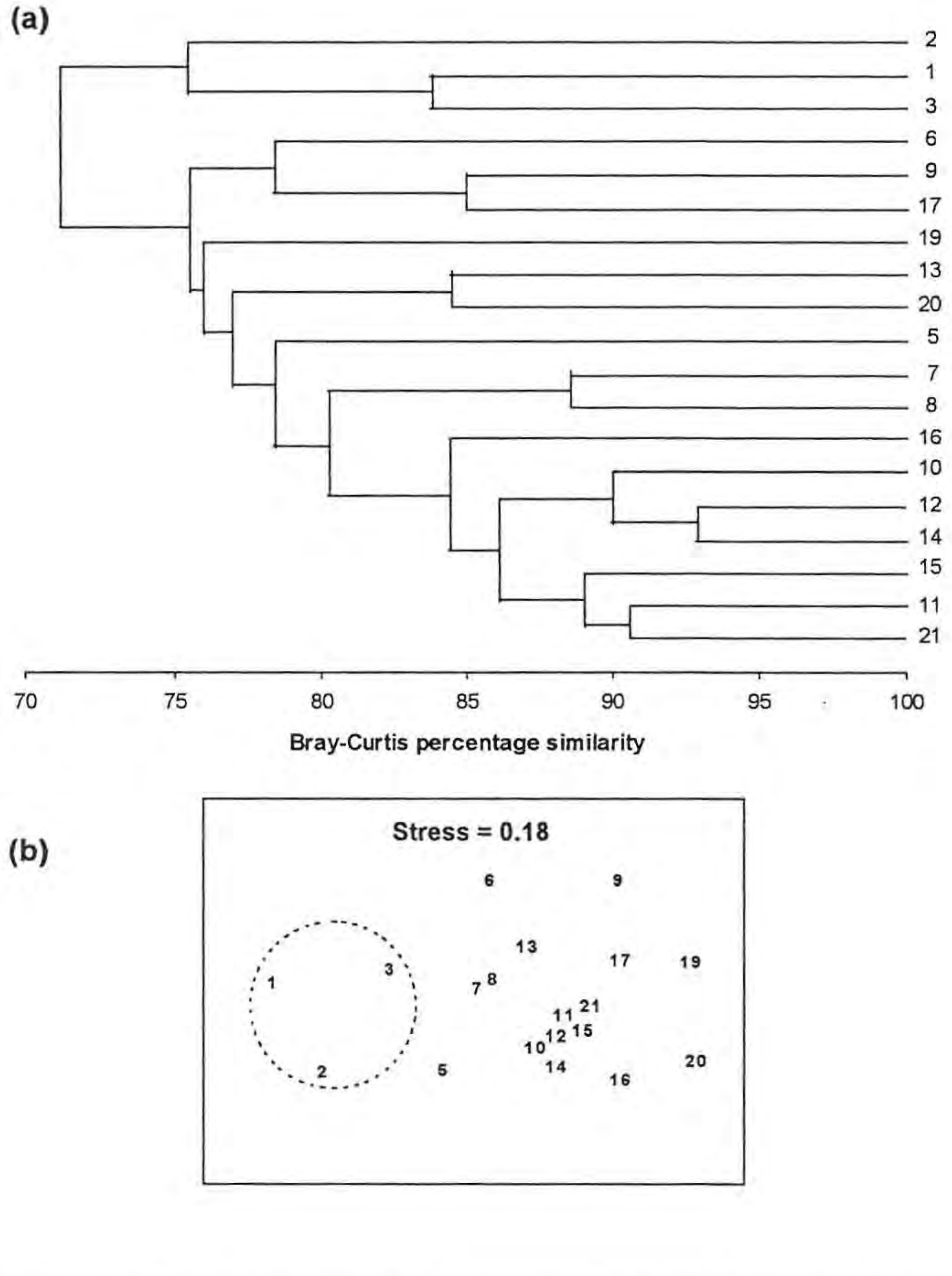

Figure 4.9 (a) Dendrogram showing the classification and (b) ordination by means of multi-dimensional scaling of the large mesh seine net fish assemblage. The sites with a sandy substratum in the lower reaches are encircled with a dashed line.

4.3.4 Gill nets

Catch composition

A total of 284 fishes from 10 species and six families were recorded in the gill nets catches (Table 4.6). According to their estuarine association categories, marine-spawning species which are dependent on estuaries (category IIa) dominated the catch composition with six species, while categories IIb, IIc, IV and Vb were each represented by a single species. No estuarine-spawning species were recorded in the gill nets due to the small size of these fish. The gill net assemblage was not analysed spatially due to the paucity of data.

Table 4.6 The catch composition in order of family abundance and size composition (mean, standard deviation and range) of the fish taxa sampled with the gill nets in the East Kleinemonde estuary.

Species	Number caught	% catch composition	Rank	Mean SL (mm)	Standard deviation	Length range
Mugilidae			**1**			
Liza richardsonii	41	14.4	3	244.8	34.2	189 - 303
Mugil cephalus	59	20.8	2	299.2	62.3	181 - 450
Myxus capensis	26	9.2	5	254.7	38.2	193 - 303
Monodactylidae			**2**			
Monodactylus falciformis	75	26.4	1	111.6	14.1	69 - 128
Sparidae			**3**			
Rhabdosargus holubi	38	13.4	4	108.1	7.2	94 - 123
Lithognathus lithognathus	8	2.8	7	250.1	64.8	195 - 383
Cichlidae			**4**			
Oreochromis mossambicus	17	6.0	6	222.2	59.3	115 - 300
Haemulidae			**5**			
Pomadasys commersonnii	8	2.8	7	349.9	142.7	150 - 540
Carangidae			**6**			
Lichia amia	2	0.7	8	448.0	82	390 - 506

The catch composition was dominated by four mullet species which collectively contributed 47.9%. At the species level *Monodactylus falciformis* dominated the catch composition (26.4%), followed by *Mugil cephalus* (20.8%), *Liza richardsonii* (14.4%) and *Rhabdosargus holubi* (13.4%).

Although the species composition differed greatly between the gill and seine net samples, the most striking difference between the catches from the two gear types was the size composition. In most cases the largest individuals for each species were recorded in the gill nets (Figures 4.6 and 4.7) and this was attributed to net selectivity.

4.4 DISCUSSION

A range of sampling gear, including a small mesh seine net, a large mesh seine net and gill nets of various mesh sizes, were used to sample the fishes of the East Kleinemonde estuary. Rozas & Minello (1997) state that all sampling techniques have advantages and disadvantages which influence the collection efficiencies of individual species. Therefore, the use of different gear types allowed for improved representation of the community in terms of diversity and size ranges, but made quantitative comparisons of the fish assemblages for each collection technique highly subjective. As a result, the fish assemblage for each gear type was treated separately.

The use of multivariate techniques of classification and ordination have been used to describe the structure of fish communities in several South African estuarine systems. Bennett (1989a) identified distinct species groups on the basis of season in three Western Cape estuaries, and Whitfield *et al.* (1989) noted similarities within the fish assemblages of the Knysna and Swartvlei estuaries based on the presence or absence of vegetated substrata. The ichthyofaunal assemblages within the East Kleinemonde estuary revealed a high degree of similarity throughout the estuary, but a distinct species grouping was identified in association with sandy substrata in the lower reaches of the system. The identification of this grouping was recorded at a similarity level of 70% and 72% for the small and large seine net assemblages respectively (Figures 4.5 and 4.9).

An analysis of the estuarine association categories revealed that the fish community of the East Kleinemonde estuary was dominated by juvenile euryhaline marine species (categories IIa, IIb and IIc) which collectively comprised 60%. The estuarine species (categories Ia and Ib) constituted 20%, the marine species which are not dependent on estuaries (category III) comprised 10%, while the euryhaline freshwater species (category IV), the obligate catadromous species (category Va) and the facultative catadromous species (category Vb) each contributed 3.3% to the overall community. Despite the inferior contribution by category III marine species, due to the predominantly closed mouth conditions, the East Kleinemonde fish assemblage is characteristic of a typical warm temperate southern African estuary. The overall species diversity is however lower when compared with equivalent subtropical systems. For example, Harrison & Whitfield (1995) recorded 47 and 56 species in the Mhlanga and Zotsha estuaries, respectively. Furthermore, temporarily open/closed estuaries usually have a lower species diversity than permanently open estuaries (Bennett 1989a; Whitfield & Kok 1992). Whitfield *et al.* (1994) recorded a total of 31 and 39 species in the neighbouring permanently open Great Fish and Kowie estuaries respectively, while 30 species were recorded from the East Kleinemonde estuary.

The small mesh seine net assemblage was numerically dominated by two small shoaling planktivorous species (*Gilchristella aestuaria* and *Atherina breviceps*) which collectively constituted 82.6% of the catch. The numerical dominance of these species has been recorded in many South African estuarine environments (Beckley 1984; Bennett 1989a; Whitfield *et al.* 1989). The success of these species can be ascribed to their typically altricial life-history style (Balon 1981) and possession of a number of eurytopic traits which include wide distribution and a broad habitat tolerance range (Whitfield 1994b). Both species are strongly euryhaline (0 - > 40 ‰) and have been found to breed in estuaries throughout the year (Talbot 1982; Ratte 1989; Whitfield 1996b). Despite their similar life-history styles, the two species showed inverse distributional trends in the East Kleinemonde estuary. *Gilchristella aestuaria* was almost five times more abundant in the upper reaches than in the lower reaches, while the abundance of *Atherina breviceps* was more than two fold greater in the lower reaches (Figure 4.4). Although the distribution of *Gilchristella aestuaria* has been linked to the abundance of suitable prey (Ter Morshuizen *et al.* 1996), as well as spawning behaviour (Talbot 1982), it generally prefers the upper reaches of estuaries (Branch & Grindley 1979; Harrison & Whitfield 1995).

Glossogobius callidus and *Psammogobius knysnaensis* in the East Kleinemonde estuary revealed a similar distribution pattern to that of *Gilchristella aestuaria* and *Atherina breviceps*. The numerically dominant goby species (*G. callidus*) occurred throughout the estuary but was more abundant in the upper reaches (Figure 4.4). This finding is mirrored by several studies in other South African estuaries (Whitfield 1980a; Beckley 1984; Ter Morshuizen *et al.* 1996). Harrison & Whitfield (1995) studied the fish communities of three KwaZulu-Natal estuaries (Damba, Mhlanga and Zotsha) and found that *G. callidus* was only an important component of the ichthyofauna in those estuaries which were characterized by a predominantly muddy substratum. *Psammogobius knysnaensis*, on the other hand, prefers sandy substrata (this study; Whitfield 1988; Ter

Morshuizen & Whitfield 1994; Ter Morshuizen *et al.* 1996), a habitat which usually predominates in the mouth region of most estuaries. Therefore, the distribution and abundance of Gobiidae in South African estuarine systems appear to be linked to substratum type.

A noteworthy inclusion in the East Kleinemonde fish assemblage was the estuarine pipefish *Syngnathus watermeyeri*. This estuarine-spawning species, previously known as the river pipefish, was declared extinct according to the 1994 IUCN Red List of Threatened Animals (Groombridge 1993). However, it should not have been classified as extinct, since 50 years have not elapsed since the last specimens were collected (Whitfield 1995). *Syngnathus watermeyeri* was known only from the Bushmans, Kariega and Kasouga estuaries, and the last specimens were collected in 1963. The disappearance of *S. watermeyeri* from these estuaries (localized extinction) is attributed to the prolonged absence of freshwater inflow and the influence of these conditions on the available planktonic food supply (Ter Morshuizen & Whitfield 1994; Whitfield 1994b). Based on the limited knowledge of the Bushmans/Kariega population, it appears that this species has specialized needs in terms of the physical characteristics of an estuary. These include sufficient macrophytic plant beds and a regular freshwater supply. Whitfield (1995) suggests that pulses of freshwater supply are essential to provide nutrients for phytoplankton development, which together with particulate organic material brought down by the rivers, support zooplankton communities on which Syngnathidae depend for food. At present, the East Kleinemonde estuary offers asylum to the only known viable population of *Syngnathus watermeyeri*. Based on the above mentioned criteria, this estuary offers a number of favourable characteristics for it's existence. These include dense stands of the submerged macrophyte *Ruppia cirrhosa*, limited freshwater abstraction, low human recreational and development pressures and low levels of piscivorous predation. The absence of the longsnout pipefish *Syngnathus acus* from the East Kleinemonde estuary indicates that potential competition between the two syngnathids is also lacking, in contrast to the situation in the Kariega estuary where these species lived sympatrically (Whitfield & Ter Morshuizen 1992).

The presence of life-history stages, ranging from early juvenile to adult size classes (Table 4.4), of the dominant estuarine-spawning species (*Gilchristella aestuaria*, *Atherina breviceps*, *Glossogobius callidus* and *Psammogobius knysnaensis*) indicated that they all bred successfully in the East Kleinemonde estuary during the study period. Although it is proposed that a viable breeding population of *Syngnathus watermeyeri* occurs in the East Kleinemonde estuary, no juveniles were recorded.

The fishes recorded in the large mesh seine were dominated by *Rhabdosargus holubi* which constituted 75.3% of the overall catch. It was also the most abundant taxon within the ichthyoplanktonic component of the surf zone adjacent to the estuary mouth (Chapter 3). It is hypothesized that the numerical dominance of this species is a result of a suite of specialized life-history characteristics. *R. holubi* exhibits serial spawning, which allows for an almost continuous supply of post larvae which not only recruit during open mouth phases but also during bar overwash events. Therefore, this species has evolved to optimally utilize 'blind' estuaries because of the temporal uncertainty of open mouth phases. The size composition of *R. holubi* (Table 4.5) in the East Kleinemonde estuary indicates that it primarily utilizes this estuary during the first year of it's life cycle. Similar results have been documented from other South African estuaries, e.g. West Kleinemonde (Blaber 1973b), Sundays (Beckley 1984), Knysna and Swartvlei (Whitfield & Kok 1992), and Great Fish and Kowie (Whitfield *et al.* 1994).

Rhabdosargus holubi was reported to be more abundant in the middle and upper reaches of the Knysna, Swartvlei and Kariega estuaries (Whitfield & Kok 1992; Ter Morshuizen & Whifield 1994). Hankom & Baird (1984), recorded significantly higher numbers of *R. holubi* in vegetated (*Zostera*) areas than in non-vegetated areas within the Kromme estuary. Whitfield *et al.* (1989) also found it to be closely associated with *Zostera* beds in the Knysna and Swartvlei estuaries. The distribution of *R. holubi* in estuaries therefore appears to be linked to the presence of macrophytic beds, which are used as foraging and refuge areas. However, this ubiquitous species in the East Kleinemonde estuary showed a preference for the lower reaches which is not as heavily vegetated as the middle and upper reaches. It is possible that the abundance of *R. holubi* in the lower reaches was associated with the epipsammic filamentous algal mats which develop between late winter and early summer. Under these conditions frequent catches of more than 200 individuals per seine haul were recorded in the lower reaches of the East Kleinemonde estuary. Whitfield (1988) reported a similar abundance of *R. holubi* in association with filamentous algal mats in the sandy upper reaches of the Swartvlei estuary.

The distribution of the other Sparidae (*Diplodus sargus capensis*, *Lithognathus lithognathus* and *Sarpa salpa*) in the East Kleinemonde estuary also showed a preference for the lower reaches. The abundance of *L. lithognathus*, a macroinvertebrate feeder, in the lower reaches can be attributed to the dominance of sand prawns (*Callianassa kraussi*) in this region. *Diplodus sargus capensis* and *Sarpa salpa* were almost exclusively recorded in the lower reaches, possibly in response to the slightly elevated salinity levels within this region (see Figure 2.5).

The Mugilidae are among the most abundant marine-spawning fishes found in South African estuaries (Blaber 1987; Bennett 1989a; Whitfield *et al.* 1994; Harrison & Whitfield 1995). Most species are strongly euryhaline (Whitfield 1996b), have extended spawning seasons (Wallace *et al.* 1984; Blaber 1987; Whitfield & Kok 1992) and are able to recruit into estuaries with a range of mouth conditions (Hall *et al.* 1987; Harrison & Whitfield 1995). These traits, together with the fact that they occupy a primary position in the food chain (i.e. detrivores), provide the attributes for their successful adaptation to estuarine environments.

The distribution of the dominant mugilids in the East Kleinemonde estuary showed some interesting trends (Figure 4.7). *Liza richardsonii* was common throughout the system, but CPUE values for *Liza dumerilii* were higher in the lower reaches than in the middle and upper reaches. Conversely, *Myxus capensis* and *Mugil cephalus* revealed a distinct preference for the upper reaches. A similar distribution of these two species was recorded from the Great Fish and Kowie estuaries (Whitfield *et al.* 1994). Marais (1981, 1983) also recorded higher numbers of *M. cephalus* in the upper reaches of the Sundays and Gamtoos estuaries. Bok (1979) states that *M. capensis* and *M. cephalus* are catadromous species, and therefore show a distinct preference for the riverine areas of estuaries in the Eastern Cape. It is tempting to suggest that the distributional trend of Mugilidae in the East Kleinemonde estuary is a consequence of resource partitioning, but this requires further detailed investigation.

Monodactylus falciformis (16 - 141 mm SL) was the fifth most dominant taxa in the large mesh seine net catches in the East Kleinemonde estuary (Table 4.5). This species showed a distinct preference for the upper reaches of the estuary. Similar trends have been documented by several authors (*inter alia* Beckley 1983, 1984; Whitfield 1984; Whitfield & Kok 1992; Ter Morshuizen *et al.* 1996). Ter Morshuizen & Whitfield (1994) also reported a higher abundance of this species in the upper reaches of the Kariega estuary which was characterized by a reversed salinity gradient. Consequently, they indicated that factors other than salinity attract *M. falciformis* to the upper reaches of estuaries.

Gill netting provided an alternative collection method which is known to be effective in sampling larger individuals and highly mobile fish which actively avoid seine nets (Marais 1985). A distinct difference in the size and species composition was observed between the gill net and the seine net fish assemblages. The gill net catch composition consisted mostly of marine-spawning species that were consistently larger than those represented in the seine net catches (Figures 4.6 and 4.7).

The numerical dominance of *Monodactylus falciformis* and *Mugil cephalus* in the gill nets suggest that these species actively avoid seine nets. *M. falciformis*, which is known to be associated with vegetated areas (Beckley 1984; Hanekom & Baird 1984; Whitfield 1984), has a decreased seine net catch efficiency. It is also possible that the elevated gill net catches of this species are a result of increased nocturnal activity. *Mugil cephalus*, on the other hand, actively avoids seine nets by jumping over the bouyed head rope of the encircling net. Catches of *Pomadasys commersonnii* and larger individuals (180 - 300 mm SL) of other mugilid species (e.g. *Liza richardsonii*, *Liza dumerilii* and *Myxus capensis*) were also higher in the gill nets than in the seine nets.

4.5 SUMMARY

- The fish community of the East Kleinemonde estuary is dominated by estuarine dependent marine-spawning species and represents that of a typical warm temperate southern African estuary.
- The low species diversity is a consequence of the estuary being closed to the sea for much of the year.
- Multivariate analyses (classification and ordination) of the catches revealed a high degree of similarity throughout the estuary, except for samples collected at sites with a sandy substratum in the lower reaches of the estuary.
- The marine-spawning group of fishes were dominated by juvenile size classes.
- The dominant estuarine-spawning species were represented by all post larval life-history stages, which suggests that they bred successfully in the estuary.
- The numerical dominance of *Rhabdosargus holubi* and several Mugilidae species was attributed to the fact that they exhibit an extended breeding season and are able to recruit under adverse (overwash) mouth conditions.
- The East Kleinemonde estuary offers asylum to the only known viable population of *Syngnathus watermeyeri*.

CHAPTER 5

DYNAMICS OF THE ESTUARINE-SPAWNING SPECIES

5.1 INTRODUCTION

Estuarine fish communities in southern African are characterized by numerous migratory marine-spawning species and relatively few resident estuarine-spawning species (Blaber 1981; Day *et al.* 1981; Whitfield 1994b). According to Whitfield (1998), species which spawn in estuaries account for 27% of the total estuarine ichthyofauna, while 39% consists of those taxa which utilize estuaries as nursery or foraging areas and the remaining 34% include catadromous species, euryhaline freshwater species and a group of marine stragglers. Despite their low species diversity, certain estuarine-spawning species (e.g. *Gilchristella aestuaria*) are major contributors towards the overall abundance and biomass of fishes in both permanently open and temporarily open/closed estuaries (Beckley 1983; Bennett 1989a; Whitfield *et al.* 1994; Harrison & Whitfield 1995).

Temporarily open/closed systems such as the East Kleinemonde estuary are subjected to rapid habitat alteration over very short time periods. Mouth opening events, often associated with periods of high rainfall result in sudden drops in water level. During the open mouth phase, marine-spawning species which have been trapped in the estuary are able to return to the marine environment and postlarval individuals are afforded the opportunity to recruit into the estuary. The changes within fish communities arising from mouth opening and closing events have been documented from two large temporarily open/closed estuaries in the Western Cape (Bennett *et al.* 1985; Kok & Whitfield 1986). These studies highlighted the benefits of frequent openings for the marine species. However, little is known about the effects of mouth opening and closing events on the population dynamics of resident estuarine-spawning species.

The aim of this study was to compare the temporal changes in species composition, size composition and abundance of the estuarine-spawning species in the East Kleinemonde estuary. The results are based on seine net catches, which represent a series of snapshots taken over a period of two years.

5.2 MATERIALS AND METHODS

Quantitative sampling of the estuarine-spawning species was conducted during daylight hours at eight selected sites in the East Kleinemonde estuary (see Figure 4.1) on seven occasions between April 1995 and January 1997, using a seine net. The net (30m x 2m with a 5mm bar mesh) was laid in a semi-circle using a boat and swept an area of approximately 100 m^2. The fish sampled were brought back to the laboratory and measured to the nearest mm standard length (SL), with the exception of *Syngnathus watermeyeri* specimens which were measured and released in the field. A sub-sample for each species was retained and individually weighed to the nearest 0.01 g to obtain length-mass relationships (Appendix 2). The relative abundance of each species is expressed in terms of numbers per square meter ($n\ m^{-2}$) and biomass estimates were standardized to grams (wet mass) per square meter ($g\ m^{-2}$). The mean density estimates obtained for each species captured in the three different geographical regions was multiplied by it's corresponding area and then collectively summed to obtain a density extrapolated population size estimate for the entire estuary.

The species included in this study were those which have been reported to breed in estuaries. According to Whitfield's (1998) estuary-association classification they include species from category Ia (resident estuarine species which have not been recorded spawning in marine or freshwater environments) and category Ib (resident species which also have marine and/or freshwater breeding populations).

5.3 RESULTS

5.3.1 Taxonomic composition

A total of six estuarine-spawning species from four families were recorded in the East Kleinemonde estuary (Chapter 4). The category Ia species (after Whitfield 1998) were *Atherina breviceps*, *Gilchristella aestuaria*, and *Syngnathus watermeyeri* and the category Ib species were *Caffrogobius gilchristi*, *Glossogobius callidus* and *Psammogobius knysnaensis*.

5.3.2 Temporal changes in size composition

Gilchristella aestuaria

The sizes of *Gilchristella aestuaria* collected during this study ranged from 15 mm to 60 mm SL, with a mean $\pm$ standard deviation of 35.1 $\pm$ 7.7 mm (see Table 4.3). Most *G. aestuaria* collected between April and August 1995 ranged between 35 mm and 50 mm SL, with all subsequent samples including individuals of less than 30 mm SL. The widest size range (17 - 60 mm) was recorded in December 1995 (Figure 5.1).

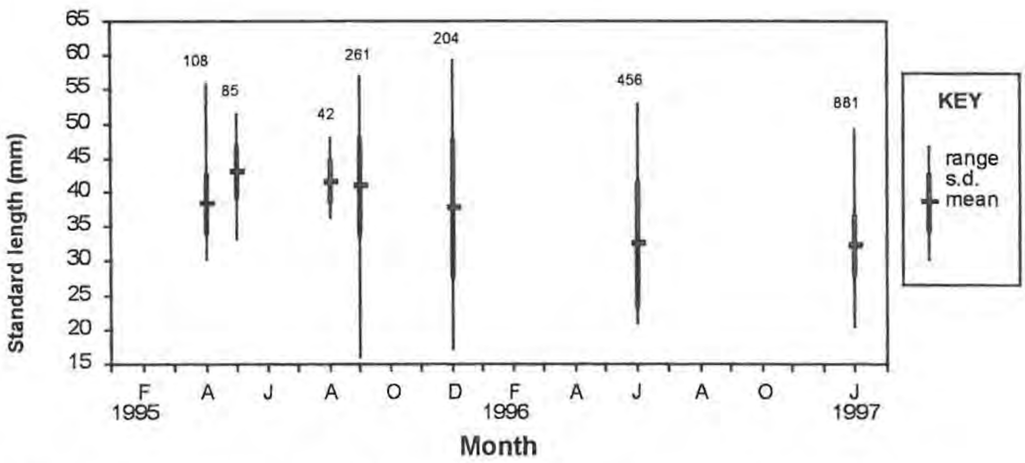

Figure 5.1 The size composition and number of *Gilchristella aestuaria* sampled on seven separate occasions between April 1995 and January 1997.

Atherina breviceps

The sizes of *Atherina breviceps* collected during this study ranged from 19 mm to 62 mm SL, with a mean $\pm$ standard deviation of 35.3 $\pm$ 8.2 mm (see Table 4.3). Specimens captured between April and September 1995 were all in the larger (>30 mm SL) size classes. A significant ($F = 57.6$: $p < 0.001$) decrease in the mean individual size was observed between September and December 1995 which dropped from 46.8 mm to 32.8 mm SL, due to the inclusion of smaller size classes. The size composition of *A. breviceps* collected in June 1996 and January 1997 were similar to the December 1995 sample which consisted mostly of the smaller (25 - 35 mm) size classes (Figure 5.2).

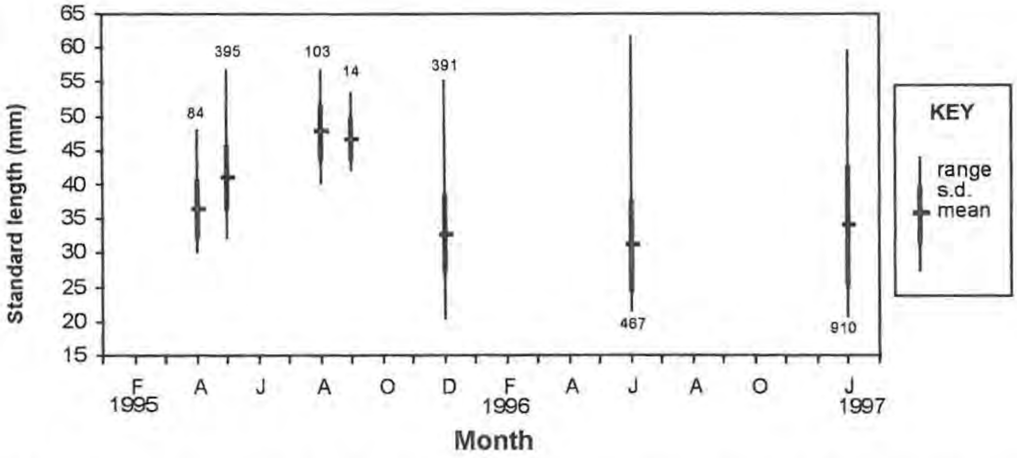

Figure 5.2 The size composition and number of *Atherina breviceps* sampled on seven separate occasions between April 1995 and January 1997.

Glossogobius callidus

The sizes of *Glossogobius callidus* collected during this study ranged between 10 mm and 92 mm SL, with a mean $\pm$ standard deviation of 41.6 $\pm$ 12.8 mm (see Table 4.3). Larger size classes (30 - 50 mm) of *G. callidus* predominated in the April to September 1995 samples. Similar to *Atherina breviceps* and *Gilchristella aestuaria*, smaller size classes were observed in the December 1995 sample. The mean individual size decreased significantly ($F = 9.0$: $p = 0.003$) from 45.2 mm to 35.2 mm SL between September and December 1995. The samples collected in June 1996 and January 1997 included a wide range of size classes, but the mean values were similar to those recorded on previous sampling occasions (Figure 5.3).

Other species

Monthly size composition comparisons were not possible for *Caffrogobius gilchristi*, *Psammogobius knysnaensis* and *Syngnathus watermeyeri* due to the low numbers of fish in each sample. Most (97%) of the *P. knysnaensis* specimens were collected in June 1996 and included a wide range of size classes (21 - 55 mm SL). No individuals smaller than 84 mm and 33 mm SL of *S. watermeyeri* and *C. gilchristi* respectively, were recorded during the study period.

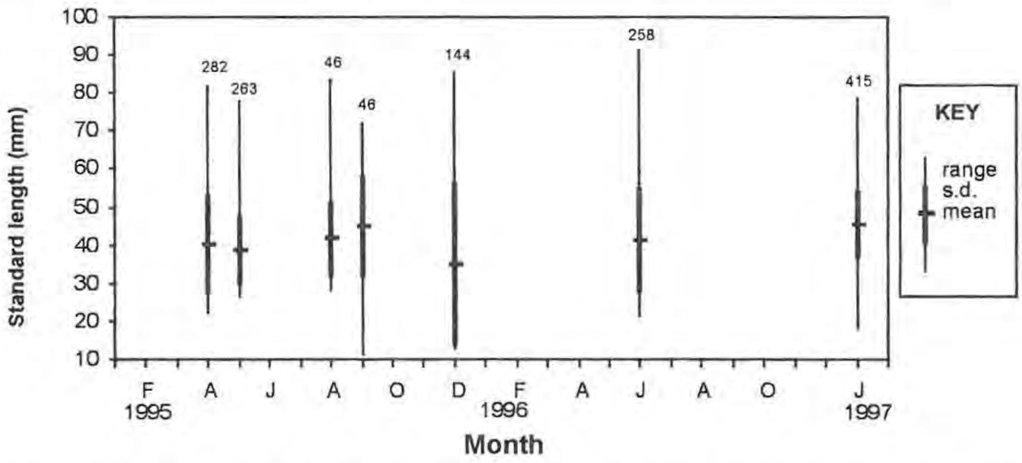

Figure 5.3 The size composition and number of *Glossogobius callidus* sampled on seven separate occasions between April 1995 and January 1997.

5.3.3 Relative abundance, biomass and population size estimates

Gilchristella aestuaria was the most abundant species with an overall mean density of 2.88 m^{-2}, followed by *Atherina breviceps* (1.11 m^{-2}), *Glossogobius callidus* (0.69 m^{-2}), *Psammogobius knysnaensis* (0.12 m^{-2}), *Syngnathus watermeyeri* (0.02 m^{-2}) and *Caffrogobius gilchristi* (0.002 m^{-2}). The mean density of the various species caught at each sampling station and geographical region (lower, middle and upper reaches) of the estuary are given in Table 5.1. Catches of *P. knysnaensis* were restricted to the lower reaches, particularly stations *a* and *b*. *Atherina breviceps* was also more abundant in the lower reaches (57%) than in the middle (22%) and upper (21%) reaches of the estuary. Conversely, *G. aestuaria* (60%) and *G. callidus* (49%) were most abundant in the upper reaches. The abundance of *S. watermeyeri*, on the other hand, was site specific and the highest abundance was recorded at station *f* (71%) and station *c* (19%).

Biomass and density extrapolated population size estimates for the estuarine-spawning species in the East Kleinemonde estuary are given in Table 5.2. *Gilchristella aestuaria* was the principal species in terms of total biomass (45.5%), followed by *Glossogobius callidus* (32.7%) and *Atherina breviceps* (18.3%), while *Psammogobius knysnaensis*, *Syngnathus watermeyeri* and *Caffrogobius gilchristi* collectively contributed less than 4%. In terms of population size, *Gilchristella aestuaria* was also the dominant species (55.8%), followed by *Atherina breviceps* (26.3%) and *Glossogobius callidus* (14.4%). The contribution by the other three minor species was again collectively less than 4%. The total biomass and population size of all estuarine-spawning species in the East Kleinemonde estuary was 582 kg (wet mass) and 754217 individuals respectively.

Table 5.1 Mean density (n m^{-2}) and percentage composition of the estuarine-spawning taxa caught at each sampling station (a - h) and geographical region (lower, middle and upper) in the East Kleinemonde estuary.

Sampling	*G. aestuaria*		*A. breviceps*		*G. callidus*		*P. knysnaensis*		*C. gilchristi*		*S. watermeyeri*	
station	n m^{-2}	%	n m^{-2}	%	n m^{-2}	%	n m^{-2}	%	n m^{-2}	%	n m^{-2}	%
a	1.527	7.9	1.957	22.8	0.180	3.6	0.63	66.3	0	0	0	0
b	0.398	2.1	1.395	16.3	0.178	3.6	0.32	33.5	0	0	0.005	2.1
c	1.963	10.1	1.880	21.9	1.260	25.1	0.01	0.5	0.01	58.8	0.045	18.8
Lower	1.275	13.9	1.725	56.7	0.572	27.1	0.29	100	0.003	56.9	0.018	36.0
d	3.153	16.3	0.440	5.1	0.383	7.6	0.00	0	0	0	0	0
e	2.230	11.5	0.833	9.7	0.647	12.9	0.00	0	0	0	0.017	7.1
f	0.780	4.0	0.930	10.8	0.520	10.4	0.00	0	0	0	0.17	70.8
Middle	2.419	26.4	0.679	22.3	0.516	24.5	0.00	0	0	0	0.031	62.0
g	1.353	7.0	0.313	3.6	0.503	10.0	0.00	0	0.007	41.2	0.003	1.3
h	7.958	41.0	0.836	9.7	1.334	26.6	0.00	0	0	0	0	0
Upper	5.481	59.7	0.640	21.1	1.023	48.5	0.00	0	0.003	43.1	0.001	2.0
Total	2.877		1.109		0.695		0.12		0.002		0.017	

Table 5.2 Biomass (grams wet mass) and population size estimates for the estuarine-spawning species in the East Kleinemonde estuary.

Species	Biomass (g m^{-2})	Total biomass (g)	Percentage contribution	Population size	Percentage contribution
Gilchristella aestuaria	1.575	264696	45.5	420973	55.8
Atherina breviceps	0.61	106756	18.3	198275	26.3
Glossogobius callidus	1.121	190400	32.7	108808	14.4
Psammogobius knysnaensis	0.092	18332	3.1	22253	2.9
Caffrogobius gilchristi	0.0002	37	< 0.1	324	<0.1
Syngnathus watermeyeri	0.016	2042	0.4	3584	0.5
Total	3.414	582263	100	754217	100

During this study, records of an additional two marine-spawning species (*Solea bleekeri* and *Heteromycteris capensis*) were kept. The reason for this was that they were too small to be captured in the large mesh seine net (bar mesh size of 15 mm) used to target the other marine-spawning species (see Chapter 4). Although these species are not regarded as estuarine-spawning (category I, after Whitfield 1998), *S. bleekeri* has been recorded spawning in Lake St Lucia (Cyrus 1991). Adults of *H. capensis*, on the other hand, occur only at sea while the larvae and juveniles utilize estuaries as nursery areas (Cyrus & Martin 1991). Analysis of the data revealed that *S. bleekeri* had a density of 0.003 m^{-2} in the middle reaches and zero in the lower and upper reaches. A density extrapolated population estimate of 200 individuals with a total biomass of 290 grams was calculated for *S. bleekeri*. *H. capensis* had a mean density of 0.007 m^{-2} and 0.0013 m^{-2} in the lower and middle reaches, with none recorded from the upper reaches. A density extrapolated population estimate was calculated at 607 individuals with a total biomass of 2858 grams.

5.4 DISCUSSION

5.4.1 Species and size composition

A total of six estuarine-spawning species were recorded in the East Kleinemonde estuary, which accounted for only 20% of the overall species composition (Chapter 4). The diversity of estuarine-spawning species in the East Kleinemonde estuary was similar to that found in two neighbouring permanently open estuaries, each less than 15 km away. Whitfield *et al.* (1994) using similar sampling techniques recorded six estuarine-spawning species (*Atherina breviceps, Gilchristella aestuaria, Glossogobius callidus, Psammogobius knysnaensis, Hyporhamphus capensis* and *Syngnathus acus*) in the Kowie estuary and four (*Atherina breviceps, Gilchristella aestuaria, Glossogobius callidus* and *Psammogobius knysnaensis*) in the Great Fish estuary.

The estuarine-spawning species captured during this study included both juveniles and adults for most species. The absence of the very small size classes (< 10 mm SL) for all species can be attributed to gear selectivity. On several occasions small individuals of several species were observed escaping through the net which had a bar mesh size of 5 mm. Analysis of length frequency distributions for the principal species (*Atherina breviceps, Gilchristella aestuaria, Glossogobius callidus* and *Psammogobius knysnaensis*) revealed the presence of only the larger size classes in the samples taken between April and August 1995. The absence of smaller size classes (20 - 35 mm SL) for these species suggests that spawning and recruitment did not take place during the first half of 1995. Although estuarine-spawning species have peak periods of breeding activity, they are often capable of spawning throughout the year (Blaber 1979; Whitfield 1980a; Talbot 1982; Bennett 1989a; Ratte 1989; Harrison & Whitfield 1995). The lack of reproductive activity during late summer and autumn of 1995 can be attributed to the physical conditions in the estuary. The water level in the system was very low during the early part of 1995 following a 13 day open mouth phase from 27 December 1994 to 8 January 1995 (see Figure 2.7). Unstable physical conditions predominated until May 1995 due to the semi-open mouth conditions and frequent over topping of the bar. A large sand bar developed at the mouth during May and the estuary level rose slowly following a series of small overwash events in June and July. After closure at the end of July, the physical conditions of the estuary stabilized and the water level remained fairly high until the next mouth opening at the end of November 1996. These stable conditions allowed for an extended reproductive season for the estuarine-spawning species. As a result, the samples collected in December 1995, June 1996 and January 1997 included specimens of the smaller size classes.

The smaller size classes present in the January 1997 sample were probably recruited prior to the mouth opening event in November 1996. Whitfield (1980a) also found that *Gilchristella aestuaria* and *Glossogobius callidus* bred during the stable closed phase in the Mhlanga estuary. Therefore, unlike the marine-spawning species, which benefit from mouth opening events (Bennett *et al.* 1985), estuarine-spawning species appear to exhibit reproductive dormancy during these events. Bennett & Branch (1990) indicated that mouth opening events in the Bot estuary result in reductions in weedbed areas and the biomass of invertebrate populations. Therefore, periods of mouth closure and physically stable conditions in temporarily open/closed estuaries are more beneficial for estuarine-spawning species as they allow for increased invertebrate (food) productivity, a prolonged breeding season and maximum habitat availability for larval and juvenile forms.

5.4.2 Density, biomass and population size

The utilization and abundance of fishes in southern African estuarine systems are determined by both biotic and abiotic variables (for a review see Whitfield 1996b). This study has shown that certain species (e.g. *Psammogobius knysnaensis*) have an affinity for the sandy areas in the lower reaches of the East Kleinemonde estuary. Similarly, *Syngnathus watermeyeri* are strongly associated with the aquatic macrophyte *Ruppia cirrhosa*. These associations with different habitats suggest that effective sampling is important when attempting to estimate relative abundance of the smaller estuarine species.

The efficiency of seine net sampling, in terms of species, size composition and estimation of absolute abundance has been the attention of much research (Jacobsen & Kushlan 1987; Allen *et al.* 1992; Rozas & Minello 1997). In a review of sampling gear efficiency (Rozas & Minello *op cit.*) state that seine nets exhibit low and variable catch efficiencies and are ineffective over soft substrates and vegetated areas. As a result, unbiased estimates of population densities can only be made if calibration for gear selectively is made or if all the fish are removed from the study site. Such an exercise is often difficult or impossible to perform in large estuarine environments. Furthermore, it is likely that sampling effectiveness as a result of net avoidance is species specific.

In the East Kleinemonde estuary many of the estuarine-spawning species (e.g. *Glossogobius callidus*, *Psammogobius knysnaensis* and *Syngnathus watermeyeri*) have a low escape response because of poor mobility. However, possible escape by these species can be attributed to their demersal habits or seeking cover in submerged macrophytes. This was partially overcome by ensuring that the lead line of the seine net dragged on the bottom at all times during net recovery and all collected vegetation was carefully examined. The escape response of *Gilchristella aestuaria* and *Atherina breviceps* was likely to be low because these species typically form midwater shoals which are easily encircled. None of the estuarine-spawning species were observed trying to swim under or around the net. Therefore, the density extrapolated seine net catches probably provide a fairly reliable, but conservative estimate, of abundance in the area swept by the net.

Quantitative information on southern African estuarine fishes is limited to a few studies. A summary of density (n m^{-2}) and/or biomass (g m^{-2}) estimates of estuarine-spawning species from various estuarine habitats is given in Table 5.3. The principal species in all studies were the zooplanktivorous *A. breviceps* and *G. aestuaria*, which collectively accounted for 64 - 92% of the biomass of estuarine-spawning species. The abundance of these species highlights their adaptability to fluctuating estuarine conditions (Ter Morhuizen & Whitfield 1994). In this context, Bennett & Branch (1990) suggested that the abundance of *A. breviceps* in the Bot estuary was a result of their broad dietary habits.

A comparison of each estuarine system revealed considerable differences in the density and biomass of most species (Table 5.3). The large differences in the overall density of estuarine-spawning species in the Kariega (7.225 m^{-2}) when compared to other estuaries are probably due to different sampling efficiencies. In the Kariega estuary, Ter Morshuizen & Whitfield (1994) used a small highly effective net (0.5 mm bar mesh), which sampled even the larvae of species such as *G. aestuaria* and *A. breviceps*. These findings suggest that standardized sampling techniques are imperative prior to making quantitative comparisons between estuarine systems.

Table 5.3 A summary of density (n m^{-2}; values in open blocks) and/or biomass (g m^{-2}; values in shaded blocks) estimates of estuarine-spawning species from various estuarine systems in southern Africa. *G.a* = *Gilchristella aestuaria*, *A.b* = *Atherina breviceps*, *G.c* = *Glossogobius callidus*, *P.*k = *Psammogobius knysnaensis*, C.*g* = *Caffrogobius gilchristi* and *S.w* = *Syngnathus watermeyeri*. Where necessary (*) dry mass values were converted to wet mass assuming that water comprises 71% fish wet mass (Marais 1990). Literature sources: 1 = this study, 2 = after Bennett & Branch (1990), 3 = Ratte (1989), 4 = Whitfield (1993), 5 = Ter Morhuizen & Whifield (1994), 6 = after Whitfield & Harrison (1996).

Estuary and literature source	Species							Total
	G.a	*A.b*	*G.c*	*P.k*	*C.g*	*S.w*	Others	
East Kleinemonde 1	2.42 1.58	1.07 0.61	0.63 1.12	0.12 0.09	0.002 0.0002	0.03 0.016		4.27 3.41
Bot 2	0.35 *0.07	1.72 *0.98		0.05 *0.03	0.003 *0.007		0.43 *0.06	2.54 *1.13
Groenvlei 3	1.0 0.27	4.1 1.96						
Swartvlei 3	1.4 0.44	1.7 0.62						
Swartvlei 4	0.99	0.38	0.02	0.005	0.41		0.05	1.84
Kariega 5	0.8	4.19	1.53	0.04	0.08		0.59	7.23
Sundays 6	1.64							

Bennett (1989a) investigated the fish communities in three Western Cape estuaries with different periods of mouth closure and found that the abundance of estuarine-spawning species was greatest in the estuary with the longest period of closure. These findings suggest that the abundance of estuarine-spawning species is greater in temporarily open/closed estuaries than in permanently open estuaries. Possible reasons for this can be attributed to the following: (1) during the closed mouth phase, the populations of estuarine-spawning species are capable of increasing due to continuous reproductive activity but the populations of marine-spawning species cannot increase because recruitment is curtailed, (2) temporarily open/closed estuaries are known to have lower species diversity (Bennett 1989a; Whitfield & Kok 1992) which implies less competition by marine taxa for available food resources. Furthermore, Bennett & Branch (1990) suggested that as far as estuarine-spawning species are concerned, temporarily open/closed estuaries are physically more stable than permanently open estuaries because the former type generally have smaller catchment areas thus making them less prone to flooding or more regular changes in salinity, temperature and turbidity regimes.

Several southern African studies have estimated the relative abundance of estuarine-spawning fishes (Table 5.3) but none have provided estimates of actual population size. This study provides the first estimates of population size for various resident estuarine dependent fish species in the East Kleinemonde estuary. The density extrapolated population size estimates are considered to be conservative because of the exclusion of the very small (larval and early juvenile) sizes of all species. Therefore, the total population size of 754217 individuals represents only that portion of the population which was effectively sampled with the 5 mm bar mesh seine net.

CHAPTER 6

POPULATION DYNAMICS OF THE MARINE-SPAWNING SPECIES

6.1 INTRODUCTION

One of the most important requirements for any ecological study is to have knowledge of population size of the various organisms in an ecosystem. This information is vital to obtain a thorough understanding of ecological processes, such as energy transfers between various organisms at different trophic levels, within an ecosystem. Furthermore, reliable population size estimates of exploited organisms (e.g. fish) provide biologists with information to effectively manage their populations. In South Africa, this quantitative approach to ichthyofaunal studies has not received much attention in the inshore marine and estuarine environments. The abundance of fish occurring in estuaries has been inferred from catches using a variety of techniques including seine nets, gill nets, lift nets, anglers catches and/or a combination of different methods (*inter alia* Marais & Baird 1980; Bennett & Branch 1990; Whitfield 1993; Whitfield *et al.* 1994). Quantitative estimates of population size in an entire estuary has been done for only one species. Blaber (1973a) investigated the population dynamics of *Rhabdosargus holubi* in the West Kleinemonde estuary over a two year period.

Population size estimation is not easy, particularly when dealing with aquatic animals which can't be seen and require specialized sampling techniques to capture them. Mark-recapture data to estimate fish population sizes was first used just over a century ago (Peterson 1896). This procedure has been widely adopted and is commonly known as the Peterson method or single census method. Population size estimation procedures have evolved considerably since the turn of century and today a wide variety of models are available. Consequently the choosing of an appropriate model to best describe the data becomes most important. Lebreton *et al.* (1992) recommended the use of several similar, but different models which are nearly equally applicable to the data. However, it must be remembered that the estimates obtained from a model(s) are not reality, but rather an appropriate representation of the data obtained to achieve a set objective. Therefore, the best model for population estimation is the simplest one which does not contain assumptions that are not met (Otis *et al.* 1978).

This study provides population size estimates, using mark-recapture techniques, for the marine-spawning fish species of the East Kleinemonde estuary for three distinct time periods. Estimates were made using a variety of methods, including three calculated models, a derived method using recapture data from the most abundant species, and a density extrapolation method which was based on catches per unit area.

6.2 MATERIALS AND METHODS

6.2.1 Sampling procedure

The general sampling procedure is the same as that described in Chapter 4 and was designed to satisfy a typical multiple census (Schnabel type) mark-recapture experiment as described by Ricker (1975). Fish were sampled using a 50 m seine net deployed randomly at 21 selected sites throughout the estuary (see Figure 4.1). A total of three mark-recapture experiments were conducted during the closed mouth phase of the estuary between 1993 and 1996. The estuary mouth conditions preceding and following each mark-recapture experiment are given in Figure 2.7 (Chapter 2). The first experiment (MR1) was conducted between 19 April 1993 and 15 September 1993 and included 16 sampling days. The second mark-recapture experiment (MR2) was conducted between 4 October 1994 and 15 December 1994 which included 26 sampling days and the third mark-recapture experiment (MR3) was conducted between 17 October 1995 and 16 February 1996, with 50 sampling days.

All the fish caught during these experiments were identified, measured and marked by means of clipping a single pelvic fin. This method of marking was chosen because the process is easy and rapidly performed, thereby minimizing handling induced stress and associated mortality (Nielson 1992). To ensure maximum survival, only fish above a certain minimum size were fin clipped. A minimize size of 100 mm standard length (SL) was selected for Mugilidae and 50 mm SL for all other species these sizes represent the maximum length of fish that could not escape through, or be injured (gill netted) by the 15 mm mesh of the seine net. Consequently, the final population estimates are conservative and do not include the contribution of the smaller size classes for each species.

6.2.2 Population size estimates

An estimate of population size for all the marine-spawning species during each mark-recapture period was made using a variety of methods. These included three calculated methods, a derived method and a density extrapolated method.

Calculated methods

a) Schnabel's method

$$N = \frac{\sum^{n}_{i=1} n_i M_i}{\sum^{n}_{i=1} r_i}$$

Where $\mathbf{i}$ = i'th sample,

$\mathbf{n_i}$ = total number of fish in the i'th sample,

$\mathbf{r_i}$ = total number of recaptures in the i'th sample,

$\mathbf{M_i}$ = total number of marked fish in the estuary just before the i'th sample, and

$\mathbf{N}$ = the population size during the experiment.

b) Schumacher & Eschmeyer's method

$$N = \frac{\sum^{n}_{i=1} M_i^2 n_i}{\sum^{n}_{i=1} M_i r_i}$$

The above methods (Schnabel and Schumacher & Eschmeyer) are described in detail by Ricker (1975) and Seber (1973). The basic assumptions required for mark-recapture studies using these methods include the following :

i) marked and unmarked fish become randomly mixed and are equally vulnerable to sampling,
ii) recruitment and mortality to the population is negligible during the mark-recapture experiment, and
iii) the marked fish do not lose their marks and that all marked fish are recognized in the

recapture sample.

c) Sum-of-squares procedure

This method estimates the population size ($\mathbf{N_0}$) at time 0 and total mortality ($\mathbf{Z}$) using the following formulas and assumptions :

$$N_t = N_{(t-1)}.e^{-Zt}$$

where $\mathbf{t}$ = a time period of 1 day

- Assuming that marked and unmarked fish die at the same rate :

$$\Sigma M_t = (\Sigma M_{t-1} + M_{t-1}).e^{-Zt}$$

where : $\mathbf{M_t}$ = number of marked fish at time $\mathbf{t}$

$\Sigma \mathbf{M_t}$ = total number of marked fish alive in the estuary at time $\mathbf{t}$

- Assuming the marked fish mix freely in the population :

$$R^*_t = C_t \ \Sigma M_t / N_t$$

where : $\mathbf{R^*_t}$ = predicted number of recaptures at time $\mathbf{t}$

$\mathbf{C_t}$ = number of fish caught at time $\mathbf{t}$

$\mathbf{N_t}$ = population size at time $\mathbf{t}$

(note - if all fish caught were marked, then $\mathbf{C_t = M_t}$)

- Compute the sum-of-squares (SS) using :

$$SS = \Sigma(R^*_t - R_t)^2$$

where $\mathbf{R_t}$ = the observed number of recaptures at time $\mathbf{t}$

From the data, therefore, $\mathbf{C_t}$, $\mathbf{M_t}$, $\mathbf{R_t}$ and $\mathbf{t}$ are known. Values for $\mathbf{Z}$ and $\mathbf{N_0}$ were then computed by non-linear minimization of the sum-of-squares using *Microsoft Excel's solver®*.

Derived method

This method was used to obtain a population size estimate for species from which no recaptures or very few recaptures were obtained during the respective mark-recapture periods. The percentage catch representation of such a species was compared with a 'control species' from which calculated population size estimates were obtained. For example, if 50 individuals of a species with no recaptures was caught, and 100 individuals of the 'control species', with a calculated population size of 1000, was caught during the mark-recapture period, then the derived population size estimate for the species with no recaptures equals 500 [i.e. (50 / 100)1000 = 500].

Rhabdosargus holubi was chosen as the 'control species' for the following reasons:

- it was the most abundant marine spawning species in the East Kleinemonde estuary,
- it was the only species with recaptures, from which calculated estimates could be made, during all three mark-recapture experiments.

The basic assumptions required for the derived estimate method were :

i) all species have equal probability of capture, and
ii) the species under investigation has the same distribution as the 'control species'.

Density extrapolated method

The estuary was divided into three regions (lower, middle and upper reaches; see Figure 4.1). The total seine net catch from each of the three regions was divided by the total area sampled. These values were then multiplied by the corresponding area of each region of the estuary and summed to give a density extrapolated population estimate for the entire estuary.

This method assumes that all species are equally distributed within each region of the estuary and that the area swept by the net is a true reflection of this distribution.

6.3 RESULTS

A total of 2539 fishes were fin clipped during the first mark-recapture experiment (MR 1) of which 39 were recaptured. During the second (MR 2) and third (MR 3) mark-recapture experiments, 5834 and 15567 fishes were marked, and 921 and 877 fish were recaptured, respectively. Unfortunately, recaptures were obtained for only a few species during each mark-recapture experiment. Therefore, population estimates using the calculation methods could only be made for those species from which marked fish were recaptured. However, the derived method was used to obtain a population size estimate for species from which no recaptures or very few recaptures were obtained during each mark-recapture period.

6.3.1 Calculated and derived population size estimates

The species from which recaptured fish were obtained during each of the mark-recapture experiments are given in Table 6.1.

Table 6.1 The number of individuals marked, recaptured and the percent recapture rate for those species from which recaptures were obtained during the three mark-recapture experiments (MR 1, MR 2 and MR 3).

	Species	Number marked	Number recaptured	Recapture rate (%)
MR 1	*Rhabdosargus holubi*	1396	32	2.3
	Liza richardsonii	275	3	1.1
	Myxus capensis	630	4	0.6
MR 2	*Rhabdosargus holubi*	4895	878	17.9
	Monodactylus falciformis	493	39	7.9
	Liza dumerilii	95	4	4.2
MR 3	*Rhabdosargus holubi*	12914	758	5.9
	Lithognathus lithognathus	406	23	5.7
	Sarpa salpa	220	9	4.1
	Liza dumerilii	821	37	4.5
	Liza richardsonii	424	21	5.0
	Myxus capensis	410	22	5.4
	Monodactylus falciformis	271	7	2.6

Rhabdosargus holubi

Rhabdosargus holubi was the principal species during all three mark-recapture experiments. It was recorded in 50%, 96% and 94% of the total number of seines during MR 1, MR 2 and MR 3 respectively. Population size estimates for this species using the three calculated methods are given in Figure 6.1. The estimates during MR 1 ranged from 26708 to 39491 with a mean of 34595. The estimates obtained during MR 2 ranged from 12833 to 14367 with a mean of 13882 and for MR 3 from 105149 to 111673 with a mean of 108150. The variance, indicated by the 95% confidence limits, of the population estimates obtained from the three calculated methods were lower during MR 2 and MR 3 due to better sampling efficiency as reflected by the higher recapture percentages obtained during these mark-recapture experiments.

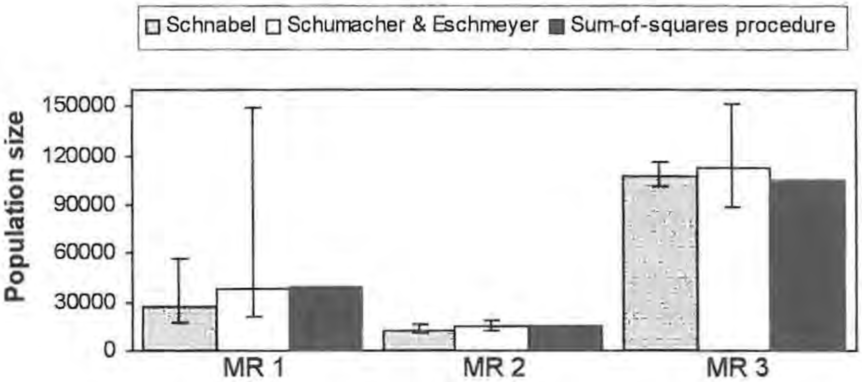

Figure 6.1 The calculated population size estimates for *Rhabdosargus holubi* during the three mark-recapture experiments (MR 1, MR 2 and MR 3). Error bars represent 95% confidence limits.

An estimate of population size using the derived method was not calculated for *Rhabdosargus holubi* because this species was used as the 'control species' for all others recorded during the three mark-recapture periods.

Lithognathus lithognathus

Lithognathus lithognathus was marked in all three mark-recapture experiments but none were recaptured during MR 1 and MR 2. Therefore, population estimates for these mark-recapture periods were made by means of the derived estimate method. However, during MR 3 estimates were also obtained using the calculated methods. The population estimates obtained from the various methods during the three mark-recapture periods are given in Figure 6.2. The similar population estimates obtained from the derived (3384) and calculated (3260, 3355 and 3953) methods during MR 3 suggest that the derived estimates of 707 obtained during MR 1 and 322 during MR 2 are realistic indicators of the population size for this species during these periods.

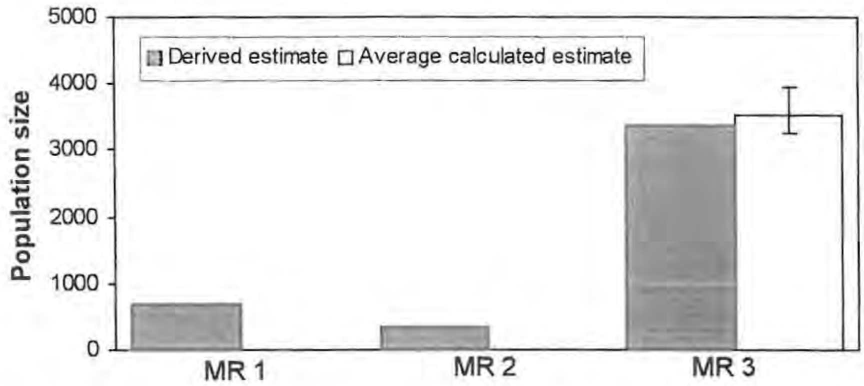

Figure 6.2 Population size estimates for *Lithognathus lithognathus* during the three mark-recapture periods (MR 1, MR 2 and MR 3). Error bar represents the minimum and maximum calculated value.

Sarpa salpa

No catches of *Sarpa salpa* were made during MR 1 and MR 2, but during MR 3 a total of 220 individuals were caught and marked, of which 9 (4.1%) were recaptured (Table 6.1). The calculated population size estimates ranged from 440 to 517 with mean of 483, while the derived estimate method yielded an estimate of 1842. The large variation obtained from the different methods can be attributed to the fact the *Sarpa salpa* had a limited distribution within the estuary. Catches of this species were restricted to the lower reaches and recorded from only two sampling sites near the mouth. Therefore, the estimate obtained from the derived method is probably not a true indication of the population size because it was related to the catches of *Rhabdosargus holubi* which were recorded throughout the estuary.

Diplodus sargus capensis

The catches of *Diplodus sargus capensis* constituted a small portion of the overall catch during the three mark-recapture periods. Only three, two and four individuals were recorded during MR 1, MR 2 and MR 3 respectively. Population size estimates, using the derived estimate method, were calculated at 74, 6 and 33 during the three mark-recapture experiments respectively. Similar to *Sarpa salpa*, the catches of *Diplodus sargus capensis* were restricted to the lower reaches of the estuary, suggesting that these derived values are unrealistic.

Liza dumerilii

No marked *Liza dumerilii* were recaptured during MR 1, but during MR 2 and MR 3 recapture rates of 4.2% and 4.5% respectively, were obtained. The population size estimates using the derived method (MR 1, MR 2 and MR 3) and the calculated methods (MR 2 and MR 3) are given in Figure 6.3. The population estimates obtained from the two different methods during MR 2 and MR 3 indicate that the derived value represents a conservative estimate of the population size.

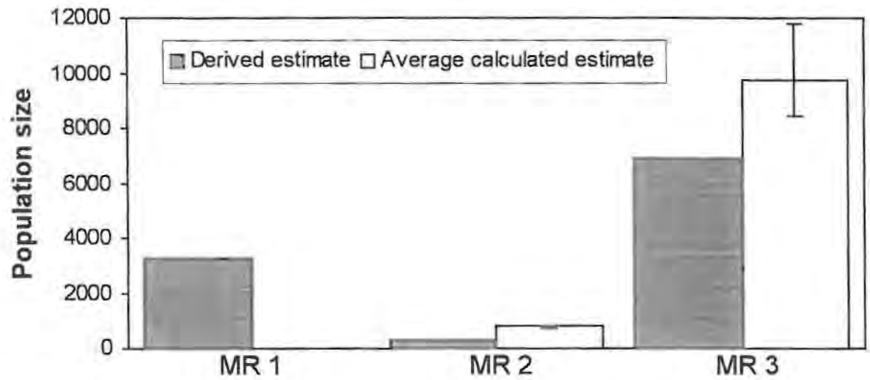

Figure 6.3 Population size estimates for *Liza dumerilii* during the three mark-recapture periods (MR 1, MR 2 and MR 3). Error bars represent the minimum and maximum calculated values.

Liza richardsonii

Population size estimates for *Liza richardsonii* were made using the derived method for all three mark-recapture periods and the calculated method for MR 1 and MR 3 only (Figure 6.4). The large variation obtained from the three calculated estimates (8137 to 13359) during MR 1 are probably a result of the low recapture rate (1.1%) suggesting that this estimate is inaccurate. The calculated estimate obtained during MR 3, with a recapture rate of 5%, compared favourably with the derived estimate. Therefore, the derived estimates for this species probably provide a realistic estimate of the actual population size.

Liza tricuspidens

Catches of *Liza tricuspidens* were low and restricted to MR 1 and MR 3. No recaptures were recorded and population size estimates of 332 during MR 1 and 117 during MR 3 were obtained using the derived method.

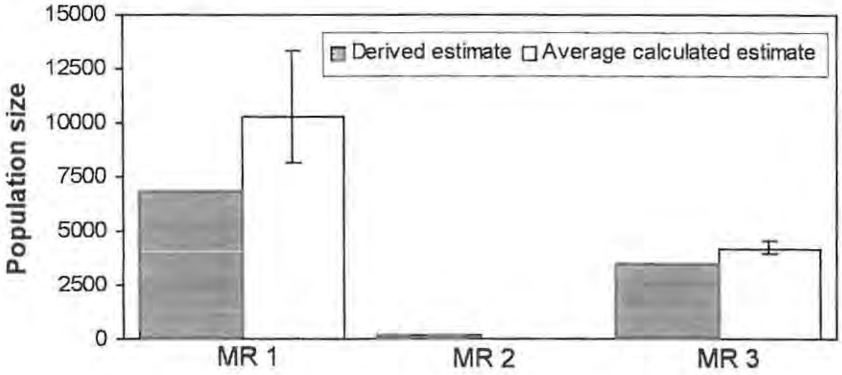

Figure 6.4 Population size estimates for *Liza richardsonii* during the three mark-recapture periods (MR 1, MR 2 and MR 3). Error bars represent the minimum and maximum calculated values.

Mugil cephalus

Mugil cephalus was recorded during all three mark-recapture periods in low numbers. Population size estimates, using the derived method, were 149 during MR 1, 17 during MR 2 and 544 during MR 3. It is believed that these values represent conservative estimates because this species was often observed jumping out of the net. Therefore, the recorded catches, on which these estimates are based, were not a true reflection of the abundance of this species.

Myxus capensis

No *Myxus capensis* were recaptured during MR 2, but MR 1 and MR 3 yielded recapture rates of 0.6% and 5.4% respectively. The estimates obtained from the calculated methods during MR 3 revealed little variation (3124 to 3827) and were similar to the estimate obtained from the derived method (Figure 6.5). However, the variation (18982 to 46996) was much greater during MR 1. The reasons for this can be ascribed to the low recapture rate (0.6%) and possible immigration due to marine topping of the bar during the experiment. The latter is supported by the change in catch rate which increased from 1.2 fish per seine (April, May and June) to 21.3 fish per seine (July, August and September) during the course of the experiment. Based on these results, the derived values probably represent a better reflection of the actual population size for

Myxus capensis during MR 1.

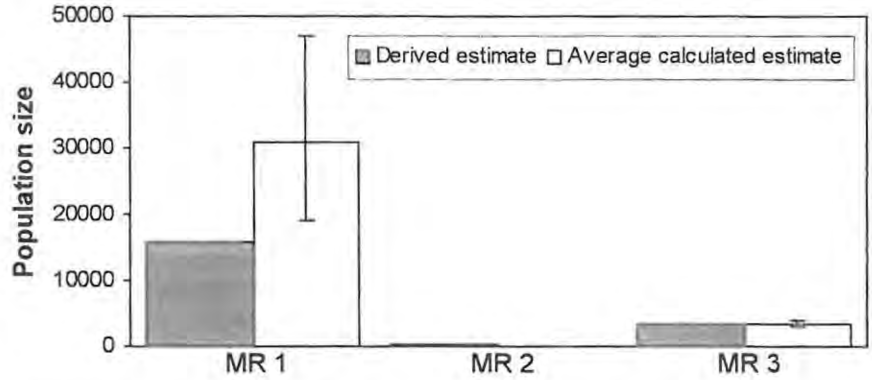

Figure 6.5 Population size estimates for *Myxus capensis* during the three mark-recapture experiments (MR 1, MR 2 and MR 3). Error bars represent the minimum and maximum calculated values.

Monodactylus falciformis

Monodactylus falciformis was recorded during all three mark-recapture periods but marked fish were only recaptured in MR 2 and MR 3. The population size estimates obtained for this species during the three mark-recapture experiments are given in Figure 6.6. The low variation between the three calculated estimates during both MR 2 (2758 to 3115) and MR 3 (4814 to 5101) suggests that these estimates are good indicators of population size. The estimates obtained from the derived method were a proportionately similar amount less than the average calculated values during MR 2 and MR 3. The difference between the two methods equated to a factor of 2.12 during MR 2 and 2.19 during MR 3. Therefore, to obtain a more realistic estimate of the population size during MR1, the mean of the above factors was multiplied by the derived estimate. The adjusted population size estimate for MR 1 was calculated at 481.

Lichia amia

Lichia amia was recorded in low numbers during all three mark-recapture periods. Population size estimates, using the derived method, were 942, 77 and 25 during MR 1, MR 2 and MR 3 respectively.

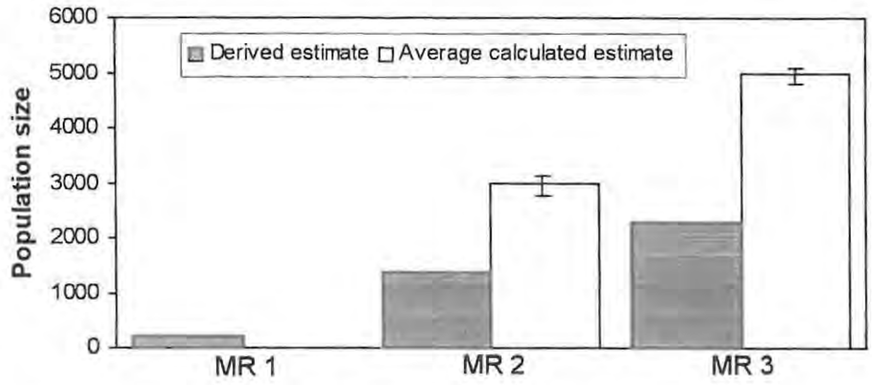

Figure 6.6 Population size estimates for *Monodactylus falciformis* during the three mark-recapture experiments (MR 1, MR 2 and MR 3). Error bars represent the minimum and maximum calculated values.

Pomadasys commersonnii

Pomadasys commersonnii was also recorded in low numbers during the three mark-recapture experiments. The derived population size estimates were calculated at 25, 54 and 126 during MR 1, MR 2 and MR 3 respectively.

6.3.2 Density extrapolated population size estimates

The estimates obtained from density extrapolation and the most reliable estimates obtained from either the calculated or derived method for each species (as given in the paragraphs above) are shown in Table 6.2. The results obtained from density extrapolation were inconsistent for the three mark-recapture periods and for certain species were as much as 10 times lower than those obtained from either the calculated or derived estimates during MR 1 and MR 3. The total population size of all marine-spawning species, using the density extrapolated method, was calculated at 15599 and 11830 during MR 1 and MR 3 respectively. These values represented approximately 25% and 9% of the total estimate obtained from the more reliable estimates (calculated or derived) for the same periods. Conversely, during MR 2 the density extrapolated estimate (21069) was similar but slightly higher than the more reliable estimate of 18592. Based on these findings, the density extrapolated method is believed to be an inaccurate estimator of population size which is highly reliant on the assumptions that fish are uniformly distributed in the estuary and that all fish within the sampled area are captured.

Table 6.2 Population size estimates obtained from density extrapolation and the calculated or derived method for the marine-spawning species in the East Kleinemonde estuary during the three mark-recapture periods (MR 1, MR 2 and MR 3), where * = average calculated estimate and ** = derived estimate.

	MR 1		MR 2		MR 3	
Species	Density extrapol. estimate	Most reliable estimate	Density extrapol. estimate	Most reliable estimate	Density extrapol. estimate	Most reliable estimate
Rhabdosargus holubi	8630	34959*	18179	13882*	9758	108150*
Lithognathus lithognathus	214	707**	508	322**	320	3523*
Sarpa salpa	0	0	0	0	176	483*
Diplodus sargus capensis	18	74**	4	6**	3	33**
Liza dumerilii	883	3246**	365	773*	629	9718*
Liza richardsonii	1880	6815**	209	179**	330	4127*
Liza tricuspidens	77	332**	0	0	11	117**
Mugil cephalus	35	149**	24	17**	49	544**
Myxus capensis	3574	15612**	308	315**	329	3460*
Monodactylus falciformis	57	481**	1290	2967*	212	4986*
Lichia amia	225	942**	107	77**	2	25**
Pomadasys commersonnii	6	25**	75	54**	11	126**
Total	15599	63342	21069	18592	11830	135192

6.3.3 Temporal changes in population structure and size

The marine-spawning fishes of the East Kleinemonde estuary are dominated by *Rhabdosargus holubi*, which constituted approximately 55%, 75% and 80% of the total population during MR 1, MR 2 and MR 3 respectively. Other dominant species included *Myxus capensis* which represented almost 25% of the population during MR 1, *Liza richardsonii* (11% during MR 1), *Monodactylus falciformis* (16% during MR 2 and almost 4% during MR 3) and *Liza dumerilii* (5% during MR 1, 4% during MR 2 and 7% during MR 3).

Based on the most reliable population estimates (given in Table 6.2), the total population size of the marine-spawning species revealed considerable fluctuations over a period of three years. The total population size declined by two thirds between MR 1 and MR 2 but then increased more than seven fold from MR 2 to MR 3. The species groups which revealed the greatest change were the sparids (mostly *Rhabdosargus holubi*) and the mugilids (Figure 6.7). The sparid population dropped from 35740 to 14210 between

MR 1 and MR 2 but increased to 112189 during MR 3. Similarly, the mugilid population declined from 26154 (MR 1) to 1284 (MR 2) and increased again in MR 3 to 17966. The combined contribution by the other species (*Lichia amia*, *Monodactylus falciformis*, and *Pomadasys commersonnii*) revealed the least variation, ranging from 1448 during MR1 to 3098 and 5137 during MR 2 and MR 3 respectively.

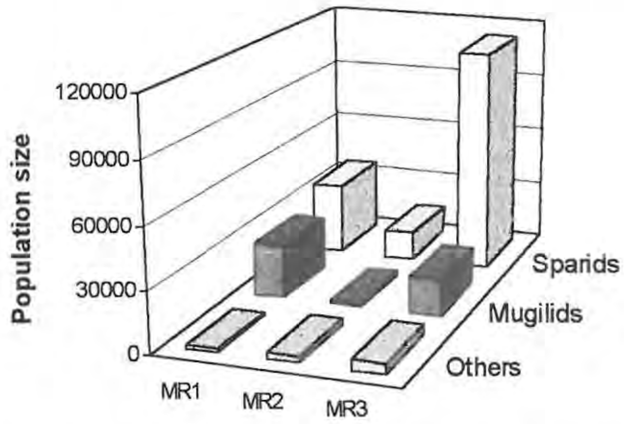

Figure 6.7 The population size for Sparids, Mugilids and other species (*Lichia amia*, *Monodactylus falciformis* and *Pomadasys commersonnii*) during the three mark-recapture periods (MR 1, MR 2 and MR 3).

These results highlight the dynamic nature of the marine-spawning fish populations in the East Kleinemonde estuary. This dynamic condition is attributed to the fact that recruitment is highly variable and restricted to periods of mouth opening and overwash (bar topping) events. However, the drastic population decline between MR 1 and MR 2 is probably the result of bird predation. During the winter of 1994 the East Kleinemonde estuary and many other estuaries along the south-eastern Cape coastline were subject to a major invasion of Cape cormorants *Phalacrocorax capensis* (see Chapter 7).

6.4 DISCUSSION

Population size estimates of marine-spawning fish species in the East Kleinemonde estuary during the closed mouth phase were obtained using a variety of methods for three distinct periods. For several species a wide range of estimates were obtained for particular periods. The main reason for this can be attributed to the different methods used to obtain the population size estimates, which are discussed in the following paragraphs.

6.4.1 Calculated population estimates

The dissimilar estimates of population size obtained for several species during the respective mark-recapture experiments highlights some of the problems faced by ecologists when attempting to calculate population size. The commonly posed questions when conducting such an exercise include: how big a sample is needed or how much effort is needed to achieve statistically valid results? Burnham *et al.* (1987) set out a protocol of effort and sample size considerations in an attempt to answer the above questions. However, working in the natural environment does not always allow for a rigid sampling strategy because the constraints which affect the protocol are often dynamic and unavoidable. For example, in the present study, sampling during MR 1 and MR 2 had to be terminated prematurely because the estuary breached its mouth thereby breaking the underlying assumption that the population under investigation was closed. Furthermore, a wealth of literature exists on different mathematical techniques or models to estimate population size (for reviews see: Ricker 1975; Otis *et al.* 1978; Blower *et al.* 1981; White *et al.* 1982; Burnham *et al.* 1987; Seber 1992), which present additional problems when attempting to select the correct model(s). The dilemma is compounded by the fact that mark-recapture models have recently evolved to rather estimate survival rates and not population sizes (Lebreton *et al.* 1992). In an attempt to assess the correct choice of model and it's applicability, the basic aims of this study influenced model selection. The primary objective was to obtain an estimate of the population size for various marine-spawning fish species in the East Kleinemonde estuary. An important consideration here was that the population under investigation was closed. Therefore, simplified mark-recapture methods, in which model assumptions could be met satisfactorily, were used. The basic assumptions required for the calculated estimates (particularly the Schnabel and Schumacher & Eschmeyer methods) and an explanation on how and what methods were used to meet them, are outlined below:

a) *The population is subject to no recruitment.* Recruitment into the East Kleinemonde estuary was considered to be negligible on the following grounds. The mark-recapture experiments were conducted during the closed mouth phase of the estuary and the fish under investigation during these experiments were all marine-spawning species which are unable to reproduce in the estuary. However, it must be noted that recruitment was possible during overwash events or from the freshwater reaches of the East Kleinemonde river. The latter was probably responsible for the increased catches for the catadromous *Myxus capensis* during MR 1. Topping of the bar occurred on six, two and one day(s) during MR 1, MR 2 and MR 3 respectively. Several species, particularly *Rhabdosargus holubi*, are able to recruit as post-flexion larvae during these overwash events. The possible contribution to the population from these events is likely to be minimal because the recruited fish were still too small to be considered for fin clipping and hence were not part of the mark-recapture experiments. The population was however subject to some recruitment as a consequence of growth (i.e. individuals entering the fin clipping size range during the mark-recapture period). Once again the contribution by these individuals was considered to be minimal because of the low variability between the estimates obtained by the three calculated methods (where the sum-of-squares procedure provides a population estimate at time 0, and the Schnabel and Schumacher & Eschmeyer's methods provide an estimate at the end of the experimental period).

b) *No emigration or mortality occurs in the population*. This assumption applies only to the Schnabel and Schumacher & Eschmeyer calculations because the sum-of-squares procedure allows for mortality. The estuary was closed during the mark-recapture experiments making anadromous migrations impossible. However, as explained above it was possible for fish to leave the estuary during topping of the bar events. It is proposed that emigration during overwash events was insignificant during MR 2 and MR 3 because these events (all minor) occurred within the first week of commencing the experiments and any losses to the population at such an early stage would have been compensated for by the calculations. However, losses to the population, although unquantifiable, during MR 1 could have been more severe. The low recapture percentages and greater variation between the three calculated estimates for each species recorded during MR 1 reinforces the possibility of such losses. Other forms of losses, such as from recreational angling, were considered to be negligible because most of the fish captured during the mark-recapture experiments are not sought after recreational linefish species and only a few exceeded the gazetted minimum size limit. Natural mortality during the mark-recapture experiments, which were conducted over relatively short periods of time were likely to be insufficient to necessitate adjustments to the final calculations.

c) *Marked fish do not loose their marks and are all recognizable in the recapture sampling*. Fish were marked by means of clipping off a single pelvic fin at it's base. Unlike external tags, the mark was permanent which negated the fears of mark loss. Although the regeneration of fins was fairly rapid, marked fish were easily identified by their wave-like deformed pelvic fins. The sampling procedure (multiple census mark-recapture) was designed so that each fish captured and/or recaptured throughout the mark-recapture experiments was individually checked for a mark. Therefore violations of these assumptions were probably insignificant.

d) *Marked and unmarked fish suffer the same mortality.* Although speculative, it is probable that the sampling and fin clipping procedure was performed cautiously enough not to subject marked fish to differential mortality compared to unmarked fish. Nielson (1992) states that mortality of fin-clipped fish is highly variable depending on the size, the species and which fin is clipped. The most important species in this study (*Rhabdosargus holubi*), was the subject of a detailed study by Blaber (1973b) who stated that the use of Floy tags and fin clipping apparently had no significant differential effect on mortality. Furthermore, several investigations have provided little evidence that predation is an important source of excess mortality among fin-clipped fish (Coble 1967). In addition, throughout the study period no captured fish revealed signs of infection or ill health as a result of the fin clipping process.

e) *Marked and unmarked fish are equally vulnerable to sampling.* Ricker (1975) stated that the sources of error which cause marked or unmarked fish to be either more or less vulnerable to sampling are a result of (i) the fish under investigation were not part of the original population being estimated, (ii) the type of mark used and (iii) the differences in behaviour as a result of tagging or marking. During this study all fish marked were native to the environment in which they were released and unlike many external tags, fin clips have little effect on the catchability of marked fish (Young *et al.* 1988). Furthermore, no noticeable difference in swimming or shoaling behaviour of fin-clipped fish were observed during this study.

f) *Marked fish become randomly mixed with unmarked fish.* In an attempt to satisfy randomization, sampling (and hence marking) was conducted throughout the estuary where it was possible to seine effectively. Furthermore, the daily sampling routine did not follow any strict site specific (geographical) sequence. According to Young *et al.* (1988) improved mixing of marked and unmarked fish can be achieved by delayed recapture effort. Therefore, if sampling was conducted on consecutive days, the same sites and nearby sites were avoided on the second day. In addition, a 24-h sampling session was conducted at three different sites in the estuary to investigate whether marked fish mixed freely within the population. The catch composition and presence of marked fish was compared between samples taken every four hours at each of the three locations. The findings indicated that the marked fish mixed freely with unmarked fish and moved away from the release site soon after being released.

In summary, therefore, it is felt that the assumptions for the calculated estimates were adequately met and the results are a true reflection of the population size, particularly during MR 2 and MR 3. The variability, as indicated by the range of the three estimates obtained from the calculated methods, was directly related to the recapture rate. Recapture rates of less than four percent tended to result in undesirable variability. Therefore, calculated estimates for species which yielded recapture rates of less than four percent were placed subordinate to the value obtained from the derived method in terms of a more reliable population size estimate (Table 6.2).

6.4.2 Derived population estimates

Population size estimates obtained using the derived method were considered to be reliable estimates for several species because they agreed well with the calculated estimates. Therefore, for these species the assumption that their distribution was similar to *Rhabdosargus holubi* (the 'control species') was adequately met. However, the estimates for species which had a limited distribution in the estuary (e.g. *Sarpa salpa*) are believed to be artificially enhanced. In the case of *Monodactylus falciformis*, which also had a different distribution to the 'control species', the derived estimate during MR 1 could be adjusted using a correction factor obtained from the difference between the calculated and derived estimates during MR 2 and MR 3. The high variability obtained from the three calculated estimates for the 'control species' during MR1 suggests that the derived estimates used during this period are not accurate and should be treated with caution.

6.4.3 Density extrapolated population estimates

The use of density extrapolation or swept area techniques to obtain population size estimates rely on the assumptions that all fish are uniformly distributed and equally vulnerable to capture. These assumptions are seldom accurately met for marine-spawning species because they are highly mobile and variously distributed within an estuary. Young *et al.* (1988) state that density extrapolation techniques require standardized quantitative sampling in randomized designs with knowledge of catch efficiency. They also recommend that a mark-recapture study should be considered for at least a one-time calibration of the density extrapolated estimates. Despite this, the accuracy of the population size estimates obtained from density extrapolation during this study were difficult to predict. Comparisons with the other population size estimates revealed enormous inter-specific variability for any one mark-recapture period and also intra-specifically for different analysis periods. A similar trend was observed by Blaber (1973a), who showed no significant difference in the catch per unit effort (mean number of fish caught per seine) for *Rhabdosargus holubi* at levels of low or high population size. Therefore, estimates obtained from density extrapolation are probably inaccurate and sometimes appear to be density independent.

6.4.4 The overall population size

The total population of marine-spawning fishes (above a certain minimum size) in the East Kleinemonde estuary displayed large fluctuations over the study period, ranging from 18592 individuals during MR 2 to 135192 individuals during MR 3. These fluctuations may be related to abiotic and/or biotic conditions which are highly variable and unpredictable. Similar conditions probably apply to all temporarily open/closed estuaries which are subject to highly variable salinity and temperature regimes, evaporation/precipitation ratios and frequency of open mouth phases which result in rapid and extensive habitat variation. The seasonal variability of open mouth phases or even topping of the bar events allow for unpredictable immigration and emigration of marine-spawning fish species. The seasonal timing of these events also play a significant role in the occurrence and abundance of individual species.

The numerical dominance of *Rhabdosargus holubi* and several mugilids in the East Kleinemonde estuary during all three mark-recapture periods is ascribed to the fact that they are serial spawners or have prolonged breeding seasons. These species are able to recruit for a larger part of the year and are not restricted by the short open mouth phases which occur sporadically throughout the year (see Chapter 2). The recruitment success of species such as *Lichia amia*, *Lithognathus lithognathus* and *Pomadasys commersonnii*, on the other hand, is diminished because they exhibit distinct reproductive seasonality which may or may not coincide with a mouth opening event.

CHAPTER 7

PREDATION

7.1 INTRODUCTION

The importance of South African estuaries as nursery areas for many marine-spawning fish species is well known (*inter alia* Beckley 1984; Wallace *et al.* 1984; Whitfield & Kok 1992). The abundance of these juvenile migrant species together with other small resident species often account for high density and biomass values within estuaries (Bennett 1989a; Whitfield *et al.* 1994; Harrison & Whitfield 1995). As a result, estuarine environments provide rich feeding grounds for a number of piscivorous predators. For example, Whitfield (1978) found a significant correlation between fish and piscivorous bird densities in Lake St Lucia. Similarly, Blaber (1973b) postulated that the numbers of piscivorous birds at the West Kleinemonde and Kasouga estuaries were related to the densities of *Rhabdosargus holubi*.

Estuarine-associated fishes are not only important dietary items of piscivorous birds, but also several of predatory fishes. The feeding ecology of piscivorous fishes has been documented from several South African estuarine systems (Whitfield & Blaber 1978a; Whitfield 1980c; Marais 1984; Whitfield 1988). According to Marais (1984) *Argyrosomus japonicus*, *Lichia amia*, *Elops machnata* and *Pomatomus saltatrix* are the most important piscivorous fishes in temperate estuaries, while subtropical estuaries include additional species such as *Sphyraena barracuda*, *S. jello*, several *Caranx* species and the elasmobranch *Carcharinus leucas* (Whitfield & Blaber 1978a). Similar to fish predators, the diversity and abundance of other piscivores is greater in subtropical estuaries. These include higher densities of penaeid prawns (*Penaeus japonicus* and *P. monodon*), the portunid crab *Scylla serrata* and the inclusion of other major piscivores such as the Nile crocodile *Crocodylus niloticus* (Whitfield & Blaber 1979a; Cyrus & Forbes 1996).

The objective of this study was to quantify fish predation by the two dominant predator groups (birds and piscivorous fish) as part of the overall aim of gaining a better understanding of the dynamics of the fishes in the temporarily open/closed East Kleinemonde estuary.

7.2 MATERIALS AND METHODS

7.2.1 Piscivorous birds

The number of piscivorous birds at the East Kleinemonde estuary was assessed by means of visual counts conducted between March 1994 and March 1996. The number of counts made during each month are given in Appendix 3. The counts were made by two people on a motorized boat following a fixed route from the mouth to the head of the estuary. Counts were made between 08h00 and 10h30 and the duration of each count ranged between 15 and 25 minutes. No counts were conducted between January and March 1995 due to very low water levels as a result of an extended open mouth phase of the estuary. No attempts were made to flush birds roosting in trees or marginal vegetation but more often than not the noise of the boat caused the birds to fly off, notably the swimming (e.g. cormorants) and aerial diving birds (e.g. kingfishers). The flight of these birds facilitated the counts because they generally occurred in low densities and may sometimes have been overlooked if they remained stationary. However, the typical underwater diving escape response displayed by the dabchick (*Tachybaptus ruficollis*) made it very difficult to count. Therefore, this species was excluded from the census. Although *T. ruficollis* is known to prey on fishes (Junor 1969), it's main dietary items include other small aquatic vertebrates and invertebrates (Maclean 1993).

As a means of evaluating their dependence on the estuary as a feeding ground, the birds were categorized into four groups based on their percentage frequency of occurrence (% FO) in the counts. The groups were assigned as follows: rare visitor (0 - 24% FO), occasional visitor (25 - 49% FO), frequent visitor (50 - 74% FO) and resident (75 - 100% FO).

The daily food consumption of each avian predator was calculated from the following expression given by Nagy (1987) :

$$\mathbf{FR = 0.495\ BM^{0.704}}$$

Where **FR** = feeding rate (grams dry mass per day)
BM = body mass (grams)

Based on the assumption that water comprises 71% of fish wet mass (Marais 1990), dry mass values were multiplied by 3.448 to convert to wet mass. Mean body mass values for each bird species were taken from Berruti (1983) and Maclean (1993). The monthly consumption by each bird species was calculated by multiplying the individual daily consumption estimate by the mean number of birds recorded per month, and then extrapolated to a full month by multiplying by the number of days in each month.

During July 1994 large numbers of Cape cormorants, which usually occur in marine waters, invaded the East Kleinemonde estuary. The number of bird counts during this unusual event was increased in an attempt to quantify the ichthyofaunal predation by these birds. The very high numbers of Cape cormorants recorded during this period overemphasized the overall predatory importance of this species. Therefore, the data collected for Cape cormorants was treated separately to that of the other avian predators.

7.2.2 Piscivorous fishes

The piscivorous fishes of the East Kleinemonde estuary were sampled using seine net gear (Chapter 4) and estimates of their population sizes were obtained from the results of a series of mark-recapture experiments (Chapter 6). Biomass values of these fish populations were calculated using both the population size estimates and information relating to the size (weight) composition of the fishes in the population. An estimate of daily food consumption was made using the following equation given by Palomares & Pauly (1989):

$$\ln Q/B = -0.1775 - 0.2018 \ln W_{\alpha} + 0.6121 \ln T + 0.5156 \ln A + 1.26 F$$

where Q/B is the daily food consumption of a fish population as a percentage of its biomass, W_{α} the mean asymptotic (or maximum) weight (g) of the fish in the population in question, T is its mean habitat temperature (in °C), A is the aspect ratio of the caudal fin (as a measure of the average activity and/or metabolic levels of the fish) and F its food type (a dummy variable which equals 0 in carnivores). The method of calculating the aspect ratio of the caudal fin of *Lichia amia* is shown in Figure 7.1.

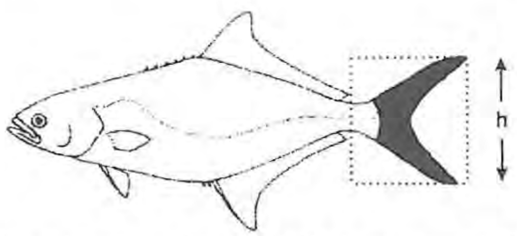

Figure 7.1 Diagrammatic representation of the method to calculate aspect ratio ($A = h^2/s$) of the caudal fin of *Lichia amia* (**h** = height and **s** = surface area, in black).

7.3 RESULTS

7.3.1 Piscivorous birds

Species composition, abundance and biomass

A total of 16 piscivorous bird species (excluding Cape cormorant) were recorded at the East Kleinemonde estuary during 62 bird counts conducted between March 1994 and March 1996 (Table 7.1). The species composition was numerically dominated by five species, namely reed cormorant (mean number per count = 9.5), pied kingfisher (3.5), whitebreasted cormorant (2.9), common tern (2.7) and darter (2.3). The mean number per count of all the other species combined was only 5.5. The dominant species gravimetrically were whitebreasted cormorant (mean biomass per count = 5522 g), reed cormorant (5111 g), darter (3303 g) and African fish eagle (928 g). The collective mean biomass of all other species was 2397 g per count (Table 7.1).

Table 7.1 Mean numbers and biomass of the piscivorous birds recorded at the East Kleinemonde estuary between March 1994 and March 1996 (values in parentheses indicate numerical ranking).

Species	Common name	Individual mass (g)	mean number per count	mean biomass (g) per count
Phalocrocorax carbo	Whitebreasted cormorant	1904	2.9 (3)	5522 (1)
Phalocrocorax africanus	Reed cormorant	538	9.5 (1)	5111 (2)
Anhinga melanogaster	Darter	1326	2.5 (5)	3315 (3)
Ardea cinerea	Grey heron	1436	2.3 (6)	3303 (4)
Ardea melanocephala	Blackheaded heron	1135	0.1 (12)	114 (11)
Ardea goliath	Goliath heron	4505	< 0.1 (13)	225 (10)
Ardea purpurea	Purple heron	920	< 0.1 (14)	28 (15)
Egretta alba	Great white egret	1100	0.7 (8)	770 (6)
Egretta garzetta	Little egret	480	0.9 (7)	432 (7)
Haliaeetus vocifer	African fish eagle	3092	0.3 (10)	928 (5)
Hydroprogne caspia	Caspian tern	587	< 0.1 (13)	29 (14)
Sterna hirundo	Common tern	138	2.7 (4)	373 (8)
Sterna albifrons	Little tern	100	0.4 (9)	40 (13)
Ceryle rudis	Pied kingfisher	77	3.5 (2)	270 (9)
Megaceryle maxima	Giant kingfisher	361	0.3 (10)	108 (12)
Alcedo semitorquata	Half collared kingfisher	39	0.2 (11)	8 (16)
		Total	26.4	20576

The proportion of counts when each bird species was seen (percentage frequency of occurrence; % FO) is given in Figure 7.2. The species with the highest frequency of occurrence were pied kingfisher (87.1% FO), darter (87.1% FO), reed cormorant

(85.5% FO), grey heron (83.9% FO) and whitebreasted cormorant (75.8% FO). These species were classed as being resident (> 75% FO) because of their presence on almost a daily basis. The great white egret (50% FO) was the only species in the frequent visitor category. Similarly, only one species (little egret) occurred in the occasional visitor category. Species which were classed as rare visitors (less than 25% FO) dominated, and included common tern, giant kingfisher, African fish eagle, half collared kingfisher, blackheaded heron, little tern, goliath heron, caspian tern and purple heron.

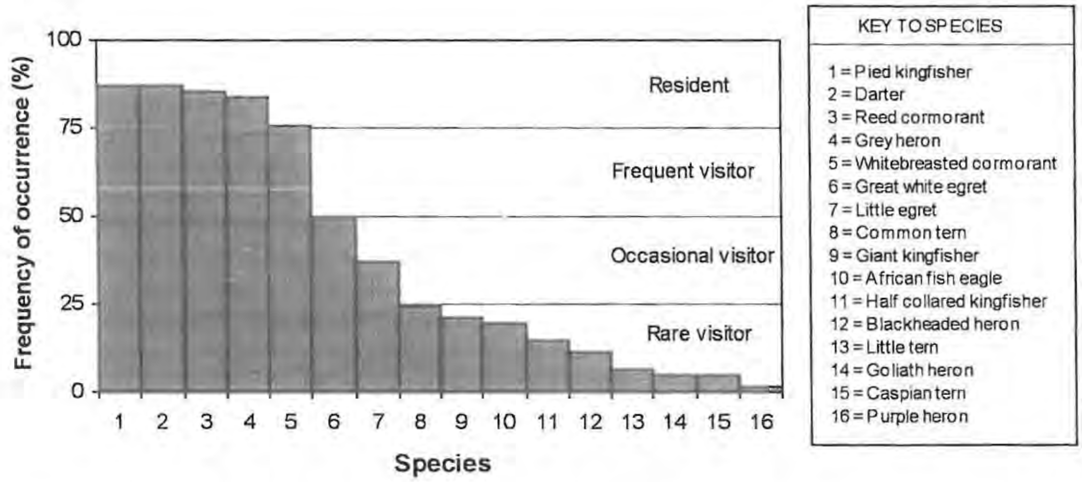

Figure 7.2 The percentage frequency of occurrence (% FO) of piscivorous birds recorded at the East Kleinemonde estuary during 62 bird counts between March 1994 and March 1996. Birds were grouped into the following four categories: rare visitor (0 - 24% FO), occasional visitor (25 - 49% FO), frequent visitor (50 - 74% FO) and resident (75 - 100% FO).

Feeding guilds and food consumption

All species recorded during the counts foraged in the estuary and an analysis of their feeding guilds (after Berruti 1983) revealed that 35.3% were waders, followed by pursuit swimmers (23.5%), aerial divers (23.5%) and aerial dippers (17.7%). An additional seven species which are also known to prey on fish were observed at times other than during the bird counts. These included six waders (*viz.* yellowbilled egret *Myteria ibis*, greenbacked heron *Ardea melanocephala*, hamerkop *Scopus umbretta*, black stork *Ciconia nigra*, African spoonbill *Platalea alba* and kelp gull *Larus dominicanus*) and one pursuit swimmer (dabchick *Tachybatus ruficollis*).

The estimates of daily food consumption by individuals, and the mean monthly food consumption by the population of each piscivorous bird species are given in Table 7.2.

Table 7.2 The daily food consumption by individuals and mean monthly consumption rates by the population of each piscivorous bird species recorded at the East Kleinemonde estuary between March 1994 and March 1996.

Species	Calculated daily food consumption (g) *	Mean monthly consumption of population (kg)	Numerical rank
Whitebreasted cormorant	347.6	34.2	2
Reed cormorant	142.8	45.5	1
Darter	269.4	19.5	3
Grey heron	285.0	16.7	4
Blackheaded heron	241.5	1.0	11
Goliath heron	637.4	0.5	13
Purple heron	208.3	0.1	15
Great white egret	236.2	4.4	6
Little egret	131.8	3.6	8
African fish eagle	489.0	3.3	9
Caspian tern	151.8	0.2	14
Common tern	54.8	4.6	5
Little tern	43.7	1.0	10
Pied kingfisher	36.3	3.9	7
Giant kingfisher	107.8	1.0	12
Half collared kingfisher	22.5	0.1	16

* Calculated using the expression given by Nagy (1987) and multiplied by 3.448 to convert to wet mass.

The reed cormorant was the most important bird predator with a mean monthly food consumption of 45.5 kg, followed by whitebreasted cormorant (34.2 kg month^{-1}), darter (19.5 kg month^{-1}) and grey heron (16.7 kg month^{-1}). The mean monthly food consumption by all other piscivorous birds totaled 26.7 kg month^{-1}.

The monthly food consumption rates by all piscivorous birds (excluding Cape cormorants) during the study period ranged from 31.6 to 466.3 kg month^{-1}, with a mean value of 142.6 kg month^{-1} (Figure 7.3). Analysis of monthly food consumption rates revealed no seasonal trends. However, food consumption rates were highest during the period April and June 1995 following an extended open mouth phase of the estuary. The mean consumption during these three months was 394.6 kg month^{-1}.

Cape cormorant invasion

During July 1994 an unusual invasion of Cape cormorants was recorded at the East Kleinemonde estuary. Although this species was recorded from July to October 1994, the birds were present in large numbers for only one month (July). The mean numbers per count, biomass and food consumption estimates for Cape cormorant during this period are summarized in Table 7.3. The number of birds per count (n = 6) during July 1994 ranged from 190 to 534, with a mean of 279. The total food consumption by these birds was estimated at 2211.5 kg for July 1994 and 2246.3 kg for the entire period of their visit (July to October). A solitary Cape cormorant was also recorded during one of the bird counts in July 1995.

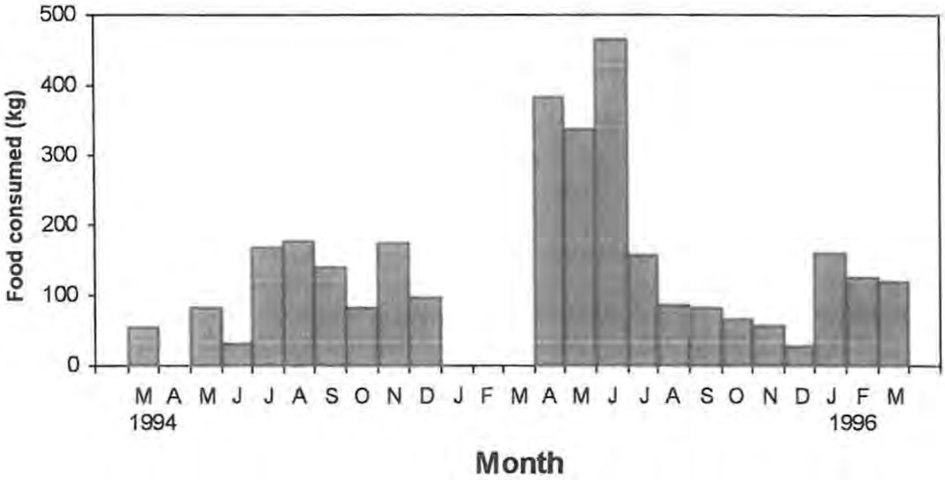

Figure 7.3 Monthly food consumption estimates of all piscivorous birds species (excluding Cape cormorants) recorded at the East Kleinemonde estuary between March 1994 and March 1996.

Table 7.3 Mean numbers, biomass and monthly food consumption estimates for Cape cormorant at the East Kleinemonde estuary between July and October 1994.

Month	Mean number per count	Mean biomass per count (g)	Food consumption of population (kg)
July	279	343449	2211.5
August	2.3	2831	18.2
September	1.3	1600	10.3
October	0.8	985	6.3
		Total	2246.3

7.3.2 Piscivorous fishes

Although a number of piscivorous fish species were recorded from the East Kleinemonde estuary (see Chapter 4), only one species (*Lichia amia*) was abundant enough to obtain population size estimates using the mark-recapture data. The population size estimates for *L. amia* were 77 individuals between October and December 1994 and 25 individuals between October 1995 and February 1996 (Chapter 6). The population parameters and food consumption estimates for *L. amia* during these time periods are given in Table 7.4. The estimated monthly food consumption of the population was 68.1 kg month^{-1} between October and December 1994 and 57.9 kg month^{-1} between October 1995 and February 1996.

Table 7.4 *Lichia amia* population parameters and food consumption estimates for two time periods between 1994 and 1996.

Time period	Population size	Population biomass, B	Maximum individual mass, W	Daily food consumption of population as a % of its biomass, Q/B *	Daily food consumption of population (g)	Monthly food consumption of population (kg)
Oct - Nov '94	77	89.3 kg	3279 g	2.54%	2270	68.1
Oct '95 - Feb '96	25	79.3 kg	4102 g	2.43%	1930	57.9

* Calculated using the expression by Palomares & Pauly (1989) where T = 21 °C and A = 5.5.

7.4 DISCUSSION

7.4.1 Piscivorous birds

The East Kleinemonde estuary is utilized as a feeding ground by a wide variety of piscivorous birds. The species composition is representative of other estuarine habitats along the southern and eastern Cape coasts as described by Boshoff *et al.* (1991a,b) at the Wilderness-Sedgefield estuarine lakes complex and Martin & Baird (1987) at the Swartkops estuary. Although the East Kleinemonde estuary is small (175000 m^2), the abundance of well vegetated gentle sloping banks provide ideal feeding grounds for wading piscivorous birds. Wading species accounted for the highest diversity of species, but generally occurred in low numbers. It is proposed that their low abundance is not related to a shortage of suitable prey items but as a consequence of their hunting method. These birds typically remain motionless in the shallow waters along the banks of the estuary and ambush their prey as it passes. Therefore, large numbers of birds employing these tactics would cause increased disturbance in the water and ultimately diminish the overall success rate of capturing prey. The grey heron was the most abundant wading species, which Whitfield & Blaber (1979a) described as being a solitary feeder which chased little egrets away from its fishing area. The numerically dominant species recorded at the East Kleinemonde estuary (reed cormorant, pied kingfisher, whitebreasted cormorant, common tern and darter), on the other hand, all actively pursue their prey by either swimming or diving. The rankings of gravimetrically important bird species is mainly a consequence of body size. For example, the African fish eagle was ranked fifth in terms of gravimetric importance but numerically was ranked only tenth. The dominant species in terms of their biomass were whitebreasted cormorant, reed cormorant, darter and grey heron.

Although the categories in which each species were assigned according to their frequency of occurrence are subjective, they were intended only to provide an importance grading of the East Kleinemonde estuary as a feeding ground. Most of the species (56.3%) were classed as being rare visitors and are not dependent on the estuary as a feeding ground on a regular basis. However, the high frequency of occurrence of pied kingfisher, darter, reed cormorant, grey heron and whitebreasted cormorant highlights their dependence on this estuary as a feeding ground. The results obtained for the African fish eagle (19.4% FO) are misleading because it is the only truly resident piscivorous bird which has been observed breeding at the East Kleinemonde estuary. During this study, birds were counted between 08h00 and 09h30, but Whitfield & Blaber (1978b) found that the African fish eagle at Lake St Lucia foraged between 09h00 and 17h00, with a peak in activity at 12h00. Therefore, the presence of this and possibly other species may be underestimated because their feeding periodicity was outside the census period.

The mean monthly food consumption by all piscivorous birds at the East Kleinemonde estuary between March 1994 and March 1996 was estimated at 142.6 kg $month^{-1}$. During the study period, food consumption rates revealed large monthly variations, ranging from 31.6 to 466.3 kg $month^{-1}$. This variance is ascribed to the fact that few avian predators were classed as being resident and that most of the piscivorous birds use this estuary opportunistically as a feeding ground. For example, monthly food consumption rates peaked subsequent to an extended open mouth phase (January to March 1995) when large scale recruitment of juvenile fishes from the marine environment would have ensured an abundance of suitable prey. By virtue of its high biomass, the reed cormorant was identified as the most important bird predator which accounted for approximately 32% of the monthly consumption of fish by all piscivorous birds. This species also accounted for the highest biomass of piscivorous birds at the Bot estuary (Heÿl & Currie 1985) and was the most abundant piscivore at the Wildernes-Sedgefield lakes complex (Boshoff *et al.* 1991a).

The use of birds as indicators of ecosystem quality has been identified from several aquatic environments (*inter alia* Heÿl & Currie 1985; Crawford *et al.* 1992; Springer *et al.* 1996). The numbers and/or biomass of piscivorous birds have been positively correlated to fish abundance at Lake St Lucia (Whitfield 1978) and Lake Kyle in Zimbabwe (Junor & Marshall 1987). Similarly, Blaber (1973a) suggested that a closed population of *Rhabdosargus holubi* in the West Kleinemonde estuary during 1971 was reduced by 80% over a seven month period, in a density-dependent fashion, by piscivorous birds. However, in the East Kleinemonde estuary there was no observed difference in the mean number of avian piscivores between two time periods when the number of *R. holubi* were known. The mean number of piscivorous birds per count between October and December 1994 was 25.6 with a corresponding *R. holubi* population of 13882 individuals, while between October 1995 and February 1996 the mean number of birds per count was 20.4 and the number of *R. holubi* totaled 108150 individuals. These results suggest that *R. holubi* is not important in the diets of avian piscivores (excluding Cape cormorant; see below) foraging in the East Kleinemonde estuary. The importance of the freshwater fish *Oreochromis mossambicus*, some estuarine-spawning species such as *Gilchristella aestuaria* and *Atherina breviceps* and Mugilids in the diet of piscivorous birds has been identified from several estuarine habitats (Whitfield & Blaber 1978b, 1979a,b; Jackson 1984; Whitfield 1986), and possibly holds true for the East Kleinemonde estuary. However, this will only be elucidated subsequent to an investigation into the dietary preferences of the piscivorous birds at this estuary.

7.4.2 Cape cormorant invasion

The Cape cormorant is a coastal marine species which occasionally enters harbours and estuaries (Sinclair 1987; Maclean 1993). However, Martin & Baird (1987) and Boshoff *et al.* (1991a) noted that this species is an annual winter visitor to estuarine habitats. During the winter of 1994, thousands of Cape cormorants invaded estuaries along the south-eastern Cape coast due to a shortage of an important prey species (Cape anchovy *Engraulis capensis*) in the marine environment. Egg and larval acoustic surveys in Algoa Bay revealed very low *E. capensis* recruitment during the first half of 1994 due to adverse environmental conditions (N. Klages, Port Elizabeth Museum, pers. comm.). The Cape cormorants, therefore, utilized the estuaries along the south-eastern Cape coast as alternative feeding grounds. The predatory impact of this invasion was quantified at the East Kleinemonde estuary. During their visit (July to October 1994), it was estimated the Cape cormorants consumed 2246.3 kg of fish. The fish consumption estimate during July 1994 (2211.5 kg) by these birds was more than 15 fold greater than the mean monthly consumption (142.6 kg) by all other avian piscivores between March 1994 and March 1996. These findings suggest that this unusual invasion of Cape cormorants impacted heavily on the closed population of fishes (including *Rhabdosargus holubi*), and are mirrored by the findings of the mark-recapture experiments (Chapter 6). The total population size of marine-spawning fishes in the East Kleinemonde estuary declined from 63342 to 18592 subsequent to the predation by these birds.

7.4.3 Piscivorous fishes

A total of five predominantly piscivorous fish (*Lichia amia*, *Argyrosomus japonicus*, *Pomatomus saltatrix*, *Elops machnata*, and a single *Caranx* species) were recorded from the East Kleinemonde estuary, which collectively constituted a very small portion of the total fish assemblage (Chapter 4). *Lichia amia* was by far the most abundant piscivore with a total biomass ranging between 80 and 90 kg. Dietary studies from several South African estuaries have revealed that fish dominated the diet of *L. amia*, with frequency of occurrence values ranging between 90 and 100 percent for fish larger than 200 mm TL (Whitfield & Blaber 1978a; Smale & Kok 1983; Marais 1984; Bennett 1989b). Therefore, it is safe to assume that the diet of *L. amia* (size range: 264 - 580 mm SL) in the East Kleinemonde estuary also consists mainly of fish and that the food consumption estimates represent an estimate of fish losses due to predation by this species.

Despite considerable research into the dietary preferences of the dominant piscivorous fishes in South African estuaries, no attempt has been made to quantify their daily or monthly food consumption. Making use of the predictive model by Palomares & Pauly (1989) it was estimated that the *L. amia* population in the East Kleinemonde estuary consumes approximately 2.5% of its biomass per day. Monthly food consumption estimates by the population were 68.1 kg month^{-1} between October and December 1994 and 57.9 kg month^{-1} between October 1995 and February 1996. These estimates, which accounted for 36.5% and 39.7% of the total fish predation losses by all major predators (birds and fish) over the two time periods respectively, suggest that *L. amia* is the top piscivorous predator in the East Kleinemonde estuary.

7.5 CONCLUSION

This study has provided a quantitative account of fish utilization in the East Kleinemonde estuary by piscivorous birds and a dominant piscivorous fish, which collectively had a food consumption rate of approximately 206 kg $month^{-1}$. The fish fauna is however vulnerable to predation by a number of other minor predators and also a limited amount of exploitation by recreational anglers. The mortality and/or loss of fish by these sources were not quantified but are believed to comprise a small portion of the total losses from this estuary. In addition, an invasion of Cape cormorants during July 1994 was identified as an unusual episodic event which was responsible for large scale mortality of fish over a relatively short time period.

CHAPTER 8

GROWTH, BIOMASS AND PRODUCTION OF THE MARINE-SPAWNING SPECIES

8.1 INTRODUCTION

Throughout the scientific literature, estuarine habitats are referred to as being 'nutrient traps' that support high primary productivity which in turn promote high levels of secondary production (e.g. Nixon *et al.* 1986). Studies worldwide have revealed that estuaries support high biomasses of secondary consumers and provide high fishery yields (Houde & Rutherford 1993). However, the calculation of production rates for estuarine fishes at the community level and even species level are limited to a few studies (*inter alia* Meredith & Lotrich 1979; Warburton 1979; Weinstein & Walters 1981; Weinstein *et al.* 1984).

Production is defined as the total amount of tissue produced in a population per unit time. It is a dynamic quantity that can rarely be measured directly, therefore, requiring indirect methods of calculation (Allen 1971). The most commonly used method incorporates knowledge of numbers and weights of population members over time. Although the use of quantitative data (i.e. population size data) is preferable for the calculation of fish production rates, estimates are also obtainable from information on food consumption and conversion efficiency, or from estimates of food consumption by predators (Chapman 1978). The general lack of quantitative information has precluded the estimation of production by South African estuarine fish populations. Quantitative information that can be used for estimating productivity is known for only one estuarine-associated fish species. Blaber (1973a, 1974) estimated the population size, rate of growth and the changes in the mortality rate for a closed population of *Rhabdosargus holubi* in the West Kleinemonde estuary during 1971 and 1972. Day *et al.* (1981) took advantage of this information to show that despite high levels of mortality, the closed *R. holubi* population revealed a net increase in biomass of approximately 1 g m^{-2} over a six month period in 1971 and 2.3 g m^{-2} over a nine month period in 1972.

This study evaluates production of the marine-spawning fish species (above a certain minimum size) in the East Kleinemonde estuary by making use of quantitative population size, biomass and growth data over a distinct census period.

8.2 METHODS

8.2.1 Population size estimates

A series of three 'closed population' mark-recapture experiments were conducted to obtain population size estimates for the marine-spawning fishes in the East Kleinemonde estuary. The results of these experiments and the reliability of the population size estimates obtained during each mark-recapture period are discussed in Chapter 6. In summary, it was felt that the results obtained during the second and third mark-recapture experiments yielded reliable population size estimates. However, the fish population during the second mark-recapture period was severely depressed following a period of high mortality caused by an unusual invasion of Cape cormorants (see Chapter 7). Therefore, only the results obtained from the third experiment, conducted over a 123 day period between October 1995 and February 1996, were used to calculate production rates of the marine-spawning fishes in the estuary. The population size estimates were obtained for all size classes except specimens < 100 mm SL for mugilids and < 50 mm SL for all other species. Therefore population size estimates, and hence calculated fish production, are conservative representations of the actual values during this period.

8.2.2 Growth rates

Length-frequency data collected during the census period was used to determine monthly growth rates. Where possible, the mean monthly size of a cohort (i.e. a group of individuals of a similar size that are assumed to be of the same age) was analysed. However, the identification of distinct cohorts was not always possible due to non-discrete pulses of recruitment by the marine-spawning species into the estuary. In these cases, the size groups were combined to obtain multiple-cohort growth rates. Mean monthly growth rates, expressed as mm month^{-1}, were calculated with the assumption that growth was linear between the mean lengths of single or multiple-cohorts between consecutive months during the census period.

8.2.3 Biomass estimates

Fish length (mm SL) was converted to fish weight (grams) by using the formula:

$$W = a\,L^{b}$$

Where W = the derived weight,

a = a constant (intercept of regression curve),

L = standard length, and

b = an exponent (the regression coefficient).

The length-weight relationships for the marine-spawning fish species captured during this study are given in Appendix 4.

Biomass estimates for each species were obtained for either identifiable cohorts (if possible), or else for the entire size range captured during the census period. The mean individual weight of the distinct cohort (or the entire catch) was multiplied by the most reliable population size estimate (given in Chapter 6) to obtain a total biomass (standing stock) estimate for each species.

8.2.4 Production estimates

Production estimates were calculated on a monthly basis during a distinct census period when the population size of each species was known. Monthly biomass production for each species was calculated using the formula (after Allen 1971):

$$P = N_t \; dW$$

Where P = production,

N_t = the number of individuals of a distinct cohort or all size groups combined in the population during the census period, and

dW = the weight-specific growth rate of the mean individual weight within the cohort or the entire population over a time period of one month.

The production values obtained for fishes in the East Kleinemonde estuary, with a surface area of approximately 175000 m^2, are expressed as g m^{-2} $month^{-1}$.

8.3 RESULTS

Mean monthly growth rates, population size, total biomass and monthly production rates for all the marine-spawning fish species recorded in the East Kleinemonde estuary during the census period are given in Table 8.1. The combined production by the marine-spawning fishes (n = 135192) in the estuary was calculated at 4.45 g m^{-2} $month^{-1}$.

Table 8.1 Mean monthly growth, population size, biomass and production estimates for the marine-spawning species in the East Kleinemonde estuary during the census period (17 October 1995 - 16 February 1996).

Species	Cohort	Size range (mm SL)	Monthly growth (mm)	Monthly growth (g)	Population size	Biomass (g)	Production (g m^{-2} $month^{-1}$)	Production (% of total)
Rhabdosargus holubi	I	20-85	9.2	3.48	27731	299246	0.551	[16.3]
	II	50-150	6.2	6.14	80419	2462598	2.822	[83.7]
Total					**108150**	**2761844**	**3.373**	**75.7**
Lithognathus lithognathus	I	34-102	10.3	4.51	1484	16278	0.038	[14.9]
	II	118-202	8.7	16.45	1753	181339	0.165	[64.4]
	III	217-272	7.7	31.78	243	82383	0.044	[17.2]
	IV	305-382	4.5	36.19	43	41929	0.009	[3.5]
Total					**3523**	**321929**	**0.256**	**5.7**
Sarpa salpa	All	37-107	12.2	6.47	483	12637	0.018	0.4
Diplodus sargus capensis	All	27 - 80	9	4.39	33	381	0.001	< 0.1
Liza dumerilii	All	51 - 248	3.1	2.93	9718	469520	0.163	3.7
Liza richardsonii	All	49 - 300	8.4	14.45	4127	467931	0.341	7.7
Liza tricuspidens	All	93 - 187	2.7	1.73	117	3031	0.001	< 0.1
Mugil cephalus	All	106 - 159	4.8	2.99	544	15320	0.009	0.2
Myxus capensis	All	88 - 306	3.9	5.24	3460	266677	0.104	2.3
Monodactylus falciformis	All	17-128	4.4	4.37	4986	152916	0.125	2.8
Lichia amia	All	460 - 580	18.3	338.01	25	79288	0.048	1.0
Pomadasys commersonnii	All	79 - 493	12.8	22.79	126	40434	0.016	0.4
Total					**135192**	**4591908**	**4.454**	**100**

Rhabdosargus holubi

Rhabdosargus holubi was numerically and gravimetrically the most dominant marine-spawning species in the East Kleinemonde estuary during the census period (Table 8.1). Two distinct size cohorts were identified for *R. holubi*. Mean monthly growth during the census period was calculated at 9.2 mm $month^{-1}$ for the size range 20 - 85 mm SL and 6.2 mm $month^{-1}$ for sizes ranging between 50 and 150 mm SL (Figure 8.1). The weight-specific growth rates for the two cohorts were 3.48 g $month^{-1}$ and 6.14 g $month^{-1}$ respectively.

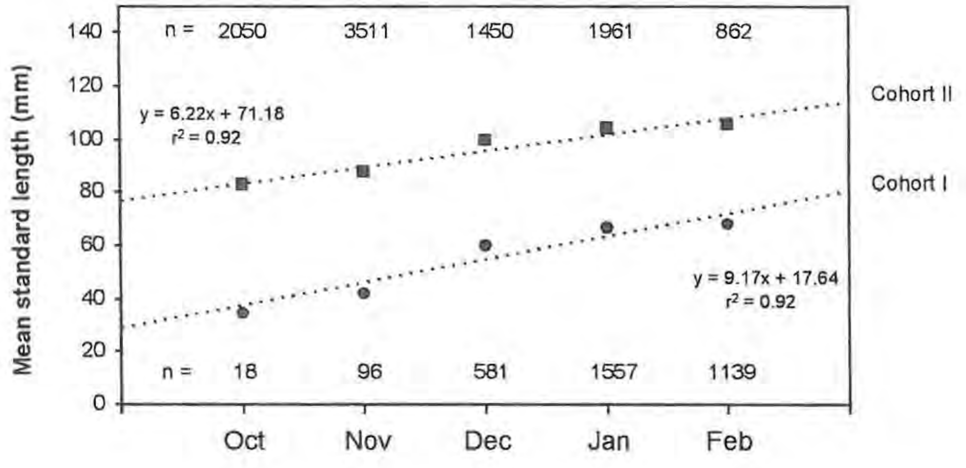

Figure 8.1 Mean monthly size composition of two cohorts for *Rhabdosargus holubi* captured in the East Kleinemonde estuary between October 1995 and February 1996 (census period).

The smaller size cohort (20 - 85 mm SL; mean = 54.3 mm SL) with a production rate of 0.551 g m^{-2} $month^{-1}$ accounted for 16.3% of the total production for this species, while the larger cohort (50 - 150 mm SL; mean = 96.1 mm SL) with a production rate of 2.882 g m^{-2} $month^{-1}$ comprised 83.7% of this production. Collectively, the two cohorts accounted for 75.7% of the total monthly production of all marine-spawning species in the East Kleinemonde estuary during the census period (Table 8.1).

Lithognathus lithognathus

During the census period, the *Lithognathus lithognathus* population (n = 3523) had a total biomass of 321929 grams (Table 8.1). Monthly growth during the census period was difficult to determine for *L. lithognathus* due to low sample sizes. However, monthly growth increments were determined for four distinct year class cohorts over the entire study period from April 1993 to March 1996 (Figure 8.2). Mean growth rates of 10.3, 8.7, 7.7 and 4.5 mm $month^{-1}$ were calculated for the year class cohorts I to IV respectively. The corresponding weight-specific growth rates of these cohorts were 4.51, 16.45, 31.78 and 36.19 g $month^{-1}$ respectively. A production rate of 0.256 g m^{-2} $month^{-1}$ was calculated for *Lithognathus lithognathus* during the census period (Table 8.1). This value accounted for 5.7% of the total production by all marine-spawning species in the estuary. The dominant cohort during the census period (cohort II; 118 -

202 mm SL) accounted for 56.3% of the total biomass and 64.4% of the total production for this species.

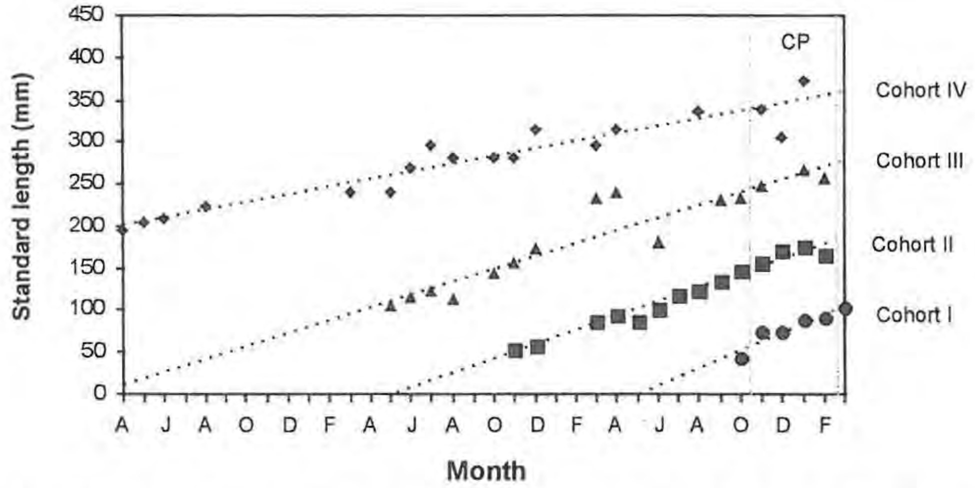

Figure 8.2 The mean monthly size composition of four year class cohorts for *Lithognathus lithognathus* captured in the East Kleinemonde estuary over the entire study period (April 1993 to March 1996; CP = census period).

Sarpa salpa

A single cohort population (37 - 107 mm SL) of 483 individuals with a total biomass of 12637 grams was recorded in the East Kleinemonde estuary during the census period (Table 8.1). A mean growth rate of 12.2 mm month^{-1} (or 6.47 g month^{-1}) was calculated for the period between October 1995 and February 1996 (Figure 8.3). The production for *Sarpa salpa* was calculated at 0.018 g m^{-2} month^{-1}, which accounted for only 0.4% of the total production by all marine-spawning species in the estuary during the census period.

Diplodus sargus capensis

A small population (n = 33) of *Diplodus sargus capensis* with a biomass of 381 g was recorded in the East Kleinemonde estuary during the census period (Table 8.1). Calculation of mean monthly growth rates was not possible due to very low sample sizes. Growth information for *D. s. capensis* was therefore obtained from published records. No growth information is available from the estuarine environment, but Smale & Buxton (1989) estimated that this species attained 100 - 120 mm TL in one year (i.e. 8 - 10 mm month^{-1}) in the intertidal marine environment. Therefore, for the purposes of production estimation, growth was assumed to be 9 mm $month^{-1}$. The corresponding weight-specific growth rate was calculated at 4.39 g $month^{-1}$. Production for this species was calculated at 0.001 g m^{-2} $month^{-1}$, which accounted for < 0.1% of the production of all marine-spawning fishes over the census period.

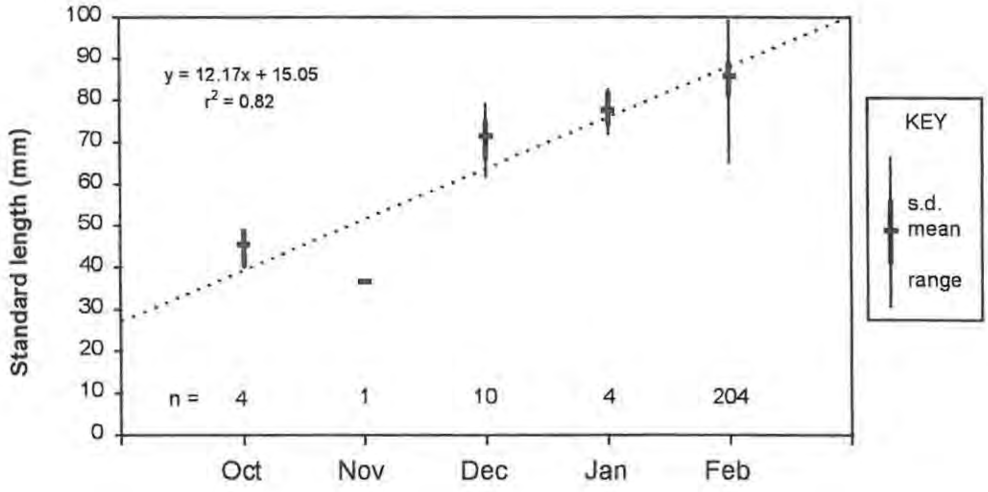

Figure 8.3 Monthly size composition (mean, standard deviation and range) for *Sarpa salpa* captured in the East Kleinemonde estuary between October 1995 and February 1996 (the census period).

Liza dumerilii

During the census period, *Liza dumerilii* was the second most abundant species in the East Kleinemonde estuary. The population of 9718 individuals had a biomass of 469520 grams (Table 8.1). Growth for *L. dumerilii* was difficult to determine due to a lack of distinct cohorts as a result of variable recruitment. However, an estimate of monthly growth of the dominant cohort (80 - 160 mm SL) was possible between November 1995 and January 1996. Length frequency analyses during this period revealed a growth rate of 3.1 mm $month^{-1}$ (Figure 8.4). The corresponding weight-specific growth rate was calculated at 2.93 g $month^{-1}$. The calculated production rate for *Liza dumerilii* was 0.163 g m^{-2} $month^{-1}$, which accounted for 3.7% of the production by all marine-spawning species in the estuary during the census period (Table 8.1).

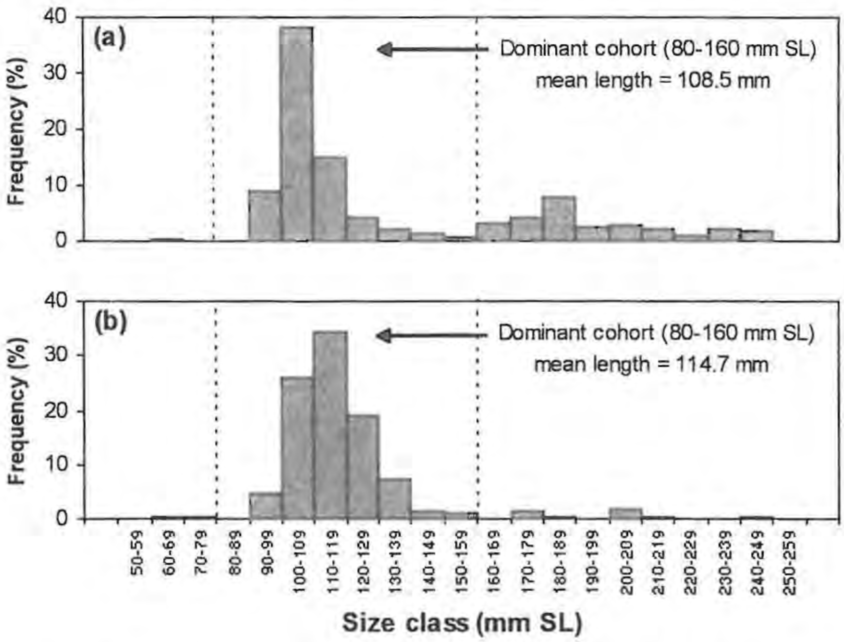

Figure 8.4 Length frequency histograms for *Liza dumerilii* captured in the East Kleinemonde estuary during (a) November 1995 and (b) January 1996. The mean individual lengths of the dominant size cohort, from which growth was determined, are also shown.

Liza richardsonii

During the census period, the *Liza richardsonii* population (n = 4127) had a total biomass of 467931 grams (Table 8.1). A multiple-cohort (49-300 mm SL; mean = 162.7 mm SL) growth rate of 8.4 mm month^{-1} (or 14.45 g month^{-1}) was calculated for this species (Figure 8.5). Production for *L. richardsonii* was calculated at 0.341 g m^{-2} month^{-1}, which accounted for 7.7% of the production by all marine-spawning species in the estuary during the census period (Table 8.1).

Liza tricuspidens

A small population (n = 117) of *Liza tricuspidens* with a biomass of 30311 g was recorded in the East Kleinemonde estuary during the census period (Table 8.1). A mean growth rate of sizes ranging between 83 mm and 134 mm SL (mean = 112.4 mm SL) was calculated at 2.7 mm month^{-1} between November 1995 and January 1996 (Figure 8.6). The corresponding weight-specific growth rate was calculated at 1.73 g month^{-1} (Table 8.1). The two individuals captured during December 1995 were unrepresentative of the size range used for growth calculation and hence were not considered. This species had a production rate of 0.001 g m^{-2} $month^{-1}$ which accounted for < 0.1% of the total production by all marine-spawning species in the estuary during the census period (Table 8.1). Whitfield & Kok (1992) indicated that *Liza tricuspidens* attains 140 mm TL in their first year (i.e. 12 mm $month^{-1}$) in the Knysna estuary. Therefore, the production value obtained for this species possibly represents a conservative estimate.

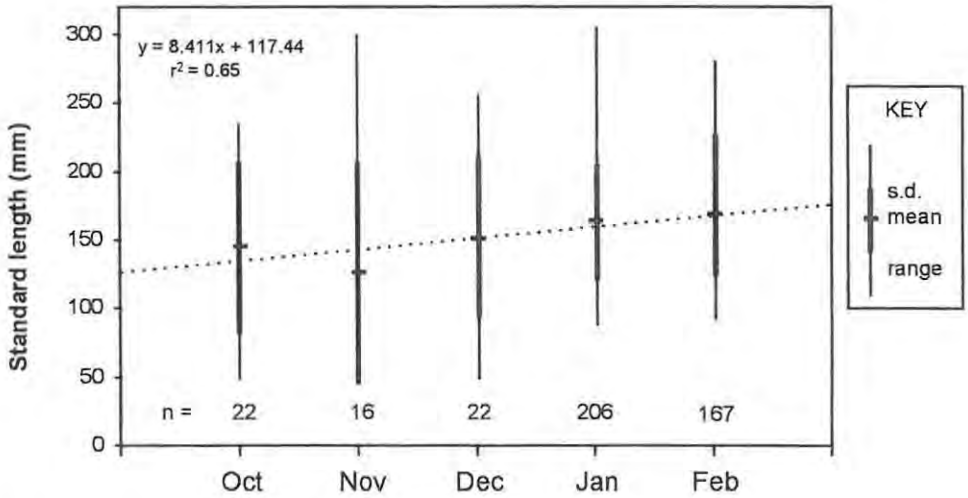

Figure 8.5 Monthly size composition (mean, standard deviation and range) for *Liza richardsonii* captured in the East Kleinemonde estuary between October 1995 and February 1996 (census period).

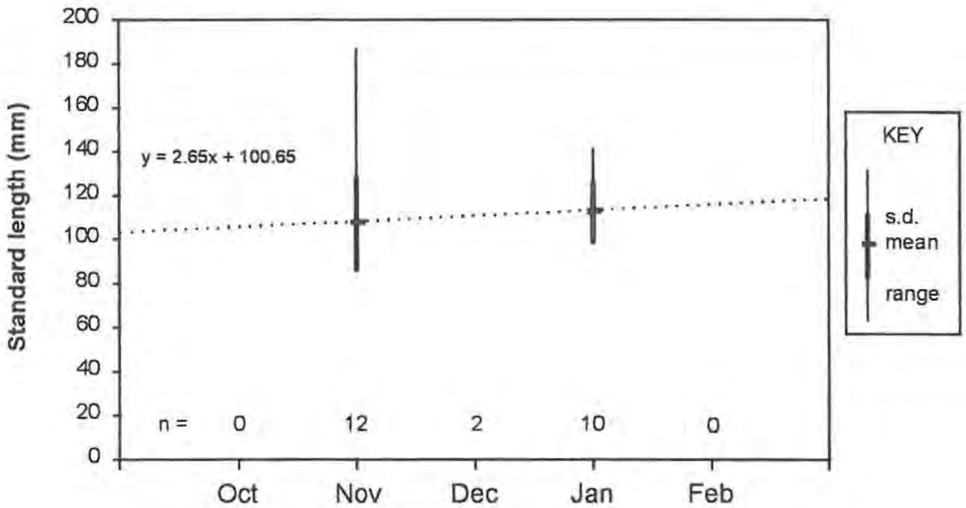

Figure 8.6 Monthly size composition (mean, standard deviation and range) for *Liza tricuspidens* captured in the East Kleinemonde estuary during the census period (excluding December 1995).

Mugil cephalus

The *Mugil cephalus* population of 544 individuals in the estuary during the census period had a biomass of 15320 grams (Table 8.1). A mean growth rate of 4.8 mm month^{-1} was calculated for the dominant cohort with sizes ranging between 106 mm SL and 159 mm SL (Figure 8.7). The corresponding weight-specific growth rate was calculated at 2.99 g month^{-1}. Data from December 1995, January and February 1996 were excluded due to low sample sizes and unrepresentative catch compositions. A production rate of 0.009 g m^{-2} month^{-1} was calculated for *M. cephalus*, which comprised 0.2% of the total production by all marine-spawning species in the estuary during the census period (Table 8.1). It is possible that the production value for this species is underestimated due to a low growth rate. Analysis of length frequency data from the Knysna estuary indicated that *Mugil cephalus* grows at approximately 15 mm month^{-1} during its first year (Whitfield & Kok 1992).

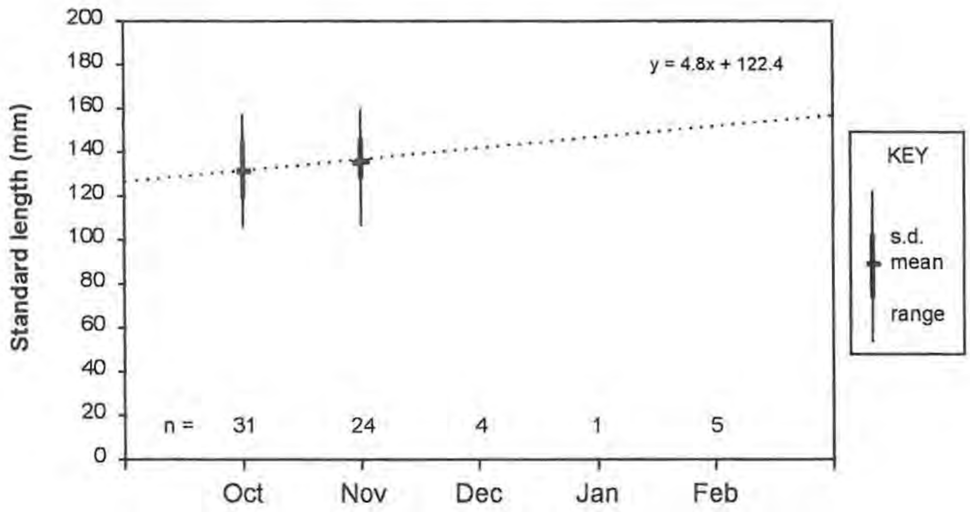

Figure 8.7 Monthly size composition (mean, standard deviation and range) for *Mugil cephalus* captured in the East Kleinemonde estuary between October and November 1995.

Myxus capensis

During the census period, the *Myxus capensis* population of 3460 individuals had a total biomass of 266677 grams (Table 8.1). Although sizes ranging from 88 mm SL to 306 mm SL were captured during this period, growth was calculated from a single dominant cohort (90-200 mm SL). A mean monthly growth rate of 3.9 mm month^{-1} (or 5.24 g month^{-1}) was calculated for *M. capensis* (Figure 8.8). Production for this species was calculated at 0.104 g m^{-2} month^{-1}, which accounted for 2.3% of the total production by all marine-spawning fishes in the estuary during the census period. The production estimate obtained for this species is possibly also conservative due to a low growth rate. Bok (1983) revealed that *Myxus capensis* grows at 9.4 mm month^{-1} in its first year and 8.2 mm month^{-1} in its second year.

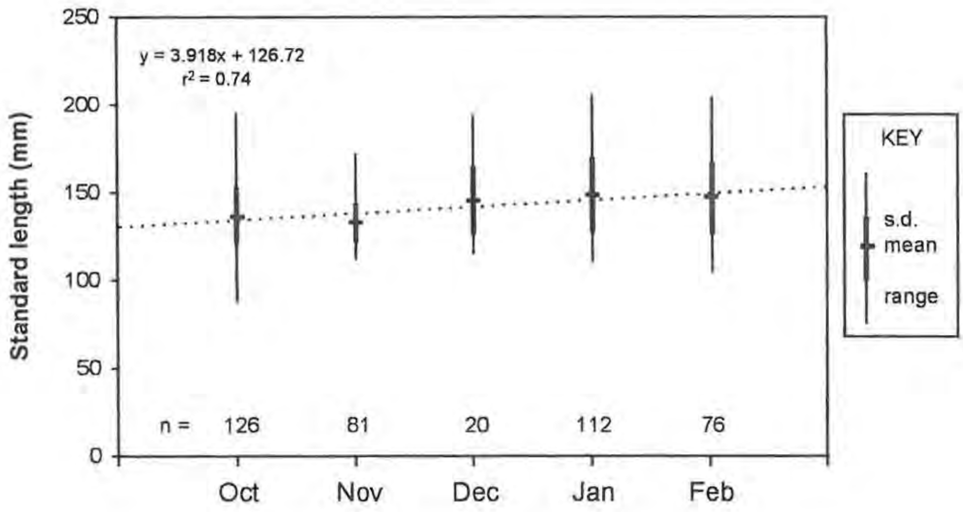

Figure 8.8 Monthly size composition (mean, standard deviation and range) for *Myxus capensis* captured in the East Kleinemonde estuary between October 1995 and February 1996 (census period).

Monodactylus falciformis

The *Monodactylus falciformis* population of 4986 individuals in the East Kleinemonde estuary during the census period had a total biomass of 152916 grams (Table 8.1). A mean growth rate of 4.4 mm month^{-1} was calculated for the entire catch (17 - 128 mm SL; mean = 86.7 mm SL) between October 1995 and February 1996 (Figure 8.9). The corresponding weight-specific growth rate was calculated at 4.37 g month^{-1}. The production value obtained for this species (0.125 g m^{-2} month^{-1}) accounted for 2.8% of the total production by all marine-spawning species in the estuary during the census period (Table 8.1).

Lichia amia

A small population (n = 25) of *Lichia amia* with a total biomass of 79288 grams was recorded in the East Kleinemonde estuary during the census period (Table 8.1). Monthly sample sizes were inadequate to calculate growth rates for *L. amia* during this study. However, Blaber (1974) recorded a length increase of 110 mm in six months (i.e. 18.3 mm $month^{-1}$) in the West Kleinemonde estuary. Making use of this data, a production rate of 0.048 g m^{-2} $month^{-1}$ was calculated for *L. amia* in the East Kleinemonde estuary. This value accounted for 1% of the total production by all marine-spawning species in the estuary during the census period (Table 8.1).

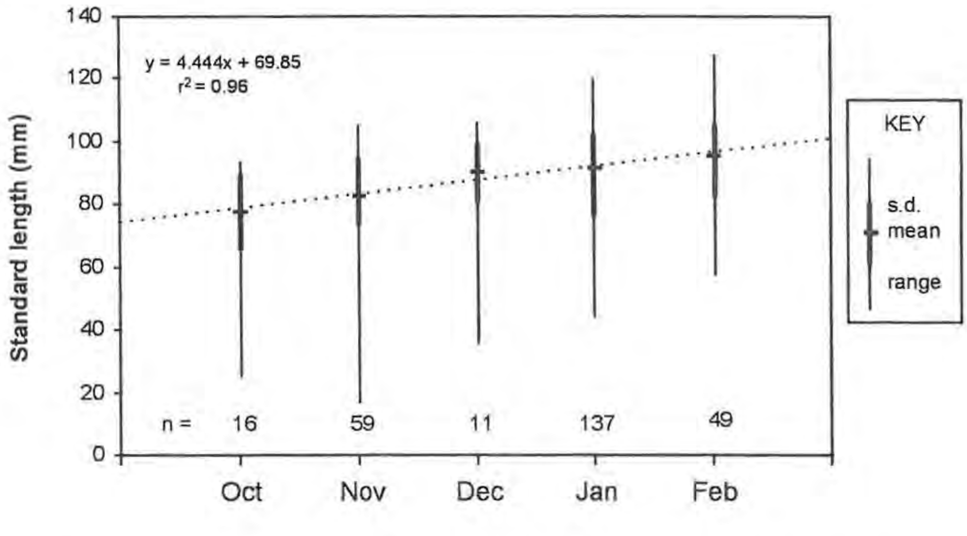

Figure 8.9 Monthly size composition (mean, standard deviation and range) for *Monodactylus falciformis* captured in the East Kleinemonde estuary between October 1995 and February 1996 (census period).

Pomadasys commersonnii

The population of *Pomadasys commersonnii* (n = 126) in the East Kleinemonde estuary during the census period had a total biomass of 40434 grams (Table 8.1). Inadequate sample sizes also prevented the calculation of growth rates for this species in the East Kleinemonde estuary. Therefore, information on the growth rate of *P. commersonnii* was obtained from the literature. Wallace & van der Elst (1975) state that this species attains a length of approximately 200 mm TL (153 mm SL) in their first year (i.e. 12.8 mm $month^{-1}$). Most of the individuals captured during the census period were 0+ aged fish (mean = 146.2 mm SL), hence the above growth rate was considered appropriate for the calculation of a production rate. The calculated production rate for *P. commersonnii* was 0.016 g m^{-2} $month^{-1}$, which accounted for 0.4% of the total production by all marine-spawning species in the estuary during the census period (Table 8.1).

8.4 DISCUSSION

The general life-history pattern of estuarine-associated marine fishes in southern Africa is one of recruitment (immigration) followed by an estuarine residence phase and then emigration (Wallace *et al.* 1984). During the period of estuarine residence many species (e.g. *Rhabdosargus holubi*) are known to occur at high densities which account for high biomass values (Blaber 1973a; Day *et al.* 1989). The ecological significance of the above life-history pattern is that emigrating fishes transfer large amounts of energy, accumulated in estuaries, to coastal marine ecosystems (Weinstein & Walters 1981; Deegan 1993). Furthermore, unlike the export of detritus, fish exports from estuaries are of high nutritive value and can provide a direct link to higher trophic levels (Nixon *et al.* 1986). These emigrating fishes are also known to contribute significant amounts of biomass for coastal recreational and commercial fisheries (Deegan 1993; Houde & Rutherford 1993).

Despite the apparent importance of estimating estuarine fish productivity, very few studies have evaluated their contribution to secondary production within these systems. This can be ascribed to the fact that production estimates for estuarine fish populations are difficult to calculate. The main sources of error encountered while estimating estuarine fish production and their influence on this study are discussed below.

8.4.1 Sources of calculation error

Population size estimates

According to Egglishaw (1970) the main source of inaccuracy for fish production estimation lies in the error associated with determining population sizes and their changes. Estuarine fish populations are known to be dynamic due to fluctuating levels of recruitment and emigration which are difficult to quantify (Robertson & Duke 1990). Hence, reliable population size estimates for estuarine-associated fishes are seldom achieved. The population size estimates for the dominant marine-spawning species in the East Kleinemonde estuary obtained during this study were regarded as reliable estimates, particularly during the second and third mark-recapture experiments (see Chapter 6). However, during the second mark-recapture period, the fish population was severely deflated due to high levels of mortality prior to the experimental period (see Chapter 7). Therefore, the results obtained from the third mark-recapture experiment (here referred to as the census period) formed the basis of the production assessment. It must be emphasized that the estimated population size is less than the actual population size due to the exclusion of individuals below a certain minimum length during the mark-recapture experiments. Consequently, the contribution of these smaller individuals to fish production in the estuary is not included in the analysis. The 4.45 g m^{-2} $month^{-1}$ marine fish productivity estimate must therefore be viewed as a conservative value for the East Kleinemonde estuary during the census period (i.e. between October 1995 and February 1996).

Growth rates

Growth rates of most fishes vary seasonally, and in relation to age, as well as in response to a number of environmental factors such as temperature, salinity and food availability. Furthermore, growth rate calculations of single or multiple cohorts of marine-spawning fishes in estuaries are affected by size specific emigration, mortality and/or prolonged recruitment periods (Weinstein & Walters 1981).

The analysis of length frequency data has been used to provide information on growth for many estuarine-associated fishes (e.g. Whitfield & Kok 1992). The use of such data is most applicable when recruitment occurs in discrete pulses (Worthington *et al.* 1992) and even more powerful when sample sizes are large (Erzini 1990). In this study, low sample sizes and unrepresentative catches of distinct size cohorts prevented the calculation of growth for distinct cohorts for all species. However, in most cases growth estimates were obtained over a distinct time period which coincided with the census period, thus facilitating more reliable calculation of production rates. It should be emphasized that the census period was conducted mainly during the summer months when growth rates for most species peaks (see Blaber 1974; Beckley 1984). Therefore, despite the exclusion of the smaller size classes (see above), the monthly production estimates represent maximum values for the populations of each species included in the mark-recapture experiments. The obtained growth rates for several species were lower in the East Kleinemonde estuary compared with the findings of studies conducted in other South African estuaries (e.g. Bok 1983; Whitfield & Kok 1992). However, the use of this data was considered to be of doubtful values because of the overwhelming gravimetric dominance of *Rhabdosargus holubi* which accounted for 76% of the total production by all marine-spawning species in the East Kleinemonde estuary.

Mortality rates

During the census period the East Kleinemonde estuary mouth was closed, with the result that no significant losses (emigration) or gains (immigration) to the fish population were possible. However, losses due to natural mortality (piscivorous bird and fish predation) and to a lesser extent recreational angling in the estuary did take place. The total mortality of all fishes (resident estuarine-spawning and migrant marine-spawning species) in the estuary during the census period was quantified (Chapter 7). The mean monthly consumption by piscivorous fishes (*Lichia amia*) during the census period was calculated at 57.9 kg month^{-1}, while the consumption by piscivorous birds during this period ranged between 29.0 and 160.4 kg month^{-1} (mean = 87.9 kg month^{-1}). Estimates of instantaneous mortality rates during the census period were also obtained for species which yielded recaptures during the mark-recapture study. The 'sum-of-squares procedure' for population size estimation (given in Chapter 6) provided an estimate of daily mortality (Z). For example, the Z value for *Rhabdosargus holubi* was 0.00166, which equated to a mortality rate of 14 individuals per day. Therefore, over the 123 day census period the total mortality of this species was 1722 individuals with an estimated biomass of 44556 grams. The inclusion of this mortality factor (approximately 1.6% of the total population size) is of doubtful value unless the relationship between the losses (natural mortality) and gains by individuals entering the size group considered for marking during the course of the mark-recapture period (cohort growth) can be measured. The compensatory effects of cohort growth and mortality suggest that the resultant net loss or gain over the census period would not have altered the monthly production estimates significantly.

8.4.2 Annual production

Production estimates are usually calculated on an annual unit area basis and expressed in terms of grams, kilojoules or grams carbon (i.e. g m^{-2} yr^{-1}, kJ m^{-2} yr^{-1} or gC m^{-2} yr^{-1}; see Chapman 1978). The calculation of annual production (over one calendar year) in estuaries is often not possible due to continuous emigration and recruitment variability. This shortcoming is compounded in temporarily open/closed estuaries which are subject to mass emigration of fishes during mouth opening events.

The monthly production rates of the marine-spawning fishes in the East Kleinemonde estuary were converted to grams (wet mass) per m^2 per year (Table 8.2) and compared with other published accounts of estuarine fish productivity. However, prior to making these comparisons attention is drawn to the following:

- the production estimates for each species in the East Kleinemonde estuary excludes the contribution by the smaller size classes (i.e. < 100 mm SL for mugilids and < 50 mm SL for the other species),
- the annual estimates are based on monthly production estimates obtained during the summer (October - February) when the growth rate for most species is at or near a maximum, and
- the total fish community productivity estimate also excludes the contribution by the estuarine-spawning species in the estuary.

At the species level, Warburton (1979) reported production values ranging between 0.8 and 9.2 g m^{-2} yr^{-1} for some important fishes in a Mexican lagoon system. However, the highest reported value for an estuarine fish (*Fundulus heteroclitus*) is 64 g m^{-2} yr^{-1} (Valiela *et al.* 1977). This high value is supported by the findings of Meredith & Lotrich (1979) who, during an independent study, estimated the productivity of *F. heteroclitus* at 40.7 g m^{-2} yr^{-1}.

Table 8.2 Production estimates (g m^{-2} yr^{-1}) for the marine-spawning fishes in the East Kleinemonde estuary (calculations based on estimates made during the summer dominated census period and only of fishes above a certain minimum size).

Species	Annual production (g m^{-2} yr^{-1})
Rhabdosargus holubi	40.48
Lithognathus lithognathus	3.07
Sarpa salpa	0.21
Diplodus sargus capensis	0.01
Liza dumerilii	1.95
Liza richardsonii	4.09
Liza tricuspidens	0.01
Mugil cephalus	0.11
Myxus capensis	1.24
Monodactylus falciformis	1.49
Lichia amia	0.58
Pomadasys commersonnii	0.20
Total	**53.46**

The production estimate obtained for *Rhabdosargus holubi* in the East Kleinemonde estuary (40.5 g m^{-2} yr^{-1}) is high compared with any estuarine-associated fish. However, the high value for *R. holubi* is not surprising considering it's numerical and biomass dominance in the East Kleinemonde estuary. During the census period, this species had a population size of 108150 and a biomass of 15.8 g m^{-2}. It is possible that these population parameters represent maximum values because the census period was conducted shortly after a period of excellent recruitment (i.e. an extended open phase of the estuary mouth followed by numerous topping of the bar events; see Figure 2.7). The population parameters for *Rhabdosargus holubi* were much lower during the first (MR 1) and second (MR 2) mark-recapture experimental periods (Chapter 6). During MR 1 (April - September 1993), this species had a population size of 34959 and a biomass of 6.7 g m^{-2}, and following a period of high bird predation (MR 2; October - December 1994) the population size was 13882 with a biomass of 1.3 g m^{-2}. Blaber (1973a) determined the population size for *R. holubi* in the neighbouring West Kleinemonde estuary, with a surface area of approximately 25.5 ha. His findings revealed that in 1971 the population decreased from 55360 to about 11485 over a period of six months and in 1972 the population decreased from 14674 to about 12000. Day *et al.* (1981) made use of the information provided by Blaber (1973a, 1974) to show the biomass changes of this population over the two experimental periods. Despite heavy bird predation (with mortality rates varying between 9% and 49% $month^{-1}$ during 1971 and about 3% $month^{-1}$ during 1972), the biomass of this population increased from 1.7 g m^{-2} to 2.7 g m^{-2} and 0.5 g m^{-2} to 2.8 g m^{-2} during 1971 and 1972 respectively. Therefore, as a result of the seemingly high population conditions of *Rhabdosargus holubi* during the census period, the annual productivity estimate of 53.5 g m^{-2} yr^{-1} for the marine-spawning fish community (above a certain minimum size) in the East Kleinemonde estuary possibly represents a maximum value.

Table 8.3 provides a review of documented studies on total fish community productivity in selected temperate, subtropical and tropical estuaries (after Day *et al.* 1989). These findings suggest that estuarine fish community productivity increases with decreasing latitude (i.e. towards the tropics). However, as pointed out by Day *et al.* (*op cit.*) it is difficult to make comparisons of total fish community productivity based on existing information because of factors such as the use of different methods of estimating standing stock and hence productivity, and the time-space scale differences of the various studies.

Despite a need for more detailed investigations, the data presented in Table 8.3 (after Day *et al.* 1989) suggest that values ranging between 5 and 125 g m^{-2} yr^{-1} are representative of total fish community productivity in estuarine environments. More recently, Houde & Rutherford (1993) estimated total fish production in 10 estuarine systems by applying primary production and fish catch information (provided by Nixon *et al.* 1986) to Iverson's (1990) equation at a trophic level of 2.5 (i.e. midway between primary and secondary carnivores). Their estimates of fish community productivity ranged between 17.7 and 64.6 g m^{-2} yr^{-2} (mean = 39.3 g m^{-2} yr^{-2}). The production estimate of 53.5 g m^{-2} yr^{-2} from the East Kleinemonde estuary therefore compares favourably with those quoted in the literature. However, it must be borne in mind that this estimate excludes the contribution by both the resident estuarine-spawning species and the smaller size classes of the marine-spawning species which were not considered during the mark-recapture experiments.

Table 8.3 Fish community productivity estimates (g m^{-2} yr^{-1}) in selected temperate, subtropical and tropical estuaries (after Day *et al.* 1989).

Location	Fish production (g m^{-2} yr^{-1})	Reference
TEMPERATE		
Southern North Sea	5.2 *	Korringa (1967)
Chesapeake Bay, Maryland	9.0 *	Mansueti (1961)
Wadden Sea, Netherlands	10.0	Postma & Rauck (1979)
Italy	9.0 - 17.0 *	DeAngelis (1960)
Flax Pond, New York	108 - 146 **	Hall & Woodwell (unpublished data)
SUBTROPICAL		
Texas coastal lagoons	12.1 - 57.6 **	Jones *et al.* (1963); Hellier (1962)
Barataria Bay, Louisiana	35.0 - 72.8 **	Wagner (1973); Day *et al.* (1973)
Mexican Pacific coast	34.5 **	Warburton (1979)
TROPICAL		
India	5.8 - 124.0 *	Pakrasi *et al.* (1964)
Phillipines	47.0 - 50.0 *	Rabanal (1961)
Cuban lagoons	22.0 - 27.6 **	Holcik (1970)
Mexican Pacific lagoons	24.6 - 66.7 **	Yanez-Arancibia (1978)
Terminos Lagoon, Mexico	20.0 **	Yanez-Arancibia & Lara Dominguez (1983)

* based on information from fisheries yield
** based on summation of production estimates of selected component species

8.5 CONCLUSION

This study has provided the first attempt at calculating production estimates for several estuarine-associated marine fishes in South Africa and highlights the difficulties associated with obtaining reliable estimates. The results also highlight the dynamic and complex nature of estuarine fish production due to fluctuating levels of population biomass arising from recruitment variability and mortality. The high production value obtained for *Rhabdosargus holubi* indicates that this ubiquitous species plays an important role in energy flow within the East Kleinemonde estuary. More importantly, attention is drawn to the dominant role of *R. holubi* as a means of exporting estuarine production (energy) to the nearshore coastal environment after mouth opening events.

CHAPTER 9

GENERAL DISCUSSION AND MANAGEMENT CONSIDERATIONS

A large amount of information is available on estuarine-associated fishes in southern Africa and research findings have provided a better understanding on how and why fishes utilize estuarine environments. Whitfield (1998) provides a comprehensive review of much of this information, particularly on the biology and ecology of individual species and the fish assemblages of different estuary types in the different biogeographical regions. In this review, he also provides a synopsis of ichthyological estuarine research in South Africa over the past five decades. Commenting on future research priorities, Whitfield (1996a, 1998) emphasizes the need to conduct quantitative studies by repeating the words of Day (1977) who states that: "We know the dominant plants and animals that live in our estuaries. We must now study them individually and in great detail - their rates of recruitment, their tolerance to environment conditions, how much food they consume, their biomass and productivity". Although several recent studies have provided quantitative density and biomass estimates for estuarine-associated fishes (e.g. Whitfield 1993; Paterson & Whitfield 1996), most assessments have not extended beyond providing relative abundance estimates.

The lack of truly quantitative studies on estuarine-associated fishes can be ascribed to a number of reasons. Foremost, is the fact that ichthyologists still depend on nets to provide quantitative data (Allen *et al.* 1992). The diverse nature of estuarine habitats often makes quantitative sampling of fish populations very difficult. The results of many studies on gear selectivity and sampling techniques have shown that nets consistently generate biased information which varies greatly in time and space (e.g. Young *et al.* 1988; Pierce *et al.* 1990). In an attempt to overcome the associated bias with net sampling it has been suggested that gear (collection) efficiency studies should become an integral part of estuarine fish studies (Allen *et al.* 1992). Rozas & Minello (1997) also highlight the problem of gear selection and recommend that each study should be goal orientated including the sampling protocol. In other words, the sampling gear must be appropriate for the targeted species (or species groups) and habitats as well as for the overall objectives of the study. During this study, consideration was given to the above recommendation. However, the problems associated with collection efficiency were circumvented by using mark-recapture techniques to estimate absolute abundance (i.e.

the total number of individuals in the estuary) for the marine-spawning species in the East Kleinemonde estuary.

The overall aim of this study was to quantitatively assess various population parameters of the fishes associated with the small temporarily open/closed East Kleinemonde estuary. The population parameters investigated included density, biomass and population size for all the fishes in the estuary, as well as growth and productivity estimation for the dominant marine-spawning species. The study also included a quantitative assessment of fish losses due to piscivorous predation. A summary of some of the population parameters calculated at various time periods during this study are diagrammatically illustrated in Figure 9.1.

According to Day (1977) quantitative information is important to assist with the understanding of ecological processes (i.e. energy transfers between various organisms) within estuarine ecosystems. This study has provided a quantitative assessment of two important groups of secondary consumers (i.e. fishes and piscivorous birds) that will assist in the understanding of the trophic dynamics within a single estuary. More importantly, however, this study has illustrated the dynamic nature of these consumer populations which is characterized by a high degree of variability over very short periods of time. For example, the total population size of the marine-spawning fishes (above a certain minimum size) in the East Kleinemonde estuary declined from 63342 individuals during 1993 to 18592 individuals during 1994 and increased again to 135192 individuals during 1995/6. Paterson & Whitfield (1996) also revealed a large inter-annual difference in the numbers and biomass of fish utilizing an intertidal salt marsh in the permanently open Kariega estuary. These authors recorded a decrease of approximately 50% in the average number of fish utilizing Taylor's salt marsh from one year to the next. These findings pose a question which is fundamental to the understanding of estuarine fish ecology : why do estuarine fish populations display large temporal variability?

Estuaries are often described as being hostile environments with rapidly changing physical and chemical conditions, yet, they are known to be more productive than adjacent freshwater and marine environments (Day *et al.* 1989). Clearly, estuarine-associated fishes and other organisms have evolved in a number of ways (morphologically and physiologically) to successfully spend part or all of their lives in these apparently unpredictable environments. The spatial and temporal abundance of these nekton in estuaries, however, are not only influenced by their adaptive tolerance to varying abiotic conditions, but also a number of biotic factors (Whitfield 1996b).

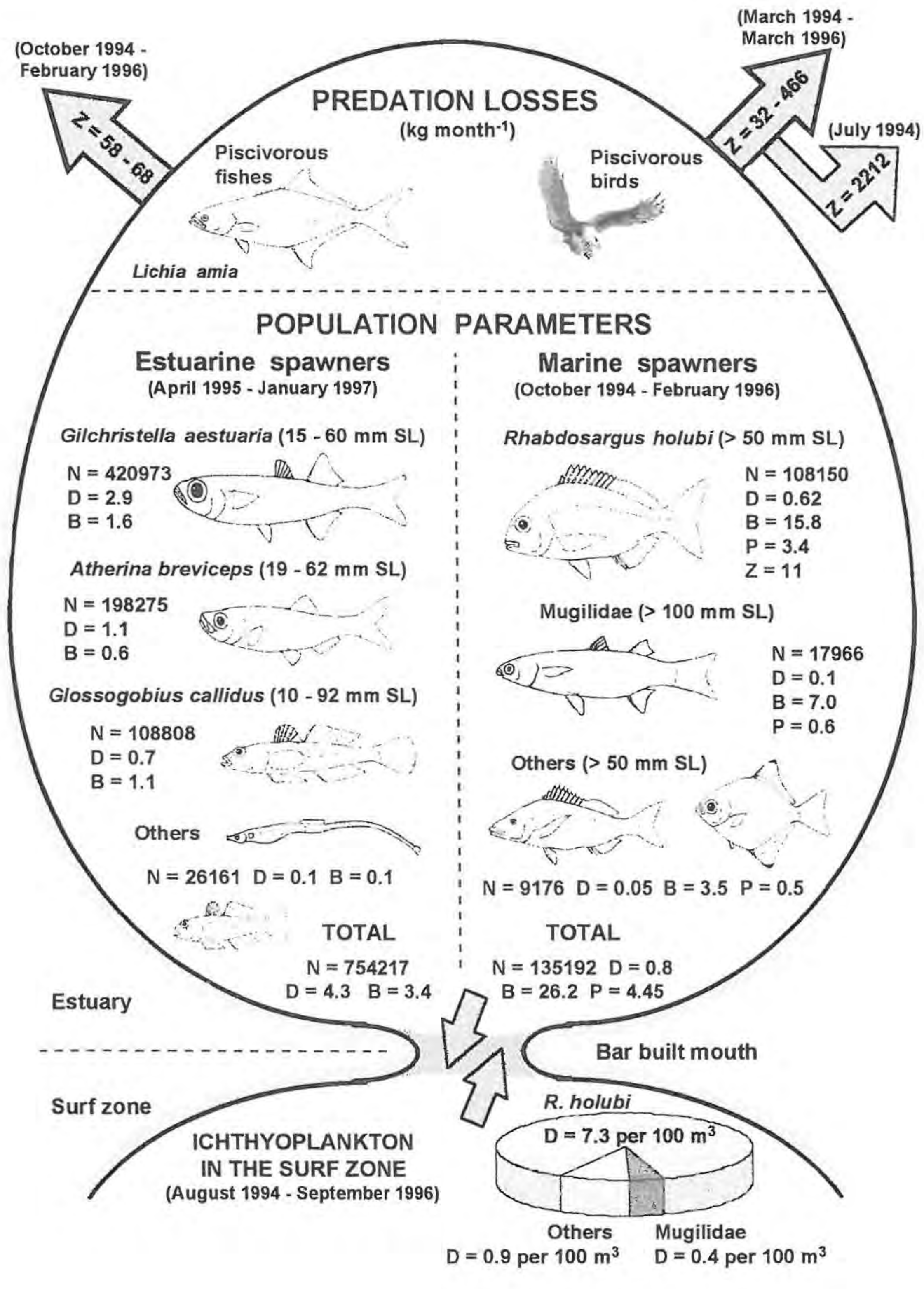

Figure 9.1 Diagrammatic representation of various population parameters of the ichthyofauna associated with the East Kleinemonde estuary. Where: N = population size (number; n), D = density (n m^{-2}), B = biomass (g m^{-2}), P = production (g m^{-2} month) and Z = mortality (kg $month^{-1}$).

The findings presented in the study suggest that the main factors determining the abundance (and its variability) of fishes in the East Kleinemonde estuary are predation and estuary mouth conditions. These factors and their influence on the closed fish populations associated with this estuary are discussed in more detail below.

Piscivorous birds are important components of estuarine ecosystems (Whitfield & Blaber 1978b, 1979a,b). Because of their relatively large size, these predators are easily observed and quantitative data on their numbers provides sufficient information to estimate their biomass and hence food consumption rates. The numbers of piscivorous birds at the East Kleinemonde estuary were recorded over a two year period (March 1994 to March 1996). Only 31% of the species recorded were considered to be resident, suggesting that food consumption (i.e. fish predation) values should display large variability. The calculated monthly food consumption rates ranged from 32 kg $month^{-1}$ to 466 kg $month^{-1}$. Furthermore, during the winter of 1994 an unusual invasion of Cape cormorants accounted for additional predation losses of 2246 kg, of which 2212 kg were consumed in a single month (July 1994). The impact of this episodic event was clearly observed in the results of the fish mark-recapture experiments. The total population size of marine-spawning fishes declined by 70% subsequent to the Cape cormorant invasion. The predatory impact of piscivorous birds on closed estuarine fish populations was also documented by Blaber (1973a). He showed that the *Rhabdosargus holubi* population in the neighbouring West Kleinemonde estuary was reduced by 80% due to density-dependent bird predation over a period of six months in 1971. However, during 1972 the population of *R. holubi* was reduced by only 18% over a nine month period (Blaber *op cit.*).

Several studies have shown that temporarily open/closed estuarine systems have lower species diversity than permanently open estuaries due to the absence of a permanent link to the sea (e.g. Begg 1984; Bennet 1989a; Whitfield *et al.* 1989). Furthermore, Harrison & Whitfield (1995) showed that species diversity was significantly correlated ($p < 0.05$) to the duration of the open mouth phase in two temporarily open/closed estuaries in KwaZulu-Natal. Clearly, the size and duration of the mouth opening in an estuary is an important factor influencing ichthyofaunal diversity. Apart from the influence on species diversity, mouth condition also affects the abundance and biomass of individual migratory marine-spawning species. Whitfield & Kok (1992) indicated that catch per unit effort (CPUE) values for most marine migrants were higher in the permanently open Knysna estuary than in the nearby seasonally open Swartvlei estuary. However, the findings of this study suggest that the abundance of certain migratory species are comparable to and sometimes even higher than those obtained from various habitats in larger seasonally open and/or permanently open estuarine systems. For example, Whitfield (1993) estimated the biomass of *Rhabdosargus holubi* at 1.7 g m^{-2} in the littoral zone of the Swartvlei estuarine lake system. This estimate was however considered to be conservative due to the absence of the macrophyte (*Potamogeton*) canopy during the sampling period. Paterson (1998) working in the permanently open Kariega estuary calculated biomass values for *R. holubi* at 0.1 g m^{-2} in Taylor's intertidal salt marsh creek and 2.3 g m^{-2} in the adjacent littoral zone (*Zostera* beds). The biomass values for this species in the East Kleinemonde estuary were 6.7 g m^{-2}, 1.3 g m^{-2} and 15.8 g m^{-2} during the three respective mark-recapture experiments conducted between 1993 and 1996. These conflicting results are arguably subjective due to different sampling methods and comparisons of different habitats. However, they do suggest that the abundance of species such as *Rhabdosargus holubi*, particularly in temporarily open/closed systems is dependent on the temporal recruitment success, or more specifically the way in which they optimally utilize periods of marine influence (i.e. mouth opening events and overwash conditions).

The marine-spawning fishes associated with the East Kleinemonde estuary were overwhelmingly dominated by a single species (*Rhabdosargus holubi*) which:

- comprised 77.6% of the ichthyoplankton catch composition in the surf zone adjacent to the mouth of the estuary,
- comprised 75.3% of the estuarine catch composition sampled with the large mesh seine net,
- accounted for approximately 55%, 75% and 80% of the total population size of marine-spawning species above a certain minimum size during three independent mark-recapture experiments, and
- accounted for 75.7% of the total secondary production by all marine-spawning species between October 1995 and February 1996.

The numerical and gravimetrical dominance by *Rhabdosargus holubi* solicits a closer examination of aspects relating to its biology. According to Blaber (1973b) *R. holubi* is an endemic species which tolerates a wide range of environmental conditions, including salinity ranges of 0.7 - 70 ‰ and temperatures ranging between 10 and 30 °C. It is also a strong osmoregulator and when exposed to a new salinity the internal osmotic concentration does not change until after 10 hours. Furthermore, Bennett (1985) revealed that *R. holubi* was one of the few species to survive prolonged low salinities (<

3 ‰) in the Bot River estuary. The diet of postlarval *R. holubi* (approximately 15 - 30 mm SL) consists mainly of copepods, whereas juveniles (> 30 mm SL) feed mainly on filamentous algae, aquatic macrophytes and epibenthic invertebrates (Whitfield 1984, 1985). Blaber (1973b) found that juvenile *R. holubi* in the West Kleinemonde estuary feed mainly on aquatic vegetation that is not digested, whereas the assimilated portion of their diet comprises epiphytic diatoms. The abundance of submerged macrophytes (*Ruppia cirrhosa*) in the East Kleinemonde estuary suggests therefore that food organisms are not in short supply. Besides providing an abundance of food, the dense stands of submerged plants offer an ideal refuge when pursued large predatory fishes such as *Lichia amia*.

Blaber (1974) revealed that *Rhabdosargus holubi* has a winter/spring peak spawning period with a spring/summer influx of 0+ individuals to the West Kleinemonde estuary. During this study, the abundance of postflexion larvae and early juveniles (length range : 9 - 21 mm) peaked in early spring (August and September) but were recorded throughout the year in the surf zone adjacent to the mouth of the East Kleinemonde estuary. These findings are in agreement with numerous other studies which have shown that recruiting *R. holubi* with lengths ranging between 10 and 40 mm are recorded throughout the year (*inter alia* Melville-Smith & Baird 1980; Beckley 1983; Whitfield & Kok 1992). It seems clear, therefore, that this species exhibits serial spawning habits which allows for improved recruitment success, particularly considering that mouth opening events are not strictly seasonal, but can occur sporadically throughout the year. Furthermore, this study has provided evidence to suggest that *R. holubi* also recruit successfully under adverse mouth conditions (i.e. during overwash conditions).

The importance of overwash (bar topping) events for recruiting and emigrating fishes associated with temporarily open/closed estuaries has not received much attention in the scientific literature and further mention of their significance is necessary. Overwash conditions in the mouth regions of temporarily open/closed estuaries usually occur over spring high tides and in association with rough sea conditions. Large swells create surging waves that penetrate the estuary. These waves range from several centimeters to 0.5 m in depth (see Plate 9.1). During storm sea conditions, major topping of the bar events often alter the sandbar conditions in the mouth regions, which may provide the catalyst for a mouth opening event if coinciding with or followed by a period of high precipitation. Marine-spawning fishes take advantage of these conditions to recruit into and emigrate from the estuary. On several occasions small shoals of fish were observed leaving the estuary to enter the marine environment, and once (5 June 1997) a small shoal of *Liza richardsonii* (41 - 83 mm SL in length) were stranded on the sandbar until the next pulse of waves washed them into the estuary. Whitfield (1992b) also recorded numerous postlarval fishes (*Rhabdosargus holubi* and Mugilidae) with lengths ranging between 9 and 12 mm recruiting into the Haga Haga estuary. Considering the size of the swells and strong current associated with these rough sea conditions, it seems that the fishes either entering of leaving the estuary are 'running the gauntlet' to do so. However, the process of recruitment and emigration are important for the completion of the life cycle by many marine-spawning species. The significance of these events is accentuated by the fact that the mouth of the East Kleinemonde estuary was open for only 43 days between March 1993 and August 1997. Small topping of bar events occurred on an additional 390 days, while large overwash events (duration exceeding three hours) occurred on 31 days.

The relatively few days available for recruitment ultimately dictates the recruitment success and the species that can recruit. The serial spawning species, with potential recruits available for a greater part of the year are therefore better suited to utilize temporarily open/closed systems. This trend was apparent in the fish assemblage of the East Kleinemonde estuary. *Rhabdosargus holubi* and Mugilidae both have extending spawning seasons (Whitfield & Kok 1992) and constituted the bulk of the fishes in this system. Therefore, the success of *Rhabdosargus holubi* in the East Kleinemonde estuary is linked to aspects of its biology, notably an extended breeding season and the ability to recruit under physically harsh (overwash) conditions. A thorough investigation into the importance of overwash events to recruiting and emigrating marine migratory species would be a worthwhile extension of this study, especially considering that more than 70% of South African estuaries are classified as being temporarily open/closed systems.

Despite the obvious benefits of periods of marine influence for migratory marine-spawning fishes, several authors have indicated that distinct benefits also exist during the closed lagoonal phase of temporarily open/closed estuaries. Firstly, the aquatic area (i.e. available nursery habitat) during the closed phase is increased due to elevated water levels (Bennett *et al.* 1985; Kok & Whitfield 1986). Secondly, due to elevated water levels, the inundated intertidal and supratidal habitats also provide greater foraging area which include important detrital, plant and invertebrate food resources (Whitfield 1980c). Thirdly, (Whitfield 1996b) proposed that the nursery function of the estuary is further enhanced because the inundated shallow, vegetated littoral habitats are often inaccessible to large predatory fishes.

Plate 9.1 Photograph of overwash conditions in the mouth region of the East and West Kleinemonde estuaries taken on 21 June 1994. Note the rough sea conditions, surging wave pulses and alteration of the sandbar.

The resident estuarine-spawning species have also adapted in numerous ways to complete their entire life cycle within the estuary. Apart from the obvious ability to tolerate wide salinity, temperature and turbidity ranges (Whitfield 1998), certain species exhibit reproductive specializations which enhance the chances of their eggs being retained within estuaries (Bennett 1985). For example, *Psammogobius knysnaensis*, *Caffrogobius gilchristi* and *Atherina breviceps* all lay large eggs with threads which are attached to some fixed substratum, while the Sygnathidae retain their eggs and larvae in a brood pouch. Furthermore, most estuarine-spawning species attain sexual maturity and reproduce within the first year of their life (Bennett 1989a), while certain species are able to alter their spawning periodicity during the year, possibly to suit prevailing conditions.

Bennett & Branch (1990) suggested that temporarily open/closed estuaries are physically more stable than permanently open systems when closed and therefore are preferred habits for species which complete their life cycle within estuaries. The open versus closed mouth phase in temporarily open/closed estuaries is important for the success of these resident species. The results presented in this study suggest that reproductive activity is halted during low water level conditions following a mouth opening event. However, during the closed mouth phase most resident species bred in the East Kleinemonde estuary. This finding is supported by studies conducted in other temporarily open/closed estuaries (Whitfield 1980a; Bennett 1989a; Harrison & Whitfield 1995). The advantages of the closed phase for the resident species are similar to those for the migratory species and include more stable physical conditions, elevated water levels with increased habitat availability (i.e. less competition for food and space), increased abundance of food organisms and a lower vulnerability to predation by piscivorous fishes.

Finally, it would appear that there is no easy answer to the question as to why estuarine fish populations reveal large temporal variability. It is possibly more appropriate to suggest that estuarine fish populations are and always will be as dynamic as the environment itself. This sentiment is reinforced by the words of Leaky & Lewin (1996) who state that: "Ecological communities do not exist in a benign harmony, but, instead, are shaped by many forces, some of them chaotic, some random. Above all, there is constant, dynamic change".

MANAGEMENT CONSIDERATIONS

Estuaries are considered to be one of the most threatened components of the South African coastline because of both land- and sea-based impacts (Heydorn 1992). Cowley *et al.* (1998) state that the increasing human demand for estuarine space and specific resources often leads to user conflict situations and potential habitat destruction. According to Whitfield (1997) each of South Africa's 250 functional estuaries require careful management and protection if they are to be maintained as a vital natural resource. Therefore, this thesis would be incomplete without making some recommendations for the management of the East Kleinemonde estuary and it's resources. The important considerations in this regard are discussed in the following paragraphs.

Conservation of *Syngnathus watermeyeri*

The estuarine pipefish *Syngnathus watermeyeri* was previously known from three Eastern Cape estuaries (Bushmans, Kariega and Kasouga), but now the East Kleinemonde estuary offers asylum to the only known viable population of this species. Therefore, an appropriate management plan for this estuary is crucial for its long-term survival.

According to Bruton (1995) each threatened species requires a unique suite of conservation measures to ensure its survival. A conservation strategy for an individual fish species is often complicated by virtue of its mobility and wide use of aquatic habitats (Whitfield 1997). A conservation strategy for *Syngnathus watermeyeri* is possibly less complicated due to the fact that it is confined to a single estuary and is strongly associated with the submerged macrophyte (*Ruppia cirrhosa*) beds in the middle and upper reaches. Subsequent to the rediscovery of *S. watermeyeri* in 1996, the management board of Seafield township under the auspices of the Western Region District Council adopted the proposed conservation measures with immediate effect. These measures included the following:

- the proclamation of an estuarine conservancy,
- a public awareness programme including the erection of a notice board highlighting the significance of the estuarine conservancy for the survival of *Syngnathus watermeyeri*,
- to discourage the excessive use of power boats above the road bridge (i.e. in the middle and upper reaches), and
- to restrict boating to the main channel (above the road bridge) to avoid disturbing the *Ruppia* beds.

The survival of *Syngnathus watermeyeri* in the East Kleinemonde estuary is also subject to a ongoing monitoring programme by the Estuarine Research Group (ERG) from the J.L.B. Smith Institute of Ichthyology. Furthermore, a small population of *S. watermeyeri* were successfully relocated to the neighbouring West Kleinemonde estuary which also has dense *Ruppia* beds along the margins of the middle reaches.

Management of catchment area

In recent years numerous studies have provided evidence to suggest that freshwater inputs are crucial for the maintenance of estuarine ecosystem functioning (*inter alia* Whitfield & Wooldridge 1994; Allanson & Read 1995; Schlacher & Wooldridge 1996). Clearly, the development of an overall estuarine conservation strategy warrants the integration of a catchment management plan. However, the main problem at this stage is the quantification of freshwater requirements for individual estuarine systems - a field of study that requires and is receiving urgent attention.

The small catchment area of the East Kleinemonde estuary (approximately 46 km^2) is relatively undisturbed with no significant impoundments restricting the flow of freshwater into the estuary. Most of the area consists of natural vegetation, particularly on the steep stream and river valleys along the banks of the estuary in the upper reaches. Furthermore, agricultural activities within the catchment area consist mainly of extensive cattle grazing with relatively low freshwater demands. Therefore, a rare opportunity exists to develop a proactive integrated estuary conservation strategy for the East Kleinemonde estuary aimed at mitigating negative anthropogenic impacts on water quality and quantity from the catchment area.

Sedimentation

Badenhorst (1988) noted that a natural process of sedimentation was taking place in the East Kleinemonde estuary and due the fact that it is a flood tide dominated system, most of the sediment is of marine origin (i.e. enters the mouth when it is open). The removal of excess sediment is only possible by means of mouth opening (flushing) events and the magnitude of these events will determine the effectiveness of sediment scour. An examination of a series of historical aerial photographs has revealed that only in recent years do the East and West Kleinemonde estuaries share a common outlet during mouth opening events. Consequently the effectiveness of sediment removal has diminished. During a mouth opening event, the exact location of the outlet determines which of the two estuaries is better scoured. The reason why the two estuaries share a common outlet is ascribed to the destabilization and ultimately the eradication of the fore dune which once separated the two estuaries. Therefore, it is recommended that a vegetated frontal dune be re-established between the mouths of the two estuaries and that both beach vehicle traffic and pedestrians be confined to appropriately placed access routes.

Residential development

Estuaries are sought after areas for human habitation, and development (residential and associated structures, e.g. jetties) often results in habitat alteration, impoverishment or even destruction. In an attempt to alleviate the pressures of development on the East Kleinemonde estuary it is recommended that:

- all the marginal vegetation (natural habitats) be retained to support a higher diversity and abundance of estuarine-associated wildlife,
- areas with steep slopes are protected to prevent erosion and sedimentation. In other words, soil erosion and run-off control measures should be prescribed for all developments on or near the estuary banks,
- appropriate recreational facilities including a concrete slipway, picnic sites, braai areas etc. be provided on the grass lawns in the mouth region on the north eastern bank. These facilities should accommodate both residents and visitors in order to channel disturbances into suitable areas. All other private jetties and slipways along the banks of the estuary should be prohibited.

Furthermore, much of the area zoned for future residential development (particularly in Island Beach and Island Beach North; see Figure 2.2) consists of clay dominated soils which do not allow for effective removal of septic tank and other waste water by means of French drains. Therefore, measures to replace the currently used septic tank systems with conservancy tanks, particularly for houses on or near the estuary banks, should be considered. In this regard, it would be worthwhile to implement a programme to monitor bacterial concentrations and other nutrients in the estuary.

Concluding comment

As part of a nationwide assessment of the health of individual estuarine systems, Harrison *et al.* (1996) described the East Kleinemonde estuary as being in a moderately good condition. The biological status and overall water quality of the estuary were both rated as good while its aesthetic appearance was considered acceptable. The future health of this system and its resources, however, depends on the implementation of an appropriate estuarine conservation strategy. The success of such a strategy requires the cooperation and active involvement by a range of interested parties, including policy-makers, scientists, environmental managers, local residents and visitors.

REFERENCES

ADAMS, J.A. 1997 - Botanical survey of the Mpekweni and East Kleinemonde estuaries, January 1997. Unpublished report. 11 pp.

ALLANSON, B.R. & G.H.L. READ. 1995 - Further comment on the response of Eastern Cape Province estuaries to variable freshwater flows. *Sth. Afr. J. aquat. Sci.* **21**(1/2): 56-70.

ALLEN, K.R. 1971 - Relation between production and biomass. *J. Fish. Res. Board Can.* **28**: 1573-1581.

ALLEN, D.M., SERVICE, S.K. & M.V. OGBURN-MATTHEWS. 1992 - Factors influencing the collection efficiency of estuarine fishes. *Trans. Amer. Fish. Soc.* **121**: 234-244.

BADENHORST, P. 1988 - Report on the dynamics of the Kleinemonde West and East estuaries (CSE 13 & 14). CSIR Report EMA/T 8805. 14 pp.

BALON, E.B. 1981 - Saltatory processes and altricial to precocial forms of ontogeny of fishes. *Amer. Zool.* **21**: 573-596.

BECKLEY, L.E. 1983 - The ichthyofauna associated with *Zostera capensis* (Setchell) in the Swartkops estuary, South Africa. *S. Afr. J. Zool.* **18**: 15-24.

BECKLEY, L.E. 1984 - The ichthyofauna of Sundays estuary, South Africa, with particular reference to the juvenile marine component. *Estuaries* 7(3): 248-258.

BECKLEY, L.E. 1985 - Tidal exchange of ichthyoplankton in the Swartkops estuary mouth, South Africa. *S. Afr. J. Zool.* **20**(1): 15-20.

BECKLEY, L.E. 1993 - Linefish larvae and the Agulhas Current. In: *Fish, Fishers and Fisheries.* Beckley L.E. & R.P. van der Elst (Eds). Proceedings of the 2nd Linefish Symposium, Durban. pp. 57-63.

BECKLEY, L.E. & A.D. CONNELL. 1996 - Early life history of *Pomatomus saltatrix* off the east coast of South Africa. *Mar. Freshwater Res.* **47**(2): 319-322.

BEGG, G.W. 1978 - The estuaries of Natal. Natal Town and Regional Planning Report **41**: 657 pp.

BEGG, G.W. 1984 - The comparative ecology of Natal's smaller estuaries. Natal Town and Regional Planning Report **62**: 182 pp.

BENNETT, B.A. 1985 - A mass mortality of fish associated with low salinity conditions in the Bot River estuary. *Trans. R. Soc. S. Afr.* **45**(3/4): 437-447.

BENNETT, B.A. 1989a - A comparison of the fish communities in nearby permanently open, seasonally open and normally closed estuaries in the south-western Cape, South Africa. *S. Afr. J. mar. Sci.* **8**: 43-55.

BENNETT, B.A. 1989b - The diets of fish in three south-western Cape estuarine systems. *S. Afr. J. Zool.* **24**(3): 163-176.

BENNETT, B.A. & G.M. BRANCH. 1990 - Relationships between production and consumption of prey species in the Bot, a cool temperate South African estuary. *Estuar. coast. Shelf Sci.* **31**: 139-155.

BENNETT, B.A., HAMMAN, K.C.D., BRANCH, G.M. & S. THORPE. 1985 - Changes in the fish fauna of the Bot River estuary in relation to opening and closure of the estuary mouth. *Trans. R. Soc. S. Afr.* **45**(3/4): 449-464.

BERRUTI, A. 1983 - The biomass, energy consumption and breeding of waterbirds relative to hydrological conditions at Lake St. Lucia. *Ostrich.* **54**. 65-82.

BLABER, S.J.M. 1973a - Population size and mortality of the marine teleost *Rhabdosargus holubi* (Pisces: Sparidae) in a closed estuary. *Mar. Biol.* **21**: 219-225.

BLABER, S.J.M. 1973b - The ecology of juvenile *Rhabdosargus holubi* (Steindachner) (Teleostei: Sparidae). PhD Thesis, Rhodes University. 123 pp.

BLABER, S.J.M. 1974 - The population structure and growth of juvenile *Rhabdosargus holubi* (Steindachner) (Teleostei: Sparidae) in a closed estuary. *J. Fish Biol.* **6**: 455-460.

BLABER, S.J.M. 1979 - The biology of filter feeding teleosts in lake St Lucia, Zululand. *J. Fish Biol.* **15**: 37-59.

BLABER, S.J.M. 1981 - The zoogeographic affinities of estuarine fishes in south-east Africa. *S. Afr. J. Sci.* **77**: 305-307.

BLABER, S.J.M. 1987 - Factors affecting recruitment and survival of mugilids in estuaries and coastal waters of southeastern Africa. *Amer. Fish. Soc. Sym.* **1**: 507-518.

BLABER, S.J.M., BREWER, D.T. & J.P. SALINI. 1989 - Species composition and biomasses of fishes in different habitats of a tropical northern Australian estuary: their occurrence in the adjoining sea and estuarine dependence. *Estuar. coast. Shelf Sci.* **29**: 509-531.

BLOWER, J.G., COOK, L.M. & J.A. BISHOP. 1981 - *Estimating the size of animal populations.* George Allen and Unwin Limited, London. 128 pp.

BOEHLERT, G.W. & B.C. MUNDY. 1988 - Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. In: *Larval Fish and Shellfish Transport through Inlets.* Weinstein, M.P. (Ed). *Amer. Fish. Soc. Sym.* **3**: 51-67.

BOK, A.H. 1979 - The distribution and ecology of two mullet species in some freshwater rivers in the eastern Cape, South Africa. *J. Limnol. Soc. sthn. Afr.* **5**: 97-102.

BOK, A.H. 1983 - The demography, breeding biology and management of two mullet species (Pisces: Mugilidae) in the eastern Cape, South Africa. PhD Thesis, Rhodes University. 268 pp.

BOSHOFF, A.F., PALMER, N.G. & S.E. PIPER. 1991a - Spatial and temporal abundance patterns of waterbirds in the southern Cape Province. Part 1: Diving and surface predators. *Ostrich*. **62**: 156-177.

BOSHOFF, A.F., PALMER, N.G. & S.E. PIPER. 1991b - Spatial and temporal abundance patterns of waterbirds in the southern Cape Province. Part 3: Wading birds. *Ostrich*. **62**: 197-214.

BRANCH, G.M. & J.R. GRINDLEY. 1979 - Ecology and southern African estuaries. Part XI. Mngazana: a mangrove estuary in Transkei. *S. Afr. J. Zool.* **14**: 149-170.

BROWNELL, C.L. 1979 - Stages in the early development of 40 marine fish species with pelagic eggs from the Cape of Good Hope. *Ichthyol. Bull. Smith Inst. Ichthyol.* **40**: 1-84.

BRUTON, M.N. 1995 - Have fishes had their chips? The dilemma of threatened fishes. *Env. Biol. Fish.* **43**: 1-27.

BURNHAM, K.P., ANDERSON, D.A., WHITE, G.C., BROWNIE,C. & K.H. POLLOCK. 1987 - Design and analysis methods for fish survival experiments based on mark-recapture. *Amer. Fish. Soc. Monogr.* **5**: 437 pp.

CHAPMAN, D.W. 1978 - Production in fish populations. In: *Ecology of freshwater fish production*. Gerking S.D. (Ed). Blackwell Scientific Publications, London. pp. 5-25.

CLARKE, K.R. & R.M. WARWICK 1994 - *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Natural Environmental Research Council, Bournemouth.

COBLE, D.W. 1967 - Effects of fin-clipping on mortality and growth of yellow perch with a review of similar investigations. *J. Wildl. Mgmt.* **31**(1): 178-180.

COOPER, J.A.G., RAMM, A.E.L. & T.D. HARRISON. 1994 - The estuarine health index: a new approach to scientific information transfer. *Ocean coast. Mgmt.* **25**: 103-141.

COWLEY, P.D., A.K. WHITFIELD & T. HECHT. 1998 - Estuarine Mariculture in South Africa Strategic Options for Development and Management. *S. Afr. Network coast. Oceanic Res.. Occ. Rep.* **4**: 80pp.

CRAWFORD, R.J.M., UNDERHILL, L.G., RAUBENHEIMER, C.M., DYER, B.M. & J. MARTIN. 1992 - Top predators in the Benguela ecosystem - implications of their trophic position. In: *Benguela Trophic Functioning*. Payne, A.I.L., Brink, K.H., Mann, K.H. & R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 675-687.

CYRUS, D.P. 1991 - The reproductive biology of *Solea bleekeri* (Teleostei) in Lake St Lucia on the south-east coast of Africa. *S. Afr. J. mar. Sci.* **10**: 45-51.

CYRUS, D.P. & A.T. FORBES. 1996 - Preliminary results on the role of KwaZulu-Natal harbours as nursery grounds for juveniles of selected marine organisms which utilize estuaries. *S. Afr. J. Wildl. Res.* **26**(1): 26-33.

CYRUS, D.P. & T. MARTIN. 1991 - The importance of estuaries in the life histories of flatfish species on the southern coast of Africa. *Neth. J. Sea Res.* **27**(3/4): 255-260.

DAY, J.H. 1977 - Marine biology in South Africa. In: *A History of Scientific Endeavour in South Africa*. Brown, A.C. (Ed) Cape Town. pp. 86-108.

DAY, J.H. 1981 - The nature, origin and classification of estuaries. In: *Estuarine Ecology with particular reference to southern Africa*. Day, J.H. (Ed). Balkema, Cape Town. pp. 1-6.

DAY, J.H., SMITH, W., WAGNER, P. & W. STOWE. 1973 - Community structure and carbon budget of a salt marsh and shallow bay estuarine system in Louisiana. Publ. No. LSU-56-72-04. Center for Wetland Resources, Louisiana State University. 79pp.

DAY, J.H., BLABER, S.J.M. & J.H. WALLACE. 1981 - Estuarine fishes. In: *Estuarine Ecology with particular reference to southern Africa*. Day, J.H. (Ed). Balkema, Cape Town. pp. 345-372.

DAY, J.H., HALL, C.A.S., KEMP, W.M. & A. YANEZ-ARANCIBIA (Eds). 1989 - *Estuarine Ecology.* Wiley Publishers. 558 pp.

DEANGELIS, R. 1960 - Brackish-water lagoons and their exploitation. *Stud. Rev. gen Fish. Coun. Mediterr.* **12**.

DEEGAN, L.A. 1993 - Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. *Can. J. Fish. aquat. Sci.* **50**: 74-79.

DICKEY-COLLAS, M., GOWEN, R.J. & C.J. FOX. 1996 - Distribution of larval and juvenile fish in the western Irish Sea: relationship to phytoplankton, zooplankton biomass and recurrent physical features. *Mar. Freshwater Res.* **47**(2): 169-181.

DUNDAS, A. 1994 - A comparative analysis of fish abundance and diversity in three semi-closed estuaries in the Eastern Cape. MSc Thesis, University of Port Elizabeth. 81 pp.

EGGLISHAW, H.J. 1970 - Production of salmon and trout in a stream in Scotland. *J. Fish Biol.* **2**: 117-136.

ERZINI, K. 1990 - Sample size and grouping of data for length-frequency analysis. *Fish. Res.* **9**: 355-366.

GRIFFITHS, M.H. 1996 - Life history of the dusky kob *Argyrosomus japonicus* (Sciaenidae) off the east coast of South Africa. *S. Afr. J. mar. Sci.* **17**: 135-154.

GRIMES, C.B. & M.J. KINGSFORD, 1996 - How do riverine plumes of different sizes influence fish larvae: do they enhance recruitment? *Mar. Freshwater Res.* **47**(2): 191-208.

GROOMBRIDGE, B. (Ed.). 1993 - *1994 IUCN red list of threatened animals.* IUCN, Gland. 286pp.

HALL, C.M., WHITFIELD, A.K. & B.R. ALLANSON. 1987 - Recruitment, diversity and the influence of constrictions on the distribution of fishes in the Wilderness Lakes system, South Africa. *S. Afr. J. Zool.* **22**: 163-169.

HANEKOM, N. & D. BAIRD. 1984 - Fish community structures in *Zostera* and non-*Zostera* regions of the Kromme estuary, St Francis Bay. *S. Afr. J. Zool.* **19**: 295-301.

HARRIS, S.A. 1996 - Larval fish assemblages of selected estuarine and coastal systems in KwaZulu-Natal, South Africa. PhD Thesis, University of Zululand. 208 pp.

HARRIS, S.A. & D.P. CYRUS. 1995 - Occurrence of fish larvae in the St. Lucia estuary, KwaZulu-Natal, South Africa. *S. Afr. J. mar. Sci.* **16**: 333-350.

HARRIS, S.A. & D.P. CYRUS. 1996 - Larval and juveniles fishes in the surf zone adjacent to the St. Lucia estuary mouth, KwaZulu-Natal, South Africa. *Mar. Freshwater Res.* **47**(2): 465-482.

HARRISON, T.D. 1993 - Ecology of the ichthyofauna in three temporarily open/closed estuaries on the Natal coast. MSc Thesis, Rhodes University. 193 pp.

HARRISON, T.D. & A.K. WHITFIELD. 1990 - Composition, distribution and abundance of ichthyoplankton in the Sundays River estuary. *S. Afr. J. Zool.* **25**(3): 161-168.

HARRISON, T.D. & A.K. WHITFIELD. 1995 - Fish community structure in three temporarily open/closed estuaries on the Natal coast. *Ichthyol. Bull. Smith Inst. Ichthyol.* **64**: 1- 80.

HARRISON, T.D., COOPER, J.A.G., RAMM, A.E.L. & R.A. SINGH. 1996 - *Health of South African estuaries, Groot (Wes) - Great Fish, Executive Report.* Coastal and Catchment Environmental Programme. CSIR. Durban. 102 pp.

HELLIER, T.R. 1962 - Fish production and biomass studies in relation to photosynthesis in the Lagun Madre of Texas. *Publ. Inst. Mar. Sci. Univ. Texas.* **8**: 212-215.

HEYDORN, A.E.F. 1992 - The conservation status of southern African estuaries. In: *Biotic Diversity in Southern Africa.* Huntley, B.J. (Ed). Oxford University Press. Cape Town. pp. 290-297.

HEYDORN, A.E.F. & K.L. TINLEY. 1980 - Estuaries of the Cape. Part 1. Synopsis of the Cape coast. CSIR Research Report **380**. CSIR, Pretoria.

HEYL, C.W. & M.H. CURRIE. 1985 - Variations in the use of the Bot River estuary by water-birds. *Trans. Roy. Soc. S. Afr.* **45**(3/4): 397-417.

HOLCIK, J. 1970 - Standing crop, abundance, production, and some ecological aspects of fish population in some waters of Cuba. *Vestn. Cs. Spol. Zool. (Acta Zoc. Zool. Bohemuslov.)*. **34**: 184-201.

HOUDE, E.D. & E.S. RUTHERFORD. 1993 - Recent trends in estuaries fisheries: Predictions of fish production and yield. *Estuaries*. **16**(2): 161-176.

IVERSON, R.L. 1990 - Control of marine fish production. *Limnol. Oceanogr.* **35**: 1593-1604.

JACKSON, S. 1984 - Predation by Pied kingfishers and Whitebreasted cormorants on fish in the Kosi estuary system. *Ostrich*. **55**: 113-132.

JACOBSEN, T & J.A. KUSHLAN. 1987 - Sources of sampling bias in enclosed fish trapping: effects on estimates of density and diversity. *Fish. Res.* **5**: 401-412.

JONES, EM. 1969 - Further notes on "The chronicle of Jeremiah Goldswain". *Africana Notes and News*. **18**(5): 183-194.

JONES, R., OGLETREE, W., THOMPSON, J. & W. FLENNILSEN. 1963 - Helicopter borne purse net for population sampling of shallow marine bays. *Publ. Inst. Mar. Sci. Univ. Texas*. **9**: 1-6.

JOUBERT, C.S.W. 1981 - Aspects of the biology of five species of inshore reef fishes on the Natal coast, South Africa. *Invest. Rep. oceangr. Res. Inst.* **51**: 1-16.

JUNOR, F.J.R. 1969 - Aspects of the ecology of piscivorous birds of Lake Kyle, Rhodesia. MSc Thesis, Rhodes University.

JUNOR, F.J.R. & B.E. MARSHALL. 1987 - Factors influencing the abundance of piscivorous birds on Lake Kyle, Zimbabwe. *Ostrich*. **58**: 168-175.

KENDALL, A.W., AHLSTROM, E.H. & H.G. MOSER. 1984 - Early life history stages of fishes and their characters. In: *Ontogeny and Systematics of Fishes*. Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.P., Kendall, A.W. and S.L. Richardson (Eds). *Spec. Publ. Am. Soc. Ichthyol. Herpetol.* **1**: 11-22 (Proceedings of an International Symposium in La Jolla, California, August 1983).

KOK, H.M. & A.K. WHITFIELD. 1986 - The influence of open and closed mouth phases on the marine fish fauna of the Swartvlei estuary. *S. Afr. J. Zool.* **21**: 309-315.

KOPKE, D. 1988 - The climate of the Eastern Cape. In: *Towards an environmental plan for the Eastern Cape*. Bruton, M.N. & F.W. Gess (Eds). Rhodes University. Grahamstown.

KORINGA, P. 1967 - Estuarine fisheries in Europe as affected by man's multiple activities. In: *Estuaries*. Lauff, G. (Ed). *Amer. Assoc. Adv. Sci. Spec. Publ.* **83**: 608-666.

LASIAK, T.A. 1981 - Nursery grounds of juvenile Teleosts: evidence from the surf zone of King's beach, Port Elizabeth. *S. Afr. J. Sci.* **77**: 388-390.

LEAKEY, R & R. LEWIN. 1996 - *The Sixth Extinction - Biodiversity and its Survival*. Weidenfeld and Nicolson. London. 271 pp.

LEBRETON, J-D., BURNHAM, K.P., CLOBERT, J. & D.R. ANDERSON. 1992 - Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**(1): 67-118.

LUTJEHARMS, J.R.E. 1998 - Coastal Hydrography. In: *Field Guide to the Eastern and Southern Cape Coasts*. Lubke, R. & I. De Moor (Eds). University of Cape Town Press, Cape Town. pp. 50-61.

MACLEAN, G.L. (Ed). 1993 - *Robert's Birds of Southern Africa*. John Voelcker Bird Book Fund, Cape Town. 871 pp.

MARAIS, J.F.K. 1981 - Seasonal abundance, distribution and catch per unit effort using gill nets, of fishes in the Sundays estuary. *S. Afr. J. Zool.* **16**: 144-150.

MARAIS, J.F.K. 1983 - Fish abundance and distribution in the Gamtoos estuary with notes on the effect of floods. *S. Afr. J. Zool.* **18**: 103-109.

MARAIS, J.F.K. 1984 - Feeding ecology of major carnivorous fish from four eastern Cape estuaries. *S. Afr. J. Zool.* **19**(3): 210-223.

MARAIS, J.F.K. 1985 - Some factors influencing the size of fishes caught in gill nets in eastern Cape estuaries. *Fish. Res.* **3**: 251-261.

MARAIS, J.F.K. 1990 - Body composition of ten marine migrants and one freshwater fish species caught in the estuaries of the eastern Cape, South Africa. *S. Afr. J. mar. Sci.* **9**: 135-140.

MARAIS, J.F.K. & D. BAIRD. 1980 - Analysis of angler's catch data from the Swartkops estuary. *S. Afr. J. Zool.* **15**: 61-65.

MARTIN, A.P. & D. BAIRD. 1987 - Seasonal abundance and distribution of birds on the Swartkops Estuary, Port Elizabeth. *Ostrich.* **58**: 122-134.

MARTIN, T.J., CYRUS, D.P. & A.T. FORBES. 1992 - Episodic events: the effects of cyclonic flushing on the ichthyoplankton of St Lucia estuary on the southeast coast of Africa. *Neth. J. Sea Res.* **30**: 273-278.

MELVILLE-SMITH, R. 1978 - Aspects of the ecology of fish larvae in the Swartkops estuary, Port Elizabeth. MSc Thesis, University of Port Elizabeth. 163 pp.

MELVILLE-SMITH, R. & D. BAIRD. 1980 - Abundance, distribution and species composition of fish larvae in the Swartkops Estuary. *S. Afr. J. Zool.* **15**(2): 72-78.

MEREDITH, W.H. & V.A. LOTRICH. 1979 - Production dynamics of a tidal creek population of *Fundulus heteroclitus* (Linnaeus). *Estuar. coast. mar. Sci.* **8**: 99-118.

NAGY, K.A. 1987 - Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monogr.* **57**(2): 111-128.

NEIRA, F.J. & I.C. POTTER. 1992 - The ichthyoplankton of a seasonally closed estuary in temperate Australia. Does an extended period of opening influence species composition? *J. Fish Biol.* **41**: 935-953.

NEIRA, F.J. & I.C. POTTER. 1994 - The larval fish assemblage of the Nornalup-Walpole Estuary, a permanently open estuary on the southern coast of western Australia. *Austr. J. Mar. Freshwater Res.* **45**: 1193-1207.

NEIRA, F.J., POTTER, I.C. & J.S. BRADLEY. 1992 - Seasonal and spatial changes in the larval fish fauna within a large temperate Australian estuary. *Mar. Biol.* **112**(1): 1-16.

NIELSON, L.A. 1992 - Methods of marking fish and shellfish. *Amer. Fish. Soc. Spec. Publ.* **23**. 208 pp.

NIXON, S.W., OVIATT, C.A., FRITHSEN, J. & B. SULLIVAN. 1986 - Nutrients and the productivity of estuarine and coastal marine ecosystems. *J. Limnol. Soc. sthn. Afr.* **12**: 43-71.

NORCROSS, B.L. & R.F. SHAW. 1984 - Oceanic and estuarine transport of fish eggs and larvae: a review. *Trans. Amer. Fish. Soc.* **113**(2): 153-165.

OLIVAR, M.P. & J.M. FURTUNO. 1991 - Guide to ichthyoplankton of the Southeast Atlantic (Benguela Current Region). *Scientia Marina*. **55**(1): 1-383.

OLIVAR, M.P. & P.A. SHELTON. 1993 - Larval fish assemblages of the Benguela current. *Bull. mar. Sci.* **53**(2): 450-474.

OLIVAR, M.P. & L.E. BECKLEY. 1994 - Investigations on the occurrence of larvae of *Symbolophorus* species (Myctophidae) off Southern Africa. *S. Afr. J. mar. Sci.* **14**: 349-359.

OTIS, D., BURNHAM, K.P., WHITE, G.C. & D.R. ANDERSON. 1978 - Statistical inference from capture data on closed populations. *Wildl. Monogr.* **62**. 135 pp.

PAKRASI, B.B., DAS, P.R. & T. HAKRTA. 1964 - Culture of brackish-water fishes in impoundments in West Bengal. *Publ. Indo-Pacific Fish. Coun.* **2**.

PALOMARES, M.L. & D. PAULY. 1989 - A multiple regression model for predicting the food consumption of marine fish populations. *Austr. J. mar. Freshwater Res.* **40**: 259-273.

PATERSON, A.W. 1998 - Aspects of the ecology of fishes associated with salt marshes and adjacent habitats in a temperate South African estuary. PhD Thesis, Rhodes University. 200 pp.

PATERSON, A.W. & A.K. WHITFIELD. 1996 - The fishes associated with an intertidal salt marsh creek in the Kariega estuary, South Africa. *Trans. Roy. Soc. S. Afr.* **51**: 195-218.

PETERSON, C.G.J. 1896 - The yearly immigration of young plaice into Limfjord from the German Sea. *Rep. Dan. biol. Stn.* **6**: 1-48.

PIERCE, C.L., RASMUSSEN, J.B. & W.C. LEGGETT. 1990 - Sampling littoral fish with a seine: corrections for variable capture efficiency. *Can. J. Fish. aquat. Sci.* **47**: 1004-1010.

POSTMA, H. & G. RAUCK. 1979 - The fishery in the Wadden Sea. In: *Fishes and Fisheries of the Wadden Sea.* Dankers, N., Wolff, W. & J. Zijlstra (Eds.). A.A. Balkema, Rottedam. pp. 139-157.

RABANAL, H.R. 1961 - Status and progress of *Chanos* fisheries in the Philippines. *Occ. paper Indo-pacific Fish. Coun.* **61/8**.

RATTE, T.W. 1989 - Population structure, production, growth, reproduction and the ecology of *Atherina breviceps* Valenciennes, 1935 (Pisces:Atherinidae) and *Gilchristella aestuaria* (Gilchrist, 1914) (Pisces: Clupeidae), from two southern Cape coastal lakes. PhD Thesis, University of Port Elizabeth. 332 pp.

RICKER, W.E. 1975 - Computation and interpretation of biological statistics of fish populations. *Info. Can. Bull.* **191**. 382 pp.

ROBERTSON, A.I. & N.C. DUKE. 1990 - Recruitment, growth and residence time of fishes in a tropical Australian Mangrove system. *Estuar. coast. Shelf Sci.* **31**: 723-743.

ROZAS, L.P. & T.J. MINELLO. 1997 - Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. *Estuaries.* **20**(1): 199-213.

RUPLE, D.L. 1984 - Occurrence of larval fishes in the surf zone of a northern Gulf of Mexico barrier island. *Estuar. coast. Shelf Sci.* **18**: 191-200.

SCHLACHER, T.A. & T.H. WOOLDRIDGE. 1996 - Ecological responses to reductions in freshwater supply and quality in South Africa's estuaries: lessons for management and conservation. *J. coast. Conserv.* **2**: 115-130.

SEBER, G.A.F. 1973 - *Estimation of animal abundance and related parameters.* Griffin, London. 506 pp.

SEBER, G.A.F. 1992 - A review of estimating animal abundance II. *Int. Stat. Rev.* **60**(2): 129-166.

SHORT, A.D. & L.D. WRIGHT. 1983 - Physical variability of sandy beaches. In: *Sandy Beaches as Ecosystems.* McLachlan, A. & T. Erasmus (Eds). Junk Publishers, The Hague. 757 pp.

SINCLAIR, I. 1987 - *Field guide to the birds of southern Africa.* Struik Publishers, Cape Town. 367 pp.

SMALE, M.J. & H.M. KOK. 1983 - The occurrence and feeding of *Pomatomus saltatrix* (elf) and *Lichia amia* (leervis) juveniles in two Cape south coast estuaries. *S. Afr. J. Zool.* **18**: 337-342.

SMALE, M.J. & C.D. BUXTON. 1989 - The subtidal gulley fish community of the eastern cape and the role of this habitat as a nursery area. *S. Afr. J. Zool.* **24**: 58-67.

SMITH, M.M. & P.C. HEEMSTRA. 1986 - *Smiths' Sea Fishes*. Macmillan Publishers, Johannesburg. 1047 pp.

SPRINGER, A.M., PIATT, J.F. & G. VAN VLIET. 1996 - Sea birds as proxies of marine habitats and food webs in the western Aleutian Arc. *Fish. Oceanogr.* **5**(1): 45-55.

STONE, A.W. 1988 - The Eastern Cape's infinite variety, an introduction to the physical environment of the Eastern Cape. In: *Towards an environmental plan for the Eastern Cape*. Bruton, M.N. & F.W. Gess (Eds). Rhodes University, Grahamstown. pp. 9-11.

STONE, A.W., WEAVER, A.v.B. & W.O. WEST. 1998 - Climate and weather. In: *Field Guide to the Eastern and Southern Cape Coasts*. Lubke, R. & I. De Moor (Eds). University of Cape Town Press, Cape Town. pp. 41-49.

SWART, D.H. & J.de V. SERDYN. 1981 - Statistical analysis of visually observed wave data from voluntary observing ships (VOS) for the South African east coast. NRIO Vol. **34** (unpublished report) 141 pp.

TALBOT, M.M.J-F. 1982 - Aspects of the ecology and biology of *Gilchristella aestuaria* (Pisces: Clupeidae) in the Swartkops estuary, Port Elizabeth. MSc Thesis, University of Port Elizabeth. 128 pp.

TER MORSHUIZEN, L.D. & A.K. WHITFIELD. 1994 - The distribution of littoral fish associated with eelgrass *Zostera capensis* in the Kariega estuary, a southern African system with a reversed salinity gradient. *S. Afr. J. mar. Sci.* **14**: 95-105.

TER MORSHUIZEN, L.D., A.K. WHITFIELD & A.W. PATERSON. 1996 - Distribution patterns of fishes in an eastern Cape estuary and river with particular emphasis on the ebb and flow region. *Trans. Roy. Soc. S. Afr.* **51**: 257-280.

TILNEY, R.L. & C.D. BUXTON. 1994 - A preliminary ichthyoplankton survey of the Tsitsikamma National Park. *S. Afr. J. Zool.* **29**: 204-211.

THORPE, C. 1977 - An eastern Cape farm - Tharfield 1976. *Toposcope* **8**: 3-8.

VALIELA, I., WRIGHT, J., TEAL, J. & S.B. VOLKMAN. 1977 - Growth, production and energy transformations in the salt marsh killifish, *Fundulus heteroclitus*. *Mar. Biol.* **40**: 135-144.

VAN DER ELST, R. P. & J.H. WALLACE. 1976 - Identification of the juvenile mullet of the east coast of South Africa. *J. Fish Biol.* **9**: 371-374.

WAGNER, P. 1973 - Seasonal biomass, abundance, and distribution of estuarine dependent fishes in the Caminada Bay system of Louisiana. PhD Dissertation, Louisiana State University. 193 pp.

WALLACE, J.H. 1975 - The estuarine fishes of the east coast of South Africa. I. Species composition and length distribution in the estuarine and marine environments. II. Seasonal abundance and migrations. *Investl. Rep. oceanogr. Res. Inst.* **40**: 1-51.

WALLACE, J.H. & R.P. VAN DER ELST. 1975 - The estuarine fishes of the east coast of South Africa. IV. Occurrence of juveniles in estuaries. V. Ecology, estuarine dependence and status. *Invest. Rep. oceanogr. Res. Inst.* **42**: 1-63.

WALLACE, J.H., KOK, H.M., BECKLEY, L.E., BENNETT, B., BLABER, S.J.M. & A.K. WHITFIELD. 1984 - South African estuaries and their importance to fishes. *S. Afr. J. Sci.* **80**: 203-207.

WARBURTON, K. 1979 - Growth and production of some important species of fish in a Mexican coastal lagoon system. *J. Fish Biol.* **14**: 449-464.

WEINSTEIN, M.P. & M.P. WALTERS. 1981 - Growth, survival and production in young-of-year populations of *Leiostomus xanthurus* (Lacepede) residing in tidal creeks. *Estuaries* **4**(3): 185-197.

WEINSTEIN, M.P., SCOTT, L., O'NEIL, S.P., SIEGFRIED, R.C. & S.T. SZEDLMAYER. 1984 - Population dynamics of Spot, *Leiostomus xanthurus*, in polyhaline tidal creeks of the York River estuary, Virginia. *Estuaries* 7(4): 444-450.

WHITE, G.C., ANDERSON, D.R., BURNHAM, K.H. & D.L. OTIS. 1982 - *Capture-recapture and removal methods for sampling closed populations*. Los Alamos National Laboratory, LA 8787-NERP, Los Alamos, New Mexico. 235 pp.

WHITFIELD, A.K. 1978 - Relationship between fish and piscivorous bird densities at Lake St. Lucia. *S. Afr. J. Sci.* **74**: 478.

WHITFIELD, A.K. 1980a - Distribution of fishes in the Mhlanga estuary in relation to food resources. *S. Afr. J. Zool.* **15**: 159-165.

WHITFIELD, A.K. 1980b - Factors influencing the recruitment of juvenile fishes into the Mhlanga estuary. *S. Afr. J. Zool.* **15**: 166-169.

WHITFIELD, A.K. 1980c - A quantitative study of the trophic relationships within the fish community of the Mhlanga estuary, South Africa. *Estuar. coast. mar. Sci.* **10**: 417-435.

WHITFIELD, A.K. 1984 - The effects of prolonged aquatic macrophyte senescence on the biology of the dominant fish species in a southern African coastal lake. *Estuar. coast. Shelf Sci.* **18**: 315-329.

WHITFIELD, A.K. 1985 - The role of zooplankton in the feeding ecology of fish fry from some South African estuaries. *S. Afr. J. Zool.* **20**: 166-171.

WHITFIELD, A.K. 1986 - Predation by Whitebreasted Cormorant on fishes in a southern Cape estuarine system. *Ostrich*. **57**: 248-249.

WHITFIELD, A.K. 1988 - The fish community of the Swartvlei estuary and the influence of food availability on resource utilization. *Estuaries*. **11**: 160-170.

WHITFIELD, A.K. 1989a - Fish larval composition, abundance and seasonality in a southern African estuarine lake. *S. Afr. J. Zool.* **24**(3): 217-224.

WHITFIELD, A.K. 1989b - Ichthyoplankton interchange in the mouth region of a southern African estuary. *Mar. Ecol. Prog. Ser.* **54**: 25-33.

WHITFIELD, A.K. 1989c - Ichthyoplankton in a southern African surf zone: nursery area for the postlarvae of estuarine associated fish species? *Estuar. coast. Shelf Sci.* **29**: 533-547.

WHITFIELD, A.K. 1992a - A characterization of southern African estuarine systems. *S. Afr. J. Aquat. Sci.* **18**(1/2): 89-103.

WHITFIELD, A.K. 1992b - Juvenile fish recruitment over an estuarine sand bar. *Ichthos* **36**: 23.

WHITFIELD, A.K. 1993 - Fish Biomass estimates from the littoral zone of an estuarine coastal lake. *Estuaries* **16**(2): 280-289.

WHITFIELD, A.K. 1994a - Abundance of larval and 0+ juvenile marine fishes in the lower reaches of three southern African estuaries with differing freshwater inputs. *Mar. Ecol. Prog. Ser.* **105**: 257-267.

WHITFIELD, A.K. 1994b - Fish species diversity in southern African estuarine systems: an evolutionary perspective. *Env. Biol. Fish.* **40**: 37-48.

WHITFIELD, A.K. 1995 - Threatened fishes of the world: *Syngnathus watermeyeri* Smith, 1963 (Syngnathidae). *Env. Biol. Fish.* **43**: 152.

WHITFIELD, A.K. 1996a - A review of estuarine ichthyology in South Africa over the past 50 years. *Trans. Roy. Soc. S. Afr.* **51**: 79-89.

WHITFIELD, A.K. 1996b - A review of factors influencing fish utilization of South African estuaries. *Trans. Roy. Soc. S. Afr.* **51**: 115-137.

WHITFIELD, A.K. 1997 - Fish conservation in South African estuaries. *Aquat. Conserv.* **7**: 1-11

WHITFIELD, A.K. 1998 - Biology and Ecology of Fishes in Southern African Estuaries. *Ichthyol. Monogr. Smith Inst. Ichthyol.* **2**: 223 pp.

WHITFIELD, A.K. & S.J.M. BLABER. 1978a - Food and feeding ecology of piscivorous fishes at Lake St Lucia, Zululand. *J. Fish Biol.* **13**: 675-691.

WHITFIELD, A.K. & S.J.M. BLABER. 1978b - Feeding ecology of piscivorous birds at Lake St Lucia, Part 1: Diving birds. *Ostrich* **49**: 185-198.

WHITFIELD, A.K. & S.J.M. BLABER. 1979a - Feeding ecology of piscivorous birds at Lake St Lucia, Part 2: Wading birds. *Ostrich* **50**: 1-9.

WHITFIELD, A.K. & S.J.M. BLABER. 1979b - Feeding ecology of piscivorous birds at Lake St Lucia, Part 3: Swimming birds. *Ostrich* **50**: 10-20.

WHITFIELD, A.K. & H.M. KOK. 1992 - Recruitment of juvenile marine fishes into permanently open and seasonally open estuarine systems on the southern coast of South Africa. *Ichthyol. Bull. Smith Inst. Ichthyol.* **57**: 1-17.

WHITFIELD, A.K. & L.D. TER MORSHUIZEN. 1992 - Is the river pipefish extinct? *Conserva* **7**: 21.

WHITFIELD, A.K., BECKLEY, L.E., BENNETT, B.A., BRANCH, G.M., KOK, H.M., POTTER, I.C. & R.P. VAN DER ELST. 1989 - Composition, species richness and similarity of ichthyofaunas in eelgrass *Zostera capensis* beds of southern Africa. *S. Afr. J. mar. Sci.* **8**: 251-259.

WHITFIELD, A.K. & T.D. HARRISON. 1996 - *Gilchristella aestuaria* (Pisces: Clupeidae) biomass and consumption of zooplankton in the Sundays estuary. *S. Afr. J. mar. Sci.* **17**: 49-53.

WHITFIELD, A.K., PATERSON, A.W., BOK, A.H. & H.M. KOK. 1994 - A comparison of the ichthyofaunas in two permanently open eastern Cape estuaries. *S. Afr. J. Zool.* **29**(2): 175-185.

WHITFIELD, A.K. & T.H. WOOLDRIDGE. 1994 - Changes in freshwater supplies to southern African estuaries: some theoretical and practical considerations. In: *Changes in Fluxes in estuaries: Implications from Science to Management.* Dyer, K.R. & R.J. Orth (Eds). Olsen and Olsen, Fredensborg. pp. 41-50.

WORTHINGTON, D.G., FERRELL, D.J., McNEILL, S.E. & J.D. BELL. 1992 - Growth of four species of juvenile fish associated with seagrass *Zostera capricorni* in Botany Bay, New South Wales. *Austr. J. mar. Freshwater Res.* **43**: 1189-1198.

YANEZ-ARANCIBIA, A. 1978 - Taxonomy, ecology and structure of fish communities in coastal lagoons with ephemeral inlets on the Pacific Coast of Mexico. *Centro. Cienc. del Mar. y Limnol. Univ. Nal. Auton. Mexico, Publ. Esp.* **2**: 1-306.

YANEZ-ARANCIBIA, A. & A.L. LARA-DOMINGUEZ. 1983 - Environmental dynamic of Estero Pargo Inlet and structure of fish communities in daily and seasonal changes in *Rhizophora mangle*/ *Thalassia testudinum* habitats (Terminos Lagoon, southern Gulf of Mexico). *An. Inst. Cienc. del Mar. y Limnol. Univ. Nal. Auton. Mexico.* **10**: 85-116.

YOKLAVIC, M.M., STEVENSON, M & G.M. CAILLIET. 1992 - Seasonal and spatial patterns of ichthyoplankton abundance in Elkhorn Slough, California. *Estuar. coast. Shelf Sci.* **34**: 109-126.

YOUNG, J.R., KLAUDA, R.J. & W.P. DEY. 1988 - Population estimates for striped bass and white perch in the Hudson river estuary. *Amer. Fish. Soc. Monogr.* **4**: 89-101.

YOUNG, G.C., POTTER I.C., HYNDES, G.A. & S. DE LESTANG. 1997 - The ichthyofauna of an intermittently open estuary: implications of bar breaching and low salinities on faunal composition. *Estuar. coast. Shelf Sci.* **45**: 53-68.

APPENDICES

Appendix 1 Date, time of sampling, number of sample hauls and environmental conditions on the days when ichthyoplankton samples were collected in the surf zone adjacent to the mouth of the East Kleinemonde estuary.

Date	Estuary mouth condition	Time at sampling	Number of 2 min. hauls	High tide at	Temperature (degrees C)	Wind direction	Estimated wind speed (knots)	Wave height (m)
26-Aug-94	open	16h30-17h30	5	18h20	not taken	SW	< 5	1-2
4-Sep-94	topping	14h45-15h30	5	14h55	19		0	< 1
14-Sep-94	closed	14h00-14h40	5	11h55	18	SW	5-10	1-2
21-Sep-94	topping	16h30-17h10	5	16h25	17	NE	5-10	< 1
27-Sep-94	closed	17h00-17h40	5	19h45	17		0	< 1
13-Oct-94	closed	11h20-12h10	5	11h30	14	NE	< 5	1-2
19-Oct-94	closed	13h55-14h50	5	15h30	16.5		0	< 1
25-Oct-94	closed	18h05-18h40	5	18h25	16.5		0	< 1
3-Nov-94	closed	15h20-15h55	5	15h15	17	SW	< 5	< 1
10-Nov-94	closed	08h30-09h05	5	09h10	19		0	1-2
18-Nov-94	closed	13h55-14h30	5	15h35	21	SW	< 5	< 1
5-Dec-94	closed	16h10-16h45	5	17h00	18.5		0	1-2
16-Jan-95	topping	14h20-14h55	5	15h40	19.5	SE	< 5	< 1
25-Jan-95	topping	09h05-09h40	5	10h10	16	SW	10-15	< 1
3-Feb-95	topping	15h35-16h05	5	17h50	19	NE	5-10	1-2
11/12-Feb-95	topping	10h00-07h30	24	13h40 & 02h15	18-20	SW	5-10	< 1
20-Feb-95	topping	07h45-08h15	5	06h35	19	SW	5-10	< 1
6-Mar-95	topping	16h10-16h40	5	18h20	18.5	SW	5-10	1-2
13-Mar-95	topping	13h00-13h30	5	13h55	16	SW	10-15	1-2
22-Mar-95	topping	07h20-07h50	5	07h00	17	SW	< 5	1-2
4-Apr-95	topping	17h00-17h30	5	17h55	17	SE	< 5	1-2
17-Apr-95	topping	16h00-16h30	5	17h05	16.5		0	1-2
26-Apr-95	topping	13h45-14h15	5	14h05	18	SW	5-10	1-2
11-May-95	topping	12h30-13h00	5	13h20	18	SW	< 5	< 1
15/16-May-95	topping	07h30-05h00	24	17h25 & 07h00	17-18	NW	0-5	< 1
25-Jul-95	topping	15h00-15h30	5	14h50	17.5	NE	< 5	1-2
3-Aug-95	closed	09h00-09h30	5	07h40	18.5		0	< 1
20-Aug-95	closed	12h10-12h40	4	12h10	18.5	SW	< 5	1-2
29-Aug-95	closed	16h30-17h10	5	17h30	18	SE	5-10	1-2
20-Sep-95	closed	13h10-13h40	4	13h30	16	SW	5-10	< 1
21-Sep-95	closed	14h10-14h45	4	14h00	17	NE	< 5	< 1
24-Oct-95	closed	14h35-15h05	5	15h35	21	SW	5-10	1-2
8-Nov-95	closed	15h40-16h20	5	16h05	20	SW	5-10	1-2
13-Nov-95	closed	07h40-08h10	5	06h35	20.5	SW	< 5	< 1
20-Dec-95	closed	11h25-12h00	5	14h20	15	SW	< 5	1-2
15-Jan-96	closed	17h20-17h35	3	10h45	20		0	< 1
31-Jan-96	closed	13h05-13h25	3	13h35	18.5	SW	5-10	< 1
5-Feb-96	closed	15h30-15h50	3	16h20	22	SE	< 5	< 1
12-Mar-96	closed	07h40-07h55	2	08h05	18	SW	< 5	< 1
8-May-96	closed	07h15-07h35	5	06h55	16		0	1-2
13-May-96	closed	13h45-14h15	5	13h10	17.5	SW	5-10	< 1
24-Jun-96	closed	07h45-08h15	5	09h00	17		0	< 1
11-Jul-96	closed	13h30-14h15	5	13h15	18	SE	< 5	< 1
26-Aug-96	closed	12h15-12h45	5	14h05	17	SW	5-10	< 1
30-Sep-96	closed	15h40-16h10	5	17h35	19	SE	< 5	< 1

Appendix 2 The length-mass relationships obtained from power curve regression analyses for the estuarine-spawning species captured in the East Kleinemonde estuary (a = intercept, b = slope, n = number of specimens).

Species	a	b	r^2	n
Atherina breviceps	0.000009	3.0906	0.9173	795
Gilchristella aestuaria	0.00003	2.8153	0.9457	519
Glossogobius callidus	0.00004	2.7943	0.9689	437
Psammogobius knysnaensis	0.000008	3.1999	0.989	9
Syngnathus watermeyeri	0.0000002	3.2271	0.8758	38

Appendix 3 The monthly number of bird counts and water level at the East Kleinemonde estuary between March 1994 and March 1996.

Month	Number of counts	Water level
1994		
March	1	medium
April	0	medium
May	2	high
June	1	high
July	6	high
August	3	high
September	3	low
October	4	medium
November	5	medium
December	2	high
1995		
January	0	low
February	0	low
March	0	low
April	2	medium
May	2	medium
June	2	medium
July	3	high
August	4	high
September	4	high
October	5	high
November	3	high
December	2	high
1996		
January	4	high
February	2	high
March	1	high

Appendix 4 The length-mass relationships obtained from regression analyses by various authors for the marine-spawning species recorded in the East Kleinemonde estuary, (a = intercept, b = slope and n = number of specimens).

Species	a	b	r^2	n	Reference
Rhabdosargus holubi	0.00007	2.851	-	-	Blaber (1973b)
Lithognathus lithognathus					
< 120 mm SL	0.00001	3.122	-	-	Blaber (1973b)
>120 mm SL	0.00003	2.945	-	-	Blaber (1973b)
Sarpa salpa	0.000059	2.793	-	-	Joubert (1981)
Diplodus sargus capensis	0.000033	2.990	-	-	Joubert (1981)
Liza dumerilii	0.00002604	2.948	0.994	148	Harrison (1993)
Liza richardsonii	0.00003	2.931	0.989	27	unplubl. data
Liza tricuspidens	0.00001597	3.007	0.986	38	Harrison (1993)
Mugil cephalus	0.00002942	2.951	0.989	255	Harrison (1993)
Myxus capensis	0.00001577	3.038	0.992	753	Harrison (1993)
Monodactylus falciformis	0.0000329	3.050	0.987	20	Harrison (1993)
Lichia amia	0.00001491	3.054	0.998	18	Harrison (1993)
Pomadasys commersonnii	0.00001398	3.112	0.997	95	Harrison (1993)