BIOGEOGRAPHY AND COMMUNITY STRUCTURE OF FISHES IN SOUTH AFRICAN ESTUARIES

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ABSTRACT

The biogeography and community structure of the fishes of South African estuaries was investigated. In all, 109 systems were examined representing two broad types: temporarily closed and permanently open estuaries.

Multivariate analyses of the fish communities identified three biogeographic regions. A cool-temperate region extended along the west and southwest coasts; a warm-temperate zone stretched along the south, southeast and east coasts and a subtropical region occurred along the east coast. The boundaries of these biogeographic regions were also delineated.

The general physico-chemical characteristics of the estuaries within the three biogeographic regions also reflected regional differences in climate, rainfall and ocean conditions. Estuarine temperatures followed the trend for marine coastal waters, decreasing from subtropical estuaries toward cool-temperate systems. The low rainfall and runoff in the warm-temperate region together with high evaporation rates and strong seawater input resulted in higher salinities in these estuaries. These factors also accounted for the predominantly clearer waters in warm-temperate estuaries.

The estuaries in the three biogeographic regions were also shown to contain somewhat distinctive fish assemblages. Temperature and salinity appeared to be the two main factors affecting the distribution and abundance of fishes in South African estuaries. Subtropical systems were characterised by fishes mostly of tropical origin as well as certain south coast endemic species. Warm-temperate estuaries were dominated by endemic taxa with some tropical species also present. The fish fauna of cool-temperate estuaries mostly comprised south coast endemic species with cosmopolitan and temperate taxa also present.

Certain functional components of the ichthyofauna also exhibited slight differences between regions. Freshwater fishes were a major component of closed subtropical estuaries while estuarine resident species were more abundant in warm-temperate estuaries. Overall, estuarine-dependent marine species dominated the fish fauna of the estuaries in all biogeographic regions, signifying that South African estuaries perform a vital nursery function for this group of fishes. Slight differences were also apparent in the trophic structure of the fishes; these were related to environmental differences between regions. Zooplanktivores and fishes that feed on aquatic macrophytes/invertebrates assumed a relatively higher importance in warm-temperate systems. Overall, detritivores dominated the estuarine fish fauna in all regions, indicating that detritus forms the main energy source in South African estuaries.

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CONTENTS

CHAPTER 1
GENERAL INTRODUCTION

The Southern African coast spans a number of climatic zones from humid, predominantly summer rainfall conditions in the east and northeast, to a Mediterranean climate in the south and southwest, to arid conditions in the northwest (Tinley, 1985). This coastline is also intersected by numerous estuaries, which vary from large, permanently open systems to small water bodies that are only occasionally connected to the ocean (Heydorn, 1991). Estuarine environments and their associated ichthyofauna are not uniformly distributed along the South African coast; many estuarine fish species are confined to specific geographic regions, or even to estuaries within these regions (Whitfield, 1994a).

Research on South African estuarine fish communities has included a wide range of studies. A number of basic ecological surveys have been undertaken in several estuaries around the country (e.g. Branch & Grindley, 1979; Branch & Day, 1984; Plumstead *et al.*, 1985; 1989a; 1989b; 1991; Ter Morshuizen *et al.*, 1996a; Cowley & Whitfield, 2001) thus laying the foundations for more detailed single species studies. The seasonal abundance and distribution of fishes in selected estuaries has also been investigated (e.g. Marais & Baird, 1980; Marais, 1981; 1983a), with particular emphasis on the larger size classes of marine species found in these systems. Some studies (e.g. Marais, 1983b; Bennett, 1994; Ter Morshuizen *et al.*, 1996b) considered the effects of reduced river inflows and floods on estuarine fish communities. Several workers have studied the fish community structure in submerged macrophyte and salt marsh habitats within estuaries (e.g. Beckley, 1983; Hanekom & Baird, 1984; Whitfield *et al.*, 1989; Ter Morshuizen & Whitfield, 1994; Paterson & Whitfield, 1996), particularly the potential nursery role that these habitats perform. The fish communities in degraded or polluted estuaries have been examined (e.g. Blaber *et al.*, 1984; Ramm *et al.*, 1987) and the sources of these anthropogenic disturbances identified. A number of comparative studies have also been undertaken in various parts of the country (e.g. Begg, 1984a; Bennett, 1989a; Dundas, 1994; Whitfield *et al.*, 1994; Harrison & Whitfield, 1995; Vorwerk *et al.*, 2001), with particular emphasis on structural and functional differences between the different fish communities and estuary types.

While a great deal of estuarine fish research has been conducted across the South African region, each investigation has had its own specific focus with regards the estuaries investigated and the aims and objectives of each study. No dedicated studies have been undertaken that consider the southern African subcontinent in its entirety. Furthermore, in spite of the considerable amount of research that has taken place, scientific information on almost 70% of South Africa's estuaries is classified as poor or lacking altogether (Whitfield, 1995a; 2000).

Regional analyses of estuarine fish communities have been undertaken in other parts of the world such as Australia (e.g. Pease, 1999), Europe (e.g. Elliott & Dewailly, 1995), South and Central America (e.g. Viera & Musick, 1993; 1994) and the United States (e.g. Monaco *et al.*, 1992). These studies, however, have largely relied on limited field collections and/or existing data from other research.

Estuarine ecosystems are under ever-increasing pressure and demand from human growth and development; this includes activiries in both the catchment and in the adjacent marine environment. In order to manage these resources effectively, paticularly at a national (and global) level, an understanding of the biodiversity, and function of estuaries at a regional scale is required. Such regional studies require extensive data; this is lacking in both the South African context and internationally. Through the collection of a comprehensive set of data, this study aims to examine the role of South African estuaries at a regional scale and to explain geographic variations in fish biodiversity, community structure and function spanning the entire coastline. The data will also add considerably to the state of scientific information on South African estuaries.

The main objectives are to 1) describe and delineate zoogeographic patterns of ichthyofaunal assemblages; 2) explain and compare the physico-chemical attributes of the estuaries along the coast; 3) describe and contrast estuarine fish compositions in relation to abiotic factors along the coast; 4) describe and evaluate functional aspects of the fish communities along the coast.

Key climatic and marine characteristics of the South African coastal environment are presented in Chapter 2. In Chapter 3, the general field sampling approach and analyses are described. A zoogeographic analysis of the estuarine fish communities along the South African coast is presented in Chapter 4, and in Chapter 5, various physico-chemical parameters of the estuaries within each biogeographic region are described and compared. The fish species composition of the estuaries within the zoogeographic regions are described and compared in Chapter 6, with relationships between key taxa and abiotic parameters also being examined. Functional aspects of the fish communities in each biogeographic region are presented in Chapters 7 and 8, primarily an estuary-association analysis of the ichthyofauna within each region in Chapter 7 and an analysis of the trophic composition of fish communities in Chapter 8. Finally, key findings are synthesised in Chapter 9.

CHAPTER 2
STUDY AREA

The South African coastline stretches for some 3400 km from the Orange River mouth (28° 38'S; 16° 27'E) on the west (Atlantic Ocean) coast to Kosi Bay (26° 54'S; 32° 48'E) on the east (Indian Ocean) coast (Figure 2.1). Over 400 outlets intersect this coastline (Allanson *et al*., 1999); some rivers and streams flow over a series of rapids before entering the sea, other systems are represented by dry riverbeds for most of each year, and yet others plunge over a waterfall directly into the sea. In a South African context, Day (1980) defined an estuary as 'a partially enclosed coastal body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixture of sea water with fresh water derived from land drainage'. Since estuaries are characterised by both riverine and marine processes, the above systems cannot be classified as estuaries according to the definition of Day (1980) but there are at least 250 other South African outlets to the sea that do fulfil the criteria for a fully functional estuary.

2.1 CLIMATE AND RAINFALL

The KwaZulu-Natal coast, from Kosi Bay to Port Edward, has a warm and humid climate and is one of the best-watered regions of South Africa (Schulze, 1984). The average annual rainfall exceeds 1000 mm, most of which falls in summer (October-March), with a peak occurring from February to March (Day, 1981a; Schulze, 1984). Average daily air temperatures vary from 19-28 °C in summer to 9-22 °C in winter (Schulze, 1984). The Eastern Cape region, from Port Edward to the Great Kei River has a temperate to warm and humid climate. This region also receives predominantly summer rainfall, which reaches a maximum in March; rainfall varies from about 800 to 1250 mm per annum (Heydorn & Tinley, 1980; Day, 1981a). Average daily air temperatures in this region range from 17-28 °C in January to 8-21 °C in July (Schulze, 1984). From East London to Cape Agulhas, rainfall decreases to approximately 500 mm per year and occurs almost equally in all seasons although slightly higher rainfall occurs during autumn (March) and spring (October/November) (Heydorn & Tinley, 1980; Schulze, 1984). The Tsitsikamma sector (west of Port Elizabeth) comprises a discrete sub-region and experiences good year-round rainfall of between 700 and 1000 mm per annum. Average daily air temperatures in this south coast region range from 15-26 °C in summer to 7-19 °C in winter (Schulze, 1984). The southwest Cape, from Cape Agulhas to Cape Columbine, has a Mediterranean climate with cool, wet winters and hot, dry summers (Schulze, 1984; Tinley, 1985). Most rainfall falls from May to September and is usually between 400 and 700 mm per year (Heydorn & Tinley, 1980; Day, 1981a). Average daily air temperatures in the region range between 15-28 °C in summer and 6-17 °C in winter (Schulze, 1984). The west coast of South Africa, north of Cape Columbine, has an arid climate and receives less than 300 mm rainfall per year (Heydorn & Tinley, 1980; Day, 1981a). When rain does fall, it occurs mostly in winter (Tinley, 1985). The average daily temperatures in the region range between 17-35 °C in January to 3-18 °C in July (Schulze, 1984).

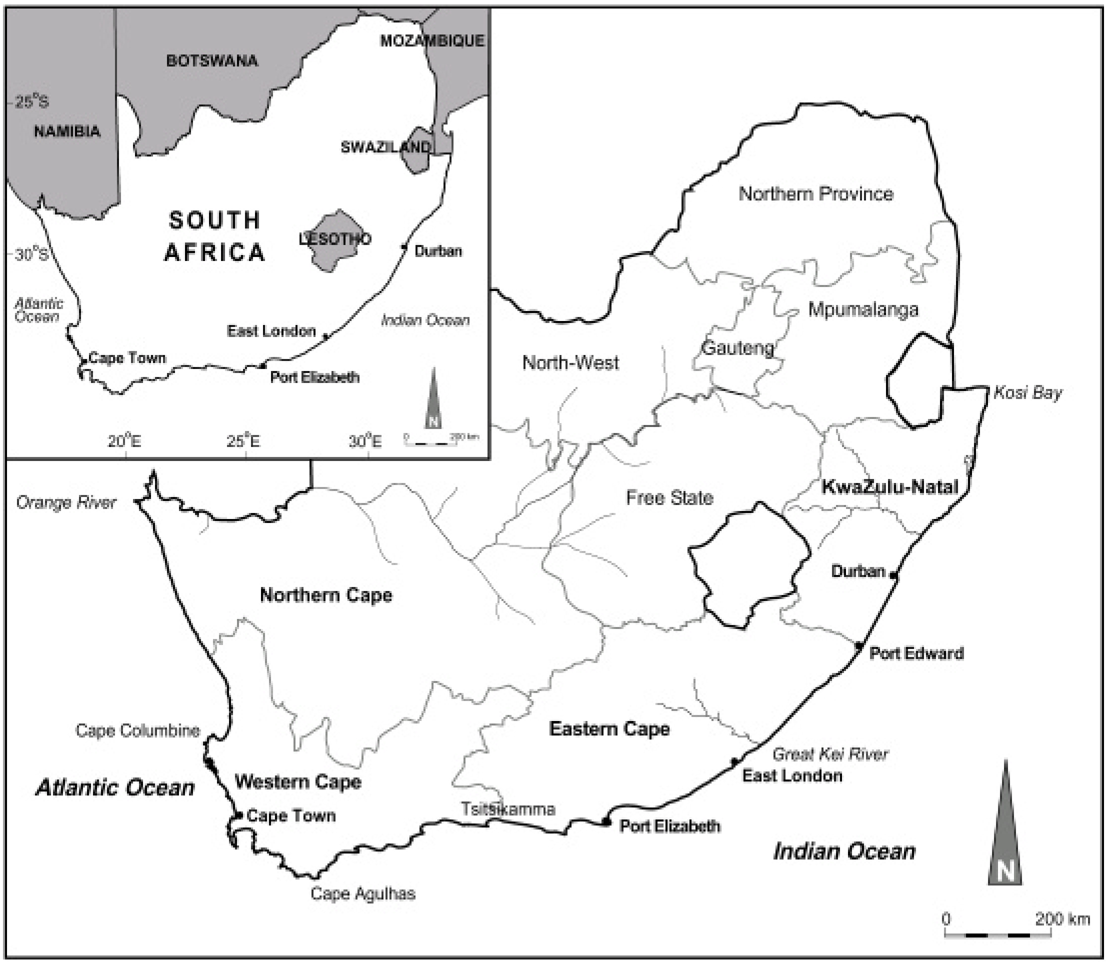


Figure 2.1. Map of South Africa indicating place names mentioned in the text.

2.2 OCEAN CURRENTS

The coastal waters of southern Africa are influenced by two major current systems (Figure 2.2).

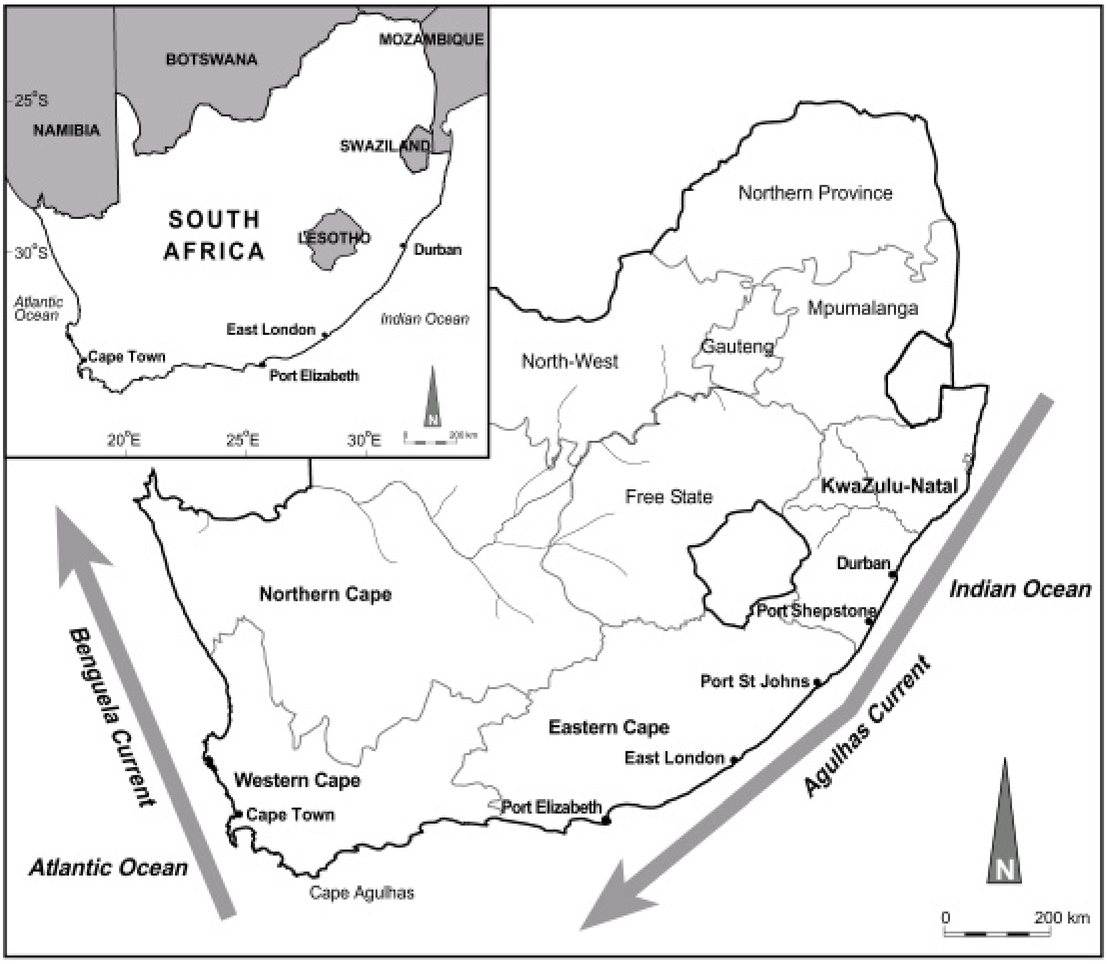


Figure 2.2. Major ocean currents off the coast of South Africa.

The east coast, which borders the Indian Ocean, is influenced by the south-flowing Agulhas Current. In general, the Agulhas Current follows the edge of the continental shelf. Off northern KwaZulu-Natal, the continental shelf is narrow and the current flows a few kilometres off the shore. North of Durban, the shelf widens to 45 km and as a result, the current tends to move offshore and flow more slowly (Shannon, 1989). Between Port Shepstone and East London, the shelf again narrows and the current flows close to the shore. Near East London the current slowly progresses seawards as the shelf broadens toward Port Elizabeth. When it reaches the southern limit of the Agulhas Bank, the main body of the current turns backward and then flows eastwards and northwards as the Agulhas Return Current (Shannon, 1989). Being tropical in origin, the waters of the Agulhas Current are relatively warm, however, as this water flows south it tends to cool. Inshore temperatures north of Port St Johns in the Eastern Cape normally vary seasonally between 18 and 25 °C and seldom fall below 16 °C (Day, 1981b). Average summer and winter sea temperatures off Durban (KwaZulu-Natal) range between 24 and 19 °C (Whitfield, 1998). Further to the south where upwelling may occur (Shannon, 1989; Lutjeharms *et al*., 2000), temperatures are lower and more variable. Between East London and Cape Agulhas inshore temperatures vary between 11 and 25 °C (Day, 1981b). Mean summer and winter sea temperatures off Port Elizabeth vary between 16 and 22 °C (Whitfield, 1998).

The west (Atlantic) coast is influenced by the cold, north-flowing Benguela Current of upwelled inshore waters (Tinley, 1985; Shannon, 1989). The surface water temperatures of the Benguela system average between 13 and 15 °C with a pronounced upwelling 'season' during the summer (September - March) (Shannon, 1989).

CHAPTER 3

GENERAL MATERIALS & METHODS

3.1 FIELD METHODS

3.1.1 Ichthyofauna

The ichthyofauna of some 250 coastal outlets between the Orange River and Kosi Bay were sampled over the period 1993 to 1999. Using information contained in Begg (1978), Heydorn & Tinley (1980) and Whitfield (1995a), the coastline was divided into arbitrary sections, each containing approximately 40 estuaries (Figure 3.1). This grouping was based on the number of systems that could be adequately surveyed within each annual sampling period.

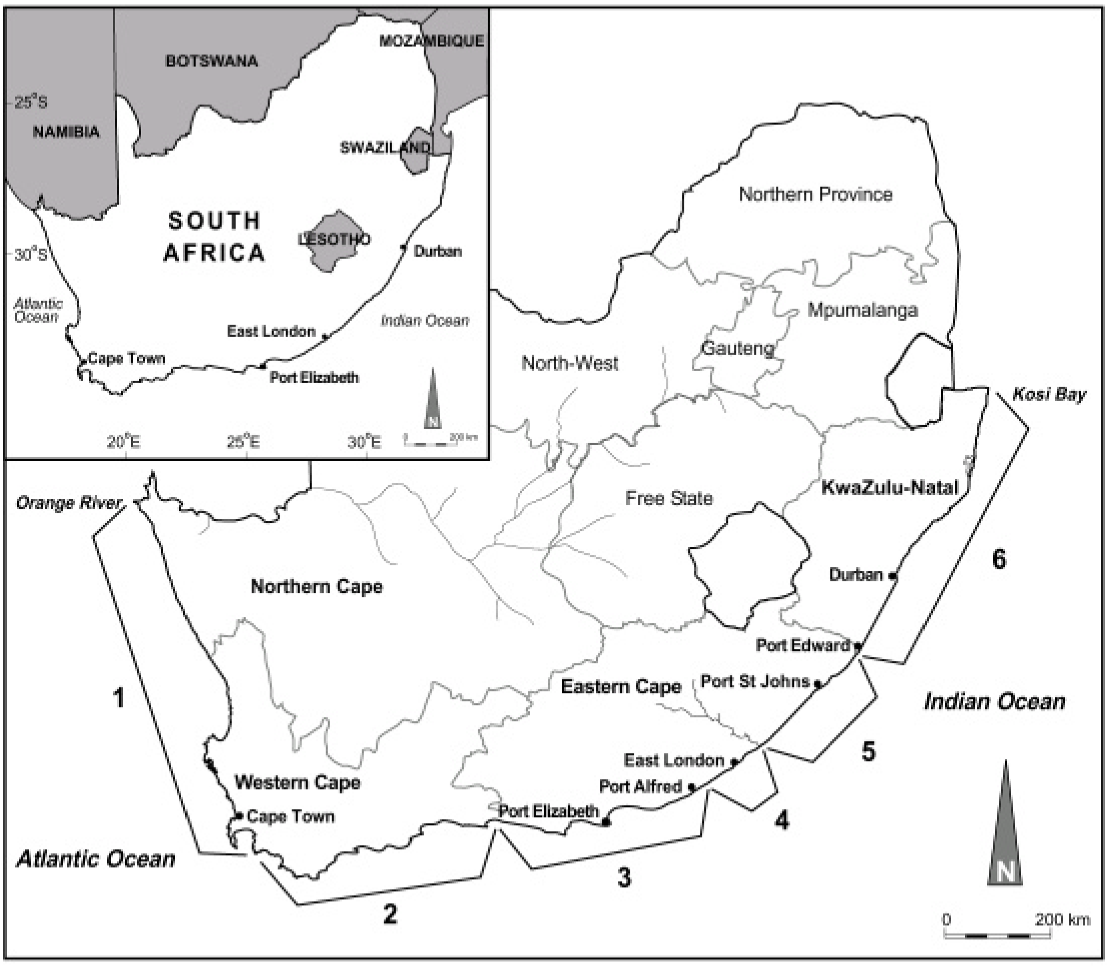


Figure 3.1. Map of South Africa showing the division of the coastline into six sampling sectors.

The estuaries in each section of coast were sampled during the spring/summer period and a new section was sampled each year until the entire coastline was covered (Table 3.1).

Table 3.1. Ichthyofaunal field sampling program for South African estuaries.

Section	Number of systems	Sampling period
1) Northern/Western Cape (Orange River - Buffels (Oos))	44	September - November 1993
2) Western Cape (Palmiet - Sout)	36	September - November 1994
3) Eastern Cape (Groot (Wes) - Great Fish)	43	September - November 1995
4) Eastern Cape (Old Woman's - Great Kei)	44	September - November 1996
5) Eastern Cape (Transkei) (Gxara - Mtentwana)	43	October 1997 - February 1998
6) KwaZulu-Natal (Mtamvuna - Kosi Bay)	47	October 1998 - March 1999

Studies of fish communities depend on equipment and methods that provide a representative sample of the community as a whole. Most techniques for sampling fishes, however, are selective, especially with respect to species and size of individuals, and can result in a catch that is not representative of the population as a whole (Lagler, 1971).

A comparison of the effectiveness of various sampling methods, namely a 1 metre beam trawl, a 2 metre otter trawl, a 30 m seine net, and gill nets made of panels of different mesh sizes, in three small estuaries revealed that each sampling technique varied in the number, biomass, and range of species collected (Harrison & Whitfield, 1995). Overall, trawling, which samples bottom fishes and fishes of limited mobility, appeared to be the least effective sampling method. Seine netting, which is effective in sampling small fishes that inhabit shallow waters, captured the most specimens and the greatest variety of species. This method is not suitable for catching larger, faster swimming fish typically found in deeper waters but gill nets are effective in sampling this group (Harrison & Whitfield, 1995).

The different methods required for sampling shallow and deep waters makes it difficult to obtain catches in which the relative species composition can be regarded as entirely representative of an estuary (Potter *et al.*, 1990). In an attempt to obtain as representative a sample of the overall fish community in each estuary, two sampling methods were employed during this study.

The ichthyofauna of each estuary was sampled using a 30 m x 1.7 m x 15 mm bar mesh seine net fitted with a 5 mm bar mesh purse and, where possible, a fleet of gill nets. Each gill net had a range of mesh sizes and comprised three 45 mm, 75 mm and 100 mm stretch mesh monofilament panels and were either 10 m or 20 m in length and 1.7 m deep.

Seine netting was carried out during daylight hours and was limited to shallow (<1.5 m deep), unobstructed areas with gently sloping banks. Gill netting was generally carried out in deep (>1 m) open, mid-channel waters with the nets being deployed in the evening (18h00-19h00) and lifted the following morning (06h00-07h00). In most cases, only the larger, deeper systems were sampled with gill nets. The sampling effort undertaken in each estuary varied depending on the size of the system, and usually took one to three days to complete. Sampling was carried out until no new species were collected or until all habitats within each estuary had been sampled.

Specimens collected by seine netting were, where possible, identified in the field, measured to the nearest mm standard length (SL) and returned alive to the system. At least 25 specimens of the abundant species as well as those specimens that could not be identified in the field were placed in labelled plastic bags and preserved in 4% formaldehyde for transport to the laboratory. Specimens collected in the gill nets were identified, measured (mm SL) and weighed (g wet mass). Specimens that could not be identified in the field were placed in labelled plastic bags and preserved in 4% formaldehyde for later processing in the laboratory.

3.1.2 Physico-chemical

Selected physico-chemical parameters were measured at various sites within each system during each survey. Depending on the size of each estuary, the number of physico-chemical sampling sites varied but generally included the lower, middle and upper reaches of each system. Water depth and transparency was measured using a 20 cm diameter Secchi disc attached to a weighted shot line graduated at 10 cm intervals. Temperature (˚C), salinity (‰), dissolved oxygen (mg l^{-1}) and turbidity (NTU) was recorded using a Horiba U-10 Water Quality Checker. Where water depth permitted, both surface and bottom waters were measured. The mouth condition of each system at the time of sampling was also noted.

3.2 LABORATORY METHODS

In the laboratory, preserved specimens were identified by reference to Smith & Heemstra (1995) and Skelton (1993). At least 25 specimens of the abundant species were measured (mm SL) and weighed to the nearest 0.01g; the remaining specimens were counted and batch weighed. Voucher specimens were also sent to the J.L.B. Smith Institute of Ichthyology, Grahamstown for verification.

3.3 DATA ANALYSES

3.3.1 Estuary classification

The occurrence and diversity of fishes in South African estuaries essentially varies according to two broad parameters: latitude (biogeography) and the individual characteristics of each estuary (estuary type) (Blaber, 1985). In order to account for the effect of the latter, representative estuaries were selected according to a broad agreement between two physical/morphological classification schemes.

Harrison *et al.* (2000) classified South Africa's estuaries into six categories based on the main forms of morphological variability among these systems along the coast. These were:

- open non-barred estuaries
- predominantly open small estuaries (mean annual runoff (MAR) <15 x 10^6 m^3)
- predominantly open moderate to large estuaries (MAR >15 x 10^6 m^3)
- predominantly closed small estuaries (surface area <2 Ha)
- predominantly closed moderately sized estuaries (surface area 2-150 Ha)
- predominantly closed large estuaries (surface area >150 Ha)

Whitfield (1992; 2000) identified and classified South Africa's estuaries into five broad types based on a combination of physiography, hydrography and salinity:

- permanently open estuaries
- temporarily open/closed estuaries
- estuarine lakes
- estuarine bays
- river mouths

Representative estuaries were then selected according to a broad agreement between both classification schemes. This was to ensure that similar estuarine types were compared on a regional basis. The classification of the 251 estuaries sampled during this survey is presented in Appendix 1. These results are summarised in Table 3.2.

According to Harrison *et al*. (2000), 44 systems (18%) were not considered estuaries on the basis of their very small size, regular dry or hypersaline conditions, extensive human modification or almost permanent isolation from the sea. Eleven systems (4%) were classified as open non-barred estuaries, 34 (14%) were small open estuaries and 62 (25%) were large open systems. Twenty-seven estuaries (11%) were classified as small closed systems, 71 (28%) were moderately sized closed estuaries, and only two (1%) were large closed systems. From Whitfield (2000), 51 (20%) of the systems were not considered estuaries either due to a loss of function or due to their extremely small size. Forty-five systems (18%) were classified as permanently open estuaries, 134 (53%) were temporarily open/closed estuaries, 12 (5%) were river mouths, eight (3%) were estuarine lakes and one was an estuarine bay (Table 3.2).

Table 3.2. Comparison of classification of South African estuaries after Harrison *et al.* (2000) and Whitfield (2000).

	Whitfield (2000)						
Harrison *et al.* (2000)	Non-estuary	Permanently open	Temporarily open/closed	River mouth	Estuarine lake	Estuarine bay	**Total**
Non-estuary	42	-	2	-	-	-	**44**
Open, non-barred	-	3	2	6	-	-	**11**
Open, small	2	-	31	-	1	-	**34**
Open, large	-	42	11	5	3	1	**62**
Closed, small	5	-	21	1	-	-	**27**
Closed, medium	2	-	67	-	2	-	**71**
Closed, large	-	-	-	-	2	-	**2**
Total	**51**	**45**	**134**	**12**	**8**	**1**	**251**

Based on a comparison between the two classification schemes, 109 estuaries were selected for further analysis. These were divided into two basic types namely 'open' estuaries and 'closed' estuaries. Forty-two systems were open estuaries and comprised representatives of permanently open estuaries (Whitfield, 2000) and large open estuaries (Harrison *et al.*, 2000). Sixty-seven estuaries were closed systems representing temporarily open/closed estuaries (Whitfield, 2000) and medium closed estuaries (Harrison *et al.*, 2000) (Table 3.2). The remaining systems were excluded from further analysis.

3.3.2 Sampling effort

The sampling effort undertaken in each estuary varied depending on the size of the system, and usually took one to three days to complete. A summary of the sampling effort (as number of seine net hauls and the metres of gill net set) in the selected estuaries is provided in Appendix 2.

Sampling in each estuary was carried out until no new species were collected or until all habitats within each system had been sampled. An example of the relationship between sampling effort and the number of taxa captured in representative closed and open estuaries from each coastal sector are given in Figures 3.2 and 3.3.

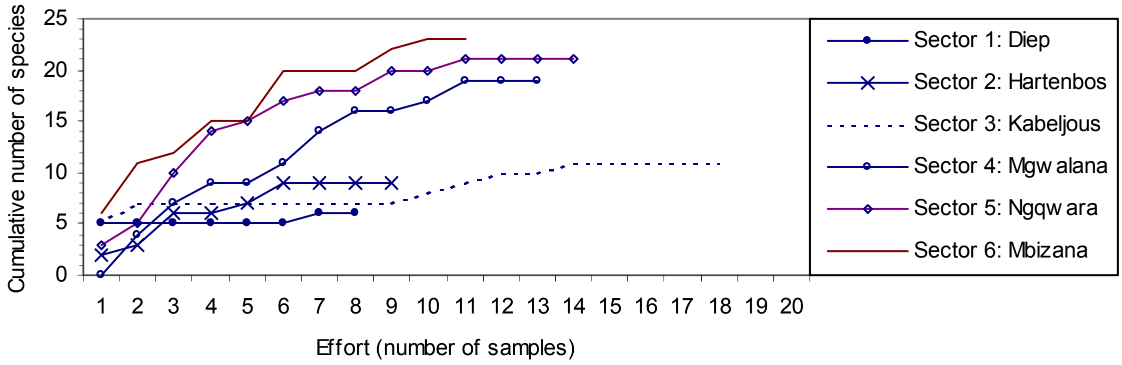


Figure 3.2. Relationship between sampling effort (seine netting and gill nets) and number of species captured in representative closed estuaries from each coastal sector.

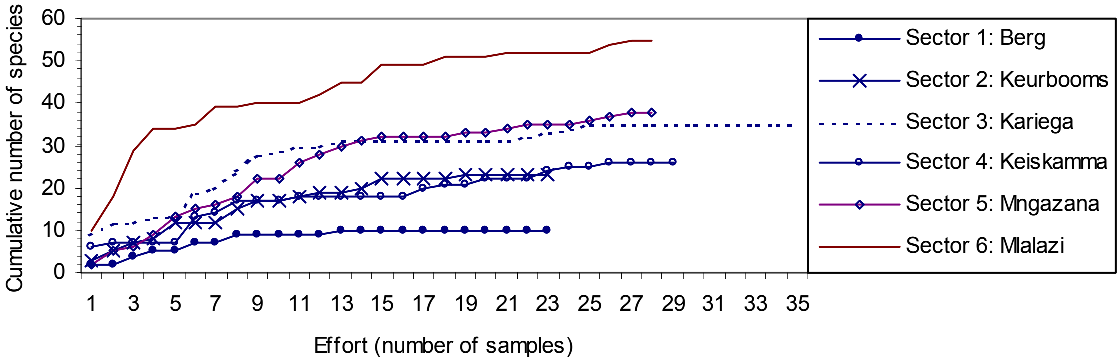


Figure 3.3. Relationship between sampling effort (seine netting and gill nets) and number of species captured in representative open estuaries from each coastal sector.

3.3.3 Ichthyofauna

Only taxa that were identified to species level were considered for further investigation. All alien species were also omitted from the analysis while translocated indigenous taxa (e.g. *Oreochromis mossambicus*) were adjusted by removing occurrences outside their natural range. An initial analysis of the inclusion/exclusion of this group revealed that they contributed very little to the overall abundance or biomass of the fish community in the estuaries (generally <0.1%).

The total species composition, both by number and by mass, of the fish community within each system was established. The relative biomass contribution of each species was calculated using actual recorded masses and masses derived from length-weight relationships presented in Harrison (2001).

Although the sampling strategy adopted during this study was designed to capture all available taxa that were susceptible to the gear used, the sampling effort within each estuary varied somewhat. To ensure that the fish communities of the various estuaries were comparable, all the data was standardised by computing the relative (%) abundance/biomass of each species within each estuary. Such standardisation is essential if the sampling effort in each estuary was different as was the case during this study (Clarke & Warwick, 1994).

CHAPTER 4
BIOGEOGRAPHY

4.1 INTRODUCTION

The approximately 3400 km South African coastal zone, from the Orange River in the west to Kosi Bay in the east (Figure 4.1) covers a wide range of climatic and oceanic conditions and as such, supports a great diversity of plants and animals. The coast of South Africa, including estuaries, encompasses at least three distinct biogeographic regions, namely a subtropical, warm temperate and cool temperate zone.

Stephenson & Stephenson (1972) examined the distribution of rocky-shore biota and identified three biogeographic provinces: a subtropical East Coast Province from Mozambique to approximately Port St Johns (characterised by warm-water species); a warm-temperate South Coast Province from Port St Johns southward to approximately Cape Point (comprising mainly cooler water species); and a West Coast Province from Cape Point up the west (Atlantic) coast (characterised by cold water forms).

Brown & Jarman (1978) regarded the east coast of southern Africa from 31°S (approximately Port Edward) northwards to 26°S as subtropical; the warm-temperate region was suggested as extending from 31°S on the east coast southward and westwards at least to Cape Point; whilst the cold-temperate (or Namaqua) West Coast Province extended from Cape Point to beyond Walvis Bay (Namibia).

Emanuel *et al*. (1992), on the basis of an analysis of marine invertebrates, divided the South African coast into three zoogeographic regions: a cool-temperate Namaqua Province from Lüderitz (Namibia) to Cape Point; a warm-temperate Agulhas Province from Cape Point eastward to East London; and a subtropical Natal Province from East London north to Mozambique. This latter region was subdivided into two sub-provinces, one from Durban southward and the other from Durban northward.

Analyses of rocky shore biota also yielded three biogeographic groupings (Bustamante, 1994): the west coast Namaqua Province between Lüderitz and Cape

Columbine; a south coast Agulhas Province from Cape Infanta to approximately the Mbashe River; and an east coast Natal Province from Ballito Bay (just north of Durban) to Inhaca Island in Mozambique.

Analyses of intertidal fishes yielded four major biogeographic regions (Prochazka, 1994): a Namaqua Province, extending from Lüderitz at least to Koppie Alleen (just east of Cape Agulhas); the warm-temperate Agulhas Province between Tsitsikamma and Port Alfred; and two east-coast Natal Provinces, one from Pennington (just south of Durban) to Durban and the other from Durban northward to Kosi Bay.

From the distribution and ordination of shelf-associated marine fish species, Turpie *et al.* (2000) identified three biogeographic regions: a cool-temperate region along the west coast from the Orange River to Cape Point; a warm-temperate region from Cape Point to approximately Port Edward; and a subtropical region from Port Edward north to Kosi Bay.

Day *et al*. (1981) also identified three faunistic provinces based on estuarine fishes: a subtropical region, characterised by high numbers of tropical taxa, from southern Mozambique as far as the Great Kei River; a warm-temperate zone from the Great Kei to False Bay (near Cape Point); and a cold-temperate region from Cape Point northward along the west (Atlantic) coast.

Whitfield (1994a) suggested that the cold-temperate region be referred to as cool-temperate since estuarine water temperatures in this zone are always above 10 °C. He also suggested that the division between the subtropical and warm-temperate regions be placed at the Mbashe estuary. This boundary coincides with the presence of a strong, inshore subsurface temperature front, which maintains a fixed location in the vicinity of the Mbashe system (Beckley & van Ballegooyen, 1992).

In terms of freshwater fishes, a west coast region, characterised by a temperate (Karroid) fauna was found to extend from the Orange River to approximately Cape Columbine, while a temperate endemic (Cape) fauna occurred from Cape Columbine to approximately Port Elizabeth (Skelton, 1993). From Port Elizabeth to the Tugela

River the fauna comprises a mixture of tropical (Zambezian) and temperate (Karroid) species. A tropical Zambezian fauna extends from the Tugela River northwards.

Based on fish, aquatic invertebrates and riparian vegetation, Eekhout *et al*. (1997) identified ten biogeographic regions for South African rivers. The coastal region from the Orange River south to the Olifants River comprised the Arid Interior; the catchments of the Olifants River system (to Cape Columbine) comprised the Namaqua Capensis region while the coastal section from Cape Columbine to Plettenberg Bay fell within the Capensis region. The Eastern Seaboard extended from Plettenberg Bay to the Mzimkulu River and the Sub-tropical East Coast region occurred from the Mzimkulu River northwards.

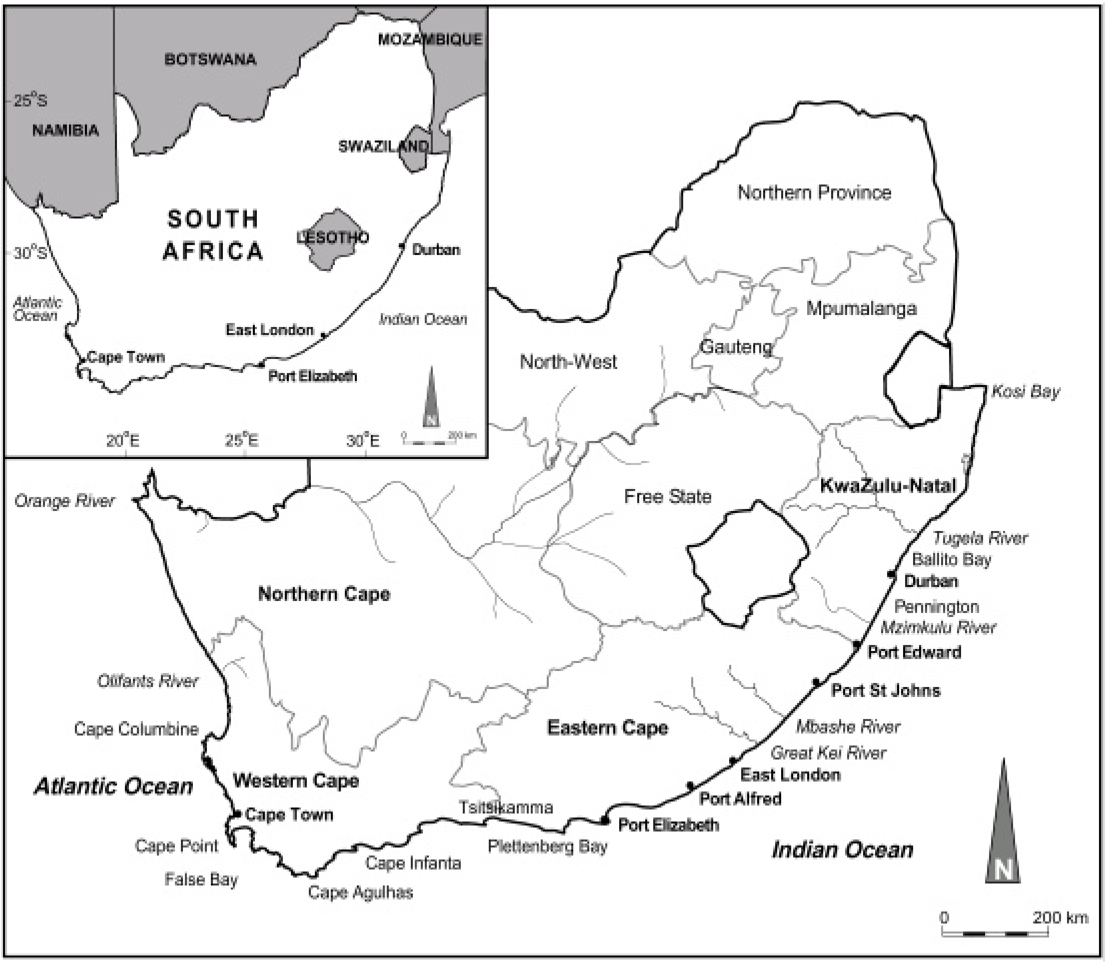


Figure 4.1. Locality map of South Africa indicating place names mentioned in the text.

Although there appears to be a broad agreement that the South African coast covers at least three biogeographical regions, there is still some question regarding the boundaries of these faunistic provinces (Figure 4.2). Furthermore, many of the studies outlined above have relied on a combination of limited field collections, historical data, and existing distribution records. The aim of this chapter is to examine whether estuarine fish communities collected during this study conform to current zoogeographic provinces identified for the coastal environment and to delineate the boundaries between these zones.

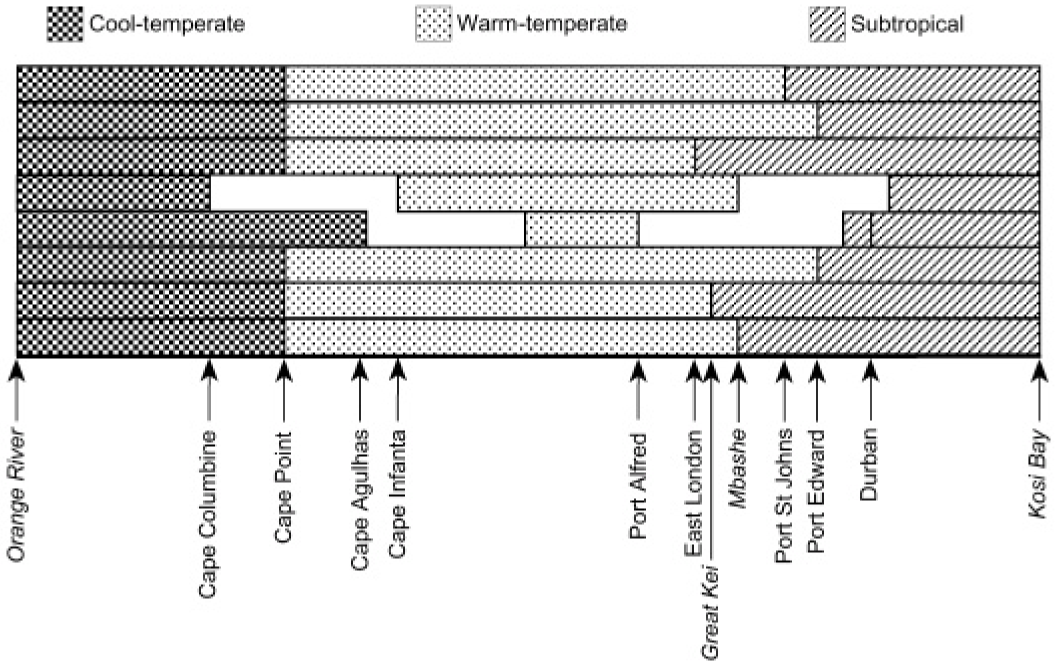


Figure 4.2. Summary diagram indicating South African marine biogeographic provinces after: (a) Stephenson & Stephenson (1972); (b) Brown & Jarman (1978); (c) Emanuel *et al*. (1992); (d) Bustamante (1994); (e) Prochazka (1994); (f) Turpie *et al*. (2000); (g) Day *et al*. (1981); (h) Whitfield (1994a).

4.2 MATERIALS & METHODS

4.2.1 Species richness and distribution

In each of the selected estuaries, the taxa were grouped into one of the following four categories based on their origin and distribution:

- Tropical species: Tropical Indian Ocean and Indo-Pacific species.
- Temperate species: Temperate East Atlantic species.
- Endemic species: Species with a distribution limited to southern Africa (south of 20° S).
- Cosmopolitan species: Species with a worldwide distribution.

Information on species origin and distribution was derived from Smith (1950), Wallace (1975a), Day *et al.* (1981), van der Elst (1988), Potter *et al.* (1990), Skelton (1993), Smith & Heemstra (1995) and Whitfield (1998), as well as data from this study. The classification of the origin (tropical, temperate, endemic, cosmopolitan) of the species captured during this study is presented in Appendix 3.

The total number of species and relative (%) contribution of each category to the ichthyofauna of each estuary was then calculated in terms of number of taxa, abundance and biomass.

4.2.2 Multivariate analyses

The fish catches from selected estuaries were also subject to multivariate statistical analyses using the Plymouth Routines in Multivariate Ecological Research package (PRIMER) (Clarke & Warwick, 1994). Multivariate methods compare two (or more) samples on the extent to which they share particular species, at comparable levels of abundance. Multivariate techniques are founded on similarity coefficients calculated between every pair of samples which then facilitates a classification or clustering of samples into groups which are similar, or an ordination plot in which the samples are ‘mapped’ (in two or more dimensions) in such a way that the distances between pairs of samples reflect their relative similarity of species composition (Clarke & Warwick, 1994).

The similarity coefficient used in this analysis is the Bray-Curtis (IS_{BC}) measure:

$$IS_{BC} = \frac{2c}{A+B}$$

Where c is the sum of the smaller (abundance/biomass) values of the species common to two samples; A is the sum of the (abundance/biomass) values of all the species in the one sample, and B is the sum of the (abundance/biomass) values of all the species in the other sample. The reason why only the smaller values of the common species are used is because only the smaller value is contained in or is common to both samples (Mueller-Dombois & Ellenberg, 1974). The Bray-Curtis measure takes all the species in a sample into consideration but has the advantage in that it is not affected by joint absences of species (Field *et al.*, 1982).

Hierarchical agglomerative clustering is a classification method which results in the production of a dendrogram in which samples are clustered into distinct groups based on their similarities, although the cut-off levels are arbitrary and depend upon convenience (Field *et al.*, 1982). Dendrograms, however, have a number of disadvantages and in view of this, it is advisable to employ an additional method of presentation to show individual relationships. If the two complimentary methods agree, then discontinuities can be accepted as real (Field *et al.*, 1982).

Non-metric multi-dimensional scaling (MDS) produces a two-dimensional graphical representation or 'map' of the similarity relationships between samples. The distance between two samples on the ordination plot is a reflection of the similarity between those two samples (Field *et al.*, 1982). The 'goodness-of-fit' of the resultant scatter plot is measured by the stress formula. If the stress value is large, the 'map' tallies poorly with the observed dissimilarities while a low stress value indicates that the sample relationship is well represented by the 'map' (Field *et al.*, 1982). Clarke & Warwick (1994) suggest that a stress of approximately 0.1 or less allows for fairly confident interpretation of the ordination plot. Although a stress of less that 0.2 still gives a potentially useful two-dimensional picture, a crosscheck of any conclusions should be made against those from an alternative technique (Clarke & Warwick, 1994).

In this study, the data were analysed using a combination of hierarchical agglomerative clustering and non-metric multi-dimensional scaling (MDS). Before calculating the Bray-Curtis similarity coefficient, the standardised data (% abundance/biomass) was 4th root transformed, which has the effect of scaling down the importance of abundant species so that they do not swamp the other data (Field *et al.*, 1982; Clarke & Warwick, 1994). The data for each group of estuary types was then analysed using a combination of hierarchical agglomerative clustering and non-metric multi-dimensional scaling (MDS).

For the results of the multivariate analyses, the estuaries were labelled according to their geographic position where: W = west coast from the Orange River to Cape Columbine; SW = southwest coast from Cape Columbine to Cape Agulhas; S = south coast from Cape Agulhas to Cape Padrone; SE = southeast coast from Cape Padrone to, and including the Great Kei estuary; E = east coast between the Great Kei and Mtamvuna estuaries; and NE = northeast coast from, and including the Mtamvuna estuary to Kosi Bay (Figures 4.3 and 4.4).

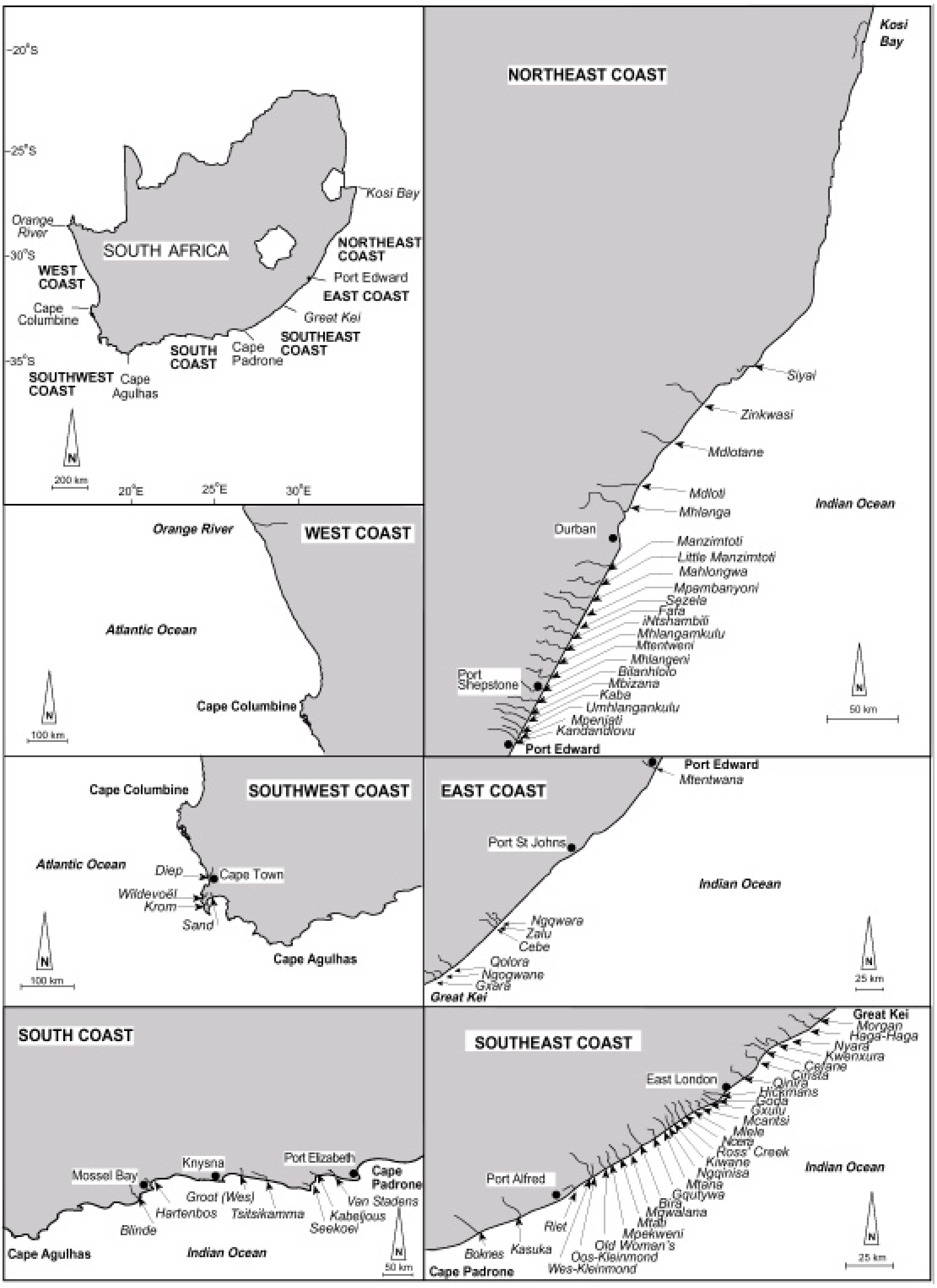


Figure 4.3. The South African coastline divided into the west, southwest, south, southeast, east, and northeast coasts. The relative positions of the closed estuaries included in the study are indicated with arrows.

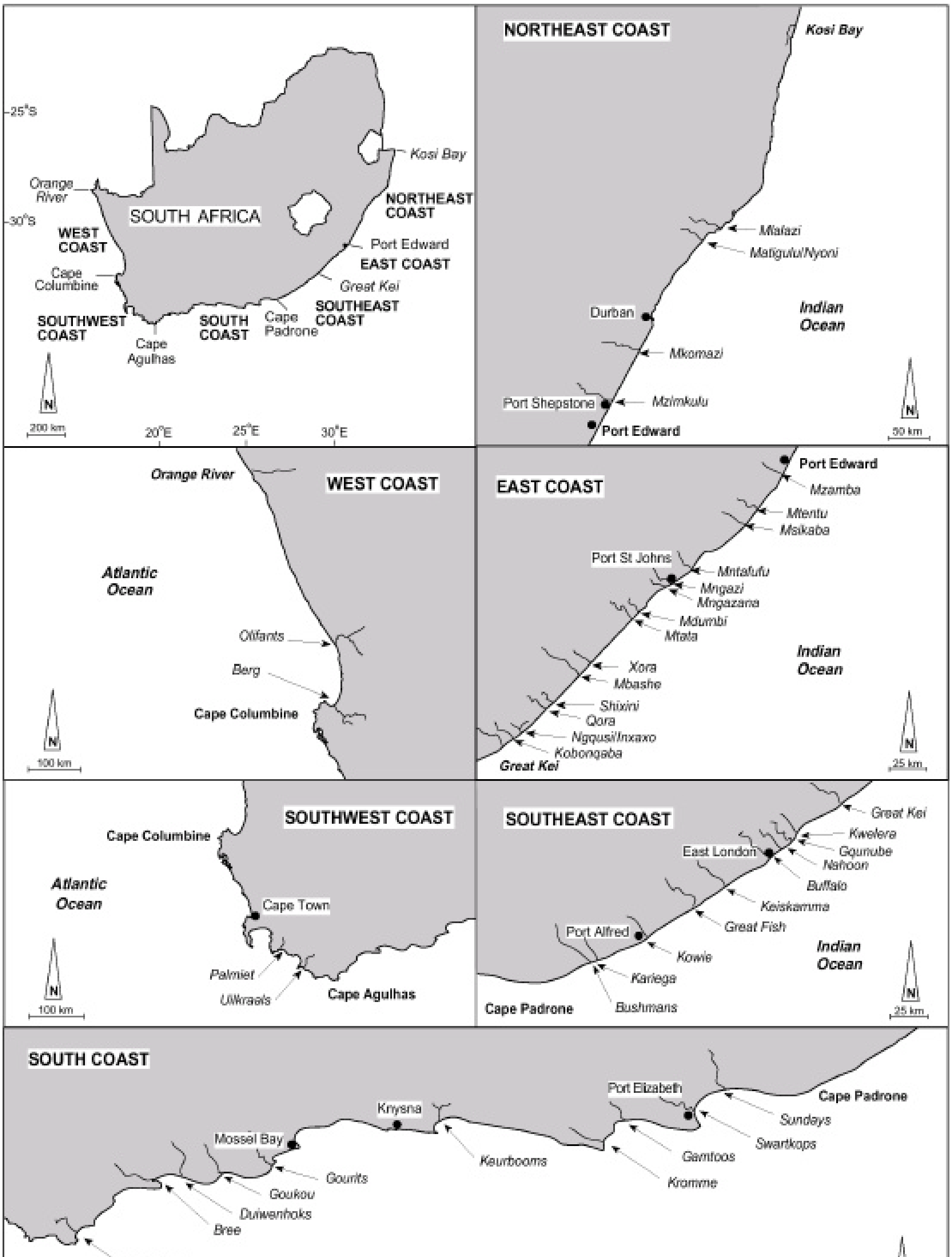


Figure 4.4. The South African coastline divided into the west, southwest, south, southeast, east, and northeast coasts. The relative positions of the open estuaries included in this study are indicated with arrows.

4.3 RESULTS

4.3.1 Species richness and distribution

4.3.1.1 Closed estuaries

The number of taxa captured in the closed estuaries ranged between 1 and 31 (Figure 4.5). The highest numbers were reported in the Zinkwasi and Qolora estuaries on the northeast and east coasts respectively. Low values were recorded in the Krom, Wildevoël and Diep systems on the southwest coast.

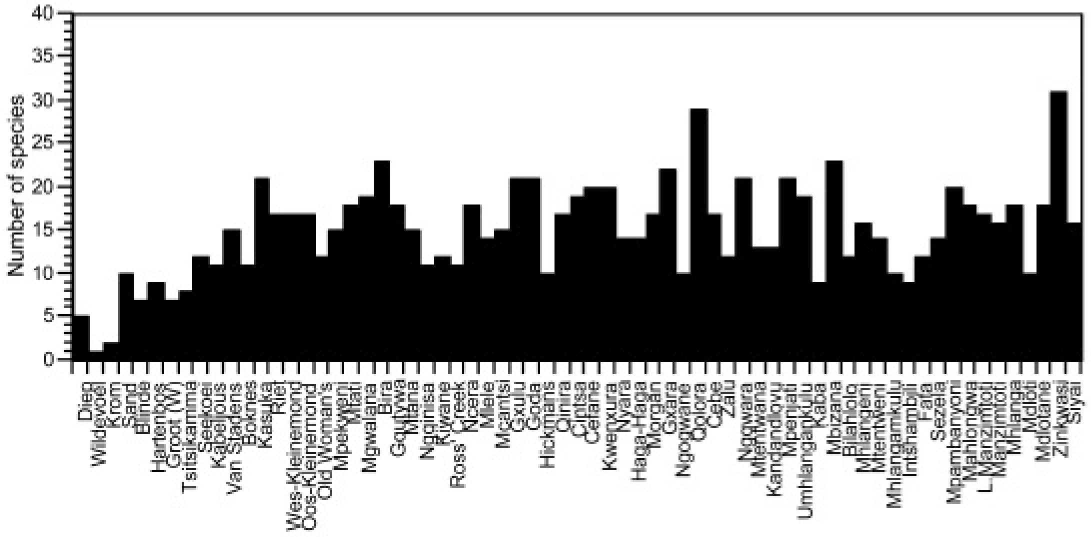


Figure 4.5. Number of fish species recorded in closed estuaries during this study.

The proportion of tropical species declined from the northeast coast toward the southwest coast with a distinct decrease occurring between the Kandandlovu estuary (on the northeast coast) and the Mtentwana system (on the east coast) (Figure 4.6a). North of the Kandandlovu, the proportion of tropical species generally exceeded 50% while from the Mtentwana south, this group usually did not comprise more than 40% of the taxa. No tropical species were recorded beyond the Hartenbos estuary (on the south coast). The proportion of endemic species decreased from the southwest coast toward the northeast coast. A marked decrease was also reported between the Mtentwana and Kandandlovu estuaries. North of the Kandandlovu this group of fishes did not comprise more than 45% of the taxa while from south of the Mtentwana, they generally constituted more than 60% of the species. The proportion of temperate species showed a similar trend, decreasing from the southwest coast toward the northeast coast, although they generally did not comprise more than 10% of the taxa. No temperate species were recorded beyond the Ngwara estuary, on the east coast. The proportion of cosmopolitan species was also low and generally did not comprise more than 10% of the taxa throughout (Figure 4.6a).

In terms of abundance, the contribution of tropical species declined rapidly from 90 % at the Siyai estuary (on the northeast coast) to just over 10% at the Mtentwana (Figure 4.6b). Endemic species dominated the catch of most of the estuaries throughout the study area and south of the Mtentwana this group generally comprised over 90% of the catch. Apart from the Ncera estuary, on the southeast coast, temperate species did not contribute more than 1% to the catch throughout the study area. The contribution of cosmopolitan species was also generally low but appeared to increase from the Nyara estuary (on the southeast coast) northwards (Figure 4.6b).

Tropical species dominated the biomass composition of estuaries north of the Mtentwana and generally accounted for over 50% of the catch (Figure 4.6c). South of the Mtentwana, this component typically accounted for less that 30% of the species mass although there was an increase in the relative contribution between the Mtana and Kasuka estuaries on the southeast coast. Endemic species generally comprised more than 50% of the biomass of estuaries south of the Mtentwana, while to the north they comprised less than 50%. Temperate species did not make a notable contribution to the fish biomass composition of those estuaries north of the Cebe (on the east coast). The biomass contribution of cosmopolitan species was variable and comprised a notable proportion of the catch in the Krom and Sand estuaries on the southwest coast, as well as the Seekoei system on the south coast (Figure 4.6c).

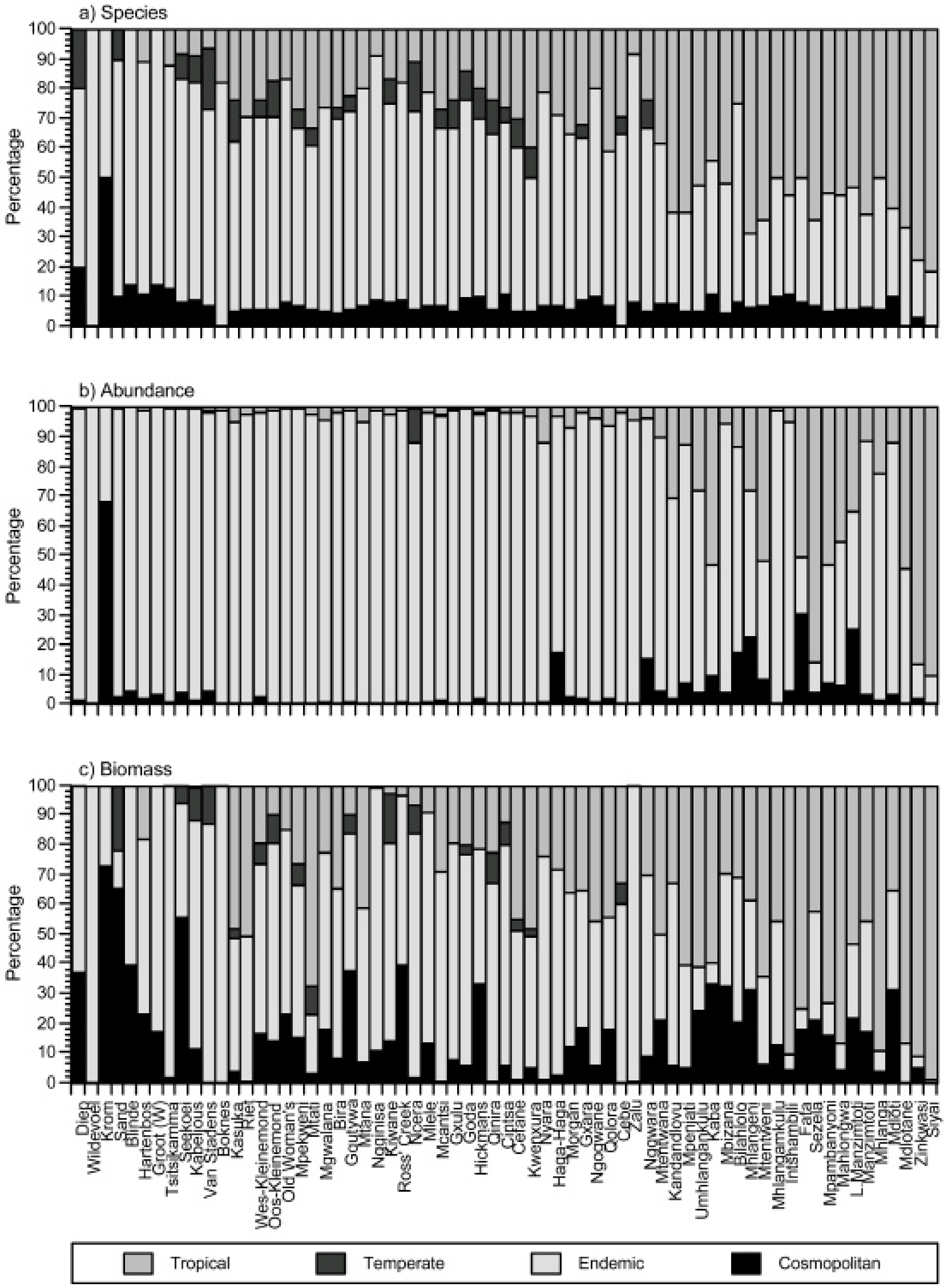


Figure 4.6. Relative composition of tropical, temperate, endemic and cosmopolitan species to the ichthyofauna of closed estuaries by (a) species, (b) abundance and (c) biomass.

4.3.1.2 Open estuaries

The number of taxa recorded in open estuaries ranged between 4 and 55 (Figure 4.7). A notable decline in the number of species occurred between the Matigulu/Nyoni and Mkomazi estuaries on the northeast coast. Another less distinct decline occurred at Cape Agulhas, between the Heuningnes estuary on the south coast and the Uilkraals system on the southwest coast. Between the Mkomazi and Heuningnes estuaries, the number of species recorded was variable.

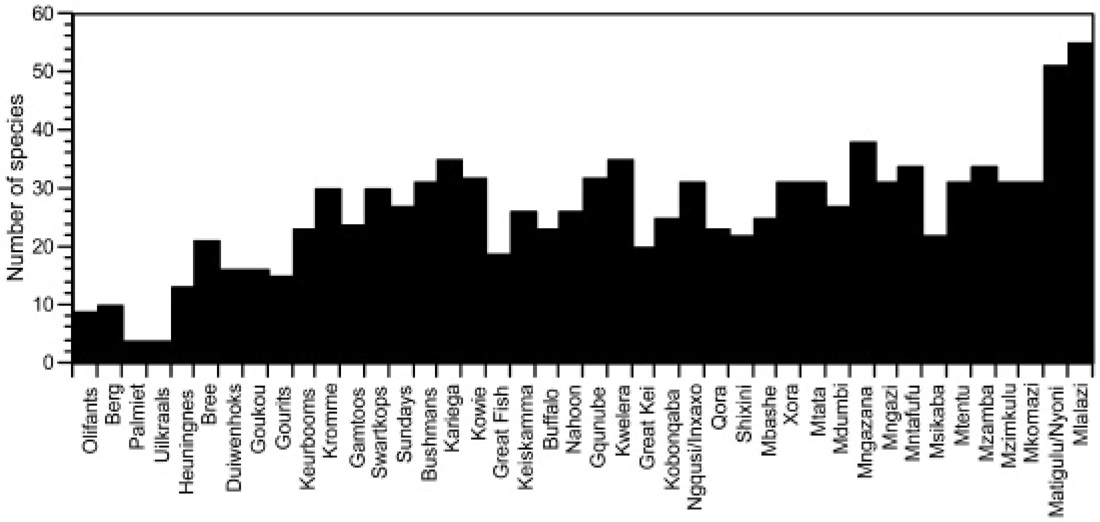


Figure 4.7. Fish species richness reported in open estuaries.

The proportion of tropical species showed a clear decline from the northeast coast toward the west coast (Figure 4.8a). North of the Mngazana estuary (on the east coast) the proportion of tropical species generally exceeded 60% while south of the Mngazana, their contribution was usually less than 40%. No tropical species were captured beyond the Heuningnes estuary near Cape Agulhas. The proportion of endemic species showed the opposite trend and decreased from the west coast toward the northeast coast. South of the Mdumbi estuary (on the east coast), this group of fishes generally comprised more than 50% of the taxa recorded while north of the Mdumbi they comprised less than 30% of the species. The proportion of temperate species showed a similar trend with a notable decline occurring between the Mdumbi and Mngazana systems. Apart from the estuaries on the west and southwest coast such as the Olifants, Palmiet and Uilkraals systems, the proportion of cosmopolitan species remained fairly constant and generally comprised less than 10 % of the taxa recorded (Figure 4.8a).

In terms of relative abundance, the contribution of tropical species declined from over 88% of the catch in the Mlalazi estuary (on the northeast coast) to just over 16% in the Mngazi system (on the east coast) (Figure 4.8b). South of the Mngazi estuary, the contribution of tropical species was usually less than 10% although there was a slight increase between the Great Kei and Swartkops estuaries, on the southeast and south coasts. Endemic species dominated the fish fauna of the estuaries between the Olifants estuary (on the west coast) and the Mntafufu system (on the east coast) and generally comprised over 70% of the catch. North of the Mntafufu estuary the contribution of this group was typically less than 50%. Apart from the Keurbooms and Bushmans estuaries (on the south and southeast coasts respectively), the contribution of temperate species was generally low (mostly<1%). With the exception of a few south coast (Goukou, Keurbooms), southeast coast (Bushmans, Nahoon) and east coast (Mtata) estuaries, the contribution of cosmopolitan species usually did not exceed 10% (Figure 4.8b).

The relative biomass contribution of tropical species generally exceeded 70% in those systems north of the Xora estuary (on the east coast) (Figure 4.8c). Apart from a few southeast coast systems (Kariega, Great Fish, Nahoon), this group typically comprised less than 50% of the catch south of the Xora estuary. The biomass composition of endemic species did not comprise more than 20% of the catch in estuaries north of the Mbashe estuary (on the east coast). Between the Mbashe estuary and the Keurbooms system, this group generally comprised between 30 and 60% of the biomass while south of the Keurbooms, it increased to over 70% of the catch. The biomass contribution of temperate species was variable but generally did not comprise more than 1% the catch of estuaries north of the Mntafufu estuary. The biomass contribution of cosmopolitan species was also somewhat variable and comprised a major proportion of the catch in the Great Kei, Mbashe and Mtata estuaries (Figure 4.8c).

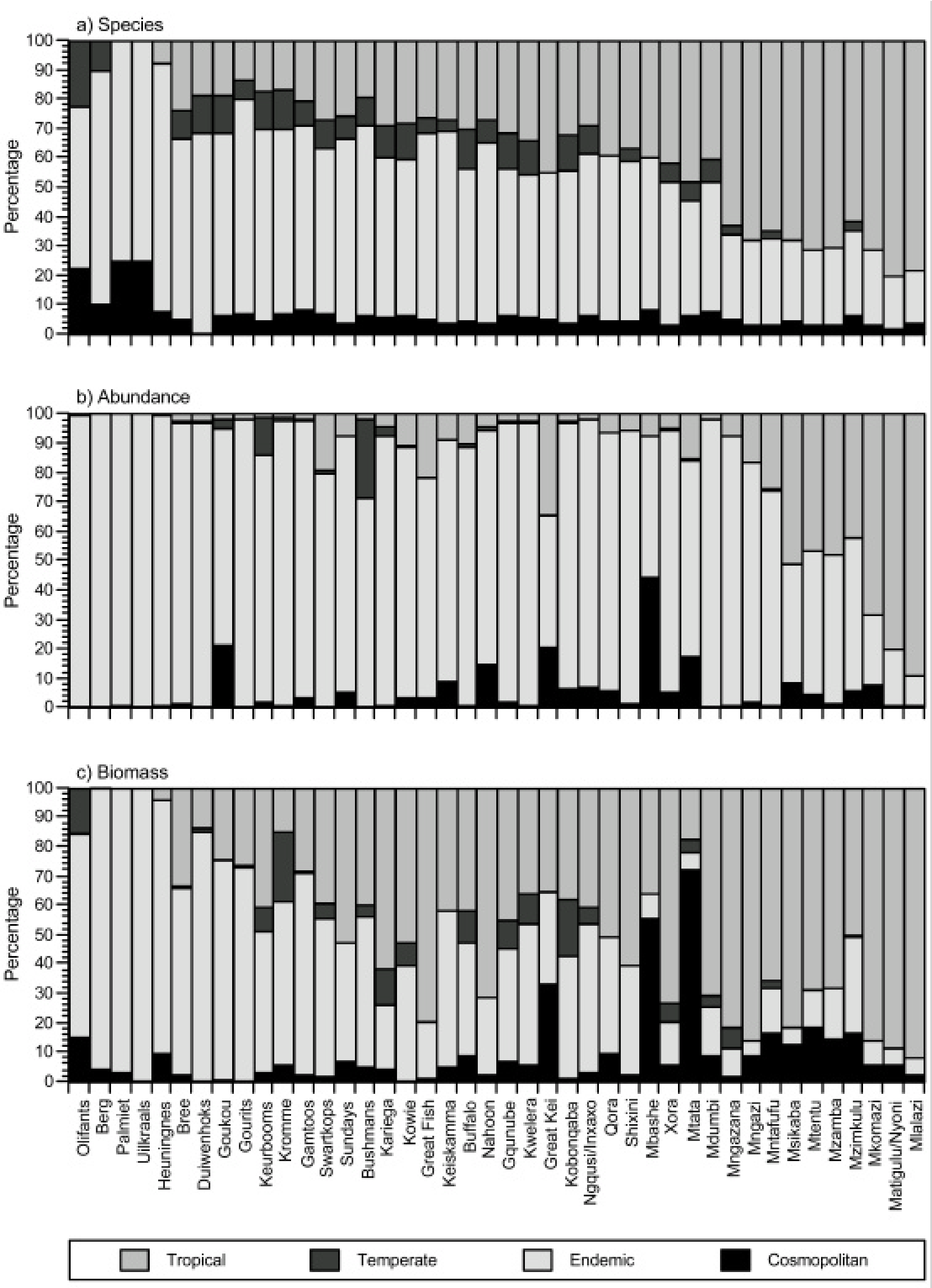


Figure 4.8. Relative composition of tropical, temperate, endemic and cosmopolitan species to the ichthyofauna of open estuaries by (a) species, (b) abundance and (c) biomass.

4.3.2 Multivariate analyses

4.3.2.1 Closed estuaries

From cluster analysis, based on fish species presence/absence, estuaries mostly on the southwest coast separated from the remainder at just over 20% similarity (Figure 4.9a). The remaining estuaries formed two groups at approximately 45% similarity. One group comprised systems predominantly on the northeast coast, while the other group consisted of estuaries from the south, southeast and east coasts. In the ordination of the presence/absence data, estuaries on the southwest coast were situated to the left of the plot (Figure 4.9b). Estuaries from the south, southeast and east coast regions were clustered in the centre of the ordination while the remaining estuaries, predominantly from the northeast coast, formed a loose grouping to the right of the plot.

The cluster analysis based on relative abundance had estuaries predominantly on the southwest coast separating from the remainder at approximately 15% similarity (Figure 4.10a). At about 40% similarity, estuaries predominantly from the northeast coast formed a separate grouping from the rest. In the ordination, the estuaries on the southwest coast were situated in the upper left of the plot (Figure 4.10b). In the middle of the plot, there was a gradation from left to right of estuaries from the south coast through to systems on the southeast and east coasts. Systems predominantly from the northeast coast formed a broad grouping to the right of the ordination.

Based on relative biomass, estuaries predominantly from the southwest coast separated out at approximately 25% similarity in the cluster analysis (Figure 4.11a). The remaining systems formed two groups at approximately 40% similarity. One group comprised estuaries predominantly from the northeast coast while the remaining systems were those from the south, southeast and east coasts. In the ordination of the biomass data, the estuaries on the southwest coast were situated to the left of the plot with a gradation to estuaries on the south, southeast and east coasts toward the centre of the plot (Figure 4.11b). The estuaries mostly from the northeast coast formed a loose group to the right of the plot.

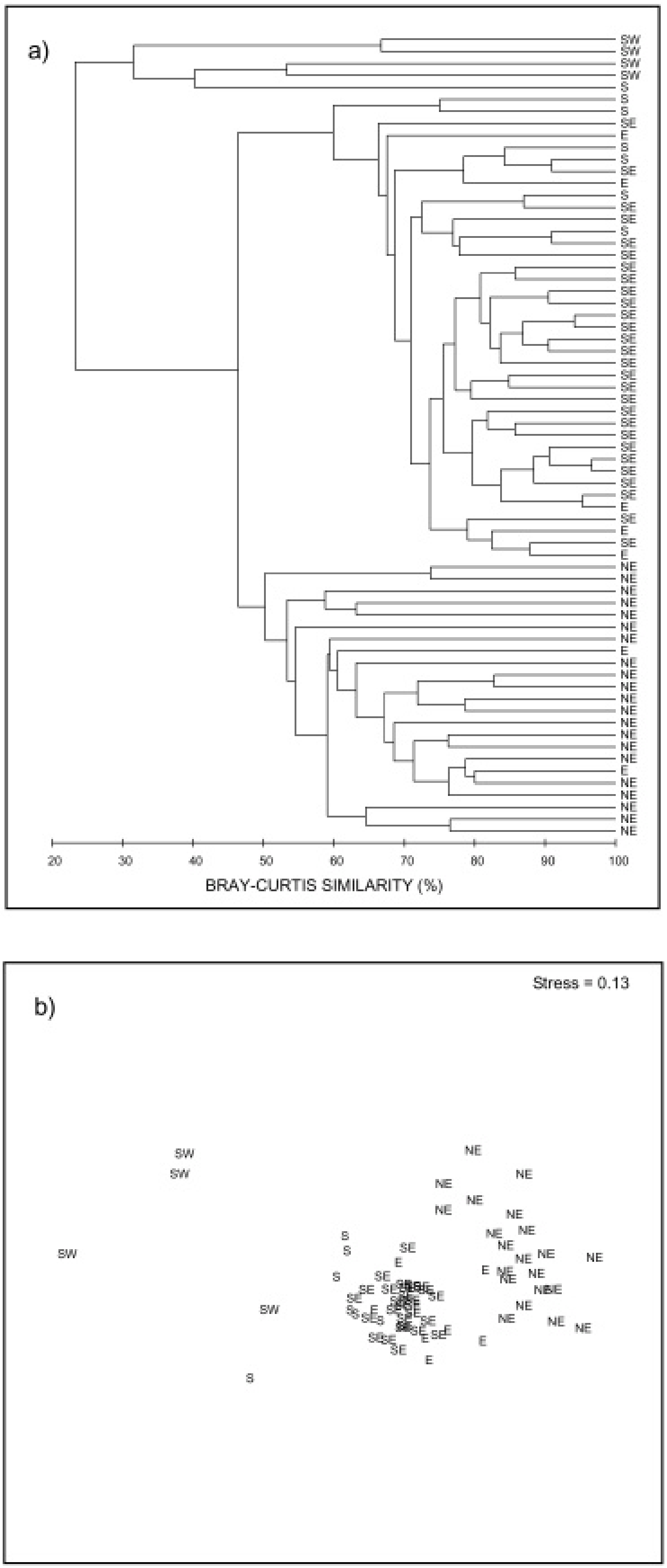


Figure 4.9. Results of cluster analysis (a) and MDS ordination (b) of closed estuaries based on presence/absence data.

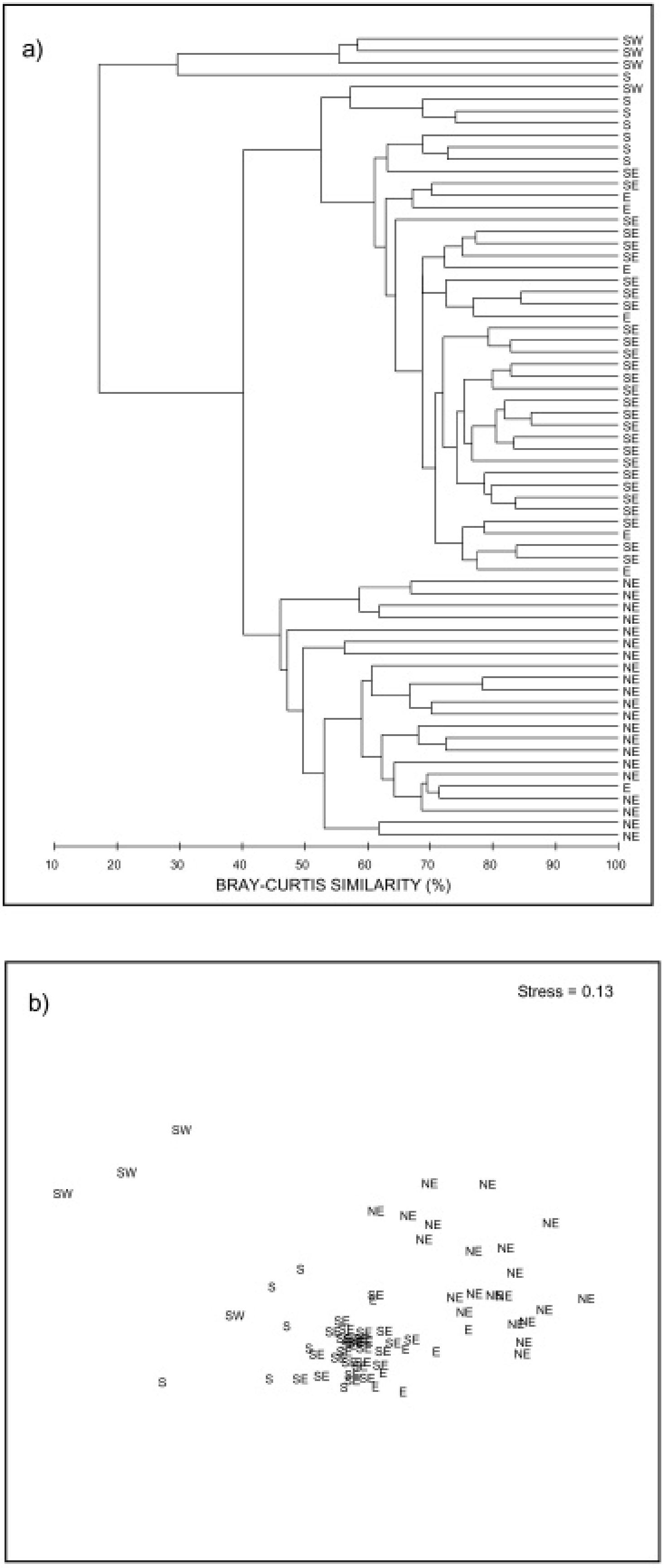


Figure 4.10. Results of cluster analysis (a) and MDS ordination (b) of closed estuaries based on abundance data.

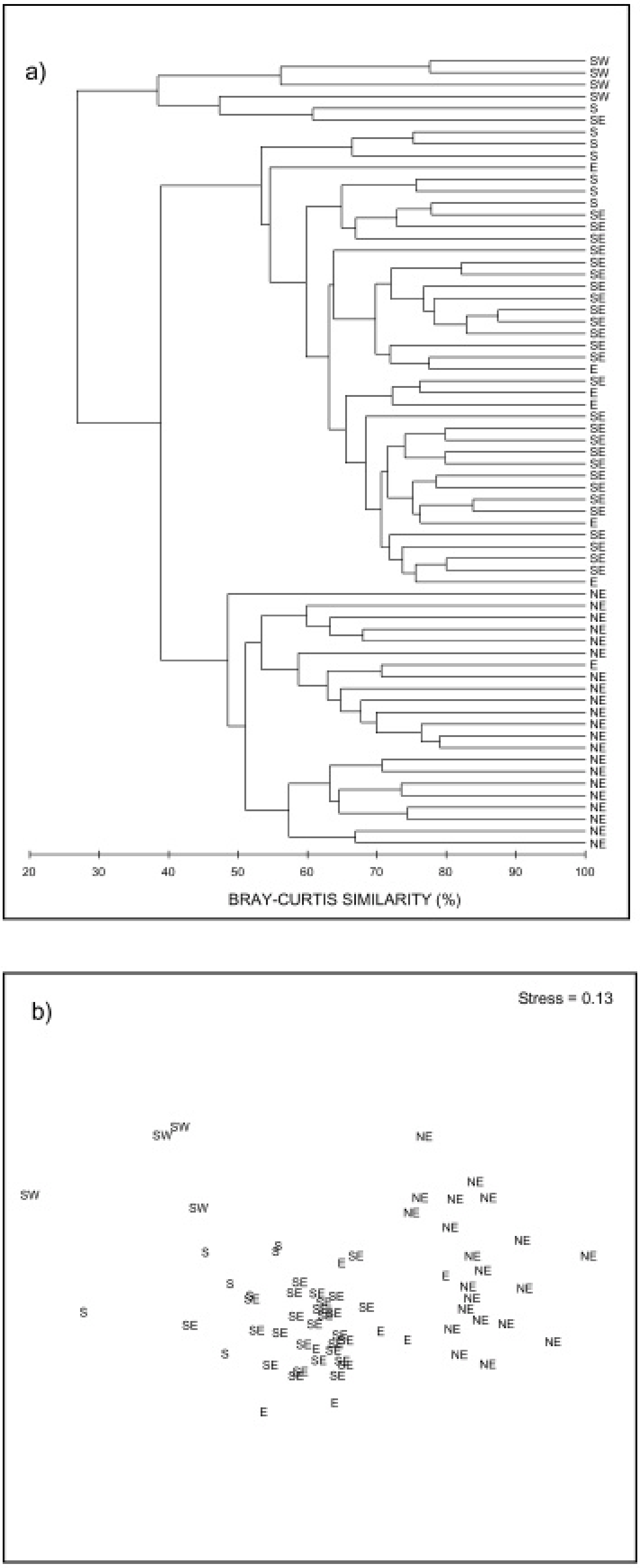


Figure 4.11. Results of cluster analysis (a) and MDS ordination (b) of closed estuaries based on biomass data.

4.3.2.2 Open estuaries

The results of the cluster analysis based on fish species presence/absence, had estuaries on the west and southwest coast separating out at roughly 20% similarity (Figure 4.12a). The remaining estuaries formed two groups at just over 40% similarity. One group comprised a mixture of estuaries from the east and northeast coasts, while the other group consisted of estuaries mainly from the south, southeast and east coast regions. In the ordination of the presence/absence data, estuaries on the west and southwest coast were situated to the left of the plot (Figure 4.12b). The remaining systems formed a gradation from those on the south and southeast coasts to estuaries on the east and northeast coasts.

Based on relative abundance, the cluster analysis had west and southwest coast estuaries separating from the remaining systems at approximately 20% similarity (Figure 4.13a). Two groups were formed at roughly 40% similarity. One group comprised estuaries mostly from the east and northeast coasts, while the other group consisted of a mixture of estuaries from the south, southeast and east coasts. In the MDS analysis, the estuaries on the west and southwest coast formed a grouping to the left of the ordination (Figure 4.13b). The remaining systems appeared to form a gradation, from left to right, of estuaries from the south and southeast coasts to those on the east and northeast coasts.

The results of the cluster analysis based on biomass, had estuaries from the west and southwest coast separating from the remainder at about 20% similarity (Figure 4.14a). The outstanding estuaries formed two groups at approximately 40% similarity. The one group comprised estuaries on the northeast and east coasts, while the other group consisted of estuaries from the south, southeast and east coast regions. In the ordination, the estuaries on the west and southwest coast formed a broad grouping to the left of the plot (Figure 4.14b). The remaining systems formed a gradation from those on the south and southeast coast to the east and northeast coasts.

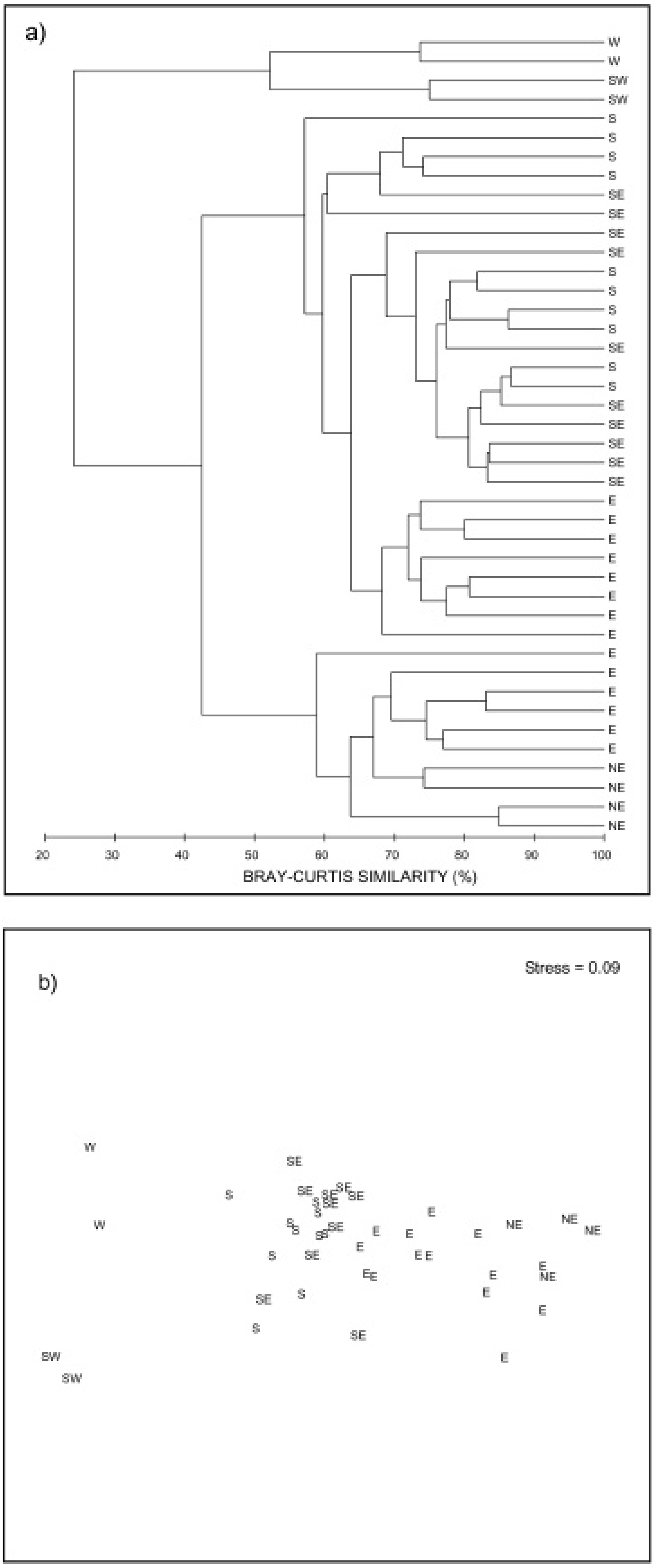


Figure 4.12. Results of cluster analysis (a) and MDS ordination (b) of open estuaries based on presence/absence data.

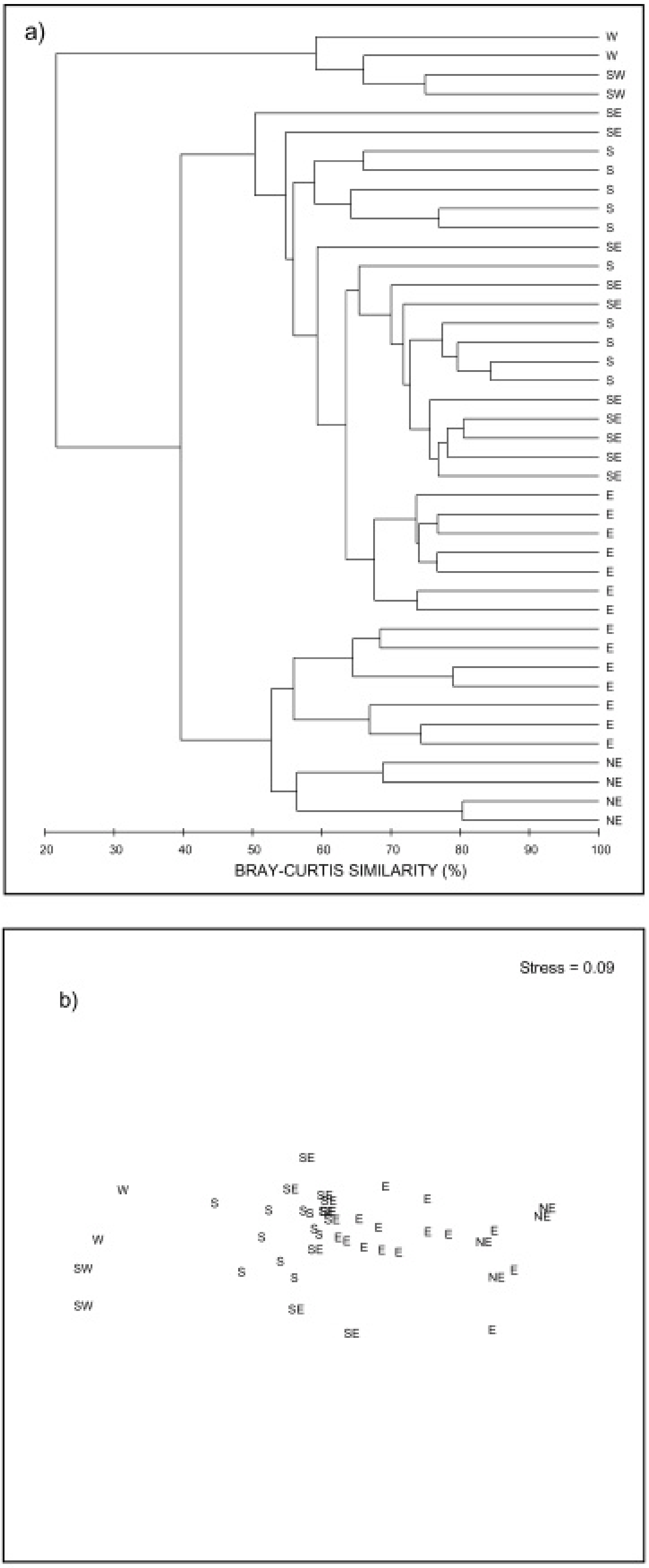


Figure 4.13. Results of cluster analysis (a) and MDS ordination (b) of open estuaries based on abundance data.

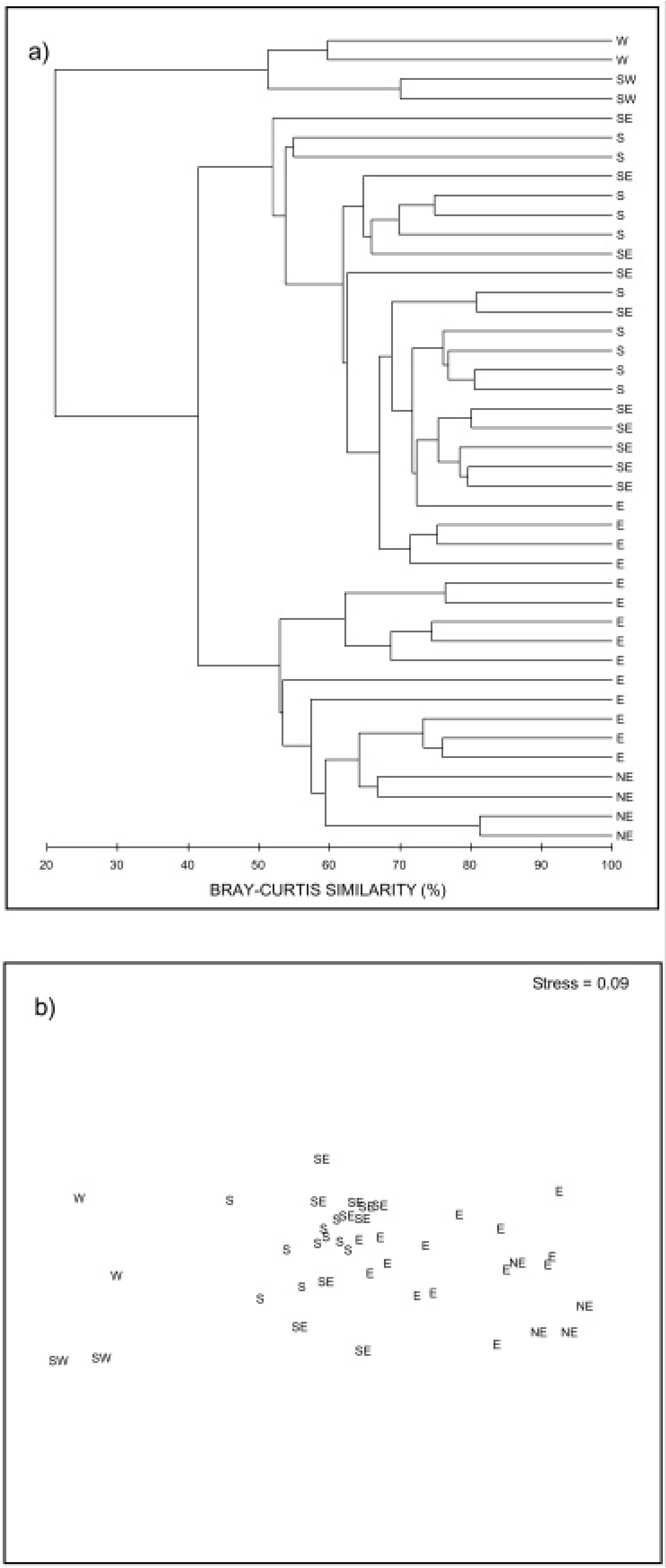


Figure 4.14. Results of cluster analysis (a) and MDS ordination (b) of open estuaries based on biomass data.

4.4 DISCUSSION

4.4.1 Species richness and distribution

Along the South African coast, there is a decline in taxonomic richness as one proceeds from the subtropical northeast (Indian Ocean) coast toward the temperate west (Atlantic Ocean) coast. Stephenson & Stephenson (1972) found that, although the distributions of rocky shore plant and animal species around the coast showed minor irregularities, the general trend was a steady decline in the number of taxa from east to west. Emanuel *et al*. (1992) also reported a decrease in species richness of marine intertidal and subtidal invertebrates from the Mozambique coast in the east to the Namibian coast in the west. The marine mollusc fauna of the west coast of South Africa was also found to be less diverse than that of the warmer south coast (Kilburn & Rippey, 1982).

Burger (1990) reported a decrease in the number of intertidal fish species from Sodwana Bay on the northeast coast toward Cape Pont (on the southwest coast). Prochazka & Griffiths (1992) noted a similar pattern where the numbers of species and families of intertidal fish decreased from Port Alfred on the southeast coast toward Groenrivier on the west coast. A decrease in the number of families and species of intertidal fishes was also reported around the southern African coast from Bhanga Nek near Kosi Bay to Namibe in southern Angola (Prochazka, 1994). Hockey & Buxton (1991) found the diversity of rock pool fishes decreased from the warmer waters of the northeast coast to the cooler southwest coast. This trend was also observed for shelf-inhabiting fish species where there was a stepped decrease in the numbers of species from the northeast coast to the west coast (Turpie *et al*., 2000). The diversity of southern African indigenous freshwater fishes was also found to decrease from north to south, with most southern (Cape) rivers having only a few indigenous freshwater species (O'Keeffe *et al*., 1991; Skelton, 1993) that are mostly confined to the Cape Fold Mountain region.

In terms of estuaries, Day (1974) noted that the total of number of benthic invertebrate species of south coast systems was higher than either the estuaries on the northeast/east coast or the west coast. De Villiers *et al*. (1999) found a similar trend when comparing the richness of macrobenthic species only in permanently open estuaries. Invertebrate species diversity, however, was found to increase again in tropical Mozambique estuaries (Day, 1981b). In terms of birds, Siegfried (1981) reported that the percentage of resident bird species was relatively low in west coast estuaries, increasing toward the Mozambique border in the northeast.

For estuarine fishes, a decline in species diversity has been reported from northeast systems around the southeast and south coast to those on the west coast (Day, 1974; Wallace & van der Elst, 1975; Whitfield *et al*., 1989; Whitfield, 1994a; 1994b; 1998; Maree *et al*., 2000). A steady decline in ichthyoplankton family representation was also observed in estuaries between Kosi Bay and the Swartvlei system (on the south coast) (Whitfield & Marais, 1999).

The decline in estuarine fish diversity in South Africa from the east (Indian Ocean) coast around to the west (Atlantic Ocean) coast is a result of the subtraction of tropical marine species (which comprise the bulk of the estuary-associated ichthyofauna) and is linked to the Agulhas Current through its influence on sea temperatures and the dispersal of these fishes in a southerly direction (Wallace & van der Elst, 1975; Blaber, 1981; Day *et al*., 1981; Whitfield *et al*., 1989; Whitfield, 1998; 1999). Maree *et al*. (2000) observed a major change in the number of species at the Swartkops estuary near Port Elizabeth and this was attributed to the presence of tropical 'vagrants' at the most southern limit of their distribution. A sudden decrease in the number of species south of the Swartkops was ascribed to lower inshore temperatures resulting from the Agulhas Current diverging from the coast as the continental shelf break moves further offshore (Maree *et al*., 2000). Along the west coast, the cold upwelled waters associated with the Benguela Current system probably acts as a barrier to the distribution of tropical and subtropical taxa from both the west and east African coasts and thus accounts for the low species richness in the region (Whitfield, 1983; 1996; 1999).

In this study, high numbers of fish species were captured in both closed and open estuaries on the northeast coast, with few taxa reported from the southwest and west coasts. The number of species in the intermediate area, however, was somewhat variable (Figures 4.5 & 4.7).

Considering only the numbers of tropical, endemic, temperate, cosmopolitan species reported during this study separately, there was a clear decline in the number of tropical taxa from the northeast coast toward the west coast in both closed and open estuaries (Figures 4.15 & 4.16). The numbers of endemic species, on the other hand, increased from the northeast coast southwards before declining again along the southwest and west coasts. The overall numbers of temperate species remained relatively low throughout with higher numbers reported on the south and southeast coasts. The numbers of cosmopolitan species also remained low with a fairly even distribution throughout (Figures 4.15 & 4.16).

The overall species richness observed during this study is therefore largely a result of a combination of the distribution of tropical and endemic taxa. As the numbers of tropical species declined from the northeast coast toward the west coast, there was an increase in the numbers of endemic species until both groups declined toward the southwest and west coasts. The relatively high species richness recorded on the south and southeast coasts is also probably a result of the mixing of tropical species from the north together with endemic species from the south.

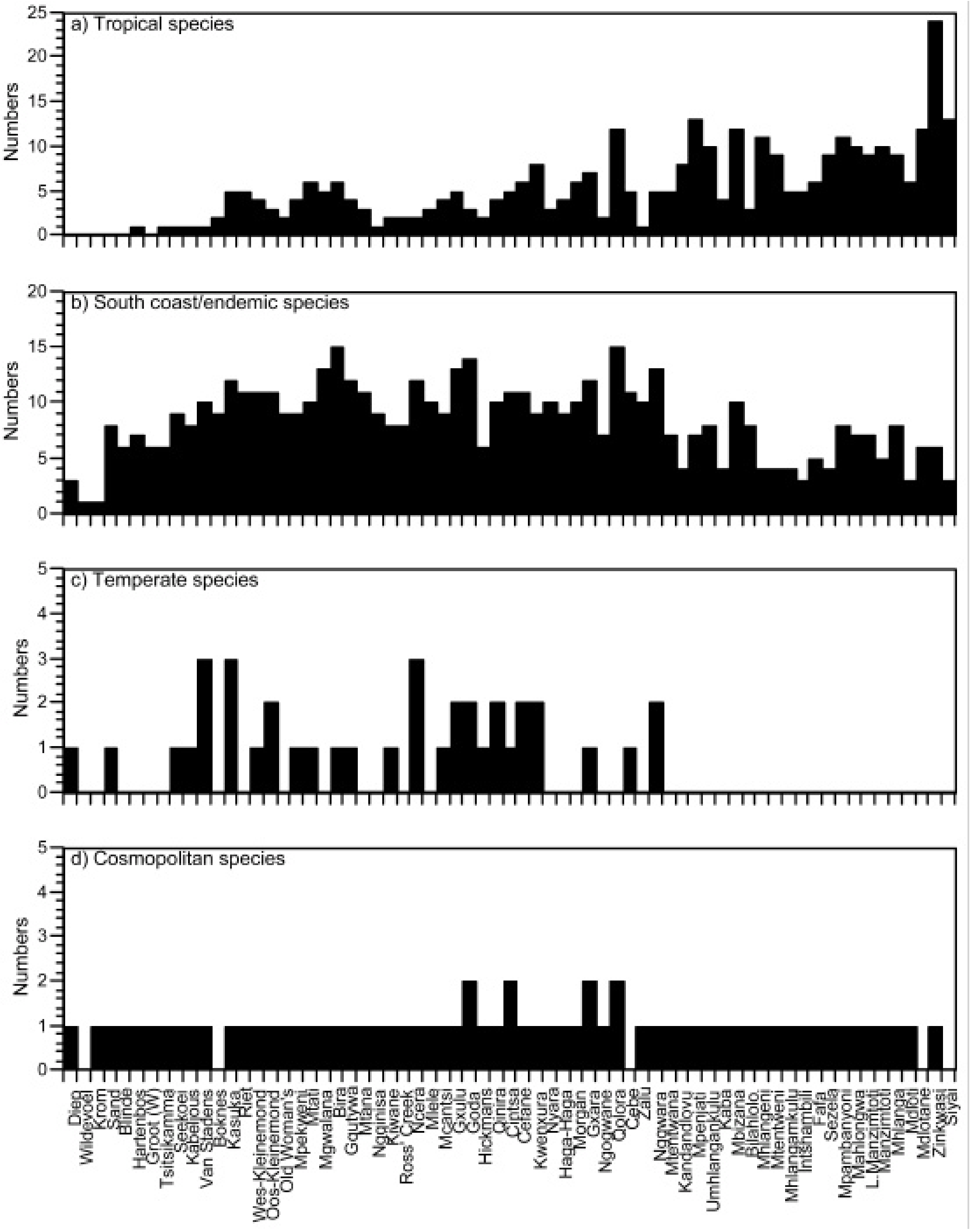


Figure 4.15. Species richness of (a) tropical species, (b) endemic species, (c) temperate species and (d) cosmopolitan species in closed estuaries.

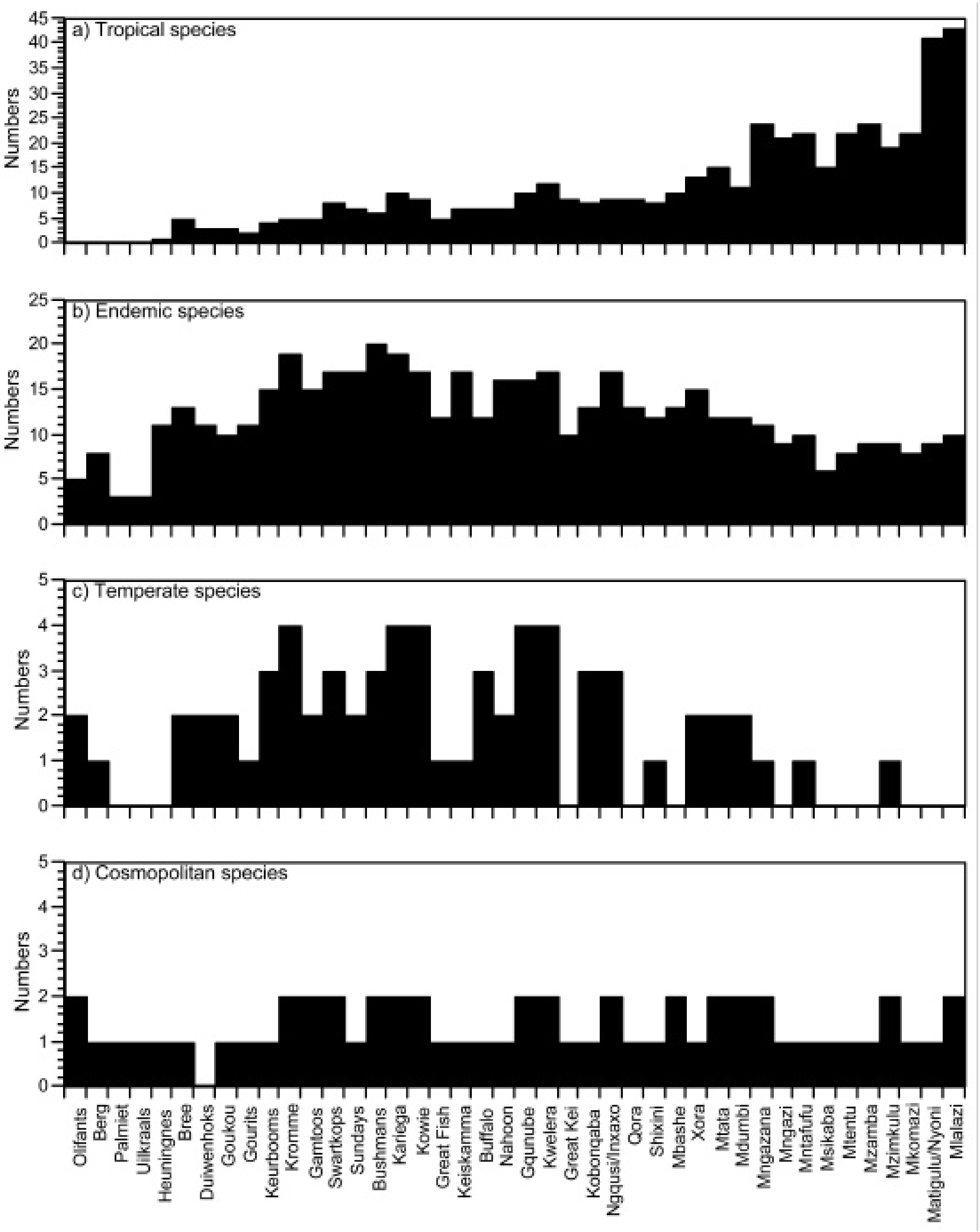


Figure 4.16. Species richness of (a) tropical species, (b) endemic species, (c) temperate species and (d) cosmopolitan species in open estuaries.

In terms of their relative composition, tropical species decreased from the northeast coast to the southwest and west coasts and generally dominated the ichthyofauna of closed estuaries north of the Mtentwana system (near Port Edward) (Figure 4.6). In open systems tropical species mostly dominated the fish communities of those systems north of the Mngazana estuary (near Port St Johns) (Figure 4.8). The composition of endemic species showed the opposite trend where the proportion of this group decreased from the west and southwest coasts toward the northeast coast. In closed estuaries this group generally dominated the ichthyofauna of systems south of the Mtentwana estuary while in open estuaries they commonly dominated the fish communities south the Mngazana system, particularly with respect to the number of taxa and their relative abundance. The contribution of both temperate and cosmopolitan species to the fish fauna of both closed and open estuaries was generally low throughout the study area, with a decline in the contribution of temperate species from west to east. Overall, tropical species dominated the fish communities of the estuaries on the northeast and east coasts down to approximately Port St Johns (Mngazana). South of Port St Johns, the contribution of tropical species declined while the proportion of endemic forms increased, dominating those systems on the southeast, southwest and west coasts (Figures 4.6 & 4.8).

Stephenson & Stephenson (1972) reported a similar trend, with a rapid decline in the proportion of warm-water rocky-shore species between Port St Johns and Qolora, just north of the Great Kei estuary. There was also a comparable decrease of west-coast (cold-water) species in the region between Hermanus on the southwest coast and Arniston on the south coast. Wooldridge *et al.* (1981) noted a major change in sandy beach macrofaunal composition between Mpande (near Port St Johns) and Cebe (near the Great Kei estuary) where the subtropical fauna was replaced by temperate species. From Cebe south and westward, the warm temperate fauna extended to an overlap region with the temperate fauna of the west coast between Cape Agulhas and Cape Point (McLachlan *et al.*, 1981). Kilburn & Rippey (1982) found that endemic species accounted for over 88% of the marine molluscs of the west (Atlantic) coast, False Bay and Cape Agulhas and of these, cold-water species declined from 25% on the west coast to 12% at False Bay and 5% at Cape Agulhas. Tropical species, on the other hand increased from 0% on the west coast to 62% on the northeast coast.

Penrith (1970) noted that almost all the intertidal clinid fishes of the west and south coasts of South Africa are endemic to the region. The east coast has some endemic clinids but from the Mbashe estuary northwards their percentage declines with a greater number of Indo-Pacific tropical species occurring. Burger (1990) also observed a decrease in the proportion of endemic intertidal fish species from Cape Point, along the south coast and up the east coast to Sodwana Bay (on the northeast coast). Prochazka (1994) found a similar pattern where the percentage of southern African endemic intertidal fish species rose sharply from zero in southern Angola to approximately 90% between Lüderitz (Namibia) and False Bay and then decreased steadily again eastward to only 1% at Bhanga Nek (Kosi Bay). Turpie *et al.* (2000) reported high numbers of tropical shelf-associated fish taxa along the northeast coast, with a notable decline occurring near Port Edward. However, this decline was largely a result of an artefact of many poorly known species distributions. Furthermore, although peak numbers of endemic species were reported near Port Elizabeth, the proportion of this group decreased from about 45% on the west coast to 34% at Port Elizabeth and 9% on the northeast coast (Turpie *et al.*, 2000).

A similar situation has also been described for southern African freshwater fish species where the number of tropical (Zambezian) taxa decreases markedly from north to south with only a few hardy species occurring south of the St Lucia basin in the northeast coastal region (Skelton, 1990; 1993). Additionally, about 61% of the primary and secondary freshwater fishes are endemic to southern Africa with the greatest concentration located in the eastern and southern (Cape) regions (Skelton, 1993).

Day (1981b) found that in open estuaries between the Morrumbene system (in southern Mozambique) and Knysna (on the south coast), the percentage of tropical benthic macroinvertebrate and fish species declined southwards with an associated increase in the percentage of endemic species. This change was very marked between the Mngazana and Knysna estuaries (Day, 1981b). Based on the zoogeographic distribution of 59 common estuarine fishes, Day *et al.* (1981) also established that the number of tropical and subtropical species declined from southern Mozambique toward the Atlantic coast. A similar pattern was described by Whitfield *et al.* (1989) where the contribution of subtropical/tropical teleosts declined from 79% in the Richards Bay and Mngazana estuaries on the northeast and east coasts respectively to 38% in systems along the south coast and no tropical fishes from Langebaan Lagoon on the west coast. Whitfield (1994a; 1994b; 1998) also found that the percentage endemicity increased from approximately 20% on the northeast coast to about 64% on the west coast. Finally, Maree *et al*. (2000) observed that the ichthyofaunal assemblages of estuaries between the Kromme on the south coast and the Great Kei were dominated by temperate (mostly endemic) species while the systems on the east coast, between the Mbashe and Mntafufu estuaries, were dominated by tropical/subtropical species.

Estuaries along the northeastern coast of South Africa were also found to support more 'tropical' bird species than Atlantic coast estuaries (Siegfried, 1981). In addition, these tropical species formed a higher percentage of the total taxa found at estuaries along the northeastern coast than those along the west coast.

4.4.2 Multivariate analyses

The results of the multivariate analyses indicate that, based on their fish communities, both closed and open estuaries on the west and southwest coasts were distinct from other South African systems. The remaining estuaries appeared to form a gradation from systems on the south coast to those on the southeast, east and northeast coasts (Figures 4.7-4.12). In closed estuaries, those from the northeast coast appeared to comprise a more discrete grouping. This, however, is probably due to the lack of closed estuaries represented on the east coast between the Mbashe estuary and Port Edward (Figure 4.3).

On the west coast, multivariate analysis of shelf-associated fish species established an ordination break at Cape Point, while to the east of Cape Point the analysis suggested a gradual turnover of species (Turpie *et al*., 2000). On the east coast, Marais (1988) found that geographical affinity had a strong influence on the clustering of 14 estuaries between the Kromme estuary and the Mtata system, with the estuaries north of the Great Kei grouping separately from the remaining systems. Multivariate analyses of eight permanently open estuaries between the Kromme and the Mntafufu systems also showed that the ichthyofaunal communities of the estuaries north of the Great Kei estuary differed from those to the south (Maree *et al*., 2000). Whitfield *et al*. (1989) found that zoogeographical factors are of major importance in determining the ichthyofaunal composition of eelgrass beds in South African estuaries;

multivariate analyses of nine systems from Richards Bay on the northeast coast to Langebaan Lagoon on the west coast revealed that estuaries on the south and southeast coast clustered together while Richards Bay, Mngazana and Langebaan Lagoon were distinct. It is interesting to note that a cluster analysis of bird data revealed that the avifaunas of west and northeast coast estuaries were also distinct (Siegfried, 1981).

4.4.3 General

The east coast, between Port St Johns and the Great Kei estuary, is generally regarded as a zone of overlap between the warm-temperate and subtropical regions. Stephenson & Stephenson (1972) found that a change from subtropical to warm-temperate rocky shore fauna occurred somewhere between Port St Johns and Qolora, just north of the Great Kei. A similar change in beach macrofauna was also found to occur between Mpande (near Port St Johns) and Cebe (near the Great Kei) (Wooldridge *et al.*, 1981). For rocky intertidal biota, Bustamante (1994) considered the area between Dwesa (near the Mbashe) and Ballito Bay (on the northeast coast) as a transition zone between the warm-temperate and subtropical provinces. Kilburn & Rippey (1982) found that, for marine molluscs, the region between the Great Kei and Mtata estuaries was a transitional zone between the subtropical and warm-temperate regions. Penrith (1970) reported major changes in the nature of intertidal clinid fish fauna between East London and the Mbashe River while Turpie *et al.* (2000) suggested that, for shelf-associated marine fish species, the subtropical/warm-temperate boundary occupies a broad transition zone within the east coast region. For freshwater fishes, the region from Port Elizabeth to approximately the Tugela River comprises a zone of overlap between tropical and temperate faunas (Skelton, 1993).

Maree *et al.* (2000) suggested that, for estuary-associated marine fishes, the transition between the subtropical and warm-temperate regions occurred between the Mbashe and Great Kei estuaries. The transitional nature of the Mbashe estuary was also highlighted by the presence of both mangroves that favour subtropical conditions, and saltmarshes that are normally associated with temperate systems. Colloty (2000) found that, between Port Alfred and Port Edward, there was a change in estuarine plant communities from salt marsh to mangrove/swamp forest and that this transition took place between the Great Kei estuary and the Mzimvubu River (at Port St Johns). In terms of birds, however, the area between Cape Point and the Great Kei estuary was found to represent an overlap zone between the avifaunas of the west and northeast coast estuaries (Siegfried, 1981). Hockey & Turpie (1999) also concluded that the avifaunas of both estuaries and sandy beaches reinforce the south coast as a zone of overlap.

The area between Cape Point and Cape Agulhas has also been shown to represent a zone of overlap between the cool-temperate and warm-temperate faunal provinces (Brown & Jarman, 1978). Stephenson & Stephenson (1972) found that the area between Kommetjie, to the west of Cape Point, and Cape Agulhas showed a marked overlap between the rocky shore biota of the cool-temperate and warm-temperate faunal provinces. McLachlan *et al*. (1981) also found that the area between Cape Point and Cape Agulhas represented an overlap region between the cool-temperate and warm-temperate provinces for beach macrofauna. Kilburn & Rippey (1982) recognized the region between Cape Point and Cape Agulhas as a transitional zone where west and south coast marine mollusc faunas intermingle. Changes in the nature of intertidal clinid fish fauna was also found to occur between Cape Point and Cape Agulhas (Penrith, 1970) while the area between False Bay and Koppie Alleen formed a transition zone between the cool-temperate and warm-temperate provinces for intertidal fishes (Prochazka, 1994). Although Whitfield (1998) tentatively proposed Cape Point as the boundary between the warm and cool temperate biogeographic regions for estuary-associated fish species, the lack of detailed ichthyological information from many estuaries in the Western Cape precluded a detailed analysis of the situation.

To determine if any clear boundary between the various biogeographic regions could be established from this study, an analysis of similarities (ANOSIM) was performed on the fish data. This analysis utilises the (rank) similarity matrix underlying the clustering or ordination procedure and tests for differences between and within *a priori* groupings (Clarke & Warwick, 1994). A test statistic (*R*) is computed, which reflects the observed differences between groupings, contrasted with differences within groupings. The *R* statistic falls within the range -1 to 1 but is usually between

0 and 1. If $R = 1$ then all sites within a group are more similar to each other than any sites from different groups and if $R = 0$ then the similarities between and within groups are the same on average (Clarke & Warwick, 1994).

For the cool-temperate/warm-temperate region, the analysis was performed on estuaries between the Orange River and the Great Kei using Cape Point and Cape Agulhas as the potential biogeographic boundaries respectively. For the warm-temperate/subtropical section, the test was performed on estuaries between Cape Agulhas and Kosi Bay using the Great Kei, Mbashe, Mdumbi, Mngazi, and Mzamba (east coast) estuaries as potential boundaries. The test was performed on both closed and open estuaries using presence/absence, abundance and biomass data. The null hypothesis assumes that there is no difference between regions.

The result of the ANOSIM test suggests that, for closed estuaries, the break between the cool-temperate and warm-temperate zones occurred at Cape Point (Table 4.1). This difference was due to the inclusion/exclusion of the Sand estuary, which lies in the northwest corner of False Bay (on the southwest coast) (Figure 4.4). Of the 11 systems that enter False Bay, the Sand has the highest recorded fish species diversity (Morant, 1991). Stephenson & Stephenson (1972) found a peak in the number of rocky shore taxa between Cape Agulhas and Cape Point and that this peak coincides with warmer temperatures recorded in the northwestern corner of False Bay. To the east of False Bay the number of taxa declined again, indicating a return to colder conditions along this stretch of coast (Stephenson & Stephenson, 1972). Brown & Jarman (1978) reported a similar situation in Langebaan Lagoon, on the west coast, where the species associated with this warmer body of water were found to be more characteristic of the warm-temperate south coast region. Conditions in False Bay therefore are probably atypical for the region as a whole. For the open estuaries, the break between the cool-temperate and warm-temperate zones occurred at Cape Agulhas (Table 4.1). This division is slightly east of Cape Point, the cool-temperate/warm-temperate division suggested by Day *et al.* (1981) and Whitfield (1994a) for fish in South African estuaries.

Table 4.1. Test statistic (R) (and significance) of the ANOSIM test applied to presence/absence, abundance and biomass data in (a) closed estuaries and (b) open estuaries using Cape Point and Cape Agulhas as the cool-temperate/warm-temperate biogeographic break.

(a) Closed estuaries	Cape Point	Cape Agulhas
Presence/absence	0.995 ($p < 0.001$)	0.958 ($p < 0.001$)
Abundance	0.990 ($p < 0.001$)	0.927 ($p < 0.001$)
Biomass	0.923 ($p < 0.001$)	0.890 ($p < 0.001$)
(b) Open estuaries	Cape Point	Cape Agulhas
Presence/absence	0.679 ($p = 0.022$)	0.998 ($p < 0.001$)
Abundance	0.655 ($p = 0.018$)	0.983 ($p = 0.001$)
Biomass	0.717 ($p = 0.018$)	0.996 ($p < 0.001$)

The break between the warm-temperate and subtropical zones for closed estuaries was found to lie in the region of the Mbashe estuary (Table 4.2), which corresponds to the location proposed by Whitfield (1994a). This break, however, is most likely a result of the lack of closed estuaries represented between the Mbashe estuary and Port St Johns (Figure 4.4). For open estuaries, this break was found to lie further north at the Mdumbi estuary, south of Port St Johns (Table 4.2). It should be noted here, however, that no open estuaries were sampled between the Mdumbi system and Port St Johns (Figure 4.3) and it is possible that this boundary may lie further north, extending even to Port St Johns as suggested by the abundance data (Table 4.2). Branch & Grindley (1979) reported that the fish fauna in the Mngazana estuary (near Port St Johns) exhibited a seasonal variation, with many tropical species occurring only in summer and those with southern affinities appearing most often in winter. Recent studies, however, have shown that the fish fauna of this system is overwhelmingly dominated by tropical taxa (both in summer and winter), thus indicating that it lies well within the subtropical region (Whitfield, personal communication).

Table 4.2. Test statistic (R) (and significance) of the ANOSIM test applied to presence/absence, abundance and biomass data in (a) closed estuaries and (b) open estuaries using Great Kei, Mbashe, Mdumbi, Mngazi and Mzamba estuaries as the warm-temperate/subtropical biogeographic boundary.

(a) Closed estuaries	Great Kei	Mbashe	Mdumbi	Mngazi	Mzamba
Presence/absence	0.579	0.826			0.817
	($p < 0.001$)	($p < 0.001$)			($p < 0.001$)
Abundance	0.578	0.824			0.813
	($p < 0.001$)	($p < 0.001$)			($p < 0.001$)
Biomass	0.589	0.824			0.794
	($p < 0.001$)	($p < 0.001$)			($p < 0.001$)
(b) Open estuaries	Great Kei	Mbashe	Mdumbi	Mngazi	Mzamba
Presence/absence	0.638	0.812	0.874	0.795	0.617
	($p < 0.001$)	($p < 0.001$)	($p < 0.001$)	($p < 0.001$)	($p < 0.001$)
Abundance	0.517	0.698	0.837	0.850	0.699
	($p < 0.001$)	($p < 0.001$)	($p < 0.001$)	($p < 0.001$)	($p < 0.001$)
Biomass	0.541	0.807	0.881	0.783	0.616
	($p < 0.001$)	($p < 0.001$)	($p < 0.001$)	($p < 0.001$)	($p < 0.001$)

4.5 SUMMARY AND CONCLUSIONS

Based on their fish communities, three biogeographic provinces are identified for South African estuaries. A cool-temperate region extends along the west and southwest coasts from the Orange River estuary to Cape Agulhas; a warm-temperate region stretches from Cape Agulhas along the south, southeast and east coasts to approximately the Mdumbi estuary; and a subtropical region along the east coast from just north of the Mdumbi system to Kosi Bay (Figure 4.17). It is possible, however, that these biogeographic boundaries may shift seasonally.

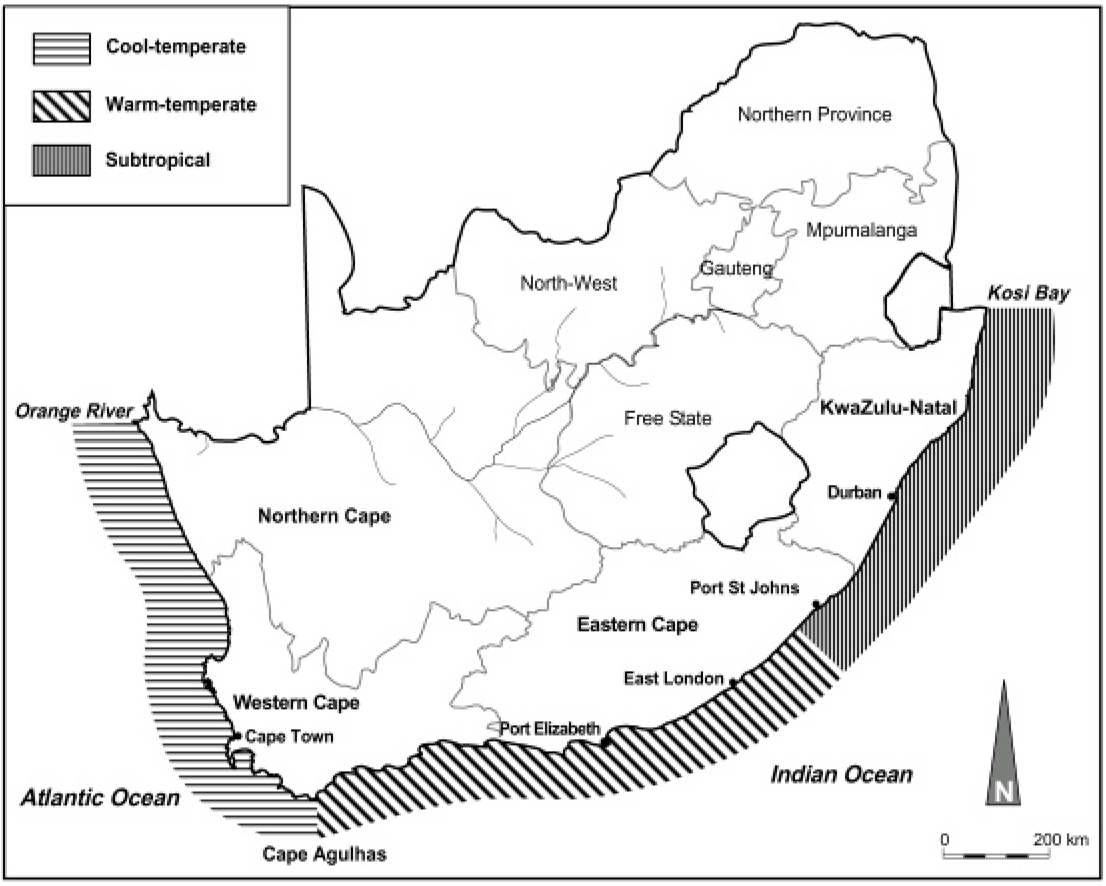


Figure 4.17. Map of South Africa indicating the three biogeographic provinces, based on estuarine fish communities.

CHAPTER 5

PHYSICO-CHEMICAL CHARACTERISTICS

5.1 INTRODUCTION

Since estuaries are formed where rivers meet the sea, they act as an interface between both terrestrial and marine environments and are affected by variations in both processes (Day, 1981a; Cooper, 2001). The southern African subcontinent spans a number of climatic zones from humid, predominantly summer rainfall conditions in the east and northeast to a Mediterranean climate in the south and southwest, to arid conditions in the northwest (Tinley, 1985).

The marine environment also exhibits a range of conditions with the warm Agulhas Current maintaining the nearshore water temperatures of the northeast and east coasts above 20 °C. As this current flows southward, it cools and moves offshore, resulting in cooler nearshore waters off the southeast and south coasts which also experience occasional upwelling. The southwest and west coast is strongly influenced by the Benguela Current system feeding cool, upwelled waters into the inshore zone (Day, 1981a; Shannon, 1989).

These features of climate, geomorphology, and tidal and fluvial patterns play a major role in determining the chemical properties of South African estuaries (Day, 1981c; Allanson, 1999). The aim of this chapter is to describe and compare the physico-chemical characteristics of the estuaries in the three biogeographic zones identified.

5.2 MATERIALS & METHODS

The selected open and closed estuaries were divided into the three biogeographic regions determined in the previous chapter. These were: cool-temperate estuaries (Orange estuary-Cape Agulhas), warm-temperate estuaries (Cape Agulhas-Mdumbi estuary) and subtropical estuaries (north of the Mdumbi estuary-Kosi Bay) (Figures 5.1 & 5.2).

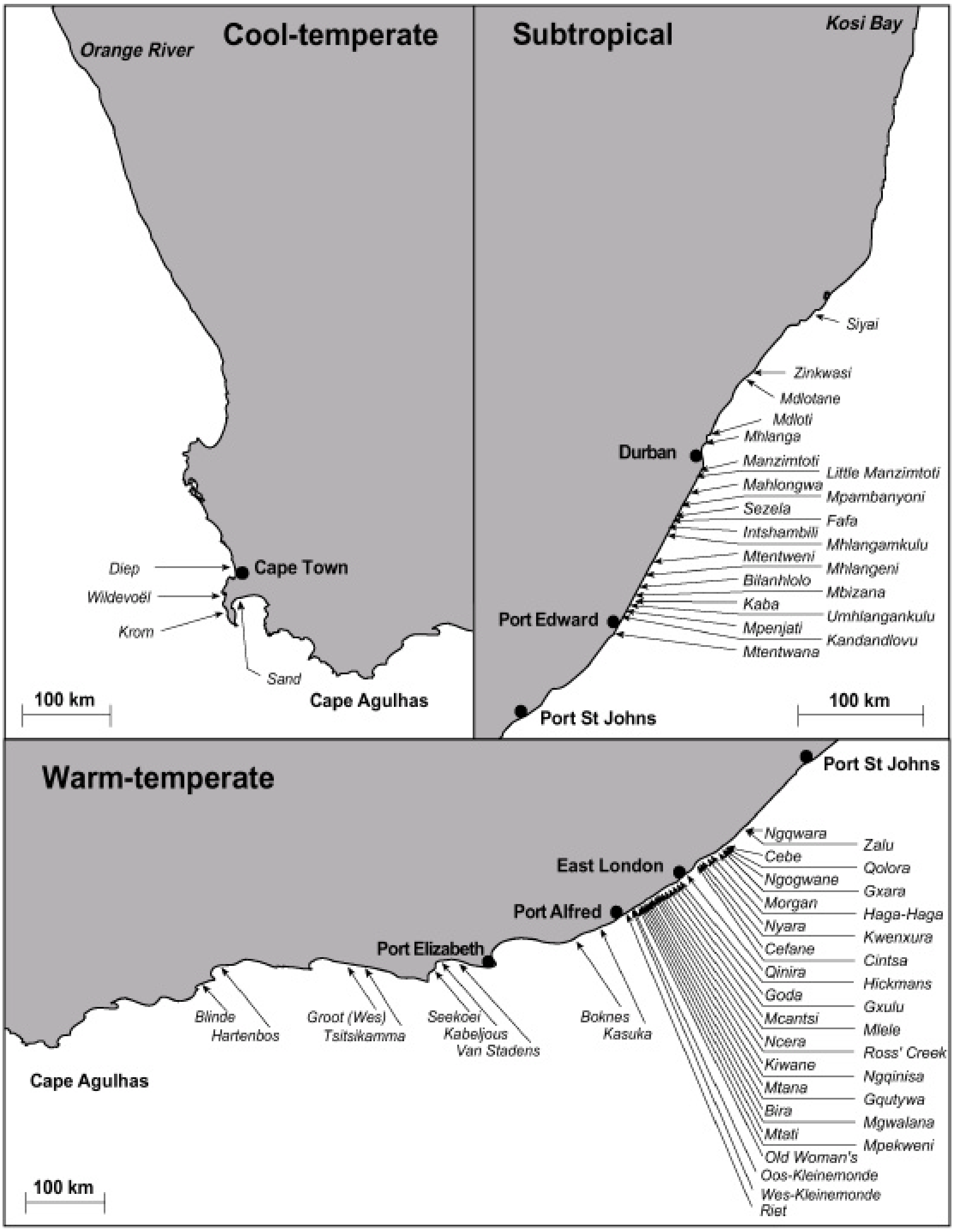


Figure 5.1. Map of closed estuaries in the cool-temperate, warm-temperate and subtropical biogeographic regions included in this study. The relative positions of the estuaries included in the study are indicated with arrows.

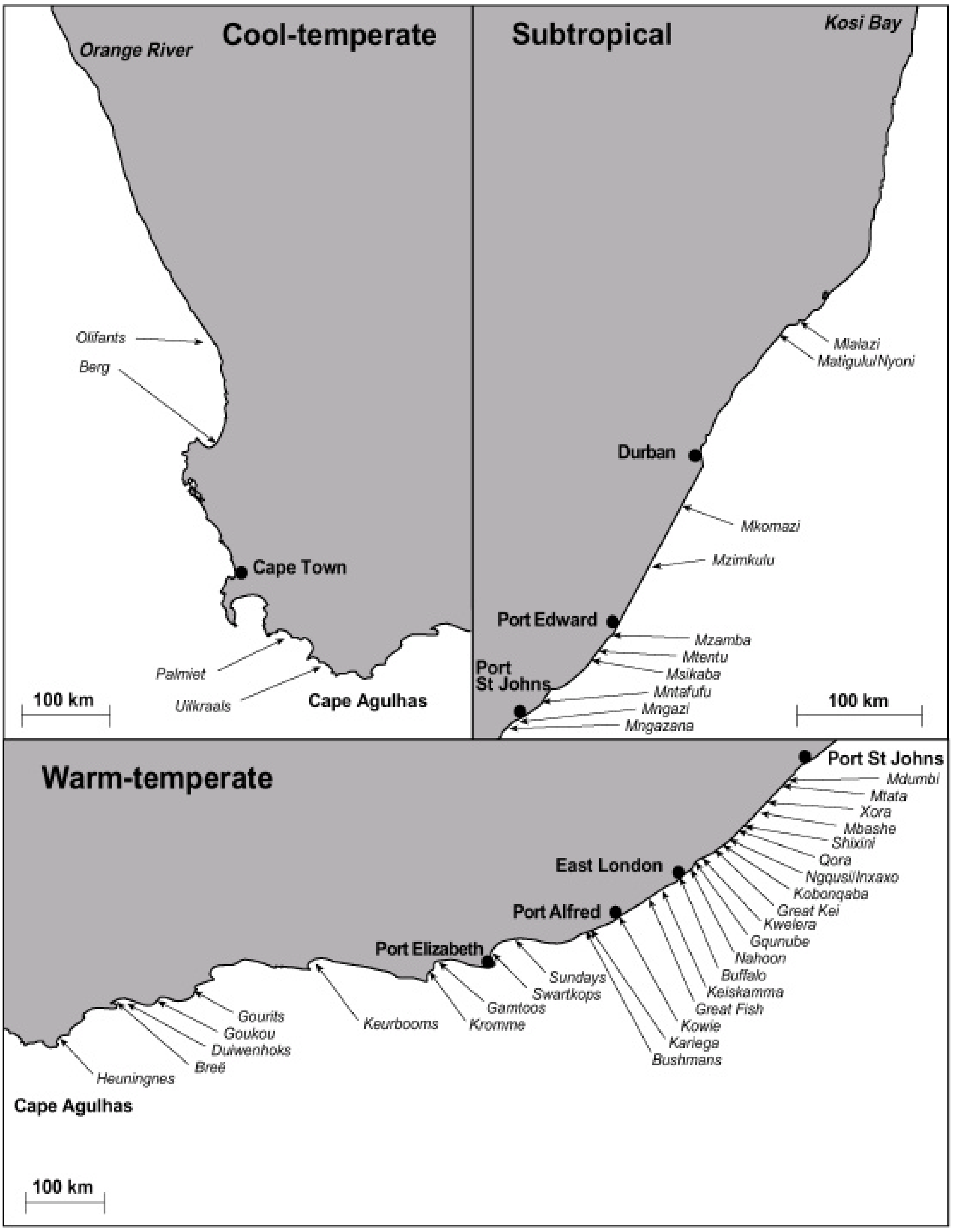


Figure 5.2. Map of open estuaries in the cool-temperate, warm-temperate and subtropical biogeographic regions included in this study. The relative positions of the estuaries included in the study are indicated with arrows.

5.2.1 Physico-chemical characteristics

Physico-chemical parameters included both horizontal and vertical measurements within each estuary. However, since the aim of this chapter is to describe and compare systems at a regional scale, the average conditions within each system were assessed. The mean (±SD) depth (m), water temperature (°C), salinity (‰), dissolved oxygen (mg l^{-1}), and turbidity (NTU) was calculated for each estuary within each biogeographic region. Because disturbance of the sediments during field sampling often resulted in high bottom water turbidity values, only surface measurements were considered. Furthermore, in some warm-temperate estuaries, turbidity readings were not taken. In these cases turbidity values were estimated from mean Secchi disc measurements taken at the time of sampling using the formula derived by Cyrus (1988a):

$$SD = 135.0 - 26.8 \ln T$$

Where SD is the Secchi disc measurement (cm) and lnT is the natural logarithm of the turbidity value (NTU).

5.2.1 Multivariate analysis

The physico-chemical data were also subject to principal component analysis (PCA) using PRIMER. Principal component analysis is a multivariate ordination method that produces a low-dimensional summary of the inter-relationships between a number of variables and is most suited to environmental data (Clarke & Warwick, 1994). Prior to conducting the PCA analysis, the physico-chemical parameters were first examined for normality. Apart from turbidity, most parameters were more or less normally distributed. Turbidity values were log- transformed (ln[1+x]). The data were also tested for any inter-correlations (Pearson *r*). In both closed and open estuaries, dissolved oxygen was significantly negatively correlated with temperature ($p<0.05$); dissolved oxygen was therefore omitted from the analysis. A PCA analysis, based on the normalised Euclidean distance, was then performed on closed and open estuaries using the following parameters: depth, temperature, salinity and turbidity. Clarke & Warwick (1994) have suggested that a PCA that accounts for approximately 70-75% of the original variation provides an adequate description of the overall structure of the inter-relationships.

5.3 RESULTS

5.3.1 Closed estuaries

5.3.1.1 Physico-chemical characteristics

Four closed estuaries were represented in the cool-temperate region (Figure 5.1). One system, the Diep estuary was open at the time of this survey. Average water depths ranged between 0.5 and 1.2 m with most systems not exceeding 1.0 m. Mean water temperatures varied between 16.9 °C recorded in the Diep estuary and 20.8 °C measured in the Sand system. Salinities measured between 2.3 ‰ in the Wildevoël system and 21.5 ‰ in the Diep estuary. Generally, mean salinities did not exceed 12 ‰. Mean dissolved oxygen levels ranged between 4.9 mg l^{-1} recorded in the Krom estuary and 8.7 mg l^{-1} in the Wildevoël system. Mean turbidities were between 6 and 20 NTU measured in the Krom and Sand estuaries respectively (Table 5.1).

Table 5.1. Mean physico-chemical parameters recorded in closed cool-temperate estuaries (number of samples; ±SD).

System	Depth (m)	Temperature (°C)	Salinity (‰)	Dissolved Oxygen (mg l^{-1})	Turbidity (NTU)
Diep	0.77 (4; 0.36)	16.86 (8; 2.45)	21.53 (8; 12.77)	5.69 (8; 1.94)	14.25 (4; 17.35)
Wildevoël	0.45 (3; 0.21)	19.75 (6; 1.91)	2.28 (6; 2.53)	8.68 (6; 0.72)	6.67 (3; 6.43)
Krom	0.53 (2; 0.29)	19.25 (4; 0.27)	9.08 (4; 0.40)	4.92 (4; 0.35)	6.00 (2; 5.66)
Sand	1.23 (3; 0.82)	20.78 (6; 0.08)	11.32 (6; 1.91)	7.90 (6; 1.32)	20.00 (3; 7.00)

Forty-one closed estuaries were included in the warm-temperate region (Figure 5.1). Seven systems, Tsitsikamma, Mcantsi, Kwenxura, Nyara, Haga-Haga, Morgan, and Qolora, were open at the time of this study. Mean water depths ranged from 0.4 m recorded in the Haga-Haga estuary to 3.4 m measured in the Qolora system. Most estuaries were between 1.0 and 2.0 m deep. Average water temperatures were between 16.3 °C recorded in the Groot (Wes) system and 26.1 °C measured in the Kasuka estuary, with most systems having temperatures between 18.0 and 24.0 °C. Mean salinities ranged between 0.6 ‰ measured in the Tsitsikamma estuary and 49.3 ‰ recorded in the Gqutywa system. Most estuaries had salinities of between 15 and 30 ‰. Mean surface dissolved oxygen levels measured between 3.5 mg l^{-1} recorded in the Nyara estuary and 11.0 mg l^{-1} recorded in the Kiwane system. Dissolved oxygen concentrations were generally in the range 5-8 mg l^{-1}. Mean turbidities varied between 0 NTU recorded in the Groot (Wes) estuary and 100 NTU in the Morgan system; most estuaries had turbidities below 10 NTU (Table 5.2).

Table 5.2. Average physico-chemical parameters recorded in closed warm-temperate estuaries (number of samples; ±SD). Turbidity values estimated from Secchi disc measurements are denoted by an asterisk (*).

System	**Depth (m)**	**Temperature (°C)**	**Salinity (‰)**	**Dissolved Oxygen (mg l^{-1})**	**Turbidity (NTU)**
Blinde	1.77 (3; 0.51)	20.85 (6; 0.65)	12.33 (6; 0.99)	5.46 (6; 1.63)	7.67 (3; 3.79)
Hartenbos	1.35 (4; 0.49)	20.19 (8; 1.22)	17.64 (8; 2.01)	7.05 (8; 1.25)	3.00 (4; 0.82)
Groot (Wes)	1.97 (3; 0.23)	16.28 (6; 1.34)	13.93 (6; 8.51)	4.29 (6; 2.45)	0.00 (3; 0.00)
Tsitsikamma	0.65 (2; 0.35)	17.73 (3; 0.64)	0.63 (3; 0.40)	8.45 (3; 0.42)	34.6*
Seekoei	1.08 (4; 0.46)	19.26 (8; 1.26)	6.13 (8; 2.22)	10.59 (8; 1.95)	9.4*
Kabeljous	1.00 (3; 0.10)	17.65 (6; 0.44)	16.45 (6; 0.66)	5.45 (6; 1.11)	2.5*
Van Stadens	2.20 (4; 0.91)	20.69 (8; 1.18)	14.55 (8; 1.64)	6.07 (8; 1.44)	0.0*
Boknes	1.80 (3; 0.20)	21.12 (6; 0.54)	16.67 (6; 0.31)	7.93 (6; 0.89)	1.8*
Kasuka	1.53 (4; 0.49)	26.11 (8; 0.70)	24.84 (8; 1.10)	4.41 (8; 0.84)	0.8*
Riet	1.67 (3; 0.49)	23.98 (6; 0.53)	20.02 (6; 4.62)	4.51 (6; 2.09)	1.2*
Wes-Kleinemond	1.92 (6; 0.31)	23.20 (12; 0.69)	18.58 (12; 1.54)	4.92 (12; 1.39)	1.1*
Oos Kleinemond	1.23 (4; 0.42)	23.00 (8; 1.45)	15.13 (8; 1.48)	6.37 (8; 0.53)	3.7*
Old Woman's	2.30 (3; 0.98)	17.42 (6; 0.41)	25.87 (6; 0.18)	6.68 (6; 0.30)	2.00 (3; 1.73)
Mpekweni	1.74 (5; 0.44)	18.14 (10; 0.66)	19.57 (10; 0.45)	8.65 (10; 1.78)	8.40 (5; 4.16)
Mtati	2.20 (5; 0.50)	17.52 (10; 0.43)	19.47 (10; 1.32)	7.56 (10; 3.25)	8.40 (5; 4.34)
Mgwalana	1.04 (5; 0.25)	19.42 (10; 0.78)	27.99 (10; 1.10)	9.50 (10; 1.40)	28.20 (5; 8.04)
Bira	1.70 (7; 0.56)	19.99 (14; 0.55)	29.76 (14; 1.38)	8.14 (14; 1.07)	14.14 (7; 10.14)
Gqutywa	0.98 (4; 0.48)	20.60 (8; 0.55)	49.34 (8; 0.22)	5.82 (8; 0.49)	15.75 (4; 4.03)
Mtana	0.90 (4; 0.29)	19.28 (8; 0.53)	29.40 (8; 0.78)	7.60 (8; 0.30)	9.50 (4; 4.66)
Ngqinisa	0.37 (3; 0.23)	17.20 (3; 0.78)	31.53 (3; 0.06)	8.81 (3; 0.20)	15.00 (3; 11.14)
Kiwane	1.95 (4; 1.03)	18.45 (8; 0.45)	20.16 (8; 0.16)	11.01 (8; 0.22)	6.25 (4; 3.30)

Table 5.2 continued.

System	Depth (m)	Temperature (°C)	Salinity (‰)	Dissolved Oxygen (mg l^{-1})	Turbidity (NTU)
Ross' Creek	0.57 (3; 0.40)	18.94 (5; 0.40)	6.58 (5; 0.19)	6.62 (5; 1.23)	20.00 (3; 0.00)
Ncera	1.22 (5; 0.35)	20.46 (10; 0.40)	33.66 (10; 0.76)	7.70 (10; 2.05)	2.40 (5; 2.61)
Mlele	1.07 (3; 0.15)	19.77 (6; 0.10)	15.30 (6; 0.11)	7.51 (6; 0.22)	16.00 (3; 0.00)
Mcantsi	1.03 (3; 0.06)	23.03 (6; 0.40)	14.10 (6; 0.71)	6.96 (6; 1.25)	6.67 (3; 3.22)
Gxulu	1.37 (6; 0.22)	22.06 (12; 1.02)	29.64 (12; 0.70)	6.41 (12; 0.72)	3.17 (6; 2.56)
Goda	1.97 (3; 0.40)	21.00 (6; 0.48)	32.55 (6; 0.11)	6.09 (6; 0.52)	5.33 (3; 4.04)
Hickmans	1.60 (3; 0.36)	21.98 (6; 0.32)	18.83 (6; 1.96)	6.42 (6; 1.89)	3.67 (3; 0.58)
Qinira	1.70 (4; 0.22)	21.50 (8; 0.40)	28.01 (8; 0.56)	6.40 (8; 0.71)	4.50 (4; 1.92)
Cintsa	1.38 (4; 0.26)	23.78 (8; 1.13)	31.13 (8; 0.85)	5.53 (8; 0.60)	3.50 (4; 1.00)
Cefane	0.93 (4; 0.37)	23.50 (8; 0.91)	28.90 (8; 0.48)	5.00 (8; 0.22)	6.00 (4; 4.24)
Kwenxura	0.80 (3; 0.66)	19.70 (5; 2.49)	29.10 (5; 6.93)	6.98 (5; 0.86)	35.67 (3; 32.08)
Nyara	0.55 (2; 0.35)	19.03 (3; 1.38)	21.77 (3; 12.97)	3.50 (2; 0.29)	94.50 (2; 62.93)
Haga-Haga	0.35 (2; 0.21)	21.33 (3; 0.95)	25.80 (3; 0.72)	8.01 (3; 0.07)	23.00 (2; 12.73)
Morgan	0.57 (3; 0.12)	21.98 (6; 1.10)	8.63 (6; 13.04)	8.37 (6; 0.40)	100.33 (3; 11.24)
Gxara	1.30 (3; 0.70)	21.37 (6; 0.76)	18.97 (6; 3.08)	5.71 (6; 1.50)	16.50 (2; 9.19)
Ngogwane	1.47 (3; 0.35)	22.62 (6; 1.03)	20.58 (6; 0.77)	5.64 (6; 1.08)	0.33 (3; 0.58)
Qolora	3.40 (3; 0.75)	21.28 (6; 1.17)	16.52 (6; 10.61)	4.52 (6; 3.68)	4.33 (3; 3.79)
Cebe	1.20 (3; 0.60)	24.22 (6; 0.34)	25.67 (6; 0.21)	6.74 (6; 0.18)	11.33 (3; 7.77)
Zalu	1.10 (3; 0.62)	20.58 (6; 0.38)	20.62 (6; 0.26)	6.25 (6; 0.77)	4.33 (3; 4.04)
Ngqwara	0.90 (3; 0.26)	21.90 (6; 1.33)	25.58 (6; 0.64)	6.41 (6; 1.30)	1.00 (3; 1.00)

Twenty-two closed estuaries were represented in the subtropical region (Figure 5.1). Six systems, Kandandlovu, Mpenjati, Little Manzimtoti, Manzimtoti, Mhlanga, and Siyai were open at the time of this study. The mean water depth ranged between 0.5 m recorded in the Mhlanga estuary and 2.9 m in the Mdlotane system with most estuaries having water depths of 1.0-2.0 m. Mean water temperatures measured between 20.7 and 28.2 °C recorded in the Mhlanga and Fafa estuaries respectively. Most estuaries had water temperatures of between 22.0 and 28.0 °C. Salinities generally did not exceed 15 ‰ and ranged between 0.1 ‰ recorded in the Mdloti estuary and 16.1 ‰ in the Siyai system. Mean dissolved oxygen levels were between

1.7 mg l^{-1} measured in the Mdlotane estuary and 7.4 mg l^{-1} in the Mtentwana system. Approximately 40% of the estuaries had dissolved oxygen levels below 5.0 mg l^{-1}. Turbidities generally did not exceed 20 NTU and ranged between 4 and 58 NTU recorded in the Mtentweni and Zinkwasi estuaries respectively (Table 5.3).

Table 5.3. Average physico-chemical parameters recorded in closed subtropical estuaries (number of samples; ±SD).

System	**Depth (m)**	**Temperature (°C)**	**Salinity (‰)**	**Dissolved Oxygen (mg l^{-1})**	**Turbidity (NTU)**
Mtentwana	1.80 (3; 0.89)	28.05 (6; 1.16)	14.20 (6; 3.99)	7.43 (6; 1.21)	11.00 (3; 3.61)
Kandandlovu	1.00 (2; 0.42)	24.48 (4; 1.19)	11.38 (4; 8.70)	4.30 (4; 1.25)	8.00 (2; 7.07)
Mpenjati	1.77 (3; 0.15)	22.22 (6; 1.35)	10.10 (6; 6.50)	5.62 (6; 3.00)	8.00 (3; 1.00)
Umhlangankulu	2.00 (3; 0.50)	23.37 (6; 0.75)	4.05 (6; 0.08)	5.94 (6; 0.64)	9.00 (3; 1.73)
Kaba	0.85 (2; 0.35)	26.73 (4; 1.63)	12.08 (4; 1.13)	7.36 (4; 0.65)	9.50 (2; 2.12)
Mbizana	2.13 (4; 0.44)	24.70 (8; 1.20)	3.49 (8; 1.28)	6.15 (8; 0.72)	5.00 (4; 0.82)
Bilanhlolo	1.37 (3; 0.46)	26.37 (6; 0.94)	10.53 (6; 9.28)	6.05 (6; 1.65)	5.00 (3; 0.00)
Mhlangeni	1.07 (3; 0.25)	27.03 (6; 1.06)	13.60 (6; 5.97)	6.94 (6; 2.67)	13.00 (3; 2.65)
Mtentweni	1.50 (3; 0.30)	25.57 (6; 2.25)	10.02 (6; 6.25)	5.39 (6; 1.95)	4.33 (3; 1.16)
Mhlangamkulu	1.68 (2; 0.25)	22.90 (4; 0.78)	0.50 (4; 0.00)	4.70 (4; 1.94)	9.50 (2; 0.71)
Intshambili	1.15 (3; 0.38)	25.40 (6; 0.64)	3.17 (6; 0.14)	5.02 (6; 1.09)	9.33 (3; 0.58)
Fafa	0.73 (3; 0.59)	28.16 (5; 0.80)	2.34 (5; 1.09)	6.83 (5; 0.62)	8.67 (3; 2.31)
Sezela	1.80 (3; 0.50)	25.70 (6; 0.28)	4.27 (6; 0.22)	3.11 (6; 0.86)	18.67 (3; 7.23)
Mpambanyoni	0.68 (3; 0.49)	24.14 (5; 2.45)	4.46 (5; 2.20)	6.91 (5; 3.54)	18.33 (3; 7.77)
Mahlongwa	1.35 (3; 0.63)	26.77 (6; 0.23)	2.30 (6; 0.70)	6.10 (6; 0.37)	10.00 (3; 1.00)
Little Manzimtoti	1.23 (3; 0.15)	20.83 (6; 0.83)	1.45 (6; 1.60)	2.31 (6; 1.17)	26.33 (3; 12.10)
Manzimtoti	1.05 (3; 0.13)	21.83 (6; 0.37)	1.70 (6; 1.24)	5.24 (6; 3.46)	49.33 (3; 12.90)
Mhlanga	0.45 (3; 0.09)	20.67 (3; 0.35)	9.57 (3; 13.11)	4.22 (3; 1.74)	36.67 (3; 25.17)
Mdloti	2.33 (3; 0.81)	21.83 (6; 0.39)	0.10 (6; 0.00)	2.93 (6; 2.55)	8.33 (3; 2.52)
Mdlotane	2.93 (3; 0.31)	28.07 (6; 1.91)	0.23 (6; 0.05)	1.74 (6; 2.00)	10.67 (3; 2.08)
Zinkwasi	1.30 (4; 0.22)	27.73 (8; 1.25)	12.25 (8; 2.15)	4.40 (8; 1.83)	58.25 (4; 4.19)
Siyai	1.18 (2; 1.03)	26.10 (4; 0.61)	16.13 (4; 15.45)	4.25 (4; 2.82)	19.50 (2; 13.44)

5.3.1.2 Multivariate analysis

The results of the PCA analysis of closed estuaries revealed that the first two PC axes accounted for approximately 71% of the variation between the samples (Table 5.4). The first PC axis was strongly related to turbidity and depth, while the second axis was strongly related to salinity and temperature (Table 5. 4). The pattern produced by the ordination showed a broad gradation from the warm, turbid, relatively low salinity subtropical estuaries in the upper half of the plot toward the cooler, clearer, more saline systems of the warm-temperate region in the lower right half of the ordination (Figure 5.3).

Table 5.4. Coefficients in the linear combinations of the physico-chemical variables making up the principal components for closed estuaries; the percentage variation explained by the principal components are also shown.

Variable	**PC1**	**PC2**	**PC3**	**PC4**
Depth	0.668	0.261	-0.309	0.625
Temperature	0.034	0.677	0.734	0.043
Salinity	0.189	-0.681	0.598	0.378
Turbidity	-0.719	0.096	-0.095	0.682
% variation	36.6	34.1	17.3	12.0

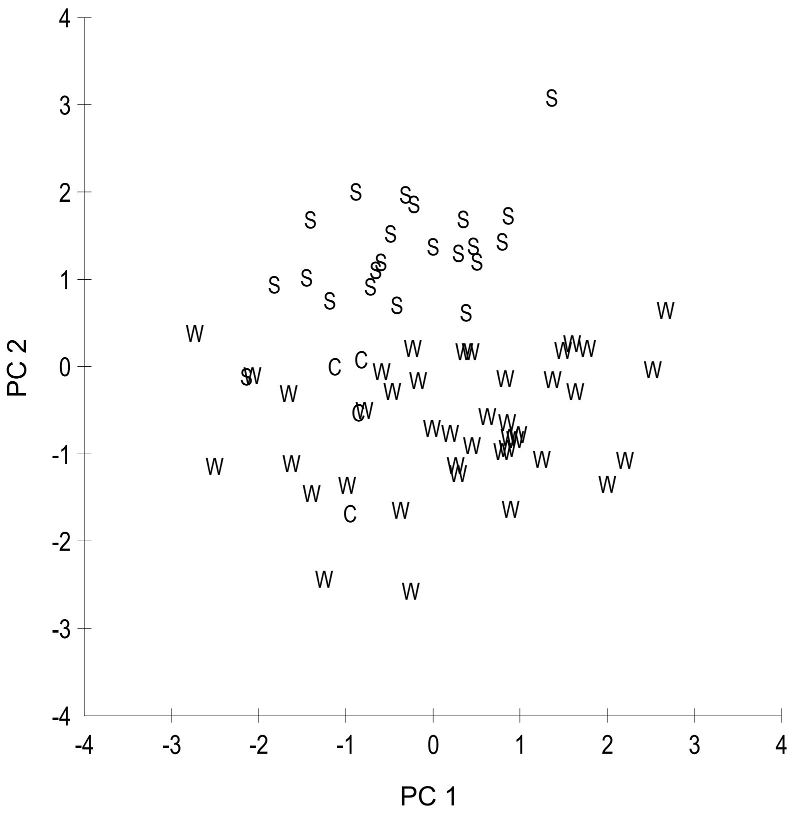


Figure 5.3. PCA ordination of physico-chemical variables for closed South African estuaries (C = cool-temperate estuaries; W = warm-temperate estuaries; S = subtropical estuaries).

5.3.2 Open estuaries

5.3.2.1 Physico-chemical characteristics

Four open estuaries were represented in the cool-temperate region (Figure 5.2). Average water depths generally exceeded 1.5 m and ranged between 0.8 m recorded in the Uilkraals system and 2.7 m measured in the Berg estuary. Mean water temperatures did not exceed 18.0 °C and varied between 14.0 °C recorded in the Olifants estuary and 17.3 °C measured in the Uilkraals system. Salinities ranged between 15.4 and 20.0 ‰ recorded in the Uilkraals and Berg estuaries respectively. Dissolved oxygen levels were normally above 8.0 mg l^{-1} and ranged between 6.8 mg l^{-1} recorded in the Berg estuary and 8.7 mg l^{-1} in the Olifants system. Average turbidities were between 4 NTU measured in the Palmiet estuary and 31 NTU recorded in the Olifants estuary; turbidities generally did not exceed 14 NTU (Table 5.5).

Table 5.5. Average physico-chemical parameters recorded in open cool-temperate estuaries (number of samples; ±SD).

System	Depth (m)	Temperature (°C)	Salinity (‰)	Dissolved Oxygen (mg l^{-1})	Turbidity (NTU)
Olifants	1.48 (5; 0.74)	13.95 (10; 2.51)	17.85 (10; 14.89)	8.73 (10; 0.92)	30.80 (5; 17.34)
Berg	2.73 (5; 1.34)	16.42 (10; 1.75)	20.00 (10; 11.25)	6.76 (10; 0.51)	13.60 (5; 7.99)
Palmiet	1.83 (3; 0.35)	14.97 (6; 0.43)	17.77 (6; 15.31)	8.43 (6; 1.41)	4.00 (3; 0.00)
Uilkraals	0.83 (3; 0.12)	17.33 (6; 0.66)	15.43 (6; 5.17)	8.49 (6; 0.26)	5.33 (3; 1.53)

Twenty-eight open estuaries were represented in the warm-temperate region (Figure 5.2). Average water depths ranged between 1.0 and 3.4 m with most systems being more than 2.0 m deep. Mean water temperatures ranged between 14.9 °C recorded in the Heuningnes estuary and 23.0 °C measured in the Kariega system and were mostly within the range 18-22 °C. Average salinities measured between 4.4 ‰ recorded in the Great Kei estuary and 33.6 ‰ measured in the Gourits estuary and mostly exceeded 20 ‰. Mean dissolved oxygen values were generally higher than 6.0 mg l^{-1} and ranged between 5.2 mg l^{-1} recorded in the Keurbooms estuary and 8.5 mg l^{-1} measured in the Nahoon estuary. Average turbidities ranged between 1 and 1300 NTU with most estuaries having turbidities less than 20 NTU (Table 5.6).

Table 5.6. Average physico-chemical parameters recorded in open warm-temperate estuaries (number of samples; ±SD). Turbidity values estimated from Secchi disc measurements are denoted by an asterisk (*).

System	**Depth (m)**	**Temperature (°C)**	**Salinity (‰)**	**Dissolved Oxygen (mg l^{-1})**	**Turbidity (NTU)**
Heuningnes	1.63 (3; 0.76)	14.85 (6; 0.24)	18.17 (6; 12.63)	7.49 (6; 0.15)	25.00 (3; 18.19)
Breë	2.52 (5; 1.07)	19.06 (10; 0.69)	10.71 (10; 5.03)	7.36 (10; 0.20)	7.40 (5; 1.67)
Duiwenhoks	2.68 (4; 1.38)	15.88 (8; 0.36)	31.63 (8; 4.27)	6.58 (8; 0.19)	5.75 (4; 0.50)
Goukou	1.48 (4; 26.30)	17.26 (7; 0.35)	23.33 (7; 8.88)	6.17 (7; 0.29)	2.75 (4; 0.50)
Gourits	2.10 (4; 0.70)	17.41 (8; 0.56)	33.64 (8; 1.91)	6.28 (8; 0.20)	10.75 (4; 8.38)
Keurbooms	1.63 (8; 0.87)	21.36 (16; 1.10)	27.19 (16; 6.24)	5.23 (16; 1.08)	0.63 (8; 0.52)
Kromme	2.39 (8; 1.05)	18.84 (18; 0.89)	30.23 (18; 1.99)	6.53 (18; 0.92)	0.0*
Gamtoos	1.59 (8; 0.69)	19.16 (16; 0.62)	19.80 (16; 10.32)	8.08 (16; 1.97)	11.4*
Swartkops	2.22 (6; 0.94)	18.58 (12; 0.32)	30.21 (12; 2.68)	6.25 (12; 0.93)	1.5*
Sundays	2.41 (7; 0.84)	20.45 (14; 1.11)	18.11 (14; 9.95)	7.61 (14; 1.63)	23.8*
Bushmans	2.44 (7; 1.00)	21.05 (13; 1.43)	32.28 (13; 1.23)	6.91 (13; 0.59)	14.5*
Kariega	2.39 (8; 0.51)	22.95 (16; 2.03)	31.59 (16; 1.88)	6.59 (16; 0.81)	4.7*
Kowie	2.75 (6; 0.89)	21.48 (13; 1.38)	30.04 (13; 3.01)	7.02 (13; 0.40)	6.9*
Great Fish	1.92 (5; 0.27)	21.55 (10; 2.65)	12.60 (10; 13.13)	7.88 (10; 0.60)	73.0*
Keiskamma	2.01 (8; 0.74)	18.41 (16; 0.34)	22.09 (16; 7.76)	6.77 (16; 1.24)	43.38 (8; 35.81)
Buffalo	3.43 (3; 1.96)	18.17 (6; 1.45)	31.17 (6; 1.57)	7.85 (6; 1.39)	10.00 (3; 3.00)
Nahoon	2.32 (5; 1.37)	19.41 (10; 0.92)	32.61 (10; 0.66)	8.45 (10; 1.20)	5.80 (5; 3.03)
Gqunube	1.68 (4; 0.61)	19.98 (8; 1.05)	32.81 (8; 0.11)	6.78 (8; 0.63)	15.75 (4; 11.70)
Kwelera	1.56 (5; 0.73)	21.01 (10; 1.71)	32.12 (10; 0.50)	6.82 (10; 0.57)	15.80 (5; 7.16)
Great Kei	1.78 (6; 0.88)	22.17 (11; 0.76)	4.43 (11; 10.13)	7.10 (11; 0.43)	1300.00 (6; 0.00)
Kobonqaba	1.53 (4; 1.21)	20.38 (8; 2.74)	28.36 (8; 7.09)	7.05 (8; 0.26)	5.50 (4; 1.73)
Ngqusi/Inxaxo	2.14 (7; 1.05)	18.06 (14; 0.96)	28.03 (14; 11.21)	6.55 (14; 1.06)	7.14 (7; 4.18)
Qora	1.03 (3; 0.21)	17.02 (6; 2.00)	23.38 (6; 10.51)	7.94 (6; 0.36)	83.33 (3; 45.24)
Shixini	1.03 (3; 0.65)	18.84 (5; 1.98)	30.86 (5; 1.18)	7.83 (5; 0.16)	14.33 (3; 5.13)
Mbashe	2.75 (4; 1.80)	20.24 (7; 1.71)	14.64 (7; 13.90)	7.36 (7; 1.54)	163.00 (4; 240.83)
Xora	2.10 (4; 0.91)	22.43 (7; 1.94)	27.84 (7; 7.05)	6.70 (7; 1.27)	17.67 (3; 9.71)
Mtata	3.08 (5; 1.84)	21.40 (10; 3.36)	12.59 (10; 11.46)	7.62 (10; 0.30)	100.20 (5; 69.84)
Mdumbi	2.08 (4; 1.37)	21.54 (8; 2.08)	27.76 (8; 6.73)	7.32 (8; 0.84)	8.00 (4; 2.83)

Ten open estuaries were represented in the subtropical region (Figure 5.2). The average water depth ranged from 0.9 m in the Mkomazi estuary to 4.1 m recorded in the Msikaba system; most estuaries had water depths exceeding 2.0 m. Mean water temperatures ranged between 23.5 °C recorded in the Mngazana, Mzimkulu and Matigulu/Nyoni estuaries and 27.0 °C measured in the Mlalazi system. Salinities ranged from 3.0 ‰ in the Matigulu/Nyoni estuary to 28.5 ‰ recorded in the Mngazana system with most estuaries having mean salinities below 20 ‰. Mean dissolved oxygen levels exceeded 5.0 mg l^{-1} and ranged between 5.2 mg l^{-1} recorded in the Matigulu/Nyoni estuary and 7.4 mg l^{-1} in the Mtentu system. Average turbidities were between 5 NTU recorded in the Mtentu estuary and 591 NTU in the Mkomazi system; most estuaries had turbidities below 20 NTU (Table 5.7).

Table 5.7. Average physico-chemical parameters recorded in open subtropical estuaries (number of samples; ±SD).

System	Depth (m)	Temperature (°C)	Salinity (‰)	Dissolved Oxygen (mg l^{-1})	Turbidity (NTU)
Mngazana	2.33 (6; 0.73)	23.48 (12; 1.39)	28.48 (12; 7.69)	5.90 (12; 1.65)	12.50 (6; 6.47)
Mngazi	2.08 (5; 1.23)	24.10 (10; 0.66)	19.25 (10; 13.73)	5.90 (10; 1.40)	86.20 (5; 35.17)
Mntafufu	3.18 (4; 2.31)	24.76 (8; 1.31)	20.30 (8; 12.58)	6.86 (8; 1.97)	19.50 (4; 2.38)
Msikaba	4.08 (4; 1.60)	25.84 (8; 1.92)	17.00 (8; 13.22)	7.33 (8; 1.58)	10.25 (4; 1.71)
Mtentu	3.85 (4; 2.45)	25.60 (8; 1.53)	18.90 (8; 12.22)	7.43 (8; 1.16)	4.50 (4; 2.08)
Mzamba	2.30 (3; 1.05)	26.75 (6; 1.62)	23.93 (6; 12.71)	7.01 (6; 1.43)	13.33 (3; 3.51)
Mzimkulu	1.06 (5; 0.38)	23.53 (10; 1.57)	14.08 (10; 13.09)	7.06 (10; 1.11)	12.00 (5; 2.00)
Mkomazi	0.85 (4; 0.62)	24.43 (7; 0.51)	3.44 (7; 8.98)	6.50 (7; 0.92)	591.25 (4; 170.91)
Matigulu/Nyoni	1.12 (7; 0.41)	23.54 (14; 0.74)	3.00 (14; 6.88)	5.21 (14; 1.81)	55.71 (7; 15.55)
Mlalazi	1.72 (5; 0.51)	26.98 (10; 0.84)	9.20 (10; 9.41)	6.66 (10; 0.59)	19.60 (5; 3.65)

5.3.2.2 Multivariate analysis

The first two axes of the PCA of open estuaries accounted for approximately 76% of the variation between the sites (Table 5.8). The first PC axis was related to salinity and turbidity, while the second axis was correlated with depth and temperature (Table 5.8). The ordination produced by the PCA showed a broad gradation from cool, clear, saline warm-temperate systems in the bottom left of the plot toward the warmer, less saline, turbid estuaries of the subtropical region in right hand of the ordination (Figure 5.4).

Table 5.8. Coefficients in the linear combinations of the physico-chemical variables making up the principal components for open estuaries; the percentage variation explained by the principal components are also shown.

Variable	**PC1**	**PC2**	**PC3**	**PC4**
Depth	-0.196	0.751	-0.629	-0.053
Temperature	0.334	0.655	0.669	0.109
Salinity	-0.659	0.031	0.180	0.730
Turbidity	0.645	-0.080	-0.353	0.673
% variation	44.9	30.8	14.9	9.4

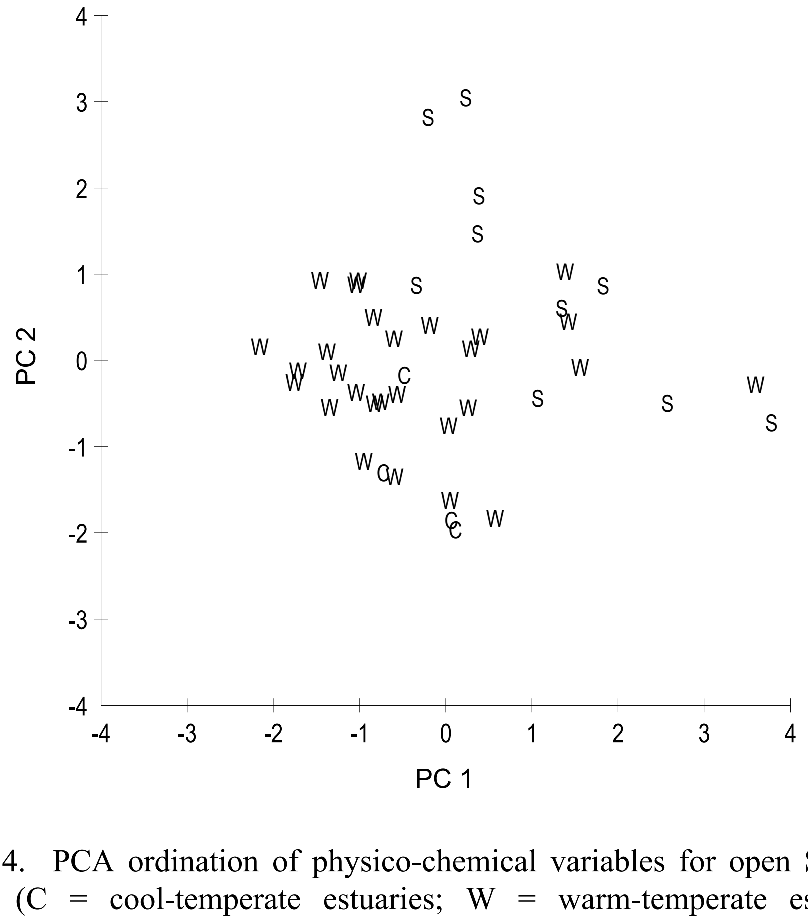


Figure 5.4. PCA ordination of physico-chemical variables for open South African estuaries (C = cool-temperate estuaries; W = warm-temperate estuaries; S = subtropical estuaries).

5.4 DISCUSSION

5.4.1 Closed estuaries

Closed estuaries, also sometimes referred to as blind estuaries (Day, 1981d) or lagoons (Begg, 1984a), have small catchments (<500 km^2) and river flow is insufficient during most months to prevent closure of the mouth by a bar built up from longshore and/or onshore movement of sand (Whitfield, 1992). The closed estuaries selected during this study had catchments ranging between 8 and 1495 km^2 with the vast majority being less than 300 km^2. The mean annual runoff (MAR) into these estuaries ranged between 1 and 117 x 10^6 m^3 with most systems receiving less than 30 x 10^6 m^3 (Eksteen *et al.*, 1979; NRIO, 1986; 1987a; 1987b; 1987c).

Only four closed estuaries were represented in the cool-temperate region during this study; all these systems were situated on the southwest coast between Cape Columbine and Cape Agulhas (Figure 5.2). Although many systems on the west coast, north of Cape Columbine have relatively large catchments, due to the arid climate, most comprise dry riverbeds and only carry water at times of exceptional rainfall (Heydorn, 1991). Systems such as the Holgat, Swartlintjies and Spoeg, for example have catchments of over 1500 km^2 but the MAR of these systems does not exceed 3 m^{3}x10^6 (NRIO, 1988).

The cool-temperate southwest coast is very dry in late summer and during this period, runoff is generally insufficient to maintain an open mouth condition in these estuaries. Systems such as the Diep and Sand, for example, are usually open during the winter rainfall period but are closed by a sandbar in summer (Millard & Scott, 1954; Morant & Grindley, 1982; Morant, 1991; Quick & Harding, 1994). Only one cool-temperate estuary, the Diep was open at the time of this study.

Rainfall (and runoff) in the warm-temperate region is relatively low and it is only during periods of high fluvial discharge that closed estuaries in this region tend to breach. Bickerton & Pierce (1988), for example, found that the sandbar at the mouth of the Seekoei estuary is only breached during rare major floods. In the Oos-Kleinemond estuary, mouth-opening events were generally found to occur during or shortly after periods of high rainfall (usually exceeding 100 mm) (Cowley &

Whitfield, 2001). Perissinotto *et al*. (2000) observed that mouth breaching in the Nyara estuary also occurred following heavy rains. Dundas (1994), however, noted that mouth opening in the Seekoei, Kabeljous and Van Stadens estuaries was not only related to freshwater inflow but also resulted from high seas overtopping and lowering the sand bar. Seven systems (Tsitsikamma, Mcantsi, Kwenxura, Nyara, Haga-Haga, Morgan, Qolora) were open during this study and most of these had breached as a result of recent heavy rains; many of these estuaries were also located in the relatively higher rainfall area north of East London.

Subtropical estuaries are normally closed during the dry winter season but frequently open following increased river discharge during the summer rainy period (Cooper *et al.* 1999). Begg (1984b) reported a close relationship between mouth condition and rainfall in many closed KwaZulu-Natal estuaries. Systems such as the Umhlangankulu, Mhlangeni, iNtshambili, and Little Manzimtoti frequently opened after heavy summer downpours (Begg, 1984b). The Mhlanga estuary also frequently opens during the summer rainy period but is normally closed during the winter (Whitfield, 1980a; 1980b; 1980c; Begg, 1984b; Harrison & Whitfield, 1995). The Mdloti estuary is also normally completely closed during winter (Blaber *et al*., 1984). The Siyai estuary is closed for most of the year and only opens for short periods after major rainfall events (van der Elst *et al*., 1999). Although rainfall and river flow is usually responsible for breaching the mouths of these estuaries, overwash-induced breaching, through lowering of the barrier to a point which enables rising water levels to form an outlet has also been observed in the Mhlanga estuary (Begg, 1984a). Six systems (Kandandlovu, Mpenjati, Little Manzimtoti, Manzimtoti, Mhlanga, Siyai) were open at the time of this study and these had breached following recent rains in the catchment.

Average water depths in closed cool-temperate estuaries were generally below 1.0 m, with only the Sand estuary having a mean depth exceeding 1.0 m (Table 5.1). This system, however, has been subject to various degrees of dredging (Morant & Grindley, 1982), with Harding (1994) reporting an average depth of 1.4 m. Water depths recorded in the Diep estuary were generally below 1.0 m (Millard & Scott, 1954; Day 1981a) while Heinecken (1985) found that the Wildevoël system did not exceed 0.6 m deep.

Closed warm-temperate estuaries were generally deeper than cool-temperate systems and average water depths were mostly 1-2 m (Table 5.2). Other workers reported similar conditions; the depth of the Hartenbos estuary was between 1.0 and 3.0 m (Day, 1981a) while the average depth of the Groot (Wes) system was approximately 1.0 m (Morant & Bickerton, 1983). In both the Seekoei and Kabeljous estuaries, water depths generally exceeded 1.6 m (Bickerton & Pierce, 1988). The depth of the Wes-Kleinemond estuary exceeded 2.0 m (Blaber, 1973) while the Oos-Kleinemond estuary is between 1.0 and 2.0 m deep (Cowley & Whitfield, 2001). The mean depths of the Mpekweni, Mtati, Mgwalana, Bira, and Gqutya estuaries generally varied between 1.0 to 2.0 m (Vorwerk *et al.*, 2001).

Closed estuaries along the warm-temperate south and southeast coasts develop behind low-elevation barriers fronted by wide, gently sloping beaches (Cooper, 2001). These systems are impounded at or close to high tide level, and as a result, breaching does not result in a dramatic reduction in water level (Cooper, 2001). Perissinotto *et al.* (2000), however, noted that after the mouth of the Nyara estuary opened, following heavy rains, water depths were reduced from an average of 2.2 m to a maximum of 1.0 m. Many of the relatively shallow estuaries reported during this study, such as the Tsitsikamma, Nyara, Haga-Haga and Morgan were also systems that had recently breached following heavy rains.

Closed estuaries that occur along the subtropical northeast (KwaZulu-Natal) coast develop behind steep beaches and have high berms that maintain a water level above high tide level (Cooper, 2001). Due to their bed levels being elevated above mean sea level, water depths in these systems rapidly decline when they open and many estuaries tend to drain (Cooper *et al.*, 1999; Cooper, 2001). Begg (1984b) noted that following breaching the Umhlangankulu system rapidly empties and virtually drains completely. A drop in water level of over 1.0 m has also been reported in the Mhlangeni, Sezela and Mahlongwa estuaries following mouth opening (Begg, 1984b). In the Mhlanga estuary, a drop in water level of approximately 1.0 m has been reported following breaching (Whitfield, 1980a; 1980b; 1980c; Begg 1984b), thus exposing large areas of the estuary bed (Cooper, 1989; Cooper & Harrison, 1992). The Mhlanga estuary, which had opened just prior to this survey, was the shallowest recorded system in the subtropical region (0.5 m) (Table 5.3). During periods of mouth closure, water levels increase and the adjacent floodplain often becomes inundated (Begg, 1984a). During this study, most estuaries had average water depths of between 1.0 and 2.0 m. Begg (1984a) also reported average water depths of over 1.0 m for most of the closed estuaries included in this study.

Water temperatures in closed estuaries are influenced by both riverine and marine conditions during the open phase, while throughout the closed phase solar heating and evaporative cooling are the main factors that determine water temperatures (Day, 1981e; Whitfield, 1992; 1998). Mean water temperatures of estuaries in the cool-temperate region usually did not exceed 20 °C (Table 5.1). Clark *et al.* (1994) reported mean temperatures of 15 °C in winter and 23-24 °C in summer in the Sand estuary. Temperatures in the Diep estuary reach a summer maximum of 24 °C and in winter decline to a mean of 11 °C (Day, 1981a). Millard & Scott (1954) found that, when the mouth was open, marine waters exerted a cooling influence in the lower reaches of the Diep estuary. The cooler temperatures reported in the Diep estuary during this study (17 °C) is probably a result of the open mouth condition.

Average water temperatures in closed warm-temperate estuaries during this study were generally in the range 18-24 °C (Table 5.2). Bickerton (1982) reported mean seasonal temperatures in the Hartenbos estuary of 15 °C in winter to 26 °C in summer. Summer temperatures recorded in the Groot (Wes) measured 20-23 °C while winter temperatures were 17-20 °C (Morant & Bickerton, 1983). Mean monthly temperatures recorded in the Seekoei, Kabeljous and Van Stadens estuaries measured 14-18 °C in winter and 17-25 °C in summer (Dundas, 1994). Water temperatures in the Wes-Kleinemond estuary also showed a clear annual cycle with winter temperatures of 12-17 °C and summer temperatures of 22-27 °C (Blaber, 1973). In the Oos-Kleinemond estuary, mean water temperatures ranged from 15-16 °C in winter to 26-27 °C in summer (Cowley & Whitfield, 2001; Vorwerk *et al.*, 2001). Mean water temperatures in the Mpekweni, Mtati, Mgwalana, Bira, and Gqutya estuaries measured 13-18°C in winter and 28-29 °C in summer (Vorwerk *et al*., 2001). Perissinotto *et al*. (2000) recorded water temperatures of 28-30 °C in the Nyara estuary in late summer but by early winter, these values had declined to 18-20 °C.

Water temperatures in subtropical estuaries were higher than those recorded in warm- and cool-temperate estuaries and were mostly between 22 and 28 °C (Table 5.3). From Begg (1984b) average water temperatures of those KwaZulu-Natal estuaries included in this study generally fell within the range 15-19 °C during winter and 25-32 °C in summer. Whitfield (1980c) recorded a maximum temperature of 30 °C in the Mhlanga estuary in summer with a minimum of 14 °C in winter while Harrison & Whitfield (1995) found that water temperatures in the system were generally above 27 °C in summer and below 19 °C in winter. In the Mdloti estuary, temperatures as low as 13 °C have been reported in winter but rose to 27 °C in summer (Blaber *et al*., 1984; Cyrus, 1988b).

Although tidal exchange and salinity gradients may be present when closed systems open, during the normally closed phase, salinities in these systems depend on the ratio between losses through evaporation and seepage through the sand bar, and gains through river discharge plus direct precipitation (Day, 1981e). If the gains exceed the losses, the salinity decreases and the level of the estuary rises until it breaches the bar at the mouth. If the losses by evaporation exceed the gains of fresh water (e.g. during droughts) then the salinity of the estuary may become hypersaline (>40 ‰) (Whitfield & Bruton, 1989).

Average salinities recorded in closed cool-temperate estuaries during this study were generally low (<12 ‰) (Table 5.1) with the high salinity reported in the Diep system (>20 ‰) probably a result of marine input due to the open mouth condition. Conditions in the Diep estuary can change from almost fresh in winter to hypersaline (>35 ‰) in late summer (Millard & Scott, 1954; Day, 1981a; Grindley & Dudley, 1988). Heinecken (1985) also found that the salinities in the Wildevoël fluctuated considerably according to the seasons due to a high evaporative loss during summer and fresh water input from the catchment in winter. Harding (1994) reported mean salinities of 6-11 ‰ in the Sand estuary with values of below 1 ‰ being reported at the end of the rainfall season. During closed phases, seawater may occasionally enter these systems by overtopping the sand bar as has been observed in the Diep estuary (Millard & Scott, 1954).

Mean salinities in closed warm-temperate estuaries were generally between 15 and 30 ‰ (Table 5.2). One system, the Gqutya, was hypersaline (49 ‰). Hypersaline conditions have also been reported in the Hartenbos, Seekoei and Kabeljous estuaries (Bickerton, 1982; Dundas, 1994). Cowley & Whitfield (2001) found that salinities in the Oos-Kleinemond estuary declined prior to mouth opening due to riverine input. Blaber (1973) reported a similar drop in salinity (from 24 to 2 ‰ within 24 hours) in the Wes-Kleinemond estuary during a flood event. Perissinotto *et al.* (2000) recorded salinities above 20 ‰ in the Nyara estuary during the closed phase. However, following a flood event, the system breached and salinities were reduced to almost fresh (<0.5 ‰) throughout. High river runoff was probably responsible for the relatively low salinities recorded in the Tsitsikamma and Morgan estuaries during this study (Table 5.2).

Due to the low berm height and gentle beach profiles associated with warm-temperate estuaries, overwashing during high tides frequently introduces seawater into these systems and, as a result, salinities are typically high (Cooper *et al.*, 1999; Cooper, 2001). Cowley & Whitfield (2001) found that after mouth closure, salinities in the Oos-Kleinemond estuary rose rapidly following a number of bar topping events; salinity levels also increased during the closed mouth phase due to evaporation. Vorwerk *et al.* (2001) reported mostly polyhaline (18-30 ‰) conditions in the Oos-Kleinemond, Mpekweni, Mtati, Mgwalana, Bira, and Gqutya estuaries. Mean salinities in these systems fell within the range 13-35 ‰ with summer salinities being slightly higher than those recorded in winter (ascribed to their shallow nature and high evaporative potential). Salinities recorded during this study were also mostly polyhaline and were generally higher than those recorded in either cool-temperate or subtropical systems (Table 5.2).

In subtropical estuaries, mean salinities generally did not exceed 15 ‰ (Table 5.3). Cooper (2001) noted that perched estuaries, characteristic of the subtropical region, are typically fresh to brackish. According to Begg (1984a), salinities in closed estuaries in KwaZulu-Natal were generally oligohaline (0.5-5.0 ‰) to mesohaline (5-18 ‰). Salinities below 10 ‰ (usually <5 ‰) were characteristic of systems such as the Mbizana, Bilanhlolo, Mhlangamkulu, iNtshambili, Fafa, Mhlangeni, and Manzimtoti (Begg, 1984b). The salinity of the Mhlanga estuary is also reported to be characteristically low, generally less than 10 ‰ (Whitfield, 1980a; 1980b; 1980c; Harrison & Whitfield, 1995). In the Siyai estuary, salinities seldom exceed 10 ‰, becoming progressively fresh during the closed phase (van der Elst *et al.*, 1999).

Although salinities in subtropical estuaries are generally low, seawater penetration often occurs when these systems open (Whitfield, 1990). In estuaries such as the Kandandlovu, Umhlangankulu, Kaba and Mpambanyoni average salinities did not exceed 10 ‰ during the closed phase but following breaching higher salinities (13-27 ‰) were reported, particularly in the bottom waters (Begg, 1984b). Blaber *et al.* (1984) also found that surface water salinity in the Mdloti estuary was usually very low except when the mouth was open. In the Siyai estuary, increases in salinity to 12-13 ‰ have been recorded in the lower reaches due to the ingress of seawater (van der Elst *et al.*, 1999). Seawater can also enter subtropical closed estuaries via barrier overwash as observed in the Zinkwasi estuary (Begg, 1984a).

Mixing of the water column in closed estuaries is primarily wind-induced although river and tidal mixing may occur when they are open (Whitfield, 1992; 1998). In broad, shallow systems, the fetch of the wind may be sufficient to ensure complete mixing from surface to bottom but where estuaries are protected from the wind, stratification may develop and result in depressed dissolved oxygen levels, particularly in the bottom waters (Day, 1981c; Begg, 1984b).

Closed cool-temperate estuaries during this study appeared to be well oxygenated with mean values generally exceeding 5.0 mg l^{-1} (Table 5.1). Millard & Scott (1954) found that the oxygen content of the surface waters of the Diep showed a fairly normal range, but low bottom values were also recorded. Mean dissolved oxygen levels in the Sand measured between 6.4 and 8.7 mg l^{-1} with a distinct seasonality of winter maxim values and summer minimum values (Harding, 1994).

Dissolved oxygen values in closed warm-temperate estuaries were mostly within the range 5.0-8.0 mg l^{-1} (Table 5.2). Other workers have also reported a range in dissolved oxygen levels, often with a distinct seasonal pattern, e.g. dissolved oxygen concentrations in the Hartenbos estuary averaged 6.4 mg l^{-1} in winter while in summer relatively low values (<5.0 mgl^{-1}) were reported (Bickerton, 1982). In the Groot (Wes) estuary, dissolved oxygen measurements generally exceeded 5.0 mg l^{-1}, with winter values usually exceeding those in summer (Morant & Bickerton, 1983). Bickerton & Pierce (1988) reported summer dissolved oxygen values of 7.4-8.0 mg l^{-1} in the Seekoei estuary and 8.3-10.5 mgl^{-1} in the Kabeljous system. The high concentrations in the Kabeljous were attributed to photosynthetic activity by extensive macrophyte (*Ruppia*) and filamentous algal beds in the estuary (Bickerton & Pierce, 1988). Dundas (1994) found that mean monthly dissolved oxygen values in the Seekoei, Kabeljous, and Van Stadens estuaries ranged between approximately 4.0 and 11.0 mgl^{-1}, with the lowest values occurring during summer.

In closed subtropical estuaries, mean dissolved oxygen levels ranged between 1.7 and 7.4 mg l^{-1}, with values of below 5 mg l^{-1} often recorded (Table 5.3). Begg (1984b) found that dissolved oxygen levels in closed KwaZulu-Natal estuaries varied seasonally with the highest values reported during winter, when water temperatures were minimal. Mean dissolved oxygen concentrations in the Kandandlovu estuary, for example, were generally below 4 mg l^{-1} in summer but increased to 5.3-7.7 mg l^{-1} in winter (Begg, 1984b). Maximum mean dissolved oxygen concentrations (8.5 mg l^{-1}) were reported in winter in the Mtentweni estuary, coinciding with minimal water temperatures. The levels of oxygen throughout the Kaba and Mhlangamkulu estuaries were also markedly higher in winter (Begg, 1984b). In the Mhlanga estuary, monthly average dissolved oxygen concentrations were generally above 5.0 mg l^{-1} with peak values (9.0- 13.3 mg l^{-1}) being recorded during winter (Harrison & Whitfield, 1995).

Begg (1984b) also found that some estuaries were well mixed and well oxygenated throughout the year. The waters of the Mpambanyoni estuary, for example, averaged between 7.5-8.9 mg l^{-1} and this was attributed to its shallow condition (Begg, 1984b). Relatively high dissolved oxygen values (6.9 mg l^{-1}) were also recorded in the

Mpambanyoni estuary during this study (Table 5.3). In other estuaries such as the iNtshambili and Mdlotane, however, reduced oxygen levels (generally <5 mg l^{-1}) were ascribed to poor water circulation, protection from the wind and the decomposition of leaf litter (Begg, 1984a; 1984b). Low oxygen levels (1.7 mg l^{-1}) were also reported in the Mdlotane during this study (Table 5.3).

A number of factors influence the turbidity of estuarine waters and these include river flow, substratum type, wind and tides (Cyrus, 1988b). Turbidities in closed cool-temperate estuaries during this study were generally below 15 NTU with only the Sand estuary having a turbidity of 20 NTU (Table 5.1). Clark *et al.* (1994) reported similar turbidities in the Sand estuary where mean values ranged between 24 and 40 NTU. In the Diep estuary, Millard & Scott (1954) found that the system was generally turbid following the winter rains but cleared when river flow ceased in summer.

Turbidities in closed warm-temperate estuaries were mostly below 10 NTU although high turbidities (>80 NTU) were reported in those systems that had recently breached following heavy rains (e.g. Nyara, Morgan) (Table 5.2). Bickerton (1982) reported moderate water transparency in the Hartenbos estuary, with Secchi disc readings measuring between 0.6 and 1.3 m. In the Groot (Wes) estuary, Secchi disc measurements also generally exceeded 1.0 m (Morant & Bickerton, 1983) while in the Seekoei and Kabeljous estuaries Secchi disc readings were mostly above 0.7 and 1.6 m respectively (Bickerton & Pierce, 1988). Dundas (1994) found that water transparencies in the Seekoei and Kabeljous estuaries were slightly higher in winter than in summer. Mean Secchi disc measurements in the Van Stadens estuary varied between 0.9 and 2.5 m, with winter values generally higher than those in summer (Dundas, 1994). Vorwerk *et al.* (2001) also found that the Oos-Kleinemond, Mpekweni, Mtati, Mgwalana, Bira, and Gqutya estuaries were generally clear systems with mean winter turbidities (4-9 NTU) normally lower than those recorded in summer (6-13 NTU).

Although mean turbidities in closed subtropical estuaries during this study were generally below 20 NTU (Table 5.3) Cyrus (1988b) reported a wide range of turbidities in closed KwaZulu-Natal estuaries. Systems such as the Mpambanyoni, Mpenjati, and Mtentweni were classified as clear systems with mean turbidities of less than 10 NTU; estuaries such as the Zinkwasi (29 NTU), Mdloti (51 NTU) and Manzimtoti (35 NTU) were classified as semi-turbid (10-50 NTU) estuaries; and the Mbokodweni, with a mean turbidity of 58 NTU was classified as a predominantly turbid (50-80 NTU) system (Cyrus, 1988b).

In some estuaries, turbidities decreased during the closed phase (Cyrus, 1988b). Begg (1984a; 1984b) also found that water transparency in KwaZulu-Natal estuaries (e.g. Mbizana, Bilanhlolo, Mlangeni, Mahlongwa, Little Manzimtoti, Zinkwasi) declined during the rainy season while the rivers were flowing but were much clearer in winter, particularly during the closed phases. Whitfield (1980a) also found that during the closed phase, water transparency in the Mhlanga estuary is relatively high but decreased following rains in the catchment. Turbidities reported in the Mhlanga estuary by Harrison & Whitfield (1995) were generally low (<1 NTU) but were higher in summer than in winter. Blaber *et al.* (1984) reported turbidities of mostly above 10 NTU in the Mdloti estuary and found that high values coincided with high rainfall periods. The estuaries with relatively high turbidities during this study (Little Manzimtoti, Manzimtoti, Mhlanga) were those that had breached following recent rains in the catchment. The higher overall turbidities relative to warm-temperate systems during this study are probably a result of the higher rainfall and runoff that occurs in the subtropical region. The coastal hinterland in KwaZulu-Natal is very steep, rising to over 3000 metres within 300 kilometres of the coast, this together with high rainfall leads to high erosion and sediment yield to the rivers that drain this area (McCormick *et al.*, 1992).

5.4.2 Open estuaries

Open estuaries are relatively large systems with catchments usually exceeding 500 km^2 and a perennial river flow (Whitfield, 1992; 1998). Open estuaries during this study had catchment areas between 178 and 46220 km^2 with a MAR of between 16 and 1751 x10^6 m^3 (Eksteen *et al.*, 1979; NRIO, 1986; 1987a; 1987b; 1987c; 1988).

Four open estuaries were represented in the cool-temperate region; two systems (Olifants, Berg) were situated on the west coast, and two (Palmiet, Uilkraals) were located on the southwest coast. The estuaries on the west coast have large catchments that drain areas beyond the arid coastal zone and thus river flow is generally sufficient to maintain a near permanent outlet to the sea (Cooper *et al.*, 1999). The Olifants and Berg estuaries have catchment areas of 46220 and 7715 km^2 respectively with a MAR exceeding 1000 m^{3}x10^6 (NRIO, 1988).

The estuaries on the cool-temperate southwest coast have smaller catchments (and MAR) than those on the west coast. The position of the mouth of the Palmiet estuary is situated against a rocky promontory and this, together with an almost continuous run-off throughout the year helps maintain an open mouth condition. The system may, however, close briefly during the dry summer months (Branch & Day, 1984; Bennett, 1989a). Little is known about the Uilkraals estuary; this system opens to the sea over a beach with a relatively flat profile and does not appear to close (Heydorn & Bickerton, 1982). Strong tidal currents probably contribute toward maintaining an open mouth condition in this estuary.

Tidal currents play a major role in maintaining a connection with the sea in warm-temperate estuaries (Cooper *et al.*, 1999; Cooper, 2001). These tide-dominated estuaries have large tidal prisms and are characterised by well-developed flood-tidal deltas in the lower reaches (Reddering & Rust, 1990; Cooper 2001). The mouth of the Breë estuary is maintained by strong tidal scour (Carter, 1983), while the tidal prism of both the Duiwenhoks and Goukou estuaries is sufficiently large to keep the mouth open (Carter & Brownlie, 1990). The mouth of the Swartkops estuary is also kept open by the action of strong tidal currents, which exceed the average river flow by sixty times (Baird *et al.*, 1986). Estuaries such as the Keurbooms (Duvenage & Morant, 1984), Kromme (Bickerton & Pierce, 1988), Bushmans (Day, 1981a), and Nahoon, Qinira and Gqunube (Wiseman *et al.*, 1993) also have well-developed flood-tidal deltas, characteristic of tide-dominated estuaries. Floods are important in removing accumulated sediments in these estuaries, causing a temporary deepening of the estuary channel (Reddering & Esterhuysen, 1987; Carter & Brownlie, 1990; Cooper *et al.*, 1999).

In subtropical (KwaZulu-Natal) estuaries, river flow is the major factor responsible for maintaining an open mouth condition (Cooper *et al.*, 1999; Cooper, 2001). The steep hinterland and moist climate promotes elevated fluvial sediment yields that contribute to rapid sediment infilling of these river maintained inlets (Cooper, 2001). The estuaries of this region have small tidal prisms and flood-tidal deltas, with river flooding being important in removing accumulated fluvial sediment from these systems (Cooper *et al.*, 1999). Unlike tide-dominated estuaries, river-dominated systems may close under low flow or drought conditions. Begg (1984b) has noted that, although both the Mzimkulu and Mkomazi estuaries are normally open, they have been known to close for a few days during low flow periods.

The mean water depth of open cool-temperate estuaries generally exceeded 1.5 m and only the Uilkraals had a mean depth of less than 1.0 m. (Table 5.5). This system is characterised by extensive sandflats (flood-tidal delta), which may be inundated or exposed depending on the state of tide (Heydorn & Bickerton, 1982). The depth of the Olifants estuary is mostly between 2.0 and 3.0 m (Day, 1981a) while the average depth of the Berg estuary is approximately 3.0 m (Slinger & Taljaard, 1994). The main channel of the Palmiet system is also between 2.0 and 3.0 m deep (Taljaard *et al.*, 1986).

Average water depths in open warm-temperate systems generally exceeded 2.0 m (Table 5.6). Water depths of between 2-3 m have also been reported in the Heuningnes (Bickerton, 1984), Breë (Carter, 1983), Gourits (Heydorn, 1989), Keurbooms (Day, 1981a), Kromme (Bickerton & Pierce, 1988), Gamtoos (Marais, 1984), Swartkops (Baird *et al.*, 1986), Sundays (Marais, 1984), Bushmans (Day, 1981a) and Kowie (Heinecken & Grindley, 1982) estuaries. Vorwerk *et al.* (2001) recorded an average depth of 1.4 m in both the Great Fish and Keiskamma estuaries while mean depths reported for the Nahoon, Gqunube, and Kwelera estuaries were between 1.3 and 2.2 m (Reddering & Esterhuysen, 1987). Plumstead *et al.* (1985) recorded average depths of 1.2-1.7 m in the Great Kei estuary, 1.2-2.0 m in the Mbashe estuary (Plumstead *et al.*, 1989a) and 1.1-5.4 m in the Mtata estuary (Plumstead *et al.*, 1989b).

The average water depth of the majority of subtropical estuaries exceeded 2.0 m (Table 5.7). Water depths reported in the Mngazana estuary generally exceeded 2.0 m (Branch & Grindley, 1979) and average depths in both the Mntafufu and Mzamba estuaries also tended to exceed 2.0 m (Plumstead *et al.*, 1991). Connell (1974) reports that mean depths in the Mtentu estuary were fairly constant, ranging between 4.3 and 5.2 m. Maximum water depths reported in the Mzimkulu and Mkomazi estuaries were 2.2 and 2.3 m respectively (Begg, 1984b).

Water temperatures in open estuaries are largely determined by a combination of tidal inflow and river discharge, with the coastal sea temperatures having a greater influence at the mouth, and river temperatures causing greater variation in the upper reaches (Day, 1981e). Mean water temperatures in cool-temperate estuaries did not exceed 18 °C (Table 5.5). Seasonal temperatures in the Olifants estuary were found to vary between 9-12 °C in winter and 10-22 °C in summer (Morant, 1984). The low temperatures reported in summer were attributed to the influence of cold seawater (resulting from oceanic upwelling) penetrating the lower reaches. In the Berg estuary, Day (1981a) reported a seasonal temperature range of 12 °C in winter to 27 °C in summer. Cold seawater (14-15 °C) was also reported entering the mouth of this system in summer (Bennett, 1994; Slinger & Taljaard, 1994). In the Palmiet estuary, Branch & Day (1984) found that surface water temperatures were generally above 20 °C in summer and below 15 °C in winter.

Average water temperatures in warm-temperate estuaries were generally higher than those recorded in cool-temperate systems and were mostly between 18 and 22 °C (Table 5.6). Mean seasonal water temperatures recorded in the Heuningnes estuary varied between 20 °C in summer and 13 °C in winter (Day, 1981a; Bickerton, 1984). In the Breë estuary, mean water temperatures ranged from 22-24 °C in summer and about 13 °C in winter (Day, 1981a; Carter, 1983). Summer temperatures in the Duiwenhoks estuary measured 19-22 °C while winter water temperatures were approximately 14 °C. In the Goukou system, summer temperatures measured 20-23 °C and 14-15 °C in winter (Carter & Brownlie, 1990). Day (1981a) reported a summer temperature of approximately 25 °C in the Gourtis while Heydorn (1989) recorded temperatures of 14-15 °C during winter. Summer temperatures recorded in the Keurbooms estuary measured 23-28 °C while winter temperatures were 12-16 °C (Duvenage & Morant, 1984).

Further to the east, average summer temperatures in the Kromme estuary measured 20-24 °C while winter temperatures averaged 17-18 °C (Scharler *et al.,* 1997). Day (1981a) reported a seasonal temperature range of 14 to 24 °C in the Gamtoos system. Mean summer temperatures in the Swartkops estuary varied between 21 and 26 °C while mean winter temperatures were 11-18 °C (Marais & Baird, 1980; Emmerson, 1985; Scharler *et al.*, 1997). Water temperatures recorded in the Sundays estuary averaged 22-24 °C in summer and 16-18 °C in winter (Scharler *et al.*, 1997).

In the Kariega estuary, Hecht & van der Lingen (1992) report a mean temperature range of 15 °C in winter and 19 °C in summer. Seasonal temperatures in the Kowie estuary range from 11-16 °C during winter to 20-28 °C in summer (Day, 1981a; Heinecken & Grindley, 1982). Mean temperatures in the Great Fish estuary varied between 15-16 °C during winter and 20-24 °C in summer (Hecht & van der Lingen, 1992; Vorwerk *et al.*, 2001). In the Keiskamma estuary, mean water temperatures ranged between 17-18 °C during winter and 21-29 °C in summer (Read, 1983; Vorwerk *et al.*, 2001).

Mean seasonal temperatures in the Great Kei estuary were found to range between 16 °C in winter and 20-22 °C in summer (Plumstead *et al.*, 1985). In the Mbashe estuary, water temperatures averaged 20-23 °C in summer and 17-19 °C in winter (Plumstead *et al.*, 1989a). Mean summer temperatures in the Mtata estuary measured 21-23 °C while winter temperatures were 16-19 °C (Plumstead *et al.*, 1989b). Although summer water temperatures are generally warmer than those during winter, coastal upwelling can sometimes result in low summer temperatures being reported, particularly in the mouth area. Plumstead *et al.* (1989a), for example, recorded water temperatures of less than 15 °C in the lower reaches of the Mbashe estuary during summer and attributed this to coastal upwelling.

Mean water temperatures recorded in subtropical estuaries were higher than those recorded in either cool- and warm-temperate systems and measured between 24 and 26 °C (Table 5.7). Seasonal temperatures recorded in the Mngazana estuary ranged from 16-19 °C in winter to 21-29 °C in summer (Branch & Grindley, 1979). In the Mntafufu estuary, mean temperatures measured between 21-24 °C in summer and 17-20 °C in winter (Plumstead *et al.*, 1991). Summer water temperatures recorded in the Mtentu exceeded 21 °C while winter temperatures were below 19 °C (Connell, 1974). Mean summer water temperatures in the Mzamba estuary were approximately 24 °C and winter temperatures averaged between 18 and about 21 °C (Plumstead *et al.*, 1991). Water temperatures recorded in the Mzimkulu estuary averaged between 16 °C in winter and 26 °C in summer while in the Mkomazi estuary, water temperatures averaged 27 °C in summer and 16-18 °C in winter (Begg, 1984b). Seasonal water temperatures in the Mlalazi estuary averaged 26-29 °C in summer and 16-17 °C in winter (Hill, 1966; Cyrus, 1988b).

Salinities in permanently open estuaries are governed primarily by the mixing of freshwater inflow from the catchment and seawater inputs driven by tidal currents. Rainfall and river discharge in many South African estuaries varies seasonally such that an estuary may be river dominated during one season and at another, it may be marine dominated (Day, 1981e). During extreme droughts hypersaline conditions (>40 ‰) may occur due to very low river inflow and high evaporation rates (Whitfield & Bruton, 1989), while during periods of high river flow and floods, low salinities may extend far downstream (Whitfield, 1992).

Mean salinities in cool-temperate estuaries were within the range 15-20 ‰ (Table 5.5). Branch & Day (1984) note that in summer, bottom water salinities in the Palmiet estuary measured 31-35 ‰ while at the surface they decreased from 35 ‰ near the mouth to 0 ‰ at the head. In winter, when the river was flowing very strongly, the upper layers of the entire estuary were fresh while the bottom remained saline (20-35 ‰) (Branch & Day, 1984). However, winter floods can flush all seawater from the system (Clarke, 1989). Extreme seasonal changes in salinity have also been reported in the Berg and Olifants estuaries. In the latter system, seawater penetration is very limited during winter and low salinity conditions (<3 ‰) generally predominate. As river flow decreases during the summer, seawater penetration into the estuary increases (Morant, 1984). The Berg estuary is also fluvially dominated during winter and the intrusion of seawater is limited to the lower reaches of the estuary; as river flow decreases during the summer, salinities in the estuary increase (Slinger & Taljaard, 1994).

In warm-temperate estuaries, mean salinities were mostly above 20 ‰ (Table 5.6). Because these systems are marine dominated and have large tidal prisms, salinities are generally high, although seasonal variations may also occur. Day (1981a) reports that mean salinities in the Heuningnes estuary vary between 24 and 38 ‰. During the dry summer months the lower reaches of the Heuningnes system are dominated by seawater, and at times a reversed salinity gradient due to evaporation exceeding freshwater inflow can occur (Bickerton, 1984). Increased runoff during winter flushes the system, resulting in lowered salinities throughout the estuary (Bickerton, 1984). Day (1981a) also found that during dry summers salt water extends high up the Breë estuary, while during heavy winter floods the whole estuary may be fresh. Mean summer salinities in the lower to middle reaches of the system ranged between 35 and 25 ‰ while average salinities in the same regions during winter were between 5 and 18 ‰ (Day, 1981a).

Hanekom & Baird (1984) report that salinities in the Kromme were normally about 33 ‰, declining to 1 ‰ during winter floods. Following the construction of several major dams in the catchment, average salinities in the Kromme estuary have tended to vary between 26 and 33 ‰ (Emmerson & Erasmus, 1987; Scharler *et al.*, 1997). Bickerton & Pierce (1988) have also found that during the dry summer months, high evaporation rates and lack of river flow cause hypersaline (>39 ‰) conditions in the upper reaches of the system, thus giving rise to a reversed salinity gradient.

In the Swartkops estuary, mean salinities varied between 23 and 34 ‰ (Marais, 1984; Emmerson, 1985). Hypersaline conditions (42 ‰) sometimes occur in the upper part of the system during the summer due to high evaporation and low freshwater inflow, while river flooding can reduce salinities to below 3 ‰ in the upper and middle reaches of the estuary (Marais & Baird, 1980; Baird *et al.*, 1986).

Day (1981a) reports that the Bushmans estuary is marine-dominated, with surface salinities measuring 30-34 ‰ for most of its length. Similar conditions were reported in the adjacent Kariega estuary where Hecht & van der Lingen (1992) recorded mean salinities of 34-35 ‰ throughout the year. Ter Morshuizen & Whitfield (1994) reported a reversed salinity gradient in the system during summer, with mean salinities increasing from 37 ‰ in the lower reaches to 40 ‰ in the upper reaches.

Salinities in the Kowie estuary are also usually above 30 ‰ and may increase to 40 ‰ in dry years (Day, 1981a). During floods, however, the surface waters of the system are almost fresh (Whitfield *et al.* 1994). Mean salinities recorded in the Great Fish estuary by Hecht & van der Lingen (1992) measured between 34 and 35 ‰ throughout the year. Whitfield *et al* (1994), however, reported overall mean salinities of between 10 and 16 ‰ in the Great Fish system. In the Keiskamma estuary, Colloty (2000) recorded an average salinity of 30 ‰ while Vorwerk *et al.* (2001) measured mean salinities of between 12 and 20 ‰.

Mean salinities reported in the Great Kei, Mbashe and Mtata estuaries varied between 1 and 36 ‰ (Plumstead *et al.*, 1985; 1989a; 1989b), with floods often reducing the salinities in these systems to almost fresh. Low salinities were also reported in the Great Kei, Mbashe and Mtata estuaries during this study, primarily due to increased runoff following rains in the catchment.

Salinities in subtropical estuaries were generally lower than those recorded in warm-temperate systems and were mostly below 20 ‰ (Table 5.7). Branch & Grindley (1979) reported that salinity in the lower and middle reaches of the Mngazana estuary remained high (35 ‰) and, although the heaviest rains fall in summer, seasonal variations in salinity were small. Mean salinities recorded in the Mntafufu estuary varied between 13 and 38 ‰ while those in the Mzamba system ranged between 5 and 35‰ (Plumstead *et al.*, 1991).

The river-dominated estuaries on the subtropical KwaZulu-Natal coast have small tidal prisms (Cooper *et al.*, 1999; Cooper, 2001) and consequently salinities in these estuaries are often reduced. Begg (1984b) recorded mean salinities in the Mzimkulu estuary of 0-13 ‰ while in the Mkomazi system, mean salinities varied between 0 and 26 ‰. Low salinities in these systems occur as a result of heavy rains in the catchment, particularly during summer. Hill (1966) reports that bottom salinities in the lower reaches of the Mlalazi estuary seldom drop below 30 ‰ although after short periods of heavy rainfall, freshwater forms a layer over the deeper saline waters. Relatively low salinities (<15 ‰) were recorded in the Mzimkulu, Mkomazi, Matigulu/Nyoni, and Mlalazi estuaries during this study (Table 5.7), probably due to rains in the catchment prior to sampling.

Tidal currents and river flow are the major driving forces governing mixing processes in open estuaries (Whitfield, 1992; 1998). Dissolved oxygen levels in cool-temperate estuaries during this study mostly exceeded 8.0 mg l^{-1} (Table 5.5). Morant (1984) noted that both summer and winter dissolved oxygen concentrations in the Olifants estuary were close to saturation while Slinger & Taljaard (1994) reported average dissolved oxygen concentrations of between 5.8 and 7.4 mg l^{-1} in the Berg estuary. Dissolved oxygen levels in the Palmiet estuary measured between 58 and 104% saturation (Branch & Day, 1984). Heydorn & Bickerton (1982) recorded high oxygen levels (9.8-13.0 mg l^{-1}) in the Uilkraals estuary and suggested that this was a result of high phytoplankton concentrations.

The warm-temperate estuaries were also well oxygenated with mean dissolved oxygen values exceeding 6.0 mg l^{-1} (Table 5.6). Carter (1983) found that summer dissolved oxygen values in the Breë estuary were all near saturation (generally >5.0 mg l^{-1}). In the Duiwenhoks estuary, both summer and winter dissolved oxygen concentrations exceeded 6.0 mg l^{-1} while in the Goukou oxygen values were generally above 5.0 mg l^{-1} (Carter & Brownlie, 1990). The water in the Gourtis estuary during winter was generally well oxygenated with dissolved oxygen values above 6.0 mg l^{-1} (Heydorn, 1989). In the Keurbooms estuary, Duvenage & Morant (1984) reported dissolved oxygen values of mostly above 5.0 mg l^{-1}.

The waters of the Kromme estuary were also well oxygenated with overall dissolved oxygen values exceeding of 6.0 mg l^{-1} (Emmerson & Erasmus, 1987; Bickerton &

Pierce, 1988; Scharler *et al.*; 1997). In the Swartkops estuary, Baird *et al.* (1981) reported a more or less constant dissolved oxygen value of approximately 4.5 mg l^{-1}. Emmerson (1985) and Scharler *et al.* (1997) both reported a mean dissolved oxygen concentration of 7.2 mg l^{-1} in the Swartkops estuary, with the waters being slightly less oxygenated during summer. Mean dissolved oxygen concentrations in the Sundays estuary exceeded 7.0 mg l^{-1} (Emmerson, 1989; Scharler *et al.*, 1997).

Hecht & van den Lingen (1992) recorded high dissolved oxygen concentrations in the Kariega estuary, with mean values ranging between 8.5 and 10.4 mg l^{-1}. Heinecken & Grindley (1982) also report that the surface waters in the Kowie are normally well oxygenated and are often supersaturated (>10 mg l^{-1}) during winter. Dissolved oxygen concentrations recorded in the Great Fish estuary averaged between 7.8 and 8.9 mg l^{-1} (Hecht & van den Lingen, 1992). Dissolved oxygen levels recorded in the Great Kei, Mbashe, and Mtata estuaries were also high, with mean values ranging between 7.2 and 9.4 mg l^{-1} (Plumstead *et al.*, 1985; 1989a; 1989b).

Subtropical estuaries were also well oxygenated with average dissolved oxygen concentrations exceeding 5.0 mg l^{-1} (Table 5.7). Branch & Grindley (1979) reported that dissolved oxygen levels in the Mngazana were moderately high throughout the system, measuring between 7.3 and 8.5 mg l^{-1} during summer and 4.2-6.9 mg l^{-1} in winter. Mean oxygen values recorded in both the Mntafufu and Mzamba estuaries exceeded 6.0 mg l^{-1} (Plumstead *et al.*, 1991). In the Mtentu estuary, Connell (1974) found that mean oxygen levels exceeded 84 % saturation at all times. Begg (1984b) also found that the Mkomazi estuary was a well-oxygenated system with average oxygen levels exceeding 7.3 mg l^{-1}, primarily due to the strong river and tidal flows in the system. Good water column mixing in the Mzimkulu estuary also resulted in well-oxygenated waters, with mean dissolved oxygen levels generally exceeding 6.0 mg l^{-1} (Begg, 1984b).

Turbidities in cool-temperate estuaries during this study did not exceed 30 NTU and were mostly below 14 NTU (Table 5.5). Seasonal variations in turbidity have been reported in a number of estuaries and this is primarily linked to rainfall and runoff. Morant (1984) reports that in winter, after heavy rain in the catchment, the Olifants system is very turbid while Day (1981a) states that the water in the Berg is very muddy during winter, becoming clearer in summer. Clarke (1989) notes that the water entering the Palmiet estuary is dark brown in colour due to the presence of dissolved humic substances. The water in the system, however, is usually very clear due to its limited sediment load, and only during peak winter flows is the water turbid due to the suspension of bottom material (Clarke, 1989).

Turbidities in warm-temperate estuaries were generally below 20 NTU (Table 5.6). Being strongly marine influenced, open warm-temperate estuaries are relatively clear systems although increased turbidities have also been noted during high river flow periods. Bickerton (1984) recorded a high water transparency (Secchi disc) in the Heuningnes estuary and attributed this to the strong influence of the sea high up into the estuary. Day (1981a) found that turbidity in the Breë estuary varies with river flow and the state of the tide. During periods of high river flow, the waters are generally turbid, while during low flow conditions seawater penetrates far upstream and the system is clear.

Water transparencies in the Gourits estuary were also reported to be high with Secchi disc values exceeding 1.0 m (Heydorn, 1989). In the Keurbooms estuary, Secchi disc measurements also tended to exceed 1.0 m (Duvenage & Morant, 1984) while in the Kromme system mean Secchi disc values varied between 0.8 and 1.8 m (Marais, 1984; Bickerton & Pierce, 1988; Scharler *et al.*, 1997). In the Gamtoos estuary, Heinecken (1981) reported Secchi disc readings estuary of 0.8 m throughout. Marais (1983b), however, noted that turbidities in the system increased during flood events and also reported relatively low water transparency during periods of normal flow when phytoplankton blooms were present. Baird *et al.* (1986) found that the waters of Swartkops estuary were relatively clear with mean Secchi disc measurements varying between 1.0 and 1.5m. In the Sundays estuary, mean Secchi disc values varied between 0.3 and 1.0 m (Marais, 1984; Scharler *et al.*, 1997).

Mean turbidities recorded in the Kariega estuary by Hecht & van der Lingen (1992) ranged between 3 and 7 NTU. Whitfield (1994c) reported mean turbidities of between 5 and 7 NTU in both the Kariega and Kowie estuaries. The Great Fish estuary has high suspensoid levels due to an elevated riverine input, with mean turbidities ranging between 21 and 200 NTU (Hecht & van der Lingen, 1992; Whitfield, 1994c; Whitfield *et al*., 1994; Ter Morshuizen *et al*., 1996a; Vorwerk *et al*., 2001). In the Keiskamma estuary, Vorwerk *et al*. (2001) noted a seasonal trend where mean summer turbidities (75 NTU) were generally higher than those in winter (16 NTU). Plumstead *et al*. (1985; 1989a; 1989b) also reports that the Great Kei, Mbashe and Mtata estuaries are relatively turbid systems and that water transparency was severely reduced during flood events. High turbidities were also recorded in the Great Kei, Mbashe and Mtata estuaries during this study (Table 5.6), probably linked to heavy rains in the catchments prior to sampling.

Turbidities recorded in subtropical estuaries during this study were generally below 20 NTU although high turbidities were recorded in those systems that were sampled following heavy rains in the catchment (e.g. Mngazi, Mkomazi, Matigulu/Nyoni) (Table 5.7). Branch & Grindley (1979) report that the water in the Mngazana is very clear, and is probably because of the strong marine influence in this system. High water transparency was also reported in the Mntafufu and Mzamba estuaries but water clarity in the Mntafufu system was reduced following rains in the catchment (Plumstead *et al*., 1991).

In the Mzimkulu estuary, low transparency was also reported while the river was flowing moderately but this improved when river flow decreased and seawater penetration increased (Begg, 1984b). A similar pattern was reported for the Mkomazi system where water transparencies reached a minimum in summer and a maximum in winter (Begg, 1984b). Hill (1966) also reported that water transparency in the Mlalazi estuary was sharply reduced following heavy rainfall. Cyrus (1988b) reported an average turbidity of 25 NTU in the Mlalazi, with the highest turbidities occurring when the river was flowing strongly.

5.4.4 General

The PCA analyses suggest that the estuaries in each biogeographic region have somewhat distinctive physico-chemical characteristics (Figures 5.3 & 5.4). The general physico-chemical features of closed and open estuaries during this study are summarised below.

Closed estuaries in the cool-temperate region were generally shallow systems with water depths not exceeding 1.0 m. Water levels in warm-temperate and subtropical estuaries were generally higher with mean water depths of between 1.0 and 2.0 m (Table 5.9). When closed estuaries breach there is usually a strong outflow to sea followed by a fall in water level. Because closed warm-temperate estuaries are impounded close to high tide level, these systems do not drain as dramatically as perched subtropical systems do when they breach (Cooper, *et al.*, 1999; Cooper, 2001). During the closed phase, water levels in subtropical estuaries are high and the adjacent floodplain often becomes inundated (Begg, 1984a). Most estuaries were closed during this study and many of the shallow systems were those that had recently breached.

Estuarine water temperatures generally decreased from the subtropical region toward the cool-temperate zone. This corresponds to the trend for marine coastal waters, although solar heating can result in relatively high temperatures in both cool- and warm-temperate systems. Mean water temperatures of cool-temperate estuaries usually did not exceed 20 °C; those in the warm-temperate region were mostly within the range 18-24 °C, while subtropical estuaries frequently had water temperatures of 22-28 °C (Table 5.9).

Salinities in the cool-temperate estuaries varied from oligohaline (<5 ‰) to polyhaline (18-30 ‰). Increased winter runoff reduces salinities in these closed systems while elevated temperatures and high evaporation rates increases salinities during the summer (Millard & Scott, 1954; Day, 1981a). Warm-temperate estuaries were mostly polyhaline and this is due to a combination of low freshwater input, high evaporation rates and seawater introduction via barrier overwash (Dundas, 1994; Cooper *et al.*, 1999; Cowley & Whitfield, 2001; Vorwerk *et al.*, 2001). Occasional heavy rains may reduce salinities in these systems, especially during the outflow phase after mouth breaching (Blaber, 1973; Perissinotto *et al.*, 2000; Cowley & Whitfield, 2001). High rainfall and runoff together with limited seawater input results in perched subtropical estuaries having typically low salinities (Begg, 1984a; Cooper, 2001). Closed subtropical estuaries were mostly oligohaline to mesohaline (5-18 ‰) (Table 5.9).

Dissolved oxygen concentrations generally declined from cool-temperate to subtropical estuaries, mirroring the general increase in water temperature (Table 5.9). Dissolved oxygen was significantly negatively correlated with temperature.

Most closed estuaries were clear (<10 NTU) to semi-turbid (10-50 NTU) (Table 5.9). Turbidities in these estuaries are generally low during the closed phase but increase during the rainy season. This occurs during winter in cool-temperate estuaries (Millard & Scott, 1954) and during summer in subtropical systems (Begg, 1984a; 1984b). Warm-temperate estuaries, which experience more evenly distributed rainfall and runoff events, were predominantly clear systems (Table 5.9).

Table 5.9. General physico-chemical characteristics of closed cool-temperate, warm-temperate and subtropical estuaries.

	Cool-temperate	**Warm-temperate**	**Subtropical**
Depth	<1.0 m	1.0-2.0 m	1.0-2.0 m
Temperature	<20 °C	18-24 °C	22-28 °C
Salinity	oligohaline (0.5-5 ‰) to polyhaline (18-30 ‰)	mesohaline (5-18 ‰) to polyhaline (18-30 ‰)	oligohaline (0.5-5 ‰) to mesohaline (5-18 ‰)
Dissolved oxygen	>5 mgl-1	5-8 mgl-1	4-7 mgl-1
Turbidity	clear (<10 NTU) to semi-turbid (10-50 NTU)	clear (<10 NTU)	clear (<10 NTU) to semi-turbid (10-50 NTU)

Tidal currents and/or river flow serve to maintain a connection with the sea in open estuaries (Cooper *et al.*, 1999; Cooper, 2001) and most of these systems had water depths exceeding 1.5 m (Table 5.10). Water temperatures showed a clear decline from subtropical systems to cool-temperate systems, corresponding to the decline in coastal sea temperatures. Temperatures in cool-temperate systems did not exceed 18 °C; warm-temperate systems had water temperatures mostly within the range 18-22 °C, while temperatures in subtropical estuaries exceeded 24 °C (Table 5.10). In both cool- and warm-temperate estuaries, coastal upwelling can result in low summer temperatures (Morant, 1984; Plumstead *et al.*, 1989).

Salinities in cool-temperate estuaries were generally polyhaline (Table 5.10). High evaporation and strong marine influence results in high salinities in these estuaries during summer, while increased runoff in winter can rapidly reduce estuarine salinities (Morant, 1984; Slinger & Taljaard, 1994). In warm-temperate systems salinities were higher, mostly polyhaline to euhaline (>30 ‰). This is probably a result of the relatively low rainfall and freshwater flows in the region and the strong marine influence in these systems (Reddering & Rust, 1990; Cooper, 2001). Salinities in subtropical estuaries were oligohaline to polyhaline. Tidal prisms in these river-dominated systems are usually small (Cooper *et al.*, 1999; Cooper, 2001) and high river flow during summer can drastically reduce salinities in these systems (Begg, 1984b).

All the open estuaries were well oxygenated with dissolved oxygen concentrations exceeding 5.0 mg l^{-1}. Dissolved oxygen concentrations, which were negatively correlated with temperature, showed a general decline from cool-temperate estuaries toward subtropical systems (Table 5.10).

Most open estuaries were clear to semi-turbid (Table 5.10). Heavy winter rainfall can increase turbidities in cool-temperate systems (Day, 1981a; Morant, 1984) while in subtropical estuaries high summer inflows leads to elevated turbidities (Begg, 1984b; Plumstead *et al.*, 1991; Cyrus, 1988b). Marine-dominated warm-temperate systems generally tend have relatively clear waters (Bickerton, 1984; Heydorn, 1989; Hecht & van der Lingen, 1992; Whitfield, 1994c; Scharler *et al.*, 1997), although river flooding can lead to periods with high turbidities (Day, 1981a; Marais, 1983b; Plumstead *et al.*, 1985; 1989a; 1989b).

Table 5.10. General physico-chemical characteristics of open cool-temperate, warm-temperate and subtropical estuaries.

	Cool-temperate	Warm-temperate	Subtropical
Depth	>1.5 m	>2.0 m	>2.0 m
Temperature	<18 °C	18-22 °C	>24 °C
Salinity	mesohaline (5-18 ‰) to polyhaline (18-30 ‰)	polyhaline (18-30 ‰) to euhaline (>30 ‰)	mesohaline (5-18 ‰) to polyhaline (18-30 ‰)
Dissolved oxygen	>8.0 mgl^{-1}	>6.0 mgl^{-1}	>5.0 mgl^{-1}
Turbidity	clear (<10 NTU) to semi-turbid (10-50 NTU)	clear (<10 NTU) to semi-turbid (10-50 NTU)	semi-turbid (10-50 NTU)

The general physico-chemical characteristics of the estuaries in each biogeographic region appears to be linked to the variation in climatic, marine and geomorphologic conditions that typify the South African coastal zone.

Day (1981a) grouped southern African estuaries into three main provinces based mainly on water temperature, rainfall and river flow. The estuaries of southern Mozambique from the Morrumbene to the Great Kei were classified as subtropical and were characterised by warm waters (>16 °C), a predominantly summer rainfall pattern and high river discharge during this season. Warm-temperate estuaries from the Great Kei to Cape Point have minimum winter temperatures of between 12 and 14 °C and experience variable rainfall. The estuaries on the west coast, between Cape Point and the Orange River; are characterised by very low summer rainfall and high evaporation during this period.

An ordination of environmental variables of 55 Eastern Cape estuaries between Port Alfred and Port Edward revealed that estuaries could be grouped according to similar physical characteristics that were a function of geomorphology (surface area) and physico-chemical factors (average salinity, nitrate and light attenuation) (Colloty, 2000). Both open and closed estuaries could be divided into three broad groups: those systems south of the Great Kei River; estuaries between the Great Kei River and approximately Port St Johns; and those estuaries between Port St Johns and Port Edward (Colloty, 2000).

Based on a PCA analysis of eight physical/environmental attributes Pease (1999) classified the estuaries of New South Wales (Australia) into three regions that also broadly corresponded to the biogeographic provinces of that region. Key parameters identified in the analysis included mouth depth and width, and latitude. Mouth depth and width were related to estuary size, geomorphology, runoff, and the degree of marine influence while latitude was related to temperature, rainfall and wind patterns (Pease, 1999).

5.5 SUMMARY AND CONCLUSIONS

The range in oceanographic and climatic conditions that characterise the South African coast also results in distinct estuarine physico-chemical conditions that broadly coincide with the biogeographic regions along the coast. Subtropical estuaries experience high summer rainfall and humid conditions, followed by a cooler, dry winter period. Rainfall in the warm-temperate region is less predictable and is mostly bi-modal or year round. Estuaries in the cool-temperate region experience predominantly winter rainfall followed by a warm, dry summer period. Estuarine temperatures follow the trend for marine coastal waters, decreasing from the subtropical east coast, along the warm-temperate south coast and up the cool-temperate west coast. Lower rainfall and runoff, together with higher seawater input and evaporative loss, results in generally elevated salinities in warm-temperate estuaries when compared to either cool-temperate or subtropical systems. High rainfall and runoff, particularly in subtropical estuaries, often results in high turbidities, the duration and intensity of which varies according to river flow regimes.

CHAPTER 6
SPECIES COMPOSITION

6.1 INTRODUCTION

Estuaries are regions where marine and fresh waters meet and, as such, experience great environmental variation. Consequently, the often abrupt changes in salinity, temperature, dissolved oxygen and turbidity place considerable physiological demands on the fishes that utilise these systems (Whitfield, 1999). A variety of factors influence the utilisation of South African estuaries by fishes (Whitfield, 1983; Blaber, 1985; Marais, 1988) with the relative importance of each factor differing according to species (Blaber & Blaber, 1980). The advantages of living in estuaries are therefore available only to those fishes that are broadly tolerant of this abiotic (and biotic) variability (Blaber, 1981; Whitfield, 1999).

Because no two estuaries are identical in terms of either biotic or abiotic characteristics, it could be argued that the ichthyofaunas of each estuary will also differ. Whitfield (1999), however, postulated if the fishes in estuaries respond to the environment in a consistent manner, then the communities occupying similar types of estuaries in a particular region would be expected to reflect this similarity. Monaco *et al.* (1992) also noted that estuaries with similar habitats and environmental regimes often support similar species assemblages.

In this chapter, the fish assemblages of estuaries from the different biogeographic regions are described and compared. The relationships between key species and environmental parameters (taken at the time of sampling) are also investigated.

6.2 MATERIALS & METHODS

6.2.1 Species composition

The open and closed estuaries selected during this study were divided into cool-temperate, warm-temperate and subtropical systems as described in the previous chapters. The average number of taxa (±SD) as well as the frequency of occurrence of each species within each biogeographic region was calculated. The relative proportions of each species, both in terms of abundance and biomass within each estuary was calculated and the mean (±SD) contribution of each species to the overall fish assemblage within each biogeographic region determined.

A similarity breakdown (SIMPER) (Clarke & Warwick, 1994) was also performed on the data. In this analysis, the closed and open estuaries were grouped into the three biogeographic regions and the average Bray-Curtis similarity coefficient for each group calculated based on presence/absence, abundance and biomass. For both abundance and biomass analyses, the data was first 4th root transformed; this has the effect of scaling down the importance of abundant species so that they do not swamp the other data (Field *et al.*, 1982; Clarke & Warwick, 1994). The contribution of each species to the average similarity within a group of estuaries (*S*) was calculated and the major species that account for this similarity identified (Clarke, 1993; Clarke & Warwick, 1994). The more abundant a species (*i*) is within a group, the more it will tend to contribute to the intra-group similarity. A species typifies that group if it is found at a consistent abundance throughout; so the standard deviation of its contribution (SD (*Si*)) is low and the ratio of its average similarity to the standard deviation (*Si*/SD (*Si*)) high (Clarke, 1993).

6.2.2 Inter-regional comparisons

The SIMPER analysis was also used to identify those species that account for the differences (or dissimilarities) between the estuaries in the various biogeographic regions. In this analysis, the dissimilarity contribution of each species (δ*i*) to the average dissimilarity (δ) between two groups of estuaries is calculated. If the standard deviation of the contribution of a species (SD (δ*i*)) is small, and the ratio of its average dissimilarity (δ*i*) to the standard deviation (SD (δ*i*)) high, then that species not only contributes much to the dissimilarity between two groups of estuaries but it also does so consistently (Clarke, 1993; Clarke & Warwick, 1994). Cool-temperate and warm-temperate estuaries, and warm-temperate and subtropical systems were compared using the SIMPER routine.

6.2.3 Physico-chemical relationships

Relationships between the relative abundance and biomass of key species and the mean physico-chemical characteristics of the estuaries were also examined using the

Spearman rank correlation coefficient. This is a non-parametric test that is based on ranked data and tests for any correlation between two sets of ranked scores. Key species were identified as those taxa that had a relative abundance/biomass of more than 1% and/or a frequency of occurrence of over 50% in any one biogeographic region.

6.3 Results

6.3.1 Closed estuaries

6.3.1.1 Species composition

Eleven species representing eight families were recorded in closed cool-temperate estuaries with an average of 4.5 (SD±4.04) taxa being captured per estuary (Table 6.1). *Liza richardsonii* was the most frequently captured species (100%), followed by *Mugil cephalus* (75%), *Caffrogobius nudiceps* (50%) and *Heteromycteris capensis* (50%). In terms of abundance, *L. richardsonii* (56.7%), *Gilchristella aestuaria* (19.5%), *M. cephalus* (18.1%), *C. nudiceps* (3.0%) and *Atherina breviceps* (2.2%) were the dominant species. *Liza richardsonii* (49.9%), *M. cephalus* (43.8%) and *Lichia amia* (5.4%) dominated the overall species mass composition (Table 6.1).

Table 6.1. Percent frequency of occurrence, mean percent abundance and mean percent biomass composition of fishes in closed cool-temperate estuaries (n = number of estuaries, SD = standard deviation).

Family	**Species**	**Frequency**		**Abundance**		**Biomass**	
		%	**n**	**%**	**SD**	**%**	**SD**
Atherinidae	*Atherina breviceps*	25	1	2.21	4.41	0.11	0.23
Carangidae	*Lichia amia*	25	1	0.08	0.16	5.43	10.86
Clupeidae	*Gilchristella aestuaria*	25	1	19.50	39.00	0.54	1.07
Gobiidae	*Caffrogobius nudiceps*	50	2	3.01	5.94	0.14	0.28
	Psammogobius knysnaensis	25	1	0.02	0.03	0.00	0.01
Mugilidae	*Liza dumerilii*	25	1	0.06	0.13	0.05	0.11
	Liza richardsonii	100	4	56.69	43.60	49.85	39.84
	Mugil cephalus	75	3	18.09	33.60	43.83	33.03
Soleidae	*Heteromycteris capensis*	50	2	0.24	0.37	0.01	0.01
Sparidae	*Rhabdosargus globiceps*	25	1	0.05	0.10	0.00	0.00
Syngnathidae	*Syngnathus acus*	25	1	0.05	0.10	0.03	0.06

Closed cool-temperate estuaries had average similarities ranging between 38.3% and 54.2% (Table 6.2). Four species accounted for over 90% of the similarity within this group, namely *C. nudiceps*, *H. capensis*, *L. richardsonii* and *M. cephalus*.

Table 6.2. Major species accounting for the similarity within closed cool-temperate estuaries; *Si* is the average similarity contribution of each species; *% Si* is the percent contribution to the overall similarity (*S*); SD (*Si*) is the standard deviation of each species to the total similarity. Similarities are based on presence/absence, abundance and biomass.

	Presence/absence			**Abundance**			**Biomass**		
Species	***Si***	**% *Si***	***Si* / SD*(Si)***	***Si***	**% *Si***	***Si* / SD*(Si)***	***Si***	**% *Si***	***Si* / SD*(Si)***
C. nudiceps				1.4	3.69	0.41			
H. capensis	2.2	5.09	0.41						
L. richardsonii	29.5	67.47	1.49	26.4	69.06	1.84	35.8	66.15	2.26
M. cephalus	9.8	22.36	0.82	9.2	24.15	0.85	17.3	31.92	0.89
Total *S*	**43.67**			**38.26**			**54.19**		

In the warm-temperate region, 43 species and 20 families were represented with an average of 15.5 (SD±4.85) species being captured per estuary (Table 6.3). The most frequently recorded taxa included *G. aestuaria* and *L. richardsonii* (100%), *Rhabdosargus holubi* (98%), *Monodactylus falciformis* (93%), *M. cephalus* and *Myxus capensis* (90%), *A. breviceps* and *Glossogobius callidus* (88%), *Liza dumerilii* (83%), *Lithognathus lithognathus* and *Liza tricuspidens* (76%), *Psammogobius knysnaensis* (71%), and *O. mossambicus* and *Pomadasys commersonnii* (61%) (Table 6.3).

In terms of abundance, *G. aestuaria* (35.8%), *A. breviceps* (18.3%), *R. holubi* (17.6%), *L. richardsonii* (6.7%), *M. capensis* (5.6%), *G. callidus* (3.2%), *L. lithognathus* (2.9%), *L. dumerilii* (2.6%), *M. cephalus* (1.8%), *L. tricuspidens* (1.1%) and *P. knysnaensis* (1.1%) were the dominant taxa. The biomass composition was dominated by *L. richardsonii* (28.4%), *M. cephalus* (11.5%), *R. holubi* (10.3%), *L. tricuspidens* (7.1%), *O. mossambicus* (6.6%), *Argyrosomus japonicus* (6.5%), *M. capensis* (5.8%), *P. commersonnii* (4.5%), *L. dumerilii* (4.4%), *L. lithognathus* (3.7%), *Lichia amia* (3.3%), *Elops machnata* (1.7%) and *G. aestuaria* (1.6%) (Table 6.3).

Table 6.3. Percent frequency of occurrence, mean percent abundance and mean percent biomass composition of fishes in closed warm-temperate estuaries (n = number of estuaries; SD = standard deviation).

Family	**Species**	**Frequency**		**Abundance**		**Biomass**	
		%	**n**	**%**	**SD**	**%**	**SD**
Ambassidae	*Ambassis gymnocephalus*	2	1	0.00	0.01	0.00	0.00
Ariidae	*Galeichthys feliceps*	20	8	0.02	0.05	0.36	1.31
Atherinidae	*Atherina breviceps*	88	36	18.33	18.61	0.84	1.17
Blenniidae	*Parablennius lodosus*	2	1	0.00	0.01	0.00	0.00
Carangidae	*Caranx sexfasciatus*	5	2	0.02	0.15	0.34	1.96
	Lichia amia	41	17	0.05	0.10	3.26	4.60
Cichlidae	*Oreochromis mossambicus*	61	25	0.79	1.83	6.56	10.47
Clupeidae	*Gilchristella aestuaria*	100	41	35.78	22.29	1.62	1.63
Elopidae	*Elops machnata*	17	7	0.04	0.14	1.73	6.71
Gerreidae	*Gerres methueni*	2	1	0.00	0.01	0.01	0.05
Gobiidae	*Caffrogobius gilchristi*	27	11	0.13	0.26	0.02	0.05
	Caffrogobius natalensis	5	2	0.00	0.02	0.00	0.00
	Caffrogobius nudiceps	5	2	0.06	0.37	0.01	0.04
	Glossogobius callidus	88	36	3.24	3.91	0.41	0.67
	Oligolepis keiensis	5	2	0.01	0.03	0.00	0.00
	Psammogobius knysnaensis	71	29	1.12	3.91	0.05	0.07
Haemulidae	*Pomadasys commersonnii*	61	25	0.24	0.48	4.52	5.73
	Pomadasys olivaceum	7	3	0.01	0.03	0.00	0.01
Lutjanidae	*Lutjanus argentimaculatus*	2	1	0.00	0.01	0.14	0.89
Monodactylidae	*Monodactylus falciformis*	93	38	0.71	0.82	0.94	1.11
Mugilidae	*Liza alata*	2	1	0.01	0.04	0.08	0.50
	Liza dumerilii	83	34	2.58	3.55	4.41	5.48
	Liza macrolepis	27	11	0.12	0.33	0.35	0.96
	Liza richardsonii	100	41	6.65	8.68	28.36	22.99
	Liza tricuspidens	76	31	1.13	1.76	7.11	10.31
	Mugil cephalus	90	37	1.80	3.67	11.46	13.36
	Myxus capensis	90	37	5.58	12.27	5.80	6.28
	Valamugil buchanani	5	2	0.01	0.02	0.16	0.75
	Valamugil cunnesius	5	2	0.03	0.17	0.02	0.11
	Valamugil robustus	7	3	0.04	0.19	0.04	0.19
Pomatomidae	*Pomatomus saltatrix*	15	6	0.09	0.48	0.72	2.92
Sciaenidae	*Argyrosomus japonicus*	44	18	0.14	0.29	6.45	9.92
Soleidae	*Heteromycteris capensis*	29	12	0.23	0.77	0.01	0.03
	Solea bleekeri	37	15	0.09	0.18	0.03	0.13
Sparidae	*Acanthopagrus berda*	2	1	0.00	0.01	0.02	0.11
	Diplodus sargus	29	12	0.34	1.74	0.02	0.05
	Lithognathus lithognathus	76	31	2.91	7.56	3.70	5.13
	Rhabdosargus globiceps	5	2	0.00	0.01	0.00	0.01
	Rhabdosargus holubi	98	40	17.64	15.72	10.28	8.55
	Rhabdosargus sarba	5	2	0.00	0.02	0.18	0.94
	Sarpa salpa	17	7	0.04	0.11	0.00	0.01
Teraponidae	*Terapon jarbua*	7	3	0.03	0.13	0.01	0.05
Tetraodontidae	*Amblyrhynchotes honckenii*	2	1	0.00	0.01	0.00	0.02

Average similarities in closed warm-temperate estuaries varied between 60.6% and 69.1% (Table 6.4). Fourteen species accounted for over 90% of the similarity within this group and these included *A. breviceps*, *G. aestuaria*, *G. callidus*, *L. lithognathus*, *L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. falciformis*, *M. capensis*, *O. mossambicus*, *P. commersonnii*, *P. knysnaensis* and *R. holubi* (Table 6.4).

Table 6.4. Major species accounting for the similarity within closed warm-temperate estuaries; *Si* is the average similarity contribution of each species; % *Si* is the percent contribution to the overall similarity (*S*); SD (*Si*) is the standard deviation of each species to the total similarity. Similarities are based on presence/absence, abundance and biomass.

	Presence/absence			**Abundance**			**Biomass**		
Species	***Si***	**% *Si***	***Si* / SD*(Si)***	***Si***	**% *Si***	***Si* / SD*(Si)***	***Si***	**% *Si***	***Si* / SD*(Si)***
A. breviceps	5.2	7.48	1.71	6.9	11.13	1.41	3.0	4.99	1.55
G. aestuaria	6.8	9.78	4.05	9.8	15.90	2.84	4.4	7.32	2.72
G. callidus	4.6	6.65	1.52	4.1	6.67	1.41	2.2	3.68	1.48
L. lithognathus	3.5	5.10	1.01	2.2	3.54	0.99	3.3	5.45	0.92
L. dumerilii	4.5	6.56	1.39	3.7	5.98	1.30	3.9	6.43	1.29
L. richardsonii	6.9	10.00	4.23	6.4	10.37	3.25	10.7	17.68	2.88
L. tricuspidens	3.7	5.36	1.11	2.5	4.06	1.06	3.3	5.53	0.94
M. falciformis	5.4	7.86	1.97	3.5	5.61	1.84	3.2	5.32	1.75
M. cephalus	5.7	8.22	1.87	3.9	6.37	1.63	5.6	9.25	1.40
M. capensis	5.5	7.90	1.86	4.4	7.18	1.65	4.8	7.95	1.55
O. mossambicus	2.0	2.89	0.70				2.2	3.58	0.66
P. commersonnii							2.3	3.72	0.72
P. knysnaensis	2.7	3.90	0.80	1.8	2.95	0.81			
R. holubi	6.7	9.77	3.10	7.6	12.29	2.79	6.8	11.15	2.37
Total *S*	**69.05**			**61.84**			**60.61**		

Forty-nine species representing 22 families were reported in closed subtropical estuaries; an average of 15.9 (SD±5.19) species were captured per estuary (Table 6.5). Frequently recorded taxa included *M. capensis* and *O. mossambicus* (100%), *M. cephalus* (91%), *Valamugil cunnesius* (86%), *G. callidus* and *R. holubi* (82%), *L. dumerilii* and *M. falciformis* (77%), *G. aestuaria* (73%), *Liza macrolepis* and *P. commersonnii* (68%), *Liza alata* (64%), *Terapon jarbua* and *Valamugil robustus* (55%), and *Ambassis productus* (50%) (Table 6.5).

In terms of abundance, *G. aestuaria* (25.8%) was the dominant species overall followed by *O. mossambicus* (18.7%), *M. capensis* (14.1%), *M. cephalus* (7.8%), *R. holubi* (6.7%), *V. cunnesius* (5.2%), *L. dumerilii* (3.7%), *G. callidus* (3.3%), *M. falciformis* (2.6%), *L. macrolepis* (2.2%), *V. robustus* (2.0%) and *A. productus* (1.9%). The overall species mass composition was dominated by *Clarias gariepinus* (18.1%), *O. mossambicus* (17.7%), *M. cephalus* (15.2%), *M. capensis* (14.0%), *L. alata* (6.6%), *L. macrolepis* (5.1%), *V. cunnesius* (3.9%), *P. commersonnii* (3.1%), *L. dumerilii* (2.9%), *V. robustus* (2.8%), *R. holubi* (2.6%), *A. japonicus* (2.2%), *G. aestuaria* (1.4%) and *A. productus* (1.0%) (Table 6.5).

Table 6.5. Percent frequency of occurrence, mean percent abundance and mean percent biomass composition of fishes in closed subtropical estuaries (n = number of estuaries, SD = standard deviation).

Family	**Species**	**Frequency**		**Abundance**		**Biomass**	
		%	**n**	**%**	**SD**	**%**	**SD**
Ambassidae	*Ambassis gymnocephalus*	9	2	0.18	0.60	0.00	0.01
	Ambassis natalensis	23	5	0.37	1.14	0.01	0.02
	Ambassis productus	50	11	1.86	5.29	1.04	1.49
Carangidae	*Caranx ignobilis*	5	1	0.05	0.22	0.19	0.88
	Caranx papuensis	5	1	0.02	0.11	0.01	0.03
	Caranx sexfasciatus	36	8	0.17	0.39	0.51	0.99
Chanidae	*Chanos chanos*	5	1	0.03	0.14	0.17	0.80
Cichlidae	*Oreochromis mossambicus*	100	22	18.72	22.79	17.67	13.75
	Tilapia rendalli	9	2	0.18	0.73	0.15	0.63
Clariidae	*Clarias gariepinus*	41	9	0.88	1.85	18.13	28.02
Clupeidae	*Gilchristella aestuaria*	73	16	25.82	32.52	1.37	3.89
Cyprinidae	*Barbus natalensis*	5	1	0.01	0.03	0.00	0.00
Eleotridae	*Eleotris fusca*	9	2	0.01	0.03	0.00	0.00
Elopidae	*Elops machnata*	5	1	0.01	0.03	0.03	0.15
Gerreidae	*Gerres methueni*	18	4	0.35	1.14	0.09	0.34
Gobiidae	*Awaous aeneofuscus*	14	3	0.01	0.04	0.01	0.03
	Caffrogobius natalensis	18	4	0.07	0.21	0.00	0.00
	Glossogobius callidus	82	18	3.27	4.72	0.14	0.16
	Glossogobius giuris	27	6	0.18	0.57	0.01	0.02
	Mugillogobius durbanensis	5	1	0.00	0.02	0.00	0.00
	Oligolepis acutipennis	14	3	0.09	0.25	0.01	0.03
	Oligolepis keiensis	9	2	0.05	0.19	0.00	0.00
	Oxyurichthys opthalmonema	5	1	0.01	0.03	0.00	0.00
	Psammogobius knysnaensis	14	3	0.24	0.70	0.01	0.02
	Redigobius dewaali	5	1	0.01	0.03	0.00	0.00
Haemulidae	*Pomadasys commersonnii*	68	15	0.64	1.35	3.10	4.17
	Pomadasys kaakan	5	1	0.02	0.09	0.02	0.07
Leiognathidae	*Leiognathus equula*	9	2	0.06	0.28	0.02	0.09
Lutjanidae	*Lutjanus argentimaculatus*	14	3	0.02	0.05	0.05	0.14
	Lutjanus fulviflamma	5	1	0.00	0.02	0.00	0.00
Megalopidae	*Megalops cyprinoides*	9	2	0.12	0.42	0.39	1.26
Monodactylidae	*Monodactylus argenteus*	5	1	0.02	0.09	0.01	0.03
	Monodactylus falciformis	77	17	2.64	8.06	0.94	1.72
Mugilidae	*Liza alata*	64	14	0.48	0.68	6.57	11.53
	Liza dumerilii	77	17	3.70	5.54	2.92	3.84
	Liza macrolepis	68	15	2.21	4.26	5.09	10.20
	Liza tricuspidens	14	3	0.04	0.13	0.01	0.03
	Mugil cephalus	91	20	7.80	8.49	15.17	11.09
	Myxus capensis	100	22	14.08	12.71	13.97	13.34
	Valamugil buchanani	18	4	0.08	0.25	0.37	1.27
	Valamugil cunnesius	86	19	5.19	8.74	3.91	8.05
	Valamugil robustus	55	12	1.97	3.24	2.78	5.64
	Valamugil seheli	14	3	0.18	0.56	0.04	0.14
Sciaenidae	*Argyrosomus japonicus*	36	8	0.14	0.23	2.23	4.28
Sillaginidae	*Sillago sihama*	5	1	0.01	0.03	0.00	0.01
Soleidae	*Solea bleekeri*	27	6	0.29	0.83	0.02	0.06
Sparidae	*Acanthopagrus berda*	14	3	0.07	0.23	0.13	0.55
Sparidae	*Rhabdosargus holubi*	82	18	6.67	10.98	2.55	5.82
	Rhabdosargus sarba	9	2	0.11	0.45	0.01	0.02
Teraponidae	*Terapon jarbua*	55	12	0.86	1.65	0.16	0.38

Closed subtropical estuaries had average similarities of between 52.3% and 58.7% (Table 6.6). Fifteen species accounted for over 90% of the similarity within this group. These taxa included *C. gariepinus*, *G. aestuaria*, *G. callidus*, *L. alata*, *L.*

dumerilii, *L. macrolepis*, *M. falciformis*, *M. cephalus*, *M. capensis*, *O. mossambicus*, *P. commersonnii*, *R. holubi*, *T. jarbua*, *V. cunnesius*, and *V. robustus* (Table 6.6).

Table 6.6. Major species accounting for the similarity within closed subtropical estuaries; *Si* is the average similarity contribution of each species; *% Si* is the percent contribution to the overall similarity (*S*); SD (*Si*) is the standard deviation of each species to the total similarity. Similarities are based on presence/absence, abundance and biomass.

	Presence/absence			**Abundance**			**Biomass**		
Species	***Si***	**% *Si***	*Si* / SD(*Si*)	***Si***	**% *Si***	*Si* / SD(*Si*)	***Si***	**% *Si***	*Si* / SD(*Si*)
C. gariepinus							2.0	3.56	0.40
G. aestuaria	3.7	6.35	0.97	5.0	9.56	0.81	1.6	2.93	0.80
G. callidus	4.5	7.60	1.32	3.6	6.82	1.19	1.8	3.29	1.19
L. alata				1.2	2.37	0.74	2.7	4.93	0.78
L. dumerilii	4.0	6.77	1.14	3.2	6.18	1.10	3.1	5.60	1.10
L. macrolepis	2.1	3.51	0.75	1.8	3.48	0.79	2.1	3.78	0.76
M. falciformis	3.0	5.10	0.98	2.3	4.37	1.11	2.2	4.02	1.02
M. cephalus	6.1	10.42	1.87	5.1	9.79	1.67	8.0	14.56	1.84
M. capensis	7.3	12.44	4.37	7.8	14.89	2.92	7.7	14.00	2.30
O. mossambicus	6.8	11.59	2.70	7.1	13.65	2.27	9.4	17.02	2.86
P. commersonnii	3.0	5.20	0.88	1.8	3.47	0.88	2.3	4.17	0.77
R. holubi	4.1	6.92	1.18	3.5	6.64	1.10	2.8	5.15	1.17
T. jarbua	1.6	2.80	0.61						
V. cunnesius	5.1	8.72	1.56	4.0	7.71	1.48	3.9	7.13	1.50
V. robustus	1.6	2.73	0.60	1.2	2.29	0.60			
Total *S*	**58.67**			**52.34**			**54.93**		

6.3.1.2 Inter-regional comparisons

In terms of their dissimilarities, the SIMPER analysis revealed that closed cool-temperate and closed warm-temperate systems had average dissimilarities of between 68.3% and 75.3% (Table 6.7). Taxa that accounted for over 50% of this dissimilarity included *A. breviceps*, *G. aestuaria*, *G. callidus*, *L. lithognathus*, *L. dumerilii*, *L. tricuspidens*, *M. falciformis*, *M. cephalus*, *M. capensis*, *O. mossambicus*, and *R. holubi*.

Table 6.7. Major species accounting for the dissimilarity between closed cool-temperate and closed warm-temperate estuaries; δ*i* is the average dissimilarity contribution of each species; % δ*i* is the percent contribution to the overall dissimilarity (δ); SD (δ*i*) is the standard deviation of each species to the total dissimilarity. Dissimilarities are based on presence/absence, abundance and biomass.

	Presence/absence			**Abundance**			**Biomass**		
Species	**δ*i***	**% δ*i***	δ*i* / SD(δ*i*)	**δ*i***	**% δ*i***	δ*i* / SD(δ*i*)	**δ*i***	**% δ*i***	δ*i* / SD(δ*i*)
A. breviceps	4.03	5.52	1.36	7.45	9.89	1.43			
G. aestuaria	4.58	6.28	1.51	9.11	12.10	1.81	3.51	5.14	1.72
G. callidus	4.44	6.09	1.96	5.02	6.67	1.69			
L. lithognathus	4.06	5.57	1.38				4.24	6.21	1.21
L. dumerilii				4.13	5.48	1.49	4.03	5.91	1.56
L. tricuspidens	3.99	5.47	1.55				4.41	6.45	1.31
M. falciformis	4.89	6.71	2.28						
M. cephalus							5.62	8.22	1.40
M. capensis	4.95	6.79	2.10	4.87	6.47	1.99	5.07	7.42	1.90
O. mossambicus							3.64	5.32	1.00
R. holubi	5.57	7.64	2.61	7.78	10.33	2.75	6.37	9.32	2.63
Total δ	**72.90**			**75.30**			**68.31**		

Closed warm-temperate and subtropical estuaries had average dissimilarities of between 54.7% and 62.4% (Table 6.8). Taxa that accounted for over 50% of the dissimilarity included *A. productus*, *A. japonicus*, *A. breviceps*, *C. gariepinus*, *G. aestuaria*, *G. callidus*, *L. lithognathus*, *L. alata*, *L. dumerilii*, *L. macrolepis*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *O. mossambicus*, *P. commersonnii*, *P. knysnaensis*, *R. holubi*, *T. jarbua*, *V. cunnesius* and *V. robustus*.

Table 6.8. Major species accounting for the dissimilarity between closed warm-temperate and closed subtropical estuaries; δ*i* is the average dissimilarity contribution of each species; % δ*i* is the percent contribution to the overall dissimilarity (δ); SD (δ*i*) is the standard deviation of each species to the total dissimilarity. Dissimilarities are based on presence/absence, abundance and biomass.

	Presence/absence			**Abundance**			**Biomass**		
Species	**δ*i***	**% δ*i***	**δ*i* / SD(δ*i*)**	**δ*i***	**% δ*i***	**δ*i* / SD(δ*i*)**	**δ*i***	**% δ*i***	**δ*i* / SD(δ*i*)**
A. productus	1.49	2.72	0.89						
A. japonicus							2.38	3.82	1.06
A. breviceps	3.08	5.62	2.31	5.63	9.30	1.77			
C. gariepinus							2.87	4.59	0.77
G. aestuaria				4.61	7.61	1.47			
G. callidus				2.33	3.84	1.25			
L. lithognathus	2.55	4.66	1.50	1.90	3.13	1.34	2.78	4.46	1.30
L. alata	1.61	2.95	1.08				2.69	4.31	1.20
L. dumerilii				2.16	3.56	1.28			
L. macrolepis	1.87	3.42	1.13						
L. richardsonii	3.56	6.50	4.19	4.03	6.65	3.45	6.17	9.89	2.84
L. tricuspidens	2.41	4.40	1.39	2.22	3.66	1.42	2.96	4.74	1.34
M. cephalus							2.30	3.68	1.13
O. mossambicus	1.71	3.13	0.88	3.22	5.32	1.28	3.38	5.42	1.30
P. commersonnii	1.85	3.38	1.01				2.36	3.79	1.23
P. knysnaensis	2.13	3.89	1.16						
R. holubi				3.07	5.07	1.40	2.57	4.12	1.47
T. jarbua	1.75	3.20	1.03						
V. cunnesius	2.95	5.38	1.93	2.91	4.80	1.62	2.80	4.48	1.84
V. robustus	1.74	3.18	1.02						
Total δ	**54.72**			**60.58**			**62.42**		

6.3.1.3 Physico-chemical relationships

The relative abundance and biomass of *H. capensis* exhibited a slight positive correlation with average estuary depth; the relative abundance of *G. aestuaria* and the biomass of *M. capensis* were also slightly positively correlated with depth (Table 6.9). Nine species (*A. productus*, *C. gariepinus*, *L. alata*, *L. macrolepis*, *M. capensis*, *O. mossambicus*, *T. jarbua*, *V. cunnesius*, *V. robustus*) were slightly positively correlated with temperature both in terms of abundance and biomass; *L. dumerilii*, *M. cephalus* and *P. commersonnii* exhibited a slight positive correlation with temperature in terms of abundance only. Four species (*A. breviceps*, *C. nudiceps*, *L. lithognathus*, *L. richardsonii*) exhibited a slight negative correlation with temperature both in terms of abundance and biomass; the relative biomass of *G. aestuaria* was also slightly negatively correlated with temperature (Table 6.9).

The abundance and biomass of eight species (*A. breviceps*, *E. machnata*, *L. amia*, *L. lithognathus*, *L. richardsonii*, *L. tricuspidens*, *P. knysnaensis*, *R. holubi*) was slightly positively correlated with salinity; the relative biomass of *A. japonicus*, *C. nudiceps*, *G. aestuaria*, *G. callidus* and *L. dumerilii,* was also slightly positively correlated with salinity. Eight species (*A. productus*, *C. gariepinus*, *L. alata*, *M. cephalus*, *O. mossambicus*, *T. jarbua*, *V. cunnesius*, *V. robustus*) were negatively correlated with salinity both in terms of abundance and biomass; the relative abundance of *L. macrolepis* was also slightly negatively correlated with salinity (Table 6.9).

Atherina breviceps, *L. lithognathus* and *L. richardsonii* exhibited a slight positive correlation with dissolved oxygen both in terms of abundance and biomass. The relative abundance and biomass of six species (*A. productus*, *C. gariepinus*, *L. alata*, *M. capensis*, *O. mossambicus*, *V. cunnesius*) were negatively correlated with dissolved oxygen. The relative abundance of *L. macrolepis* and *T. jarbua* was also slightly negatively correlated with dissolved oxygen (Table 6.9).

The relative abundance and biomass of *A. breviceps*, *H. capensis*, *L. lithognathus* and *P. knysnaensis* was negatively correlated with turbidity; the relative biomass of *L. richardsonii* was also slightly negatively correlated with turbidity. The abundance and biomass of *C. gariepinus*, *E. machnata*, *L. machnata*, *O. mossambicus* and *V. cunnesius* was slightly positively correlated with turbidity while the abundance of *C. nudiceps*, *P. commersonnii* and *T. jarbua* also exhibited a slight positive correlation with turbidity (Table 6.9).

Table 6.9. Spearman rank correlation coefficient between the relative abundance (n) and biomass (g) of key taxa and the mean physico-chemical parameters in closed estuaries (*p<0.05, **p<0.01).

Species	**Depth**		**Temperature**		**Salinity**		**Dissolved oxygen**		**Turbidity**	
	n	**g**	**n**	**g**	**n**	**g**	**n**	**g**	**n**	**g**
A. productus	0.07	0.08	0.47**	0.47**	-0.32**	-0.31**	-0.29*	-0.27*	0.15	0.12
A. japonicus	0.05	0.07	0.22	0.17	0.22	0.33	-0.09	-0.02	0.00	0.01
A. breviceps	0.09	0.09	-0.39**	-0.41**	0.66**	0.68**	0.32**	0.34**	-0.37**	-0.34**
C. nudiceps	-0.07	-0.07	-0.24*	-0.25*	0.18	0.24*	0.22	0.18	0.24*	0.20
C. gariepinus	-0.02	-0.02	0.34**	0.34**	-0.41**	-0.42**	-0.36**	-0.36**	0.33**	0.33**
E. machnata	0.07	0.07	-0.14	-0.15	0.27*	0.28*	0.22	0.24	0.30*	0.30*
G. aestuaria	0.33**	0.17	-0.23	-0.28*	0.15	0.31**	0.16	0.19	-0.05	-0.11
G. callidus	-0.08	-0.06	0.07	0.04	0.23	0.35**	0.24	0.19	0.14	0.04
H. capensis	0.31**	0.26*	-0.15	-0.10	0.20	0.13	0.00	-0.05	-0.27*	-0.29*
L. amia	0.15	0.18	-0.18	-0.20	0.37**	0.38**	0.16	0.18	-0.20	-0.21
L. lithognathus	0.12	0.13	-0.44**	-0.49**	0.33**	0.37**	0.29*	0.35**	-0.37**	-0.30*
L. alata	0.14	0.18	0.40**	0.40**	-0.46**	-0.47**	-0.42**	-0.44**	0.24	0.21
L. dumerilii	0.13	0.06	0.30*	0.22	0.14	0.27*	0.07	0.13	0.05	-0.04
L. macrolepis	0.08	0.07	0.43**	0.40**	-0.27*	-0.22	-0.24*	-0.18	0.31*	0.28*
L. richardsonii	-0.20	-0.13	-0.58**	-0.69**	0.38**	0.49**	0.25*	0.38**	-0.20	-0.25*
L. tricuspidens	-0.07	-0.01	-0.14	-0.22	0.65**	0.67**	0.16	0.21	-0.15	-0.19
M. falciformis	-0.06	0.13	0.16	0.10	0.10	0.19	-0.01	-0.02	0.14	0.00
M. cephalus	-0.14	-0.03	0.32**	-0.08	-0.48**	-0.24*	-0.10	0.10	0.15	0.13
M. capensis	0.03	0.25*	0.57**	0.44**	-0.15	-0.20	-0.28*	-0.35**	0.05	-0.04
O. mossambicus	-0.03	-0.02	0.67**	0.57**	-0.37**	-0.26*	-0.37**	-0.33**	0.33**	0.25*
P. commersonnii	-0.03	0.13	0.33**	0.19	-0.01	0.16	-0.13	-0.07	0.26*	0.09
P. knysnaensis	0.10	0.03	-0.16	-0.15	0.31**	0.33**	0.14	0.15	-0.33**	-0.27*
R. holubi	-0.18	-0.07	-0.07	-0.08	0.49**	0.61**	0.22	0.22	0.01	-0.12
T. jarbua	0.15	0.21	0.46**	0.48**	-0.32**	-0.31**	-0.25*	-0.20	0.27*	0.20
V. cunnesius	0.23	0.24	0.47**	0.46**	-0.55**	-0.57**	-0.42**	-0.44**	0.28*	0.29*
V. robustus	0.04	0.06	0.42**	0.44**	-0.32**	-0.32**	-0.12	-0.11	0.06	0.05

6.3.2 Open estuaries

6.3.2.1 Species composition

Twelve species, representing 10 families were recorded in open cool-temperate estuaries with an average of 6.8 (SD±3.2) species captured per estuary (Table 6.10). *Liza richardsonii* and *P. knysnaensis* were the most frequently reported taxa (100%), followed by *A. breviceps*, *Galeichthys feliceps* and *M. cephalus* (75%) and, *G. aestuaria*, *Pomatomus saltatrix* and *Syngnathus acus* (50%). Numerically dominant species included *L. richardsonii* (85.7%), *A. breviceps* (11.5%) and *G. aestuaria* (1.2%) with *L. richardsonii* (76.1%), *A. breviceps* (10.1%), *Argyrosomus* sp. (3.9%), *P. saltatrix* (3.8%), *M. cephalus* (1.9%), *G. feliceps* (1.8%), and *Haploblepharus pictus* (1.3%) dominating the overall biomass (Table 6.10).

Table 6.10. Percent frequency of occurrence, mean percent abundance and mean percent biomass composition of fishes in open cool-temperate estuaries (n = number of estuaries, SD = standard deviation).

Family	Species	Frequency		Abundance		Biomass	
		%	n	%	SD	%	SD
Ariidae	*Galeichthys feliceps*	75	3	0.05	0.05	1.80	1.55
Atherinidae	*Atherina breviceps*	75	3	11.52	16.22	10.10	17.15
Clupeidae	*Gilchristella aestuaria*	50	2	1.20	1.76	0.90	1.55
Gobiidae	*Caffrogobius nudiceps*	25	1	0.30	0.59	0.21	0.43
	Psammogobius knysnaensis	100	4	0.88	0.97	0.07	0.05
Mugilidae	*Liza richardsonii*	100	4	85.72	18.01	76.08	23.80
	Mugil cephalus	75	3	0.19	0.25	1.86	2.25
Pomatomidae	*Pomatomus saltatrix*	50	2	0.07	0.10	3.79	5.08
Scianidae	*Argyrosomus* sp.	25	1	0.01	0.02	3.89	7.79
Scyliorhinidae	*Haploblepharus pictus*	25	1	0.01	0.02	1.29	2.57
Syngnathidae	*Syngnathus acus*	50	2	0.03	0.04	0.01	0.02
Triglidae	*Chelidonichthys capensis*	25	1	0.01	0.03	0.00	0.00

Open estuaries in the cool-temperate region had average similarity values of between 55.8% and 59.9% (Table 6.11). Species that accounted for over 90% of the overall similarity within these systems included *A. breviceps*, *G. feliceps*, *L. richardsonii*, *M. cephalus* and *P. knysnaensis*.

Table 6.11. Major species accounting for the similarity within open cool-temperate estuaries; *Si* is the average similarity contribution of each species; % *Si* is the percent contribution to the overall similarity (*S*); SD (*Si*) is the standard deviation of each species to the total similarity. Similarities are based on presence/absence, abundance and biomass.

	Presence/absence			Abundance			Biomass		
Species	***Si***	**% *Si***	*Si* / SD(*Si*)	***Si***	**% *Si***	*Si* / SD(*Si*)	***Si***	**% *Si***	*Si* / SD(*Si*)
A. breviceps	6.9	11.51	0.89	4.4	7.65	0.75	3.8	6.86	0.62
G. feliceps	6.9	11.51	0.89	2.8	4.89	0.86	5.5	9.93	0.91
L. richardsonii	16.1	26.95	3.40	34.4	59.84	3.73	33.2	59.44	2.95
M. cephalus	9.6	15.97	0.87	4.2	7.25	0.90	4.6	8.17	0.76
P. knysnaensis	16.1	26.95	3.40	8.5	14.79	2.55	5.1	9.09	2.61
Total *S*	**59.92**			**57.50**			**55.78**		

Seventy-three species representing 35 families were captured in open warm-temperate estuaries with an average of 25.3 (SD±6.18) species being captured per system (Table 6.12). *Argyrosomus japonicus*, *L. dumerilii* and *L. tricuspidens* were the most frequently reported species (100%), followed by *Caffrogobius gilchristi*, *L. richardsonii*, *P. knysnaensis* and *R. holubi* (96%), *G. aestuaria* and *M. cephalus* (93%), *P. commersonnii* (89%), *A. breviceps*, *M. falciformis* and *S. bleekeri* (86%), *L. lithognathus* (79%), *E. machnata* (71%), *G. feliceps*, *G. callidus*, *H. capensis*, *L. amia* and *M. capensis* (64%), *Diplodus sargus* (57%), *C. nudiceps* (54%) and *L. macrolepis* (50%) (Table 6.12).

In terms of abundance, *G. aestuaria* (30.4%), *R. holubi* (15.1%), *L. richardsonii* (12.0%), *L. dumerilii* (7.8%), *M. cephalus* (6.4%), *A. breviceps* (4.7%), *C. gilchristi* (3.1%), *P. commersonnii* (3.0%), *G. callidus* (2.9%), *P. knysnaensis* (1.7%), *M. capensis* (1.5%), *S. bleekeri* (1.4%), *D. sargus* (1.3%), *A. japonicus* (1.2%) and *L. tricuspidens* (1.1%) were the dominant taxa. The overall biomass composition was dominated by *L. richardsonii* (15.5%), *E. machnata* (14.1%), *A. japonicus* (12.7%), *P. commersonnii* (8.9%), *M. cephalus* (8.9%), *G. feliceps* (8.7%), *L. tricuspidens* (7.2%), *L. dumerilii* (4.9%), *L. amia* (4.6%), *R. holubi* (3.2%), *Valamugil buchanani* (2.9%), *L. lithognathus* (1.8%) and *G. aestuaria* (1.1%) (Table 6.12).

Table 6.12. Percent frequency of occurrence, mean percent abundance and mean percent biomass composition of fishes in open warm-temperate estuaries (n = number of estuaries, SD = standard deviation).

Family	Species	Frequency		Abundance		Biomass	
		%	n	%	SD	%	SD
Ambassidae	*Ambassis gymnocephalus*	14	4	0.21	0.83	0.01	0.02
	Ambassis natalensis	4	1	0.00	0.02	0.00	0.00
	Ambassis productus	7	2	0.00	0.02	0.00	0.01
Anguillidae	*Anguilla mossambica*	7	2	0.01	0.05	0.01	0.05
Antennariidae	*Antennarius striatus*	4	1	0.00	0.00	0.00	0.00
Ariidae	*Galeichthys feliceps*	64	18	0.58	1.03	8.74	13.08
Atherinidae	*Atherina breviceps*	86	24	4.68	9.53	0.17	0.37
Blenniidae	*Omobranchus woodi*	4	1	0.00	0.00	0.00	0.00
Carangidae	*Caranx ignobilis*	4	1	0.00	0.01	0.00	0.00
	Caranx sexfasciatus	11	3	0.01	0.04	0.28	1.35
	Lichia amia	64	18	0.11	0.14	4.60	5.96
	Trachinotus spp.	4	1	0.00	0.02	0.00	0.00
	Trachurus trachurus	4	1	0.00	0.00	0.00	0.00
Cichlidae	*Oreochromis mossambicus*	7	2	0.02	0.09	0.02	0.12
Clinidae	*Clinus superciliosus*	36	10	0.36	1.25	0.03	0.11
Clupeidae	*Etrumeus whiteheadi*	4	1	0.00	0.01	0.00	0.00
	Gilchristella aestuaria	93	26	30.42	21.82	1.07	1.55
	Sardinops sagax	18	5	0.03	0.07	0.00	0.02
Dasyatidae	*Dasyatis kuhlii*	4	1	0.00	0.00	0.14	0.75
Elopidae	*Elops machnata*	71	20	0.27	0.34	14.14	14.56
Engraulidae	*Stolephorus holodon*	18	5	0.03	0.07	0.00	0.01
Gobiidae	*Caffrogobius gilchristi*	96	27	3.10	4.45	0.13	0.16
	Caffrogobius natalensis	36	10	0.17	0.41	0.01	0.01
	Caffrogobius nudiceps	54	15	0.60	1.18	0.03	0.06
	Glossogobius callidus	64	18	2.86	4.64	0.17	0.31
	Oligolepis acutipennis	11	3	0.02	0.11	0.00	0.00
	Oligolepis keiensis	21	6	0.08	0.18	0.00	0.00
	Psammogobius knysnaensis	96	27	1.73	1.65	0.04	0.04
Haemulidae	*Pomadasys commersonnii*	89	25	3.02	4.85	8.92	11.62
	Pomadasys kaakan	7	2	0.01	0.02	0.00	0.01
	Pomadasys olivaceum	29	8	0.31	0.91	0.04	0.13
Hemiramphidae	*Hemiramphus far*	11	3	0.03	0.15	0.00	0.01
Leiognathidae	*Leiognathus equula*	7	2	0.01	0.05	0.03	0.16
	Secutor ruconius	4	1	0.00	0.02	0.00	0.00
Lutjanidae	*Lutjanus argentimaculatus*	4	1	0.00	0.02	0.05	0.25
Monodactylidae	*Monodactylus falciformis*	86	24	0.44	0.45	0.72	1.07
Mugilidae	*Liza dumerilii*	100	28	7.76	8.46	4.86	3.38
	Liza macrolepis	50	14	0.23	0.80	0.42	0.68
	Liza richardsonii	96	27	12.03	17.94	15.46	15.38
	Liza tricuspidens	100	28	1.09	1.61	7.21	6.49
	Mugil cephalus	93	26	6.38	9.73	8.89	16.88
	Myxus capensis	64	18	1.54	4.52	0.88	1.37
	Valamugil buchanani	39	11	0.08	0.21	2.89	6.43
	Valamugil cunnesius	18	5	0.04	0.11	0.01	0.03
	Valamugil robustus	32	9	0.10	0.30	0.15	0.56
Myliobatidae	*Myliobatis aquila*	4	1	0.01	0.05	0.05	0.26
Odontapididae	*Eugomphodus taurus*	7	2	0.00	0.01	0.72	2.88
Platycephalidae	*Platycephalus indicus*	21	6	0.09	0.41	0.11	0.27
Pomatomidae	*Pomatomus saltatrix*	46	13	0.10	0.29	0.47	1.68
Rajidae	*Raja miraletes*	4	1	0.00	0.00	0.00	0.00
Sciaenidae	*Argyrosomus japonicus*	100	28	1.15	1.88	12.69	9.01
	Johnius dorsalis	4	1	0.00	0.02	0.01	0.05
Siganidae	*Siganus sutor*	4	1	0.00	0.01	0.00	0.00
Sillaginidae	*Sillago sihama*	4	1	0.00	0.00	0.00	0.00
Soleidae	*Heteromycteris capensis*	64	18	0.46	0.77	0.01	0.01
	Solea bleekeri	86	24	1.39	3.28	0.04	0.05

Table 6.12 continued.

Family	**Species**	**Frequency**		**Abundance**		**Biomass**	
		%	**n**	**%**	**SD**	**%**	**SD**
Sparidae	*Acanthopagrus berda*	21	6	0.39	1.92	0.20	0.64
	Diplodus cervinus	21	6	0.02	0.06	0.00	0.02
	Diplodus sargus	57	16	1.29	3.75	0.03	0.08
	Gymnocrotaphus curvidens	4	1	0.00	0.01	0.00	0.00
	Lithognathus lithognathus	79	22	0.73	1.17	1.81	3.74
	Rhabdosargus globiceps	39	11	0.30	0.72	0.03	0.10
	Rhabdosargus holubi	96	27	15.06	13.39	3.24	2.49
	Rhabdosargus sarba	4	1	0.00	0.01	0.06	0.29
	Sarpa salpa	32	9	0.52	1.97	0.08	0.26
Sphyraenidae	*Sphyraena jello*	4	1	0.01	0.03	0.09	0.47
Syngnathidae	*Hippichthys spicifer*	4	1	0.00	0.01	0.00	0.00
	Syngnathus acus	32	9	0.04	0.09	0.00	0.01
	Syngnathus watermeyeri	4	1	0.00	0.01	0.00	0.00
Teraponidae	*Terapon jarbua*	11	3	0.02	0.06	0.01	0.06
Tetraodontidae	*Amblyrhynchotes honckenii*	21	6	0.02	0.04	0.01	0.03
Torpedinidae	*Torpedo fuscumaculata*	14	4	0.01	0.02	0.11	0.31
	Torpedo sinusperci	14	4	0.01	0.01	0.08	0.23

Open warm-temperate estuaries had overall similarities ranging between 57.9% and 63.0% (Table 6.13). Twenty-one species accounted for over 90% of the similarity within this group. These taxa included *A. japonicus*, *A. breviceps*, *C. gilchristi*, *D. sargus*, *E. machnata*, *G. feliceps*, *G. aestuaria*, *G. callidus*, *H. capensis*, *L. amia*, *L. lithognathus*, *L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. falciformis*, *M. cephalus*, *M. capensis*, *P. commersonnii, P. knysnaensis*, *R. holubi*, and *S. bleekeri* (Table 6.13).

Table 6.13. Major species accounting for the similarity within open warm-temperate estuaries; *Si* is the average similarity contribution of each species; % *Si* is the percent contribution to the overall similarity (*S*); SD (*Si*) is the standard deviation of each species to the total similarity. Similarities are based on presence/absence, abundance and biomass.

	Presence/absence			**Abundance**			**Biomass**		
Species	***Si***	**% *Si***	***Si* / SD(*Si*)**	***Si***	**% *Si***	***Si* / SD(*Si*)**	***Si***	**% *Si***	***Si* / SD(*Si*)**
A. japonicus	1.4	2.15	0.97	1.5	2.52	2.47	7.0	11.46	4.39
A. breviceps	2.7	4.35	1.38	2.9	4.97	1.24	1.0	1.71	1.13
C. gilchristi	2.8	4.39	1.47	2.4	4.15	1.63	1.7	2.72	2.20
D. sargus	1.3	2.02	0.67	0.9	1.60	0.64			
E. machnata	1.9	3.04	0.98	1.3	2.27	0.92	3.4	5.58	0.96
G. feliceps	1.8	2.82	0.80	1.2	2.11	0.77	2.5	4.03	0.76
G. aestuaria	3.8	5.99	2.19	4.7	8.13	2.04	2.7	4.39	2.07
G. callidus	1.6	2.49	0.82	1.7	2.94	0.75			
H. capensis	1.6	2.52	0.80	1.1	1.98	0.77			
L. amia	1.6	2.62	0.81	0.9	1.60	0.81	2.1	3.37	0.79
L. lithognathus	2.7	4.22	1.20	1.7	2.93	1.13	1.7	2.72	0.90
L. dumerilii	4.5	7.07	5.13	5.3	9.19	3.53	5.2	8.49	4.29
L. richardsonii	4.1	6.58	2.89	5.1	8.79	1.85	6.3	10.29	2.19
L. tricuspidens	3.2	5.00	1.83	2.1	3.71	2.62	5.4	8.91	3.57
M. falciformis	3.1	4.87	1.58	2.1	3.56	1.48	1.7	2.78	1.21
M. cephalus	3.6	5.79	2.15	3.4	5.83	1.81	4.1	6.79	1.71
M. capensis	1.6	2.54	0.79	1.1	1.91	0.74			
P. commersonnii	2.3	3.68	1.19	1.8	3.10	1.36	4.2	6.93	1.42
P. knysnaensis	4.1	6.56	2.89	3.9	6.68	2.73	1.4	2.21	2.37
R. holubi	4.1	6.46	2.94	6.3	10.82	2.48	4.0	6.55	2.47
S. bleekeri	3.0	4.82	1.58	2.3	4.03	1.42	1.0	1.64	1.42
Total *S*	**62.97**			**57.86**			**61.07**		

In open subtropical estuaries, 76 species representing 31 families were captured with an average of 35.8 (SD±9.96) species being captured per estuary (Table 6.14). The most frequently recorded species included *A. japonicus*, *E. machnata*, *G. callidus*, *L. alata*, *L. dumerilii*, *L. macrolepis*, *M. cephalus*, *P. commersonnii*, *R. holubi*, *T. jarbua* and *V. cunnesius* (100%), followed by *Acanthopagrus berda*, *Caranx sexfasciatus*, *Hilsa kelee*, *Leiognathus equula* and *M. capensis* (90%), *Ambassis natalensis*, *Caranx ignobilis*, *G. aestuaria*, *Oligolepis acutipennis* and *Oligolepis keiensis* (80%), *L. tricuspidens*, *Scomberoides lysan*, *S. bleekeri*, *V. buchanani* and *V. robustus* (70%), *Amblyrhynchotes honckenii* (60%), and *Ambassis gymnocephalus*, *C. gilchristi*, *Lutjanus argentimaculatus*, *Thryssa vitrirostris* and *Valamugil seheli* (50%) (Table 6.14).

The most abundant species overall were *G. aestuaria* (15.7%), *L. dumerilii* (14.7%), *A. gymnocephalus* (6.9%), *R. holubi* (6.9%), *V. cunnesius* (6.8%), *L. macrolepis* (6.0%), *G. callidus* (4.2%), *M. cephalus* (3.4%), *P. commersonnii* (3.3%), *L. equula*

(3.2%), *A. natalensis* (2.2%), *C. sexfasciatus* (1.8%), *C. ignobilis* (1.6%), *S. lysan* (1.6%), *C. gilchristi* (1.5%), *T. jarbua* (1.5%), *S. bleekeri* (1.3%), *M. capensis* (1.1%), *V. buchanani* (1.1%), *A. honckenii* (1.0%), *V. robustus* (1.0%) and *H. kelee* (1.0%) (Table 6.14).

The biomass composition was dominated by *Liza alata* (14.9%), *E. machnata* (10.3%), *M. cephalus* (10.2%), *A. japonicus* (9.0%), *V. buchanani* (8.7%), *H. kelee* (4.7%), *L. dumerilii* (4.6%), *P. commersonnii* (4.2%), *L. macrolepis* (3.9%), *M. capensis* (3.6%), *C. sexfasciatus* (3.6%), *V. cunnesius* (3.5%), *Megalops cyprinoides* (3.1%), *L. argentimaculatus* (2.3%), *C. gariepinus* (2.2%), *A. berda* (1.2%), *T. vitrirostris* (1.1%), *L. amia* (1.0%), *L. tricuspidens* (1.0%) and *R. holubi* (1.0%) (Table 6.14).

Table 6.14. Percent frequency of occurrence, mean percent abundance and mean percent biomass composition of fishes in open subtropical estuaries (n = number of estuaries, SD = standard deviation).

Family	**Species**	**Frequency**		**Abundance**		**Biomass**	
		%	**n**	**%**	**SD**	**%**	**SD**
Ambassidae	*Ambassis gymnocephalus*	50	5	6.94	11.72	0.35	0.56
	Ambassis natalensis	80	8	2.17	2.70	0.05	0.06
	Ambassis productus	40	4	0.20	0.27	0.21	0.43
Atherinidae	*Atherina breviceps*	20	2	0.61	1.30	0.02	0.04
Bothidae	*Pseudorhombus arsius*	10	1	0.05	0.16	0.01	0.04
Carangidae	*Caranx heberi*	10	1	0.00	0.01	0.00	0.00
	Caranx ignobilis	80	8	1.62	1.56	0.94	1.84
	Caranx papuensis	30	3	0.03	0.06	0.19	0.39
	Caranx sexfasciatus	90	9	1.77	1.92	3.59	5.21
	Lichia amia	20	2	0.02	0.04	1.03	2.40
	Scomberoides lysan	70	7	1.55	3.81	0.03	0.06
Cichlidae	*Oreochromis mossambicus*	30	3	0.16	0.35	0.26	0.64
	Tilapia rendalli	10	1	0.01	0.04	0.00	0.00
Clariidae	*Clarias gariepinus*	30	3	0.07	0.11	2.17	3.81
Clupeidae	*Gilchristella aestuaria*	80	8	15.70	22.85	0.52	1.00
	Hilsa kelee	90	9	0.95	0.95	4.67	4.52
Eleotridae	*Eleotris fusca*	10	1	0.01	0.02	0.00	0.00
Elopidae	*Elops machnata*	100	10	0.41	0.31	10.34	8.17
Engraulidae	*Engraulis japonicus*	20	2	0.16	0.44	0.00	0.00
	Stolephorus holodon	40	4	0.77	1.91	0.01	0.02
	Thryssa setirostris	20	2	0.02	0.04	0.00	0.00
	Thryssa vitrirostris	50	5	0.93	1.33	1.14	1.91
Gerreidae	*Gerres acinaces*	10	1	0.07	0.23	0.00	0.01
	Gerres filamentosus	10	1	0.01	0.04	0.00	0.00
	Gerres methueni	30	3	0.88	1.67	0.07	0.18
Gobiidae	*Caffrogobius gilchristi*	50	5	1.54	3.27	0.03	0.07
	Caffrogobius natalensis	20	2	0.05	0.10	0.00	0.00
	Favonigobius reichei	20	2	0.07	0.17	0.00	0.00
	Glossogobius biocellatus	10	1	0.02	0.06	0.00	0.00
	Glossogobius callidus	100	10	4.19	5.57	0.07	0.11
	Glossogobius giuris	40	4	0.24	0.54	0.01	0.02
	Oligolepis acutipennis	80	8	0.69	0.92	0.01	0.01
	Oligolepis keiensis	80	8	0.61	0.73	0.01	0.01
	Periopthalmus koelreuteri	20	2	0.01	0.03	0.00	0.00
	Psammogobius knysnaensis	30	3	0.10	0.27	0.00	0.00
	Silhouettea sibayi	10	1	0.04	0.14	0.00	0.00
Haemulidae	*Pomadasys commersonnii*	100	10	3.33	3.01	4.15	5.03
	Pomadasys kaakan	30	3	0.23	0.50	0.23	0.48
	Pomadasys olivaceum	10	1	0.90	2.86	0.02	0.06
Leiognathidae	*Leiognathus equula*	90	9	3.21	4.64	0.64	0.79
Lutjanidae	*Lutjanus argentimaculatus*	50	5	0.06	0.08	2.33	5.24
	Lutjanus fulviflamma	10	1	0.01	0.02	0.00	0.00
Megalopidae	*Megalops cyprinoides*	40	4	0.12	0.20	3.14	6.71
Monodactylidae	*Monodactylus argenteus*	20	2	0.03	0.06	0.02	0.03
	Monodactylus falciformis	40	4	0.05	0.12	0.05	0.11
Mugilidae	*Liza alata*	100	10	0.92	0.94	14.86	14.31
	Liza dumerilii	100	10	14.73	11.57	4.57	3.08
	Liza macrolepis	100	10	6.04	6.95	3.88	2.74
	Liza melinoptera	20	2	0.01	0.03	0.06	0.13
	Liza tricuspidens	70	7	0.34	0.63	1.03	2.82
	Mugil cephalus	100	10	3.36	3.06	10.16	6.19
	Myxus capensis	90	9	1.13	1.29	3.63	4.51
	Valamugil buchanani	70	7	1.06	1.52	8.69	11.57
	Valamugil cunnesius	100	10	6.77	9.73	3.50	4.70
	Valamugil robustus	70	7	0.96	1.83	0.78	0.87
	Valamugil seheli	50	5	0.85	2.43	0.04	0.07

Table 6.14 continued.

Family	Species	Frequency		Abundance		Biomass	
		%	n	%	SD	%	SD
Mullidae	*Upeneus vittatus*	20	2	0.09	0.20	0.01	0.01
Platycephalidae	*Platycephalus indicus*	30	3	0.13	0.24	0.24	0.49
Polynemidae	*Polydactylus plebeius*	10	1	0.00	0.01	0.03	0.08
Pomatomidae	*Pomatomus saltatrix*	30	3	0.06	0.09	0.10	0.31
Scianidae	*Argyrosomus japonicus*	100	10	0.72	0.71	8.97	11.40
Serranidae	*Epinephelus malabaricus*	30	3	0.04	0.07	0.01	0.03
Silliaginidae	*Sillago sihama*	20	2	0.07	0.19	0.01	0.03
Soleidae	*Solea bleekeri*	70	7	1.26	1.76	0.03	0.04
Sparidae	*Acanthopagrus berda*	90	9	0.88	0.74	1.21	1.54
	Diplodus sargus	10	1	0.02	0.06	0.05	0.15
	Lithognathus lithognathus	10	1	0.00	0.01	0.06	0.19
	Rhabdosargus holubi	100	10	6.91	6.12	0.99	1.02
	Rhabdosargus sarba	40	4	0.35	0.82	0.24	0.48
Sphyraenidae	*Sphyraena jello*	30	3	0.05	0.08	0.30	0.66
Syngnathidae	*Hippichthys heptagonus*	10	1	0.01	0.02	0.00	0.00
	Hippichthys spicifer	10	1	0.01	0.02	0.00	0.00
Teraponidae	*Terapon jarbua*	100	10	1.46	1.31	0.13	0.08
Tetraodontidae	*Amblyrhynchotes honckenii*	60	6	0.99	1.70	0.07	0.10
	Arothron immaculatus	20	2	0.03	0.05	0.01	0.03
	Chelonodon laticeps	40	4	0.12	0.27	0.04	0.13

The average similarities in open subtropical region estuaries ranged between 58.2% and 61.9% (Table 6.15). Thirty species accounted for over 90% of the similarity within this group and these were represented by *A. berda*, *A. natalensis*, *A. honckenii*, *A. japonicus*, *C. ignobilis*, *C. sexfasciatus*, *E. machnata*, *G. aestuaria*, *G. callidus*, *H. kelee*, *L. equula*, *L. alata*, *L. dumerilii*, *L. macrolepis*, *L. tricuspidens*, *L. argentimaculatus*, *M. cephalus*, *M. capensis*, *O. acutipennis*, *O. keiensis*, *P. commersonnii*, *R. holubi*, *S. lysan*, *S. bleekeri*, *T. jarbua*, *T. vitrirostris*, *V. buchanani*, *V. cunnesius*, *V. robustus*, and *V. seheli* (Table 6.15).

Table 6.15. Major species accounting for the similarity within open subtropical estuaries; *Si* is the average similarity contribution of each species; % *Si* is the percent contribution to the overall similarity (*S*); SD (*Si*) is the standard deviation of each species to the total similarity. Similarities are based on presence/absence, abundance and biomass.

	Presence/absence			**Abundance**			**Biomass**		
Species	***Si***	**% *Si***	***Si* / SD(*Si*)**	***Si***	**% *Si***	***Si* / SD(*Si*)**	***Si***	**% *Si***	***Si* / SD(*Si*)**
A. berda	2.5	3.97	1.87	1.9	3.23	1.75	1.8	2.90	1.74
A. natalensis	1.8	2.93	1.17	1.6	2.71	1.16	0.7	1.10	1.05
A. honckenii	0.6	0.92	0.44	0.7	1.14	0.54			
A. japonicus	1.3	2.07	1.11	1.4	2.40	2.71	3.9	6.48	3.70
C. ignobilis				0.7	1.21	1.03	1.1	1.85	1.10
C. sexfasciatus	1.3	2.17	1.29	1.2	2.13	1.74	2.1	3.39	1.25
E. machnata	3.2	5.22	5.65	2.2	3.76	4.95	4.2	7.01	2.58
G. aestuaria	1.9	3.01	1.23	2.0	3.48	1.00	0.9	1.55	1.00
G. callidus	3.2	5.22	5.65	3.2	5.42	2.79	1.1	1.90	3.24
H. kelee	2.5	3.97	1.87	1.9	3.32	1.83	3.0	5.02	1.90
L. equula	2.5	3.97	1.87	2.1	3.68	1.64	1.6	2.72	1.69
L. alata	3.2	5.22	5.65	2.4	4.20	4.02	4.9	8.09	2.67
L. dumerilii	3.2	5.22	5.65	5.5	9.43	3.84	4.0	6.55	4.09
L. macrolepis	3.2	5.22	5.65	3.6	6.26	4.44	3.6	5.97	3.82
L. tricuspidens	0.9	1.41	0.67	0.7	1.26	0.84	0.6	1.05	0.80
L. argentimaculatus	0.6	0.96	0.52				0.6	0.97	0.49
M. cephalus	2.2	3.60	2.07	1.8	3.14	3.11	5.0	8.20	3.30
M. capensis	0.8	1.30	0.86	1.0	1.73	1.54	2.1	3.46	1.23
O. acutipennis	1.9	3.10	1.23	1.4	2.43	1.18	0.6	0.97	1.16
O. keiensis	1.9	3.01	1.23	1.3	2.30	1.18			
P. commersonnii	3.2	5.22	5.65	3.0	5.12	4.83	3.0	5.03	3.39
R. holubi	3.2	5.22	5.65	3.8	6.51	2.51	2.3	3.77	2.65
S. lysan	1.0	1.55	0.71	0.8	1.34	0.84			
S. bleekeri	1.4	2.26	0.90	1.3	2.15	0.84			
T. jarbua	2.5	4.05	2.40	2.2	3.86	2.46	1.7	2.83	7.27
T. vitrirostris	0.6	1.00	0.52						
V. buchanani	0.9	1.40	0.77	0.9	1.47	0.82	1.9	3.20	0.79
V. cunnesius	3.2	5.22	5.65	3.2	5.45	3.94	2.7	4.49	2.87
V. robustus	1.5	2.36	0.91	1.2	1.99	0.88	1.1	1.84	0.80
V. seheli	0.8	1.37	0.53						
Total *S*	**61.85**			**58.21**			**60.51**		

6.3.2.2 Inter-regional comparisons

Open cool-temperate and warm-temperate estuaries had average dissimilarities of between 68.6% and 73.6% (Table 6.16). *Argyrosomus japonicus*, *A. breviceps*, *C. gilchristi*, *E. machnata*, *G. feliceps*, *G. aestuaria*, *G. callidus*, *H. capensis*, *L. amia*, *L. lithognathus*, *L. dumerilii*, *L. macrolepis*, *L. richardsonii*, *L. tricuspidens*, *M. falciformis*, *M. cephalus*, *M. capensis*, *P. commersonnii*, *R. holubi* and *S. bleekeri* were among the species that accounted for over 50% of the dissimilarity.

Table 6.16. Major species accounting for the dissimilarity between open cool-temperate and open warm-temperate estuaries; δ*i* is the average dissimilarity contribution of each species; % δ*i* is the percent contribution to the overall dissimilarity (δ); SD (δ*i*) is the standard deviation of each species to the total dissimilarity. Dissimilarities are based on presence/absence, abundance and biomass.

	Presence/absence			**Abundance**			**Biomass**		
Species	**δ*i***	**% δ*i***	**δ*i* / SD(δ*i*)**	**δ*i***	**% δ*i***	**δ*i* / SD(δ*i*)**	**δ*i***	**% δ*i***	**δ*i* / SD(δ*i*)**
A. japonicus							5.75	7.82	3.66
A. breviceps				3.71	5.18	1.37	2.91	3.95	1.26
C. gilchristi	2.80	4.08	1.85	2.69	3.75	1.58			
E. machnata	2.23	3.25	1.51				4.16	5.66	1.45
G. feliceps							2.89	3.93	1.23
G. aestuaria	1.91	2.78	0.94	3.31	4.62	1.31			
G. callidus	2.01	2.92	1.30	2.72	3.80	1.15			
H. capensis	2.10	3.06	1.26						
L. amia	2.11	3.08	1.25				2.86	3.89	1.24
L. lithognathus	2.73	3.98	1.66	2.14	2.99	1.45			
L. dumerilii	3.54	5.16	3.88	5.01	6.99	3.30	4.37	5.94	4.08
L. macrolepis									
L. richardsonii				4.98	6.96	1.92	3.69	5.01	1.83
L. tricuspidens	2.98	4.34	2.17				4.74	6.44	3.26
M. falciformis	2.88	4.19	2.15	2.19	3.06	1.94			
M. cephalus				2.31	3.22	1.62			
M. capensis	2.09	3.05	1.24						
P. commersonnii	2.49	3.63	1.74				4.42	6.00	1.68
R. holubi	3.37	4.91	3.09	5.94	8.29	2.95	3.65	4.96	3.05
S. bleekeri	2.85	4.16	2.16	2.51	3.51	1.65			
Total δ	**68.59**			**71.61**			**73.56**		

Average dissimilarities between warm-temperate subtropical systems ranged between 61.5% and 64.3% (Table 6.17). Species accounting for over 50% of this dissimilarity included *A. berda*, *A. natalensis*, *A. breviceps*, *C. gilchristi*, *C. sexfasciatus*, *D. sargus*, *E. machnata*, *G. feliceps*, *G. aestuaria*, *G. callidus*, *H. capensis*, *H. kelee*, *L. equula*, *L. amia*, *L. lithognathus*, *L. alata*, *L. macrolepis*, *L. richardsonii*, *L. tricuspidens*, *M. falciformis*, *M. cephalus*, *M. capensis*, *O. acutipennis*, *O. keiensis*, *P. commersonnii*, *P. knysnaensis*, *R. holubi*, *S. lysan*, *T. jarbua*, *V. buchanani*, *V. cunnesius*, *V. robustus* and *V. seheli*.

Table 6.17. Major species accounting for the dissimilarity between open warm-temperate and open subtropical estuaries; δ*i* is the average dissimilarity contribution of each species; % δ*i* is the percent contribution to the overall dissimilarity (δ); SD (δ*i*) is the standard deviation of each species to the total dissimilarity. Dissimilarities are based on presence/absence, abundance and biomass.

	Presence/absence			**Abundance**			**Biomass**		
Species	**δ*i***	**% δ*i***	**δ*i* / SD(δ*i*)**	**δ*i***	**% δ*i***	**δ*i* / SD(δ*i*)**	**δ*i***	**% δ*i***	**δ*i* / SD(δ*i*)**
A. berda	1.36	2.18	1.56	1.26	1.96	1.88	1.35	2.20	1.92
A. natalensis	1.40	2.25	1.67	1.33	2.07	1.62			
A. breviceps	1.26	2.04	1.42	2.00	3.12	1.44			
C. gilchristi	1.33	2.14	1.83	1.36	2.11	1.44			
C. sexfasciatus	1.14	1.84	1.73				1.82	2.97	1.41
D. sargus	1.01	1.62	1.08	1.10	1.71	0.99			
E. machnata							1.71	2.77	1.22
G. feliceps	1.20	1.93	1.28	1.10	1.71	1.16	2.06	3.35	1.14
G. aestuaria				1.43	2.22	1.06			
G. callidus				1.64	2.55	1.50			
H. capensis	1.14	1.83	1.27						
H. kelee	1.64	2.64	2.64	1.45	2.26	2.44	2.28	3.71	2.66
L. equula	1.54	2.49	2.12	1.74	2.71	1.91	1.27	2.07	2.05
L. amia	1.07	1.73	1.14				1.67	2.71	1.21
L. lithognathus	1.36	2.19	1.53	1.28	1.98	1.40	1.31	2.13	1.16
L. alata	1.88	3.02	5.27	1.59	2.47	3.11	3.39	5.52	2.65
L. macrolepis	1.43	2.31	1.82	1.72	2.68	2.22	1.73	2.82	1.81
L. richardsonii	1.81	2.92	3.65	3.07	4.78	2.09	3.31	5.38	2.43
L. tricuspidens							1.98	3.21	1.82
M. falciformis	1.09	1.76	1.12	1.10	1.71	1.51			
M. cephalus				1.22	1.90	1.48	1.25	2.03	1.20
M. capensis							1.49	2.43	1.38
O. acutipennis	1.35	2.18	1.57	1.09	1.70	1.52			
O. keiensis	1.22	1.97	1.36						
P. commersonnii							1.30	2.12	1.20
P. knysnaensis	1.28	2.07	1.38	1.74	2.70	2.06			
R. holubi				1.71	2.66	1.61			
S. lysan	1.06	1.71	1.16						
T. jarbua	1.59	2.56	2.62	1.46	2.02	2.27			
V. buchanani							1.98	3.23	1.18
V. cunnesius	1.63	2.62	2.36	2.10	3.27	2.26	1.93	3.13	2.58
V. robustus	1.07	1.73	1.11						
V. seheli	1.03	1.65	0.98						
Total δ	**62.09**			**64.31**			**61.48**		

6.3.2.3 Physico-chemical relationships

The relative abundance and biomass of *V. buchanani* and the abundance of *C. nudiceps*, *L. amia* and *L. dumerilii* was slightly positively correlated with mean estuary depth (Table 6.18). Two species (*C. gariepinus* and *M. cyprinoides*) were negatively correlated with depth both in terms of abundance and biomass.

The relative abundance and biomass of 25 species (*A. berda*, *A. gymnocephalus*, *A. natalensis*, *A. honckenii*, *C. ignobilis*, *C. sexfasciatus*, *C. gariepinus*, *E. machnata*, *H. kelee*, *L. equula*, *L. alata*, *L. macrolepis*, *L. argentimaculatus*, *M. cyprinoides*, *M.*

cephalus, *M. capensis*, *O. acutipennis*, *O. keiensis*, *S. lysan*, *T. jarbua*, *T. vitrirostris*, *V. buchanani*, *V. cunnesius*, *V. robustus*, *V. seheli*) was slightly positively correlated with temperature; the relative abundance of *G. callidus*, *L. dumerilii* and *P. commersonnii* was also slightly positively correlated with temperature. The relative abundance and biomass of *A. breviceps*, *G. feliceps*, *L. richardsonii*, *P. knysnaensis* and *S. acus* and the biomass of *L. lithognathus* were slightly negatively correlated with temperature (Table 6.18).

Thirteen species (*A. breviceps*, *C. gilchristi*, *C. nudiceps*, *D. sargus*, *G. feliceps*, *G. aestuaria*, *G. callidus*, *L. amia*, *L. lithognathus*, *L. tricuspidens*, *M. falciformis*, *P. knysnaensis* and *R. holubi*) were slightly positively correlated with salinity both in terms of abundance and biomass. The abundance of *H. capensis* and the biomass of *L. dumerilii* were also slightly positively correlated with salinity. The abundance and biomass of eight species (*A. natalensis*, *C. gariepinus*, *H. kelee*, *L. alata*, *M. cyprinoides*, *O. acutipennis*, *T. jarbua* and *V. cunnesius*) was negatively correlated with salinity. The abundance of *L. equula*, *O. keiensis*, *P. commersonnii*, and the biomass of *M. cephalus* and *S. lysan* were also slightly negatively correlated with salinity (Table 6.18).

The relative abundance and biomass of *C. gariepinus*, *H. kelee*, *L. equula* and *L. amia*, and the abundance of *C. sexfasciatus* and the biomass of *L. macrolepis* showed a slight negative correlation with dissolved oxygen (Table 6.18).

Ambassis gymnocephalus, *S. bleekeri* and *V. cunnesius* all showed a positive correlation with turbidity, both in terms of relative abundance and biomass. The abundance of *A. japonicus*, *L. macrolepis*, *O. keiensis* and *P. commersonnii*, and the biomass of *M. cephalus* and *M. capensis* were also positively correlated with turbidity. The relative abundance and biomass of *L. amia* was negatively correlated with turbidity. The abundance of *D. sargus* and the biomass of *G. feliceps* and *P. knysnaensis* were also slightly negatively correlated with turbidity (Table 6.18).

Table 6.18. Spearman rank correlation coefficient of the relative abundance (n) and biomass (g) of key taxa and the mean physico-chemical parameters in open estuaries (*p<0.05, **p<0.01).

Species	**Depth**		**Temperature**		**Salinity**		**Dissolved oxygen**		**Turbidity**	
	n	**g**	**n**	**g**	**n**	**g**	**n**	**g**	**n**	**g**
A. berda	0.03	-0.01	0.70**	0.61**	-0.24	-0.23	-0.26	-0.28	0.18	0.28
A. gymnocephalus	-0.02	-0.03	0.31*	0.35*	-0.15	-0.19	-0.30	-0.25	0.32*	0.38*
A. natalensis	0.03	-0.11	0.65**	0.62**	-0.45**	-0.45**	-0.15	-0.15	0.14	0.10
A. honckenii	0.18	0.14	0.43**	0.37*	-0.02	-0.01	0.08	0.07	-0.16	-0.12
A. japonicus	0.09	-0.08	0.26	0.16	-0.17	0.13	0.07	-0.27	0.41**	0.25
A. breviceps	0.09	0.07	-0.34*	-0.37*	0.50**	0.56**	-0.08	-0.12	-0.20	-0.27
C. gilchristi	0.19	0.06	-0.19	-0.30	0.42**	0.59**	0.04	-0.15	-0.00	-0.15
C. nudiceps	0.31*	0.27	-0.17	-0.15	0.35*	0.42**	-0.07	-0.11	-0.16	-0.23
C. ignobilis	0.25	0.22	0.67**	0.67**	-0.24	-0.25	-0.21	-0.23	0.04	0.05
C. sexfasciatus	0.17	0.16	0.70**	0.66**	-0.26	-0.21	-0.31*	-0.30	0.10	0.06
C. gariepinus	-0.32*	-0.32*	0.38*	0.38*	-0.44**	-0.44**	-0.32*	-0.33*	0.30	0.30
D. sargus	0.02	-0.03	-0.06	0.12	0.49**	0.43**	-0.11	-0.17	-0.38*	-0.30
E. machnata	0.22	0.15	0.52**	0.32*	0.20	0.38*	0.03	-0.02	0.01	-0.06
G. feliceps	0.09	0.10	-0.53**	-0.58**	0.33*	0.38*	-0.10	-0.16	-0.30	-0.33*
G. aestuaria	0.05	0.09	-0.03	-0.20	0.59**	0.54**	-0.13	-0.12	0.02	0.02
G. callidus	0.02	-0.07	0.41**	0.29	0.35*	0.44**	-0.19	-0.24	-0.07	-0.09
H. capensis	0.06	0.10	-0.24	-0.18	0.31*	0.19	-0.08	-0.09	-0.05	-0.07
H. kelee	-0.07	-0.02	0.68**	0.68**	-0.36*	-0.32*	-0.32*	-0.33*	0.17	0.16
L. equula	-0.12	-0.09	0.70**	0.69**	-0.33*	-0.29	-0.37*	-0.39*	0.20	0.22
L. amia	0.32*	0.25	-0.09	0.00	0.62**	0.63**	-0.33*	-0.32*	-0.37*	-0.38*
L. lithognathus	0.14	0.10	-0.28	-0.36*	0.36*	0.35*	0.00	-0.05	-0.21	-0.23
L. alata	0.03	0.06	0.73**	0.73**	-0.41**	-0.39*	-0.29	-0.28	0.18	0.18
L. dumerilii	0.42**	0.20	0.55**	0.29	0.08	0.47**	-0.02	-0.16	0.06	-0.20
L. macrolepis	0.00	-0.07	0.74**	0.69**	-0.32*	-0.18	-0.25	-0.39*	0.34*	0.27
L. richardsonii	-0.20	-0.25	-0.78**	-0.82**	0.10	0.16	0.23	0.20	-0.20	-0.24
L. tricuspidens	0.15	-0.03	-0.11	-0.20	0.47**	0.38*	0.15	0.07	-0.11	-0.10
L. argentimaculatus	0.13	0.15	0.49**	0.48**	-0.25	-0.22	0.13	-0.20	0.23	0.22
M. cyprinoides	-0.39*	-0.39*	0.41**	0.41**	-0.47**	-0.47**	-0.26	-0.26	0.24	0.24
M. falciformis	0.19	0.02	-0.12	-0.20	0.40*	0.56**	0.19	-0.13	-0.08	-0.30
M. cephalus	-0.07	0.09	0.31*	0.46**	-0.30	-0.41**	0.07	0.11	0.26	0.47**
M. capensis	0.05	0.07	0.51**	0.46**	-0.22	-0.27	-0.06	-0.08	0.30	0.31*
O. acutipennis	0.04	0.05	0.63**	0.60**	-0.47**	-0.39*	-0.13	-0.10	0.30	0.21
O. keiensis	-0.25	-0.16	0.49**	0.37*	-0.36*	-0.25	-0.19	-0.16	0.46**	0.26
P. commersonnii	0.14	-0.20	0.55**	0.23	-0.34*	-0.10	-0.07	-0.25	0.39*	0.12
P. saltatrix	0.25	0.06	0.00	-0.08	0.12	0.25	-0.03	0.01	0.02	0.01
P. knysnaensis	0.01	0.02	-0.56**	-0.63**	0.37*	0.42**	0.06	-0.04	-0.20	-0.41**
R. holubi	0.02	-0.04	0.08	-0.03	0.36*	0.65**	0.01	-0.12	0.08	-0.22
S. lysan	0.21	0.11	0.64**	0.54**	-0.30	-0.32*	-0.18	-0.11	0.09	0.00
S. bleekeri	-0.03	0.00	0.22	0.09	-0.14	0.03	0.04	0.00	0.49**	0.32*
S. acus	0.15	0.04	-0.31*	-0.35*	0.20	0.06	-0.06	-0.11	-0.22	-0.13
T. jarbua	0.15	0.11	0.73**	0.64**	-0.38*	-0.36*	-0.26	-0.30	0.16	0.14
T. vitrirostris	-0.08	-0.07	0.46**	0.45**	-0.30	-0.28	-0.21	-0.22	-0.01	-0.02
V. buchanani	0.31*	0.34*	0.64**	0.59**	-0.04	0.07	-0.11	-0.09	0.02	-0.04
V. cunnesius	0.09	0.08	0.74**	0.77**	-0.56**	-0.51**	-0.22	0.08	0.40*	0.38*
V. robustus	-0.04	-0.07	0.44**	0.43**	-0.09	-0.05	0.04	0.05	0.20	0.15
V. seheli	0.21	0.21	0.50**	0.50**	-0.26	-0.26	-0.12	-0.12	0.12	0.12

6.4 DISCUSSION

6.4.1 Closed estuaries

6.4.1.1 Cool-temperate estuaries

Mugilids, *L. richardsonii* and *M. cephalus*, were the most frequently recorded species in closed cool-temperate estuaries and were also among the dominant taxa both in terms abundance and biomass. Other important taxa included *A. breviceps*, *C. nudiceps*, *G. aestuaria* and *L. amia*, with *H. capensis* also occasionally recorded (Table 6.1).

Similar fish communities have also been reported from closed cool-temperate estuaries, e.g. in the Diep estuary, *L. richardsonii* was found to be the commonest species with *M. cephalus* also present in lower numbers (Millard & Scott, 1954). Other frequently reported species include *A. breviceps*, *C. nudiceps*, *G. aestuaria*, *H. capensis*, *L. lithognathus*, *P. knysnaensis*, and *R. globiceps* (Millard & Scott, 1954; Grindley & Dudley, 1988). Limited sampling in the Wildevoël estuary revealed the presence of both *L. richardsonii* and *M. cephalus* (Heinecken, 1985). In the Sand estuary, *L. richardsonii* and *M. cephalus* along with other smaller species such as *A. breviceps*, *C. nudiceps* and *P. knysnaensis* were common, with *L. amia*, *L. lithognathus*, *P. saltatrix* and *R. globiceps* reported in smaller numbers (Morant & Grindley, 1982). The numerically dominant species reported in the Sand by Clark *et al.* (1994) included *A. breviceps*, *G. aestuaria*, *L. richardsonii* and *P. knysnaensis*. Quick & Harding (1994) found that juvenile *L. richardsonii* occur in the Sand estuary in very large numbers and that the system is also an important nursery area for *L. amia*, *L. lithognathus* and *M. cephalus*.

6.4.1.2 Warm-temperate estuaries

Important taxa in terms of frequency of occurrence, numerical contribution and biomass in closed warm-temperate estuaries included *G. aestuaria*, *L. lithognathus*, *L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus, M. capensis* and *R. holubi*. Frequently captured species that were also numerically important were *A. breviceps*, *G. callidus* and *P. knysnaensis* while *O. mossambicus* and *P. commersonnii* were important in terms of biomass. *Argyrosomus japonicus*, *E. machnata* and *L. amia*, were among the important taxa in terms of biomass but were not regularly recorded.

Although it did not contribute significantly toward the overall abundance or biomass in closed warm-temperate estuaries, *M. falciformis* was frequently captured in these systems (Table 6.3).

From gill netting in the Hartenbos system, Bickerton (1982) found that *L. dumerilii*, *L. richardsonii* and *M. falciformis* were among the most abundant species. Further to the east, Bickerton & Pierce (1988) recorded *G. feliceps*, *L. lithognathus*, *L. dumerilii* and *R. holubi* as being numerically dominant in the Seekoei estuary. Dundas (1994) found that important species, in terms of abundance and/or biomass, in the Seekoei estuary included *A. breviceps*, *G. aestuaria*, *L. amia*, *L. lithognathus*, *L. richardsonii*, *M. falciformis*, *M. cephalus* and *R. holubi*. The most abundant species reported in the Kabeljous estuary included *A. japonicus*, *L. richardsonii* and *Pomadasys olivaceum* (Bickerton & Pierce, 1988). According to Dundas (1994) important taxa in the Kabeljous estuary, either numerically and/or in terms of biomass, included *A. breviceps*, *G. aestuaria*, *L. amia*, *L. lithognathus*, *L. richardsonii*, *L. tricuspidens*, *M. falciformis*, *M. cephalus*, *O. mossambicus*, *P. commersonnii* and *R. holubi*. Important species captured in the Van Stadens estuary included *A. breviceps*, *L. amia*, *L. lithognathus*, *L. dumerilii*, *L. richardsonii*, *M. falciformis*, *M. cephalus*, *Myliobatis aquila*, *P. commersonnii* and *R. holubi* (Dundas, 1994).

Cowley & Whitfield (2001) documented the numerically dominant fishes in the Oos-Kleinemond estuary, including *A. breviceps*, *G. aestuaria*, *G. callidus*, *L. lithognathus*, *L. dumerilii*, *L. richardsonii*, *M. falciformis*, *M. cephalus*, *M. capensis* and *R. holubi*. Similarly, Vorwerk *et al*. (2001) found that *A. breviceps*, *G. aestuaria*, *G. callidus*, *L. dumerilii, L. richardsonii*, *M. falciformis, M. capensis*, *O. mossambicus*, and *R. holubi* were generally the most abundant fishes in the Oos-Kleinemond, Mpekweni, Mtati, Mgwalana, Bira, and Gqutywa estuaries. Taxa such as *E. machnata*, *L. lithognathus*, *M. cephalus*, *P. commersonnii* and *P. saltatrix* were also among the dominant species in some of these systems.

6.4.1.3 Subtropical estuaries

Taxa that were frequently captured and were also important in terms of abundance and biomass in closed subtropical estuaries included *A. productus, G. aestuaria*, *L.*

dumerilii, *L. macrolepis*, *M. cephalus*, *M. capensis*, *O. mossambicus*, *R. holubi*, *V. cunnesius*, and *V. robustus*. Species such as *G. callidus* and *M. falciformis* were regularly recorded and were also numerically important, while *L. alata*, and *P. commersonnii* were among the dominant species in terms of biomass. *Argyrosomus japonicus* and *C. gariepinus* were seldom captured but were important in terms of biomass. Although it did not comprise an important component, either numerically or by mass, *T. jarbua* was frequently reported in these systems (Table 6.5).

Ramm *et al.*, (1987) found that the most abundant fishes recorded in the Sezela estuary included *A. productus*, *O. mossambicus*, *V. cunnesius*, *M. capensis*, *M. falciformis* and *G. aestuaria*. Important species, either numerically and/or in terms of biomass in the Mhlanga estuary included *A. commersonnii*, *A. japonicus*, *G. aestuaria*, *G. callidus*, *L. amia*, *L. alata, L. dumerilii*, *L. macrolepis*, *M. cephalus*, *M. capensis*, *O. mossambicus*, *P. commersonnii*, *R. holubi*, *T. jarbua* and *V. cunnesius* (Whitfield, 1980a; 1980b; 1980c; Harrison & Whitfield, 1995). *Ambassis productus*, *L. alata*, *L. macrolepis*, *M. cephalus*, *M. capensis*, *O. mossambicus* and *V. cunnesius* were also among the most frequently reported species in the Mdloti estuary (Blaber *et al.*, 1984). Overall, Begg (1984a; 1984b) found that normally closed systems in KwaZulu-Natal were commonly dominated by species such as *G. aestuaria*, *Glossogobius* spp. and *O. mossambicus*.

6.4.2 Open estuaries

6.4.2.1 Cool-temperate estuaries

In open cool-temperate estuaries, *A. breviceps* and *L. richardsonii* were important species in terms of frequency of occurrence, numerical contribution and biomass. *Gilchristella aestuaria* was also frequently recorded and was an important species in terms of abundance, while *G. feliceps*, *M. cephalus* and *P. saltatrix* were important in terms of biomass. *Argyrosomus* sp. and *H. pictus* were also important in terms of biomass but were uncommon. *Argyrosomus* sp. was only recorded in the Olifants estuary, and *H. pictus* in the Berg estuary. Although not well represented either numerically or in terms of biomass, *P. knysnaensis* and *S. acus* were recorded in a number of estuaries during this study (Table 6.10).

Day (1981a) found that the commonest species reported in the Olifants estuary were *A. breviceps*, *G. aestuaria* and *L. richardsonii* with a few *L. lithognathus* also reported. In the Berg estuary, *A. breviceps*, *G. aestuaria* and *L. richardsonii* were also found to be among the commonest species (Day, 1981a). Similarly, the most abundant species reported in a seine net survey of this system included *L. richardsonii*, *G. aestuaria*, *A. breviceps*, *C. nudiceps* and *P. knysnaensis* (Bennett, 1994). Seine net surveys of the Palmiet estuary also revealed that *A. breviceps*, *L. lithognathus*, *L. richardsonii* and *P. knysnaensis* were the dominant taxa, both in terms of abundance and/or biomass, with also among the most abundant species captured (Branch & Day, 1984; Bennett, 1989a). Taxa such as *C. nudiceps*, *L. lithognathus*, Mugilidae and *P. knysnaensis* have also been reported from the Uilkraals estuary (Heydorn & Bickerton, 1982).

6.4.2.2 Warm-temperate estuaries

In open warm-temperate estuaries, *A. japonicus*, *G. aestuaria*, *L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *P. commersonnii* and *R. holubi* were all taxa that were frequently reported and were also important in terms of abundance and biomass. Frequently captured species that were also numerically important included *A. breviceps*, *C. gilchristi*, *D. sargus*, *G. callidus*, *M. capensis*, *P. knysnaensis* and *S. bleekeri*, while *E. machnata*, *G. feliceps*, *L. amia* and *L. lithognathus* made major contributions to the overall biomass. *Valamugil buchanani* was not frequently recorded but it was important in terms of biomass. Although they did not contribute to the overall abundance or biomass, *C. nudiceps*, *H. capensis*, *L. macrolepis* and *M. falciformis* were frequently captured during this study (Table 6.12).

Numerically important species captured in a survey of the Breë estuary, using both gill and seine netting, included *G. feliceps*, *L. lithognathus*, *L. richardsonii* and *M. cephalus* (Ratte, 1982). These species were also abundant during a gill net study in the system (Coetzee & Pool, 1991), with large numbers of *A. japonicus*, *L. amia*, *M. falciformis* and *P. commersonnii* also being documented. In a Kromme estuary gill net study, Marais (1983a) found that *A. japonicus*, *G. feliceps*, *L. amia*, *M. falciformis*, Mugilidae (mostly *L. dumerilii*, *L. richardsonii* and *L. tricuspidens*), *P. commersonnii* and *R. holubi* were the dominant taxa either numerically and/or in terms of biomass.

A gill net survey by Bickerton & Pierce (1988) also found that *G. feliceps*, *L. amia* and *L. richardsonii* were the most abundant species. Important species recorded by Hanekom & Baird (1984) in a Kromme seine net study included *A. breviceps*, *C. gilchristi*, *G. aestuaria*, *G. callidus*, *L. dumerilii*, *P. knysnaensis* and *R. holubi*. Important taxa, both numerically and in terms of biomass, recorded in a Gamtoos estuary gill net study included *A. japonicus*, *G. feliceps*, *L. amia* and Mugilidae (*L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus* and *M. capensis*) (Marais, 1983b).

From Baird *et al*. (1988) the most abundant fishes from netting in the Swartkops estuary over the period 1915-1916 were *A. japonicus*, *G. feliceps*, *L. amia*, *L. lithognathus*, Mugilidae, *P. commersonnii*, *P. saltatrix* and *R. holubi*. The most abundant taxa recorded from a seine net study during 1973-1975 included *A. breviceps*, mullet (mostly *L. dumerilii*) and *R. holubi*. A seine net study over the period 1977-1979 reported *A. breviceps*, *D. sargus*, *Engraulis japonicus*, *G. aestuaria*, Mugilidae and *R. holubi* as the most abundant taxa with mugilids (*L. dumerilii* and *L. richardsonii*) and *R. holubi* dominating the biomass (Baird *et al*., 1988). Abundant taxa reported in *Zostera* beds in the Swartkops estuary included *A. breviceps*, *D. sargus*, *G. aestuaria*, Gobiidae (mostly *C. gilchristi* and *P. knysnaensis*), Mugilidae (*L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*) and *R. holubi* (Beckley, 1983). From gill netting in the system, Marais & Baird (1980) recorded *P. commersonnii* as the dominant species both numerically and in terms of mass; other important species included *E. machnata*, *G. feliceps*, *L. amia*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, and *R. holubi*.

Important gill net captured species, either numerically and/or in terms of biomass, in the Sundays estuary included *A. japonicus*, *G. feliceps*, *L. richardsonii*, *M. cephalus* and *P. commersonnii* (Marais, 1981). Abundant taxa recorded by Beckley (1984) during a seine net study in the same estuary were *G. aestuaria*, Gobiidae (*P. knysnaensis* and *C. gilchristi*), *M. falciformis*, Mugilidae (*L. dumerilii*, *L. richardsonii* and *M. cephalus*), *R. holubi*, and Soleidae (*H. capensis* and *S. bleekeri*).

Ter Morshuizen & Whitfield (1994), in a small mesh seine net study of *Zostera* beds in the Kariega estuary, found that the numerically dominant taxa included *A. breviceps*, *C. superciliosus*, *G. aestuaria*, *G. callidus*, *D. sargus*, *M. falciformis*, Mugilidae and *R. holubi*. Dominant species associated with intertidal saltmarshes in the same system were *A. breviceps*, *G. aestuaria*, *L. dumerilii*, *M. cephalus*, and *R. holubi* (Paterson & Whitfield, 1996). In the Kowie estuary, numerically important species included *A. breviceps*, *A. japonicus*, *D. sargus*, *G. feliceps*, *G. aestuaria*, *L. amia*, *L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *M. capensis*, *P. commersonnii*, *P. olivaceum* and *R. holubi* (Whitfield *et al.*, 1994).

The most abundant species reported in the Great Fish estuary were *A. japonicus*, *G. feliceps*, *G. aestuaria*, *L. lithognathus*, *L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *M. capensis*, *P. commersonnii*, *P. olivaceum*, *R. holubi*, and *S. bleekeri* (Whitfield *et al.*, 1994). Numerically dominant fishes reported in the Great Fish estuary by Ter Morshuizen *et al.* (1996a; 1996b) included *A. gymnocephalus*, *A. japonicus*, *C. nudiceps*, *G. feliceps*, *G. aestuaria*, *L. lithognathus*, *L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, Mugilidae (<30 mm SL), *M. cephalus*, *M. capensis*, *P. commersonnii*, *P. knysnaensis* and *R. holubi*. According to Vorwerk *et al.* (2001) numerically dominant fishes in this estuary included *A. japonicus*, *G. aestuaria*, *H. capensis*, *L. lithognathus*, *L. dumerilii*, *L. richardsonii*, *M. cephalus*, *P. commersonnii*, *P. knysnaensis*, *R. holubi* and *S. bleekeri*.

Numerically important species in the Keiskamma estuary were *A. breviceps*, *A. japonicus*, *C. gilchristi*, *C. nudiceps*, *G. feliceps*, *G. aestuaria*, *L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *M. capensis*, *P. commersonnii*, and *R. holubi* (Vorwerk *et al.*, 2001). Dominant species, both in terms of number and biomass, from gill netting in the Great Kei estuary included *A. japonicus*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *M. capensis* and *P. commersonnii* (Plumstead *et al.*, 1985). Gill net catches in the Mbashe estuary were dominated by *A. japonicus*, *E. machnata*, *L. amia*, *L. tricuspidens*, *M. cephalus*, *M. capensis*, *P. commersonnii* and *V. buchanani*; species such as *L. dumerilii*, *L. richardsonii*, *R. holubi* and *V. robustus* were also fairly common (Plumstead *et al.*, 1989a). The dominant taxa, both numerically and in terms of biomass, reported from gill netting in the Mtata estuary were *A. japonicus*, *C. leucas*, *E. machnata*, *J. dorsalis*, *L. equula*, *L. amia*, *L. alata*, *M. cephalus*, *P. commersonnii*, *P. kaakan*, *T. vitrirostris* and *V. buchanani* (Plumstead *et al*., 1989b).

6.4.2.3 Subtropical estuaries

Important taxa in open subtropical estuaries in terms of frequency of occurrence, abundance and biomass included *C. sexfasciatus*, *H. kelee*, *L. dumerilii*, *L. macrolepis*, *M. cephalus*, *M. capensis*, *P. commersonnii*, *R. holubi*, *V. buchanani* and *V. cunnesius*. Frequently reported species that were also abundant included *A. gymnocephalus*, *A. natalensis*, *A. honckenii*, *C. gilchristi*, *C. ignobilis*, *G. aestuaria*, *G. callidus*, *L. equula*, *S. lysan*, *S. bleekeri*, *T. jarbua* and *V. robustus*. Species such as *A. berda*, *A. japonicus*, *E. machnata*, *L. alata*, *L. tricuspidens*, *L. argentimaculatus*, and *T. vitrirostris* were also regularly reported and were important in terms of biomass. Although they did not contribute greatly to the overall abundance or biomass, *O. acutipennis*, *O. keiensis* and *V. seheli* were frequently reported in these estuaries. *Clarias gariepinus*, *L. amia* and *M. cyprinoides* were infrequently recorded but did make important contributions to the overall biomass in these systems (Table 6.14).

On an individual estuary basis Branch & Grindley (1979) found that the following species were common to abundant in the Mngazana estuary; *A. natalensis*, *A. breviceps*, *C. gilchristi*, *C. nudiceps*, *Eleotris fusca*, *G. aestuaria*, *G. callidus*, *L. dumerilii*, *L. macrolepis*, *M. argenteus*, *M. cephalus*, *O. acutipennis*, *P. knysnaensis*, *R. holubi*, *S. salpa* and *T. jarbua*. In the Mntafufu estuary, *A. japonicus*, *Caranx* spp., *Chanos chanos*, *E. machnata*, *H. kelee*, *L. equula*, *L. amia*, *L. alata*, *L. macrolepis*, *L. tricuspidens*, *M. falciformis*, *M. cephalus*, *M. capensis*, *P. commersonnii*, *P. saltatrix*, *R. sarba*, *Sphyraena acutipinnis*, *T. vitrirostris*, *V. buchanani* and *V. cunnesius* dominated the overall gill net catch composition both numerically and/or in terms of biomass (Plumstead *et al*., 1991). The dominant species captured in the Mzamba estuary included *A. japonicus*, *Caranx* spp., *C. chanos*, *H. kelee*, *L. equula, L. amia*, *L. alata*, *L. macrolepis*, *M. cephalus*, *M. capensis*, *P. saltatrix*, *Scomberoides tol*, *T. vitrirostris* and *V. buchanani* (Plumstead *et al*., 1991).

Moving northwards, Hemens *et al*. (1986) documented the important taxa in the Matigulu system, namely Ambassidae, *A. japonicus*, *E. machnata*, *L. equula*, *L. macrolepis* and *Pomadasys* spp. Common to abundant fishes reported in the Mlalazi estuary by Hill (1966) comprised Ambassidae, *Arothron immaculatus*, *L. dumerilii M. cephalus*, *Periopthalmus* sp., *R. holubi*, *T. jarbua*, and *V. seheli*. According to Begg (1984a; 1984b), open estuaries on the subtropical KwaZulu-Natal coast are dominated by a wide variety of marine teleosts including *A. berda*, *A. japonicus*, *Pomadasys* spp., *Rhabdosargus* spp. and Mugilidae.

6.4.3 Physico-chemical relationships

Fish in estuaries appear to show a preference for relatively shallow waters (Wallace & van der Elst, 1975; Blaber, 1985) that provide shelter and refuge from larger fish predators, which are normally confined to deeper waters (Whitfield & Blaber, 1978). Most species during this study did not show any clear or consistent correlation with average depth in either closed or open estuaries. The relative abundance and/or biomass of *G. aestuaria*, *H. capensis* and *M. capensis* exhibited a slight positive correlation with average estuary depth in closed estuaries (Table 6.9) while *C. nudiceps*, *L. amia*, *L. dumerilii* and *V. buchanani* was slightly positively correlated with mean estuary depth in open systems. Two species (*C. gariepinus* and *M. cyprinoides*) were also negatively correlated with depth in open estuaries (Table 6.18).

The relative abundance and/or biomass of 30 species exhibited a slight positive correlation with temperature during this study, including *A. berda*, *A. gymnocephalus*, *A. natalensis*, *A. productus*, *A. honckenii*, *C. ignobilis*, *C. sexfasciatus*, *C. gariepinus*, *E. machnata*, *G. callidus*, *H. kelee*, *L. equula*, *L. alata*, *L. dumerilii*, *L. macrolepis*, *L. argentimaculatus*, *M. cyprinoides*, *M. cephalus*, *M. capensis*, *O. acutipennis*, *O. keiensis*, *O. mossambicus*, *P. commersonnii*, *S. lysan*, *T. jarbua*, *T. vitrirostris*, *V. buchanani*, *V. cunnesius*, *V. robustus* and *V. seheli* (Tables 6.9 & 6.18). Cyrus & Blaber (1987a) also reported a positive relationship between the abundance of *A. berda*, *C. sexfasciatus*, *E. machnata*, *L. macrolepis*, *L. equula*, *M. cephalus*, *T. jarbua*, *T. vitrirostris*, and *V. cunnesius* and water temperature in the St Lucia system (KwaZulu-Natal).

The vast majority of the species (26) that exhibited a positive correlation with temperature are tropical Indo-Pacific species (Smith & Heemstra, 1995). Most of these occur in estuaries along the east coast of South Africa with some species reaching as far south as Cape Agulhas and False Bay (e.g. *M. falciformis*, *P. commersonnii*) (Smith & Heemstra, 1995; Whitfield, 1998). *Amblyrhynchotes honckenii* has even been recorded in the Berg estuary on the west coast (Bennett, 1994). Maree *et al*. (2000) reported a number of tropical taxa such as *A. gymnocephalus*, *A. natalensis*, *C. ignobilis*, *C. sexfasciatus*, *L. alata*, *L. argentimaculatus* and *M. cyprinoides* extending as far south as the Swartkops estuary. These species, however, were represented only by a few sporadic individuals.

The subtraction in distribution of tropical species is strongly linked to the decrease in sea temperatures along the southeast coast of South Africa (Wallace & van der Elst, 1975; Blaber, 1981; Day *et al*., 1981; Whitfield *et al*., 1981; Whitfield, 1998; 1999). A rapid decline in tropical 'vagrant' species was also reported south of Algoa Bay and this was attributed to the reduction in inshore temperature as the Agulhas Current diverges from the coast (Maree *et al*., 2000). Average summer and winter sea temperatures off Port Elizabeth vary between 16 and 22 °C (Whitfield, 1998). Briggs (1974) noted that in tropical shelf regions, many tropical species are unable to live in waters where the average temperature for the coldest month drops below 20 °C.

Low water temperatures have also occasionally resulted in mass mortalities of tropical fishes in subtropical estuaries. Cyrus & McLean (1996), for example, reported a fish kill in the St Lucia estuary following a rapid drop in water temperature (<14 °C) in winter. The dominant species killed were *H. kelee*, *L. equula* and *T. vitrirostris* with *Ambassis*, *Caranx*, *Scomberoides*, *T. jarbua* and *V. cunnesius* also recorded (Cyrus & McLean, 1996). Numerous tropical species were also recorded dying in Kosi Bay in winter when water temperatures decreased from 14 to 10 °C overnight (Kyle, 1989).

The abundance and/or biomass of a number of species (*A. breviceps*, *C. nudiceps*, *G. feliceps*, *G. aestuaria L. lithognathus*, *L. richardsonii*, *P. knysnaensis* and *S. acus*) exhibited a slight negative correlation with temperature (Tables 6.9 & 6.18). Most of these are endemic species that appear to prefer cooler waters. Species such as *A.*

breviceps, *L. lithognathus* and *L. richardsonii*, for example, are found from the west coast to northern KwaZulu-Natal (Smith & Heemstra, 1995). They are, however, most abundant in temperate South African estuaries and are rare in subtropical systems (Day *et al*. 1981; Whitfield, 1998). Maree *et al*. (2000) also reported a strong negative correlation between the number of temperate (endemic) species and the mean monthly minimum temperatures of eight estuaries between the Kromme and Mntafufu systems.

Eighteen species (*A. japonicus*, *A. breviceps*, *C. gilchristi*, *C. nudiceps*, *D. sargus*, *E. machnata*, *G. feliceps*, *G. aestuaria*, *G. callidus*, *H. capensis L. amia*, *L. lithognathus*, *L. dumerilii, L. richardsonii L. tricuspidens*, *M. falciformis P. knysnaensis*, *R. holubi*) exhibited a slight positive correlation with salinity in terms of abundance and/or biomass (Tables 6.9 & 6.18). Many of these were also species that prefer cooler waters and generally do not occur in subtropical estuaries (e.g. *A. breviceps*, *C. gilchristi*, *C. nudiceps*, *G. feliceps*, *H. capensis*, *L. lithognathus*, *L. richardsonii*, *P. knysnaensis*) (Whitfield, 1998). Bennett (1985) reported a mass mortality of fishes, including species such as *D. sargus*, *G. feliceps*, *L. lithognathus* and *L. richardsonii* in the closed Bot estuary on the southwest coast when salinities declined to 2-3 ‰. All of these are euryhaline marine species but they differ in their susceptibility to low salinities; the first fish to die were *D. sargus* and *G. feliceps* followed by *L. lithognathus* and *L. richardsonii* (Bennett, 1985). Of the taxa that were positively correlated with salinity, only *A. breviceps* and *C. gilchristi* have been recorded in salinities below 1 ‰ (Whitfield, 1996; 1998).

A number of species (*A. productus*, *A. natalensis*, *C. gariepinus*, *H. kelee*, *L. equula*, *L. alata*, *L. macrolepis*, *M. cyprinoides*, *M. cephalus*, *O. acutipennis O. keiensis*, *O. mossambicus*, *P. commersonnii*, *S. lysan*, *T. jarbua*, *V. cunnesius* and *V. robustus*) exhibited a slight negative correlation with salinity (Tables 6.9 & 6.18). Both *C. gariepinus* and *O. mossambicus* are freshwater species. *Clarias gariepinus* cannot tolerate salinities above 10 ‰ but *O. mossambicus* has been recorded in salinities of between 0-116 ‰ (Whitfield, 1996). Whitfield & Blaber (1979) found that *O. mossambicus* is abundant in closed estuaries, but is usually absent from the lower and middle reaches of permanently open estuaries. *Oreochromis mossambicus* was also an important component of the ichthyofauna of closed estuaries during this study.

The majority of the species that were negatively correlated with salinity were tropical Indo-Pacific species (Smith & Heemstra, 1995). Blaber (1981) found that many estuary-associated fishes in southeast Africa also occur in large areas of the Indian Ocean, such as the Bay of Bengal and south-east Asia where, due to monsoon rains twice a year, salinities are always less than 35 ‰. Whitfield *et al.* (1981) also noted that fishes inhabiting southern African estuaries are more tolerant of low rather than high salinities.

The relative abundance and/or biomass of *A. breviceps*, *L. lithognathus* and *L. richardsonii* exhibited a slight positive correlation with dissolved oxygen during this study while *A. productus*, *C. sexfasciatus C. gariepinus*, *H. kelee*, *L. equula*, *L. amia*, *L. alata*, *L. macrolepis M. capensis*, *O. mossambicus*, *T. jarbua* and *V. cunnesius* were negatively correlated with dissolved oxygen (Tables 6.9 & 6.18). Those species that were positively correlated with dissolved oxygen were all cool water species while those that showed a negative correlation were predominantly tropical taxa. The relationship between relative abundance/biomass, and dissolved oxygen is probably a reflection of the temperature preferences of the species, rather than dissolved oxygen. Temperature and dissolved oxygen measurements were significantly ($p<0.05$) negatively correlated in both closed and open estuaries during this study.

The relative abundance/biomass of 14 species (*A. gymnocephalus*, *A. japonicus*, *C. nudiceps*, *C. gariepinus*, *E. machnata*, *L. macrolepis*, *M. cephalus*, *M. capensis O. keiensis*, *O. mossambicus*, *P. commersonnii*, *S. bleekeri*, *T. jarbua* and *V. cunnesius*) was slightly positively correlated with turbidity (Tables 6.9 & 6.18). Cyrus & Blaber (1987a) also reported a positive correlation between the abundance of *E. machnata*, *M. cephalus*, *S. bleekeri* and *V. cunnesius* and turbidity in the St Lucia estuary. Cyrus & Blaber (1987b) noted that the vast majority of the fishes that occur in southeast African estuaries are turbid water species, occurring predominantly in waters with turbidities of over 10 NTU. Furthermore, the shallow brackish areas of the Indian Ocean such as the Bay of Bengal and southeast Asia, where many estuary-associated fishes of the Indo-Pacific also occur, have characteristically turbid waters (Blaber, 1981).

A number of cool water species (*A. breviceps*, *D. sargus*, *G. feliceps*, *H. capensis*, *L. amia*, *L. lithognathus*, *L. richardsonii* and *P. knysnaensis*) were also negatively correlated with turbidity (Table 6.9 & 6.18). Whitfield (1998) states that, although *A. breviceps* is found in a range of estuaries, it is more abundant in clear systems. Species such as *P. knysnaensis* and *H. capensis* are also reported to prefer the sandy lower reaches of open estuaries in the Western and Eastern Cape where clear marine waters tend to prevail.

6.4.4 General

The key taxa identified during this study may be divided into a number of groups, based on their occurrence, relative abundance and biomass, and relationships with environmental variables.

Group1

The first group comprises tropical species that are largely restricted to subtropical estuaries. Representatives of this group include *A. berda*, *A. gymnocephalus*, *A. natalensis*, *A. productus*, *C. ignobilis*, *C. sexfasciatus*, *C. gariepinus*, *H. kelee*, *L. equula*, *L. alata*, *L. macrolepis*, *L. argentimaculatus*, *M. cyprinoides*, *O. acutipennis*, *O. keiensis*, *S. lysan*, *T. jarbua*, *T. vitrirostris*, *V. buchanani, V. cunnesius*, *V. robustus* and *V. seheli*. The distribution of these fishes appears to be strongly linked to temperature. The relative abundance and/or biomass of the majority of these taxa were positively correlated with temperature although many species were also negatively correlated with salinity.

Group 2

This group also comprised tropical species but their distribution extends further south into warm-temperate estuaries. Species belonging to this group included *A. honckenii*, *A. japonicus*, *E. machnata*, *M. falciformis*, *O. mossambicus* and *P. commersonnii*. Briggs (1974) also noted that a conspicuous faunal element that inhabit warm-temperate shelf regions is the ‘eurythermic tropical’ group, which consists of species that range in both tropical and warm-temperate waters.

The species belonging to this group were generally positively correlated with both temperature and salinity. Martin (1988) found that the combination of temperature and salinity was a major determinant in the distribution and abundance of tropical ambassid fishes. Increased salinities (from 10 to 34 ‰) had the effect of widening the survival temperature range of *A. gymnocephalus* and *A. natalensis* in southern African waters (Martin, 1988). Whitfield (1995b; 1999) also notes that most mass mortalities of fish in estuaries on the subcontinent are associated with a combination of low salinities and low water temperatures. A mass mortality of fishes occurred in the St Lucia system when the salinity declined below 3 ‰ and the temperature dropped to 12 °C (Blaber & Whitfield, 1976).

Group 3

The third group comprises south coast endemic species that were a major component of the fish community in warm-temperate estuaries and were also important in subtropical systems. These species generally do not comprise a major component of the fish community of cool-temperate estuaries. This group included species such as *G. callidus*, *L. dumerilii*, *L. tricuspidens*, *M. capensis*, *R. holubi* and *S. bleekeri*. Most of these taxa occur from the southern Cape coast northward to Mozambique (Smith & Heemstra, 1995). Some species (e.g. *L. dumerilii*, *M. capensis*, *R. holubi* and *S. bleekeri*) have also been reported in estuaries on the southwest coast (Bennett, 1989a; Clark *et al.*, 1994). *Solea bleekeri* has been captured in the Berg estuary on the west coast but only during summer (Bennett, 1994).

Species belonging to this group were generally positively correlated with both temperature and salinity. Whitfield (1999) has suggested that the combination low salinities and temperatures that are frequently recorded in cool-temperate estuaries probably limit the colonisation of these systems by endemic species such as *R. holubi*.

Group 4

The fourth group comprised 'cool-water' endemics that were important in both warm- and cool-temperate estuaries but did not make a major contribution to the ichthyofauna of subtropical systems. These species included *A. breviceps*, *C. gilchristi*, *C. nudiceps*, *G. feliceps*, *H. capensis*, *L. lithognathus*, *L. richardsonii* and *P. knysnaensis*. The species in this group appear to prefer cooler waters (Whitfield, 1998) and relatively high salinities (Bennett, 1985). Most taxa in this group were negatively correlated with temperature and positively correlated with salinity.

Group 5

The fifth group comprised temperate species such as *D. sargus*, *L. amia* and *S. acus* that were also an important component of the fish assemblage of both cool- and warm-temperate systems but generally did not occur in subtropical estuaries. Most of these species occur in the eastern Atlantic region and extend around the South African coast to KwaZulu-Natal and sometimes further north (Smith & Heemstra, 1995). Species belonging to this group also generally exhibited a negative correlation with temperature and a positive correlation with salinity.

Group 6

The last group comprised 'widespread' species that were important components of the estuarine ichthyofauna in all the biogeographic regions. Species belonging to this category included *G. aestuaria*, *M. cephalus* and *P. saltatrix*. *Gilchristella aestuaria* is an endemic species that occurs in estuaries, coastal lakes and rivers from the Kosi system in KwaZulu-Natal to the Orange River on the west coast while *M. cephalus* is a circumglobal mullet found in all warm and temperate seas, rivers and estuaries (Smith & Heemstra, 1995). *Pomatomus saltatrix* is also a cosmopolitan species occurring in all oceans between latitudes 50° N and 50° S (Smith & Heemstra, 1995). Within southern Africa it occurs on the west coast and is common along the south and east coasts, declining in abundance towards Mozambique (van der Elst, 1976). *Pomatomus saltatrix* occurred in open estuaries throughout all regions but was only important in cool-temperate estuaries during this study.

A summary of the fish groupings outlined above is presented in Figure 6.1 below. The categorisations presented in Figure 6.1 are also supported by the results of the SIMPER analysis, where taxa that accounted for some of the dissimilarity between cool-temperate and warm-temperate systems included those tropical (e.g. *A. japonicus*, *E. machnata*, *M. falciformis*, *O. mossambicus*, *P. commersonnii*) and endemic species (e.g. *G. callidus*, *L. dumerilii*, *L. tricuspidens*, *M. capensis*, *R. holubi*, *S. bleekeri*) that were important in subtropical and warm-temperate systems but generally do not comprise a major component of the fish fauna of cool-temperate estuaries. Species that were important in both warm- and cool-temperate systems (e.g. *A. breviceps*, *G. feliceps*, *G. aestuaria*, *L. lithognathus*, *L. richardsonii*, *M. cephalus*) also accounted for some of this dissimilarity, mainly due to differences in the relative proportions of the species collected in the estuaries in each region.

Taxa that accounted for some of the dissimilarity between warm-temperate and subtropical estuaries included tropical species that were largely restricted to subtropical estuaries (e.g. *A. berda*, *Ambassis*, *C. sexfasciatus*, *C. gariepinus*, *H. kelee*, *L. equula*, *L. alata*, *L. macrolepis*, *Oligolepis*, *S. lysan*, *T. jarbua*, *V. cunnesius*, *V. robustus*, *V. seheli*). Taxa that were important in cool- and warm-temperate estuaries (e.g. *A. breviceps*, *D. sargus*, *G. feliceps*, *H. capensis*, *L. amia*, *L. lithognathus*, *L. richardsonii*, *P. knysnaensis*) also accounted for some of the dissimilarity. Tropical species that also occur in warm-temperate estuaries (e.g. *A. japonicus*, *E. machnata*, *M. falciformis*, *O. mossambicus*, *P. commersonnii*) as well as endemic taxa that extend into subtropical estuaries (*G. aestuaria*, *G. callidus*, *L. dumerilii*, *L. tricuspidens*, *M. capensis*, *R. holubi*) accounted for the dissimilarity between the estuaries in the two regions. This was mostly due to differences in the relative proportions of these species in warm-temperate and subtropical estuaries.

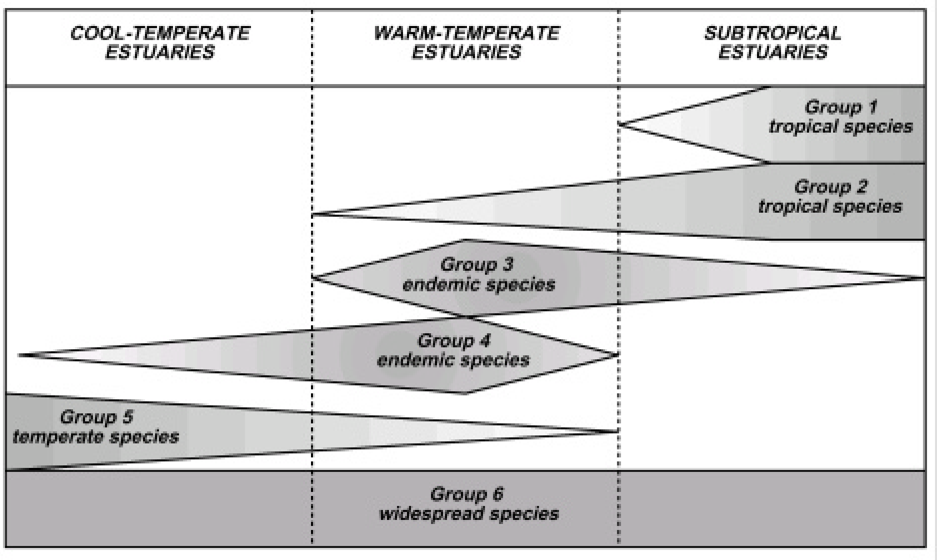


Figure 6.1. Fish groupings associated with subtropical, warm-temperate, and cool-temperate estuaries in South Africa.

This study has shown that the occurrence and abundance of the fish fauna of South African estuaries is linked to two primary environmental gradients: temperature and salinity. This is also supported by a BIOENV analysis, which identified the combination of environmental variables that best match the biotic similarities between the estuaries (Clarke, 1993; Clarke & Warwick, 1994). In both closed and open estuaries, a combination of temperature and salinity yielded the best correlation with the various biotic similarity matrices (presence/absence, abundance, biomass).

6.5 SUMMARY AND CONCLUSIONS

The estuaries in the three biogeographic regions of South Africa contain somewhat distinctive fish communities and these appear to be related to temperature and salinity. Subtropical estuaries are characterised by species of tropical origin that prefer warmer waters. The south coast endemic taxa that enter warmer waters are also important, although these species appear to have a primary preference for the more saline conditions typical of warm-temperate systems. In the warm temperate region, the fauna generally comprises those taxa that appear to prefer higher salinities although some species also appear to prefer cooler waters while others exhibit a preference for warmer water. The estuaries of the cool-temperate region do not appear contain any unique taxa but rather comprise those south coast endemic species that prefer cooler, more saline waters and are able to extend their range westwards. Fish stocks in these systems are supplemented by certain cosmopolitan species which occur mainly in the temperate waters of southern Africa, with some taxa extending into the subtropical east coast region.

CHAPTER 7

ESTUARY-ASSOCIATION ANALYSIS

7.1 INTRODUCTION

Estuaries are among the most productive ecosystems on earth (Odum, 1983; McHugh, 1985). However, they are also highly variable environments and as a result, only those fish species that are broadly tolerant of such fluctuations are able to occupy this food-rich environment (Whitfield, 1998). Estuarine fish communities are typically composed of a mixture of euryhaline freshwater species, species restricted to estuaries, euryhaline marine species and stenohaline marine species (Wallace, 1975a; Blaber, 1985). The most important function of estuaries, in terms of their utilisation by fishes, is the provision of nursery areas for certain marine fishes and the dependence of estuarine species on this environment (Wallace *et al.* 1984; Whitfield, 1998). Although estuaries serve important nursery areas for juvenile marine fishes, the adults of certain species also make use of these environments, particularly for feeding (Wallace, 1975a; Wallace *et al*., 1984; Whitfield, 1999).

While several studies have highlighted the importance of both tropical (e.g. Yáñez-Arancibia *et al*., 1982; 1985; Pauly, 1985; Blaber *et al*., 1989) and temperate (e.g. Yoklavich *et al*., 1991; Deegan & Thompson, 1985; Claridge *et al*., 1986; Elliott & Dewailly, 1995) estuaries as nursery areas for certain marine fish species, few have compared the utilisation of estuaries by fishes at a regional scale. Based on available data, Vieira & Musick (1993; 1994) established that, the majority of species present in tropical and warm-temperate estuaries of the western Atlantic were young-of-the-year maintained by recruitment waves from the adjacent marine environment. Ayvazian *et al* (1992), however, found that in the northeastern United States there was a trend toward a decrease in estuary nursery use by marine species and an increase in diadromous and resident species with increasing latitude. Dame *et al.* (2000) described a similar pattern in estuaries of the South Atlantic coast of North America, where systems in temperate North Carolina, South Carolina and Georgia were dominated by estuarine related species, while in the more subtropical Florida estuaries fish catches were slightly dominated by marine species. In the northeastern United States, Roman *et al.* (2000) found that fishes with life history strategies classified as nursery, marine, diadromous or transient appear to represent a greater percentage of fishes using estuarine habitats from more southern latitudes while resident fishes and seasonal residents dominate the fauna of estuaries in the northeast. Emmett *et al.* (2000) states that, unlike the fishes of the east coast of the United States, where most species reside in estuaries during most of their life history, many North American West Coast fishes, especially anadromous species, use estuaries only during a short period of their life cycle. These estuaries play an important role in the life histories of salmonid stocks (Emmett *et al.*, 2000). From studies in temperate New Zealand estuaries, Mac Dowall (1985) also suggest that, with increasing latitude there was a change from species of marine origin to freshwater/diadromous species.

In this chapter the estuarine fish communities within the various biogeographic regions is described and compared, based on their estuary-associations or life histories. The prime objective is to determine if estuarine utilisation by fishes differs between biogeographic regions.

7.2 MATERIALS & METHODS

7.2.1 Estuary-associations

Each species captured during this study was classified according to its degree of dependence on estuaries following an estuary-association categorisation provided by Whitfield (1998) (Table 7.1).

Table 7.1. Estuary-association categories of southern African fish fauna after Whitfield (1998).

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

The basic life cycle of estuarine-dependent marine species (category II) involves adult spawning at sea, often close inshore and in the vicinity of estuary mouths; egg and larval development also take place at sea but juveniles migrate into estuaries where they use this environment as a nursery area (Wallace *et al.*, 1984). Facultative catadromous species (category Vb) such as *Megalops cyprinoides* and *Myxus capensis* have a similar life cycles, with adults spawning at sea and juveniles migrating into estuaries; the only major difference between this group and those belonging to category II is that these species are able to enter and live in the fresh waters (Bruton *et al.*, 1987). Obligate catadromous species (category Va) includes the anguillid eels; these species also spawn at sea but use estuaries primarily as transit routes to their preferred riverine habitat (Bruton *et al.*, 1987). For this study, obligate catadromous species (category Va) were placed in the freshwater species category (category IV) while facultative catadromous species (category Vb) were combined with estuarine-dependent marine species (category IIa). The estuary-association categorisation of the species (from Whitfield, 1998) captured during this study is presented in Appendix 3.

The relative (%) contribution of each category to the ichthyofauna of each estuary was then calculated in terms of number of taxa, abundance and biomass. The mean contribution (±SD) of each group was then determined for each estuary type within each biogeographic region.

7.2.2 Multivariate analyses

Closed and open estuaries were also subject to multivariate statistical analyses using PRIMER (Clarke & Warwick, 1994). Bray-Curtis similarities, based on the ichthyofaunal estuary-association categories, between the estuaries were calculated and the data subjected to non-metric multi-dimensional scaling (MDS). Because the ichthyofaunal composition, based on taxa did not display a high degree of dominance, similarities based on percent taxa were calculated on untransformed data while percent abundance/biomass data, which exhibited strong dominance by certain groups, were first 4th root transformed. In the MDS ordinations the estuaries were labelled according to their biogeographic region where: CT = cool-temperate; WT = warm-temperate; and ST = subtropical. Cool-temperate, warm-temperate and subtropical estuaries were also compared by performing an analysis of similarities (ANOSIM) (Clarke & Warwick, 1994). For this analysis, estuaries within each biogeographic region were only considered distinct at a significance of $p<0.01$.

7.3 RESULTS

7.3.1 Closed estuaries

7.3.1.1 Cool-temperate estuaries

Estuarine species (category I) were only recorded in the Diep and Sand estuaries and comprised 40.0% of the taxa in these systems. Estuarine-dependent marine species (category II) were the dominant taxa in closed cool-temperate estuaries, averaging 80.0% of the species recorded. No marine (category III) or indigenous freshwater species (category IV) were captured during this study. In terms of abundance, estuarine species comprised 87.0% of the catch in the Sand estuary and 12.1% in the Diep system. Estuarine-dependent marine species generally dominated the ichthyofauna of closed cool-temperate estuaries both numerically (75.2%) and in terms of biomass (99.2%) (Table 7.2).

Table 7.2. Contribution of estuary-association categories to the ichthyofauna of closed cool-temperate estuaries.

	% Species				**% Abundance**				**% Biomass**			
Estuary	I	II	III	IV	I	II	III	IV	I	II	III	IV
Diep	40.00	60.00	0.00	0.00	12.11	87.89	0.00	0.00	0.69	99.31	0.00	0.00
Wildevoël	0.00	100.00	0.00	0.00	0.00	100.00	0.00	0.00	0.00	100.00	0.00	0.00
Krom	0.00	100.00	0.00	0.00	0.00	100.00	0.00	0.00	0.00	100.00	0.00	0.00
Sand	40.00	60.00	0.00	0.00	87.02	12.98	0.00	0.00	2.62	97.38	0.00	0.00
Mean	**20.00**	**80.00**	**0.00**	**0.00**	**24.78**	**75.22**	**0.00**	**0.00**	**0.83**	**99.17**	**0.00**	**0.00**
SD	23.09	23.09	0.00	0.00	41.88	41.88	0.00	0.00	1.24	1.24	0.00	0.00

7.3.1.2 Warm-temperate estuaries

The contribution of estuarine species (category I) to the taxa in closed warm-temperate estuaries ranged between 14.3% in the Blinde estuary to 41.7% in the Zalu system. Overall, this group comprised 25.7% of the taxa. Estuarine-dependent marine species (category II) were the dominant taxa, averaging 69.9% of the species captured. Marine species (category III) were infrequently recorded during this study and comprised a maximum of 5.9% of the taxa recorded in the Qinira estuary. Freshwater species (category IV) did not comprise more than 10.0% of the taxa in any one estuary during this study (Table 7.3).

In terms of abundance, estuarine species generally dominated the fish communities in closed warm-temperate systems; this group comprised 58.7% of the fishes captured. The numerical contribution of estuarine-dependent marine species varied between 5.0% recorded in the Old Woman's system to 83.8% in the Ngogwane estuary with a mean contribution of 40.5%. The numerical contribution of both marine and freshwater species was low (<1.0%). In terms of biomass, estuarine-dependent marine species were the dominant group, averaging 90.5% of the species mass. Freshwater species comprised 6.6% of the biomass followed by estuarine species (2.9%). The biomass contribution of marine taxa did not exceed 0.1% (Table 7.3).

Table 7.3. Contribution of estuary-association categories to the ichthyofauna of closed warm-temperate estuaries.

	% Species				% Abundance				% Biomass			
Estuary	I	II	III	IV	I	II	III	IV	I	II	III	IV
Blinde	14.29	85.71	0.00	0.00	58.52	41.48	0.00	0.00	2.05	97.95	0.00	0.00
Hartenbos	33.33	66.67	0.00	0.00	72.09	27.91	0.00	0.00	1.66	98.34	0.00	0.00
Groot (Wes)	28.57	71.43	0.00	0.00	25.77	74.23	0.00	0.00	0.10	99.90	0.00	0.00
Tsitsikamma	25.00	75.00	0.00	0.00	50.93	49.07	0.00	0.00	0.83	99.17	0.00	0.00
Seekoei	33.33	66.67	0.00	0.00	69.50	30.50	0.00	0.00	1.86	98.14	0.00	0.00
Kabeljous	27.27	72.73	0.00	0.00	77.15	22.85	0.00	0.00	3.06	96.94	0.00	0.00
Van Stadens	26.67	73.33	0.00	0.00	20.10	79.90	0.00	0.00	1.03	98.97	0.00	0.00
Boknes	36.36	54.55	0.00	9.09	44.35	55.11	0.00	0.54	0.78	98.90	0.00	0.32
Kasuka	19.05	76.19	0.00	4.76	71.28	24.81	0.00	3.91	6.53	78.99	0.00	14.48
Riet	23.53	70.59	0.00	5.88	59.42	40.47	0.00	0.10	1.27	93.29	0.00	5.43
Wes-Kleinemond	23.53	70.59	0.00	5.88	69.53	30.03	0.00	0.44	1.73	97.72	0.00	0.55
Oos-Kleinemond	23.53	70.59	0.00	5.88	81.35	18.40	0.00	0.26	5.09	86.12	0.00	8.79
Old Woman’s	25.00	75.00	0.00	0.00	94.99	5.01	0.00	0.00	9.35	90.65	0.00	0.00
Mpekweni	20.00	80.00	0.00	0.00	79.99	20.01	0.00	0.00	1.83	98.17	0.00	0.00
Mtati	16.67	77.78	0.00	5.56	93.63	5.89	0.00	0.48	3.16	92.74	0.00	4.11
Mgwalana	26.32	68.42	0.00	5.26	80.84	17.38	0.00	1.77	1.64	86.24	0.00	12.12
Bira	26.09	69.57	0.00	4.35	67.48	32.47	0.00	0.05	2.27	97.71	0.00	0.03
Gqutywa	22.22	72.22	0.00	5.56	80.75	19.01	0.00	0.24	1.72	98.18	0.00	0.10
Mtana	26.67	66.67	0.00	6.67	78.66	17.28	0.00	4.06	4.64	58.69	0.00	36.67
Ngqinisa	36.36	63.64	0.00	0.00	48.36	51.64	0.00	0.00	2.17	97.83	0.00	0.00
Kiwane	25.00	75.00	0.00	0.00	94.11	5.89	0.00	0.00	3.99	96.01	0.00	0.00
Ross’ Creek	27.27	63.64	0.00	9.09	41.44	58.17	0.00	0.38	1.48	95.78	0.00	2.74
Ncera	22.22	77.78	0.00	0.00	46.93	53.07	0.00	0.00	4.09	95.91	0.00	0.00
Mlele	21.43	71.43	0.00	7.14	54.38	45.50	0.00	0.12	1.81	94.78	0.00	3.41
Mcantsi	20.00	73.33	0.00	6.67	37.23	61.38	0.00	1.39	3.61	71.22	0.00	25.17
Gxulu	19.05	71.43	4.76	4.76	75.68	24.13	0.05	0.15	2.47	89.82	0.00	7.71
Goda	19.05	80.95	0.00	0.00	70.53	29.47	0.00	0.00	4.15	95.85	0.00	0.00
Hickmans	20.00	70.00	0.00	10.00	70.84	28.20	0.00	0.96	5.38	77.36	0.00	17.27
Qinira	23.53	64.71	5.88	5.88	82.17	17.34	0.04	0.46	2.84	76.73	0.10	20.33
Cintsa	26.32	68.42	0.00	5.26	61.95	37.79	0.00	0.26	1.98	97.90	0.00	0.12
Cefane	25.00	65.00	5.00	5.00	76.04	23.56	0.06	0.34	7.10	88.08	0.05	4.77
Kwenxura	20.00	75.00	0.00	5.00	63.53	36.33	0.00	0.14	1.81	97.60	0.00	0.59
Nyara	35.71	57.14	0.00	7.14	36.96	52.61	0.00	10.43	2.13	75.82	0.00	22.05
Haga-Haga	28.57	64.29	0.00	7.14	23.51	76.35	0.00	0.14	3.27	95.37	0.00	1.35
Morgan	29.41	64.71	0.00	5.88	14.98	82.45	0.00	2.57	2.18	86.18	0.00	11.64
Gxara	27.27	68.18	0.00	4.55	58.56	41.15	0.00	0.29	3.90	80.64	0.00	15.46
Ngogwane	30.00	60.00	0.00	10.00	14.10	83.81	0.00	2.09	0.40	55.85	0.00	43.74
Qolora	24.14	68.97	3.45	3.45	34.67	64.59	0.08	0.66	1.58	88.38	0.02	10.02
Cebe	29.41	70.59	0.00	0.00	25.75	74.25	0.00	0.00	0.95	99.05	0.00	0.00
Zalu	41.67	58.33	0.00	0.00	57.50	42.50	0.00	0.00	12.12	87.88	0.00	0.00
Ngqwara	23.81	71.43	4.76	0.00	39.96	59.86	0.18	0.00	0.71	99.26	0.03	0.00
Mean	**25.67**	**69.94**	**0.58**	**3.80**	**58.67**	**40.53**	**0.01**	**0.79**	**2.94**	**90.49**	**0.00**	**6.56**
SD	5.74	6.42	1.60	3.36	22.40	22.18	0.03	1.83	2.41	10.83	0.02	10.47

7.3.1.3 Subtropical estuaries

In closed subtropical estuaries, the contribution of estuarine species (category I) to the taxa recorded varied between 7.7% in the Kandandlovu estuary and 50.0% in the Bilanhlolo system. Overall, this group comprised 19.7% of the taxa recorded. Estuarine-dependent marine species (category II) averaged 67.0% of the taxa. No marine species (category III) were captured during this study. The contribution of freshwater species (category IV) varied between 4.8% in the Mpenjati system to 30.0% in the Mdloti estuary; this group averaged 13.3% of the taxa recorded (Table 7.4).

In terms of abundance, the contribution of estuarine species ranged between 0.7% in the Mhlangeni estuary to 93.1% in the Little Manzimtoti system with a mean overall contribution of 32.0%. The relative abundance of estuarine-dependent marine species was also variable, ranging between 1.4% in the Mhlangeni estuary to 98.0% in Mhlangamkulu system. The mean numerical contribution of this group was 48.0%. The abundance of freshwater species ranged between 0.2 % in the Mpenjati system to 76.9% in the Sezela estuary. The average contribution of this group was 20.0%. The biomass composition in closed subtropical estuaries was dominated by estuarine-dependent marine species (61.5%) followed by freshwater species (36.0%). Estuarine species generally did not contribute more than 5.0% to the biomass of the ichthyofauna in any estuary (Table 7.4).

Table 7.4. Contribution of estuary-association categories to the ichthyofauna of closed subtropical estuaries.

	% Species				**% Abundance**				**% Biomass**			
Estuary	I	II	III	IV	I	II	III	IV	I	II	III	IV
Mtentwana	15.38	76.92	0.00	7.69	11.14	87.43	0.00	1.43	0.11	81.90	0.00	17.99
Kandandlovu	7.69	76.92	0.00	15.38	2.24	72.84	0.00	24.92	3.12	79.81	0.00	17.07
Mpenjati	14.29	80.95	0.00	4.76	52.98	46.80	0.00	0.22	0.63	95.38	0.00	3.99
Umhlangankulu	21.05	73.68	0.00	5.26	38.91	58.36	0.00	2.74	2.01	82.77	0.00	15.22
Kaba	33.33	44.44	0.00	22.22	22.18	30.03	0.00	47.78	2.44	39.88	0.00	57.68
Mbizana	26.09	60.87	0.00	13.04	80.05	18.84	0.00	1.11	8.00	91.95	0.00	0.06
Bilanhlolo	50.00	41.67	0.00	8.33	54.42	37.93	0.00	7.65	6.82	68.29	0.00	24.89
Mhlangeni	12.50	81.25	0.00	6.25	0.68	76.36	0.00	22.95	0.57	80.53	0.00	18.90
Mtentweni	14.29	71.43	0.00	14.29	2.67	73.33	0.00	24.00	1.23	89.89	0.00	8.88
Mhlangamkulu	20.00	60.00	0.00	20.00	97.99	1.37	0.00	0.64	18.14	42.51	0.00	39.35
Intshambili	11.11	66.67	0.00	22.22	42.33	53.80	0.00	3.88	0.24	15.19	0.00	84.57
Fafa	8.33	83.33	0.00	8.33	1.74	63.91	0.00	34.35	0.06	78.31	0.00	21.63
Sezela	28.57	64.29	0.00	7.14	3.35	19.77	0.00	76.88	0.68	68.31	0.00	31.01
Mpambanyoni	15.00	70.00	0.00	15.00	1.51	91.51	0.00	6.98	0.10	37.35	0.00	62.56
Mahlongwa	16.67	66.67	0.00	16.67	19.90	52.36	0.00	27.75	0.26	18.22	0.00	81.52
Little Manzimtoti	17.65	76.47	0.00	5.88	3.59	93.05	0.00	3.36	1.50	84.26	0.00	14.24
Manzimtoti	31.25	43.75	0.00	25.00	81.47	9.31	0.00	9.23	1.97	56.81	0.00	41.22
Mhlanga	22.22	66.67	0.00	11.11	22.54	61.97	0.00	15.49	0.53	34.75	0.00	64.71
Mdloti	10.00	60.00	0.00	30.00	81.86	17.30	0.00	0.84	2.47	68.04	0.00	29.48
Mdlotane	11.11	77.78	0.00	11.11	43.14	5.99	0.00	50.87	0.93	39.18	0.00	59.89
Zinkwasi	22.58	67.74	0.00	9.68	32.13	63.24	0.00	4.63	3.33	83.00	0.00	13.67
Siyai	25.00	62.50	0.00	12.50	6.72	21.38	0.00	71.90	1.60	15.50	0.00	82.90
Mean	**19.73**	**67.00**	**0.00**	**13.27**	**31.98**	**48.04**	**0.00**	**19.98**	**2.58**	**61.45**	**0.00**	**35.97**
SD	9.95	11.94	0.00	6.98	31.19	28.90	0.00	23.23	4.04	26.39	0.00	26.79

7.3.1.4 Multivariate analyses

In all the MDS ordinations of closed estuaries, two cool-temperate estuaries (Wildevoël and Krom) appeared as outliers. These are indicated as a single point to the left of the ordination. The remaining systems formed a broad gradation from warm-temperate estuaries toward subtropical systems. In terms of percentage species, warm-temperate estuaries were situated near the centre of the plot while subtropical systems generally appeared toward the top of the ordination. In the ordinations based on percent abundance and biomass, warm-temperate estuaries were situated near the bottom left of the plot while subtropical systems appeared toward the top right of the map (Figure 7.1).

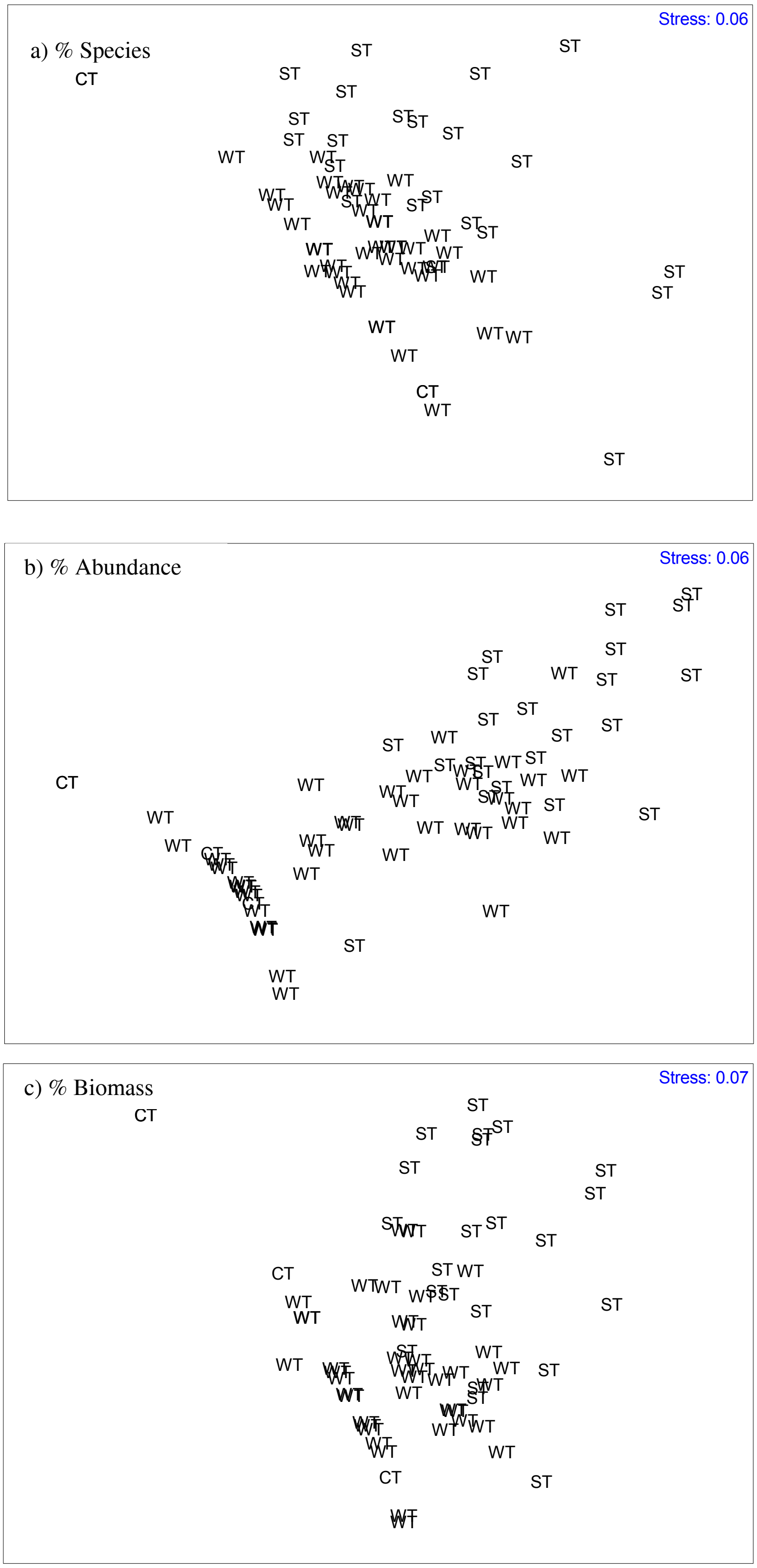


Figure 7.1. MDS ordination of closed estuaries based on (a) % species, (b) % abundance and (c) % biomass of the estuary-associations of the ichthyofauna.

The results of the ANOSIM test revealed that, in terms of taxa and relative abundance, cool-temperate estuaries were significantly distinct from both warm-temperate and subtropical systems. Warm-temperate and subtropical estuaries were also slightly ($R<0.5$) but significantly distinct. In terms of biomass, subtropical estuaries differed strongly ($R>0.9$) from cool-temperate estuaries; subtropical estuaries were also slightly ($R<0.4$) but significantly different to warm-temperate systems (Table 7.5).

Table 7.5. Results of the ANOSIM test (R) comparing closed cool-temperate, warm-temperate and subtropical estuaries based on the percent species, abundance and biomass contribution of their ichthyofaunal estuarine associations (* $p<0.01$).

	Cool-temperate versus Warm-temperate	Cool-temperate versus Subtropical	Warm-temperate versus Subtropical
% Species	0.765*	0.611*	0.396*
% Abundance	0.646*	0.754*	0.473*
% Biomass	0.295	0.919*	0.346*

7.3.2 Open estuaries

7.3.2.1 Cool-temperate estuaries

In open cool-temperate estuaries, estuarine species (category I) comprised between 25.0% of the taxa in the Palmiet estuary and 50.0% of the species in both the Berg and Uilkraals systems. Estuarine-dependent marine species (category II) comprised between 30.0 % of the taxa recorded in the Berg estuary to 75.0% of the taxa captured in the Palmiet system. Marine species were only captured in the Olifants and Berg estuaries and comprised 11.0 and 20.0% of the taxa respectively. No indigenous freshwater species were recorded in open cool-temperate estuaries during this study (Table 7.6).

Estuarine-dependent marine species were the dominant group numerically, averaging 86.0% of the catch. The numerical contribution of estuarine species varied between 1.3% in the Olifants estuary to 40.0% in the Berg system. Marine species did not comprise more than 0.1% of the catch in either the Olifants or Berg estuaries. Estuarine-dependent marine species also dominated the biomass composition of open cool-temperate systems and comprised 83.5% of the species mass. Although estuarine species comprised 39.8% of the fish biomass in the Berg estuary, this group did not comprise more than 5.0% in the remaining systems. Marine species comprised 5.2% of the fish biomass in the Berg estuary and 15.6% in the Olifants system (Table 7.6).

Table 7.6. Contribution of estuary-association categories to the ichthyofauna of open cool-temperate estuaries.

	% Species				**% Abundance**				**% Biomass**			
Estuary	I	II	III	IV	I	II	III	IV	I	II	III	IV
Olifants	44.44	44.44	11.11	0.00	1.29	98.67	0.05	0.00	0.45	83.97	15.58	0.00
Berg	50.00	30.00	20.00	0.00	39.96	59.95	0.09	0.00	39.82	55.03	5.15	0.00
Palmiet	25.00	75.00	0.00	0.00	2.28	97.72	0.00	0.00	0.05	99.95	0.00	0.00
Uilkraals	50.00	50.00	0.00	0.00	12.24	87.76	0.00	0.00	4.89	95.11	0.00	0.00
Mean	**42.36**	**49.86**	**7.78**	**0.00**	**13.94**	**86.02**	**0.03**	**0.00**	**11.30**	**83.52**	**5.18**	**0.00**
SD	11.87	18.76	9.69	0.00	18.04	18.07	0.04	0.00	19.14	20.13	7.34	0.00

7.3.2.2 Warm-temperate estuaries

Estuarine species (category I) averaged 26.3% of the taxa recorded in open warm-temperate estuaries. Estuarine-dependent marine species (category II) were the dominant group, averaging 68.3% of the taxa. Marine species (category III) were frequently reported in open warm-temperate estuaries but only comprised 4.7% of the taxa. Freshwater species (category IV) were only recorded in three estuaries, Great Fish, Great Kei and Mtata (Table 7.7).

In terms of abundance, estuarine-dependent marine species were the dominant group comprising 55.3% of the fishes captured. The numerical contribution of estuarine species ranged between 2.0% recorded in the Great Fish estuary to 83.7% in the Mdumbi system. Overall, this group averaged 44.3% of the catch. The abundance of marine species during this study was low (0.4%). Estuarine-dependent marine species also dominated the biomass composition of open warm-temperate estuaries (97.3%). The mean biomass contribution of estuarine and marine species was 1.7 and 1.0% respectively (Table 7.7).

Table 7.7. Contribution of estuary-association categories to the ichthyofauna of open warm-temperate estuaries.

	% Species				**% Abundance**				**% Biomass**			
Estuary	I	II	III	IV	I	II	III	IV	I	II	III	IV
Heuningnes	30.77	69.23	0.00	0.00	33.66	66.34	0.00	0.00	1.32	98.68	0.00	0.00
Breë	28.57	66.67	4.76	0.00	29.10	70.40	0.50	0.00	0.53	98.84	0.63	0.00
Duiwenhoks	43.75	50.00	6.25	0.00	37.66	62.20	0.14	0.00	0.69	99.16	0.15	0.00
Goukou	25.00	75.00	0.00	0.00	11.70	88.30	0.00	0.00	0.31	99.69	0.00	0.00
Gourits	20.00	80.00	0.00	0.00	46.17	53.83	0.00	0.00	0.61	99.39	0.00	0.00
Keurbooms	30.43	69.57	0.00	0.00	4.31	95.69	0.00	0.00	0.23	99.77	0.00	0.00
Kromme	30.00	66.67	3.33	0.00	66.40	33.58	0.03	0.00	2.61	97.39	0.00	0.00
Gamtoos	20.83	79.17	0.00	0.00	36.78	63.22	0.00	0.00	0.62	99.38	0.00	0.00
Swartkops	30.00	70.00	0.00	0.00	40.90	59.10	0.00	0.00	3.31	96.69	0.00	0.00
Sundays	25.93	62.96	11.11	0.00	46.08	53.82	0.10	0.00	1.01	92.99	6.00	0.00
Bushmans	29.03	61.29	9.68	0.00	38.41	61.27	0.32	0.00	1.67	98.23	0.10	0.00
Kariega	28.57	62.86	8.57	0.00	63.80	35.47	0.73	0.00	2.92	97.02	0.06	0.00
Kowie	21.88	68.75	9.38	0.00	59.10	39.80	1.10	0.00	3.45	96.51	0.05	0.00
Great Fish	15.79	73.68	5.26	5.26	2.03	97.77	0.10	0.10	0.03	99.70	0.00	0.27
Keiskamma	30.77	65.38	3.85	0.00	35.17	64.77	0.05	0.00	0.47	99.53	0.00	0.00
Buffalo	21.74	69.57	8.70	0.00	54.84	40.32	4.84	0.00	0.96	97.64	1.41	0.00
Nahoon	30.77	61.54	7.69	0.00	47.57	50.79	1.64	0.00	1.19	84.34	14.48	0.00
Gqunube	31.25	62.50	6.25	0.00	80.71	18.84	0.45	0.00	3.22	96.65	0.13	0.00
Kwelera	17.14	65.71	17.14	0.00	64.30	35.39	0.31	0.00	1.99	93.95	4.06	0.00
Great Kei	20.00	70.00	0.00	10.00	5.42	93.91	0.00	0.68	0.04	99.31	0.00	0.65
Kobonqaba	24.00	68.00	8.00	0.00	67.10	32.72	0.17	0.00	1.33	98.66	0.01	0.00
Ngqusi/Inxaxo	22.58	74.19	3.23	0.00	73.41	26.35	0.23	0.00	8.22	91.76	0.02	0.00
Qora	34.78	65.22	0.00	0.00	39.83	60.17	0.00	0.00	1.37	98.63	0.00	0.00
Shixini	27.27	63.64	9.09	0.00	55.62	44.12	0.27	0.00	1.43	98.38	0.19	0.00
Mbashe	24.00	72.00	4.00	0.00	21.84	78.08	0.08	0.00	0.44	99.55	0.01	0.00
Xora	22.58	74.19	3.23	0.00	61.04	38.89	0.06	0.00	1.23	98.77	0.00	0.00
Mtata	25.81	67.74	3.23	3.23	33.18	66.48	0.22	0.11	0.48	99.50	0.00	0.02
Mdumbi	22.22	77.78	0.00	0.00	83.69	16.31	0.00	0.00	5.05	94.95	0.00	0.00
Mean	**26.27**	**68.33**	**4.74**	**0.66**	**44.28**	**55.28**	**0.41**	**0.03**	**1.67**	**97.32**	**0.97**	**0.03**
SD	5.85	6.34	4.41	2.16	22.32	22.46	0.95	0.13	1.77	3.31	2.97	0.13

7.3.2.3 Subtropical estuaries

In open subtropical estuaries, estuarine species (category I) averaged 20.3% of the taxa recorded. Estuarine-dependent marine species (category II) were the dominant group, averaging 70.7% of the taxa. Marine (category III) and freshwater (category IV) species comprised 6.4 and 2.6% of the taxa respectively (Table 7.8).

In terms of abundance, estuarine-dependent marine species were the dominant group averaging 64.2% of the fishes captured. The numerical contribution of estuarine species ranged between 2.9% recorded in the Msikaba system to 76.4% in the

Mngazana estuary. Overall, the mean numerical contribution of this group was 33.0%. Marine species averaged 2.4% of the fish abundance while freshwater species comprised 0.5%. Estuarine-dependent marine species also dominated the fish biomass in open subtropical estuaries (96.1%). Although freshwater species had the next highest the biomass contribution (2.4%), this group only made a notable contribution to three systems, Mkomazi, Matigulu/Nyoni and Mlalazi. The biomass contribution of estuarine species averaged 1.3% while that of marine species was 0.2% (Table 7.8).

Table 7.8. Contribution of estuarine association categories to the ichthyofauna of open subtropical estuaries.

	% Species				**% Abundance**				**% Biomass**			
Estuary	I	II	III	IV	I	II	III	IV	I	II	III	IV
Mngazana	21.05	71.05	5.26	2.63	76.36	23.48	0.08	0.08	3.27	96.45	0.28	0.00
Mngazi	25.81	67.74	3.23	3.23	53.80	46.06	0.07	0.07	1.82	97.71	0.00	0.48
Mntafufu	23.53	70.59	5.88	0.00	52.58	46.67	0.75	0.00	1.98	97.94	0.08	0.00
Msikaba	18.18	77.27	4.55	0.00	2.91	93.59	3.50	0.00	0.02	99.80	0.19	0.00
Mtentu	16.13	74.19	9.68	0.00	6.69	87.95	5.35	0.00	0.07	99.61	0.32	0.00
Mzamba	20.59	70.59	8.82	0.00	22.80	76.07	1.12	0.00	0.50	99.44	0.06	0.00
Mzimkulu	16.13	74.19	9.68	0.00	26.71	63.65	9.64	0.00	0.57	99.24	0.19	0.00
Mkomazi	25.81	67.74	0.00	6.45	22.22	75.84	0.00	1.94	0.36	94.39	0.00	5.25
Matigulu/Nyoni	21.57	64.71	5.88	7.84	36.28	61.94	0.38	1.40	3.09	85.79	0.07	11.05
Mlalazi	14.55	69.09	10.91	5.45	29.21	66.67	2.71	1.41	1.23	90.59	0.63	7.55
Mean	**20.33**	**70.72**	**6.39**	**2.56**	**32.96**	**64.19**	**2.36**	**0.49**	**1.29**	**96.10**	**0.18**	**2.43**
SD	4.02	3.71	3.40	3.07	22.56	21.11	3.12	0.77	1.20	4.63	0.19	4.05

7.3.2.4 Multivariate analyses

The MDS ordination of open estuaries based on the relative species contribution indicated a broad spread of mostly cool-temperate estuaries (Berg, Olifants, Uilkraals) to the left of the plot. The remaining estuaries did not appear to display any clear pattern, although there was a slight gradation from left to right, of warm-temperate to subtropical estuaries. The analyses based on abundance and biomass did not display any clear pattern or trend (Figure 7.2).

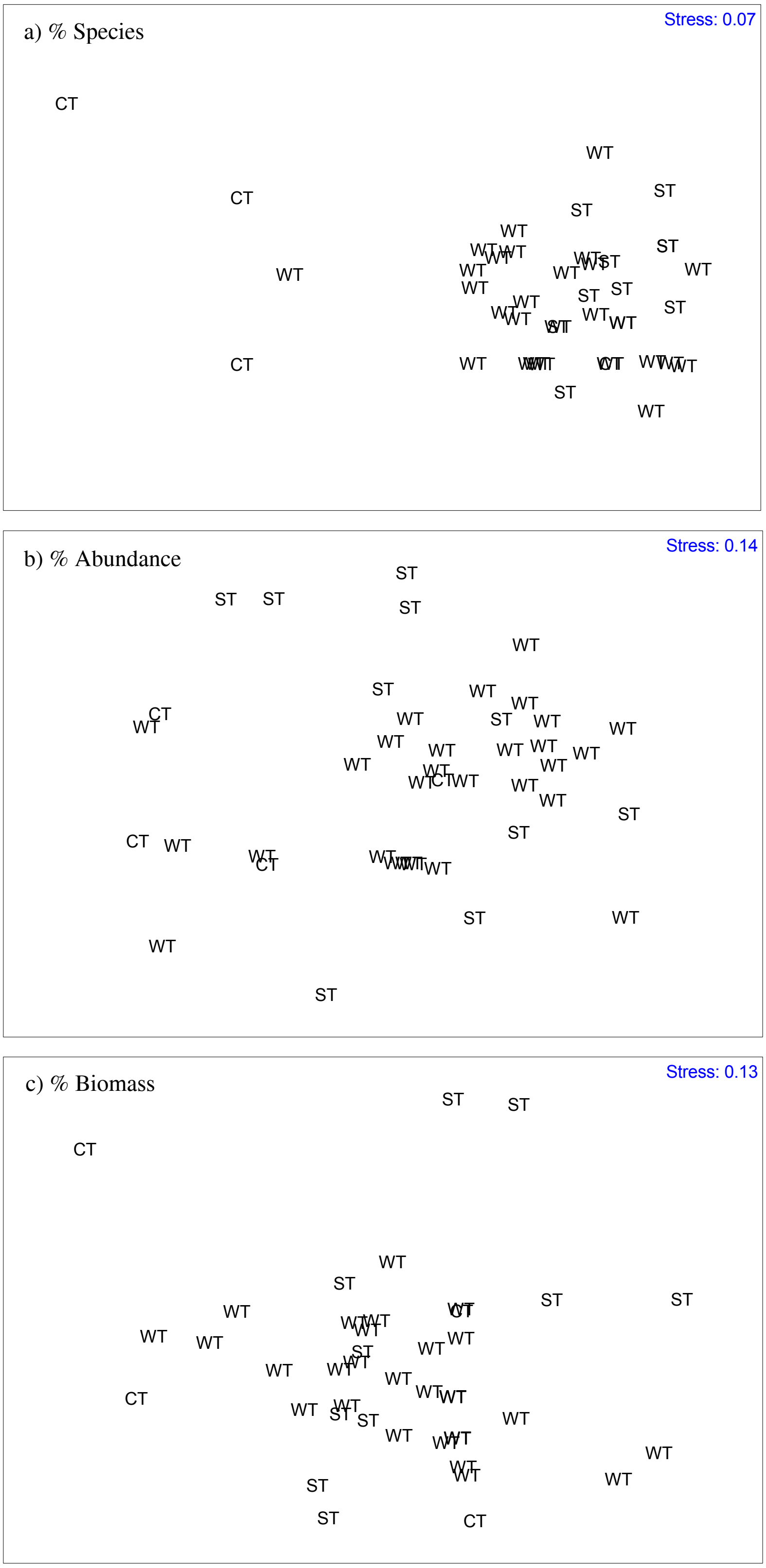


Figure 7.2. MDS ordination of open estuaries based on (a) % species, (b) % abundance and (c) % biomass of the estuary-associations of the ichthyofauna.

From the results of the ANOSIM test, cool-temperate estuaries were strongly ($R>0.6$) and significantly different to both warm-temperate and subtropical systems in terms of percentage taxa. Although there was a significant difference between subtropical and warm-temperate estuaries, in terms of abundance, this was not high ($R<0.3$). Generally, the estuaries from each biogeographic region did not appear to be significantly different in terms of abundance or biomass (Table 7.9).

Table 7.9. Results of the ANOSIM test (R) comparing open cool-temperate, warm-temperate and subtropical estuaries based on the percent species, abundance and biomass contribution of their ichthyofaunal estuarine associations (* $p<0.01$).

	Cool-temperate versus Warm-temperate	Cool-temperate versus Subtropical	Warm-temperate versus Subtropical
% Species	0.657*	0.718*	0.09
% Abundance	0.299	0.344	0.291*
% Biomass	0.414	0.348	0.266

7.4 DISCUSSION

7.4.1 Cool-temperate estuaries

7.4.1.1 Closed estuaries

Closed cool-temperate estuaries were dominated by estuarine-dependent marine species and estuarine resident species (Table 7.2). *Liza richardsonii* and *M. cephalus* were the most important estuarine-dependent marine species and together comprised 75% of the abundance and 94% of the biomass. Important estuarine species included *A. breviceps*, *C. nudiceps* and *G. aestuaria*, which together comprised 25% of the catch numerically.

Data from other studies in closed cool-temperate estuaries yielded similar estuarine-associated fish assemblages. In the Diep estuary, estuarine-dependent marine species and estuarine species were among the dominant taxa recorded (Millard & Scott, 1954; Grindley & Dudley, 1988). Estuarine-dependent mugilids (*L. richardsonii* and *M. cephalus*) have also been reported from the Wildevoël system (Heinecken, 1985). In the Sand estuary, estuarine-dependent mullet, *L. richardsonii* and *M. cephalus* were among the dominant taxa reported, with smaller estuarine species such as *A. breviceps*, *C. nudiceps* and *P. knysnaensis* also common (Morant & Grindley, 1982; Morant, 1991; Quick and Harding, 1994). Clark *et al.* (1994) found that estuarine species (mostly *A. breviceps*, *G. aestuaria* and *P. knysnaensis*) numerically dominated the fish community in the Sand estuary; this group accounted for 57% of the total catch while estuarine-dependent marine species (predominantly *L. richardsonii*, *M. cephalus* and *R. globiceps*) comprised 44%. The high abundance of estuarine species reported by Clark *et al*. (1994) is a result of sampling being restricted to seine netting, which tends to favour smaller fishes.

7.4.1.2 Open estuaries

The fish fauna in open cool-temperate estuaries were also dominated by estuarine-dependent marine species and estuarine species (Table 7.6). Important estuarine-dependent marine taxa included *G. feliceps*, *L. richardsonii*, *M. cephalus* and *P. saltatrix*. Together these taxa comprised over 85% of the fishes numerically and over 83% of the biomass. Key estuarine species during this study included *A. breviceps* and *G. aestuaria*, which together comprised approximately 13% of the abundance and 11% of the biomass. Estuarine species such as *P. knysnaensis* and *S. acus* were also frequently recorded.

Day (1981a) also reported that estuarine (*A. breviceps* and *G. aestuaria*) and estuarine-dependent marine taxa (*L. lithognathus* and *L. richardsonii*) were among the commonest species reported in the Olifants estuary. In the Berg estuary, the fish community sampled by seine netting were dominated by estuarine species (mostly *A. breviceps*, *C. nudiceps*, *G. aestuaria* and *P. knysnaensis*) and estuarine-dependent marine species (predominantly *L. richardsonii*); the latter group numerically comprised 54% of the total catch while estuarine species comprised 45% (Bennett, 1994). Estuarine-dependent marine species (mostly *L. richardsonii* and *L. lithognathus*) also numerically dominated the ichthyofauna in the Palmiet estuary and comprised over 52% of the total catch; the remainder of the assemblage (48%) comprised estuarine species, mainly *A. breviceps* and *P. knysnaensis* (Branch & Day, 1984). Similar results were reported by Bennett (1989a) where estuarine-dependent marine species dominated the catch composition of the Palmiet estuary, both numerically and in terms of biomass; this group (mainly *L. richardsonii* and *L. lithognathus*) numerically comprised over 54% of the total catch and 97% of the biomass. Estuarine species (mainly *A. breviceps* and *P. knysnaensis*) comprised the remaining 46% of the abundance and 3% of the biomass (Bennett, 1989a). The low biomass contribution of estuarine species is due to their small size.

7.4.2 Warm-temperate estuaries

7.4.2.1 Closed estuaries

Estuarine-dependent marine species dominated the taxa and biomass of the fish communities of closed warm-temperate estuaries; this group was also important numerically (Table 7.3). Important estuarine-dependent marine species during this study included *A. japonicus*, *E. machnata*, *L. amia*, *L. lithognathus*, *L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *M. capensis*, *P. commersonnii* and *R. holubi*. Together, these taxa numerically comprised over 38% of the fishes in closed warm-temperate estuaries and 87% of the biomass. Estuarine species were the second most important group in terms of taxa and was the dominant group numerically (Table 7.3). Key estuarine resident species included *A. breviceps*, *G. aestuaria*, *G. callidus* and *P. knysnaensis*, which together numerically comprised 59% of the fish assemblage.

Estuarine-dependent marine species were also the dominant taxa reported in the Hartenbos (Bickerton, 1982), Groot (Wes) (Morant & Bickerton, 1983) and Seekoei and Kabeljous (Bickerton & Pierce, 1988) estuaries. In terms of abundance, Dundas (1994) found that estuarine species (mainly *A. breviceps* and *G. aestuaria*) were among the most abundant species caught by seine netting in the Seekoei, Kabeljous and Van Stadens estuaries while the biomass composition was dominated by estuarine-dependent marine species (mainly *L. richardsonii* and *R. holubi*). Estuarine-dependent marine species dominated the gill net catches in these systems both in terms of abundance and biomass (Dundas, 1994). Important estuarine-dependent marine species included *L. amia*, *L. lithognathus*, *L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. falciformis*, *M. cephalus*, *P. commersonnii* and *R. holubi*, and together comprised over 90% of the gill net catch numerically and over 80% of the biomass. Estuarine resident species are typically small fishes and are therefore not susceptible to capture by gill nets.

Cowley & Whitfield (2001) found that euryhaline marine species comprised over 60% of the taxa collected in the Oos-Kleinemond estuary. Estuarine species were the next most important group and comprised 20% of the taxa followed by marine (13%) and freshwater species (6%). The catch composition from small-mesh seine netting in the system was numerically dominated by estuarine species (mainly *A. breviceps*, *G. aestuaria*, *G. callidus* and *P. knysnaensis*), which comprised over 99% of the catch (Cowley & Whitfield, 2001). Large-mesh seine net and gill net catches, however, were dominated by estuarine-dependent marine species (*L. lithognathus*, *L. dumerilii*, *L. richardsonii*, *M. falciformis*, *M. cephalus*, *M. capensis*, *P. commersonnii* and *R. holubi*); this group numerically comprised over 90% of the catch (Cowley & Whitfield, 2001). Based on a combination of seine netting and gill netting, Vorwerk *et al*. (2001) also found that the taxa recorded in the Oos-Kleinemond, Mpekweni, Mtati, Mgwalana, Bira and Gqutywa estuaries were dominated by estuarine-dependent marine species. In terms of abundance, however, estuarine species (mostly *A. breviceps*, *G. aestuaria* and *G. callidus*) dominated the fish communities in these estuaries and comprised over 70% of the total catch (Vorwerk *et al*., 2001).

7.4.2.2 Open estuaries

The fish community in open warm-temperate estuaries were dominated by estuarine-dependent marine species and estuarine species (Table 7.7). Important estuarine-dependent marine species during this study included *A. japonicus*, *D. sargus*, *G. feliceps*, *L. amia*, *L. lithognathus*, *L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *M. capensis*, *P. commersonnii*, *R. holubi*, *S. bleekeri* and *V. buchanani*. Together, these species numerically accounted for over 52% of the fish assemblage and over 94% of the biomass. Estuarine-dependent marine species such *H. capensis* and *M. falciformis* were also frequently reported in these systems. Dominant estuarine species included *A. breviceps*, *C. gilchristi*, *C. nudiceps*, *G. aestuaria*, *G. callidus* and *P. knysnaensis*, which together comprised 43% of the fish abundance.

Carter (1983) found that, in terms of abundance, the dominant species in the Breë estuary included both estuarine-dependent marine taxa (*G. feliceps*, *L. richardsonii* and *M. cephalus*) and estuarine species (*A. breviceps*). The catch composition reported by Ratte (1982) and Coetzee & Pool (1991), however, was dominated by estuarine-dependent marine species; this is primarily a result of the sampling methods (mainly gill netting), which excludes smaller estuarine species. Gill net catches in the Kromme and Gamtoos estuaries were also dominated by estuarine-dependent marine species (Marais, 1983a; 1983b). Although estuarine species (*G. aestuaria* and *G. callidus*) were well represented in a seine net study of the Kromme system, estuarine-dependent marine species (mainly *L. dumerilii* and *R. holubi*) were the most abundant group (Hanekom & Baird, 1984).

From data presented in Baird *et al.* (1988), early collections made in the Swartkops estuary from 1915 to 1916, were dominated by estuarine-dependent marine species (predominantly mugilids and *R. holubi*); this group numerically comprised over 90% of the catch. The sampling method used in this study was regarded as similar to a combination of seine and gill netting (Baird *et al.*, 1988). Similar results were obtained from a seine net study conducted from 1973 to 1975 where Mugilidae and *R. holubi* were the dominant taxa and numerically comprised 92% of the catch. A seine net study during 1977-1979 on the other hand, revealed that estuarine species were the most abundant taxa; *A. breviceps* and *G. aestuaria* together comprised over 70% of the catch. In terms of mass, however, estuarine-dependent marine taxa (mainly mugilids and *R. holubi*) dominated (Baird *et al.*, 1988). The gill net catch composition in the Swartkops estuary was dominated by estuarine-dependent marine species (Marais & Baird, 1980) while the overall catch composition from a small haul-seine net survey was dominated by estuarine species (mostly *A. breviceps*, *C. gilchristi*, *G. aestuaria* and *P. knysnaensis*), which numerically accounted for over 58% of the catch (Beckley, 1983).

A similar situation was reported in the Sundays estuary where estuarine-dependent marine species dominated the gill net catch (Marais, 1981) while the catch composition of a seine net study was dominated by estuarine species (Beckley, 1984). *Gilchristella aestuaria* and estuarine goby species (mainly *P. knysnaensis* and *C. gilchristi*) together comprised over 82% of the total abundance (Beckley, 1984).

Estuarine species (mainly *A. breviceps*, *C. superciliosus*, *G. aestuaria* and *G. callidus*) also numerically dominated a small mesh seine net survey of the Kariega estuary and comprised over 56% of the catch (Ter Morshuizen & Whitfield, 1994). Paterson & Whitfield (1996), however, found that the fish community of intertidal saltmarshes in the system were dominated by estuarine-dependent marine species. This group comprised 46% of the taxa, 52% of the abundance and 87% of the biomass. The dominant estuarine-dependent marine species were mainly *L. dumerilii*, *M. cephalus* and *R. holubi* (Paterson & Whitfield, 1996). Estuarine species comprised 31% of the taxa with marine species also well represented (15%). Estuarine species (mainly *A. breviceps* and *G. aestuaria*) were important numerically (30%) but comprised only 5% of the biomass. Both freshwater and marine species comprised <1% of the total numbers or mass (Paterson & Whitfield, 1996).

Estuarine-dependent marine species dominated the seine net catches from both the Kowie and Great Fish estuaries (Whitfield *et al.*, 1994). The three most abundant estuarine-dependent marine species captured in the Kowie estuary included *L. dumerilii*, *L. tricuspidens* and *R. holubi*, while *L. dumerilii*, *L. richardsonii* and *R. holubi* dominated the catch in the Great Fish system. Estuarine species (*G. aestuaria*) were important in both systems (Whitfield *et al.*, 1994). Estuarine-dependent marine species (mainly *A. japonicus*, juvenile mugilids, *L. dumerilii*, *M. cephalus*, *P. commersonnii* and *R. holubi*) also numerically dominated the seine and gill net assemblages in the Great Fish estuary (Ter Morshuizen *et al.*, 1996a). This group comprised over 97% of the small seine net catch, 71% of the large seine net catch and the entire gill net catch. Estuarine species (*G. aestuaria*) were also numerically important in the large seine net catch (25%) (Ter Morshuizen *et al.*, 1996a). Based on a combination of seine and gill nets, Vorwerk *et al.* (2001) found that the dominant group in the Great Fish estuary in terms of overall abundance were estuarine species (mainly *G. aestuaria* and *P. knysnaensis*). These fishes accounted for 52% of the catch, with estuarine-dependent marine species (*A. japonicus*, *H. capensis*, *L. lithognathus*, *L. dumerilii*, *L. richardsonii*, *M. cephalus*, *P. commersonnii*, *R. holubi* and *S. bleekeri*) comprising 47% (Vorwerk *et al.*, 2001).

In the Keiskamma estuary, estuarine species (mainly *A. breviceps*, *C. gilchristi*, *C. nudiceps* and *G. aestuaria*) also numerically dominated the fish community and accounted for 74% of the catch (Vorwerk *et al.*, 2001). Estuarine-dependent marine species (*A. japonicus*, *G. feliceps*, *L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *M. capensis*, *P. commersonnii*, and *R. holubi*) comprised 26% of the catch numerically.

The species assemblages from gill net studies in a number of Transkei estuaries (Great Kei, Mbashe and Mtata) were all dominated by estuarine-dependent marine taxa (Plumstead *et al.*, 1985; 1989a; 1989b). The absence of estuarine resident species is due to gill nets not sampling these smaller taxa.

7.4.3 Subtropical estuaries

7.4.3.1 Closed estuaries

In closed subtropical systems, estuarine-dependent marine species were the dominant group in terms of taxa abundance and biomass (Table 7.4). Key estuarine-dependent marine species included *A. japonicus*, *L. alata*, *L. dumerilii*, *L. macrolepis*, *M. falciformis*, *M. cephalus*, *M. capensis*, *P. commersonnii*, *R. holubi*, *T. jarbua*, *V. cunnesius* and *V. robustus*. Together these taxa comprised over 45% of the community numerically and 59% of the biomass. Estuarine species were also numerically important during this study. This group was mainly represented by *A. productus*, *G. aestuaria* and *G. callidus*, which together comprised approximately 31% of the fish abundance. Freshwater taxa were important both numerically and in terms of biomass. Freshwater species were primarily *C. gariepinus* and *O. mossambicus* and together these two species comprised 20% of the community numerically and 36% of the biomass.

Although estuarine-dependent marine species were the dominant taxa reported in the Sezela estuary, estuarine species (*A. productus* and *G. aestuaria*) numerically dominated, comprising over 40% of the catch (Ramm *et al.*, 1987). Estuarine-dependent marine species (mainly *M. falciformis*, *M. capensis* and *V. cunnesius*) comprised 32% of the catch followed by freshwater species (*O. mossambicus*) (28%).

From Whitfield (1980c) estuarine-dependent marine species (mainly *L. alata, L. dumerilii*, *L. macrolepis*, *M. cephalus*, *M. capensis*, *R. holubi*, *T. jarbua* and *V. cunnesius*) dominated the fish fauna of the Mhlanga estuary. This group comprised

46% of the catch numerically and 71% of the biomass. Freshwater species (*O. mossambicus*) accounted for 34% of the abundance and 26% of the biomass while estuarine species (mostly *A. productus*, *G. aestuaria* and *G. callidus*) comprised 19% of the overall abundance and only 2% of the biomass (Whitfield, 1980c). Harrison & Whitfield (1995), however, found that estuarine species (mainly *G. aestuaria* and *G. callidus*) numerically dominated the fish community of the Mhlanga estuary (48%), followed by estuarine-dependent marine species (mainly *A. japonicus*, *L. amia*, juvenile mugilids, *L. alata*, *L. dumerilii*, *M. cephalus, M. capensis*, *P. commersonnii* and *V. cunnesius*) (34%) and freshwater species (*O. mossambicus*) (18%). In terms of biomass, estuarine-dependent marine species and freshwater species dominated, and accounted for 52% and 47% of the catch respectively; estuarine species comprised less than 1% of the biomass (Harrison & Whitfield, 1995).

From a comparative study of KwaZulu-Natal estuaries, Begg (1984a) concluded that resident estuarine (*G. aestuaria* and *Glossogobius* spp.) and freshwater (*O. mossambicus*) taxa commonly dominated the fish communities of normally closed systems in the region.

Begg (1984a) concluded that normally closed systems in KwaZulu-Natal were commonly dominated by resident (e.g. *G. aestuaria*, *Glossogobius* spp.) and freshwater (*O. mossambicus*) taxa and that these systems did not serve a significant nursery function for estuarine-dependent marine species. These findings, however, were based on sampling methods restricted to a one-metre beam trawl, which is not effective in sampling larger, swifter, estuarine-dependent species such as mullet. Harrison & Whitfield (1995), using a range of sampling methods, found that estuarine-dependent marine taxa were an important component of the ichthyofauna of small KwaZulu-Natal estuaries. The results of this study also support these findings.

7.4.3.2 Open estuaries

Open subtropical estuaries were dominated by estuarine-dependent marine species (Table 7.8). Key estuarine-dependent marine species during this study included *A. berda*, *A. japonicus*, *C. ignobilis*, *C. sexfasciatus*, *E. machnata*, *H. kelee*, *L. equula*, *L. amia*, *L. alata*, *L. dumerilii*, *L. macrolepis*, *L. tricuspidens*, *L. argentimaculatus*, *M.*

cyprinoides, *M. cephalus*, *M. capensis*, *P. commersonnii*, *R. holubi*, *S. lysan*, *S. bleekeri*, *T. jarbua*, *T. vitrirostris*, *V. buchanani*, *V. cunnesius* and *V. robustus*. Together, these species comprised 60% of the fish abundance and 93% of the biomass. Estuarine species were also an important group in terms of abundance. Dominant estuarine species were *A. gymnocephalus*, *A. natalensis*, *C. gilchristi*, *G. aestuaria* and *G. callidus*, which together numerically comprised 30.5% of the catch; estuarine species such as *O. acutipennis* and *O. keiensis* were also frequently recorded during this study.

In the Mngazana estuary, Branch & Grindley (1979) reported that estuarine species such as *A. natalensis*, *A. breviceps*, *C. gilchristi*, *C. nudiceps*, *Eleotris fusca*, *G. aestuaria*, *G. callidus*, *O. acutipennis* and *P. knysnaensis* were among the common to abundant taxa. Important estuarine-dependent taxa were *L. dumerilii*, *L. macrolepis*, *M. argenteus*, *M. cephalus*, *R. holubi*, *S. salpa* and *T. jarbua* (Branch & Grindley, 1979). In both the Mntafufu and Mzamba estuaries, estuarine-dependent marine species were the dominant group reported from gill net catches (Plumstead *et al.*, 1991). According to Begg (1984a), open estuaries on the subtropical KwaZulu-Natal coast are dominated by a wide variety of estuarine-dependent marine teleosts including *A. berda*, *A. japonicus*, *Pomadasys* spp., *Rhabdosargus* spp. and Mugilidae. The data presented for the Mzimkulu and Mkomazi estuaries, however, revealed that species such as estuarine gobies (mostly *Glossogobius* and *Oligolepis*) and the sole, *S. bleekeri* numerically dominated the ichthyofauna with the goby species accounting for approximately 30% of the catch. This is a reflection of the sampling method used, which tends to target demersal species. The taxa reported from gill netting in the Matigulu estuary (Hemens *et al.*, 1986) and seine netting in the Mlalazi system (Hill, 1966) were dominated by estuarine-dependent species.

7.4.4 General

From the various studies in South African estuaries outlined above, a major factor influencing the relative proportions of the fish estuary-association categories was sampling gear. Seine netting is effective in sampling small fishes such as estuarine resident species that inhabit shallow waters but is not suitable for catching larger, faster swimming marine and freshwater fish typically found in deeper waters. Gill nets, however, are effective in sampling, larger marine and freshwater species but not small fishes (Harrison & Whitfield, 1995; Vorwerk *et al*., 2000). Whitfield & Marais (1999) state that any attempt to determine the extent of utilisation of an estuary, or to compare different systems, a sampling protocol that ensures the collection of representative data should be used. The abundance and catch composition of fishes in estuaries should be determined using different methods that overlap in terms of selectivity (Whitfield & Marais, 1999). The combination of sampling methods used during this study (seine netting and gill nets) was designed to obtain a representative a sample of the overall fish community in each estuary.

Relatively few fish species are able to complete their entire life cycle within southern African estuaries; this group comprised between 20 and 26% of the taxa in closed and open subtropical and warm-temperate estuaries during this study. Whitfield (1998) reported similar proportions where estuarine resident species comprised 27% of the estuary-associated fish taxa in southern Africa. In cool-temperate estuaries, however, the contribution of estuarine species generally exceeded 40%. This is probably a result of the low species diversity in the region elevating the relative contribution of this group. Estuarine species were also relatively important numerically and typically comprised over 20% of the abundance in all regions. Estuarine taxa are characteristically small species (Wallace *et al*., 1984; Whitfield, 1990) and as a result, they did not comprise a major component of the biomass composition of the ichthyofauna in any biogeographic region. Wallace (1975b) states that the small size of estuarine species limits their physical ability to undertake migrations to and from the sea. Whitfield (1998) has further suggested that predation by adult piscivorous fishes in the sea may also deter mass migrations by these small species; in addition, the typically shallow microtidal estuaries of southern Africa tend to favour occupation by small species.

To reduce the loss of eggs and larvae to the marine environment, both by normal tidal activity or when closed estuaries open, resident estuarine species often exhibit reproductive specialisations. *Atherina breviceps*, *Caffrogobius* spp. and *P. knysnaensis* have eggs with threads that are used for attachment to aquatic plants, shells, stones and other submerged objects (Bennett, 1989a; Whitfield, 1998).

Gilchristella aestuaria spawns in the upper reaches of estuaries and as the larvae grow, their distribution extends toward the mouth (Melville-Smith & Baird, 1980; Talbot, 1982). The breeding season of resident species also serves to enhance the survival of these fishes in estuaries. In the subtropical St Lucia system, *G. aestuaria* was found to spawn throughout the year with a peak in spring and early summer corresponding with a general rise in water temperature and an increase in zooplankton food resources (Blaber, 1979). Whitfield (1980b) states that the prolonged breeding season of estuarine species is important in closed estuaries since it acts as a buffer against episodic events such as floods or unseasonal breaching. Both *G. aestuaria* and *G. callidus* were found to breed in the Mhlanga estuary (KwaZulu-Natal) during the stable (winter) closed phase (Whitfield, 1980b). Estuarine resident species also appear to spawn predominantly during the spring and summer in both the cool- and warm-temperate regions (Bennett, 1989; Whitfield, 1998). In the warm-temperate region, this occurs between the rainfall peaks in spring (October/November) and late summer (March). These rains serve to replenish nutrients needed to stimulate summer productivity (Whitfield, 1998). In the cool-temperate region, spawning coincides with the period when rainfall is at a minimum and most of the estuaries are closed or, if open, water flow is reduced; during this period maximum cover and food are available, and together with the high temperatures optimise growth of larvae and juveniles (Bennett, 1989a).

The highest abundance of estuarine species during this study was recorded in warm-temperate estuaries; this also contributed to the differences between closed warm-temperate estuaries and cool-temperate and subtropical systems. The high abundance of estuarine species also contributed to the very slight difference between open warm-temperate and subtropical systems. Potter *et al.* (1990) also noted that both temperate southern African and southwestern Australian estuaries contain moderate to large populations of estuarine resident species. Temperate southwestern Australian and southern African estuaries are similar both morphologically and hydrologically (Potter & Hyndes, 1999) and among the reasons given for the high representation of resident species was the hydrological stability of these systems and the maintenance of high salinities. From a study of seven temperate southwestern Australian estuaries, estuarine resident species comprised 19% of the total taxa reported and 34-99% of the fish assemblages numerically (Potter & Hyndes, 1999). Griffiths (2001) also found in the intermittently open Shellharbour Lagoon, southeastern Australia, where salinities were maintained at approximately 20 ‰, estuarine resident species numerically accounted for 48% of the fishes collected. The moderate rainfall and river flow together with relatively high salinities probably account for the high proportion of resident species in warm-temperate estuaries relative to cool-temperate and subtropical systems, which experience marked seasonal variations in rainfall, runoff and salinity.

It has also been suggested that the important contribution made by species that spawn in estuaries in southwestern Australia and southern Africa, may be a reflection of adaptations evolved in response to an intermittent mouth condition (Begg, 1984a; Potter *et al.*, 1990; 1993; Potter & Hyndes, 1999); most of the estuaries in southwestern Australia and southern Africa are closed systems. There would therefore be strong selection pressures for small species with short life cycles to adapt to spawning in estuaries in those years when their access to the sea is blocked (Begg 1984a; Potter *et al.*, 1990; 1993; Potter & Hyndes, 1999). It is also interesting to note that 60-80% of the resident species recorded in warm-temperate estuaries during this study are endemic species.

Estuarine-dependent marine species were the dominant taxa recorded during this study, comprising 67-80% of the species in closed estuaries, and 50-71% of the taxa in open systems. This group was also the dominant category both in terms of abundance and biomass. For southern African estuaries as a whole, Whitfield (1998) found that euryhaline marine species comprised approximately 66% of the estuary-associated fish taxa the bulk of the taxa associated with southern African estuaries.

The main feature of the life cycle of most marine species utilising southern African estuaries is a division into a juvenile phase that is predominantly estuarine and an adult phase that is predominantly marine (Wallace, 1975b). In KwaZulu-Natal, estuarine-dependent marine species generally spawn in the inshore marine environment during late autumn, winter and spring (May-November) (Wallace, 1975b) with recruitment of juveniles into estuaries taking place mainly during winter and spring (June-November) (Wallace & van der Elst, 1975). During this period, river flow is often at a minimum and although all open estuaries are available for colonisation, many closed estuaries only open after spring rains (Wallace & van der Elst, 1975; Whitfield, 1980c). The prolonged recruitment period, which is a function of the extended spawning season, is regarded as a strategy against unfavourable environmental conditions such as unseasonal floods, or droughts that could delay the breaching of closed estuaries (Wallace, 1975b; Whitfield, 1998).

In the warm- and cool-temperate regions, estuarine-dependent marine species also have an extended spawning and recruitment period; however, this appears to occur later, during spring and summer (September-February). *Liza dumerilii*, which is important in both subtropical and warm-temperate estuaries, spawns in KwaZulu-Natal waters between June and November (Wallace, 1975b) while in the Eastern Cape, spawning occurs between December and February (van der Horst & Erasmus, 1981). Similarly, spawning by *R. holubi* in KwaZulu-Natal occurs mainly between May and August (Wallace, 1975b) and between July and February in the Eastern Cape (Whitfield, 1998). Lasiak (1983) has also suggested that the spawning period of *L. richardsonii*, which is important in both cool- and warm-temperate estuaries, varies according to temperature regimes. In the Eastern Cape, *L. richardsonii* spawns during spring and summer (September-March) (Lasiak, 1983) while on the west coast, spawning takes place mostly in summer (December to March) (De Villiers, 1987). From a review of mugilid spawning seasons, van der Horst & Erasmus (1981) suggested that at higher latitudes, low winter temperatures appear to be a limiting factor with spawning occurring in summer; at lower latitudes where sea temperatures seldom drop below 16 °C, all mullet species spawn in winter. The peak recruitment period of estuarine-dependent marine fishes into cool- and warm-temperate estuaries takes place during spring/summer (October-March) (Bennett, 1989a; Whitfield & Kok, 1992). In warm-temperate estuaries, this occurs just after the spring rains. In the cool-temperate region, rainfall and runoff are reduced, but the seasonally open estuaries have yet to close. Small juveniles can therefore enter the estuaries and take advantage of the high temperatures, and food availability until the onset of the next winter (Bennett, 1989a).

The spawning and recruitment period of estuarine-dependent marine species in southern African waters ensures that juveniles occur in estuarine nursery areas during periods when environmental conditions such as food and habitat availability are optimal. The dominance of estuarine-dependent marine species in all biogeographic regions during this study indicates that estuaries throughout the country serve a viable nursery function for this group of fishes.

Although Whitfield (1998) noted that marine species (category III) comprise 25% of southern African estuary-associated fish taxa, they did not comprise an important component of the ichthyofauna in any biogeographic region during this study. Wallace (1975b) also noted that stenohaline marine fishes generally do not constitute an important component of the ichthyofauna of South African estuaries. This group was virtually absent from closed estuaries during this study and this is probably a reflection of the predominantly closed mouth condition, which reduces the potential for this group to utilise these systems. In open estuaries, where exchange with the marine environment is more regular and salinities are higher, the lack of marine taxa is somewhat surprising; this may be related to habitat availability. Over 160 fish species have been recorded in the Kosi Bay estuary, KwaZulu-Natal, the vast majority of which were stenohaline marine visitors (Blaber & Cyrus, 1981). Furthermore, over 30% of the taxa were associated with a rocky outcrop near the mouth. South African estuaries typically do not have such reef habitat and therefore, even marine-dominated estuaries are probably unable to support reef-associated marine fishes.

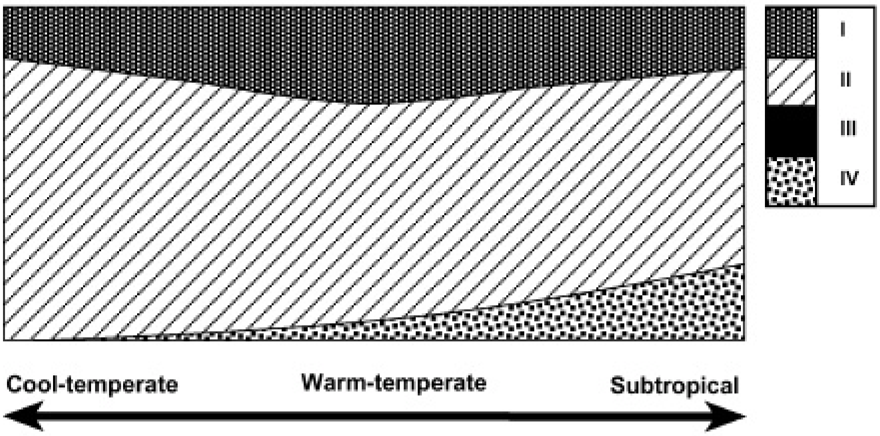
Freshwater species, including species with an obligate freshwater phase, only made a notable contribution to the fish community of closed subtropical estuaries during this study. Whitfield (1998) also found that this group comprised only 8% of the estuary-associated fish taxa in southern Africa. The dominant freshwater species in subtropical systems were *O. mossambicus* and *C. gariepinus*. Whitfield & Blaber (1979) found that *O. mossambicus* was common in seasonally closed estuaries and coastal lakes in KwaZulu-Natal but absent from open, tidal estuaries. Begg (1984a; 1984b) also noted that *O. mossambicus* was often a dominant component of the ichthyofaunal community of many closed KwaZulu-Natal estuaries. The importance of freshwater species declined in closed warm- and cool-temperate systems during this study. Whitfield (1998) also notes that freshwater species are not a major component of the ichthyofauna of warm-temperate estuaries and are virtually absent from cool-temperate estuaries. The decline in freshwater fishes from subtropical to cool-temperate estuaries also parallels the north-south decline in species richness of southern African indigenous freshwater fishes (O'Keeffe *et al.*, 1991; Skelton, 1993). The results of a SIMPER analysis revealed that the relatively high contribution of freshwater species in closed subtropical estuaries contributed toward the differences between these systems and warm- and cool-temperate estuaries. Closed subtropical estuaries typically have low salinities and this probably allows freshwater taxa, especially stenohaline species such as *C. gariepinus*, to extend into these habitats; the higher salinities in open estuaries probably restricts the utilisation of these systems by freshwater taxa. Deegan & Thompson (1985) found that the occurrence of freshwater forms in Louisiana estuaries was negatively correlated with salinity. The high salinities that characterise warm-temperate estuaries may also restrict the occurrence of freshwater taxa in these systems.

Ter Morshuizen *et al.* (1996a; 1996b) suggested that the paucity of freshwater species in southern African estuaries, even during extended periods of elevated freshwater input, may be partially due to competition with the abundant estuarine and marine fish assemblages in these systems. Another factor that may limit the utilisation of South African estuaries by freshwater fishes is the relatively high proportion of marine piscivorous fishes in estuaries. There are relatively few piscivorous freshwater fishes in southern Africa and the impact of piscivorous fishes on indigenous freshwater fishes is highlighted by the fact that introductions of alien fishes such as bass (*Micropterus*) have been responsible for the decline in some indigenous freshwater species (Skelton, 1993).

Overall, the estuaries in the three biogeographic regions exhibited a high degree of similarity, generally exceeding 60% in closed estuaries and 70% in open systems. Elliott & Dewailly (1995) also found that, although the relative proportions of species representing different life cycle categories in European estuaries varied, there were few major differences between the systems; the similarity between estuaries based on these functional guilds exceeded 70%. They concluded that similar functional types, irrespective of their taxonomic identities inhabit these estuaries (Elliott & Dewailly, 1995). The high degree of similarity, based on their ichthyofaunal estuary-associations during this study, also suggests a similar situation in southern Africa. The estuarine fish communities in all biogeographic regions were dominated by estuarine-dependent marine species demonstrating that estuaries throughout the South Africa serve as important nursery areas.

7.5 SUMMARY AND CONCLUSIONS

A summary of the ichthyofaunal composition of closed and open estuaries, based on their estuary-associations is presented in Figure 7.3 below. This diagrammatic representation is based on an importance value calculated by summing the percentage taxonomic composition, numerical abundance and biomass composition (Mueller-Dombois & Ellenberg, 1974; Krebbs, 1985).


a) Closed estuaries

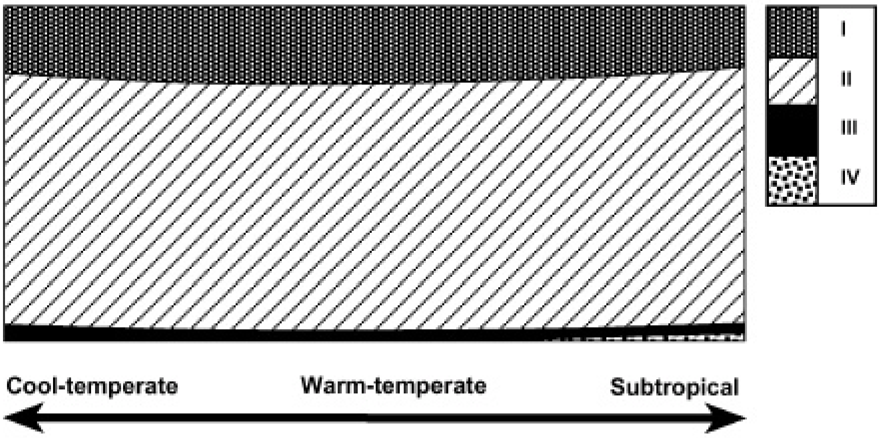

b) Open estuaries

Figure 7.3. Relative importance of the various estuary-association categories of fishes in a) closed estuaries and b) open estuaries in the cool-temperate, warm-temperate and subtropical regions. I = estuarine resident species, II = estuarine-dependent marine species, III = marine species, IV = freshwater species.

Estuarine resident taxa were well represented in all regions. These fishes have reproductive specialisations that enable them to live and breed in estuaries. The numerical importance of this group was highest in warm-temperate estuaries and this may be related to the relative stable environmental conditions of these estuaries when compared to cool-temperate and subtropical estuaries. Warm-temperate estuaries are characterised by low rainfall, runoff and relatively high salinities while cool-temperate, and subtropical estuaries are subject to distinct seasonal variations in rainfall, runoff and salinity. Estuarine-dependent marine species spawn in the marine environment with the juveniles utilising estuaries as nursery areas. This group of fishes has an extended spawning and recruitment period, which acts as a buffer against unfavourable environmental conditions such as floods or delayed opening of closed estuaries. This group of fishes dominated the ichthyofauna of all estuaries in all regions. Marine species were virtually absent from closed estuaries and this is probably a result of the lack of contact with the sea and variable salinities, particularly in cool-temperate and subtropical estuaries. This group was recorded in open estuaries but they were not an important component of the ichthyofauna. A factor that may account for their low representation, even in the relatively high salinity warm-temperate estuaries is a lack of suitable habitat such as reef. Freshwater species were a major component of the ichthyofauna of closed subtropical estuaries but their importance declined in warm- and cool-temperate estuaries; this mirrors the pattern for southern African freshwater fishes in general. Low salinity conditions in closed subtropical estuaries probably enhance the utilisation of these systems by freshwater taxa while high salinities probably restrict the occurrence of freshwater species in warm-temperate estuaries as well as open estuaries in general.

Although certain components of the ichthyofauna differed between biogeographic regions, the estuaries exhibited a high degree of similarity signifying that they perform a similar function. Overall, estuarine-dependent marine species dominated the fish fauna of the estuaries in all biogeographic regions, indicating that estuaries throughout South Africa perform a viable nursery function.

CHAPTER 8
TROPHIC COMPOSITION

8.1 INTRODUCTION

South African estuaries are recognised as productive systems that serve as important nursery areas for juvenile marine fishes (Wallace *et al.*, 1984; Whitfield, 1998). According to Whitfield & Marais (1999), one of the reasons why juvenile marine migrants as well as estuarine residents utilise estuaries successfully, is a food supply that is usually richer and more predictable than in the open sea.

There are three primary sources of food for estuarine-associated fishes, namely phytoplankton, aquatic macrophytes and detritus (Bennett, 1989b). Phytoplankton is consumed by zooplankton, which in turn is fed on by zooplanktivorous fishes (Blaber, 1980; Whitfield, 1980c; Marais, 1984). There are few, if any truly herbivorous fishes in South African estuaries; although some fishes do graze sea grasses directly, food is mostly provided indirectly through consumers feeding on epiphytic algae (Blaber, 1974; Day *et al.*, 1981). Food chains in South African estuaries are largely based on detritus (Day, 1951; Whitfield & Marais, 1999). Estuaries act as detritus traps, thus providing abundant food resources for filter and deposit-feeding invertebrate prey as well as detritivorous fish species (Blaber, 1980; Whitfield, 1980c; Marais, 1984; Whitfield, 1998; Whitfield & Marais, 1999).

The characterisation of trophic structure among fish assemblages is critical to an understanding of the interrelationships among habitat variables, productivity, associated food webs and dependence of fishes on inshore resources (Barry *et al.*, 1996; Livingston, 1997). This chapter describes and compares the trophic composition of the estuarine ichthyofauna within the various biogeographic regions. The main objective is to determine if the primary food sources, as reflected by the trophic composition of the fish fauna, differs between zoogeographic regions.

8.2 MATERIALS & METHODS

8.2.1 Trophic composition

Based on available scientific literature, the fish species captured during this study were classified into five broad categories, according to the predominant food items in their diet. These included:

- Fish: species that are primarily piscivorous
- Benthic invertebrates: fishes that feed mainly on benthic invertebrates
- Zooplankton: fishes that are predominantly zooplankton feeders
- Aquatic macrophytes/invertebrates: species that consume aquatic macrophytes, filamentous algae, and the associated invertebrate fauna
- Detritus: fishes that feed mainly on detritus, benthic microalgae, and meiofauna.

The categorisation of the species based on their predominant food items (from Whitfield, 1998) captured during this study is presented in Appendix 3. The relative (%) contribution of each category to the ichthyofauna of each estuary was then calculated in terms of number of taxa, abundance and biomass. The mean contribution (±SD) of each group was then determined for each estuary type within each biogeographic region.

8.2.2 Multivariate analyses

Closed and open estuaries were also subject to multivariate statistical analyses using PRIMER (Clarke & Warwick, 1994). Bray-Curtis similarities, based on the ichthyofaunal trophic categories, between the estuaries were calculated and the data subjected to non-metric multi-dimensional scaling (MDS). Similarities based on percent taxa were calculated on untransformed data while percent abundance/biomass data were first 4th root transformed. The percentage taxonomic composition did not exhibit strong dominance by any one trophic category while the relative abundance and biomass data did show a high dominance by certain categories. For the results of the MDS ordinations, the estuaries were labelled according to their biogeographic region where: CT = cool-temperate; WT = warm-temperate; and ST = subtropical. The estuaries in each biogeographic region were also compared by an analysis of similarities (ANOSIM) (Clarke & Warwick, 1994). In this analysis, estuaries within each biogeographic region were only considered distinct at a significance of $p<0.01$.

8.3 RESULTS

8.3.1 Closed estuaries

8.3.1.1 Cool-temperate estuaries

The taxa in closed cool-temperate estuaries were dominated by detritivores; this group comprised 67.5% of the taxa followed by species that feed on benthic invertebrates (17.5%) and zooplanktivores (10.0%). Piscivores and species that consume aquatic macrophytes/invertebrates each comprised 2.5% of the taxa (Table 8.1). In terms of abundance, detritivores were the dominant group, comprising 74.8% of the overall assemblage. Zooplanktivores were the next most abundant group (21.8%) followed by species that feed on benthic invertebrates (3.3%). Piscivorous fishes and species that consume aquatic macrophytes/invertebrates comprised less than 0.1% of the catch. The biomass composition of closed cool-temperate estuaries was also dominated by detritivores, which comprised 93.7% of the species mass followed by piscivores (5.4%). Fishes belonging to the remaining feeding groups did not constitute a major component of the fish biomass (Table 8.1).

Table 8.1. Mean contribution (±SD) of trophic categories to the ichthyofauna of closed cool-temperate estuaries.

Trophic category	% Species	% Abundance	% Biomass
Fish	2.50 (±5.00)	0.08 (±0.16)	5.43 (±10.86)
Benthic invertebrates	17.50 (±20.62)	3.27 (±5.91)	0.15 (±0.28)
Zooplankton	10.00 (±11.55)	21.76 (±43.38)	0.68 (±1.28)
Aquatic macrophytes/invertebrates	2.50 (±5.00)	0.05 (±0.10)	0.00 (±0.00)
Detritus	67.50 (±37.75)	74.84 (±42.51)	93.74 (±12.07)

8.3.1.2 Warm-temperate estuaries

Detritivores dominated the taxa in closed warm-temperate estuaries; this group comprised 36.0% of the taxa, followed by species that feed on benthic invertebrates (27.7%) and zooplanktivores (19.3%). Species that feed on aquatic macrophytes/invertebrates constituted 10.0% of the taxa while piscivores comprised 7.0% (Table 8.2). Numerically, zooplanktivores were the dominant group (54.8%), followed by detritivores (18.7%) and fishes that consume aquatic macrophytes/invertebrates (18.0%). Fishes that predominantly feed on benthic invertebrates numerically comprised 8.1% of the assemblage while piscivores only constituted 0.4%. In terms of biomass, detritivores were the dominant group and comprised 64.3% of the fish biomass. Piscivores were the next most important group (12.6%) followed by fishes that consume aquatic macrophytes/invertebrates (10.5%) and those that feed on benthic invertebrates (9.2%). Zooplanktivores made up 3.4% of the biomass (Table 8.2).

Table 8.2. Mean contribution (±SD) of trophic categories to the ichthyofauna of closed warm-temperate estuaries.

Trophic category	% Species	% Abundance	% Biomass
Fish	7.03 (±6.19)	0.35 (±0.58)	12.63 (±14.40)
Benthic invertebrates	27.74 (±8.21)	8.10 (±11.07)	9.16 (±7.85)
Zooplankton	19.27 (±4.98)	54.82 (±23.63)	3.40 (±2.58)
Aquatic macrophytes/invertebrates	9.98 (±4.48)	18.03 (±15.89)	10.48 (±8.57)
Detritus	35.99 (±8.10)	18.71 (±16.28)	64.34 (±18.30)

8.3.1.3 Subtropical estuaries

The fishes in closed subtropical estuaries were dominated by detritivores and constituted 36.0% of the taxa. Species that feed on benthic invertebrates comprised 27.7% of the taxa, followed by zooplanktivores (19.3%), species that feed on aquatic macrophytes/invertebrates (10.0%) and piscivores (7.0%) (Table 8.3). In terms of abundance, detritivores and zooplanktivores were the dominant groups and comprised 54.5 and 30.9% of the catch respectively. Species that consume aquatic macrophytes/invertebrates comprised 7.0% of the fish abundance, followed by those that feed on benthic invertebrates (6.3%) and piscivores (1.4%). Detritivores dominated the fish biomass and constituted 68.7% of the species mass. Piscivores were the next most important group (21.5%) followed by species that feed on benthic invertebrates (3.7%) and zooplanktivores (3.4%); fishes that consume aquatic macrophytes/invertebrates constituted 2.7% of the fish biomass (Table 8.3).

Table 8.3. Mean contribution (±SD) of trophic categories to the ichthyofauna of closed subtropical estuaries.

Trophic category	**% Species**	**% Abundance**	**% Biomass**
Fish	8.86 (±6.78)	1.40 (±2.11)	21.50 (±28.00)
Benthic invertebrates	24.10 (±11.10)	6.26 (±6.86)	3.70 (±4.82)
Zooplankton	15.43 (±6.59)	30.89 (±30.67)	3.37 (±4.34)
Aquatic macrophytes/invertebrates	6.49 (±3.77)	6.97 (±11.06)	2.71 (±6.39)
Detritus	45.12 (±10.02)	54.48 (±26.10)	68.70 (±25.40)

8.3.1.4 Multivariate analyses

The MDS ordination of the taxa showed two cool-temperate estuaries (Wildevoël and Krom) situated as outliers to the bottom left of the plot. The remaining systems did not exhibit any clear pattern although there did appear to be a slight gradation, from left to right, of subtropical systems toward warm-temperate estuaries. A similar pattern was also observed in the ordination of the abundance data with cool-temperate systems situated as outliers toward the bottom left of the plot and a slight left to right gradation from subtropical estuaries to warm-temperate systems. In the biomass ordination, the two cool-temperate estuaries were also depicted as outliers. The remaining systems did not show any clear pattern although subtropical systems were generally situated toward the top of the remaining group (Figure 8.1).

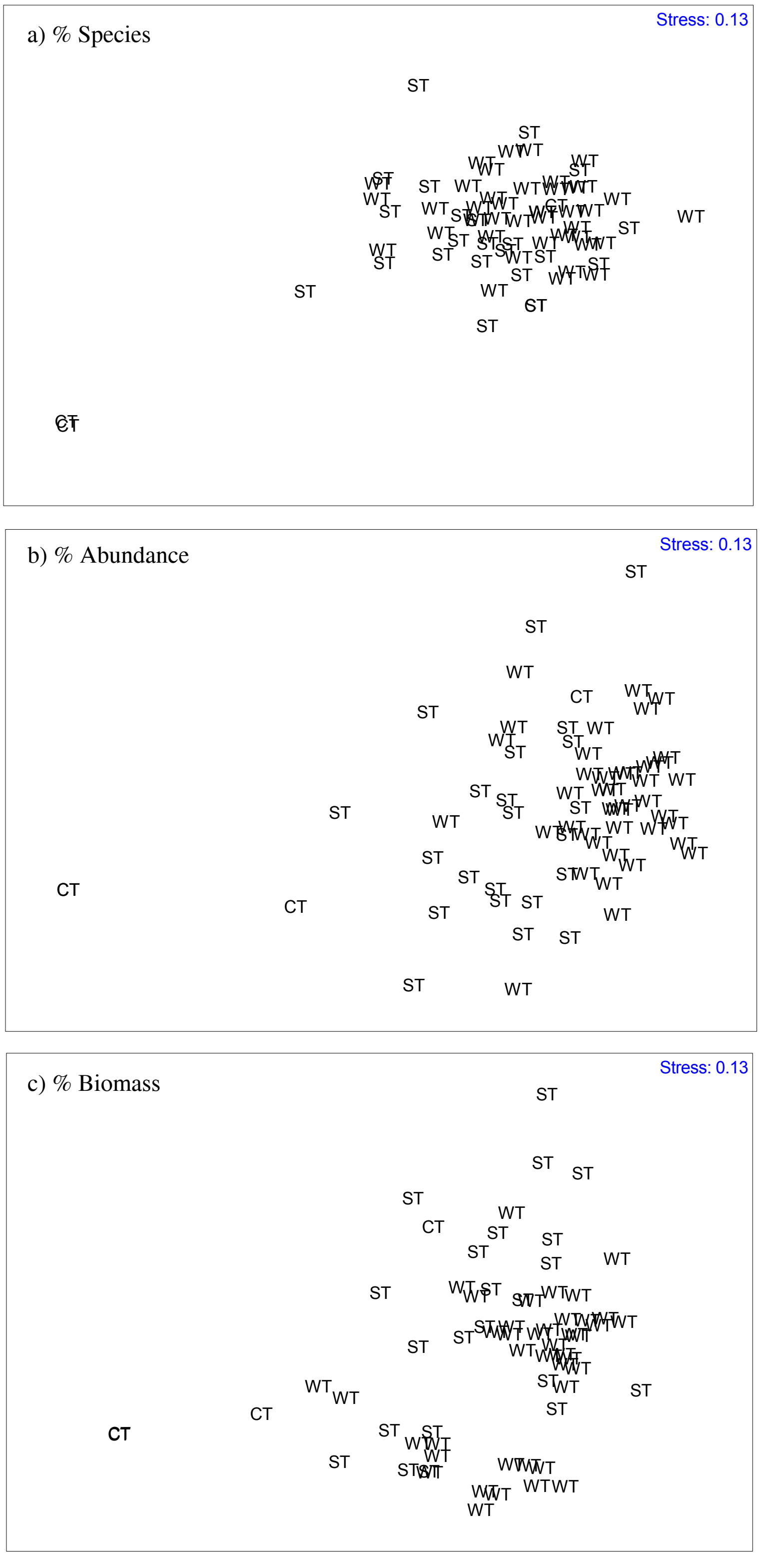


Figure 8.1. MDS ordination of closed estuaries based on (a) % species, (b) % abundance and (c) % biomass of the trophic categories of the ichthyofauna.

The results of the ANOSIM test revealed that, in terms of taxa, relative abundance, and relative biomass composition, cool-temperate estuaries were significantly distinct from both warm-temperate and subtropical systems. Warm-temperate and subtropical estuaries were also slightly (R<0.4) but significantly distinct (Table 8.4).

Table 8.4. Results of the ANOSIM test (R) comparing closed cool-temperate, warm-temperate and subtropical estuaries based on the percent species, abundance and biomass contribution of their ichthyofaunal trophic composition (* p<0.01).

	Cool-temperate versus Warm-temperate	Cool-temperate versus Subtropical	Warm-temperate versus Subtropical
% Species	0.466*	0.484*	0.202*
% Abundance	0.816*	0.647*	0.412*
% Biomass	0.837*	0.569*	0.224*

8.3.2 Open estuaries

8.3.2.1 Cool-temperate estuaries

Fishes that feed on benthic invertebrates comprised 36.8% of the taxa captured in open cool-temperate estuaries. Detritivores were the next most important group (33.1%), followed by zooplanktivores (22.1%) and piscivores (8.1%). Species that feed on aquatic macrophytes/invertebrates were not captured during this study (Table 8.5). Detritivores were the most abundant group and numerically comprised 85.9% of the catch. Zooplanktivores numerically accounted for 12.8% followed by benthic invertebrate feeders (1.3%). Piscivores were not abundant and only constituted 0.1% of the catch numerically. In terms of biomass, detritivores were the dominant group (77.9%) followed by zooplanktivores (11.0%), piscivores (7.7%) and species that consume benthic invertebrates (3.4%) (Table 8.5).

Table 8.5. Mean contribution (±SD) of trophic categories to the ichthyofauna of open cool-temperate estuaries.

Trophic category	% Species	% Abundance	% Biomass
Fish	8.06 (±10.56)	0.08 (±0.10)	7.68 (±12.60)
Benthic invertebrates	36.81 (±15.28)	1.25 (±1.07)	3.37 (±4.26)
Zooplankton	22.08 (±15.12)	12.76 (±17.73)	11.02 (±18.68)
Aquatic macrophytes/invertebrates	0.00 (±0.00)	0.00 (±0.00)	0.00 (±0.00)
Detritus	33.06 (±20.19)	85.91 (±18.15)	77.93 (±24.03)

8.3.2.2 Warm-temperate estuaries

Fishes that feed on benthic invertebrates were the dominant species in open warm-temperate estuaries and comprised 36.8% of the taxa. These were followed by followed by detritivores (24.3%), zooplanktivores (15.2%), piscivores (13.9%) and fishes that consume aquatic macrophytes/invertebrates (9.9%) (Table 8.6). In terms of abundance, zooplanktivores were the dominant group and comprised 35.9% of the fish community numerically. Detritivores numerically contributed 29.3% to the fish assemblage, followed by fishes that consume aquatic macrophytes/invertebrates (17.2%) and species that feed on benthic invertebrates (15.9%). Piscivores numerically comprised 1.8% of the fish abundance. Detritivores dominated the fish biomass, contributing 40.8% to the species mass. Piscivores and fishes that feed on benthic invertebrates comprised 33.3 and 20.5% of the fish biomass respectively. Fishes that consume aquatic macrophytes/invertebrates contributed 3.4% to the biomass while zooplanktivores comprised 2.0% (Table 8.6).

Table 8.6. Mean contribution (±SD) of trophic categories to the ichthyofauna of open warm-temperate estuaries.

Trophic category	% Species	% Abundance	% Biomass
Fish	13.87 (±5.19)	1.75 (±1.95)	33.33 (±17.14)
Benthic invertebrates	36.81 (±6.05)	15.88 (±11.96)	20.45 (±18.58)
Zooplankton	15.21 (±5.10)	35.90 (±21.85)	1.99 (±1.97)
Aquatic macrophytes/invertebrates	9.85 (±5.18)	17.20 (±15.58)	3.44 (±2.62)
Detritus	24.26 (±6.84)	29.28 (±20.01)	40.80 (±17.77)

8.8.2.3 Subtropical estuaries

In open subtropical estuaries, fishes that feed on benthic invertebrates comprised 33.6% of the taxa. Detritivores were the next most important group, comprising 26.2% of the taxa, followed by piscivores (20.5%) and zooplanktivores (15.1%). Fishes that consume aquatic macrophytes/invertebrates comprised 4.5% of the taxa (Table 8.7). In terms of abundance, detritivores were the dominant group and constituted 36.3% of the fishes numerically. Zooplanktivores comprised 28.5% of the fish abundance while species that feed on benthic invertebrates constituted 21.2%. Fishes that consume aquatic macrophytes/invertebrates numerically comprised 7.3% of the assemblage followed by piscivores (6.7%). Detritivores also dominated the fish biomass and contributed 51.5% to the species mass. Piscivores contributed 33.4% to the biomass followed by zooplanktivores (7.0%) and fishes that feed on benthic invertebrates (6.8%). Species that consume aquatic macrophytes/invertebrates comprised 1.3% of the biomass (Table 8.7).

Table 8.7. Mean contribution (±SD) of trophic categories to the ichthyofauna of open subtropical estuaries.

Trophic category	**% Species**	**% Abundance**	**% Biomass**
Fish	20.54 (±3.90)	6.65 (±5.50)	33.37 (±10.06)
Benthic invertebrates	33.59 (±3.03)	21.18 (±11.24)	6.84 (±6.63)
Zooplankton	15.13 (±4.71)	28.54 (±21.61)	7.05 (±5.83)
Aquatic macrophytes/invertebrates	4.52 (±2.23)	7.29 (±6.10)	1.27 (±1.06)
Detritus	26.23 (±5.23)	36.33 (±20.04)	51.47 (±15.39)

8.3.2.4 Multivariate analyses

The MDS ordination of the taxa showed no clear pattern; cool-temperate estuaries were situated at the periphery of the plot. Subtropical estuaries were generally situated near the bottom of the remaining group. In terms of both abundance and biomass, cool-temperate estuaries appeared as a broad spread to the left of the plot. The remaining systems did not exhibit any clear pattern although subtropical systems were mostly situated toward the top of the remaining groups (Figure 8.2).

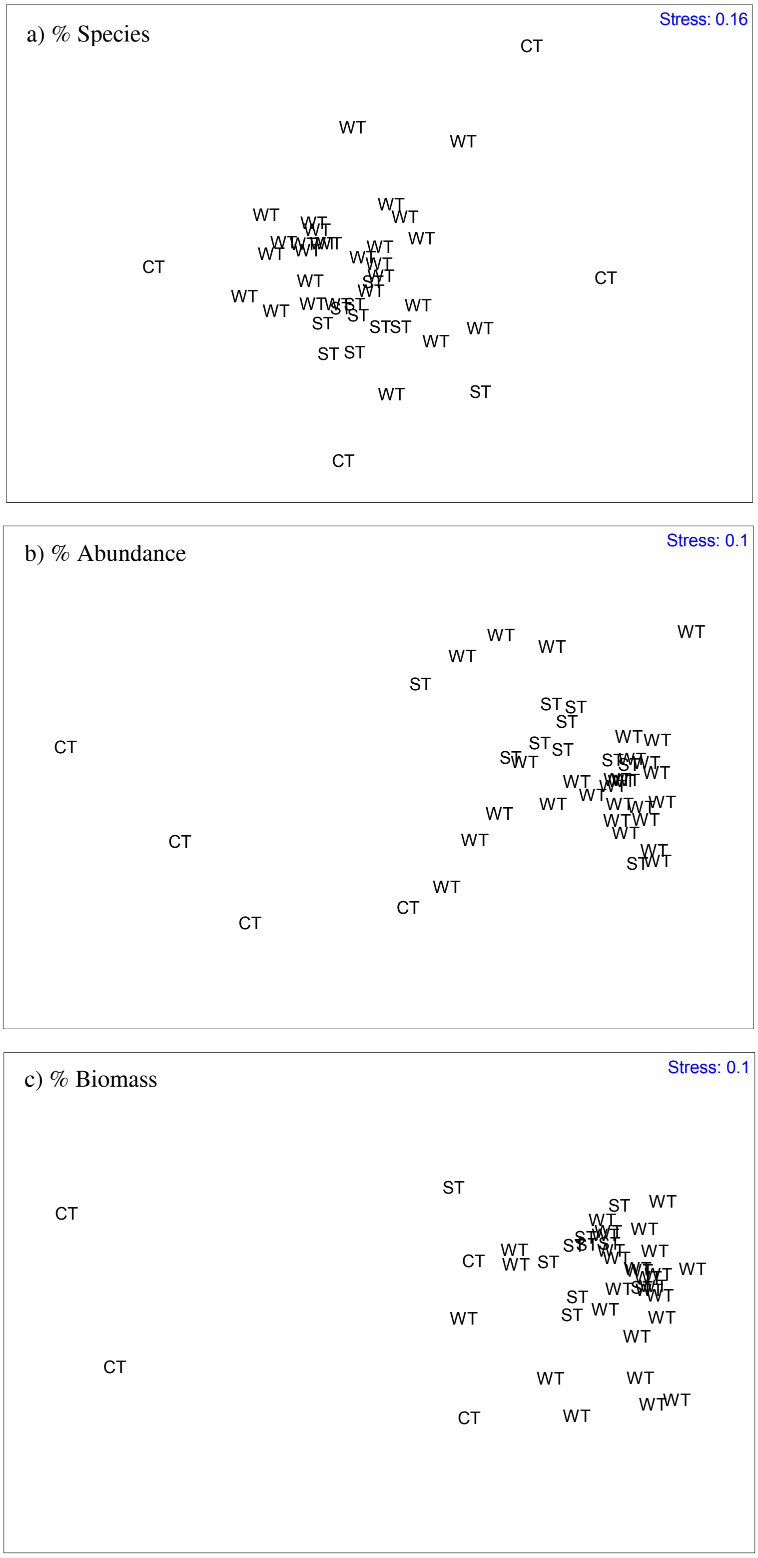


Figure 8.2. MDS ordination of open estuaries based on (a) % species, (b) % abundance and (c) % biomass of the trophic categories of the ichthyofauna.

The results of the ANOSIM test revealed that, in terms of taxa, relative abundance, and relative biomass composition, cool-temperate estuaries were significantly distinct from both warm-temperate and subtropical systems. Warm-temperate and subtropical estuaries, however, were not distinct (Table 8.8).

Table 8.8. Results of the ANOSIM test (R) comparing closed cool-temperate, warm-temperate and subtropical estuaries based on the percent species, abundance and biomass contribution of their ichthyofaunal estuarine associations (* p<0.01).

	Cool-temperate versus Warm-temperate	Cool-temperate versus Subtropical	Warm-temperate versus Subtropical
% Species	0.860*	0.817*	0.058
% Abundance	0.934*	0.963*	0.120
% Biomass	0.860*	0.752*	0.117

8.4 DISCUSSION

8.4.1 Cool-temperate estuaries

8.4.1.1 Closed estuaries

In closed cool-temperate estuaries, detritivores were the dominant group, comprising 68% of the taxa, 75% of the abundance and 94% of the biomass. The main species belonging to this group were the mugilids, *L. richardsonii* and *M. cephalus*. Zooplanktivores (mainly *A. breviceps* and *G. aestuaria*) were also important in terms of abundance (22%) but comprised less than 1% of the biomass. Benthic invertebrate feeders were well represented in terms of taxa (18%) but only comprised 3% of the fish abundance and very little to the overall biomass. Fishes that consume aquatic macrophytes/invertebrates were not an important component of the fish community of closed cool-temperate systems during this study. Piscivores were also not important in terms of taxa or abundance; this group (mainly *L. amia*) comprised over 5% of the fish biomass (Table 8.1).

Limited data from earlier fish surveys of closed cool-temperate estuaries showed a similar trophic composition to that recorded during this study. Detritivorous mullet (*L. richardsonii* and *M. cephalus*) were among the commonest fish reported in the Diep estuary (Millard & Scott, 1954; Grindley & Dudley, 1988). Benthic invertebrate feeders such as *C. nudiceps*, *H. capensis*, *L. lithognathus* and *P. knysnaensis* and zooplanktivores (*A. breviceps* and *G. aestuaria*) were also common. The only major piscivore was *P. saltatrix*, however, this species was not common (Millard & Scott, 1954; Grindley & Dudley, 1988). Detritivorous mullet (*L. richardsonii* and *M. cephalus*) were the dominant fishes reported from limited netting in the Wildevoël system (Heinecken, 1985). Mullet (*L. richardsonii* and *M. cephalus*) were also found to be the most abundant species in the Sand estuary (Morant & Grindley, 1982; Morant, 1991). Benthic invertebrate feeders such as *C. nudiceps*, *L. lithognathus* and *P. knysnaensis* were also common. *Rhabdosargus globiceps*, which consumes aquatic macrophyte/invertebrates, was relatively abundant while *A. breviceps* was a common zooplanktivore. Piscivores (*P. saltatrix* and *L. amia*) were reported in small numbers (Morant & Grindley, 1982; Morant, 1991). From Clark *et al.* (1994), the zooplanktivores, *A. breviceps* and *G. aestuaria* were the numerically dominant species in the Sand estuary, comprising 56% of the catch; detritivores (mostly *L. richardsonii*) were the next most abundant group. Although a number of benthic invertebrate feeders were represented, they did not constitute a major component of the ichthyofauna numerically (Clark *et al.* (1994).

8.4.4.2 Open estuaries

Detritivores (*L. richardsonii* and *M. cephalus*) were the dominant fishes in open cool-temperate estuaries, particularly in terms of abundance and biomass (Table 8.5). Zooplanktivores (mainly *A. breviceps* and *G. aestuaria*) were also an important group in terms of abundance (13%) and biomass (11%). Although benthic invertebrate feeders were well represented and comprised 37% of the taxa, this group was not important either numerically (1%) or in terms of biomass (3%). Species that consume aquatic macrophytes/invertebrates were not captured in open cool-temperate estuaries during this study. Piscivores were represented by *Argyrosomus* spp. and *P. saltatrix*; together these two species accounted for approximately 8% of the biomass (Table 8.5).

Detritivores (*L. richardsonii*) and zooplanktivores (*A. breviceps* and *G. aestuaria*) were among the commonest species reported in the Olifants estuary (Day, 1981a). From a seine net study in the Berg estuary, detritus feeders (mainly *L. richardsonii*) and zooplanktivores (predominantly *A. breviceps* and *G. aestuaria*) were the most abundant trophic groups (Bennett, 1994). Benthic invertebrate feeders were also relatively abundant; the dominant species belonging to this group were *C. nudiceps* and *P. knysnaensis*. The main piscivores represented were *P. saltatrix* and *L. amia*; these species, however, did not contribute much to the overall catch. In the Palmiet estuary, detritivores (mainly *L. richardsonii*) and zooplanktivores (*A. breviceps*) numerically dominated the ichthyofauna (Branch & Day, 1984; Bennett, 1989a). *Liza richardsonii* constituted approximately 50% of the catch while *A. breviceps* comprised about 44%. In terms of biomass, *L. richardsonii* comprised 87% of the catch while *A. breviceps* only comprised 3% (Bennett, 1989a). The main fish predators were *L. amia* and *P. saltatrix* but they were not important numerically.

8.4.2 Warm-temperate estuaries

8.4.2.1 Closed estuaries

The taxa and biomass of closed warm-temperate estuaries was dominated by detritivores, mainly mugilids (*L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *M. capensis*) and the cichlid, *O. mossambicus*. This group comprised 36% of the taxa and 64% of the biomass (Table 8.2). In terms of abundance, zooplanktivores (mainly *A. breviceps* and *G. aestuaria*) were the dominant group (55%). This group, however, only comprised 3% of the ichthyofauna in terms of biomass; this is because these are typically small species. Fishes that feed on benthic invertebrates were well represented in terms of taxa (28%) and comprised 8% of the abundance and 9% of the biomass. Key species belonging to this group included *G. callidus*, *L. lithognathus*, *P. commersonnii* and *P. knysnaensis*. Species that feed on aquatic macrophytes/invertebrates (primarily *R. holubi*) were relatively important both numerically (18%) and in terms of biomass (11%). Although piscivorous species were not abundant, they did comprise a notable portion of the biomass (13%). Dominant piscivores species included *A. japonicus*, *E. machnata* and *L. amia*.

In the Seekoei, Kabeljous and Van Stadens estuaries, zooplanktivores (mainly *A. breviceps* and *G. aestuaria*) were among the most abundant species caught by seine netting (Dundas, 1994). In terms of biomass, however, detritivores (mainly *L. richardsonii*) and aquatic macrophyte/invertebrate feeders (*R. holubi*) dominated. The larger fishes captured by gill netting were dominated by detritivores (*L. dumerilii*, *L.*

richardsonii, *L. tricuspidens* and *M. cephalus*) both in terms of number and mass. All other trophic groups were also well represented. Important benthic invertebrate feeders included *L. lithognathus* and *P. commersonnii* while *R. holubi* was the dominant aquatic macrophyte/invertebrate feeder. The only major zooplanktivore captured in the gill nets was *M. falciformis* while the main piscivore was *L. amia* (Dundas, 1994).

The catch composition from small-mesh seine netting in the Oos-Kleinemond estuary was numerically dominated by zooplanktivores (mainly *A. breviceps*, *G. aestuaria*); these fishes comprised approximately 83% of the catch (Cowley & Whitfield, 2001). Small benthic invertebrate feeders (mainly *G. callidus* and *P. knysnaensis*) were also numerically important, comprising about 17% of the catch. Large-mesh seine net catches were dominated by the aquatic macrophyte/invertebrate feeder, *R. holubi*; this species numerically accounted for 75% of the catch. Detritivores (mainly *L. dumerilii*, *L. richardsonii*, *M. cephalus*, *M. capensis* and *O. mossambicus*) were the next most abundant group. Detritivores numerically dominated the gill net catches in the Oos-Kleinemond estuary and constituted approximately 40% of the catch. The zooplanktivorous, *M. falciformis* comprised 26% of the gill net catch followed by the macrophyte/invertebrate feeder, *R. holubi* (13%). The main piscivore captured in both seine and gill nets was *L. amia* but it was not abundant (Cowley & Whitfield, 2001).

From Vorwerk *et al*. (2001), the fish communities in the Oos-Kleinemond, Mpekweni, Mtati, Mgwalana, Bira, and Gqutywa estuaries were dominated by zooplanktivores; *A. breviceps* and *G. aestuaria* together comprised over 60% of the fish abundance in these systems. Other important trophic groups included benthic invertebrate feeders (mainly *G. callidus*, *L. lithognathus*, *P. commersonnii*) and detritivores (*L. dumerilii, L. richardsonii*, *M. cephalus*, *M. capensis* and *O. mossambicus*). *Rhabdosargus holubi*, which feeds on aquatic macrophytes/invertebrates, was also relatively important in these systems. The dominant piscivores included *E. machnata* and *P. saltatrix* but these were not abundant (Vorwerk *et al*., 2001).

8.4.2.2 Open estuaries

Species that feed on benthic invertebrates were well represented in open cool-temperate estuaries and comprised 37% of the taxa (Table 8.6). In terms of abundance, however, zooplanktivores (predominantly *A. breviceps* and *G. aestuaria*) were the dominant group (36%) followed by detritivores (24%). Important detritivores were mostly mullet (*L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *M. capensis* and *V. buchanani*); this group also dominated the biomass composition (41%). Piscivores (mainly *A. japonicus*, *E. machnata* and *L. amia*) were an important group in terms of biomass (33%) (Table 8.6).

Day (1981a) reports that detritivorous mullet (*L. richardsonii* and *M. cephalus*) as well as the zooplanktivorous *A. breviceps* and *G. aestuaria* were common in the Heuningnes estuary. Benthic invertebrate feeders (*L. lithognathus* and *P. commersonnii*) and piscivores (*A. japonicus* and *L. amia*) were also abundant. Benthic invertebrate feeders (*G. feliceps*, *L. lithognathus* and *P. commersonnii*) and piscivores (*A. japonicus* and *L. amia*) were found to be an important component of the larger fish component captured by gill netting in the Breë estuary (Ratte, 1982; Coetzee & Pool, 1991). Detritivorous mullet (*L. richardsonii* and *M. cephalus*) were also important.

From a gill net study of the Kromme estuary, Marais (1983a) found that the piscivorous *L. amia* and *A. japonicus* were the dominant species both in terms of numbers and biomass; this was followed by larger benthic invertebrate feeders, *G. feliceps* and *P. commersonnii*. The detritivorous mullet (*L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus* and *V. buchanani*) were also important. As a group mugilids comprised 12% of the catch numerically and 6% of the biomass (Marais, 1983a). From a seine net study of the system, the numerically dominant species were detritivorous mullet; *L. dumerilii* comprised 62% of the catch (Hanekom & Baird, 1984). Piscivores (*A. japonicus* and *L. amia*) also dominated the gill net catches in the Gamtoos estuary (Marais, 1983b). Benthic invertebrate feeders (*G. feliceps* and *P. commersonnii*) were the next most important group followed by detritivorous mullet (mainly *L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus* and *M. capensis*).

The family Mugilidae comprised 28% of the fish assemblage numerically and 14% of the biomass (Marais, 1983b).

From Baird *et al.* (1988), netting in the Swartkops estuary during 1915-1916 showed that the aquatic macrophyte/invertebrate feeder, *R. holubi*, was the numerically dominant species (45%), followed by Mugilidae (34%). Three benthic invertebrate feeders, *L. lithognathus*, *G. feliceps* and *P. commersonnii* comprised 13% of the catch while the piscivores, *A. japonicus* and *P. saltatrix* constituted 6%. The most abundant taxa recorded during a seine net study from 1975 to 1979 were Mugilidae (mostly *L. dumerilii*); this group numerically comprised 42% of the catch. The benthic invertebrate feeders, *G. feliceps* and *P. commersonnii*, together comprised 23% of the abundance. In terms of biomass, however, benthic invertebrate feeders dominated (35%) followed by mullet (25%). The piscivore, *L. amia* comprised approximately 6% of the catch both numerically and in terms of mass (Baird *et al.*, 1988). A seine net study during 1977-1979 was numerically dominated by the zooplanktivores, *A. breviceps* and *G. aestuaria*; together these two species comprised 73% of the total catch. In terms of biomass, however, Mugilidae dominated and comprised 62% of the species mass. Fishes that consume aquatic macrophytes/invertebrates (*D. sargus* and *R. holubi*) were also relatively important and comprised 9% of the abundance and 13% of the biomass (Baird *et al.*, 1988).

The larger fishes captured during a gill net study of the Swartkops estuary were numerically dominated by Mugilidae (mainly *L. richardsonii*, *L. tricuspidens* and *M. cephalus*); this family comprised 42% of the catch (Marais & Baird, 1980). In terms of biomass, benthic invertebrate feeders (*G. feliceps* and *P. commersonnii*) dominated. Mullet were the next most important group followed by piscivores (*E. machnata* and *L. amia*) (Marais & Baird, 1980). The overall catch composition from a small haul-seine net survey was numerically dominated by zooplanktivorous species (mostly *A. breviceps*, and *G. aestuaria*) (Beckley, 1983). Mullet (*L. dumerilii*, *L. richardsonii*, *L. tricuspidens* and *M. cephalus*) were the next most abundant group, followed by fishes that feed on aquatic macrophytes/invertebrates (mainly *D. sargus* and *R. holubi*) (Beckley, 1983).

From a gill net study of the Sundays estuary, mullet (mainly *L. richardsonii*, *L. tricuspidens* and *M. cephalus*) numerically dominated the larger fish fauna (38%) followed by invertebrate feeders (*G. feliceps* and *P. commersonnii*) and piscivores (*A. japonicus*, *E. machnata* and *L. amia*) (Marais, 1981). In terms of biomass, benthic invertebrate feeders dominated, followed by mugilids and piscivores. The catch composition of a seine net study in the Sundays was numerically dominated zooplanktivores (mainly *G. aestuaria* and *M. falciformis*); mugilids (*L. dumerilii*, *L. richardsonii* and *M. cephalus*) were the next most abundant group (Beckley, 1984).

The fish community captured in the Kariega estuary during a small mesh seine net survey were also dominated by zooplanktivores (*A. breviceps*, *G. aestuaria* and *M. falciformis*) (Ter Morshuizen & Whitfield, 1994). Fishes that consume aquatic macrophytes/invertebrates (*D. sargus* and *R. holubi*) were the next most important group followed by mugilids and benthic invertebrate feeders (mainly *G. callidus*) (Ter Morshuizen & Whitfield, 1994). The fish community of intertidal saltmarshes in the Kariega estuary, however, were dominated by Mugilidae (mainly juveniles, *L. dumerilii*, *L. richardsonii*, *L. tricuspidens* and *M. cephalus*) both numerically and in terms of biomass (Paterson & Whitfield, 1996). Zooplanktivores (*A. breviceps* and *G. aestuaria*) were also numerically important but did not contribute much to the biomass.

Species that consume aquatic macrophyte/invertebrates (namely *D. sargus* and *R. holubi*) numerically dominated the seine net catch in the Kowie estuary (Whitfield *et al.*, 1994). The next most abundant groups were zooplanktivores (*A. breviceps* and *G. aestuaria*) and detritivorous mullet (mainly *L. dumerilii*, *L. richardsonii*, *L. tricuspidens* and *M. cephalus*). Mullet dominated the gill net assemblage followed by piscivores (*A. japonicus* and *L. amia*) and benthic invertebrate feeders (mainly *G. feliceps*, *L. lithognathus* and *P. commersonnii*) (Whitfield *et al.*, 1994).

In the Great Fish estuary, detritivorous mullet (mainly *L. dumerilii*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus* and *M. capensis*) were the numerically dominant group in seine net catches (Whitfield *et al.*, 1994; Ter Morshuizen *et al.*, 1996a; 1996b). Zooplanktivores (mainly *G. aestuaria*), benthic invertebrate feeders (mainly *G.*

feliceps, *L. lithognathus*, *P. commersonnii*, *P. olivaceum*, *S. bleekeri*) and species that consume aquatic macrophytes/invertebrates (*R. holubi*) were also relatively important. The larger fish component captured by gill nets was dominated by mugilids followed by benthic invertebrate feeders (*G. feliceps* and *P. commersonnii*) (Whitfield *et al*., 1994; Ter Morshuizen *et al*., 1996a). The major piscivore reported in the Great Fish estuary was *A. japonicus*. Vorwerk *et al*. (2001) reported that zooplanktivores were the numerically dominant group in the Great Fish and Keiskamma estuaries. *Gilchristella aestuaria* comprised 47 and 66% of the catch in the Great Fish and Keiskamma estuaries respectively. Detritivores, mainly mullet were the next most important group, followed by benthic invertebrate feeders (Vorwerk *et al*., 2001).

From gill netting in the Great Kei, Mbashe and Mtata estuaries, detritivorous mullet (*L. alata*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *M. capensis* and *V. buchanani*) were the dominant group both in terms of abundance and biomass (Plumstead *et al*., 1985; 1989a; 1989b). Benthic invertebrate species (*G. feliceps*, *J. dorsalis*, *L. equula*, *L. lithognathus* and *P. commersonnii*) and piscivores (*A. japonicus*, *E. machnata* and *L. amia*) were also relatively important.

8.4.3 Subtropical estuaries

8.4.3.1 Closed estuaries

The ichthyofauna of closed subtropical estuaries was dominated by detritivores; these were mainly represented by the mullet *L. alata*, *L. dumerilii*, *L. macrolepis*, *M. cephalus*, *M. capensis*, *V. cunnesius* and *V. robustus* as well as the cichlid, *O. mossambicus*. Detritivores comprised 36% of the taxa, 55% of the abundance and 69% of the biomass (Table 8.3). Zooplanktivores (mainly *A. productus*, *G. aestuaria* and *M. falciformis*) were also an important group in terms of abundance (31%) while piscivores (chiefly *A. japonicus* and *C. gariepinus*) were important in terms of biomass (22%). Fishes that feed on benthic invertebrates were well represented in terms of taxa (28%) but were generally not important in terms of abundance or biomass (Table 8.3).

The fish community in the Sezela estuary was numerically dominated by detritivores (mainly *M. cephalus*, *M. capensis*, *O. mossambicus* and *V. cunnesius*) and zooplanktivores (primarily *A. productus*, *G. aestuaria* and *Monodactylus* spp.) (Ramm *et al*., 1987). In the Mhlanga estuary, Mugilidae (*L. alata*, *L. dumerilii*, *L. macrolepis*, *M. cephalus*, *M. capensis* and *V. cunnesius*) and *O. mossambicus* dominated the fish community both numerically and in terms of biomass (Whitfield, 1980c). Zooplanktivores, (mainly *A. productus* and *G. aestuaria*) were also important numerically but did not contribute much to the overall biomass; the low biomass contribution of this group was attributed to the small size of these species. Small benthic invertebrate feeders such as *G. callidus* and *T. jarbua* were also numerically important. *Caranx sexfasciatus* was the only piscivore reported (Whitfield, 1980c). From Harrison & Whitfield (1995), detritivores (mainly juvenile mullet, *L. alata*, *L. dumerilii*, *M. cephalus*, *M. capensis*, *O. mossambicus* and *V. cunnesius*) dominated the ichthyofauna of the Mhlanga estuary both numerically and in terms of biomass. The zooplanktivore, *G. aestuaria* was also numerically important. Blaber *et al*. (1984) noted that iliophagous species including Mugilidae (particularly *M. cephalus*, *M. capensis* and *V. cunnesius*) and *O. mossambicus* were the most common trophic category in the Mdloti estuary.

8.4.3.2 Open estuaries

In open subtropical estuaries, detritivorous mugilids (*L. alata*, *L. dumerilii*, *L. macrolepis*, *L. tricuspidens*, *M. cephalus*, *M. capensis*, *V. buchanani* and *V. cunnesius*) dominated the ichthyofauna both numerically (36%) and in terms of biomass (52%) (Table 8.7). Zooplanktivores (*A. gymnocephalus*, *A. natalensis*, *G. aestuaria*, *H. kelee*, *T. vitrirostris*) were also an important group in terms of abundance 29%. Fishes that feed on benthic invertebrates were well represented, comprising 34% of the taxa; they were also relatively abundant (21%). Key benthic invertebrate feeders included *A. berda*, *G. callidus*, *L. equula*, *P. commersonnii*, *S. bleekeri* and *T. jarbua*. Piscivores (*A. japonicus*, *C. ignobilis*, *C. sexfasciatus*, *C. gariepinus*, *E. machnata*, *L. amia*, *L. argentimaculatus*, *M. cyprinoides* and *S. lysan*) were also relatively important in terms of biomass (33%).

Branch & Grindley (1979) noted that detritivorous mullet (*L. dumerilii*, *L. macrolepis* and *M. cephalus*) were common to abundant in the Mngazana estuary. The larger fish species captured by gill netting in the Mntafufu and Mzamba estuaries were dominated by detritivores (mainly *Chanos chanos*, *L. alata*, *L. macrolepis*, *L. tricuspidens*, *M. cephalus*, *M. capensis*, *V. buchanani* and *V. cunnesius*) both numerically and in terms of biomass (Plumstead *et al*., 1991). Piscivores (mostly *A. japonicus*, *Caranx* spp., *E. machnata* and *L. amia*) and larger zooplanktivores (*H. kelee* and *T. vitrirostris*) were also important groups. Although benthic invertebrate feeders and species that feed on aquatic macrophytes/invertebrates were well represented, they did not comprise a major proportion of the catch either numerically or in terms of biomass (Plumstead *et al*., 1991). Juvenile mullet (*L. macrolepis*) were also found to be the most common species reported in the Matigulu system with zooplanktivorous Ambassidae as well as benthic invertebrate feeders (*L. equula* and *P. commersonnii*) also present in considerable numbers (Hemens *et al*., 1986). Among the common to abundant fishes reported from the Mlalazi estuary were the zooplanktivorous Ambassidae, and detritivorous Mugilidae (Hill, 1966).

8.4.4 General

Detritivores were the dominant component of the ichthyofauna of the estuaries in all biogeographic regions. Taxa belonging to this group were primarily mullet. The freshwater cichlid, *O. mossambicus* was also important, particularly in closed subtropical estuaries. Blaber (1985) states that in all southeast African estuaries, the most numerous fishes are the iliophagous species (mainly mullet) and that detritus, together with epipsammic algae and periphyton provide a major energy input into the fish community. Whitfield (1980c) also found that, in the closed Mhlanga estuary, KwaZulu-Natal, benthic floc (detritus) accounted for 83% of the measured food resources and supported 93% of the fish biomass. The results of this study also suggest that detritus is a major food source for estuarine fishes in all biogeographic regions.

According to Whitfield (1999), a key attractiveness of estuaries to fishes lies in the fact that they act as detritus traps. Organic detritus in an estuary is derived from three primary sources. Riverine input introduces terrestrial plant material as well as freshwater plants and algae into the system while tidal action carries detached algae, sea grasses, marine plankton and decomposing material in from the sea; the estuary itself also provides material from both vascular plants and algae (Day & Grindley, 1981). Closed estuaries automatically accumulate detritus during the closed phase while in open estuaries, river flow and tidal action aid in the retention and accumulation of detrital material (Whitfield, 1988).

In river-dominated subtropical estuaries, fluvial input is probably the most important source of detritus. Organic detritus in the Mhlanga estuary, for example, was found to be mainly allochthonous in origin and entered the estuary via the river or adjacent reed swamp (Whitfield, 1980c). In South African warm-temperate estuaries, particularly those that are deprived of an adequate river flow, detritus is mainly autochthonous and is usually derived from intertidal salt marshes and submerged aquatic macrophytes (Whitfield, 1998). In the Kromme estuary, Heymans & Baird (1995) determined that marsh halophytes were responsible for 78% of primary production, of which, 90% was first broken down to detritus before entering the food web. In cool-temperate estuaries, both fluvial and marine inputs of detritus appear to be important. Branch & Day (1984) found that most detritus in the Palmiet estuary comprised plant remains brought down from the river and kelp washed in from the sea, with the latter being quantitatively more important. Most kelp species in southern Africa are restricted to the west and southwest coasts with only one small species (*Ecklonia radiata*) occurring along the south and southeast coast (Branch *et al.*, 1994). Although detritus appears to be an important food supply for fishes in South African estuaries, the primary source of this material most likely differs in each biogeographic region. In subtropical estuaries, detritus from riverine inputs is probably the main source of this material while in warm-temperate systems, detritus is most likely derived from the estuary itself; in cool-temperate estuaries, detritus is derived from both river and marine inputs with the latter, in the form of kelp, probably assuming a greater significance.

Apart from being consumed directly by fishes, detritus in estuaries also provides food for filter- and deposit-feeding invertebrate prey (de Villiers *et al.*, 1999). In estuaries where detritivorous fishes are not abundant, benthic invertebrates appear to be a major food source. Barry *et al.* (1996) found that, in contrast to many tropical and temperate estuaries worldwide, mullet (*M. cephalus*) and other detritivorous fishes were uncommon in Elkhorn Slough, California; detritus-consuming prey, however, dominated the diet of several fish species. Elliott & Dewailly (1995) also found that most European (Atlantic seaboard) estuarine fish assemblages were dominated by benthic invertebrate predators. They concluded that the predominance of detritus-based food webs for estuarine nekton was supported through the central role of small epibenthic crustaceans and infaunal invertebrates in the food chain (Elliott & Dewailly, 1995). Benthic invertebrate feeding fish taxa were well represented in estuaries from all biogeographic regions during this study. This group was an important abundance and biomass component of the ichthyofauna of open subtropical and warm-temperate estuaries. This further emphasises the (indirect) importance of detritus in South African estuaries. Whitfield (1999) also states that, although detritivorous fishes are often the dominant group in terms of biomass, South African estuaries often support a high diversity of carnivorous fishes.

Although benthic invertebrate feeding fishes were well represented in cool-temperate estuaries during this study, they were not important either in terms of abundance or biomass. This may be due to the effect of seasonal floods which can affect benthic invertebrate prey through prolonged exposure to decreased salinities, physical scouring and the deposition of fine silt (de Villiers *et al*., 1999). Branch & Day (1984) noted annual winter flooding was among the factors acting against the establishment of invertebrate populations in the cool-temperate Palmiet estuary. Breaching of closed estuaries also results in a slump in aquatic plant and invertebrate food resources (Bennett, 1989a). A significant decline in aquatic macrophyte and benthic macrofauna abundance and biomass was reported in the Bot estuary on the southwest Cape coast, following a breaching event (De Decker, 1987). The results of a SIMPER analysis showed that the relatively low abundance and biomass of benthic invertebrate feeding fishes in cool-temperate estuaries contributed toward some of the difference between these and subtropical and warm-temperate estuaries.

Benthic invertebrate feeding fishes were an important component of the ichthyofauna of warm-temperate estuaries, particularly open systems. From a study of three Eastern Cape estuaries, Scharler *et al*. (1997) found that stable estuarine conditions contributed to higher standing stocks and diversity of macroinvertebrates; this was related to a continuous low freshwater input together with high aquatic macrophyte cover. The moderate river flows associated with warm-temperate estuaries probably allow relatively high densities of invertebrates to establish and support high biomasses of carnivorous fishes. Benthic invertebrate feeding fishes were a major component of the ichthyofauna in the Kromme, Swartkops and Sundays estuaries both in terms of biomass and productivity (Scharler *et al*., 1997). Thollot *et al*. (1999) found that, in mangrove fish communities from New Caledonia, invertebrate feeders were more developed in clear waters with low variations in salt content than in turbid estuarine areas. The relatively clear, saline waters of warm-temperate estuaries may therefore also contribute to high numbers and biomass of benthic invertebrate feeding fishes in these systems.

There are very few fishes in South African estuaries that are herbivorous (Whitfield, 1998), however, aquatic macrophytes provide food through their diverse and abundant faunas as well as fishes feeding on epiphytic algae (Adams *et al*., 1999). The sparid, *R. holubi* consumes large quantities of macrophytic plant material but only digests the epiphytic diatoms that cover the leaves and not the plant material itself (Blaber, 1974). Whitfield (1999) has suggested that a factor contributing to the low abundance of herbivorous fish in southern African estuaries is the fluctuating nature or even absence of submerged plant communities within these systems. Adams *et al*. (1999) state that episodic or even minor (annual) floods can result in the loss or impaired growth of aquatic macrophytes in estuaries through scouring and smothering by silt. Branch & Day (1984) also found that aquatic macrophytes were poorly represented in the Palmiet estuary and those that were present, only occurred in summer when current velocities were lowest. Both cool-temperate and subtropical estuaries are subject to seasonal flooding and fish species that feed on aquatic macrophytes/invertebrates did not appear to be an important component of these systems.

In estuaries with low freshwater input, increased sediment stability and high water clarity promote macrophyte growth (Adams *et al*., 1999). The low runoff, high salinity and clear waters, associated with warm-temperate estuaries probably serve to enhance the establishment of submerged aquatic macrophytes in these systems. The numerical contribution of fishes that consume aquatic macrophytes/invertebrates (namely *R. holubi*) was also relatively high in warm-temperate estuaries during this study. The SIMPER analysis also showed that the abundance of this group contributed to the differences between warm-temperate and cool-temperate and subtropical systems; the relatively higher biomass contribution of this group in closed warm-temperate estuaries also accounted for the dissimilarities between these systems and closed cool-temperate and subtropical systems.

Zooplanktivorous fishes were abundant in the estuaries in all biogeographic regions during this study. Particularly high abundances of these fishes (mainly *A. breviceps* and *G. aestuaria*) were recorded in both closed and open warm-temperate estuaries. The high relative abundance of zooplanktivores in warm-temperate estuaries contributed to the difference between these systems and cool-temperate estuaries; they also contributed to the slight, but significant difference between closed warm-temperate and subtropical systems. Zooplankton abundance in estuaries has been linked to river flow and nutrient supply (Whitfield, 1998). Allanson & Read (1995) for example, reported higher standing stocks of zooplankton in the Great Fish estuary, which is subject to a sustained freshwater inflow relative to the freshwater-starved Kariega estuary. The abundance of zooplankton in the Gamtoos, Kromme and Sundays estuaries was also related to freshwater pulses entering these estuaries (Wooldridge & Bailey, 1982; Wooldridge, 1999). In the St Lucia estuary, Blaber (1979) reported peak abundances of zooplankton during the summer rainy season. Despite the positive effects of frequent freshwater pulses on estuarine productivity, floods can result in a temporary depletion of zooplankton stocks. In both the Mhlanga and Mdloti estuaries, high zooplankton densities were reported during the closed (winter) phase but decreased dramatically when the estuaries opened in summer (Whitfield, 1980a; Blaber *et al.*, 1984). Both subtropical and cool-temperate estuaries are subject to seasonal flooding. The relatively high contribution of zooplanktivores in warm-temperate estuaries may be related to the moderate river pulses in these estuaries, which enhances the retention time of nutrients and thus allows high phytoplankton and zooplankton stocks to establish.

Piscivores were an important component of the ichthyofauna of estuaries in all biogeographic regions, particularly in terms of biomass. The importance of this group, however, appeared to decline from subtropical to cool-temperate systems. This partly accounted for the difference between these systems and open warm-temperate and subtropical estuaries. The high biomass of piscivores in closed subtropical estuaries was also responsible for some of the dissimilarity between these and closed warm-temperate and cool-temperate estuaries. The dominant piscivore recorded in closed subtropical estuaries was the tropical freshwater species, *C. gariepinus*. The low salinity conditions in these estuaries probably allowed this species to capitalise on the rich food resources in these systems. In Lake Nhlange, Kosi Bay, Blaber & Cyrus (1981) reported a rise in numbers of the freshwater predator *C. gariepinus* in response to increasing freshwater conditions. The relatively low contribution of piscivores in cool-temperate estuaries may be a reflection of the relatively low number of piscivorous fish taxa found in this region.

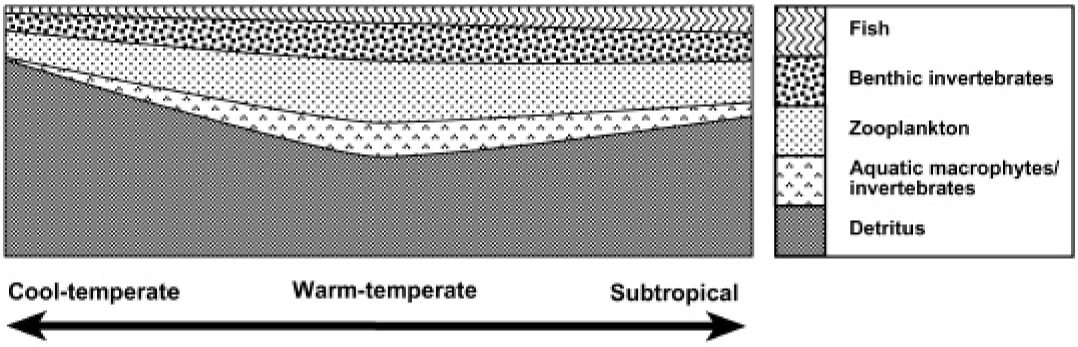
A key factor that makes estuaries important nursery areas for juvenile fishes is refuge from fish predators (Blaber, 1991; Barry *et al*., 1996; Livingston, 1997). Blaber (1986) found that estuarine piscivorous fishes fed on prey species approximately in proportion to their abundance in the environment and that these prey were not selected on the basis of species, but rather by their small size. Paterson & Whitfield (2000) have shown that shallow estuarine areas are important refugia for the juvenile life-stages of fishes that are vulnerable to predation. The data from this study indicate that piscivorous fishes were more prevalent in open estuaries than closed systems in each of the biogeographic regions. This suggests that, at least in terms of providing protection from piscivorous fishes, closed estuaries may serve a greater nursery function than open estuaries and the adjacent marine environment.

In spite of the differences in fish trophic composition, the estuaries from each biogeographic region exhibited a relatively high degree of similarity (>50% in closed estuaries and >60% in open systems). This suggests that the primary food source in estuaries throughout each biogeographic region is similar. Whitfield (1998) also states that despite the influence of biogeography and estuary type on the composition of fishes in an estuary, the basic trophic structure within southern African estuaries is usually very similar. A comparative study on the trophic structure and ecology of four tidal estuaries, the Ythan in Scotland, the Ems-Dollard in the Netherlands and the Swartkops and Kromme in South Africa also revealed that the trophic structure of all the estuaries was similar (Baird & Ulanowicz, 1993). In addition, Elliott & Dewailly (1995) found that, based on the taxonomic composition of the fish feeding guilds, the similarities between European estuaries exceeded 75%. Yoklavich *et al.* (1991) state that, although species composition may vary latitudinally, the numerically dominant fishes in estuaries along the west coast of the United States are juvenile members of similar trophic levels. Overall, detritivores were the dominant trophic category in all estuaries from all regions, during this study thus supporting the concept that this forms the main energy source in South African estuaries and estuaries in general.

8.5 SUMMARY AND CONCLUSIONS

The trophic composition of the ichthyofauna in closed and open estuaries from the three biogeographic regions is summarised in Figure 8.3 below. This diagrammatic representation is based on an importance value that includes the sum of the percentage taxonomic composition, numerical abundance and biomass composition (Mueller-Dombois & Ellenberg, 1974; Krebbs, 1985).

a) Closed estuaries



b) Open estuaries

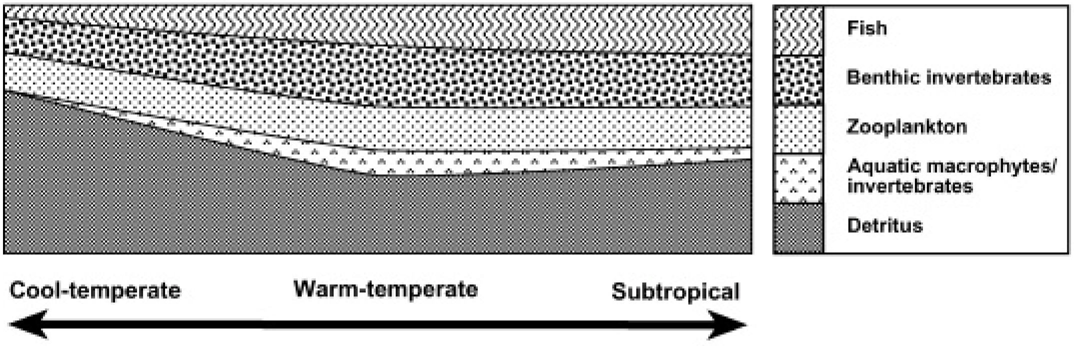


Figure 8.3. Diagrammatic representation of the trophic composition of fishes in a) closed estuaries and b) open estuaries in the cool-temperate, warm-temperate and subtropical regions.

The trophic composition of the fish communities of the estuaries within each biogeographic region exhibited slight differences; these appear to be related to the environmental characteristics of the estuaries within each region and the availability of food resources.

Piscivores were an important biomass component of the ichthyofauna in all regions; however, the relative contribution of this group was lower in cool-temperate systems. This may be a result of the relatively low species diversity of the region.

By acting as detritus sinks, estuaries provide abundant food for filter- and deposit-feeding invertebrate prey; this is also reflected in the good representation of benthic invertebrate feeding fishes in all biogeographic regions. The decline in benthic invertebrate feeding fishes in cool-temperate estuaries may be a result of seasonal flushing during winter spates while the relatively stable conditions in the warm-temperate region probably allow high densities of benthic invertebrate prey (and benthic invertebrate feeding fishes) to establish in these estuaries.

Zooplanktivores were a numerically important group in all estuaries, particularly warm-temperate systems. Zooplankton densities appear to be strongly related to river flow through the introduction of nutrients, however, the low to moderate river flows in the warm-temperate region may provide sufficient residence time for these nutrients to support high phytoplankton and zooplankton stocks. In cool-temperate and subtropical estuaries, this food source is likely to be somewhat variable due to seasonal flushing during winter and summer rainfall periods respectively.

Aquatic macrophytes are also affected by river flow through scouring and smothering by sediments; fishes that feed on aquatic macrophytes/invertebrates appeared to be more important in warm-temperate estuaries. This may also be a result of the low river flows and turbidities in the region, which serves to enhance macrophyte growth in warm-temperate estuaries.

Detritivores dominated the fish community in all biogeographic regions. Although detritus appeared to be the main food source for fishes in estuaries from all regions, the origins of this detritus most likely differs within each region. In river-dominated subtropical estuaries, detritus of fluvial origin is probably the most important source of this material. In the low rainfall warm-temperate region, detritus appears to be mainly autochthonous and is derived from the estuary itself. Cool-temperate estuaries receive detritus from both riverine inputs during winter floods and from the marine environment during low flow periods with the latter probably being more important.

Although certain components of the trophic composition of the ichthyofauna differed between biogeographic regions, the estuaries exhibited a high degree of similarity. Overall, detritivores dominated the fish fauna of the estuaries in all biogeographic regions indicating that detritus comprises the main energy source in these estuaries.

CHAPTER 9

GENERAL SYNTHESIS

In this study, the role of South African estuaries in terms of their fish fauna was examined in a regional context. Some 250 estuaries were sampled spanning the entire 2400 km coastline; the data were collected in a systematic manner, using standard methods and during similar times of year. The approach also took into account intra-regional differences in estuary type. In all, 109 estuaries were included in this study; these represented two broad categories, closed estuaries and open estuaries.

9.1 BIOGEOGRAPHY

A key objective of this study was, based on their fish communities, to verify that estuarine biogeographic regions conform to the generally recognised marine provinces. The South African coast, including estuaries, encompasses at least three distinct biogeographic provinces, namely a subtropical region, a warm temperate region and a cool temperate region (Stephenson & Stephenson, 1972; Brown & Jarman, 1978; Day *et al*., 1981; Whitfield 1994a; 1998; Turpie *et al*., 2000). While it is recognised that South African estuaries also encompass three biogeographic regions, these have been based primarily on marine zoogeographic provinces and composite regional data on estuarine biota (e.g. Day, 1974). Multivariate analyses of estuarine fish communities confirmed that South African estuaries do indeed encompass three biogeographic regions and that these conform to the zoogeographic provinces recognised for the coastal marine environment. Several authors have also found that geographical patterns of estuarine fishes correspond closely with the regional marine zoogeographic patterns, in other world regions. These included tropical and subtropical estuaries of the western Atlantic (Vieira & Musick, 1994), west coast estuaries of the United States (Monaco *et al*., 1992), European estuaries (Elliott & Dewailly, 1995) and Australian east coast (New South Wales) estuaries (Pease, 1999). The strong relationship between estuarine fish communities and marine zoogeographic provinces is not surprising since the vast majority of fishes that utilise South African estuaries are of marine origin (Day *et al*., 1981).

Although there appears to be a broad agreement that the South African coast covers at least three biogeographical regions, there is some question regarding the boundaries of these faunistic provinces. Previous studies on a variety of marine and estuarine biotas suggest that the boundary between the cool-temperate and warm-temperate regions lies at Cape Columbine (e.g. Bustamante, 1994), Cape Point (e.g. Stephenson & Stephenson, 1972; Day *et al.*, 1981; Emanuel *et al.*, 1992; Turpie *et al.*, 2000) or east of Cape Agulhas (e.g. Prochazka, 1994). The boundary between the warm-temperate and subtropical regions has been variously placed at East London (e.g. Emanuel *et al.*, 1992), the Great Kei estuary (e.g. Day *et al.*, 1981), the Mbashe estuary (e.g. Maree *et al.*, 2000), Port St Johns (e.g. Stephenson & Stephenson, 1972) and Port Edward (e.g. Turpie *et al.*, 2000). A second goal of this study was to delineate the boundaries between the various biogeographic provinces. This study established that the break between the cool-temperate and warm-temperate zones was at Cape Agulhas: this corresponds with the approximate boundary between the Agulhas and the Benguela Currents, which lies somewhere in the vicinity of Cape Infanta (east of Cape Agulhas) (Shannon, 1989). The break between the warm-temperate and subtropical zones, at the Mdumbi estuary, coincides with the northern boundary of an upwelling cell that extends from Port Alfred to the Mbashe estuary and occasionally as far north as Port St Johns (Lutjeharms *et al.*, 2000). It should be noted here, however, that no open estuaries were sampled between the Mdumbi system and the Mngazana estuary (just south of Port St Johns) and it is possible that the above boundary lies within this zone.

9.2 PHYSICO-CHEMICAL CHARACTERISTICS

This study also demonstrated that the physico-chemical characteristics of the estuaries within each zoogeographic region were distinctive; this could be related to regional variations in climate, rainfall and ocean conditions. Day (1981a) also grouped southern African estuaries into three main regions based mainly on water temperature, rainfall and river flow; Cooper (2001) found that the geomorphological variability of estuaries in South Africa followed a broad pattern around the coast that reflected regional variability in climate, topography and sediment availability. Variations in climate and oceanographic regime have also been found to be responsible for regional differences in estuary physical/environmental attributes in Australia (e.g. Kench, 1999; Pease, 1999; Potter & Hyndes, 1999) and North America (e.g. Dame *et al.*, 2000; Emmett *et al.*, 2000; Roman *et al.*, 2000).

Estuarine temperatures during this study followed the trend for marine coastal waters, decreasing from the subtropical region toward the cool-temperate zone. Mean water temperatures of closed cool-temperate estuaries usually did not exceed 20 °C; those in the warm-temperate region were mostly within the range 18-24 °C, while subtropical estuaries frequently had water temperatures of 22-28 °C. Temperatures in open cool-temperate systems did not exceed 18 °C; warm-temperate systems had water temperatures mostly within the range 18-22 °C, while temperatures in subtropical estuaries often exceeded 24 °C. In both cool- and warm-temperate estuaries, coastal upwelling can result in low summer temperatures (Morant, 1984; Plumstead *et al.*, 1989a).

Salinities in closed cool-temperate estuaries varied from oligohaline (<5 ‰) to polyhaline (18-30 ‰) while open estuaries were generally polyhaline. Increased runoff reduces salinities in both closed and open systems during winter while high evaporation rates and seawater input results in high salinities during summer (Millard & Scott, 1954; Day, 1981a; Morant, 1984; Slinger & Taljaard, 1994). Warm-temperate estuaries were mostly polyhaline to euhaline (>30 ‰). Because closed warm-temperate estuaries are impounded at or close to high tide level (Cooper, 2001), the influx of seawater via barrier overwash enhances salinities in these systems (Dundas, 1994; Cooper *et al.*, 1999; Cowley & Whitfield, 2001; Vorwerk *et al.*, 2001). Open estuaries in this region are typically tide-dominated systems and the strong marine influence contributes to the high salinities in these systems (Reddering & Rust, 1990; Cooper, 2001). Low freshwater input together with high evaporation rates also contributes to the high salinities in warm-temperate estuaries. Salinities in closed subtropical estuaries were mostly oligohaline to mesohaline (5-18 ‰); this is a result of high rainfall and runoff, together with limited seawater input. Closed estuaries also have a perched bed level, which further limits tidal exchange (Begg, 1984a; Cooper, 2001). Open subtropical estuaries were mostly oligohaline to polyhaline. These estuaries are typically river-dominated systems and their small tidal prisms limit the extent of marine influence (Cooper *et al.*, 1999; Cooper, 2001).

Most estuaries during this study were clear (<10 NTU) to semi-turbid (10-50 NTU). Turbidities can vary seasonally, particularly in areas with high rainfall. In closed estuaries, turbidities are generally low during the closed phase but increase during the rainy season; this occurs in winter in cool-temperate estuaries (Millard & Scott, 1954) and during summer in subtropical systems (Begg, 1984a; 1984b). Heavy winter and summer rainfall also results in increased turbidities in open cool-temperate and subtropical systems respectively (Day, 1981a; Begg, 1984b; Morant, 1984; Cyrus, 1988b; Plumstead *et al.*, 1991). Warm-temperate estuaries, which experience comparatively less rainfall and runoff, were predominantly clear systems.

9.3 SPECIES COMPOSITION

A further objective of this study was to describe and compare the species composition of the estuarine ichthyofauna within each biogeographic region and to identify the main abiotic factors that explain the occurrence and distribution of key species within each region. The results showed that estuaries within the three biogeographic regions contained somewhat distinctive fish assemblages and that distribution and abundance of these assemblages was related primarily to temperature and salinity. Temperature and salinity were also found to be major environmental factors affecting the distribution, abundance and composition of estuarine fishes in American (e.g. Horn & Allen, 1978; Ayvazian *et al.*, 1992; Monaco *et al.*, 1992; Emmett *et al.*, 2000; Kupschus & Tremain, 2001; Vieira & Musick, 1993) and Australian systems (Pease, 1999).

Subtropical systems were characterised by fish assemblages of predominantly tropical origin (e.g. *A. berda*, *A. japonicus*, *L. macrolepis*, *P. commersonnii*, *V. cunnesius*). The distribution and abundance of these species was strongly linked to temperature, with many species being largely restricted to the warmer waters of subtropical estuaries. Several species found in the subtropical estuaries were also negatively correlated with salinity. Blaber (1981) has suggested that the estuary-associated fishes in southeast Africa are turbid, brackish water species that also occur in shallow areas of the Indian Ocean such as the Bay of Bengal and southeast Asia. Due to monsoon rains twice a year, conditions in these areas are brackish and the waters are characteristically turbid. In southeast African waters, however, such habitats are largely restricted to estuaries (Blaber, 1981). The dispersal of these Indo-Pacific fishes is facilitated by the ocean current systems; the south-flowing Agulhas Current off the east coast of South Africa, transports tropical fishes into southern African waters (Wallace & van der Elst, 1975; Day *et al*., 1981).

As the Agulhas Current flows south, however, it moves offshore and consequently, inshore sea temperatures decline; this limits the dispersal of tropical species into warm-temperate estuaries (Wallace & van der Elst, 1975; Day *et al*., 1981; Whitfield, 1998). Maree *et al*. (2000) have suggested that summer upwelling events on the south coast also acts as a barrier to the distribution of tropical species, particularly in the Algoa Bay region. The upwelling cell that extends from Port Alfred northward to the Mbashe estuary and even as far as Port St Johns (Lutjeharms *et al*., 2000) is probably the first thermal barrier encountered by tropical species and this corresponds with the subtropical/warm-temperate biogeographic boundary. Since tropical estuarine-associated species appear to prefer turbid, brackish water conditions (Blaber, 1981), the change in estuarine conditions to clear, saline systems may further restrict the occurrence of these fishes in this region. Some tropical species (e.g. *A. japonicus*, *E. machnata*, *P. commersonnii*), however, do extend into warm-temperate estuaries and are often an important part of the ichthyofauna (Marais & Baird, 1980; Marais, 1981; Marais, 1983b; Whitfield *et al*., 1994; Vorwerk *et al*., 2001).

Warm temperate estuaries are mainly dominated by endemic taxa (e.g. *A. breviceps*, *L. richardsonii*, *M. capensis*, *P. knysnaensis*, *R. holubi*); this is probably enhanced through the restriction of tropical species to estuaries further north and thus reducing competition. Several endemic species were positively correlated with salinity. Some endemic species, however, also showed a positive correlation with temperature and many of these extended into subtropical estuaries. Cool-temperate estuaries did not appear to contain any unique taxa but rather comprised a mix of widespread (e.g. *M. cephalus*) and endemic species that appear to prefer cooler waters (e.g. *A. breviceps*, *L. richardsonii*). Many of these endemic taxa showed a negative correlation with temperature. Although the cold upwelled waters associated with the Benguela Current system has been identified as a barrier to the distribution of tropical species into southwest and west coast estuaries (Whitfield, 1983; 1996), it may also serve as a barrier to many endemic species, particularly those that appear to prefer warmer waters. The occurrence of *R. holubi* in southwest and west coast estuaries, for example, are only represented by a few 'stragglers' (Whitfield, 1999).

9.4 ESTUARY-ASSOCIATIONS

An analysis of the estuary-associations of the ichthyofauna was conducted to determine if the utilisation of estuaries by fishes differs between biogeographic regions. Several authors (e.g. Mac Dowall, 1985; Ayvazian *et al.*, 1992; Dame *et al.*, 2000; Roman *et al.*, 2000) have suggested a change in the ichthyofaunal estuary-associations with latitude. This study has indicated that, irrespective of the environmental conditions that structure estuarine fish assemblages, the estuary-associations of the ichthyofauna throughout the various zoogeographic regions was similar. Estuarine-dependent marine species were the dominant group, demonstrating that estuaries in all biogeographic regions are important nursery areas for these fishes.

Whitfield (1990) has highlighted that, relative to the nearshore marine environment, conditions in estuaries are highly variable, and the life-history styles of estuarine-dependent marine fishes reflect this. These fishes spawn at sea and produce large numbers of pelagic eggs; following larval development at sea, numerous juveniles then enter estuarine nursery areas (Wallace *et al.*, 1984). The seasonal spawning and recruitment period of this group of fishes differs slightly within each region and is adapted to ensure that juveniles occur in estuaries when conditions such as food and habitat are optimal (Whitfield, 1990). From studies in Terminos Lagoon, Mexico, Yáñez-Arancibia *et al.* (1988; 1993) reported a strong correlation between the life history patterns of marine migratory fish and the patterns of primary production; peak recruitment was found to coincide with periods of high productivity. A prolonged breeding and recruitment season is also considered a strategy against temporarily unfavourable conditions, both in the marine and estuarine environments (Wallace, 1975b; Bennett, 1989; Whitfield, 1998).

Estuarine resident species were also an important component of the ichthyofauna in all estuaries and in all regions, particularly in terms of abundance. This group of fishes have reproductive specialisations that facilitate the retention of eggs and larvae in estuaries (Whitfield, 1990; 1998). The relatively high abundance of estuarine resident fishes in warm-temperate estuaries may be a result of the high salinities and comparatively stable environmental conditions in these systems. Potter & Hyndes (1999) found that species that complete their life cycles in estuaries make far greater contributions to the total numbers of fish in temperate southwestern Australian estuaries than in temperate northern hemisphere estuaries. This was attributed in part to to the hydrological stability of temperate Australian estuaries and the maintenance of high salinities, particularly during and immediately after the spawning period of these fishes. In temperate northern hemisphere estuaries conditions are more variable; these systems experience strong tidal currents, and marked changes in salinity and turbidity following heavy seasonal freshwater discharge (Potter & Hyndes, 1999). In contrast, the abundance of estuarine resident species subtropical and cool-temperate estuaries, which experience higher levels of seasonal variation in rainfall, runoff and salinity in these estuaries, was generally lower than that of warm-temperate systems.

Freshwater species only made a notable contribution to the fish community of closed subtropical estuaries during this study and their importance declined in warm-temperate and cool-temperate estuaries. This decline parallels the north-south decline in species richness of southern African indigenous freshwater fishes (O'Keeffe *et al.*, 1991; Skelton, 1993). The typically low salinities that characterise closed subtropical probably allows freshwater taxa to extend into these habitats while the higher salinities in open subtropical estuaries and warm-temperate systems probably restricts the occurrence of freshwater taxa. The scarcity of freshwater species in southern African estuaries may also be partially due to competition with the abundant estuarine and marine fish assemblages (Ter Morshuizen *et al.*, 1996a; 1996b) as well as a relatively high proportion of marine piscivorous fishes in estuaries.

Marine species or stragglers did not comprise an important component of the ichthyofauna in any biogeographic region during this study; this group was virtually absent from closed estuaries and is probably a reflection of the predominantly closed mouth condition, which reduces the potential for this group to utilise these systems. In open estuaries, where exchange with the marine environment is more regular, the lack of marine taxa may be related to habitat availability.

9.5 TROPHIC COMPOSITION

The trophic composition of the estuarine ichthyofauna within the various biogeographic regions was described and compared to determine if the primary food sources differs between zoogeographic regions. This study established that detritus, either directly or indirectly was the dominant food source for estuarine fishes throughout all zoogeographic regions. Detritivorous fishes dominated the ichthyofauna of estuaries in all biogeographic regions; fishes that consume benthic invertebrates were also an important component of the ichthyofauna. Although detritus is the dominant food source, it is suggested that the primary origin of this material differs within each region. In river-dominated subtropical estuaries, detritus is likely to be derived primarily from fluvial inputs (Whitfield, 1980c); in the low rainfall warm-temperate region, detritus produced from primary production within the estuary itself is probably more important (Whitfield, 1998). Cool-temperate estuaries receive detritus from both riverine inputs during winter floods and from the marine environment during low flow periods (Branch & Day, 1984).

Certain trophic components of the fish communities within each region exhibited slight differences. Fishes that feed on aquatic macrophytes/invertebrates were an important component of the ichthyofauna of warm-temperate estuaries but were less so in cool-temperate and subtropical systems. Aquatic macrophytes in estuaries are affected by river flow through scouring and smothering by sediments (Adams *et al.*, 1999). The low representation of fishes that feed on aquatic macrophytes/invertebrates in cool-temperate or subtropical estuaries may be a result of high seasonal rainfall and runoff in these regions.

Zooplanktivores were a numerically important group in all estuaries and were particularly abundant warm-temperate systems. Zooplankton densities in estuaries are strongly associated with river flow through the introduction of nutrients and the stimulation of phytoplankton growth (Allanson & Read, 1995; Wooldridge, 1999). In cool-temperate and subtropical estuaries, this food source is likely to be somewhat variable due to seasonal flushing during winter and summer rainfall periods respectively. The low to moderate river flows in the warm-temperate region may provide sufficient residence time for these nutrients to support high phytoplankton and zooplankton stocks and thus zooplanktivorous fishes.

The shallow waters of estuaries are a key criterion that renders these systems important nursery areas for juvenile fishes (Blaber, 1991; Barry *et al.*, 1996; Livingston, 1997; Paterson & Whitfield, 2000). The relatively low proportion of piscivorous fishes in closed estuaries relative to open systems in all biogeographic regions during this study suggests that the nursery potential of closed estuaries should not be underestimated.

9.6 CONCLUSION

This study has demonstrated that, based on their fish communities, South African estuaries span at least three biogeographic regions and that these conform to the generally accepted marine zoogeographic provinces. The boundaries of these provinces have also been delineated. The locality of the warm-temperate/subtropical boundary, however, needs to be clarified. The permanence of these boundaries on a seasonal basis also deserves further investigation.

South Africa covers a wide range of climatic and oceanic conditions and this variation was apparent in the physico-chemical characteristics of the estuaries within each region. Both intra- and inter-regional differences in these processes as well as their seasonal variability, however, requires further study since these represent important driving forces that affect both the structure and function of estuarine biota.

This study has shown that the origin and distribution of estuarine fish communities within each biogeographic region were distinct and that the main environmental factors affecting the distribution and abundance of key species were temperature and salinity. The limiting conditions of temperature and salinity (and other variables), however, on key estuarine fish species is not well understood and deserves further attention.

The degree of environmental stability also produced differences in both fish community assemblages and trophic composition. In spite of these differences, the estuaries throughout the country appeared to perform an important nursery function for estuarine resident and estuarine-dependent marine fishes. In a South African context, however, this may be of particular relevance since many estuarine-associated species, particularly in the warm-temperate region, are endemic. This further emphasises the importance and conservation value of the estuaries within the region.

This study supported the concept that detritus forms the basis of estuarine food webs, however, both the origin and importance of this food source deserves further consideration. This is particularly relevant to the productivity of estuaries and their contribution to the bionomics of the adjacent marine environment.

CHAPTER 10

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APPENDIX

Appendix 1. List of coastal outlets sampled (from west to east) and classifications according to Harrison *et al*. (2000), Whitfield (2000) and this study.

No.	**System**	**Harrison *et al*. (2000)**	**Whitfield (2000)**	**This study**
1	Gariep (Orange)	Open, large	River mouth	
2	Holgat	Non-estuary	Non-estuary	
3	Buffels	Non-estuary	Non-estuary	
4	Swartlintjies	Non-estuary	Non-estuary	
5	Spoeg	Non-estuary	Non-estuary	
6	Bitter	Non-estuary	Non-estuary	
7	Groen	Non-estuary	Non-estuary	
8	Brak	Non-estuary	Non-estuary	
9	Sout (Noord)	Non-estuary	Non-estuary	
10	Olifants	Open, large	Permanently open	Open
11	Jakkals	Non-estuary	Non-estuary	
12	Wadrif	Non-estuary	Non-estuary	
13	Verlore	Closed, medium	Non-estuary	
14	Papkuils	Non-estuary	Non-estuary	
15	Berg	Open, large	Permanently open	Open
16	Dwars (Noord)	Non-estuary	Non-estuary	
17	Dwars (Suid)	Non-estuary	Non-estuary	
18	Modder	Non-estuary	Non-estuary	
19	Jacobsbaai	Non-estuary	Non-estuary	
20	Lêerbaai	Non-estuary	Non-estuary	
21	Bok	Non-estuary	Non-estuary	
22	Silwerstroom	Non-estuary	Non-estuary	
23	Sout (Suid)	Non-estuary	Non-estuary	
24	Diep	Closed, medium	Temporarily open/closed	Closed
25	Soutrivier	Non-estuary	Non-estuary	
26	Houtbaai	Closed, small	River mouth	
27	Wildevoël	Closed, medium	Temporarily open/closed	Closed
28	Bokramspruit	Non-estuary	Temporarily open/closed	
29	Schuster	Closed, small	Temporarily open/closed	
30	Krom	Closed, medium	Temporarily open/closed	Closed
31	Booiskraal	Non-estuary	Non-estuary	
32	Buffels (Wes)	Non-estuary	Non-estuary	
33	Elsies	Non-estuary	Non-estuary	
34	Silwermyn	Closed, small	Temporarily open/closed	
35	Sand	Closed, medium	Temporarily open/closed	Closed
36	Seekoe	Non-estuary	Non-estuary	
37	Eerste	Open, large	Temporarily open/closed	
38	Lourens	Open, small	Temporarily open/closed	
39	Sir Lowry's Pass	Open, small	Temporarily open/closed	
40	Steenbras	Open, non-barred	Permanently open	
41	Rooiels	Open, small	Temporarily open/closed	
42	Buffels (Oos)	Open, small	Temporarily open/closed	
43	Palmiet	Open, large	Permanently open	Open
44	Kleinmond	Closed, medium	Estuarine lake	
45	Bot	Closed, large	Estuarine lake	
46	Onrus	Open, small	Temporarily open/closed	
47	Mossel	Non-estuary	Non-estuary	

48	Klein	Closed, large	Estuarine lake	
49	Uilkraals	Open, large	Permanently open	Open
50	Ratel	Open, small	Temporarily open/closed	
51	Heuningnes	Open, large	Permanently open	Open
52	Klipdrifsfontein	Closed, small	Temporarily open/closed	
53	Breë	Open, large	Permanently open	Open
54	Duiwenhoks	Open, large	Permanently open	Open
55	Goukou	Open, large	Permanently open	Open
56	Gourits	Open, large	Permanently open	Open
57	Blinde	Closed, medium	Temporarily open/closed	Closed
58	Hartenbos	Closed, medium	Temporarily open/closed	Closed
59	Klein Brak	Open, large	Temporarily open/closed	
60	Groot Brak	Open, large	Temporarily open/closed	
61	Rooi	Non-estuary	Non-estuary	
62	Maalgate	Open, non-barred	Temporarily open/closed	
63	Gwaing	Open, non-barred	Temporarily open/closed	
64	Meul	Non-estuary	Non-estuary	
65	Kaaimans	Open, non-barred	Permanently open	
66	Touw	Closed, medium	Estuarine lake	
67	Swartvlei	Open, large	Estuarine lake	
68	Goukamma	Open, large	Temporarily open/closed	
69	Knysna	Open, large	Estuarine bay	
70	Noetsie	Closed, small	Temporarily open/closed	
71	Grooteiland	Non-estuary	Non-estuary	
72	Kranshoek	Non-estuary	Non-estuary	
73	Crooks	Non-estuary	Non-estuary	
74	Piesang	Open, small	Temporarily open/closed	
75	Keurbooms	Open, large	Permanently open	Open
76	Matjies	Closed, small	Temporarily open/closed	
77	Brak	Non-estuary	Non-estuary	
78	Sout	Open, non-barred	Permanently open	
79	Groot (Wes)	Closed, medium	Temporarily open/closed	Closed
80	Bloukrans	Open, non-barred	River mouth	
81	Lottering	Open, non-barred	River mouth	
82	Elandsbos	Open, non-barred	River mouth	
83	Storms	Open, non-barred	River mouth	
84	Elands	Open, non-barred	River mouth	
85	Groot (Oos)	Open, non-barred	River mouth	
86	Eerste	Non-estuary	Non-estuary	
87	Klipdrif (Wes)	Non-estuary	Non-estuary	
88	Boskloof	Non-estuary	Non-estuary	
89	Kaapsedrif	Non-estuary	Non-estuary	
90	Tsitsikamma	Closed, medium	Temporarily open/closed	Closed
91	Klipdrif (Oos)	Closed, small	Temporarily open/closed	
92	Slang	Closed, small	Temporarily open/closed	
93	Kromme	Open, large	Permanently open	Open
94	Seekoei	Closed, medium	Temporarily open/closed	Closed
95	Kabeljous	Closed, medium	Temporarily open/closed	Closed
96	Gamtoos	Open, large	Permanently open	Open
97	Van Stadens	Closed, medium	Temporarily open/closed	Closed
98	Maitland	Closed, small	Temporarily open/closed	

99	Bakens	Non-estuary	Non-estuary	
100	Papkuils	Non-estuary	Non-estuary	
101	Swartkops	Open, large	Permanently open	Open
102	Ngcura (Koega)	Non-estuary	Temporarily open/closed	
103	Sundays	Open, large	Permanently open	Open
104	Boknes	Closed, medium	Temporarily open/closed	Closed
105	Bushmans	Open, large	Permanently open	Open
106	Kariega	Open, large	Permanently open	Open
107	Kasuka	Closed, medium	Temporarily open/closed	Closed
108	Kowie	Open, large	Permanently open	Open
109	Rufane	Open, small	Temporarily open/closed	
110	Riet	Closed, medium	Temporarily open/closed	Closed
111	Wes-Kleinemond	Closed, medium	Temporarily open/closed	Closed
112	Oos-Kleinemond	Closed, medium	Temporarily open/closed	Closed
113	Great Fish	Open, large	Permanently open	Open
114	Old Woman's	Closed, medium	Temporarily open/closed	Closed
115	Thatshana	Closed, small	Non-estuary	
116	Mpekweni	Closed, medium	Temporarily open/closed	Closed
117	Mtati	Closed, medium	Temporarily open/closed	Closed
118	Mgwalana	Closed, medium	Temporarily open/closed	Closed
119	Bira	Closed, medium	Temporarily open/closed	Closed
120	Gqutywa	Closed, medium	Temporarily open/closed	Closed
121	Ngculura	Open, small	Temporarily open/closed	
122	Fresh Water Poort	Non-estuary	Non-estuary	
123	Blue Krans	Non-estuary	Non-estuary	
124	Mtana	Closed, medium	Temporarily open/closed	Closed
125	Keiskamma	Open, large	Permanently open	Open
126	Shwele-Shwele	Non-estuary	Non-estuary	
127	Ngqinisa	Closed, medium	Temporarily open/closed	Closed
128	Kiwane	Closed, medium	Temporarily open/closed	Closed
129	Tyolomnqa	Open, large	Temporarily open/closed	
130	Shelbertsstroom	Open, small	Temporarily open/closed	
131	Lilyvale	Closed, small	Temporarily open/closed	
132	Ross' Creek	Closed, medium	Temporarily open/closed	Closed
133	Ncera	Closed, medium	Temporarily open/closed	Closed
134	Mlele	Closed, medium	Temporarily open/closed	Closed
135	Mcantsi	Closed, medium	Temporarily open/closed	Closed
136	Gxulu	Closed, medium	Temporarily open/closed	Closed
137	Goda	Closed, medium	Temporarily open/closed	Closed
138	Hlozi	Closed, small	Temporarily open/closed	
139	Hickmans	Closed, medium	Temporarily open/closed	Closed
140	Mvubukazi	Non-estuary	Non-estuary	
141	Ngqenga	Non-estuary	Non-estuary	
142	Buffalo	Open, large	Permanently open	Open
143	Blind	Closed, small	Temporarily open/closed	
144	Hlaze	Closed, small	Temporarily open/closed	
145	Nahoon	Open, large	Permanently open	Open
146	Qinira	Closed, medium	Temporarily open/closed	Closed
147	Gqunube	Open, large	Permanently open	Open
148	Kwelera	Open, large	Permanently open	Open
149	Bulura	Open, small	Temporarily open/closed	

150	Cunge	Closed, small	Temporarily open/closed	
151	Cintsa	Closed, medium	Temporarily open/closed	Closed
152	Cefane	Closed, medium	Temporarily open/closed	Closed
153	Kwenxura	Closed, medium	Temporarily open/closed	Closed
154	Nyara	Closed, medium	Temporarily open/closed	Closed
155	Imtwendwe	Closed, small	Non-estuary	
156	Haga-Haga	Closed, medium	Temporarily open/closed	Closed
157	Mtendwe	Closed, small	Temporarily open/closed	
158	Quko	Open, large	Temporarily open/closed	
159	Morgan	Closed, medium	Temporarily open/closed	Closed
160	Cwili	Open, small	Temporarily open/closed	
161	Great-Kei	Open, large	Permanently open	Open
162	Gxara	Closed, medium	Temporarily open/closed	Closed
163	Ngogwane	Closed, medium	Temporarily open/closed	Closed
164	Qolora	Closed, medium	Temporarily open/closed	Closed
165	Ncizele	Closed, small	Temporarily open/closed	
166	Kobonqaba	Open, large	Permanently open	Open
167	Ngqusi/Inxaxo	Open, large	Permanently open	Open
168	Cebe	Closed, medium	Temporarily open/closed	Closed
169	Zalu	Closed, medium	Temporarily open/closed	Closed
170	Ngqwara	Closed, medium	Temporarily open/closed	Closed
171	Qora	Open, large	Permanently open	Open
172	Jujura	Open, small	Temporarily open/closed	
173	Ngadla	Open, small	Temporarily open/closed	
174	Shixini	Open, large	Permanently open	Open
175	Mbashe	Open, large	Permanently open	Open
176	Ku-Mpenzu	Open, small	Temporarily open/closed	
177	Ku-Bhula (Mbhanyana)	Open, small	Temporarily open/closed	
178	Kwa-Suku	Open, small	Non-estuary	
179	Ntlonyane	Open, small	Temporarily open/closed	
180	Nkanya	Open, small	Temporarily open/closed	
181	Sundwana	Closed, small	Non-estuary	
182	Xora	Open, large	Permanently open	Open
183	Nenga	Open, small	Temporarily open/closed	
184	Mapuzi	Open, small	Temporarily open/closed	
185	Mtata	Open, large	Permanently open	Open
186	Thsani	Closed, small	Non-estuary	
187	Mdumbi	Open, large	Permanently open	Open
188	Mpande	Open, small	Temporarily open/closed	
189	Sinangwana	Open, large	Temporarily open/closed	
190	Mngazana	Open, large	Permanently open	Open
191	Mngazi	Open, large	Permanently open	Open
192	Gxwaleni	Closed, small	Non-estuary	
193	Bulolo	Open, small	Temporarily open/closed	
194	Mtumbane	Open, small	Temporarily open/closed	
195	Mzimvubu	Open, large	River mouth	
196	Ntlupeni	Open, small	Temporarily open/closed	
197	Mntafufu	Open, large	Permanently open	Open
198	Msikaba	Open, large	Permanently open	Open
199	Butsha	Open, small	Non-estuary	
200	Mgwegwe	Open, small	Temporarily open/closed	

201	Mgwetyana	Open, small	Temporarily open/closed	
202	Mtentu	Open, large	Permanently open	Open
203	Mzamba	Open, large	Permanently open	Open
204	Mtentwana	Closed, medium	Temporarily open/closed	Closed
205	Mtamvuna	Open, large	Temporarily open/closed	
206	Sandlundlu	Open, small	Temporarily open/closed	
207	Tongazi	Open, small	Temporarily open/closed	
208	Kandandlovu	Closed, medium	Temporarily open/closed	Closed
209	Mpenjati	Closed, medium	Temporarily open/closed	Closed
210	Umhlangankulu	Closed, medium	Temporarily open/closed	Closed
211	Kaba	Closed, medium	Temporarily open/closed	Closed
212	Mbizana	Closed, medium	Temporarily open/closed	Closed
213	Mvutshini	Closed, small	Temporarily open/closed	
214	Bilanhlolo	Closed, medium	Temporarily open/closed	Closed
215	Uvuzana	Closed, small	Temporarily open/closed	
216	Kongweni	Closed, small	Temporarily open/closed	
217	Mhlangeni	Closed, medium	Temporarily open/closed	Closed
218	Zotsha	Open, small	Temporarily open/closed	
219	Mzimkulu	Open, large	Permanently open	Open
220	Mtentweni	Closed, medium	Temporarily open/closed	Closed
221	Mhlangamkulu	Closed, medium	Temporarily open/closed	Closed
222	Damba	Closed, small	Temporarily open/closed	
223	Intshambili	Closed, medium	Temporarily open/closed	Closed
224	Mhlabatshane	Open, small	Temporarily open/closed	
225	Fafa	Closed, medium	Temporarily open/closed	Closed
226	Sezela	Closed, medium	Temporarily open/closed	Closed
227	Mkumbane	Closed, small	Temporarily open/closed	
228	Mzimayi	Closed, small	Temporarily open/closed	
229	Mpambanyoni	Closed, medium	Temporarily open/closed	Closed
230	Mahlongwa	Closed, medium	Temporarily open/closed	Closed
231	Mkomazi	Open, large	Permanently open	Open
232	Lovu	Open, large	Temporarily open/closed	
233	Little Manzimtoti	Closed, medium	Temporarily open/closed	Closed
234	Manzimtoti	Closed, medium	Temporarily open/closed	Closed
235	Mbokodweni	Open, small	Temporarily open/closed	
236	Sipingo	Closed, medium	Non-estuary	
237	Mgeni	Open, large	Temporarily open/closed	
238	Mhlanga	Closed, medium	Temporarily open/closed	Closed
239	Mdloti	Closed, medium	Temporarily open/closed	Closed
240	Mhlali	Open, large	Temporarily open/closed	
241	Mvoti	Open, large	River mouth	
242	Mdlotane	Closed, medium	Temporarily open/closed	Closed
243	Zinkwasi	Closed, medium	Temporarily open/closed	Closed
244	Thukela (Tugela)	Open, large	River mouth	
245	Matigulu/Nyoni	Open, large	Permanently open	Open
246	Siyai	Closed, medium	Temporarily open/closed	Closed
247	Mlalazi	Open, large	Permanently open	Open
248	Mfolozi/Msunduzi	Open, large	River mouth	
249	St Lucia	Open, large	Estuarine lake	
250	Mgobezeleni	Open, small	Estuarine lake	
251	Kosi Bay	Open, large	Estuarine lake	

Appendix 2. Number of seine net hauls and metres of gill net set in closed and open estuaries during this study.

Year	System	Classification	Number of seine net hauls	Metres of gill net set
1993	Olifants	Open	8	120
1993	Berg	Open	12	120
1993	Diep	Closed	4	40
1993	Wildevoël	Closed	4	30
1993	Krom	Closed	6	20
1993	Sand	Closed	4	40
1994	Palmiet	Open	4	30
1994	Uilkraals	Open	4	10
1994	Heuningnes	Open	9	50
1994	Breë	Open	10	180
1994	Duiwenhoks	Open	8	60
1994	Goukou	Open	7	50
1994	Gourits	Open	5	50
1994	Blinde	Closed	3	30
1994	Hartenbos	Closed	4	50
1994	Keurbooms	Open	13	100
1995	Groot (Wes)	Closed	10	50
1995	Tsitsikamma	Closed	7	50
1995	Kromme	Open	18	180
1995	Seekoei	Closed	11	50
1995	Kabeljous	Closed	13	50
1995	Gamtoos	Open	16	150
1995	Van Stadens	Closed	11	50
1995	Swartkops	Open	19	140
1995	Sundays	Open	16	140
1995	Boknes	Closed	6	50
1995	Bushmans	Open	19	170
1995	Kariega	Open	21	150
1995	Kasuka	Closed	13	50
1995	Kowie	Open	25	150
1995	Riet	Closed	7	30
1995	Wes-Kleinemond	Closed	12	50
1995	Oos-Kleinemond	Closed	10	50
1995	Great Fish	Open	10	50
1996	Old Woman’s	Closed	5	30
1996	Mpekweni	Closed	10	90
1996	Mtati	Closed	10	80
1996	Mgwalana	Closed	8	50
1996	Bira	Closed	10	80
1996	Gqutywa	Closed	6	40
1996	Mtana	Closed	7	40
1996	Keiskamma	Open	16	130
1996	Nqinisa	Closed	5	20
1996	Kiwane	Closed	7	50
1996	Ross' Creek	Closed	4	20
1996	Ncera	Closed	8	50
1996	Mlele	Closed	5	30
1996	Mcantsi	Closed	6	30
1996	Gxulu	Closed	9	50
1996	Goda	Closed	6	50
1996	Hickmans	Closed	5	30
1996	Buffalo	Open	7	50
1996	Nahoon	Open	10	80
1996	Qinira	Closed	8	50

1996	Gqunube	Open	12	80
1996	Kwelera	Open	15	80
1996	Cintsa	Closed	8	50
1996	Cefane	Closed	8	50
1996	Kwenxura	Closed	8	40
1996	Nyara	Closed	6	20
1996	Haga-Haga	Closed	5	20
1996	Morgan	Closed	6	40
1996	Great-Kei	Open	17	90
1997/98	Gxara	Closed	8	40
1997/98	Ngogwane	Closed	6	30
1997/98	Qolora	Closed	8	40
1997/98	Kobonqaba	Open	10	50
1997/98	Ngqusi/Inxaxo	Open	21	60
1997/98	Cebe	Closed	5	30
1997/98	Zalu	Closed	6	30
1997/98	Ngqwara	Closed	9	50
1997/98	Qora	Open	11	50
1997/98	Shixini	Open	7	30
1997/98	Mbashe	Open	16	100
1997/98	Xora	Open	18	50
1997/98	Mtata	Open	15	100
1997/98	Mdumbi	Open	13	50
1997/98	Mngazana	Open	20	80
1997/98	Mngazi	Open	12	50
1997/98	Mntafufu	Open	12	50
1997/98	Msikaba	Open	8	50
1997/98	Mtentu	Open	9	50
1997/98	Mzamba	Open	11	50
1997/98	Mtentwana	Closed	6	30
1998/99	Kandandlovu	Closed	2	20
1998/99	Mpenjati	Closed	7	30
1998/99	Umhlangankulu	Closed	5	30
1998/99	Kaba	Closed	4	20
1998/99	Mbizana	Closed	6	50
1998/99	Bilanhlolo	Closed	5	30
1998/99	Mhlangeni	Closed	5	30
1998/99	Mzimkulu	Open	7	50
1998/99	Mtentweni	Closed	6	30
1998/99	Mhlangamkulu	Closed	5	20
1998/99	Intshambili	Closed	5	30
1998/99	Fafa	Closed	6	30
1998/99	Sezela	Closed	7	40
1998/99	Mpambanyoni	Closed	6	30
1998/99	Mahlongwa	Closed	6	30
1998/99	Mkomazi	Open	8	50
1998/99	Little Manzimtoti	Closed	6	30
1998/99	Manzimtoti	Closed	6	30
1998/99	Mhlanga	Closed	6	30
1998/99	Mdloti	Closed	6	50
1998/99	Mdlotane	Closed	4	50
1998/99	Zinkwasi	Closed	7	50
1998/99	Matigulu/Nyoni	Open	17	80
1998/99	Siyai	Closed	3	20
1998/99	Mlalazi	Open	18	100

Appendix 3. List of fish species captured in closed and open estuaries during this study and classifications according to origin, estuary-associations and food.

Family	**Species**	**Common name**	**Origin**	**Estuary-association**	**Food**
Ambassidae	*Ambassis gymnocephalus*	Bald glassy	Tropical	IB?	Zooplankton
Ambassidae	*Ambassis natalensis*	Slender glassy	Tropical	IB?	Zooplankton
Ambassidae	*Ambassis productus*	Longspine glassy	Tropical	IA?	Zooplankton
Anguillidae	*Anguilla mossambica*	Longfin eel	Tropical	VA	Benthic Invertebrates
Antennariidae	*Antennarius striatus*	Striped angler	Tropical	III	Fish
Ariidae	*Galeichthys feliceps*	White seacatfish	Endemic	IIB	Benthic Invertebrates
Atherinidae	*Atherina breviceps*	Cape silverside	Endemic	IB	Zooplankton
Blenniidae	*Omobranchus woodi*	Kappie blenny	Endemic	IA	Benthic Invertebrates
Blenniidae	*Parablennius lodosus*	Mud blenny	Tropical	III?	Benthic Invertebrates
Bothidae	*Pseudorhombus arsius*	Largetooth flounder	Tropical	IIC?	Benthic Invertebrates
Carangidae	*Caranx heberi*	Blacktip kingfish	Tropical	III	Fish
Carangidae	*Caranx ignobilis*	Giant kingfish	Tropical	IIB?	Fish
Carangidae	*Caranx papuensis*	Brassy kingfish	Tropical	IIC?	Fish
Carangidae	*Caranx sexfasciatus*	Bigeye kingfish	Tropical	IIB	Fish
Carangidae	*Lichia amia*	Garrick	Temperate	IIA	Fish
Carangidae	*Scomberoides lysan*	Doublespotted queenfish	Tropical	IIB?	Fish
Carangidae	*Trachinotus spp.*	Pompano	Tropical	III	Benthic Invertebrates
Carangidae	*Trachurus trachurus*	Maasbanker	Temperate	III	Zooplankton
Chanidae	*Chanos chanos*	Milkfish	Tropical	IIC	Detritus
Cichlidae	*Oreochromis mossambicus*	Mozambique tilapia	Tropical	IV	Detritus
Cichlidae	*Tilapia rendalli*	Redbreast tilapia	Tropical	IV	Macrophytes/Invertebrates
Clariidae	*Clarias gariepinus*	Sharptooth catfish	Tropical	IV	Fish
Clinidae	*Clinus superciliosus*	Super klipfish	Endemic	IB	Benthic Invertebrates
Clupeidae	*Etrumeus whiteheadi*	Redeye roundherring	Endemic	III	Zooplankton
Clupeidae	*Gilchristella aestuaria*	Estuarine roundherring	Endemic	IA	Zooplankton
Clupeidae	*Hilsa kelee*	Kelee shad	Tropical	IIC	Zooplankton
Clupeidae	*Sardinops sagax*	Pilchard	Temperate	III	Zooplankton
Cyprinidae	*Barbus natalensis*	Scaly	Endemic	IV	Benthic Invertebrates
Dasyatidae	*Dasyatis kuhlii*	Bluespotted stingray	Tropical	III	Benthic Invertebrates
Eleotridae	*Eleotris fusca*	Dusky sleeper	Tropical	IA?	Benthic Invertebrates
Elopidae	*Elops machnata*	Ladyfish	Tropical	IIA	Fish
Engraulidae	*Engraulis japonicus*	Cape anchovy	Tropical?	III	Zooplankton
Engraulidae	*Stolephorus holodon*	Thorny anchovy	Endemic	IIC	Zooplankton
Engraulidae	*Thryssa setirostris*	Longjaw glassnose	Tropical	III	Zooplankton
Engraulidae	*Thryssa vitrirostris*	Orangemouth glassnose	Tropical	IIB	Zooplankton
Gerreidae	*Gerres acinaces*	Smallscale pursemouth	Tropical	IIB	Benthic Invertebrates
Gerreidae	*Gerres filamentosus*	Longspine pursemouth	Tropical	IIB	Benthic Invertebrates
Gerreidae	*Gerres methueni*	Evenfin pursemouth	Endemic	IIB	Benthic Invertebrates
Gobiidae	*Awaous aeneofuscus*	Freshwater goby	Tropical	IV	Benthic Invertebrates
Gobiidae	*Caffrogobius gilchristi*	Prison goby	Endemic	IB	Benthic Invertebrates
Gobiidae	*Caffrogobius natalensis*	Baldy	Endemic	IB	Benthic Invertebrates
Gobiidae	*Caffrogobius nudiceps*	Barehead goby	Endemic	IB	Benthic Invertebrates
Gobiidae	*Favonigobius reichei*	Spotted sandgoby	Tropical	IB?	Benthic Invertebrates
Gobiidae	*Glossogobius biocellatus*	Sleepy goby	Tropical	IA?	Benthic Invertebrates
Gobiidae	*Glossogobius callidus*	River goby	Endemic	IB	Benthic Invertebrates
Gobiidae	*Glossogobius giuris*	Tank goby	Tropical	IV	Benthic Invertebrates
Gobiidae	*Mugillogobius durbanensis*	Durban goby	Tropical	IB?	Benthic Invertebrates

Gobiidae	*Oligolepis acutipennis*	Sharptail goby	Tropical	IA?	Benthic Invertebrates
Gobiidae	*Oligolepis keiensis*	Speartail goby	Tropical	IA?	Benthic Invertebrates
Gobiidae	*Oxyurichthys opthalmonema*	Eyebrow goby	Tropical	IB?	Benthic Invertebrates
Gobiidae	*Periopthalmus koelreuteri*	African mudskipper	Tropical	IA	Benthic Invertebrates
Gobiidae	*Psammogobius knysnaensis*	Speckled sandgoby	Endemic	IB?	Benthic Invertebrates
Gobiidae	*Redigobius dewaali*	Checked goby	Endemic	IB	Benthic Invertebrates
Gobiidae	*Silhouettea sibayi*	Barebreast goby	Endemic	IB	Benthic Invertebrates
Haemulidae	*Pomadasys commersonnii*	Spotted grunter	Tropical	IIA	Benthic Invertebrates
Haemulidae	*Pomadasys kaakan*	Javelin grunter	Tropical	IIC	Benthic Invertebrates
Haemulidae	*Pomadasys olivaceum*	Piggy	Tropical	III	Benthic Invertebrates
Hemiramphidae	*Hemiramphus far*	Spotted halfbeak	Tropical	IIC	Zooplankton
Leiognathidae	*Leiognathus equula*	Slimy	Tropical	IIB	Benthic Invertebrates
Leiognathidae	*Secutor ruconius*	Pugnose soapy	Tropical	III	Zooplankton
Lutjanidae	*Lutjanus argentimaculatus*	Mangrove snapper	Tropical	IIC	Fish
Lutjanidae	*Lutjanus fulviflamma*	Dory snapper	Tropical	IIC	Benthic Invertebrates
Megalopidae	*Megalops cyprinoides*	Oxeye tarpon	Tropical	VB	Fish
Monodactylidae	*Monodactylus argenteus*	Round moony	Tropical	IIB	Zooplankton
Monodactylidae	*Monodactylus falciformis*	Oval moony	Tropical	IIA	Zooplankton
Mugilidae	*Liza alata*	Diamond mullet	Tropical	IIB	Detritus
Mugilidae	*Liza dumerilii*	Groovy mullet	Endemic?	IIB	Detritus
Mugilidae	*Liza macrolepis*	Largescale mullet	Tropical	IIA	Detritus
Mugilidae	*Liza melinoptera*	Giantscale mullet	Tropical	IIB	Detritus
Mugilidae	*Liza richardsonii*	Southern mullet	Endemic	IIC	Detritus
Mugilidae	*Liza tricuspidens*	Striped mullet	Endemic	IIB	Detritus
Mugilidae	*Mugil cephalus*	Flathead mullet	Cosmopolitan	IIA	Detritus
Mugilidae	*Myxus capensis*	Freshwater mullet	Endemic	VB	Detritus
Mugilidae	*Valamugil buchanani*	Bluetail mullet	Tropical	IIC	Detritus
Mugilidae	*Valamugil cunnesius*	Longarm mullet	Tropical	IIA	Detritus
Mugilidae	*Valamugil robustus*	Robust mullet	Endemic?	IIA	Detritus
Mugilidae	*Valamugil seheli*	Bluespot mullet	Tropical	IIC	Detritus
Mullidae	*Upeneus vittatus*	Yellowbanded goatfish	Tropical	III	Benthic Invertebrates
Myliobatidae	*Myliobatis aquila*	Eagleray	Temperate	III	Benthic Invertebrates
Odontaspididae	*Eugomphodus taurus*	Spotted ragged-tooth	Tropical	III	Fish
Platycephalidae	*Platycephalus indicus*	Bartail flathead	Tropical	IIC	Fish
Polynemidae	*Polydactylus plebeius*	Striped threadfin	Tropical	III	Benthic Invertebrates
Pomatomidae	*Pomatomus saltatrix*	Elf	Cosmopolitan	IIC	Fish
Rajidae	*Raja miraletes*	Twineye skate	Temperate	III	Benthic Invertebrates
Sciaenidae	*Argyrosomus japonicus*	Dusky kob	Tropical	IIA	Fish
Sciaenidae	*Argyrosomus* spp.	Kob	Temperate	III	Fish
Sciaenidae	*Johnius dorsalis*	Small kob	Tropical	IIC	Benthic Invertebrates
Scyliorhinidae	*Haploblepharus pictus*	Dark shyshark	Endemic	III	Benthic Invertebrates
Serranidae	*Epinephelus malabaricus*	Malabar rockcod	Tropical	III	Fish
Siganidae	*Siganus sutor*	Whitespotted rabbitfish	Tropical	III	Macrophytes/Invertebrates
Sillaginidae	*Sillago sihama*	Silver sillago	Tropical	IIC	Benthic Invertebrates
Soleidae	*Heteromycteris capensis*	Cape sole	Endemic	IIB	Benthic Invertebrates
Soleidae	*Solea bleekeri*	Blackhand sole	Endemic	IIB	Benthic Invertebrates
Sparidae	*Acanthopagrus berda*	Estuarine bream	Tropical	IIA	Benthic Invertebrates
Sparidae	*Diplodus cervinus*	Zebra	Endemic	III	Macrophytes/Invertebrates
Sparidae	*Diplodus sargus*	Blacktail	Temperate?	IIC	Macrophytes/Invertebrates
Sparidae	*Gymnocrotaphus curvidens*	Janbruin	Endemic	III	Benthic Invertebrates
Sparidae	*Lithognathus lithognathus*	White steenbras	Endemic	IIA	Benthic Invertebrates

Sparidae	*Rhabdosargus globiceps*	White stumpnose	Endemic	IIC	Macrophytes/Invertebrates
Sparidae	*Rhabdosargus holubi*	Cape stumpnose	Endemic	IIA	Macrophytes/Invertebrates
Sparidae	*Rhabdosargus sarba*	Tropical stumpnose	Tropical	IIB	Macrophytes/Invertebrates
Sparidae	*Sarpa salpa*	Strepie	Temperate	IIC	Macrophytes/Invertebrates
Sphyraenidae	*Sphyraena jello*	Pickhandle barracuda	Tropical	IIC?	Fish
Syngnathidae	*Hippichthys heptagonus*	Belly pipefish	Tropical	IB?	Zooplankton
Syngnathidae	*Hippichthys spicifer*	Bellybarred pipefish	Tropical	IB?	Zooplankton
Syngnathidae	*Syngnathus acus*	Longsnout pipefish	Temperate	IB	Zooplankton
Syngnathidae	*Syngnathus watermeyeri*	Estuarine pipefish	Endemic	IA	Zooplankton
Teraponidae	*Terapon jarbua*	Thornfish	Tropical	IIA	Benthic Invertebrates
Tetraodontidae	*Amblyrhynchotes honckenii*	Evileye blaasop	Tropical	III	Benthic Invertebrates
Tetraodontidae	*Arothron immaculatus*	Blackedged blaasop	Tropical	III	Benthic Invertebrates
Tetraodontidae	*Chelonodon laticeps*	Bluespotted blaasop	Tropical	III	Benthic Invertebrates
Torpedinidae	*Torpedo fuscumaculata*	Blackspotted electric ray	Tropical	IIC?	Fish
Torpedinidae	*Torpedo sinusperci*	Marbled electric ray	Tropical	IIC?	Fish
Triglidae	*Chelidonichthys capensis*	Cape gurnard	Endemic	III	Benthic Invertebrates